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Fishery Bulletin

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CHEMICAL SIGNALS IN THE SEA: MARINE ALLELOCHEMICS AND EVOLUTION[1]

J. S. KITTREDGE,[2] FRANCIS T. TAKAHASHI,[3]
JAMES LINDSEY,[4] AND REUBEN LASKER[5]

ABSTRACT

Observations in chemical ecology suggest the coevolution of "natural products" of plants and the chemoreceptors of herbivorous insects. We have reviewed evidence which suggests that this coevolution extends back to the primordial protistans. Thus, the evolutionary pressure for the development of a chemosensory capability probably derived from the presence of metabolic products in the milieu. These products are considered to have been both cues to the location of prey and "membrane irritants" evolved in the initial phase of chemical protection. Sometime later this chemosensory capability provided several functions in the evolution of metazoans, i.e. the precursors of developmental signals, hormone function, and synaptic transmission.

We consider that most of the extant "natural products" of plants and marine invertebrates are protective allomones. A feature of allomone function that has been termed "antifeedant" or "feeding inhibitor" may represent the "cryptic odors" of Haldane. We provide evidence that the naphthoquinones with a juglone or naphthazarin structure have this activity. Octopus ink has a "cryptic odor" effect on moray eels. Marine Crustacea have, however, evolved an ability to perceive the orthoquinone precursors of the ink, a warning signal.

Evidence for an array of sex pheromones in a crab and a cycloid swimming pattern in a copepod that may enable it to follow a chemical gradient indicate the complexity of behavioral responses to chemical cues.

The earliest form of interaction between organisms was probably by means of chemical agents. This interaction involved both conflict and cooperation and its existence implies detection of these agents. Haldane (1955) first suggested that chemical communication is the most primitive form of communication, orginating with primordial unicellular organisms. He reasons that this primordial protistan communication was a necessary prelude to the evolution of metazoans and thus is a lineal predecessor of synaptic transmission and hormone reception. This early chemical communication may have evolved as an accessory to the active transport mechanism of the cell membrane or as a "membrane sensitivity" to metabolic by-products (Wynne-Edwards, 1962). That a more detailed understanding of transducer physiology is central to further advances in neurobiology has been emphasized by Delbrück (1970). He considers the stimulus-response system represented by chemoreception or synaptic transmission to be homologous.

We wish to examine some of the recent concepts of chemical ecology and to present examples from the marine environment. Studies of chemoreception are providing evidence for the pervasive function of chemical signals in the environment. The "membrane sensitivity" concept of Wynne-Edwards may provide a clue to both the initial evolution of a transducer function and the continuing evolution of receptor sites of greater diversity and specificity. It is evident that this diversity has resulted from a continual interplay of chemical countermeasures and the development of neurosensory and behavioral adaptations to these agents.

ALLELOCHEMICS

At all levels of life we are finding examples of attack, defense, and behavioral response

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based on chemical agents. These interactions and the characterization of the chemical agents involved are the subject of the newly developing field of chemical ecology (Sondheimer and Simeone, 1970). Chemicals that are syntheized and released by one individual of a species to alter the behavior of other members of the species are termed pheromones. These signals range in their function from trail markers and territorial markers through alarm and defense signals to those which control caste structure in social insects and the sex pheromones that are calling signals and aphrodisiacs. Chemicals also have a wide range of interspecific interactions. A substance produced by one organism may influence the behavior of members of other species. A flower scent that enhances pollination is a well-known example. This field of chemical ecology has been termed allelochemics, and the chemical agents have been subdivided on the basis of function into allomones, which give adaptive advantage to the producing organism, and kairomones, which give adaptive advantage to the receiving organism (Whittaker and Feeny, 1971). The allomones include the repellents produced by many plants and animals, suppressants which inhibit competitors (e.g., fungal antibiotics), venoms, inductants (e.g., gall producing agents), and attractants (e.g., chemical lures). The kairomones include attractants (e.g., the scent of a prey), inductants (e.g., the factor that stimulates hyphal loop development in nematode-trapping fungi), danger signals (e.g., predator scents, secondary plant substances indicating toxicity), and stimulants (e.g., hormones that induce growth in the receiving organism).

The diverse natural products, coumarins, quinones, flavonoids, acetylenes, terpenoids, saponins, cardiac glycosides, alkaloids, thiols, and cyanogenic glycosides, which were long considered metabolic waste products, are now recognized to be allelochemic agents. Examination of the function of these natural products provides some insight into their evolution. Some of these compounds are toxic, some are chemical lures, others inhibit the growth of competitive plant species, but the bulk of these compounds probably function as "feeding inhibitors" of herbivores (Gilbert, Baker, and Norris, 1967; Munakata, 1970). The coevolution of butterflies and plants is considered by Ehrlich and Raven (1964). They emphasize the role of reciprocal selective responses during this evolution and conclude that "the plant-herbivore interface may be the major zone of interaction responsible for generating terrestrial organic diversity." The "accidental" evolution of a metabolic sequence resulting in the production of a noxious substance by a plant provided a selective survival advantage in the clone carrying this capability. Decreased predation by herbivores on those individuals containing the highest concentrations of the new substance resulted in genetic selection for increased synthesis and storage of the noxious substance. Such "protected" species experience an explosive increase because of their protection from contemporary phytophagous organisms. The first evolutionary response of the herbivores must have been the development of the capability to detect the compound, i.e. sensitive external chemoreceptors. Later evolutionary events led to the development in some individuals of a tolerance for the noxious substance. The herbivores which developed this tolerance then had access to a large food supply for which there was no competition. The ability to detect the substance then had an altered function, the feeding inhibitor was now a feeding stimulant. The present evidence of the repeated occurrence of this cycle is the existence of tightly coupled herbivorous insects and their host plants, presumably arising through coadaptation.

In 1955 Haldane, in a consideration of chemical communication and visual signals, wondered if cryptic odors had ever evolved. While most of the feeding inhibitors that have evolved are probably irritants, many may be cryptic odors. It is likely that the two activities may only differ in the membrane affected. The term irritant implies membranic sensitivity and, of those membranes of an organism in immediate contact with the environment, the chemosensory membranes are likely the most sensitive to chemical irritation. In an environment in which a major fraction of the information flow is chemical, any agent capable of disrupting the chemosensory organs of a predator would provide an ideal mechanism for "hiding" from that predator. Cryptic odors may be either "negative odors" altering, for protracted periods, the membrane potential of the dendrites and blocking their normal generator potential, or they may be the chemical equivalent of a

"white noise," producing an "uncoded" array of spikes in the chemosensory neurons.

The best description of behavior suggesting a "cryptic odor" in the marine environment is that given by MacGinitie and MacGinitie (1968). The ink of an octopus is considered a "smoke screen"; however, it can also affect the olfactory sense. The MacGinities observed that after a moray eel swam through the ink cloud of an octopus it could no longer "recognize" an octopus. The moray eel apparently requires both visual and olfactory input for this recognition. They state, "We were surprised to find that the real effect of the ink of an octopus is to paralyze the olfactory sense of its enemies." The melanin of the ink is a polymer of oxidized L-DOPA. The polymerization proceeds through three orthoquinones, dopaquinone (6, Figure 1), dopachrome (7), and indole-5, 6-quinone (8). In the biosynthesis of melanin, this oxidation is catalyzed by polyphenyl oxidases; however, heavy metal ions can also catalyze the oxidation, and it can be readily demonstrated that the trace of heavy metal ions in seawater will rapidly convert L-DOPA to melanin. The octopus ink loses its potency with time, a factor that would indicate that the biological activity of the ink is due to the presence of the unstable monomer orthoquinones in the fresh ink (Kittredge, Takahashi, and Lindsey, unpublished data).

The observation of Gilbert et al. (1967) that juglone (5-hydroxy-1,4-naphthoquinone) (1, Figure 1) is a deterrent to feeding by the bark beetle, *Scolytus multistriatus*, suggested a similar function for the polyhydroxynaphthoquinones occurring in the echinoderms. These spinochromes are all derivatives of juglone (1) or naphthazarin (2). They occur as soluble salts in the tissues and may be present in considerable amounts in the larvae. They also occur as insoluble calcium salts in the spines and tests (Thompson, 1971). The echinoids have received the closest attention, but P. J. Scheuer and his group have demonstrated the presence of these compounds in the other four classes of this phylum—the holothurians, asteroids, ophiuroids, and crinoids (Singh, Moore, and Scheuer, 1967). They also demonstrated the presence of a substituted 2,5-benzoquinone (3) in the genus *Echinothrix* (Moore, Singh, and Scheuer, 1966). The crinoids are interesting in that they contain primarily a series of polyhydroxyanthroquinones (e.g., rhodocomatulin,

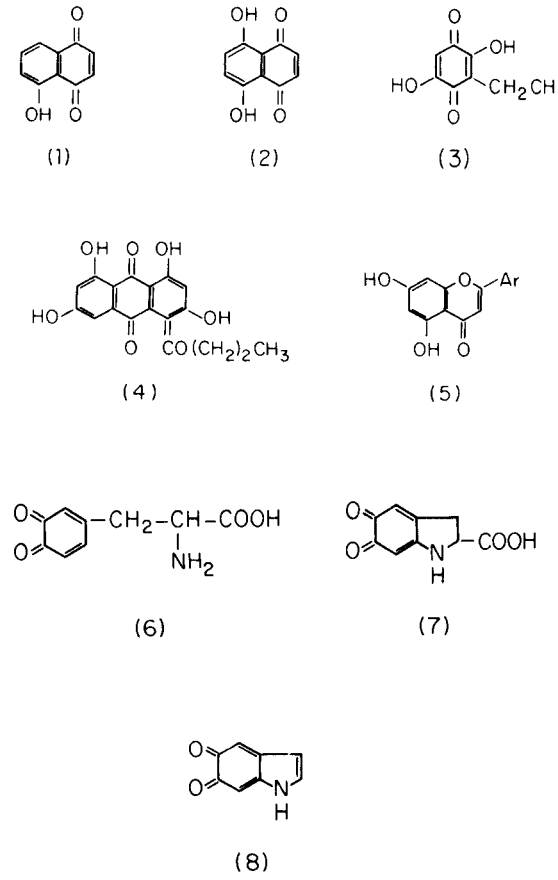

FIGURE 1.—Structures of compounds typical of those which may function as "cryptic odors." (1) juglone, (2) naphthazarin, (3) 2, 5-dihydroxy-3- ethylbenzoquinone, (4) rhodocomatulin, (5) flavone, (6) dopaquinone, (7) dopachrome, (8) indole-5,6-quinone.

4) (Sutherland and Wells, 1967; Powell, Sutherland, and Wells, 1967; Powell and Sutherland, 1967; Matsuno et al., 1972; Erdman and Thomson, 1972).

Utilizing the "feeding response" of the lined shore crab, *Pachygrapsus crassipes*, which consists of a rapid lateral movement of the mouthparts when presented with a feeding stimulus, we have bioassayed the "feeding inhibitor" activity of juglone and eight representative spinochromes. The "feeding stimulus" was a 20-μl aliquot of a 3-mM solution of taurine in seawater administered from a repeating syringe close to one of the antennules of the crab. Initially the crabs were immersed in a 1-μM solution of the naphthoquinone and tested for a feeding response. Five experimental and

one control crab were utilized for each compound. No feeding responses were observed in any of the test crabs while all of the controls were positive. A second series of bioassays was designed to determine the onset of inhibition. The crabs were placed in seawater and stimulated with 20 μl aliquots of a solution of 3 mM taurine and 1 μM quinone. The stimulus was administered at 2 sec intervals to alternate antennules. Inhibition of the "feeding response" was observed at approximately 10 sec. The naphthazarin derivatives were apparently more potent than the juglone derivatives. We interpret these results as indicative of a "cryptic odor" function; the crabs cannot detect the feeding stimulant after a brief exposure to the quinone.

Many higher plants contain juglone or other hydroxynaphthoquinones or benzoquinones. These compounds also occur in fungi, lichens, pholangids, millipedes, and insects. 1,4-benzoquinones are the most common ingredient of insect defensive secretions and the 2,5-substituted 1,4-benzoquinones are characteristic of fungi. A similar "cryptic odor" function may be predicted for these compounds.

Norris (1969) compared the feeding deterrent activity of a number of substituted naphthoquinones. Juglone (1) and naphthazarin (2) were the most potent inhibitors. The apparent effectiveness of the hydroxy groups in the 5- or 5,8-positions in these naphthoquinones suggests an examination of the function of the major group of secondary plant metabolites, the flavones (5) (Harborne, 1972) which have a marked structural similarity.

Whittaker and Feeny (1971) predict "that research into the relations of multicellular marine algae and their consumers will reveal chemical defenses and responses paralleling those of higher plants and animals on land." The most likely candidates to fulfill this prediction are the highly halogenated hydrocarbons that are synthesized by algae and stored in the tissues of the herbivorous gastropod, *Aplysia californica* (Faulkner and Stallard, 1973; Faulkner et al., 1973). We would add to the prediction of Whittaker and Feeny that research into the relations of many marine invertebrates and their predators may reveal allomones. Some of the "natural products" of marine invertebrates that have been recently characterized and that may have this function are the halogenated antibiotics that have been isolated from sponges (Sharma, Vig, and Burkholder, 1970; Fattorusso, Minale, and Sodano, 1972; Moody et al., 1972; Anderson and Faulkner, 1973). Steroid saponins that are toxicants or irritants have been characterized from holothuroids and starfish (Yasumoto, Nakamura, and Hashimoto, 1967; Tursch et al., 1967; Roller et al., 1969; Tursch, Cloetens, and Djerassi, 1970; Turner, Smith, and Mackie, 1971).

We recall a simple demonstration by the late C. F. A. Pantin of the sensitive chemosensory capability of sea anemones for saponin. The nematocysts of sea anemones require both a mechanical and a chemical stimulus for discharge. One can brush the surface of a sea anemone's tentacles with a clean glass rod without effecting any discharges. If, however the glass rod is first dipped into a dilute saponin solution, a massive discharge is effected.

An observation by Clark (1921) suggests the existence of allomones in crinoids. He discusses the avoidance of comatulid crinoids by fish and suggests the activity of glands at the base of the tentacles. The comatulids are unique in containing both polyhydroxyanthroquinones and aromatic polyketides (Kent, Smith, and Sutherland, 1970; Smith and Sutherland, 1971).

MARINE KAIROMONES

As in the terrestrial environment, invertebrates utilize chemical cues to locate hosts or to warn of predators. Davenport (1966) demonstrated the response of commensal polynoid polychaetes to a "host factor" in the water draining from tanks containing the host species of starfish. In an electrophysiological analysis of the antennular chemoreceptors of two commensal shrimps, Ache and Case (1969) demonstrated the specificity of the response to "host water" from the specific hosts, *Haliotis* spp. and *Strongylocentrotus* spp.

Predatory starfish induce an escape response in a variety of molluscs (Feder, 1967), and these behavioral responses probably effectively reduce the predation on these species that can detect the predator (Feder, 1963). The active materials in extracts of the starfish *Marthasteria glacialis* and *Asterias rubens* which induce the escape response have been shown to be steroid saponins (Mackie, Lasker, and Grant, 1968).

The threshold for response by the snail, *Buccinum undatum* is $0.2-0.4 \times 10^{-9}$ M (Mackie, 1970), and the structure of these steroid glycosides has been determined (Turner et al., 1971).

A behavioral bioassay of one of the orthoquinones derived from L-DOPA, dopachrome, utilizing the feeding response of the lined shore crab *Pachygrapsus crassipes* indicated that this quinone might also be a "cryptic odor." Electrophysiological studies, however, demonstrated that these results were misleading. Utilizing a preparation of the dactyl chemoreceptors of the spiny lobster *Panulirus interruptus*, we detected chemoreceptors for this quinone that were about a hundred times as sensitive as the general amino acid receptors in this preparation (Figure 2). While we have not explored the range of specificity of these receptors, the results suggest that these crustaceans, the natural prey of the octopus, have evolved a mechanism for detecting the presence of the predator. Our results with the bioassay likely reflect a priority of responses to the two chemical stimuli (Kittredge, Takahashi, and Lindsey, unpublished data).

PHEROMONES

Unicellular chemical communication, analogous to Haldane's primordial protistan communication, is evident in the conjugation of ciliates. The microconjugant of a peritrichous ciliate, which is free swimming, can identify the macroconjugant, which is sessile, by chemicals released by the latter. Although evidence for

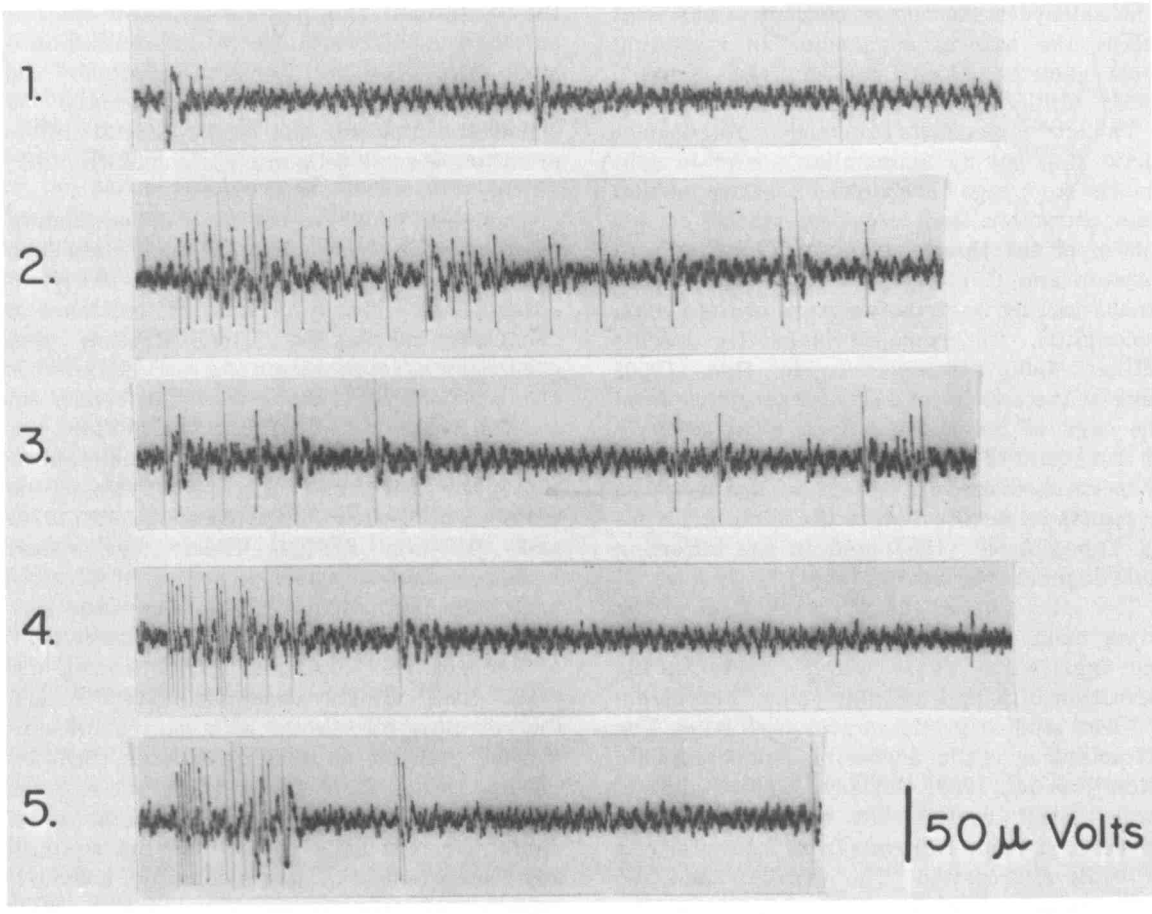

FIGURE 2.—Electrophysiological recordings from the dactyl chemoreceptors of a spiny lobster, *Panulirus interruptus*. (1) Seawater blank, (2) 10^{-5} M dopachrome in seawater, (3) Persisting spikes in dopachrome receptors (continuation of 2), (4) 10^{-3} M taurine in seawater, (5) 10^{-3} M taurine after dopachrome and a seawater wash.

the presence of a large number of agents chemotropic for male gametes exists (Machlis and Rawitscher-Kunkel, 1963), only two have been chemically characterized. Sirenin, the active compound produced by the female gametes of the water mold *Allomyces*, has been isolated and characterized as an oxygenated sesquiterpene (Machlis et al., 1966), and its structure has been uniquely established (Machlis, Nutting, and Rapoport, 1968). It is active in attracting male gametes at 10^{-10}M. The corresponding work from the marine field resulted in the characterization of the active substance released by the female gametes of the brown alga *Ectocarpus siliculosus* as allo-cis-1-(cycloheptadien -2′, 5′-yl)-butene-l (Müller et al., 1971). The receptor sites on the male algal gametes evidence a low level of specificity. Many lower hydrocarbons, esters, alcohols, and aldehydes, at higher concentrations, will mimic the natural compounds in attracting male gametes (Cook, Elvidge, and Bentley, 1951; Müller, 1968; Hlubucek et al., 1970).

Though many efforts to demonstrate a chemotactic response by mammalian sperm to substances from eggs have yielded negative results, such attraction does occur in marine forms. Sperm of the thecate hydroids *Campanularia flexuosa* and *C. calceolifera* respond to a substance issuing from the aperture of the female gonangium. The response is species specific (Miller, 1966). Observations by Dan (1950) suggest the activity of a similar substance from the eggs of the medusa *Spirocodan saltatrix* on the sperm of this species. The first examples of sperm chemotaxis in vertebrates are described in papers on fertilization in the herring *Clupea* by Yanagimachi (1957) and in the bitterling *Acheilognathus* by Suzuki (1961).

The attraction of the amoeboid form of the slime mold *Dictyostelium discoideum* during the aggregation phase which results in the formation of a multicellular "slug" represents the best studied protistan communication. The attractant is cyclic adenosine monophosphate (Konijn et al., 1968; Barkley, 1969). Pulses of cyclic AMP radiate out through the soil moisture at 5 min intervals from the center of a growing aggregation. The gradient and the pulse nature of the signal are maintained by each inward streaming amoeba. Each amoeba secretes a phosphodiesterase to break down the cyclic AMP and, on sensing a pulse of cyclic AMP, emits its own pulse of cyclic AMP about 15 sec after receiving a signal (Cohen and Robertson, 1971; Robertson, Drage, and Cohen, 1972). Bonner (1969) has indicated the likely course of the evolution of this communication in the social slime molds. Soil bacteria, the food of the solitary predecessors of the slime mold amoeba, secrete cyclic AMP. It is reasonable to assume that a mechanism which initially increased the feeding success of these amoebas developed, due to selective pressure, the requisite high sensitivity of response to a chemical signal necessary for aggregation. This capacity then facilitated the evolution of the social species. This is very close to Haldane's premise of the evolution of chemical communication prior to the evolution of metazoans. In further support of Haldane's premise of the lineage of hormones, after aggregation is complete the "metazoan" slug phase migrates to the soil surface and then certain cells differentiate into stalk cells which will eventually support the spore head. Cyclic AMP is apparently the chemical signal for the developmental differentiation of some cells into stalk cells (Bonner, 1970).

The recent rapid growth of our understanding of pheromone communication in insects was founded on half a century of acute biological observations which implicated the existence of chemical messengers. The isolation and chemical characterizations of a growing number of pheromones, and the concomitant behavioral studies, have provided the basis for our appreciation of the role of chemical communication in the life cycle of many species. Among the many recent reviews are those of Beroza (1970) and Jacobson (1972). Electrophysiological investigations of chemoreception in insects have demonstrated that the receptor cells may be divided into two groups, either "specialists" or "generalists" (Yamada, 1970). Among the "specialists" are the pheromone receptors and the receptors for specific secondary plant substances that act as phagostimulants (Schoonhoven, 1968). While remarkable success has been achieved in recording the response of single receptor cells as well as the summed receptor potential of all the antennal chemoreceptors (electroantennogram) these workers have had to contend with a technical problem inherent in studies with this material. Evaluation of the response of a chemosensory organ

or a single cell is difficult when the stimulant must be presented in the gas phase. Each species of stimulant molecule must partition between the gas phase and an aqueous film. The active concentration at the receptor membrane is unknown. A study of the physiology of pheromone reception by aquatic organisms would avoid this limitation.

A survey of the literature reveals that, as in the field of entomology, there exists a broad basis of behavioral observations suggesting the role of chemical communication in the aquatic environment. These studies suggest that marine invertebrates are primarily dependent on chemoreception for information from their environment. The input is composed of a broad spectrum of chemical messages ranging from species specific pheromones eliciting stereospecific responses, e.g., mating behavior, epidemic spawning, aggregation, or alarm behavior, through those kairomones triggering metamorphosis or migration to the cues indicating the proximity of predators or prey.

The closest parallel to insect pheromone communication observed in marine organisms are the sex pheromones of marine crustacea. The first experimental demonstration of "chemical recognition" by marine crustacea is the description of the behavior of male copepods *(Labidocera aestiva)* by Parker (1902). In a series of elegantly simple experiments he demonstrated that "they [the females] probably give rise to some substance that serves as a scent for the males; in other words, the males are probably positively chemotropic toward the females." Moreover Parker noted that "they [the males] seldom pass near the tube without some characteristic reaction. Usually they made one or two quick circles as they swam by, or even a somersault-like motion; these were observed fifteen times when the females were in the tube, never when they were not." Lillelund and Lasker (1971) observed similar swimming behavior in male *Labidocera jollae*. Although *L. jollae* females swim in a seemingly random pattern with only occasionally looped excursions, the males frequently vary their random course of a few seconds duration by swimming in circles, covering a small area intensively. Of greater interest was the observation that rather than circles, the path of the males often resembled a curtate cycloid. The males occasionally progressed for several centimeters in this curtate cycloid path (Figure 3). These observations, although obtained during feeding studies, suggest an important aspect of the physiology of pheromone response in small crustacea—the mechanism of sensing a chemical gradient. Crisp and Meadows (1962) have stated that, because of the small distance between the chemosensory organs of barnacle cyprid larvae, these larvae cannot detect a chemical gradient and thus

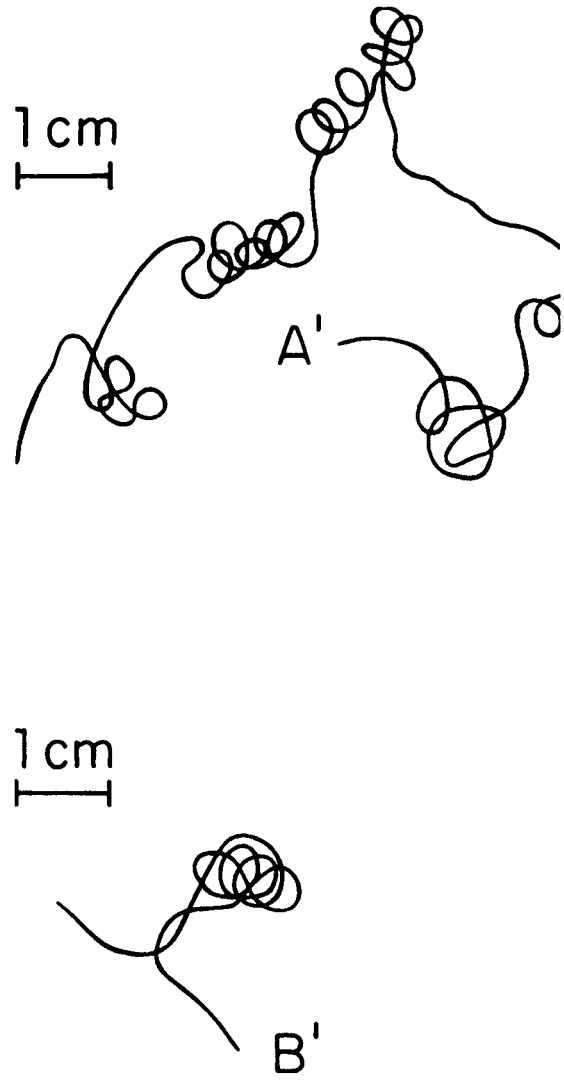

FIGURE 3.—Swimming behavior of a male copepod *Labidocera jollae*. A' and B' mark the termini of the tracings. The upper trace shows both an occasional circular swimming course, progression in a curtate cycloid course and "doubling back." The lower trace is an extreme example of the "doubling back" behavior.

cannot exhibit chemotactic behavior. This reasoning has been applied to all small marine crustacea including copepods. From the above observations it is apparent that the reasoning of Crisp and Meadows is invalid for *Labidocera* and probably for other small crustacea. The critical dimension is the diameter of the circular course, not the dimensions of the organism. A circular swimming pattern in a concentration gradient of a stimulant would result in a sinusoidal variation in the signal intensity. Alteration of the radius of curvature of the swimming course in response to this sinusoidal input would result in cycloidal progression in the gradient. It appears from the observations of the behavior of male *L. jollae* in the feeding experiment that a threshold level of stimulant will trigger a circular swimming pattern, if this circular course results in the detection of a gradient, the circular course will become a curtate cycloid with the ratio of the major to the minor radius being a function of the intensity of the gradient. A frequent observation is a doubling back. If several progressions of the cycloid result in loss of the gradient signal (as must frequently occur in a medium in which the dimensions of the turbulent flow are of the same scale as the swimming pattern), the swimming plots indicate that the male *Labidocera* can effectively loop back through the area where the signal was initially detected (Figure 3). These observations indicate some power of spatial orientation and short term memory in *Labidocera*.

In crabs the male is attracted to the premolt female. During this attraction phase he may display a stance characterized by standing on the tips of his dactyls and elevating his body. He will seize the premolt female and place her below his body. He will protect her during the vulnerable molting period and they copulate immediately after molting. Ryan (1966) demonstrated pheromone communication in this interaction. Water from a tank containing a premolt female *Portunus sanguinolentus*, when added to a tank containing a male of this species, elicited the premolt stance. Evidence that the pheromone is released from the antennule glands was provided by sealing these glands and noting the absence of the stimulating factor.

We have examined this pheromone communication in the lined shore crab, *Pachygrapsus crassipes*. We isolated an active substance and found that it behaved chromatographically like the molting hormone, crustecdysone. Pure crustecdysone is active in stimulating all of the precopulatory behavior of male lined shore crabs from an early search behavior through the display stance to seizing the female. The threshold for stimulating the stance is 10^{-13} M (Kittredge, Terry, and Takahashi, 1971). Confirmation of the identification has been obtained by injecting tritiated crustecdysone into intermolt female Dungeness crabs *(Cancer magister)* and detecting its release as the females entered premolt. Recently we have detected the presence of two additional pheromones released by the female lined shore crabs. Compound A is released in addition to crustecdysone prior to molt. After molting compound A is no longer released into the water, but, if the female is held in isolation from male crabs, a second compound, B, is released. It is likely that the postmolt female has a different message to transmit.

Evolutionary biologists concerned with the inception of pheromone communication have long been puzzled by a dilemma. This chemical communication implies two new capabilities, that to synthesize a messenger compound and the ability to receive the message and translate it into a behavioral response. The improbability of the simultaneous occurrence of these two *de novo* events suggests a stepwise sequence. The observation that the molting hormone of crustacea can function as a sex pheromone indicates that the primordial Arthropoda, through an evolutionary sequence that resulted in structuring the receptor site for the hormones on chemosensory membranes, were able to initiate pheromonal communication (Kittredge and Takahashi, 1972).

SUMMARY

Evidence from the literature supports Haldane's premise that chemical communication is the most primitive form of communication and thus the lineal predecessor of synaptic transmission and hormone function. Transducers of environmental chemical information have likely evolved in response to the metabolic products released by their prey and by competitive organisms. This coevolution of "natural products" and the respective transducers has existed from the earliest metabolic product that happened to be a membrane irritant to the

present. We thus consider it likely that most of the "natural products," not only of terrestrial plants, but also of marine plants and invertebrates, function as allomones, kairomones, or pheromones. Faulkner and Anderson (In press) have provided a review of the chemistry of the "natural products" of marine organisms.

Conceptually, in such a "chemical environment" the most effective protection from a predator would be a "cryptic odor," an irritant that disrupts chemoreception. These cryptic odors may be released into the environment, as is the active component of octopus ink, they may exist in the epidermal tissues or glands where they would function at the inception of attack, or they may be contained in the eggs or larvae. Most sessile marine invertebrates reproduce by epidemic spawning, the simultaneous release of the gonadal products of an entire local population of a species. Most sessile marine invertebrates are also filter feeders. The prime advantage of epidemic spawning is the enhancement of fertilization. However, in the densely populated benthic environment, a heavy loss of eggs or larvae to filter feeders may occur. The presence of a "feeding inhibitor" in the eggs or larvae would reduce such losses. Reiswig (1970) reported that they observed epidemic spawning of the sponge *Neofibularia nolitangere* on a Jamaican reef. At the time they were measuring the water pumping rate of other sponges. When the epidemic spawning of *N. nolitangere* started, the pumping rate of the species under study, *Verongia* sp, abruptly decreased and remained negligible for 2 days. *N. nolitangere* is known to contain toxic substances.

The evidence for chemical cooperation, from gamones to sex pheromones, suggests a pattern of increasing complexity in the function of chemical cues. The behavioral response of even a "simple" crustacean to a chemical gradient appears to involve at least some short term "memory" or a type of "chemical-spatial" sense that we have not observed in such clear-cut form in any other organism.

The study of the chemical ecology of the marine environment is scarcely in its infancy. The chemical characterization of some of the intraspecific and interspecific messages in the sea and the physiology of their perception are challenges. Solutions to these paired problems will provide insights into the evolution of chemical transduction and perhaps expose a hierarchy of perception from membrane irritation to synaptic transmission.

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A SIMPLE BIOECONOMIC FISHERY MANAGEMENT MODEL: A CASE STUDY OF THE AMERICAN LOBSTER FISHERY[1]

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ABSTRACT

The pressures of world economic expansion have led to more intensive exploitation of living marine resources as a source of protein. The exploitation of these common property resources leads, in many cases, to overfishing and depletion. This paper attempts to develop a simplified management tool to prevent overexploitation and depletion of a fishery resource. A general resource model is postulated embracing both biological and economic relationships. This bioeconomic model approximates the operation of a fishery under free access to the resource. A Schaefer type yield function is combined with a linear demand function, and other standard economic relationships and simulations are performed to evaluate the model. Using computer simulation, we imposed five management strategies on the case example, the American lobster fishery. These strategies include (1) freezing fishing effort by raising license fees; (2) reducing fishing effort to that necessary to harvest at the maximum sustainable yield by raising license fees; (3) reducing fishing effort to an "economic optimum" where marginal cost of doing business is equal to marginal revenue from sales by raising license fees; (4) instituting a "stock certificate plan" where individual fishermen would own portions of the resource and trade catch certificates on the open market; however, the total number of catch certificates would not exceed the maximum sustainable yield; and (5) doing nothing. The economic impact in terms of catch, fishing effort, number of fishermen, ex-vessel prices, license revenues, and returns per boat and fishermen were computed for each management strategy so that policymakers and industry leaders could see the alternative consequences of these management positions. The simplified model also is available for use in evaluation of other management schemes that might be suggested.

In the past few years the world community has become increasingly aware of the sea and its resources. The pressures of world economic expansion have led to more intensive exploitation and, at the same time, to increasing concern over the marine environment. Many management strategies used to protect these resources from overexploitation have resulted in inefficient use of gear and equipment as shown by Crutchfield and Pontecorvo (1969). The purpose of this paper is to develop a bioeconomic model of living marine resource exploitation which can be used to assess the economic impact of alternative management strategies for the U.S. inshore American lobster fishery. The U.S. American lobster fishery is a classic case of rapid increases in consumer demand impinging upon a limited resource (Bell, 1972). It should be made quite clear that this analysis is intended to predict the effects of alternative actions without recommending any specific policy.

SPECIFICATION OF THE GENERAL RESOURCE USE MODEL

Before we are able to evaluate the economic impact of various management strategies, it is necessary to develop a general bioeconomic model of how a fishery functions. The following general model has been developed by Fullenbaum, Carlson, and Bell (1971):

$$X = f(X, Kx) \tag{1}$$

$$Kx = Kg(X, K) \tag{2}$$

or

$$x = g(X, K)$$

$$C = K\tilde{\pi} \tag{3}$$

[1] This article was first submitted for publication 7 August 1972. At that time, all data were as current as could be obtained for purposes of the analysis. The views of the authors do not necessarily represent the official position of the U.S. Department of Commerce.

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$$\pi = pKx - C = pKg(X,K) - K\tilde{\pi} \quad (4)$$

$$\dot{K} = \delta_1 \pi, \pi > 0 \quad (5)$$

$$\delta_2 \pi, \pi < 0$$

In the above system, X is the biomass; K equals the number of homogeneous operating units or vessels; x is the catch rate per vessel; C is total industry cost (in constant dollars) or total annual cost per vessel multiplied by the number of vessels; $\tilde{\pi}$ is equal to total annual cost per vessel (in constant dollars) or opportunity cost;[4] π is industry profit in excess of opportunity cost; p is the real ex-vessel price; and δ_1, δ_2 represent the rates of entry and exit of vessels, respectively. Equation (1) represents the biological growth function in which the natural yield or net change in the biomass ($\dot{X}$) is dependent upon the size of the biomass, X, and the harvest rate, Kx. X reflects the influence of environmental factors such as available space or food, which constrain the growth in the biomass as the latter increases. The harvest rate or annual catch, Kx, summarizes all growth factors induced by fishing activity. Equations (2) present the industry and firm production function for which it is normally assumed that $\frac{\partial g}{\partial X} \equiv g_1 > 0$ and $\frac{\partial g}{\partial K} \equiv g_2 < 0$.[5] In other words, catch per vessel increases when the biomass increases and declines when the number of vessels increases. Equations (3) and (4) are the industry total cost and total profit function, respectively. Equation (5) is a very important equation since it indicates that vessels will enter the industry when excess industrial profits are greater than zero (i.e., greater than that rate of return necessary to hold vessels in the fishery, or the opportunity cost) and will leave the fishery when excess industrial profits are less than zero (i.e., below opportunity cost).

[4] Opportunity cost is defined as the necessary payment to fishermen and owners of capital to keep them employed in the industry or fishery compared to alternative employment or uses of capital.

[5] In some developing fisheries, it is possible that $g_2 > 0$. For example, in the Japanese Pacific tuna fishery, intercommunication between vessels may increase the catch rate as more vessels enter the fishing grounds.

The equilibrium condition for the industry ($\pi = 0$) may be formulated as shown below:

$$p = \frac{\tilde{\pi}}{g(X,K)} \quad (6)$$

Equation (6) merely stipulates that ex-vessel price is equal to average cost per pound of fish landed (i.e., no excess profits).

There are two important properties of the system outlined in (1) - (5). First, the optimum size of the firm is given and may be indexed by $\tilde{\pi}$. Thus, the firm is predefined as a bundle of inputs.[6] Second, the long-run catch rate per vessel per unit of time is beyond the individual firm's control.[7] It is, in effect, determined by stock or technological externalities.[8] Finally, we are assuming that the number of homogeneous vessels is a good proxy for fishing effort. Alternatively, we may employ fishing effort directly in our system by determining the number of units of fishing effort applied to the resource per vessel. This will be discussed below.

A QUADRATIC EXAMPLE OF THE RESOURCE USE MODEL

By combining the more traditional theories depicting the dynamics of a living marine resource with some commonly used economic relations, we may derive a quadratic example of the general model specified above. This example effectively abstracts from complications such as ecological interdependence and age-distribution-dependent growth of the biomass on the biological side and, furthermore, assumes the absence of crowding externalities (i.e., $g_2 \equiv 0$) in the production function on the economic side.

[6] In other words, because we are dealing with a long-run theory of the industry, we are assuming that variations in output result from the entry or exit of optimum-sized homogeneous vessels.

[7] We have implicitly assumed that such short-run changes as longer fishing seasons, etc., are all subsumed in a long-run context. Normally longer fishing seasons, for example, do not change catch rates per unit of time fished; nor do they change costs per unit of time fished. They do, however, change the effective level of K.

[8] A technological externality exists when the input into the productive process of one firm affects the output of another firm. In the context of fishing, an additional firm or vessel entering the fishery will utilize the biomass (as an input) and, as a result, in the long run will reduce the level of output for other vessels in the fleet. (See Worcester (1969)).

The dynamics of a fish stock may be depicted by the logistic growth function (Lotka, 1956).[9]

$$X(t) = \frac{L}{1 + Ce^{-KLt}} \text{ where } L>0, C>0, k>0, \quad (7)$$

where L, C, and K are assumed to be environmental constants. Differentiating (7) and substituting we obtain,

$$\dot{X} \equiv \frac{dX}{dt} = kLX - kX^2 \equiv aX - bX^2 \quad (8)$$

where $a = kL$, $b = k$.

If (8) is set equal to zero, we may solve for the nonzero steady-state biomass, a/b (i.e., L). Alternatively, the limit of $X(t)$ as $t \to \infty$ yields identical results. The maximum of (8) occurs when X is equal to $a/2b$. Thus

$$\max \frac{dX}{dt} = a^2/4b \quad (9)$$

The introduction of fishing (i.e., harvest or Kx) is assumed to have no interactive effects, so that the instataneous growth rate is reduced by the amount harvested:[10]

$$\frac{dX}{dt} = aX - bX^2 - Kx. \quad (10)$$

The economic component of the model requires the exact specification of an industry production function and an industry revenue relationship. One hypothesis regarding the fish catch is that the proportion of the biomass caught is a direct function of the number of vessels (or equivalent fishing effort) exploiting a given ground.[11] Thus, the total harvest rate is given as,

$$Kx = rKX \quad (11)$$

where r is a technological parameter.[12] Finally, the total revenue function for the industry may take the following form:

$$pKx = (\alpha - \beta Kx)Kx. \quad (12)$$

Equation (12) merely stipulates that the total revenue is a quadratic function of total landings, Kx. Dividing through by Kx will give us the familiar demand function where ex-vessel price is inversely related to landings, holding all other factors constant.[13] With total costs equal to $K\pi$, the profit function becomes

$$\pi = (\alpha - \beta Kx)Kx - K\tilde{\pi}. \quad (13)$$

Given these formulations, the system in (10) - (13) can be reduced to two steady-state functions. The first, which condenses all relevant biotechnological factors, is the ecological equilibrium equation. It plots the relationship between the biomass and the number of vessels (or fishing effort) needed to harvest the yield such that the biomass is in equilibrium. We can derive this equation by setting $\dot{X}$ equal to zero, substituting (11) into (10), and solving for K in terms of X:

$$K = \frac{1}{r}(a - bX). \quad (14)$$

Similarly, the second equilibrium function plots the relationship between X and K under a zero profit state, i.e., under conditions that $K = 0$, or that there is no entry to or exit from the fishery. Thus, by setting (13) equal to zero and substituting (11) into (13), we obtain

$$K = \frac{\alpha}{\beta rX} - \frac{\tilde{\pi}}{\beta r^2 X^2}. \quad (15)$$

[9] Graham (1935) was the first biologist to apply the logistic growth model to exploited fish populations.

[10] Schaefer, (1954) was the first population dynamicist to develop the function specified in equation (10).

[11] Alternatively, one could assume that the proportion of the biomass caught declines as the number of vessels increases:

$$Kx = [1 - (1 - t)^K]X. \qquad 0<t<1$$

With this specification, t represents the proportion of the biomass taken by the first vessel and also represents the percentage taken by each succeeding vessel of the remaining biomass. This form was first developed by E. W. Carlson (1970. An economic theory of common property resources. Unpubl. manuscr. Econ. Res. Lab., Natl. Mar. Fish. Serv., NOAA College Park, Md.).

[12] A reviewer of this article has pointed out that r is not likely to be constant over any large number of years. Since there are no time series observations on X, r cannot be tested to see whether it varies over time or is a constant. In this case, we are merely following the simplified Schaefer model.

[13] Such complicating factors as per capita income and its influence on ex-vessel prices can be introduced later as changes in the parameter, α.

These two curves are plotted in Figure 1.[14] Their intersection at (X^*, K^*) denotes bioeconomic equilibrium. The direction of the arrows describes the qualitative dynamic changes of a point in phase space. Figure 1 represents the general case of exploitation. When (15) is combined with (14), however, we can simulate either nonexploitation (Figure 2) or extinction as a possible dynamic result (Figure 3).[15] The state of the fishery—exploited, unexploited, or extinct—depends upon the parameters a, b, r, β, $\tilde{\pi}$, and α and their interrelationships. This completes our general model of how a fishery functions. Now let us turn to a specific application of the model.

AN EMPIRICAL CASE STUDY: THE U.S. INSHORE AMERICAN LOBSTER FISHERY

The U.S. inshore American lobster fishery—principally located off the coast of Maine—represents a good case study for a number of reasons. First, the American lobster is considered a high quality seafood item and is a popularly consumed species for which demand has been increasing rapidly (Bell, 1972). Second, because of intensive fishing pressure, the resource has shown signs of overexploitation.[16] Third, the inshore lobster fishery is one of the few grounds for which enough data are available so that some rough measures of needed biological and economic parameters can be derived. Fourth, according to Dow (1961),[17] the inshore lobster fishery is a relatively closed population as our production model assumes. Last, we believe that over the long run the American lobster population has not had a great divergence from the steady-state model employed in our analysis. The gross divergence from the steady-state assumption is significant only when fishing effort changes dramatically from period to period. For modest changes in fishing effort, the steady-state assumption will not yield biased estimates. A check on the fishing effort series for the American inshore northern lobster fishery reveals a steady and gradual increase. The alternative methods of Pella and Tomlinson (1969) do yield biased parameters due to nonlinear fitting methods. Gulland's (1961) method yields biased parameters since effort is averaged and then used as an independent variable. Therefore effort in period t is not independent of effort in period $t + 1$ which violates classical statistical assumptions underlying least squares. Also the predictive value (using the steady- state assumption) or goodness of fit is certainly at an acceptable level, $R^2 = 0.962$ (infra). Our discussion will be subdivided on the basis of production-related and demand-related estimates.

The Production Function and the Supply of American Lobsters

There are four parameters on the supply side for which initial estimates are required: a, b, r,

[14] In steady state, the reader should be aware that we have not constrained the population stock to its initial size or any other size. Using the Schaefer model (i.e., steady state), the stock size varies inversely with fishing effort, T. Even in a dynamic context, the biomass would asymptotically approach the steady-state solution.

[15] It should be pointed out that Schaefer (1954) discusses economic transitional states which are very similar to the bioeconomic model presented in this paper. He states:

"To arrive at a particular function to describe the change of the intensity of fishing with the size of the population, we may consider that the incentive for new investment is proportional to the return to be expected, in which case there will be a linear relation between the percentage rate of change of fishing intensity and the difference between the level of fish population and its economically critical level, b. This function will, then, be

$$\frac{dF}{dt} = k_3 F(P - b) \text{ ------ } (11)$$

where k_3 is a constant."

His process of transitional states is implicit in our diagrams in Figure 3 since adjustment (i.e., transitional states) will occur anywhere in phase space to the equilibrium values where $\dot{X} = 0$ and $\dot{K} = 0$.

[16] U.S. landings of trap-caught American lobsters increased from approximately 23 million pounds in 1950 to a peak of over 29 million pounds by 1957. Since 1957 landings have fallen off, reaching a low of 22 million pounds in 1967. In 1969 lobster production had recovered to 26.9 million pounds. Despite the poor performance of production over the 1950-69 period, the number of lobster traps fished per year (i.e., a proxy for fishing effort) has increased secularly from approximately 579,000 in 1950 to over 1,060,000 in 1969. Because of these past events, several bills have been presented in the Maine Legislature to apply some sort of stringent licensing scheme to limit entry.

[17] Dow, R. 1971. Effort, environment, supply, and yield in the Maine lobster fishery. Unpublished manuscript submitted to the U.S. Fish and Wildlife Service, Washington, D.C. 125 p. (May be obtained from Sea and Shore Fisheries, Maine.)

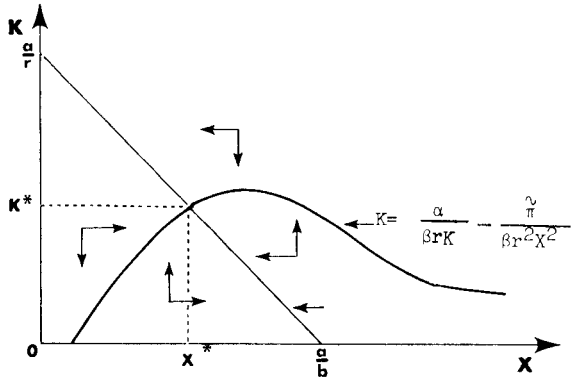

FIGURE 1.—Exploitation.

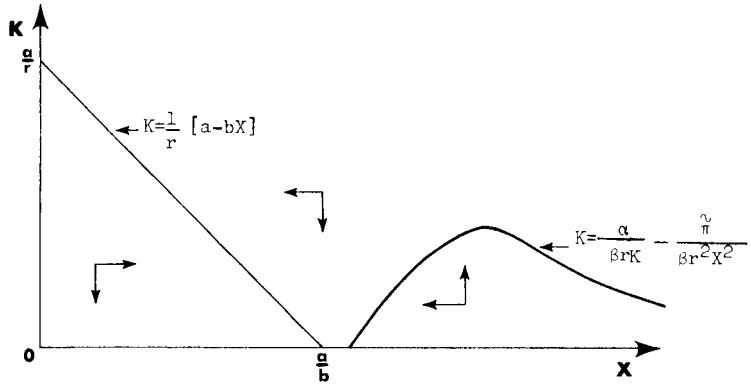

FIGURE 2.—Non-exploitation.

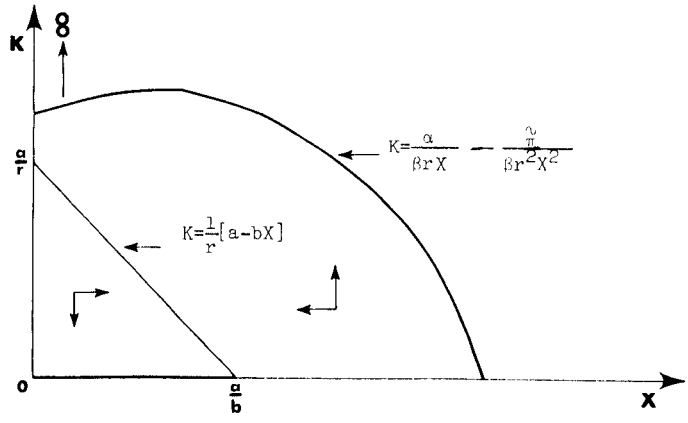

FIGURE 3.—Extinction.

and $\tilde{\pi}$.[18] The first three can be developed by combining statistical estimation and independently derived data. Assume that the biomass is instantaneously in equilibrium (i.e., $\frac{dX}{dt} = 0$).

Then, taking the inverse of (14) and substituting it for X in (11), we obtain:

$$Kx = cK - dK^2 \tag{16}$$

where $$c = \frac{ar}{b},\ d = \frac{r^2}{b}$$

and $$x = c - dK. \tag{17}$$

Equation (16) is the familiar parabolic yield function postulated by Schaefer (1954).[19] Notice that both the harvest rate, Kx, and output per vessel, x, may be specified solely in terms of the number of vessels or fishing effort. Similarly, the common property resource externality, as given in (17), is a function only of the level of K. Over a longer period of time the basic assumption underlying equations (16) and (17) may reflect a valid representation; i.e., effort or K is the only instrumental variable affecting output. There are three different parameters embedded in estimates of c and d. The only way that a, b, and r can be derived is if some independent biological information is given. More specifically, suppose that we have an estimate of the biomass consistent with maximum sustainable yield, call it $\hat{X}^\circ$. Since $\hat{X}^\circ$ is equal to $a/2b$, it follows that the following parameters may be estimated (designated by ^):

$$\hat{r} = \hat{c}/2\hat{X}^\circ \tag{18}$$

$$\hat{b} = [\hat{d}/\hat{r}^2] - 1 \tag{19}$$

$$\hat{a} = \hat{c}\hat{b}/\hat{r}. \tag{20}$$

Thus, (17) will be estimated subject to one modification concerning the introduction of an environmental variable. Several biologists, including Dow et al. (1961),[20] have argued that a long-term trend of declining seawater temperature is partially responsible for the decline in U.S. coastal catches.[21] It will be assumed in this study that seawater temperature (°F) affects the a term in the growth function so that,

$$\frac{dX}{dt} = a(^\circ\mathrm{F})X - bX^2, \tag{21}$$

where °F is equal to the mean annual seawater temperature, in degrees Fahrenheit Boothbay Harbor, Maine, with $\frac{\partial a}{\partial(^\circ\mathrm{F})} \equiv a' > 0$. Seawater temperature can easily be incorporated into (17) in the following way:

$$x = c' - dK + z(^\circ\mathrm{F}), \tag{22}$$

where z represents the change in output per boat as a result of a one-degree change in water temperature.[22]

Data on the number of traps fished per year for the entire inshore American lobster fishery

[18] An alternative approach suggested by Thomas (1970) uses the Beverton-Holt model in developing a yield/recruit relationship. However, because a stock-recruitment equation is not specified, it cannot be incorporated into our bioeconomic model at this time.

[19] The reader should recognize that it does not follow that (17) can be derived from a generalized growth equation [$\dot{X} = F(X) - Kx = 0$] and production function $Kx = f(X,K)$. Only under certain specifications of the previous two functions will it follow that x can be defined as a unique function of K (or X) only. In addition, this production function could have been more generally specified as $Kx = rK^{\alpha}X^{\beta}$. However, two compelling factors make it desirable to employ this function. First, there are no observations on the biomass, X, so that empirical tests cannot be made to estimate ß. Second, the equation $Kx = rKX$ combined with the logistic gives an excellent empirical fit to past behavior in the fishery (i.e., $R^2 = 0.962$ for yield function equation 23). In addition, Schaefer makes the same assumption as we did, and this assumption is generally accepted as plausible for most fisheries. In conclusion it is difficult for us to imagine how a different assumption could lead to superior predictive results (i.e., goodness of fit).

[20] Dow, R., D. Harriman, G. Pontecorvo, and J. Storer. 1961. The Maine lobster fishery. Unpublished manuscript submitted to the U.S. Fish and Wildlife Service, Washington, D.C. 71 p. (May be obtained from Sea and Shore Fisheries, Maine.)

[21] Higher seawater temperature can affect the natural yield of lobsters by providing a climate in which molting is facilitated. A larger number of molts will tend, *ceteris paribus*, to increase the yield associated with any given level of the biomass.

[22] Implicit in the way the effect of seawater temperature is measured is the relationship:

$$[a = a_0 + d(^\circ\mathrm{F})].$$

are available for the 1950-69 period (see Appendix Table).[23] Output per trap was regressed against the number of traps and seawater temperature on the assumption that the number of traps per boat was constant. The regression estimates yielded the following results:

$$x = -31.82 - 0.00002807(T) + 1.846(^\circ\mathrm{F}) \quad (23)$$

$$(6.55) \qquad (4.99)$$

$$R^2 = 0.962$$

$$\text{D-W} = 2.38$$

where $T = 562.8(K)$: $\hat{a} = 0.0156$; $\hat{c} = -31.82 + 1.846(^\circ\mathrm{F})$. In (23), T is equal to the number of traps fished per year, and t-ratios are in parentheses.[24] Both T and °F are statistically significant at the 5% level and exhibit the correct sign; the Durbin-Watson statistic indicates no significant autocorrelation.

The only step required to obtain the biotechnological parameters is an estimate of the biomass consistent with maximum sustainable yield. It has been calculated that (assuming a temperature of 46°F) the fishable stock of U.S. inshore American lobsters consistent with maximum sustainable yield is equal to 31 million pounds.[25] For the Gulf of Maine (where most of the resource is located), estimates of the biomass were made through sampling experiments.[26]

Finally, on the basis of recent cost studies, we have derived an estimate of $\hat{\pi}$ for 1966 equal to $12,070.[27, 28] Therefore, on the supply side, the estimated parameters for 1969 are the following:

$$\hat{a} = 1.85379$$
$$\hat{b} = 2.9899 \times 10^{-8}$$
$$\hat{r} = 5.1562 \times 10^{-4}$$
$$\hat{\pi} = \$13{,}191 \text{ (see footnote 27).}$$

The Demand Function for American Lobsters

Only knowledge of $\hat{a}$ and $\hat{\beta}$ is needed in order to complete the empirical component of the study. The estimation procedure is rather straightforward. We may specify the following demand function for all lobsters:

$$\frac{C}{N} = F - m(P'/\mathrm{CPI}) + g(Y/N) \quad (24)$$

where C is equal to consumption of all lobsters, P' is the money ex-vessel price of American lobsters, Y is aggregate U.S. personal income (1967 prices), N is U.S. population, and CPI is the consumer price index. Since there are no exports of lobster, the following identity holds:

$$C = I + Q_o + Q_{\mathrm{in}} \quad (25)$$

where I, Q_o, and Q_{in} are the level of imported lobsters, U.S. production of all other lobsters, and U.S. production of inshore American lobsters, respectively. Given (25), equation (24) may be solved in terms of P, or,

$$P = \frac{P'}{\mathrm{CPI}} = \left[\frac{F}{e} - \frac{1}{mN}(Q_{\mathrm{in}} + Q_o + I) + \frac{gY}{mN}\right] \quad (26)$$

If Q_o, I, Y, CPI, and N are held constant, equation (26) gives a unique relationship between the ex-vessel price of American lobsters and quantity landed.

Using data over the 1950-69 period (see Appendix Table), the parameters of equation (24) were estimated using least squares:

[23] The assumption of a constant number of traps per boat is necessary in order to solve for a coefficient on "K", and thereby, to obtain the biotechnological parameters embedded in the yield-effort relationship. The relationship for 1966, derived on the basis of cost data obtained from the National Marine Fisheries Service's Division of Financial Assistance was 562.8 traps per full-time equivalent northern lobster boat. However, it should be pointed out that when the stock is large and the catch high, it may pay to increase the number of traps per boat; therefore, this might bias the number of "standardized boats", but not total amount of effort.

[24] However, the reader should note that the empirical estimates themselves (1950-69) make no assumption with respect to the relation between K and T. x was regressed on T and °F. Only in the simulation was a relationship assumed ($T = 562.8K$).

[25] U.S. Department of the Interior. 1970. Joint master plan for the northern lobster fishery. Unpublished manuscript. 130 p. (May be obtained from the National Marine Fisheries Service, Washington, D.C.)

[26] No attempts were made to run the simulation model with varying sizes of the MSY biomass as this would unnecessarily complicate this paper which is intended to be simplistic as possible.

[27] Cost data from the National Marine Fisheries Service's Division of Financial Assistance (1966) reveal the following cost breakdown for a representative lobster boat: operating expenses, $4,965.16; fixed expenses, $1,180.20; returns to capital and labor, $5,825.48. This gives a total of $12,070.84. The latter figure was updated to 1969 by income increases in Maine to obtain $13,191.

[28] We will assume that $\bar{\pi}$ remains constant in real terms. This is equivalent to keeping our estimate of $\bar{\pi}$, $\hat{\pi}$ constant, while deflating all nominal variables on the demand side.

$$\frac{C}{N} = -0.0632 - \underset{(2.06)}{0.005029}\left(\frac{P'}{\text{CPI}}\right) + \underset{(5.38)}{0.00051}\,\frac{Y}{N} \quad (27)$$

$R^2 = 0.816$

D-W = 0.619

All of the independent variables are significant at the 0.05 level. However, the Durbin-Watson statistic indicates the strong possibility of positive autocorrelation. Nonetheless, we will use these estimates as rough approximations to obtain the price-dependent relationship as shown in (26). Given 1969 values of exogenous variables (N = 199,100,000; Y = \$567,635 million; CPI = 109.8 with a base of 1967 = 100; $Q_o + I$ = 158.8 million pounds), we have,

$$P = 1.179 - (0.99853 \times 10^{-8})Q_{in}. \quad (28)$$

Thus initial values for $\hat{a}$ (1.179) and $\hat{\beta}$ (0.99853 $\times 10^{-8}$) have been obtained.[29]

[29] For purposes of simplification, the parameters of the model are all assumed constant. Certainly, one could argue that the parameters, so tacitly assumed to be constants, are at best random variables. Therefore, a stochastic treatment might be used with criteria like maximal expected present value or minimal maximum expected loss for evaluating the management alternatives rather than simple deterministic computations. Possibly, the parameters are random variables and conditional on some of the suggested management alternatives. For example, freezing effort might accelerate r, leading to shifts in season or age structure harvested, hence a change in a/b.

HOW THE MODEL WORKS: THE IMPACT OF CRITICAL VARIABLES

To illustrate the power of the model in explaining the impact of changes in critical variables, we may derive initial quantitative estimates of the ecological equilibrium and economic steady-state functions. In this section we will illustrate the power of the model in explaining the impact of changes in critical variables. The year 1969 is selected for initial quantitative estimates of the ecological equilibrium and economic steady-state functions. Table 1 shows what happens to the value of (X^*, K^*) as well as the equilibrium harvest level, $(Kx)^*$, when the following changes take place:

a) A 25% increase in opportunity costs of labor caused by the development of greater regional industrial activity;
b) A 25% increase in the supply of other lobsters traceable to the discovery of a new lobster ground;
c) A 5% increase in personal per capita income; and
d) A decrease in water temperature from 48° to 47°F.

Notice that these changes are for illustrative purposes; however they do come about on a routine basis in the real world. Perhaps 25% changes in selected variables do not come about in one year so the reader can view the new equilibrium

TABLE 1.—The impact of exogenous shocks to the inshore American lobster fishery on the effort, catch, and biomass.

	Vessels, full-time equivalent K^*	Traps E^*	Catch Kx^*	Biomass X^*
	Number	*Number*	*Million pounds*	
Initial equilibrium (1969) (computed by model)	1,936	1,089,000	28.56	28.62
New equilibrium:				
(a) Increase (25%) in opportunity cost of labor	1,531	861,718	28.1	35.6
(b) Increase (25%) in exogenous supply of lobsters	947	533,000	22.3	45.7
(c) Increase (5%) in personal per capita income	2,182	1,228,310	27.4	28.0
(d) Decline in water temperature by 1°	1,851	1,041,710	26.8	29.0
(e) Changes (a)-(d) simultaneously	905	509,356	20.7	45.9

positions shown in Table 1 to result over a period of years from the 1969 initial equilibrium. We may incorporate all of the four changes given separately in (a) - (d) to ascertain their net impact. The strength of the simulation model is that we can study the separate and combined influences on the fishery of important variables. Because we have both positive and negative influences on fishing effort, it is likely to be such that complete extinction of a particular species would be somewhat difficult.[30]

ECONOMIC IMPACT OF SELECTED MANAGEMENT ALTERNATIVES

Up to this point, we have been concerned largely with building a bioeconomic model that considers all important variables. The model is based upon the fact that open access to the American lobster fishery is permitted. However, all States restrict gear to pots and traps. Each State (Maine, Massachusetts, New Hampshire, and Rhode Island) has a minimum length requirement; permitted minimum lengths vary from $3\frac{1}{8}$ to $3\frac{3}{16}$ inches. We are taking the array of existing regulations as given. We shall consider the economic impact of five alternative policies that could be adopted to manage or to limit entry to the entire American lobster fishery. These management strategies assume that some central authority such as a regional commission could impose these regulations.[31] The specific objectives of these management strategies will be discussed below. All strategies have two objectives in common which are (1) to protect the resource from overexploitation and (2) to allow maximum freedom for operators to function in a free enterprise fashion. Further, the following strategies are meant to be illustrative and do not exhaust all possible alternatives. Also, two other management strategies suggested by Reeves (1969) and Sinclair (1960) will be reviewed. As other management strategies are suggested both inside and outside government, the model formulated above may be used to predict their impact.

Some Possible Alternative Management Strategies for Inshore American Lobsters

1. *Freeze on existing (1969) fishing effort by placing a license fee on traps:* Under this scheme, the regulatory authority would calculate a license fee on traps which would keep the level of fishing effort constant despite an increase in the demand for lobsters.[32] A license fee could not be levied on the individual vessel because this would not control the number of traps fished per vessel. The increased cost of operations due to the license fee would make it uneconomical for vessels to enter the fishery even though ex-vessel prices have increased. In essence, the license fee would siphon off increased revenue (or profits) from an increase in ex-vessel prices assuming the latter increases faster than cost of operations. For purposes of illustration, let us assume that we desire to manage the inshore American lobster fishery commencing in 1974. Given the estimated trend in important variables in the fishery (i.e., $\hat{\pi}$, I, Q_0, Y, N, CPI) to the year 1974, it would be necessary to place an estimated annual license

[30] This is subject to two qualifications. First, since we are plotting only equilibrium relationships, extinction is a possible dynamic outcome (as was mentioned previously). Second, we have implicitly assumed that in the case of American lobster, the rate of technological advance is minimal. This is a fairly realistic assumption for the inshore trap fishery. However, in general, $r = r(t)$, with $r' > 0$.

[31] With the steady-state assumption, the management policies would in fact maximize the present value of the stream of net benefits over time.

[32] The model can derive the "correct tax" (or license fee) in a number of ways. Suppose, the regulatory authority wishes to freeze effort at some specified level K^0. We can derive the equilibrium yield consistent with K^0, call it $(Kx)^0$, from the yield-effort relationship. The total tax and the tax per vessel are then respectively given by:

$$T_x = (\hat{\alpha} - \hat{\beta}(Kx)^0)(Kx)^0 - K^0\hat{\pi}$$

$$T_x/K = \frac{[(\hat{\alpha} - \hat{\beta}(Kx))\,x - \hat{\pi}]}{K}$$

In similar fashion, if the regulatory authority wishes to freeze effort at a level consistent with maximum sustainable yield, we can obtain the tax that will insure this level of exploitation.

The only other taxing scheme that requires further explanation is a tax that will insure marginal cost pricing. Long-run industry marginal cost can be defined as:

$\hat{\pi}/\frac{\partial Kx}{\partial K}$, where $\frac{\partial Kx}{\partial K}$ is the first derivative of (16). Total industry cost can then be redefined as,

$$\left(\frac{\hat{\pi}}{\partial Kx/\partial K}\right)Kx$$

This expression can be substituted into the total revenue function and solution for K, Kx can be found by iteration. The tax consistent with these solutions can then be derived by using the formulas given above, i.e., Tx, Tx/K.

fee of $3.34 (in 1972 dollars) on each lobster trap fished. This is shown in Table 2. The regulatory authority would collect over $3.5 million in license fee revenue which could be used to finance resource research, enforcement, and surveillance. It should be emphasized that these calculations are merely rough estimates and only serve to give the reader some idea of the magnitude of such license fee. The illustrative license fee is also based upon an extrapolation of trends 5 yr ahead of 1969. If we did nothing, it is estimated that the catch would be lower and more fishermen and traps would be employed in the fishery by 1974. Obviously, the situation would worsen as demand for lobsters expanded and the fishery became increasingly overfished. The license fee plan does have many disadvantages. First, a license fee on traps fished does not really get at the utilization rate. One might expect that a license fee on an individual trap might induce fishermen to fish each trap more intensively and thereby reduce their number of traps. At this point, we do not have any information on utilization rates whereby the tax could be adjusted upward if utilization increased. Second, enforcement and surveillance might be difficult along the coastline from Maine to North Carolina. Third, and most important, the quantitative tools and projected figures needed to calculate a license fee are at best crude and would have to be used for calculations each year.

2. *Reduce the existing level of fishing effort to that necessary to harvest MSY by placing a license fee on traps:* With this scheme, the regulatory authority would calculate a license fee on traps which would reduce the level of existing effort to that necessary to harvest maximum sustainable yield (i.e., estimated to be about 1,011,910 traps) despite an increase in demand for lobsters.[33] Because we are actually reducing fishing effort as opposed to freezing it at the 1969 level, the estimated 1974 license fee per trap must be higher or $5.58 (in 1972 dollars). Actual catch will not be significantly higher. The regulatory authority would receive approximately $5.6 million in license fee revenue. However, this plan has the same disadvantages of a general license fee plan indicated under alternative one.

3. *Reduce the existing level of fishing effort to that necessary to make the marginal cost of*

[33] The fishing effort needed to harvest MSY was obtained from equation (23) with the 1950-69 average water temperature.

TABLE 2.—The impact of various management schemes imposed on the inshore American lobster fishery in 1974.[1]

Economic variables	Estimated values before imposition of management strategies (1969)	Impact after the imposition of selected management strategies for 1974				
		(1) Freeze at 1969 level of fishing effort	(2) Reduce fishing effort to E_{MAX}	(3) Reduce fishing effort so $MC = P$	(4) Issue "stock certificate" to vessel owner while freezing effort at 1969 level	(5) Do nothing
Catch (million lb)	28.6	28.6	28.7	23.9	28.6	28.1
Value of catch (million $)	28.0	36.8	36.9	31.9	36.8	36.4
Vessels (full-time equivalent)	1,900	1,900	1,798	1,060	1,900	2,070
Traps (million)	1.069	1.069	1.011	0.597	1.069	1.165
Ex-vessel price	0.98	1.29	1.29	1.33	1.29	1.30
Total license fees collected (million $)	0	3.56	5.58	13.3	0	0
License fee/vessel ($)[2]	0	1,877	3,119	12,622	0	0
License fee /trap ($)	0	3.34	5.54	22.43	0	0
Return per vessel and fisherman	6,365	8,400	8,400	8,400	10,278	8,400

[1] Projection of 1974 impact of selected management strategies. Assumes that $F^{\circ} = 48^{\circ}$; $Y = \$677.9$ billion, (1969 prices); POP = 212.4 million; $Q_0 + I =$ 183.6 million pounds and $\hat{\pi} = \$15{,}292$. All prices and dollar values projected for 1974 are expressed in 1972 dollars.

[2] The license fee per vessel was obtained by multiplying the tax per trap by the average number of traps (562.8) fished per full-time vessel.

landings equal to ex-vessel price by placing a license fee on traps: The idea here is to obtain the greatest "net economic benefit" and has been suggested by such economists as Crutchfield and Pontecorvo (1969).[34] If a regulatory authority were to try this for 1974, it would have a drastic impact on the fishery as the number of full-time equivalent vessels and traps would be reduced by approximately 47%. To accomplish this objective an estimated 1974 license fee of $22.43 (in 1972 dollars) per trap would be needed. This would yield the regulatory authority approximately $13.3 million in revenue. From an economic point of view, it is argued that this management strategy will result in the most efficient operation of the fishery if fishermen and vessels can easily move to other fisheries or industries. However, this strategy may be particularly unwise in rural areas such as Maine where labor mobility is low. A drastic cutback in the number of fishermen may create social problems where the cost would greatly exceed any benefits derived from this management strategy. Therefore this management strategy is difficult, if not impossible, to justify on economic grounds for many rural areas where the fishing industry is located and also has the same disadvantages of a general license fee plan on traps as discussed above.

4. *Issue "stock certificates" to each vessel owner based upon average catch over last 5 yr while freezing the existing level of fishing effort:* Under this scheme, the historic rights of each fishing firm would be recognized. In a similar manner to a private land grant procedure, the regulatory authority would simply grant each fisherman a "private" share of an existing resource or catch. The stock certificate would be evidence of private ownership. Individual fishermen would be free to catch up to their allotted share through the use of pots or other biologically permissible technology or, if they desired, trade their stock certificates to others for cash. Suppose the regulatory authority were to freeze the level of fishing effort at the 1969 level and distribute the estimated catch via a stock certificate to the existing fishermen. It should be pointed out that the regulatory authority fixes effort when it selects a given catch. The selected catch could be either MSY or any other level of catch deemed by the regulatory authority not injurious to the viability of the stock. The expansion in demand for lobsters by 1974 would generate excess profits for those individual fishermen who were initially endowed with the property right. By 1974, it is estimated that a full-time lobsterman would be earning $10,278 (in 1972 dollars) a year of which $1,878 would be excess profits (i.e., above opportunity cost). If profits become excessive a license fee would be levied on the fishermen holding stock certificates to insure against increased abnormal returns and provide the regulatory authority with funding to conduct scientific investigations and enforcement. It should be noted that this plan is identical to the license fee scheme which freezes effort at its 1969 level. However, in the latter case, excess profits are taken by the regulatory authority while for this strategy, fishermen are allowed to hold onto the profits generated in the fishery. Since many fisheries are located in rural areas where earnings are traditionally low, this strategy might be justified on the basis that it will raise income levels and thereby help improve living standards to comparable levels to those received in urban areas. This management strategy would, of course, be popular with those already in the fishery. However, new entrants would have to buy stock certificates from those initially in the fishery. This would bring up certain questions of equity and legal precedent which are beyond the scope of this article.

5. *No management strategy:* When considering the economic consequences of alternative management strategies (1-4), it is always wise to assess the results of doing nothing. This gives policymakers a better perspective in evaluating the benefits from taking action. The consequence of doing nothing would be overcapitalization by 1974 with an expansion in the number of full-time equivalent fishermen and traps fished. Approximately 96,000 excess traps (i.e., above that necessary to take MSY) would be in the fishery, and the catch would fall to 28.1 million pounds.

The fishery would grow increasingly overcapitalized, and the resource would be greatly overexploited as demand increased for lobsters during the 1970's. On economic grounds, these

[34] When price is constant, maximization of net economic benefit becomes identical to the goal of maximization of rent to the fishery. This, however, is not the case when the normally downward sloping demand curve is specified.

results are hardly acceptable because more fishermen and vessels will probably be catching less.

6. *Other suggested management strategies:* Reeves (1969) has proposed a hike in license fees to eliminate the marginal or part-time fishermen. He suggests that the present $10 yearly fee in Maine be raised $10 a year over the next 9 yr to a top of $100. In 1969, a little less than one-half of the lobster fishermen were part-time. A part-time lobster fisherman is defined as one who gains less than one-half of his annual income from lobstering. The first step in most suggested limited entry schemes is usually to restrict the fishery to full-time utilization of capital and labor. Two problems occur with this policy. First, the part-time fishermen may represent the most efficient way of taking the catch. If so, the full-time fishermen may be eliminated by increased license fees. Second, license fees do not directly control fishing effort since fishermen may fish more traps. However, Reeves also goes on to argue strongly for limiting the number of traps each fisherman is allowed to set. It is not quite clear whether anyone knows the optimum number of traps per vessel.

Rutherford, Wilder, and Frick (1967) in their study of the Canadian inshore lobster fishery endorse the system suggested by Sinclair (1960). They state:

> "An alternative management system is that suggested by Sinclair (1960) for the salmon fisheries of the Pacific Coast. This would use the licensing of fishermen to limit entry into the fishery. In the first stage, lasting about five years, licenses would be reissued at a fee but no new entries would be licensed, and it would be hoped that during the period there would take place a reduction in the labour and capital input, to take the maximum sustainable catch of salmon at a considerably lower cost. After the end of the first stage, licenses would be issued by the government under competitive bidding and only in sufficient numbers to approximate the most efficient scale of effort; the more competent fishermen would be able to offer the highest bids and it would be expected that the auction would recapture for the public purse a large portion of the rent from the fisheries that would otherwise accrue to the fishing enterprises under the more efficient production conditions in the fishery.
>
> "An arbitrary reduction in the number of fishermen by restriction of licenses to a specified number would entail injustice and inequity as well as grave administrative problems in determining who should be allowed to continue fishing. The auctioning of licenses to exploit a public property resource is justifiable in a private enterprise system of production, particularly when the state is incurring heavy expense to administer and conserve the resource; the recovery by the state of some part of the net economic yield by means of a tax on fishermen (or on the catch) would recoup at least part of such public expenditures, or could be used to assist former fishermen (see strategies discussed above) for instance, by buying their redundant equipment. A tax on fishermen through the auctioning of licenses has, at least, the merit of using economic means instead of arbitrary regulations to achieve a desired economic objective—the limitation of fishing effort to increase the net economic yield from the fishery. Regulations have to be enforced, usually at considerable cost, but economic sanctions tend to be, if not impartial, at least impersonal and automatic in their operation."

Actually, this latter management scheme is similar to the taxing scheme, but uses an auction rather than a direct tax.

Conclusions

The purpose of this article is to explain the use of bioeconomic models in assessing alternative management strategies. For this purpose the data are less than optimal. However, this does not mean that we cannot take steps in the direction of fishery management. In fact, these steps must be taken to protect the resource from destruction and to achieve a better use of vessels and fishermen. It is hoped that the following conclusions will provide a helpful framework in which to consider the merits of limited entry:

1. For the inshore American lobster resource, there is every indication that the fishery has achieved maximum sustainable yield and is fully capitalized. This has been brought about by a rapid expansion in effort (i.e., traps fished) produced by (1) free access to the resource, (2) a rising market for lobsters of all species, and (3) a secular decline in seawater temperature.

2. We have presented the bioeconomic impact of alternative management strategies to both conserve the resource and use it efficiently. The choice of which strategy to pursue is in the public domain and beyond the scope of this paper. However, the economic alternatives are pointed out.

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APPENDIX TABLE—Economic variables associated with the U.S. inshore American lobster fishery, 1950-69.

Year	Catch by traps	Value	Traps fished	Catch per trap	Ex-vessel price	Ex-vessel price divided by consumer price index	Year	Per capita consumption of lobsters	Per capita disposable personal income divided by consumer price index	Consumer price index (1967 = 100)	Mean annual seawater temperature at Boothbay Harbor, Maine
	Thousand pounds	*Thousand dollars*	*Number*	*Pounds*	*Cents per pound*	*Cents per pound*		*Pounds (live weight)*	*Dollars*		*Degrees Fahrenheit*
1950	22,914	8,283	578,930	39.6	36.1	50.1	1950	0.585	1,892	72.1	49.3
1951	25,749	9,328	512,812	50.2	36.2	46.6	1951	.651	1,888	77.8	51.4
1952	24,681	10,469	544,730	45.3	42.4	53.4	1952	.638	1,909	79.5	50.2
1953	27,509	10,687	569,081	48.3	38.8	48.5	1953	.710	1,976	80.1	52.0
1954	26,628	10,250	628,209	42.4	38.5	47.8	1954	.690	1,969	80.5	50.3
1955	27,886	11,003	669,229	41.7	39.5	49.2	1955	.734	2,077	80.2	50.0
1956	25,386	11,584	666,887	38.1	45.6	56.1	1956	.704	2,141	81.4	48.6
1957	29,358	11,263	688,815	42.6	38.4	45.6	1957	.806	2,136	84.3	48.8
1958	26,143	12,890	753,503	34.7	49.3	56.9	1958	.736	2,114	86.6	47.4
1959	27,752	14,043	856,794	32.4	50.6	58.0	1959	.763	2,182	87.3	47.0
1960	29,345	13,657	844,110	34.8	46.5	52.5	1960	.830	2,185	88.7	47.9
1961	25,621	13,662	895,098	28.6	53.3	59.5	1961	.810	2,214	89.6	47.3
1962	26,728	13,770	909,318	29.4	51.5	56.9	1962	.855	2,280	90.6	46.6
1963	27,210	15,299	866,900	31.4	56.2	61.3	1963	.938	2,333	91.7	47.9
1964	26,844	17,689	904,233	29.7	65.9	70.9	1964	.935	2,459	92.9	46.9
1965	24,737	18,764	949,045	26.1	75.9	80.3	1965	.884	2,578	94.5	45.8
1966	25,606	19,517	947,113	27.0	76.2	78.4	1966	.873	2,680	97.2	45.7
1967	22,098	18,162	907,956	24.3	82.2	82.2	1967	.882	2,751	100.0	45.1
1968	26,918	20,648	966,335	27.9	76.7	73.6	1968	.960	2,827	104.2	46.6
1969	26,930	22,997	1,061,807	25.4	85.4	77.8	1969	.999	2,851	109.8	48.0

Source: Fishery Statistics of the United States, various years, U.S. Department of Commerce, Bureau of Labor Statistics, and Robert Dow.

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DAILY ACTIVITY, MOVEMENTS, FEEDING, AND SEASONAL OCCURRENCE IN THE TAUTOG, *TAUTOGA ONITIS*[1]

BORI L. OLLA, ALLEN J. BEJDA, AND A. DALE MARTIN[2]

ABSTRACT

Observations were made on the activity and movements of adult tautog, *Tautoga onitis*, in their natural habitat using scuba and by monitoring the movements of individual fish by ultrasonic tracking. Results showed tautog to be active during the day and inactive at night. Fish larger than 30 cm moved out from the night resting place (home site) each day to feed, while younger fish (≤25 cm) remained and fed in close proximity to the home site. Examination of digestive tracts from various-sized fish showed the blue mussel, *Mytilus edulis*, to be the principal food for this population. While older fish appeared to move offshore for the winter, the younger fish remained inshore, wintering over in a torpid state. The significance of the tautog's differential responsiveness, food habits, and daily and seasonal movements are discussed.

The tautog, *Tautoga onitis* (L.), an inhabitant of the western Atlantic, ranges from Nova Scotia to South Carolina, being most abundant between Cape Cod and the Delaware Capes (Bigelow and Schroeder, 1953:478-484). Its distribution is limited primarily to inshore regions with individual populations being highly localized (Cooper, 1966). This fish lives in close association with rocky places, wrecks, pilings, jetties, or almost any bottom discontinuity and for part of its range, is a prominent member of inshore benthic communities. Unlike the majority of labrids, this species is valued as a game fish and is an excellent table fish.

Our aim in this work was to observe and describe the behavior of adult tautog in situ and to relate our findings to the animal's life habits and history. Our queries primarily concerned daily activity and movements, feeding, and seasonal occurrence. The study was carried out on a population residing in Great South Bay, N.Y., using scuba and ultrasonic tracking.

MATERIALS AND METHODS

The study area was along the south shore of Great South Bay, Long Island, N.Y., extending east from the Fire Island Inlet Bridge to 2 km east of the Fire Island Light (Figure 1). Water depth in the study area ranged from 2.4 to 8.8 m with the bottom composed primarily of sand, gravel, and shell.

Two methods were employed to observe the activity and movements of the fish: (1) ultrasonic tracking of a single fish and (2) direct underwater observations while using scuba.

Twelve fish were tracked at different times from August through September 1971 and June through October 1972 (Table 1). Fish were captured at night within the Fire Island Coast Guard basin by a scuba diver using a hand-held net, and each fish was held in a floating cage for periods ranging from 10 to 108 h before a transmitter was attached.

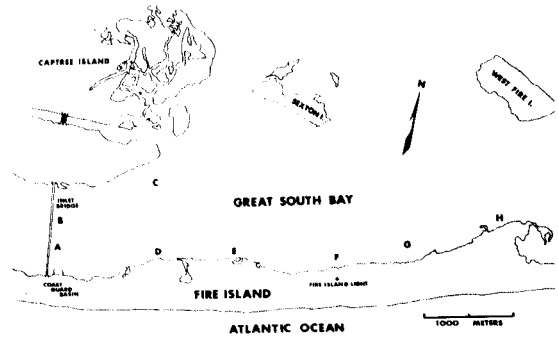

FIGURE 1.—Study area and areas (A-H) of tautog movement as presented in Table 1.

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TABLE 1.—Locations and duration of stay (h) of individual tautog during their daily movements as determined by ultrasonic tracking.

Tautog no.			Day 1	Day 2	Day 3	Day 4	Night 1	Night 2	Night 3
1	TL (cm)	45	A3[1](5.0)[2]	A1(2.2)	A4(9.8)	A4(2.6)	A1(11.4)	A1(10.0)	A1(14.1)
	Age[3]/sex	12/♀		A3(10.2)					
	Release (date/time)	7-25-72/1310		A4(1.9)					
	Track duration (h)	67.5							
	Mean temperature	19.2°C							
2	TL (cm)	42	A1(0.8)	A4(11.5)	A3(3.1)	A4(0.5)	A1(9.6)	A1(9.8)	A1(9.6)
	Age/sex	10/♀	A4(0.4)	A5(2.3)	A4(9.2)				
	Release (date/time)	8-1-72/0940	C (8.4)		A5(1.8)				
	Track duration (h)	68.3							
	Mean temperature	21.2°C							
3	TL (cm)	42	A1(3.0)	A4(0.9)	A5(6.2)	A5(0.3)	A1(11.3)	A1(11.6)	A1(10.8)
	Age/sex	10/♀	A4(3.0)	A9(10.3)	A9(7.0)				
	Release (date/time)	8-8-72/1215							
	Track duration (h)	66.5							
	Mean temperature	20.4°C							
4	TL (cm)	43	A1(1.0)	A3(2.5)	A4(0.5)		A1(12.8)	A1(15.6)	
	Age/sex	9/♂	A4(5.7)	A5(0.8)					
	Release (date/time)	9-15-71/0830	A6(0.6)	A6(4.5)					
	Track duration (h)	47.5	A7(2.3)	A7(0.8)					
	Mean temperature	22.0°C							
5	TL (cm)	38	A1(0.3)	A5(2.7)	A5(1.0)		A1(16.6)	A1(15.1)	
	Age/sex	7/♀	A4(0.2)	A6(1.4)					
	Release (date/time)	9-27-71/1400		A7(4.0)					
	Track duration (h)	41.5		A8(0.1)					
	Mean temperature	18.1°C							
6	TL (cm)	47	A1(1.4)	A2(10.9)	F (4.1)		A1(10.3)	G (12.2)	
	Age/sex	11/♂	A5(0.3)						
	Release (date/time)	8-16-71/1830							
	Track duration (h)	41.5							
	Mean temperature	21.7°C							
7	TL (cm)	20	A1(9.4)	A1(12.5)			A1(11.5)	A1(0.6)	
	Age/sex	3/♀							
	Release (date/time)	10-4-72/0930							
	Track duration (h)	34.0							
	Mean temperature	16.8°C							

The transmitter emitted pulsed signals at 70 kHz (kilohertz). Those used for small fish (20-25 cm) measured 30 × 9 mm (manufactured by Chipman Instruments[3]). Larger transmitters, 65 × 14 mm (SR-69B, Smith-Root Inc.) were used for the remaining fish (38-50 cm).

The pharyngeal mill apparatus of the fish precluded internal insertion of the transmitter. This necessitated external attachment through the dorsal musculature, with nylon monofilament line just below the midpoint of the dorsal fin. On each side of the body, rubber disks (25-mm diameter) were used to prevent the flesh from tearing. Tags were made neutrally buoyant by the addition of a styrofoam collar coated with silicone sealant. Following attachment of the transmitter, fish were held in a 50-liter tank for 15 to 30 min to insure that the fish were responsive and that the transmitter was operating normally.

Fish were released within the basin and tracked from a 5.2-m skiff. The signal was monitored with hydrophone and sonic receiver (Model SR-70-H and TA-60 respectively, Smith-Root Inc.) in a manner similar to that described by McCleave and Horrall (1970).

The location of each fish was recorded in relation to local landmarks. We considered a fish active whenever a change in transmitter signal was detected. Direct underwater observations confirmed that we were able to detect abrupt changes in the fish's orientation and straight line movement over 1 m. The data were subsequently condensed to indicate the presence of a fish for a period of time at a specific location (Table 1).

For each track, we recorded current velocity,

[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

TABLE 1.—Locations and duration of stay (h) of individual tautog during their daily movements as determined by ultrasonic tracking, continued.

Tautog no.		Day 1	Day 2	Day 3	Day 4	Night 1	Night 2	Night 3
8 TL (cm)	25	A1(7.7)	A1(12.5)	A1(12.5)	A1(0.6)	A1(11.4)	A1(11.5)	A1(11.5)
Age/sex	4/♀							
Release (date/time)	10-3-72/1115							
Track duration (h)	67.7							
Mean temperature	16.8°C							
9 TL (cm)	50	D (0.5)	D (10.1)	D (4.9)		G (8.0)	D (7.9)	
Age/sex	14/♂	E (10.9)	E (3.0)					
Release (date/time)	6-14-72/0855		F (0.6)					
Track duration (h)	48.8							
Mean temperature	14.1°C							
Renewed track		D (3.9)	D (16.8)	D (10.2)		D (7.9)	D (7.9)	
Date/time	6-19-72/1750			E (3.1)				
Track duration (h)	49.9							
Mean temperature	15.5°C							
10 TL (cm)	43	A5(8.6)	A5(9.8)			A5(10.2)	A5(8.3)	
Age/sex	9/♂		A6(5.6)					
Release (date/time)	6-27-72/1025							
Track duration (h)	42.5							
Mean temperature	17.3°C							
11 TL (cm)	44	A1(1.1)						
Age/sex	11/♀	A2(1.8)						
Release (date/time)	6-5-72/1345	B (0.6)						
Track duration (h)	3.5							
Mean temperature	13.4°C							
12 TL (cm)	45	A1(0.3)						
Age/sex	12/♀	A5(3.2)						
Release (date/time)	6-12-72/1145	A6(2.7)						
Track duration (h)	8.3	A8(0.3)						
Mean temperature	13.8°C	B (1.1)						
		C (0.7)						

[1] Location as presented in Figures 1 and 2.
[2] Hours given in parentheses.
[3] Age estimated from calculated total lengths by Cooper (1967).

stage of tide, cloud cover, water temperature, and water transparency. Current velocity was measured either with a Beauvert midget current meter or by the float method. The current velocity ranged from 0.65 to 1.75 m/s. Temperature was measured with a thermistor and transparency with a secchi disk. Cloud cover was visually estimated.

In conjunction with our tracking, we directly observed tautog in the study area with scuba for a total of 135 h (90 h daytime and 45 h nighttime).

To identify periods of feeding as well as the types and amounts of food ingested, we examined the digestive tracts of fish collected at different times of the day and night. We measured the relative digestive tract fullness of each volumetrically with the fullness index being the quotient of displacement volume of empty tract/displacement volume of tract with contents.

Determination of the maximum size of mussel that the tautog could ingest and of the maximum size it could crush was made by inserting different size mussels into the mouth and into the anterior opening of the pharyngeal mill. The maximum ingestable size was defined as the largest mussel that could be completely enclosed in the mouth. The maximum crushable size was the largest mussel that could be partially grasped by the pharyngeal teeth.

To aid in describing the method of feeding on mussels, at infrequent intervals over a 16-mo period, we directly observed and used cine analysis of three individuals 25 to 38 cm, held in a 2,200-liter aquarium.

RESULTS

Activity and Movements

The fish which we tracked were active during the day and inactive at night. There was some

degree of variation in the precise time that activity began or ceased relative to morning and evening civil twilight (Table 2). Activity began from 10 min before to 69 min after the start of morning twilight. Cessation of activity, however, was more variable, ranging from 222 min before to 69 min after the end of evening twilight. Although we were unable to arrive at the cause for this variation, there were indications that cloud cover and water transparency, both affecting light penetration, might play a role. Our direct scuba observations (135 h of observation) on untagged tautog showed that the fish were active during the day and inactive at night. Activity as well as responsiveness at night were at such a low level that we were able to touch individual fish or catch them easily with a hand-held net.

Five fish (No. 1-5, Table 1), tracked at different times from July through September 1971 and 1972, exhibited similar patterns in their daily movements. Each morning at the onset of activity or soon after, the fish moved out and usually remained within 500 m of the basin. They spent most of each day at locations in which there were large concentrations of blue mussel (*Mytilus edulis*) (areas A2-A9, Figure 2; Table 1). Towards late afternoon or early evening, the fish returned to the basin and within 1 to 198 min ($\bar{x} = 55.7$), settled in one location and remained throughout the night in an inactive state.

Another fish (No. 6, Table 1) tracked during this period returned to the basin the first night after being released, following the same pattern as fishes 1 to 5. However, after spending most of the second day in close proximity to the basin, it did not return but rather, at 172 min prior to the end of evening twilight, swam 6.2 km in a direct easterly course to an artificial reef (consisting of sunken barges and tires) where it spent the night (area G, Figure 1).

Underwater observations made during July through mid-October showed that the number of fish, measuring about 30 to 50 cm, in close proximity to the basin increased just prior to and immediately after the beginning of evening twilight in comparison to the number that were present during the day. Comparing these obser-

TABLE 2.—Onset and end of the daily activity of individual tautog relative to morning and evening civil twilight (MCT and ECT[1]).

Tautog no.	Mean time and range (min) to: Onset of activity, Prior to MCT	Onset of activity, Following MCT	End of activity, Prior to ECT	End of activity, Following ECT
1		27.0 (21.0 to 35.0)	122.0 (43.0 to 222.0)	
2		20.0 (10.0 to 30.0)	14.7 (8.0 to 26.0)	
3		26.0 (12.0 to 43.0)	71.0 (39.0 to 116.0)	
4	7.0 (4.0 to 10.0)		78.5 (72.0 to 85.0)	
5		23.0 (18.0 to 28.0)	47.5 (12.0 to 83.0)	
6		54.5 (52.0 to 57.0)	28.0 (4.0 to 52.0)	
7		35.0	68.0 (54.0 to 82.0)	
8		27.0 (13.0 to 45.0)	75.3 (51.0 to 88.0)	
9		62.0 (49.0 to 69.0)	131.0 (26.0 to 158.0)	69.0
10		14.0	51.0 (28.0 to 74.0)	

[1] MCT: start of morning civil twilight.
ECT: end of evening civil twilight.

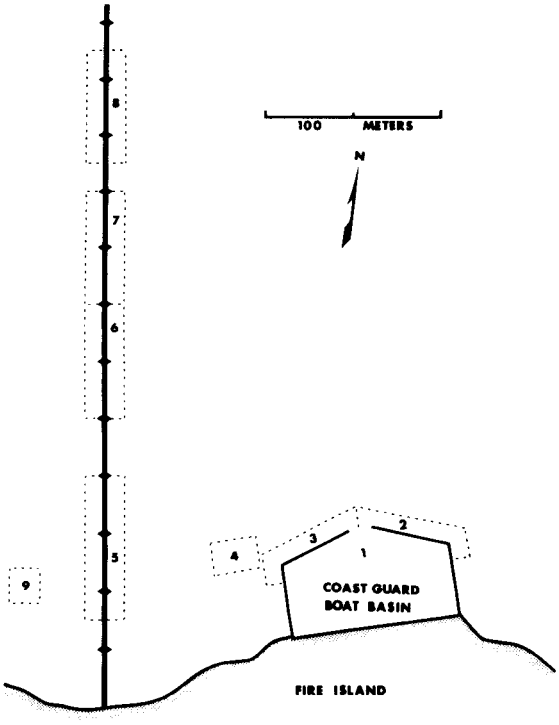

FIGURE 2.—Areas demarcating the locations of tautog during their daily movements as presented in Table 1 (an enlargement of area A, Figure 1).

vations with our tracks of similar-sized fish, we were led to conclude that this increase was the result of the normal nightly return to the basin. However the number of smaller fish (≤25 cm) appeared to remain the same throughout the day and during evening twilight, i.e., there was no discernible increase at evening twilight. To affirm whether the smaller, younger fish did in fact remain closer to the basin during the day than the larger, older ones, we tagged two fish 20 and 25 cm (No. 7 and 8, Table 1), tracking one for 34 and the other for 66.8 h. These fish exhibited the typical habit of the larger fish of being active during the day and inactive at night (Table 2). However, in contrast to the larger fish, these smaller fish remained within the basin and never ventured farther than 2 m from the walls. Examination of the digestive tract of one of these smaller fish, recaptured after tracking had been terminated, showed the presence of mussels throughout the tract, indicating that this fish had been feeding on mussels attached to the basin walls or other substrate within the basin.

These data indicate that tautog occur as an essentially localized population at least from July through mid-October. The basin acts as a focal point for the population, providing a suitable night habitat for all fish and a forage area for smaller fish.

Four fish (No. 9-12, Table 1) tracked during June 1972 exhibited quite different patterns of daily movements. Two of these (No. 9 and 10) ranged farther during the day and spent the night at various locations other than the basin. Tracking was discontinued on the other two fish of this group (No. 11 and 12) during the first day due to inclement weather. However, a search the night following tracking termination and on three successive nights failed to detect the presence of either fish in or around the basin. They, too, evidently spent the night at other locations.

The major difference in fish tracked during June from all other fish tracked was that all June fish were in spawning condition, readily extruding sperm or ova during the tagging procedure. Further, if this population bears any similarities to the Narragansett Bay population (Cooper, 1966), we surmise that during June, fish are still arriving inshore from their offshore wintering area and have not yet become localized (at least fish of the size we were tracking).

On 26 September 1972, during the day, we sighted just outside the basin (Area 3, Figure 2) a tautog with a transmitter attached. Although we could not ascertain when this fish was tagged, it had been 49 days since the last tagging. The fish, which appeared normally responsive, had either remained localized within this area for at least 49 days or possibly was one of the four fish tagged during June that had not returned to the basin at that time.

Feeding

There were varying amounts of food throughout the digestive tracts of fish sampled at various times of the day and just after evening twilight (Table 3). The tracts of fish sampled just prior to morning twilight (23-83 min), while still in an inactive night condition, were empty. Thus it appears that the fish feed throughout the day, beginning soon after morning twilight and continuing up to evening twilight. Assuming that the fish sampled just before morning

twilight had fed up to the previous evening twilight, passage through the digestive tract while the animals were quiescent took 8 h or less.

Examination of the matter ingested showed that 70% of the fish sampled contained 78.4 to 100% mussels, by volume, in various stages of digestion (Table 3). Next in abundance were remains of various decapod and cirriped crustaceans, followed by an assortment of other invertebrates and debris (vegetable matter, sand, and gravel), with some of the latter probably being ingested incidentally with the mussels. All but two of the fish examined contained over 50% mussels, by volume, indicating that mussels are the principal food for this population.

Observations on the tautog's method of feeding on mussels, in both the field and laboratory, revealed that after approaching a clump of mussels, the fish would grasp one or several at a time with the anterior canine teeth and then tear them from the substrate with an intense lateral or shaking movement of the head. In no case, in either the field or laboratory, did the initial ingestion process involve crushing with the canines. After initial ingestion, muscular contractions in the bucco-pharyngeal area were clearly seen, evidentally resulting from the shells being crushed by the pharyngeal teeth. When a clump of mussels attached by byssal threads was too large to be processed by the pharyngeal teeth, the fish would alternately ingest and egest the clump until it was separated into a smaller crushable size.

The mussels in the digestive tracts consisted primarily of specimens averaging 11.9 mm in length and estimated to be 1 to 2 yr old (Table 3). There was an obvious selection of young, small mussels by all-sized fish.

While factors such as ease of crushing and a greater digestive efficiency may be involved in the tautog's preference for small, young mussels, we found another possible cause related to the limitations imposed by the dimensions of the pharyngeal area where the mussels are crushed. The mouth can accommodate much larger mussels than the crushing apparatus is able to process. For example in the laboratory on 20 occasions, we saw fish that were starved for more than a day attempting to eat mussels

TABLE 3.—Relative fullness and contents of tautog digestive tracts.

Time of capture (EDT)	Fish length (cm)	Fullness index[1]	% of total gut contents: Mussels	Decapod and cirriped crustaceans	Other	Median length of mussels (mm)	% of mussels less than 30 mm
0400-0500	23.5	1.0					
	23.5	1.0					
	45.0	1.0					
	37.0	1.0					
	46.0	1.0					
0800-0830	24.0	0.8	85.7	5.8	8.5	14	100.0
	27.5	0.7	100.0			12	100.0
	26.5	0.7	99.5		0.5	14	100.0
	34.0	0.8	62.5		37.5	16	100.0
1200-1300	31.0	0.6	89.6	4.5	5.9	15	100.0
	36.5	0.5	65.3	27.0	7.7	8	100.0
	37.5	0.6	78.5	16.1	5.4	16	100.0
	21.0	0.7	98.6		1.4	11	100.0
	24.5	0.7	100.0			5	100.0
	32.0	0.4	95.2	4.8		15	100.0
	29.0	0.4	54.5	36.4	9.1	10	100.0
1600-1700	40.0	0.7	99.1	0.6	0.3	8	100.0
	32.0	0.4	92.2	6.0	1.8	8	100.0
	32.5	0.6	31.3	68.1	0.6	8	100.0
1930-2000	44.0	0.4	90.4	9.6		14	88.1
	36.0	0.6	45.9	41.3	12.8	12	87.5
	46.0	0.6	65.7	32.9	1.4	10	53.8
	37.0	0.6	92.3	7.7		15	100.0
	42.5	0.4	94.0	6.0		16	72.7
	[2]20.0	0.6	78.4		21.6	11	100.0

[1] Fullness index = volume empty tract/volume of tract with contents.
[2] Fish no. 7 (Table 1) captured at end of track.

larger than could be crushed by the pharyngeal teeth. The fish would ingest the mussel, unsuccessfully attempt to crush it, and then egest it, the process being repeated 20 to 30 times. We also found in a preliminary determination of the maximum crushable size that fish, 34 to 53 cm, could crush mussels that were only 0.47 times the maximum size they could ingest.

Seasonal Movements

Direct observations made during the day with scuba from October 1971 through May 1972 and from October 1972 through January 1973 indicated that there was a difference in the seasonal movement between small fish (≤25 cm, 2-3 yr old) and large fish (>25 cm, >4 yr old). The ages of fish were estimated from calculated total lengths by Cooper (1967). Tautog of varying sizes were observed in close proximity to the basin on 12 October 1971, at an average water temperature of 17.0°C (range: 15.2°-19.5°C). On 1 November with the water temperature averaging 10.0°C (range: 8.9°-10.6°C), no large tautog were sighted, but about 25 small ones were seen swimming within 1 m of the basin walls. Small fish were still active on 18 November (water temperature 10.0°C: 9.7°-10.1°C). On 9 December 1971, and 5 January 1972, with temperatures ranging from 4.0° to 5.5°C, a total of approximately 40 small tautog was sighted within the basin. These fish appeared lethargic and rested against the basin walls. When prodded by a diver, they moved only a few feet before settling to the bottom once again.

Both large and small fish were sighted on 10 May 1972 with an average temperature of 10.0°C (range: 8.5°-11.5°C) and appeared normally active.

Diving observations the following fall and winter substantially supported the fact that small fish wintered inshore. On 2 October 1972, we sighted normally active large and small tautog (water temperature 16.8°C: 16.2°-17.7°C). On 26 October with the temperature averaging 10.0°C (range: 9.6°-10.5°C), we found no large fish but sighted at least 30 small fish which appeared normally active. During dives on 27 November and 29 December 1972, and 9 January 1973, with the temperature ranging 2.0° to 4.8°C, we sighted approximately 35 small fish (≤ 25 cm) lying in a torpid state on the bottom between pilings and the basin walls or in bottom depressions within 10 cm of the wall. Some of these fish were partially covered with silt. Opercular movements were so shallow as to be almost undiscernible. Examination of the digestive tracts of five fish captured during this period showed that the fish had not eaten for some time as indicated by the empty and flaccid condition of the tracts.

We concluded from these observations that fish at least larger than 25 cm moved offshore to winter, agreeing with the conclusions of Cooper (1966) for a population residing in Narragansett Bay, Rhode Island. However, small fish (approximately ≤25 cm) remained inshore throughout the year in close proximity to the home site.

DISCUSSION

The tautog's pattern of being active during the day and inactive at night is a typical labrid trait having been observed in a number of species. For example, field observations in the Pacific by Hobson (1965, 1968, 1972) showed this pattern to be present in five species (*Bodianus diplotaenia*, *Halichoeres nicholsi*, *Labroides phthirophagus*, *Thalassoma duperrey*, and *T. lucasanum*). The pattern was presumed to be present in *Halichoeres dispilus*, *Hemipteronotus mundiceps*, and *H. pavoninus* since the fish were observed in the active state during the day but not sighted at night, having apparently buried under sand or rested in crevices. Field observations in the Atlantic by Starck and Davis (1966) on *Bodianus rufus*, *Clepticus parrai*, *Lachnolaimus maximus*, and *Thalassoma bifasciatum* also show the typical labrid day active/night inactive pattern.

Whether a labrid species spends the night buried under sand or lying in cracks or crevices, all appear to be in a state of low responsiveness. Tauber and Weitzman (1969) investigated the level of responsiveness of the slippery dick, *Irideo bivittata*, at night. They found the fish to be in a state that resembled the mammalian sleep phase characterized by decreased responsiveness to altering stimuli, diminished or irregular respiration, and eye movement activity.

The low level of responsiveness present at night in labrids and other species with a similar habit has wide ramifications with regard to

susceptibility to environmental stress. The probability that fish would be able to respond and escape potentially lethal environmental perturbations during the inactive night phase would be less than if the same stress were applied during the day. Physiological responses would also differ. Differential susceptibility to stresses as related to the daily rhythm has been clearly established (for discussion and review, see Reinberg, 1967).

During most of the summer and into early fall, fish of the colony we studied had a fairly well defined home range (Gerking, 1959) with the basin acting as a focal point or home site, providing a suitable night habitat for all-sized fish. While larger fish (≥30 cm) moved out each day to feed, the smaller fish (≤25 cm) foraged along or in close proximity to the basin walls. The adaptation of young fish remaining close to the home site may relate to effectively protecting them against predators. On one occasion while diving in early July 1972, we observed three striped bass (*Morone saxatilis*, 80-90 cm) actively pursuing and attempting to capture young tautog (≤25 cm) from a group of 30 to 40. The tautog were within 1 m of the basin wall at the onset of the attack. They escaped from the predators by swimming directly to the wall where they remained in crevices. The older fish, not as susceptible to predation, moves out to feed, resulting in a fuller utilization of the potential energy resources of the area and in the probable reduction of feeding competition among individuals. The reduction in the probability of feeding competition seemed especially critical since all sizes studied preferred, to a large extent, similar-sized mussels. This daily movement of the larger fish out of the basin also seemed to make the home site a nursery for young fish.

Our observations that tautog larger than 30 cm (approximately 5 yr or older) were not present in the vicinity of the basin after the end of October circumstantially agree with the finding of Cooper (1966) that Narragansett Bay fish of similar size wintered offshore. In contrast, our results showed that younger fish remained inshore throughout the year, wintering at the home site in a torpid, nonfeeding state. It is apparent that the younger fish are highly dependent on the home site throughout the year for at least the first 3 to 4 and perhaps 5 yr of their life. The habit of remaining inshore over the winter is not unknown in labrids. Green and Farwell (1971) found various-sized cunner, *Tautogolabrus adspersus*, lying in a torpid state inshore when temperatures fell below 5°C.

Although tautog feed readily on other types of food, the most abundant food available and found most frequently in the digestive tract was mussels. Mussels were predominantly less than 30 mm long, indicating an average age of 1 to 2 yr (Savage, 1956). The next most abundant food found in the digestive tract was various crustaceans, with only negligible amounts of other items. It seemed that, on the basis of our diving observations, the crustacean population, in terms of a potential alternate food source for the tautog in this area, did not approach the abundance of mussels in the 1 to 2 yr class. We surmise that the equilibrium of the population, in terms of food resources, is highly dependent on a single food item, with no alternate potentially serving as a sustaining element.

Environmental perturbations that would directly affect 1- to 2-yr-old mussels or any of the pre-adult stages, would lead to a high probability of stress in the tautog population. This would be especially true for young fish (3 yr or less) since they seem especially dependent upon the home site. This dependence on the home site raises the question of whether or not it is within their capability to move out and seek new feeding areas and if so, how successful would they be.

Another obvious limiting element of the population is a suitable physical structure which all-sized tautog require during their night inactive phase and upon which young tautog seem totally dependent. In areas where food resources are in relative abundance to support a population, the introduction of a suitable physical habitat could lead to the establishment of new discrete colonies.

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AN EXAMINATION OF THE YIELD PER RECRUIT BASIS FOR A MINIMUM SIZE REGULATION FOR ATLANTIC YELLOWFIN TUNA, *THUNNUS ALBACARES*

W. H. LENARZ, W. W. FOX, JR., G. T. SAKAGAWA, AND B. J. ROTHSCHILD[1]

ABSTRACT

Some of the conceptual foundations of yield-per-recruit analysis as a management tool and as applied to the Atlantic yellowfin tuna fishery were critically explored. Problems examined include: (1) estimating the current state of the fishery in terms of a knife-edged recruitment approximation, (2) inferring consequences of management action from the yield-per-recruit isopleth, (3) the difficulty in achieving a maximum yield per recruit when there exist several gear types exploiting different size ranges, (4) the difficulty in obtaining projected increases in yield per recruit when the killing and discarding (dumping) of fish smaller than the optimum size occurs, and (5) the possible interaction between a size limit and the projection of the maximum sustainable yield.

In employing yield-per-recruit analysis to the Atlantic yellowfin tuna fishery, two approaches were taken—one approach makes use of a wide range of parameter estimates and a number of simplifying assumptions, but little data, and the other approach makes use of considerably more data, but is more confined in the parameter estimates and uses fewer of the simplifying assumptions. The general results of both approaches, assuming no dumping occurs, indicate that only minor increases in yield per recruit would occur if the size at recruitment is increased from our estimate of the present size at recruitment and fishing effort remains constant; an increase in fishing effort without changing other aspects of the fishery would not appreciably increase yield per recruit; and an increase in size at recruitment and in fishing effort would result in modest gains in yield per recruit. Specifically meeting the request of the International Commission for the Conservation of Atlantic Tunas, we recommended that a minimum size limit regulation in the vicinity of 55 cm (3.2 kg) be enacted.

The second regular meeting, in Madrid, Spain, on 2-7 December 1971, of the commission of ICCAT (International Commission for the Conservation of Atlantic Tunas) authorized the "Council to recommend to the Contracting Parties that they prohibit landing of yellowfin weighing less than a minimum weight somewhere between 3.2 and 10 kg." This recommendation was based on studies by members of the Subcommittee on Stock Assessment that showed that theoretically the size at first capture which maximizes the yield per recruit of yellowfin is between 10 and 25 kg.

A special ICCAT working group on stock assessment of yellowfin tuna met in Abidjan, Ivory Coast, 12-16 June 1972, to consider further scientific aspects of size regulation and other matters pertaining to the Atlantic yellowfin fishery (ICCAT, 1972).[2] Studies on yield per recruit were presented by Hayasi, Honma, and Suzuki (1972);[3] Joseph and Tomlinson (1972);[4] and Lenarz and Sakagawa (1972).[5] A similar study was published by Wise (1972)

[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, LaJolla, CA 92037.

[2] ICCAT. 1972. Report of the meeting of the special working group on stock assessment of yellowfin tuna (Abidjan, June 12-16, 1972). Manuscript on file at ICCAT General Mola 17, Madrid, 1 Spain.

[3] Hayasi, S., M. Honma, and Z. Suzuki. 1972. A comment to rational utilization of yellowfin tuna and albacore stocks in the Atlantic Ocean. Far Seas Fisheries Research Laboratory, Orido 1000, Shimizu, Japan. Unpublished manuscript.

[4] Joseph, J., and P. K. Tomlinson. 1972. An evaluation of minimum size limits for Atlantic yellowfin. Inter-American Tropical Tuna Commission, La Jolla, Calif. Unpublished manuscript.

[5] Lenarz, W., and G. Sakagawa. 1972. A review of the yellowfin fishery of the Atlantic Ocean. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

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FISHERY BULLETIN: VOL. 72, NO. 1, 1974.

before the meeting. The report of the meeting may be considered as a summary of these papers, which indicated that increases in size at recruitment would probably increase yield per recruit but not by more than about 10%.

The special ICCAT working group also examined available evidence on the practicability of minimum size regulations. Scientists of the group were concerned that since the gears that fish for yellowfin in the Atlantic supposedly kill most fish that are captured, a minimum size regulation would reduce the number of small yellowfin that are landed but would not have the desired effect of reducing mortality rates of small yellowfin. This, of course, assumes that schools of yellowfin containing yellowfin less than any minimum size would actually be set upon. In this connection the group noted that the conditions which must be met before minimum size regulations can be effective are: (1) the fishermen must be able to estimate the size of yellowfin in a school, and (2) there must be little or no mixing of small yellowfin with large yellowfin within schools.

Very little evidence is available from the Atlantic on these subjects. Ten samples were presented at the Abidjan meeting that indicated considerable mixing of small yellowfin (<5 kg) with large yellowfin (>5 kg) within schools. The working group also took note of a study on the subject by Calkins (1965) when size regulations were being considered by the IATTC (Inter-American Tropical Tuna Commission) for the yellowfin fishery in the eastern tropical Pacific. Calkins, working with only one hypothetical minimum size out of a range of 12.7 to 25.0 kg, concluded that a 12.7-kg size regulation would be seriously complicated by size variation within sets. He also noted that a considerable amount of small yellowfin are often captured in sets that include skipjack. Thus it appears that it would not be possible to fish for skipjack without killing some small yellowfin. Evidence based on the few samples from the Atlantic indicated that sets would include yellowfin tuna larger and smaller than 5 kg; thus even if a minimum size regulation were set at this value it would be difficult to prevent the capture of fish smaller than 5 kg.

The working group recommended that more data should be collected on the subject from the Atlantic. The working group also noted that a reduction in the size at first recruitment should be prevented and that minimum size regulations of 3.2 kg that have been passed by several African nations should help prevent a reduction in size at recruitment.

The population dynamics of Atlantic yellowfin tuna are complex because the fishery is prosecuted by several types of gear: bait boats, small purse seiners, large purse seiners, and longliners. These gears tend to capture different sizes of fish and thus affect the population in different ways. FAO (1968) noted that longline gear tends to capture large yellowfin while the other gears capture small yellowfin. Lenarz (1970),[6] with more recent data, showed that American[7] purse seine gear tends to capture relatively more large yellowfin—in significant quantities—than was indicated for the earlier surface fishery. Joseph and Tomlinson (1972, see footnote 4) presented data that indicated small purse seiners of France-Ivory Coast-Senegal (FIS) tend to capture relatively more small yellowfin than the large FIS and American purse seiners. The differences among size selectivity of the four gears necessitates consideration of the physical makeup of the fleet when examining size regulations. Therefore, considerable attention was paid to this aspect of the problem during the study.

The above paragraph might be taken to imply that adequate data are available respecting the relative quantities and size distributions of fish caught by the various gears. It is our feeling that the adequacy of the data needs to be demonstrated. We cannot place much faith in the details of the relative size distributions per unit effort among the various fishing units, but we do feel that the general orders of magnitude are essentially correct. We should also point out that with the improvement in data over the last several years, the interpretations which accrue from the data and our appreciation of the considerable complexity of the fishery are more evident.

Definitions of Minimum Size

Because this paper discusses minimum size, it is necessary to define the term explicitly to

[6] Lenarz, W. 1970. Estimates of yield per recruit of Atlantic yellowfin tuna. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

[7] Refers to vessels registered in Canada, Panama, and the U.S.A.

avoid ambiguity and to prevent possible misapplications of the results of this study. "Minimum size" may be viewed from two aspects: absolute minimum size and effective minimum size. Absolute minimum size is defined as the smallest fish in the catch and is related to the concept of knife-edged recruitment in defining the size at recruitment to the fishery. Recruitment is defined as the act of becoming vulnerable to fishing. In the case of knife-edged recruitment, no fish are vulnerable to fishing prior to the size at recruitment. Fish that are larger than the size at recruitment are fully vulnerable to fishing. Since most recruitment is size specific, hence sequential, the term effective minimum size is also needed. Effective minimum size is that size whose corresponding age is used as the lower bound for integration of the yield equation as if recruitment were knife-edged, and which gives the same yield per recruit as the sequential recruitment case.

Approaches to Yield-Per-Recruit Analysis

This paper examined several of the concepts involved in yield-per-recruit analyses because the question of what is the optimum minimum size for a given rate of exploitation is usually interpreted through such analyses. Both the classical approach, in which fishing mortality is constant with knife-edged recruitment, and the more complex approach, in which fishing mortality is size specific, are explored.

Throughout the paper we have intentionally kept mathematical notation to a bare minimum. We believe that most of the equations used are well known to readers actively involved in stock assessment. Readers who are not familiar with the equations can find excellent descriptions in the cited literature.

Employing the classical approach to yield-per-recruit analysis involves: (1) estimating the age or size at recruitment which represents an approximation of the current state of the fishery in terms of knife-edged recruitment; (2) finding the age or size at recruitment which maximizes the yield per recruit at a given level of fishing mortality; (3) imposing some regulation on the fishery such to achieve as its effective minimum size, the age or size at recruitment which maximizes the yield per recruit. The advice from the yield-per-recruit isopleth (in terms of the optimal age or size at recruitment) may be interpreted as either a knife-edged absolute minimum size or as an effective minimum size. Since for the fishery under consideration (and for many other fisheries as well) recruitment is not knife-edged, then we are talking about an effective minimum size. Now, on the other hand, if we assume that the absolute minimum size, the regulated size, and the effective minimum size are all the same, then we will have an inappropriate estimate of the yield per recruit, and the optimum may not be achieved. Somehow we need to determine the relationship between the effective minimum size and the regulated size; in some instances they can roughly be the same; but this equality will usually not obtain if the regulated size is chosen to be the absolute minimum size in the catch.

The more complex approach, which estimates size-specific fishing mortality, circumvents the first difficulty encountered in the classical approach, i.e., determining a knife-edged approximation to the current state of the fishery. The problem still remains, however, as to interpretation of the advice from the yield-per-recruit isopleth in terms of an effective minimum size. Joseph and Tomlinson (1972, see footnote 4) used the more complex approach in a recent study on minimum size regulations for the Atlantic yellowfin fishery. We have updated their analysis by using data made available at the Abidjan meeting and have also examined the sensitivity of the methodology to various sources of errors in the data.

DATA, PARAMETERS, AND COMPUTER PROGRAMS

Data

Catch- and length-frequency data for each type of gear for the 1967-71 period were obtained from the report of the meeting of the special ICCAT working group (Tables 10, 11, and 12 of ICCAT, 1972, see footnote 2) with the exception of length-frequency data of the 1967-68 FIS fishery and 1971 Japanese longline fishery. Length frequencies for the 1967-68 FIS fishery were compiled from various ORSTOM (Office de la Recherche Scientique et Technique Outre-Mer) publications (Lenarz and Sakagawa, 1972, see footnote 5). Length

frequencies from the 1971 Japanese longline fishery are assumed to be the same as those of the 1970 Japanese longline fishery; this assumption appears justifiable because year to year changes in length frequencies from longline fisheries tend to be less than differences in length frequencies between longline fisheries and surface fisheries.

Length-frequency data were available only from the Japanese longline fishery, FIS surface fisheries, and American large purse seine fishery. Thus it was necessary to make several assumptions before estimating the length frequencies of the total catch of yellowfin in the Atlantic. Length frequencies for longline fisheries other than Japan are assumed to be the same as Japan's. Length frequencies for the bait boat and small purse seine fisheries other than FIS were assumed to be the same as the FIS fishery. Length frequencies for the large purse seine fisheries other than FIS and American were assumed to be the same as those two fisheries.

Parameters

The growth equation [$L = 194.8 \times (1 - e^{-0.42(t - 0.62)})$] presented in LeGuen and Sakagawa (1973) and length-weight relationship ($W = 0.0000214L^{2.9736}$) given by Lenarz (1971a)[8] were used, where L is fork length in cm, t is age in years, and W is weight in kg.

The annual instantaneous coefficient of natural mortality (M) is a difficult parameter to estimate and due to a lack of data only preliminary estimates have been made for the parameter in the Atlantic. We assume as most authors have that M is constant over the exploited phase. Estimates of $M = 2.61$ and 1.50 for the Atlantic were made by Pianet and LeHir (1971) based on data from bait boats and seiners, respectively. These estimates seem unreasonably high perhaps because their data were only from the Pointe Noire region which is a small area compared to the total region in the Atlantic where yellowfin tuna are found. Hennemuth (1961) estimated that M is 0.8 in the Pacific while Davidoff (1969) chose the upper bound of Hennemuth's estimate, 1.0. Hennemuth's work was based on estimates of instantaneous coefficient of total mortality (Z) made from age compositions of catches by primarily bait boats and an estimate of instantaneous coefficient of fishing mortality (F) from Schaefer (1957). Since bait boats appear to be selective for small yellowfin, F and Z are not constant, and methods of ageing yellowfin have not been proven correct, Hennemuth's estimate must be considered a first approximation. However, his estimate seems reasonably consistent with what is thought to be the life span of yellowfin. We assumed for the purposes of our calculations here that M is 0.8 as is conventional (based on Hennemuth's work in the Pacific); we also used values of 0.6 and 1.0 to encompass what we believe is the range of reasonable values.

Pianet and LeHir (1971) also estimated an average F of 0.88 for the segment of the Atlantic yellowfin tuna population that is exploited in the Pointe Noire region. As we have indicated, their estimate is not representative for the population as a whole.

Our range of estimates of Z for 1967-71 is 0.91 to 1.82 (Lenarz and Sakagawa, 1972, see footnote 5). If we assume that $M = 0.8$ for the Atlantic population, then F is 0.11 to 1.02. We believe that F is about 0.6 for recent years. However, we used a range of F values in our study.

Computer Programs

Most of the calculations were performed on the Burroughs 6700[9] computer at the University of California at San Diego. Programs used in the analysis, except for FRG708 (Paulik and Bayliff, 1967), were written by the authors; they are as follows:

1. Simplified Beverton and Holt yields per recuit—YPER.
2. Accuracy of knife-edged approximations of age at entry and interactions between minimum size and catch quota regulations—GXPOPS.
3. Yield-per-recruit isopleths under knife-edged recruitment—FRG708.

[8] Lenarz, W. 1971a. Length-weight relations for five Atlantic scombrids. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

[9] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

4. Size-specific rates of fishing mortality—COHORT.
5. Yield-per-recruit isopleths for multigear fisheries with size-specific F—MGEAR.
6. Optimum size at recruitment under different levels of effort by two gears—OPSIZE.

ANALYSIS

As previously mentioned in the introduction, we use two approaches in analyzing the data, the knife-edged recruitment approach and the size-specific F approach.

Knife-Edged Recruitment Approach

Introduction

Two commonly used models for computing yield per recruit and determining the size at recruitment which maximizes yield per recruit are those of Beverton and Holt (1957) and Ricker (1958). We employed both models for knife-edged approximation analyses—the simplified Beverton and Holt model, making use of a wide range of parameter estimates or extrapolations from fisheries for similar species, and the Ricker model, making use of the best parameter estimates and giving a more detailed analysis of yield per recruit. We used the Ricker model instead of the Beverton and Holt model for calculating yield-per-recruit isopleths because the Ricker model allows the use of exponents in the length-weight relationship with values other than 3. It is important to stress that the material in the simplified Beverton and Holt model involves fewer assumptions than the material in subsequent sections. This is important because as our approach becomes more complex the data requirements become more rigorous. It can be argued that we have sufficient data for this simplified approach. In the more complex approaches this assertion becomes more tenuous; because we use more assumptions in the more complex approaches we do not necessarily obtain more information, even though it may appear that way. However, it should be noted that the assumption of a constant rate of mortality over the fishable life span contained in the simplified approach may be important, and we believe that it is not fulfilled. These analyses are followed by sections discussing the problems of determining the proper parameters which represent the current situation of the fishery.

Simplified Beverton and Holt Model

The Beverton and Holt yield-per-recruit model may be simplified such that relative yield per recruit, Y', is a function of three ratios:

$$C = l_r'/L_\infty$$
$$Q = M/K$$
$$E = F/(F + M)$$
$$Y' = Y/(RW_\infty)$$

and where l_r' is the size (length) at recruitment, W_∞, L_∞, and K are parameters of the von Bertalanffy growth equation, Y is yield in weight, and R is recruitment. Y' is tabulated in Beverton and Holt (1966), but more extensive calculations were performed with program YPER.[10] Beverton and Holt (1959) concluded that, within reason, there exists a common ratio between M and K within related species groups. Therefore, a range of estimates for the various parameters is utilized along with other information obtained by examining parameter estimates for M and K for yellowfin tuna from areas other than the Atlantic.

The range of values for the various parameters is as follows: $K = 0.28$ to 0.53 and $L_\infty = 175.2$ to 223.0 cm from LeGuen and Sakagawa (1973), $Z = 0.91$ to 1.82 from Lenarz and Sakagawa (1972, see footnote 5), and $M = 0.6$ to 1.0. From these ranges of estimates, a maximum range for E is 0.0 to 0.67 and for Q is 1.13 to 3.57. Using our most reasonable parameter estimates of $K = 0.42$, $M = 0.8$, and $Z = 1.4$, however, a reasonable range for E and Q was established by allowing either the numerator or denominator of the ratio to be one of our most reasonable estimates—the reasonable ranges are $E = 0.12$ to 0.56 and $Q = 1.42$ to 2.86. With $K = 0.42$, $M = 0.8$, and $Z = 1.4$, our most reasonable estimates of E and Q are 0.43 and 1.9, respectively.

Table 1 contains optimal values of size (cm) at recruitment, $l^{*\prime}_r$, for the maximum range of estimates of E and Q (deleting the impossible $E = 0.0$) for the range and most reasonable estimates of L_∞. The dashed lines enclose the

[10] For some values of c, Table IIb of Beverton and Holt (1966) was slightly higher than computed by YPER; this may be due to differing methods of rounding.

Table 1.—Optimal values of size at recruitment (cm) as a function of the rate of exploitation (E) and the ratio of M to K (Q) for three estimates of L_∞.[1]

	E						
Q	0.1	0.2	0.3	0.4	0.5	0.6	0.7
			L_∞ = 175.2 cm				
1.0	56.6	73.1	84.4	94.3	102.3	109.5	115.8
1.5	49.4	64.1	74.8	83.4	90.8	97.1	102.8
2.0	43.8	57.1	66.9	74.8	81.5	87.2	92.5
2.5	39.4	51.7	60.4	67.8	73.9	79.4	84.1
3.0	35.9	47.1	55.4	62.0	67.6	72.7	77.1
3.5	32.9	43.3	51.0	57.1	62.4	66.9	71.1
			L_∞ = 194.8 cm				
1.0	62.9	81.2	94.3	104.8	113.8	121.8	128.8
1.5	54.9	71.3	83.2	92.7	100.9	107.9	114.4
2.0	48.7	63.5	74.4	83.2	90.6	97.0	102.8
2.5	43.8	57.5	67.2	75.4	82.2	88.2	93.5
3.0	39.9	52.4	61.6	69.0	75.2	80.8	85.7
3.5	36.6	48.1	56.7	63.5	69.4	74.4	79.1
			L_∞ = 223.0 cm				
1.0	72.0	93.0	107.9	120.0	130.2	139.4	147.4
1.5	62.9	81.6	95.2	106.2	115.5	123.5	130.9
2.0	55.8	72.7	85.2	95.2	103.7	111.0	117.7
2.5	50.2	65.8	76.9	86.3	94.1	101.0	107.0
3.0	45.7	60.0	70.5	78.9	86.1	92.6	98.1
3.5	41.9	55.1	64.9	72.7	79.4	85.2	90.5

[1] Dashed lines encompass our reasonable range of values; underlined value is our most reasonable estimate.

reasonable range of estimates (deleting the unreasonably low E = 0.12), and the underlined value in the center of Table 1 is our most reasonable estimate. One can see in Table 1 that the values are all greater than the approximate absolute minimum size of 32.5 cm[11] for the Atlantic yellowfin tuna fishery over the range of the estimates of L_∞.

For the moment let us assume that recruitment is knife-edged at 32.5 cm (0.67 kg) and that the fishery can be regulated such to obtain a knife-edged recruitment at any desired size. Therefore, the maximum possible increases in yield per recruit may be computed. Our smallest reasonable values for optimal size at recruitment are 47.1 cm (2.0 kg), 52.4 cm (2.8 kg), or 60.0 cm (4.1 kg) depending on L_∞. The respective predicted values of yield per recruit are 2.0%, 3.1%, and 4.3% higher than when size at recruitment is 32.5 cm. Our largest reasonable estimates of optimal size at recruitment are 97.1 cm (17 kg), 107.9 cm (24 kg), or 123.5 cm (36 kg). The respective predicted increases in yield per recruit are 65%, 73%, and 82%. The predicted increase in yield per recruit using all of our most reasonable parameter estimates, i.e., raising 32.5 cm to 83.2 cm (11 kg), is 23%. The bounds on an increase in yield per recruit, 2% to 82%, and the most likely value of 23%, are estimated under the assumptions of knife-edged recruitment, and that size at recruitment represents an absolute minimum size. The Atlantic yellowfin tuna fishery, however, does not have knife-edged recruitment.

We used equation 1b of this paper to obtain our most reasonable estimate of the 1967-71 average effective minimum size for the Atlantic yellowfin tuna fishery from average lengths given in Table 15 of Lenarz and Sakagawa (1972, see footnote 5). The estimate of average effective minimum size is about 55 cm (3.2 kg). Nearly all the values within the dashed lines in Table 1, however, are greater than 55. The only smallest reasonable estimate of optimal effective minimum size greater than 55 cm is 60.0 cm with L_∞ = 223.0 cm. An increase from 55 to 60.0 cm would give an increase in yield per recruit < 0.2%. The largest reasonable estimates of optimal effective minimum size predict increases in yield per recruit of 28%, 36%, or 45% with in-

[11] The value of 32.5 cm represents our selection for an approximate absolute minimum size for the Atlantic yellowfin tuna fishery, which also agrees with that chosen by Joseph and Tomlinson (1972, see footnote 4).

creases from 55 cm to 97.1, 107.9, and 123.5 cm, respectively depending on L_∞. The increase in yield per recruit by increasing the effective minimum size from 55 to 83.2 cm, our most reasonable estimate, is only 7.9%.

From the above analysis using a wide range of parameter estimates, we can conclude with reasonable assurance that virtually any increase in the effective minimum size will cause an increase in yield per recruit. Our most likely estimate of this increase in yield per recruit is only 7.9% which is bounded, with reasonable parameter estimates, by 0% and 45%.

Ricker Model

Ricker model yield-per-recruit isopleths were calculated using values of M of 0.6, 0.8, and 1.0 to illustrate our estimates of actual (rather than relative) yield per recruit (Figures 1, 2, and 3). As will be mentioned in the next section it is difficult to estimate the location of the fishery on the graphs, i.e., when fishing mortality is size specific it is not a trivial matter to make reasonable estimates of age at recruitment, t_r', and a constant total mortality coefficient, Z. Our most reasonable estimates, taken from Lenarz and Sakagawa (1972, see footnote 5), of these parameters are: t_r' is 1.41 yr and Z is 1.4.

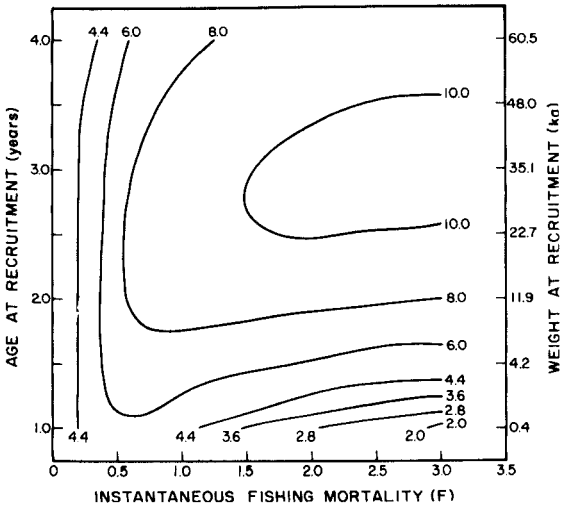

FIGURE 1.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 0.6$.

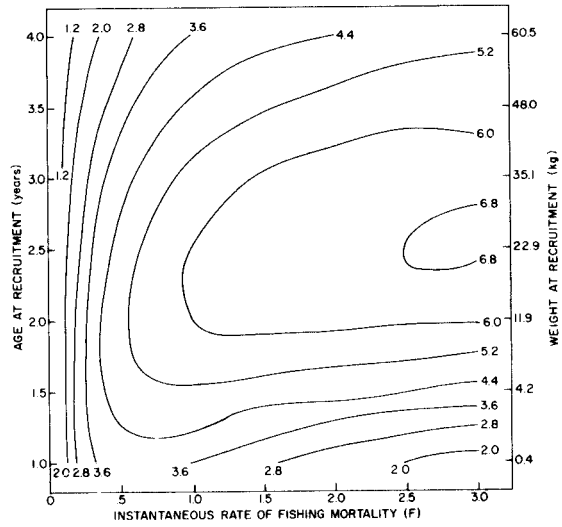

FIGURE 2.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 0.8$.

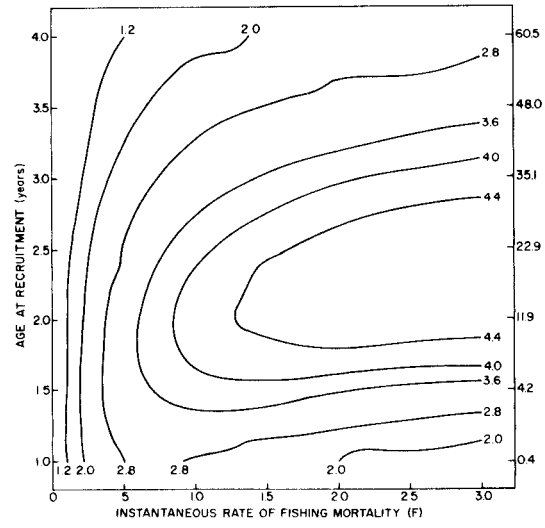

FIGURE 3.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 1.0$.

The results (Figures 1, 2, and 3) show, for example, that with $M = 0.6$ and Z remaining constant (1.4), an increase in age at recruitment from 1.41 to 1.83 yr (or 77.5 cm) raises the yield per recruit about 20%; if $M = 0.8$, the same change raises the yield per recruit on the order of 10%; and if $M = 1.0$, the same change does

not change yield per recruit. If age at recruitment is held constant and fishing mortality is doubled, when $M = 0.6$ yield per recruit decreases by some 20%; when $M = 0.8$ yield per recruit increases on the order of 5%; and when $M = 1.0$ yield per recruit increases about 30%. If effort is doubled and age at recruitment is raised to 1.83 yr, when $M = 0.6$ or $M = 0.8$ yield per recruit increases on the order of 20%; and when $M = 1.0$ yield per recruit increases by about 40%.

Estimation of t_r'

In employing a knife-edged approximation to size-specific recruitment protracted over some time period, the first problem is to determine the proper age at recruitment (t_r') such that the integration reflects the same yield per recruit as the size-specific recruitment case. There are two problems in doing so. First, there are two values for t_r' that will give the same yield per recruit as the size-specific recruitment case, unless eumetric fishing obtains. Often, however, this may be of little consequence, since one of the two values for t_r' could be obviously infeasible. Second, t_r' will depend on the fishing mortality.

Two estimators of t_r' are provided, at least implicitly, by Beverton and Holt (1957): (1) the age corresponding to the mean selection length, and (2) the resultant of a formula depending on Z and the average age, $\bar{t}$ (or average length, $\bar{l}$), in the catch. The mean selection length is the 50% selection length if the selection curve is symmetrical, and it is not dependent on the magnitude of the fishing mortality coefficient, F. The second estimator of t_r' is

$$t_r' = \bar{t} - 1/Z \qquad (1a)$$

or, in terms of length

$$l_r' = \bar{l} - K(L_\infty - \bar{l})/Z. \qquad (1b)$$

These two equations were obtained from manipulations of the Beverton and Holt yield equation.

Several computations of yield per recruit with the program GXPOPS were made utilizing $F = 0.1$ and $F = 2.0$, $M = 0.8$, the von Bertalanffy equation for Atlantic yellowfin tuna, and an arbitrary age-specific selection curve (Figure 4) in order to demonstrate the two

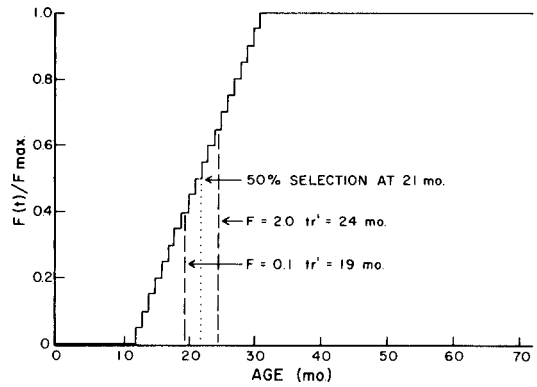

FIGURE 4.—Arbitrary age-specific recruitment curve.

problems and to evaluate the two estimators of t_r'. At $F = 0.1$, the values of t_r' giving the same yields per recruit as the selection curve are <8 mo (t_0 of the von Bertalanffy growth curve is 7.48 mo) or 24 mo, and 19 or 45 mo for $F = 2.0$. Since the state of the simulated fishery is not eumetric for either value of F, there are two knife-edged approximation locations. The effect of the magnitude of F on the true t_r' is obvious, with the lower value increasing from <8 to 19 mo and the upper value increasing from 24 to 45 mo as F is changed from 0.1 to 2.0. The reasonable values for t_r' to approximate the selection curve, however, are 24 mo for $F = 0.1$ and 19 mo for $F = 2.0$, a change of 5 mo.

Estimator 1, the mean selection age, is 21 mo and is shown along with the reasonable values in Figure 4. Using 21 mo for t_r' would result in yields per recruit that are 4% and 15% too high for $F = 0.1$ and $F = 2.0$ respectively. Estimator 1 does not change with F, of course, but in this case it lies intermediate between the true t_r' values. Estimator 2 gives 19 mo for $F = 0.1$ and 18 mo for $F = 2.0$. We emphasize that this estimator does depend on the magnitude of F.

Neither estimator is exact in this example where the catches, their ages, and the selection curve are known without error. This places doubt on their estimates from the usual catch at age data where considerable random error would be involved. Encouraging, though, is that both estimators indicate the proper direction that the fishery's selectivity should proceed to approach the optimal yield per recruit—about

15 mo for $F = 0.1$ and 30 mo for $F = 2.0$. Since estimator 1 requires size-selective data not frequently available and does not respond to changes in F, estimator 2 appears to be the most attractive for knife-edged approximations. The Atlantic yellowfin tuna fishery, however, has a much more complex recruitment pattern and size-specific F than this simple example owing to the diverse gear types. The mix of relative F among the various gear types makes the determination of the appropriate current t_r' somewhat tenuous.

Estimation of Constant Z

The yield-per-recruit isopleths shown in Figures 1, 2, and 3 were calculated under the assumption that fishing mortality and Z are constant after the fish are recruited. The value of Z was also estimated under the same assumption. The section on size-specific fishing mortality will indicate that F is not a constant, but is related to size. Thus our estimate of a constant Z may not be realistic but may be a more reasonable approach to estimating yield per recruit than the size-specific F approach given the quality of the data. It is the average of values of Z estimated for the FIS bait boat and purse seine fisheries (Lenarz and Sakagawa, 1972, see footnote 5). The size-specific F section indicates that F decreases with size for bait boats and increases with size for purse seiners. Beverton and Holt (1956) gave examples that indicated that when F decreases with age, constant Z will be overestimated and when F increases with age, constant Z will be underestimated. Hopefully we have obtained a reasonable estimate by taking the average of Z's for the two gears.

Size-Specific F Approach

Estimates of Length Frequencies

Length frequencies, numbers of yellowfin caught by 5-cm intervals starting at 35 cm (32.5 cm $\leq$ fork length $<$37.5 cm), were estimated for each gear and the total fishery for two overlapping periods, 1967-71 and 1969-71 (Figure 5). The first period was used with the hope that the effect caused by unequal strength of year classes would be minimized by averaging. The second period was used because it was felt that

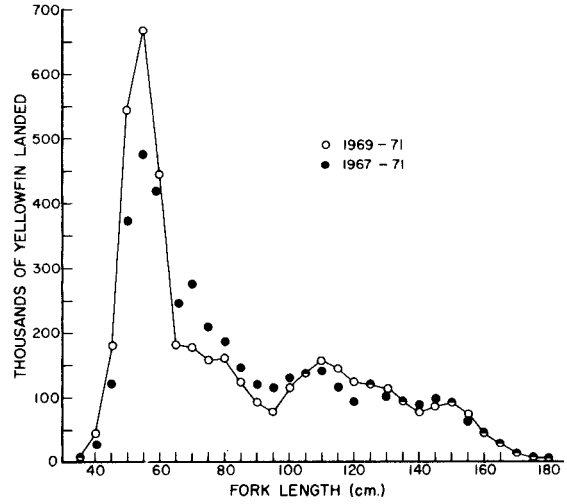

FIGURE 5.—Average length frequencies for the Atlantic yellowfin tuna fisheries for two periods, 1967-71 and 1969-71.

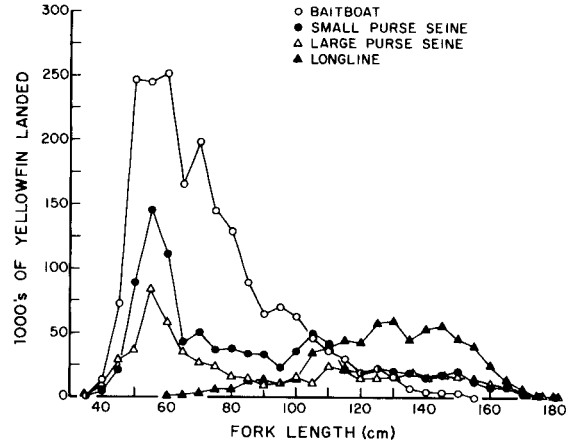

FIGURE 6.—Average length frequencies (1967-71) of Atlantic yellowfin tuna caught by four gear types.

the data are more accurate. Length frequencies of the two periods are quite similar and produce similar estimates of size-specific fishing mortality and estimates of yield per recruit. Thus, to avoid redundancy, only the data for the 1967-71 period are used. Figure 6 and Table 2 show the length frequencies for each gear. The curves are as described earlier (see introductory section.)

Estimates of Size-Specific Fishing Mortality

Size-specific instantaneous coefficients of fishing mortality were estimated with the method of Gulland (1965) and Murphy (1965) as suggested

TABLE 2.—Basic data on size (age) composition of catch of yellowfin tuna from the tropical Atlantic Ocean.

Midpoint of size interval (cm)	Weight at beginning of interval (kg)	Age at beginning of interval (yr)	1967-71 average number of yellowfin landed				
			Bait boats	Small purse seiners	Large purse seiners	Longliners	Total
35	0.67	1.0579	1,886	372	100		2,358
40	1.03	1.1325	14,551	5,445	9,057		29,053
45	1.49	1.2093	72,972	21,782	28,372		123,126
50	2.08	1.2888	246,924	89,614	36,684	7	373,229
55	2.79	1.3710	245,206	146,883	83,153	22	475,264
60	3.66	1.4562	251,017	110,755	59,648	451	421,871
65	4.69	1.5445	165,328	42,427	35,891	647	244,293
70	5.90	1.6363	197,855	49,929	26,992	2,151	276,927
75	7.30	1.7317	143,885	36,942	23,263	5,435	209,525
80	8.90	1.8310	128,810	37,082	15,528	5,694	187,114
85	10.72	1.9348	89,637	31,143	13,338	12,025	146,143
90	12.77	2.0432	64,128	31,135	9,818	13,049	118,130
95	15.06	2.1568	70,422	22,248	10,062	11,665	114,397
100	17.61	2.2761	63,619	36,483	13,323	15,074	128,499
105	20.43	2.4017	45,582	48,274	11,647	34,071	139,574
110	23.54	2.5343	36,414	42,283	24,296	40,209	143,202
115	26.95	2.6748	29,227	21,268	21,466	44,034	115,995
120	30.67	2.8240	18,877	18,311	15,144	42,859	95,191
125	34.72	2.9832	22,228	23,711	15,018	57,358	118,915
130	39.10	3.1538	15,152	20,612	16,238	58,544	110,546
135	43.84	3.3376	7,142	18,304	18,504	44,690	88,640
140	48.95	3.5368	4,137	15,790	13,569	52,070	85,566
145	54.43	3.7542	3,393	17,301	17,886	55,582	94,162
150	60.31	3.9935	3,459	20,222	16,711	45,648	86,040
155	66.60	4.2595	1,511	12,057	14,926	39,108	67,602
160	73.30	4.5590	793	8,754	10,678	24,489	44,714
165	80.44	4.9017	634	7,803	6,633	13,659	28,729
170	88.03	5.3021	327	2,470	2,918	6,265	11,980
175	96.07	5.7838	209	2,132	1,383	241	3,965
180	104.59	6.3883	49	1,429	361	55	1,894
	113.60	7.2004					
Total			1,945,374	942,961	573,207	625,102	4,086,645

by Lenarz (1971b).[12] We followed the modification of Joseph and Tomlinson (1972, see footnote 4) by using the inverse of the von Bertalanffy growth equation to convert size distributions to age distributions. This method assumes that there is a reasonably accurate relationship between length and age of yellowfin tuna. This assumption has not been verified. Ageing by modal progression would probably be more satisfactory, if more complete length composition data were available on a monthly or quarterly basis.

The reverse iterative procedure with computer program COHORT and $M = 0.8$ was used to estimate size-specific values of fishing mortality (F) starting at the 180-cm interval. Four initial values of F were tried: 0.2, 0.4, 0.6, and 0.8 (Figure 7). Estimates of F tend to converge as size of the yellowfin tuna decreases with the range of initial values tried as is characteristic

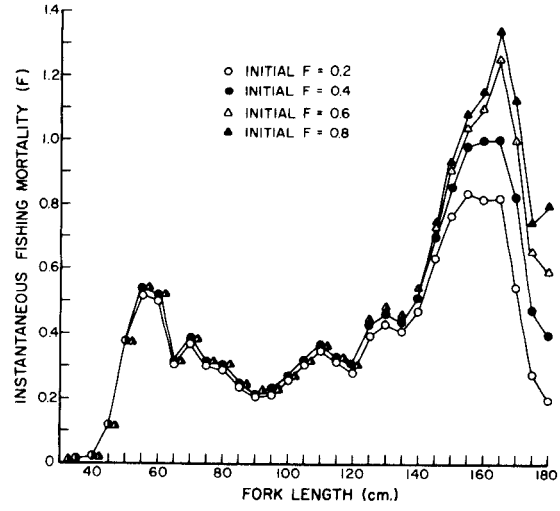

FIGURE 7.—Estimates of size-specific instantaneous fishing mortality coefficients (F) with several initial F values.

[12] Lenarz, W. 1971b. Yield per recruit of Atlantic yellowfin tuna for multigear fisheries. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

of the methodology (Tomlinson, 1970). Calculations of yield per recruit using initial values of F of 0.2 and 0.8 are shown in Figures 8 and 9 as functions of initial values of F, effort, and size at recruitment. The values of yield per recruit do not vary significantly (< 10%) with changes in the initial values of F, and the relative values are quite similar. Values of size specific F are shown for each gear in Figure 10 when initial values of F are 0.2 and 0.8. When the initial value of F is 0.8, values of F for small purse seiners increase sharply with size from 170 to 180 cm. This does not occur when the initial value of F is 0.2. Intuitively we do not expect an increase in F with size past 170 cm and thus choose to use the results when the initial value of F is 0.2 in the remainder of the

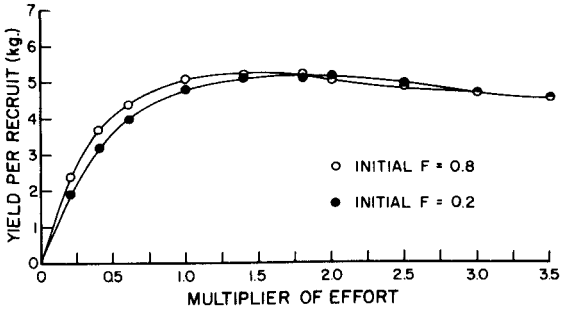

FIGURE 8.—Yield-per-recruit (kg) of Atlantic yellowfin tuna, when size at recruitment is 32.5 cm, as a function of the multiplier of fishing effort.

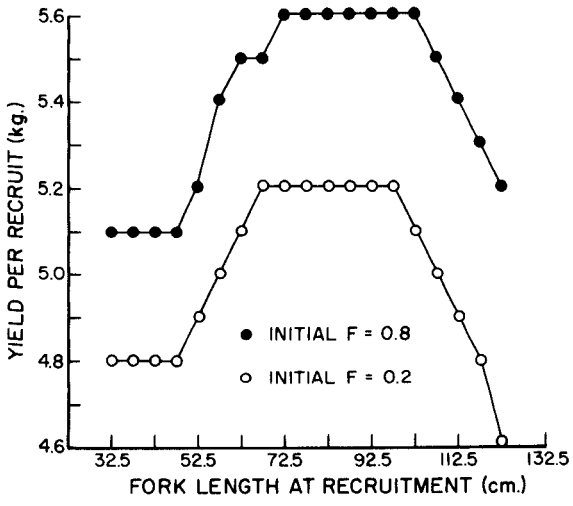

FIGURE 9.—Yield-per-recruit (kg) of Atlantic yellowfin tuna, with the current level of fishing effort, as a function of length at recruitment.

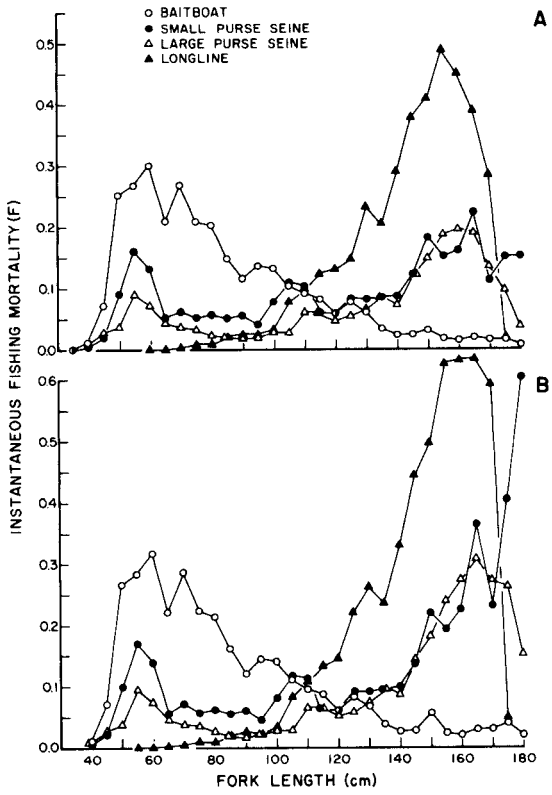

FIGURE 10.—Estimates of size-specific instantaneous fishing mortality coefficients (F) by gear type when initial values of F are (A) F = 0.2, (B) F = 0.8.

paper. Validity of the estimates of F depends on the validity of the assumption that recruitment has been fairly constant for the cohorts included in the analysis. The special ICCAT working group noted that the cohort which entered the surface fisheries in 1969 appears to be weaker than the following two cohorts (ICCAT, 1972, see footnote 2). Although inclusion of 5 yr of data in the analysis may minimize the source of error, future studies should examine the sensitivity of the results to errors of this type.

Estimates of Yield Per Recruit

Results of the yield-per-recruit calculations using the estimates of size-specific F when the initial value of F is 0.2 and with M = 0.8 are shown by gear in Table 3. Yield-per-recruit isopleths and the line of eumetric fishing (size at recruitment, $l^{*\prime}_r$, which maximizes yield per recruit at a given effort) for the entire fishery

TABLE 3.—Estimates of yield per recruit (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.08	0.15	0.21	0.31	0.39	0.46	0.49	0.56	0.62	0.68
117.5	30.6	0.09	0.17	0.24	0.36	0.46	0.54	0.58	0.66	0.73	0.80
112.5	26.9	0.11	0.21	0.29	0.43	0.55	0.65	0.69	0.80	0.89	0.96
107.5	23.5	0.13	0.24	0.33	0.50	0.64	0.75	0.80	0.92	1.02	1.11
102.5	20.4	0.15	0.27	0.38	0.57	0.73	0.86	0.92	1.06	1.17	1.27
97.5	17.6	0.17	0.31	0.44	0.66	0.85	1.01	1.08	1.24	1.38	1.50
92.5	15.0	0.19	0.35	0.50	0.75	0.96	1.15	1.23	1.41	1.58	1.72
87.5	12.7	0.20	0.38	0.54	0.81	1.04	1.24	1.32	1.52	1.69	1.84
82.5	10.7	0.22	0.41	0.58	0.88	1.12	1.34	1.43	1.64	1.82	1.98
77.5	8.9	0.24	0.45	0.63	0.95	1.22	1.45	1.55	1.78	1.97	2.13
72.5	7.3	0.26	0.48	0.68	1.02	1.30	1.54	1.64	1.87	2.07	2.23
67.5	5.9	0.27	0.51	0.72	1.08	1.38	1.62	1.73	1.96	2.14	2.30
62.5	4.7	0.29	0.53	0.75	1.12	1.41	1.65	1.76	1.98	2.16	2.30
57.5	3.7	0.30	0.56	0.78	1.15	1.43	1.66	1.76	1.96	2.11	2.22
52.5	2.8	0.31	0.57	0.79	1.15	1.42	1.63	1.72	1.88	2.00	2.08
47.5	2.1	0.31	0.58	0.80	1.15	1.42	1.61	1.69	1.84	1.94	2.00
42.5	1.5	0.31	0.58	0.80	1.15	1.41	1.60	1.68	1.82	1.91	1.97
37.5	1.0	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.96
32.5	0.7	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.34	0.58	0.75	0.97	1.09	1.16	1.19	1.24	1.28	1.31
117.5	30.6	0.35	0.60	0.77	0.99	1.11	1.18	1.21	1.27	1.30	1.33
112.5	26.9	0.36	0.61	0.79	1.01	1.13	1.20	1.23	1.28	1.31	1.34
107.5	23.5	0.38	0.64	0.83	1.06	1.20	1.28	1.32	1.38	1.43	1.47
102.5	20.4	0.40	0.67	0.87	1.12	1.27	1.37	1.41	1.49	1.55	1.60
97.5	17.6	0.41	0.69	0.89	1.14	1.30	1.40	1.44	1.52	1.59	1.64
92.5	15.0	0.41	0.70	0.90	1.15	1.30	1.39	1.43	1.50	1.56	1.61
87.5	12.7	0.42	0.71	0.91	1.16	1.31	1.40	1.44	1.51	1.56	1.60
82.5	10.7	0.42	0.71	0.91	1.16	1.30	1.39	1.43	1.49	1.53	1.57
77.5	8.9	0.43	0.71	0.91	1.15	1.29	1.37	1.40	1.45	1.49	1.51
72.5	7.3	0.43	0.71	0.91	1.14	1.27	1.34	1.36	1.41	1.43	1.44
67.5	5.9	0.43	0.72	0.91	1.13	1.24	1.30	1.32	1.35	1.36	1.35
62.5	4.7	0.43	0.71	0.90	1.11	1.22	1.27	1.28	1.30	1.29	1.28
57.5	3.7	0.43	0.71	0.90	1.10	1.19	1.23	1.24	1.24	1.23	1.21
52.5	2.8	0.44	0.72	0.89	1.08	1.16	1.19	1.20	1.19	1.17	1.14
47.5	2.1	0.44	0.71	0.89	1.06	1.13	1.15	1.15	1.14	1.11	1.07
42.5	1.5	0.44	0.71	0.88	1.06	1.12	1.14	1.14	1.11	1.08	1.05
37.5	1.0	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04
32.5	0.7	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.31	0.54	0.69	0.89	0.99	1.05	1.07	1.10	1.12	1.12
117.5	30.6	0.32	0.55	0.71	0.90	1.01	1.06	1.08	1.11	1.12	1.13
112.5	26.9	0.33	0.56	0.73	0.92	1.03	1.09	1.11	1.14	1.16	1.17
107.5	23.5	0.34	0.58	0.74	0.94	1.04	1.10	1.12	1.15	1.17	1.18
102.5	20.4	0.34	0.58	0.74	0.93	1.02	1.06	1.08	1.10	1.10	1.10
97.5	17.6	0.35	0.58	0.74	0.92	1.00	1.04	1.05	1.06	1.06	1.06
92.5	15.0	0.35	0.58	0.73	0.91	0.99	1.02	1.03	1.03	1.03	1.02
87.5	12.7	0.35	0.58	0.73	0.90	0.97	1.00	1.00	1.00	0.99	0.97
82.5	10.7	0.35	0.58	0.73	0.89	0.96	0.98	0.98	0.97	0.95	0.93
77.5	8.9	0.35	0.58	0.72	0.88	0.93	0.95	0.95	0.93	0.91	0.88
72.5	7.3	0.35	0.57	0.72	0.86	0.92	0.92	0.92	0.90	0.87	0.84
67.5	5.9	0.35	0.57	0.71	0.85	0.89	0.89	0.88	0.86	0.82	0.79
62.5	4.7	0.35	0.57	0.71	0.84	0.87	0.87	0.86	0.83	0.80	0.76
57.5	3.7	0.35	0.57	0.70	0.82	0.85	0.84	0.82	0.79	0.75	0.71
52.5	2.8	0.35	0.57	0.69	0.80	0.82	0.80	0.79	0.75	0.71	0.67
47.5	2.1	0.35	0.56	0.68	0.78	0.79	0.77	0.75	0.71	0.66	0.62
42.5	1.5	0.35	0.56	0.68	0.78	0.79	0.76	0.75	0.70	0.65	0.61
37.5	1.0	0.35	0.56	0.68	0.78	0.79	0.76	0.75	0.70	0.65	0.61
32.5	0.7	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61

TABLE 3.—Estimates of yield per recruit (kg) when M = 0.8, initial F = 0.2, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

		LONG LINERS									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.80	1.40	1.86	2.49	2.87	3.12	3.21	3.38	3.49	3.57
117.5	30.6	0.82	1.44	1.90	2.53	2.90	3.14	3.23	3.38	3.47	3.54
112.5	26.9	0.84	1.46	1.93	2.54	2.90	3.12	3.19	3.32	3.39	3.43
107.5	23.5	0.85	1.48	1.93	2.52	2.84	3.02	3.08	3.17	3.20	3.21
102.5	20.4	0.86	1.48	1.93	2.49	2.78	2.93	2.97	3.03	3.03	3.01
97.5	17.6	0.86	1.47	1.90	2.43	2.69	2.81	2.83	2.85	2.82	2.76
92.5	15.0	0.86	1.46	1.89	2.38	2.62	2.71	2.72	2.71	2.66	2.58
87.5	12.7	0.86	1.46	1.87	2.34	2.55	2.62	2.63	2.59	2.52	2.43
82.5	10.7	0.86	1.45	1.85	2.29	2.48	2.52	2.52	2.46	2.36	2.25
77.5	8.9	0.85	1.43	1.82	2.23	2.38	2.40	2.38	2.29	2.17	2.04
72.5	7.3	0.85	1.41	1.79	2.17	2.29	2.28	2.24	2.13	1.99	1.85
67.5	5.9	0.84	1.39	1.75	2.09	2.18	2.13	2.09	1.95	1.79	1.63
62.5	4.7	0.84	1.38	1.72	2.03	2.09	2.03	1.98	1.82	1.64	1.48
57.5	3.7	0.83	1.35	1.67	1.95	1.97	1.88	1.81	1.63	1.44	1.27
52.5	2.8	0.82	1.33	1.63	1.86	1.85	1.73	1.66	1.46	1.26	1.09
47.5	2.1	0.82	1.31	1.60	1.81	1.77	1.64	1.56	1.35	1.15	0.98
42.5	1.5	0.82	1.31	1.59	1.79	1.75	1.61	1.53	1.32	1.12	0.94
37.5	1.0	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
32.5	0.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94

are shown in Figure 11. Table 3 and Figures 8, 9, and 11 indicate that if size at recruitment remains constant at 32.5 cm, very little increase in yield per recruit (~5%) can be expected if effort is increased, and if effort remains constant, very little (~10%) increase in yield per recruit can be expected by increasing size at recruitment. However, if fishing effort is doubled (i.e., multiplier = 2.0) and size at recruitment increased to 55 cm (3.2 kg), yield per recruit would increase 15%, or if size at recruitment is increased to 77.5 cm (~10 kg), yield per recruit would increase about 30% (Table 3). Since the line of eumetric fishing shows that optimum size at recruitment changes with fishing effort, any "minimum size" regulation must be geared to fishing effort.

If fishermen are unable to distinguish the size of yellowfin before capturing them and a minimum size regulation prevents their landing, then the discarding of dead yellowfin will occur. Table 4 presents landings per recruit by gear and Figure 12 the landings per recruit for the total fishery when killing and discarding ("dumping") of all yellowfin smaller than the size limit occurs. If the minimum size limit is 55 cm and effort remains the same, then a 2.7% decrease in landings per recruit would occur; and a 13% decrease in landings per recruit would occur if the minimum size is set at 77.5 cm. If effort is doubled and the minimum size is 55 cm, then a 1% increase in landings per recruit would occur; with a minimum size of 77.5 cm, a 16% decline in landings per recruit would

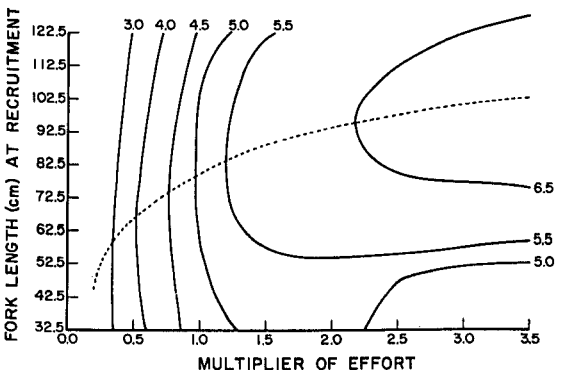

FIGURE 11.—Yield-per-recruit (kg) isopleths for the entire Atlantic yellowfin tuna fishery. Dotted curve is the line of eumetric fishing.

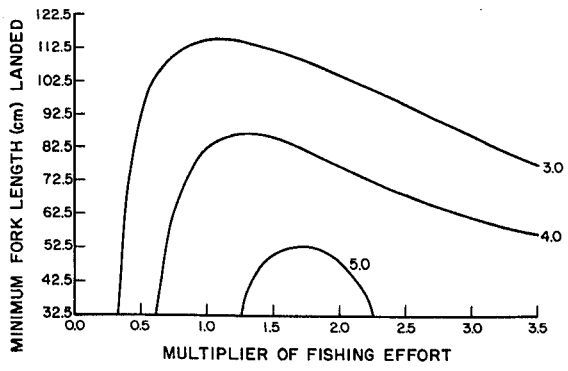

FIGURE 12.—Landings-per-recruit (kg) isopleths for Atlantic yellowfin tuna when all fish less than the minimum size that are caught are discarded dead.

TABLE 4.—Landings per recruit (kg) when M = 0.8, initial F = 0.2, growth curve of LeGuen and Sakagawa (1973) is used, and yellowfin less than the minimum size are caught and discarded dead.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.07	0.12	0.15	0.18	0.18	0.17	0.16	0.14	0.12	0.10
117.5	30.6	0.08	0.14	0.18	0.22	0.22	0.22	0.21	0.19	0.16	0.14
112.5	26.9	0.10	0.17	0.22	0.27	0.29	0.28	0.28	0.25	0.22	0.19
107.5	23.5	0.12	0.20	0.26	0.33	0.36	0.36	0.36	0.33	0.30	0.27
102.5	20.4	0.14	0.24	0.31	0.40	0.44	0.45	0.44	0.42	0.39	0.35
97.5	17.6	0.16	0.27	0.36	0.48	0.53	0.56	0.56	0.54	0.51	0.47
92.5	15.0	0.18	0.31	0.41	0.55	0.63	0.66	0.67	0.66	0.63	0.59
87.5	12.7	0.19	0.34	0.45	0.61	0.70	0.74	0.75	0.75	0.73	0.69
82.5	10.7	0.21	0.37	0.50	0.68	0.79	0.84	0.86	0.87	0.85	0.81
77.5	8.9	0.23	0.41	0.55	0.76	0.89	0.97	0.99	1.01	1.00	0.97
72.5	7.3	0.25	0.44	0.60	0.84	0.99	1.08	1.11	1.15	1.15	1.12
67.5	5.9	0.27	0.48	0.66	0.92	1.10	1.22	1.25	1.31	1.33	1.32
62.5	4.7	0.28	0.51	0.70	0.98	1.18	1.31	1.35	1.43	1.46	1.46
57.5	3.7	0.29	0.54	0.74	1.05	1.27	1.42	1.48	1.57	1.62	1.64
52.5	2.8	0.30	0.56	0.77	1.10	1.34	1.51	1.57	1.69	1.76	1.79
47.5	2.1	0.31	0.57	0.79	1.14	1.39	1.58	1.65	1.79	1.87	1.92
42.5	1.5	0.31	0.58	0.80	1.15	1.41	1.59	1.67	1.81	1.90	1.95
37.5	1.0	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95
32.5	0.7	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.31	0.47	0.54	0.56	0.50	0.43	0.40	0.31	0.25	0.19
117.5	30.6	0.32	0.49	0.57	0.60	0.55	0.48	0.44	0.36	0.29	0.23
112.5	26.9	0.33	0.51	0.60	0.64	0.59	0.53	0.49	0.41	0.33	0.27
107.5	23.5	0.35	0.55	0.65	0.71	0.68	0.62	0.58	0.50	0.42	0.35
102.5	20.4	0.37	0.58	0.70	0.78	0.76	0.71	0.68	0.60	0.52	0.45
97.5	17.6	0.38	0.61	0.73	0.82	0.81	0.77	0.74	0.66	0.59	0.51
92.5	15.0	0.39	0.62	0.75	0.84	0.84	0.80	0.78	0.70	0.62	0.55
87.5	12.7	0.40	0.63	0.76	0.87	0.88	0.84	0.82	0.75	0.67	0.60
82.5	10.7	0.40	0.64	0.78	0.90	0.91	0.88	0.85	0.79	0.71	0.64
77.5	8.9	0.41	0.65	0.80	0.92	0.94	0.91	0.89	0.83	0.76	0.69
72.5	7.3	0.41	0.66	0.81	0.94	0.96	0.94	0.92	0.86	0.79	0.73
67.5	5.9	0.42	0.67	0.82	0.96	0.99	0.98	0.96	0.90	0.84	0.77
62.5	4.7	0.42	0.68	0.83	0.98	1.01	1.00	0.98	0.93	0.87	0.81
57.5	3.7	0.43	0.69	0.85	1.01	1.05	1.05	1.04	1.00	0.95	0.89
52.5	2.8	0.43	0.70	0.87	1.04	1.10	1.10	1.10	1.07	1.03	0.98
47.5	2.1	0.44	0.71	0.88	1.05	1.11	1.13	1.13	1.10	1.07	1.03
42.5	1.5	0.44	0.71	0.88	1.05	1.12	1.13	1.13	1.11	1.08	1.04
37.5	1.0	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04
32.5	0.7	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.28	0.43	0.50	0.51	0.46	0.39	0.36	0.28	0.21	0.16
117.5	30.6	0.29	0.45	0.52	0.54	0.50	0.43	0.39	0.31	0.25	0.19
112.5	26.9	0.30	0.47	0.55	0.59	0.54	0.48	0.44	0.36	0.29	0.24
107.5	23.5	0.31	0.49	0.58	0.63	0.59	0.53	0.50	0.42	0.35	0.28
102.5	20.4	0.32	0.50	0.59	0.64	0.61	0.55	0.52	0.44	0.37	0.31
97.5	17.6	0.32	0.51	0.60	0.66	0.63	0.57	0.54	0.46	0.39	0.33
92.5	15.0	0.33	0.51	0.61	0.67	0.64	0.59	0.56	0.48	0.41	0.35
87.5	12.7	0.33	0.52	0.62	0.68	0.65	0.60	0.57	0.50	0.42	0.36
82.5	10.7	0.33	0.52	0.62	0.69	0.67	0.62	0.59	0.51	0.44	0.38
77.5	8.9	0.33	0.53	0.63	0.70	0.68	0.63	0.60	0.53	0.46	0.40
72.5	7.3	0.34	0.53	0.64	0.71	0.70	0.65	0.62	0.55	0.49	0.43
67.5	5.9	0.34	0.54	0.65	0.72	0.71	0.67	0.64	0.57	0.51	0.45
62.5	4.7	0.34	0.54	0.65	0.74	0.73	0.69	0.66	0.60	0.54	0.48
57.5	3.7	0.35	0.55	0.66	0.75	0.75	0.71	0.69	0.63	0.58	0.53
52.5	2.8	0.35	0.56	0.68	0.77	0.77	0.74	0.73	0.67	0.62	0.58
47.5	2.1	0.35	0.56	0.68	0.77	0.78	0.75	0.74	0.69	0.64	0.60
42.5	1.5	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61
37.5	1.0	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61
32.5	0.7	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61

TABLE 4.—Landings per recruit (kg) when M = 0.8, initial F = 0.2, growth curve of LeGuen and Sakagawa (1973) is used, and yellowfin less than the minimum size are caught and discarded dead.—Continued.

		LONG LINERS									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.72	1.13	1.34	1.43	1.33	1.16	1.07	0.85	0.67	0.52
117.5	30.6	0.74	1.18	1.41	1.53	1.43	1.27	1.18	0.96	0.76	0.60
112.5	26.9	0.77	1.22	1.47	1.61	1.53	1.37	1.28	1.06	0.86	0.69
107.5	23.5	0.79	1.25	1.51	1.68	1.61	1.45	1.37	1.15	0.94	0.77
102.5	20.4	0.80	1.28	1.55	1.72	1.67	1.52	1.43	1.21	1.01	0.84
97.5	17.6	0.81	1.29	1.56	1.74	1.69	1.54	1.46	1.24	1.04	0.86
92.5	15.0	0.81	1.29	1.57	1.76	1.70	1.56	1.48	1.26	1.06	0.88
87.5	12.7	0.81	1.30	1.58	1.77	1.72	1.58	1.49	1.28	1.08	0.90
82.5	10.7	0.81	1.30	1.58	1.78	1.73	1.59	1.51	1.30	1.10	0.92
77.5	8.9	0.82	1.31	1.59	1.78	1.74	1.60	1.51	1.30	1.10	0.93
72.5	7.3	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.93
67.5	5.9	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
62.5	4.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
57.5	3.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
52.5	2.8	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
47.5	2.1	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
42.5	1.5	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
37.5	1.0	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
32.5	0.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94

occur. Therefore, if effort is constant the predicted gain with no dumping is greater than the possible loss through dumping if the minimum size were 55 cm, but at 77.5 cm the opposite is true. At both size limits we predict a greater gain with no dumping than possible loss through dumping if effort is doubled.

Assuming constant recruitment, yield per recruit per unit effort is a measure of fishing success. Table 5 presents the estimated yield per recruit per effort by gear assuming no dumping. Increasing the size at recruitment to 77.5 cm at the current level of effort would result in a 17% decrease for bait boats, a 9% increase for small purse seiners, a 12% increase for large purse seiners, and a 25% increase for longliners. Yield per recruit per effort would drop by about 35% for each of the gears if effort doubled and size at recruitment increased to 77.5 cm. If effort doubled and size at recruitment remained 32.5 cm, yield per recruit per effort would decrease by 30% for bait boats, 50% for purse seiners, and 60% for longliners.

Changes in the average weight of landings should be considered because average weight affects the values of landings particularly in light of size-specific changes in the value of yellowfin tuna. Table 6 presents estimates of the average weight of catches by gear. Figure 13 shows average weight isopleths for the entire fishery. If effort remained constant and size at recruitment increased to 77.5 cm, the average weight of the catch of the total fishery would increase from 17.7 kg to 30.3 kg. If effort doubled and size at recruitment increased to 77.5 cm, the average weight would increase to 24.2 kg.

Sensitivity of Results to Errors when Ageing Large Yellowfin

The growth curve used in this study was based on the use of modal progressions to age yellowfin. Unfortunately while this method is probably reasonably accurate for ageing yellowfin less than about 130 cm long, beyond this size it becomes increasingly difficult to separate modes, and there is a reasonable probability that ages are increasingly underestimated with increases in size. In addition, because tuna apparently spawn over a large portion of the year, the exact meaning of age is not always clear. Alternative methods, such as ageing by

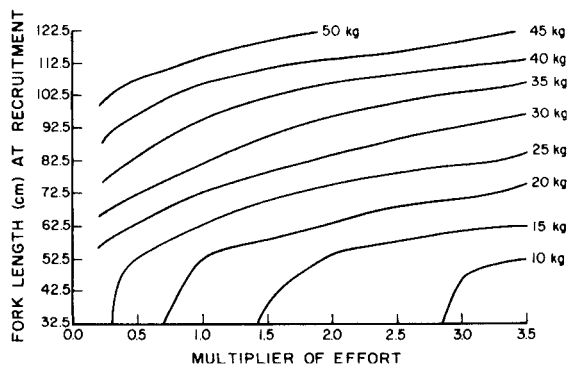

FIGURE 13.—Average weight (kg) isopleths for the entire Atlantic yellowfin tuna fishery.

TABLE 5.—Estimates of yield per recruit per effort (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.40	0.37	0.35	0.31	0.28	0.25	0.24	0.22	0.21	0.19
117.5	30.6	0.47	0.43	0.40	0.36	0.33	0.30	0.29	0.26	0.24	0.23
112.5	26.9	0.55	0.51	0.48	0.43	0.39	0.36	0.35	0.32	0.30	0.28
107.5	23.5	0.64	0.60	0.56	0.50	0.45	0.42	0.40	0.37	0.34	0.32
102.5	20.4	0.73	0.68	0.64	0.57	0.52	0.48	0.46	0.42	0.39	0.36
97.5	17.6	0.84	0.78	0.74	0.66	0.61	0.56	0.54	0.50	0.46	0.43
92.5	15.0	0.94	0.88	0.83	0.75	0.69	0.64	0.61	0.57	0.53	0.49
87.5	12.7	1.01	0.95	0.90	0.81	0.74	0.69	0.66	0.61	0.56	0.53
82.5	10.7	1.09	1.03	0.97	0.88	0.80	0.74	0.72	0.66	0.61	0.57
77.5	8.9	1.19	1.12	1.06	0.95	0.87	0.81	0.78	0.71	0.66	0.61
72.5	7.3	1.28	1.20	1.13	1.02	0.93	0.85	0.82	0.75	0.69	0.64
67.5	5.9	1.37	1.28	1.21	1.08	0.98	0.90	0.86	0.78	0.71	0.66
62.5	4.7	1.43	1.34	1.25	1.12	1.01	0.92	0.88	0.79	0.72	0.66
57.5	3.7	1.49	1.39	1.30	1.15	1.02	0.92	0.88	0.78	0.70	0.64
52.5	2.8	1.54	1.42	1.32	1.15	1.02	0.91	0.86	0.75	0.67	0.60
47.5	2.1	1.57	1.44	1.33	1.15	1.01	0.90	0.84	0.74	0.65	0.57
42.5	1.5	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.73	0.64	0.56
37.5	1.0	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.72	0.63	0.56
32.5	0.7	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.72	0.63	0.56

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	1.72	1.46	1.26	0.97	0.78	0.65	0.60	0.50	0.43	0.38
117.5	30.6	1.77	1.50	1.29	0.99	0.79	0.66	0.61	0.51	0.43	0.38
112.5	26.9	1.82	1.54	1.31	1.01	0.80	0.67	0.61	0.51	0.44	0.38
107.5	23.5	1.91	1.61	1.38	1.06	0.85	0.71	0.66	0.55	0.48	0.42
102.5	20.4	1.99	1.69	1.45	1.12	0.90	0.76	0.70	0.59	0.52	0.46
97.5	17.6	2.05	1.73	1.48	1.14	0.93	0.78	0.72	0.61	0.53	0.47
92.5	15.0	2.07	1.74	1.49	1.15	0.93	0.77	0.72	0.60	0.52	0.46
87.5	12.7	2.10	1.76	1.51	1.16	0.93	0.78	0.72	0.60	0.52	0.46
82.5	10.7	2.12	1.78	1.52	1.16	0.93	0.77	0.71	0.60	0.51	0.45
77.5	8.9	2.13	1.78	1.52	1.15	0.92	0.76	0.70	0.58	0.50	0.43
72.5	7.3	2.14	1.79	1.52	1.14	0.91	0.74	0.68	0.56	0.48	0.41
67.5	5.9	2.15	1.79	1.51	1.13	0.89	0.72	0.66	0.54	0.45	0.39
62.5	4.7	2.16	1.78	1.50	1.11	0.87	0.70	0.64	0.52	0.43	0.37
57.5	3.7	2.17	1.79	1.50	1.10	0.85	0.68	0.62	0.50	0.41	0.35
52.5	2.8	2.19	1.79	1.49	1.08	0.83	0.66	0.60	0.48	0.39	0.33
47.5	2.1	2.19	1.78	1.48	1.06	0.81	0.64	0.58	0.45	0.37	0.31
42.5	1.5	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.45	0.36	0.30
37.5	1.0	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.44	0.36	0.30
32.5	0.7	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.44	0.36	0.30

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	1.57	1.34	1.16	0.89	0.71	0.58	0.53	0.44	0.37	0.32
117.5	30.6	1.61	1.37	1.18	0.90	0.72	0.59	0.54	0.44	0.37	0.32
112.5	26.9	1.66	1.41	1.21	0.92	0.74	0.60	0.55	0.46	0.39	0.33
107.5	23.5	1.71	1.44	1.24	0.94	0.75	0.61	0.56	0.46	0.39	0.34
102.5	20.4	1.72	1.44	1.23	0.93	0.73	0.59	0.54	0.44	0.37	0.32
97.5	17.6	1.73	1.45	1.23	0.92	0.72	0.58	0.53	0.43	0.35	0.30
92.5	15.0	1.74	1.45	1.22	0.91	0.71	0.57	0.51	0.41	0.34	0.29
87.5	12.7	1.74	1.45	1.22	0.90	0.69	0.56	0.50	0.40	0.33	0.28
82.5	10.7	1.74	1.44	1.21	0.89	0.68	0.54	0.49	0.39	0.32	0.27
77.5	8.9	1.75	1.44	1.20	0.88	0.67	0.53	0.47	0.37	0.30	0.25
72.5	7.3	1.75	1.44	1.20	0.86	0.65	0.51	0.46	0.36	0.29	0.24
67.5	5.9	1.75	1.43	1.19	0.85	0.64	0.49	0.44	0.34	0.27	0.23
62.5	4.7	1.76	1.43	1.18	0.84	0.62	0.48	0.43	0.33	0.27	0.22
57.5	3.7	1.76	1.42	1.17	0.82	0.60	0.46	0.41	0.32	0.25	0.20
52.5	2.8	1.76	1.42	1.15	0.80	0.59	0.45	0.40	0.30	0.24	0.19
47.5	2.1	1.76	1.40	1.14	0.78	0.57	0.43	0.38	0.28	0.22	0.18
42.5	1.5	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.18
37.5	1.0	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.17
32.5	0.7	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.17

TABLE 5.—Estimates of yield per recruit per effort (kg) when M = 0.8, initial F = 0.2, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

LONG LINERS											
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	4.00	3.51	3.10	2.49	2.05	1.74	1.61	1.35	1.16	1.02
117.5	30.6	4.12	3.60	3.17	2.53	2.07	1.75	1.61	1.35	1.16	1.01
112.5	26.9	4.21	3.66	3.21	2.54	2.07	1.73	1.60	1.33	1.13	0.98
107.5	23.5	4.27	3.69	3.22	2.52	2.03	1.68	1.54	1.27	1.07	0.92
102.5	20.4	4.31	3.70	3.21	2.49	1.99	1.63	1.49	1.21	1.01	0.86
97.5	17.6	4.31	3.68	3.17	2.43	1.92	1.56	1.42	1.14	0.94	0.79
92.5	15.0	4.30	3.66	3.14	2.38	1.87	1.50	1.36	1.08	0.89	0.74
87.5	12.7	4.30	3.64	3.11	2.34	1.82	1.46	1.31	1.04	0.84	0.69
82.5	10.7	4.29	3.61	3.08	2.29	1.77	1.40	1.26	0.98	0.79	0.64
77.5	8.9	4.27	3.57	3.03	2.23	1.70	1.33	1.19	0.92	0.72	0.58
72.5	7.3	4.24	3.53	2.98	2.17	1.63	1.26	1.12	0.85	0.66	0.53
67.5	5.9	4.21	3.49	2.91	2.09	1.55	1.19	1.05	0.78	0.60	0.47
62.5	4.7	4.19	3.45	2.86	2.03	1.49	1.13	0.99	0.73	0.55	0.42
57.5	3.7	4.15	3.39	2.79	1.95	1.40	1.04	0.91	0.65	0.48	0.36
52.5	2.8	4.12	3.33	2.72	1.86	1.32	0.96	0.83	0.58	0.42	0.31
47.5	2.1	4.09	3.29	2.67	1.81	1.26	0.91	0.78	0.54	0.38	0.28
42.5	1.5	4.08	3.27	2.65	1.79	1.25	0.89	0.76	0.53	0.37	0.27
37.5	1.0	4.08	3.27	2.65	1.78	1.24	0.89	0.76	0.52	0.37	0.27
32.5	0.7	4.08	3.27	2.65	1.78	1.24	0.89	0.76	0.52	0.37	0.27
ENTIRE FISHERY											
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	7.70	6.68	5.86	4.65	3.82	3.22	2.98	2.51	2.17	1.91
117.5	30.6	7.97	6.90	6.04	4.78	3.91	3.29	3.05	2.57	2.21	1.94
112.5	26.9	8.25	7.12	6.22	4.90	4.00	3.36	3.11	2.61	2.25	1.97
107.5	23.5	8.53	7.34	6.40	5.02	4.08	3.42	3.16	2.65	2.27	1.99
102.5	20.4	8.75	7.51	6.53	5.10	4.14	3.46	3.19	2.67	2.28	2.00
97.5	17.6	8.92	7.64	6.62	5.16	4.17	3.48	3.20	2.67	2.28	1.99
92.5	15.0	9.04	7.73	6.69	5.19	4.19	3.48	3.21	2.67	2.27	1.98
87.5	12.7	9.14	7.80	6.74	5.21	4.19	3.48	3.20	2.65	2.26	1.96
82.5	10.7	9.24	7.86	6.78	5.22	4.18	3.46	3.18	2.62	2.22	1.92
77.5	8.9	9.34	7.92	6.81	5.22	4.16	3.42	3.14	2.58	2.18	1.88
72.5	7.3	9.42	7.96	6.82	5.19	4.12	3.38	3.09	2.52	2.12	1.82
67.5	5.9	9.49	7.99	6.82	5.15	4.06	3.30	3.01	2.44	2.04	1.74
62.5	4.7	9.54	7.99	6.80	5.10	4.00	3.23	2.94	2.37	1.97	1.66
57.5	3.7	9.58	7.98	6.75	5.01	3.88	3.11	2.81	2.25	1.84	1.55
52.5	2.8	9.60	7.95	6.68	4.90	3.75	2.98	2.68	2.11	1.71	1.42
47.5	2.1	9.61	7.91	6.61	4.81	3.65	2.87	2.58	2.01	1.62	1.33
42.5	1.5	9.60	7.90	6.59	4.78	3.62	2.84	2.54	1.98	1.59	1.31
37.5	1.0	9.60	7.89	6.59	4.77	3.61	2.83	2.53	1.97	1.58	1.30
32.5	0.7	9.60	7.89	6.59	4.77	3.61	2.83	2.53	1.97	1.58	1.30

the examination of hard parts, are extremely difficult and not easily interpreted for tropical species such as the yellowfin tuna.

The marked increase in estimates of size-specific F beyond 130 cm for the purse seine gears is a possible result of underestimating ages of older yellowfin. To examine this possibility, the growth curve of LeGuen and Sakagawa (1973) was modified. It was hypothetically assumed that the percentage of underestimation of the time interval within a size interval increased linearly from 0% at 135 cm to 100% at 180 cm. The resulting growth curve is compared to the original in Figure 14.

Values of size-specific F were then estimated as before with initial values of 0.2 and 0.8. The value of 0.2 gave the most reasonable results for reasons similar to those given before. Values of size specific F for each gear are shown in

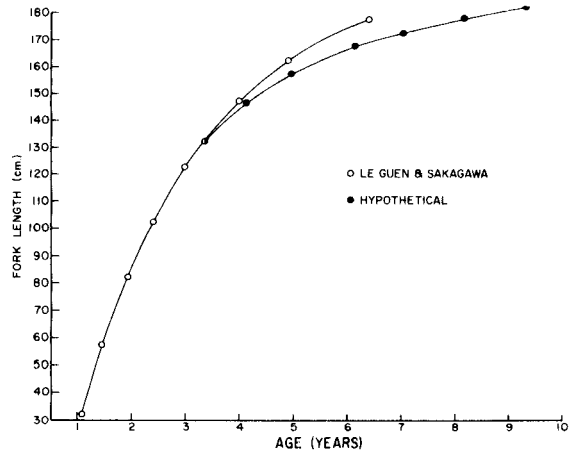

FIGURE 14.—Growth curves of Atlantic yellowfin tuna. Upper curve is from LeGuen and Sakagawa (1973). Lower curve is a modification of the upper curve (see text).

TABLE 6.—Estimates of average weight of catch (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	48.87	47.71	46.73	45.18	44.03	43.14	42.78	42.01	41.41	40.91
117.5	30.6	45.55	44.47	43.56	42.12	41.06	40.24	39.90	39.19	38.61	38.14
112.5	26.9	41.63	40.64	39.80	38.47	37.49	36.72	36.40	35.71	35.15	34.68
107.5	23.5	38.03	37.10	36.32	35.08	34.15	33.42	33.10	32.43	31.87	31.40
102.5	20.4	34.67	33.80	33.07	31.91	31.02	30.31	30.01	29.35	28.79	28.31
97.5	17.6	31.19	30.39	29.71	28.63	27.80	27.12	26.83	26.19	25.65	25.19
92.5	15.0	28.34	27.59	26.96	25.95	25.16	24.53	24.25	23.64	23.12	22.67
87.5	12.7	26.21	25.51	24.91	23.95	23.19	22.58	22.31	21.72	21.21	20.77
82.5	10.7	23.80	23.13	22.57	21.65	20.93	20.34	20.08	19.50	19.00	18.57
77.5	8.9	21.12	20.51	19.98	19.12	18.44	17.87	17.62	17.06	16.58	16.16
72.5	7.3	18.89	18.31	17.82	17.00	16.35	15.81	15.57	15.03	14.56	14.16
67.5	5.9	16.57	16.04	15.58	14.81	14.20	13.68	13.45	12.93	12.48	12.09
62.5	4.7	15.08	14.57	14.13	13.39	12.80	12.29	12.07	11.57	11.13	10.75
57.5	3.7	13.31	12.82	12.40	11.70	11.13	10.64	10.42	9.93	9.50	9.13
52.5	2.8	11.97	11.50	11.10	10.41	9.85	9.37	9.16	8.67	8.25	7.88
47.5	2.1	10.87	10.42	10.02	9.35	8.80	8.33	8.11	7.63	7.21	6.85
42.5	1.5	10.57	10.13	9.73	9.07	8.51	8.04	7.83	7.35	6.93	6.56
37.5	1.0	10.51	10.07	9.67	9.01	8.46	7.98	7.77	7.29	6.87	6.50
32.5	0.7	10.51	10.06	9.67	9.00	8.45	7.98	7.76	7.28	6.86	6.50

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	63.08	60.94	58.99	55.67	53.02	50.93	50.04	48.20	46.76	45.59
117.5	30.6	60.95	58.69	56.65	53.18	50.44	48.28	47.36	45.47	43.98	42.78
112.5	26.9	58.62	56.24	54.09	50.47	47.62	45.38	44.44	42.48	40.94	39.69
107.5	23.5	54.53	51.97	49.68	45.87	42.91	40.61	39.65	37.65	36.10	34.85
102.5	20.4	50.69	48.01	45.65	41.78	38.82	36.55	35.61	33.47	32.18	31.00
97.5	17.6	48.15	45.42	43.03	39.15	36.22	33.99	33.07	31.19	29.74	28.60
92.5	15.0	46.71	43.96	41.55	37.66	34.74	32.53	31.61	29.75	28.32	27.19
87.5	12.7	44.78	41.99	39.57	35.67	32.76	30.55	29.64	27.79	26.37	25.24
82.5	10.7	42.99	40.17	37.73	33.82	30.92	28.72	27.82	25.97	24.55	23.43
77.5	8.9	41.01	38.17	35.71	31.79	28.89	26.71	25.81	23.97	22.55	21.41
72.5	7.3	39.22	36.35	33.88	29.96	27.07	24.89	24.00	22.16	20.74	19.60
67.5	5.9	37.02	34.12	31.65	27.73	24.86	22.69	21.80	19.97	18.55	17.41
62.5	4.7	35.35	32.44	29.96	26.06	23.20	21.05	20.16	18.34	16.93	15.79
57.5	3.7	31.69	28.79	26.34	22.51	19.73	17.65	16.79	15.04	13.68	12.59
52.5	2.8	27.97	25.13	22.75	19.09	16.46	14.52	13.72	12.10	10.86	9.88
47.5	2.1	26.14	23.35	21.02	17.47	14.93	13.07	12.31	10.77	9.60	8.67
42.5	1.5	25.72	22.94	20.63	17.10	14.59	12.74	11.99	10.47	9.31	8.39
37.5	1.0	25.62	22.84	20.54	17.01	14.50	12.66	11.91	10.39	9.23	8.32
32.5	0.7	25.61	22.84	20.53	17.00	14.50	12.65	11.90	10.39	9.23	8.32

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	63.26	61.49	59.84	56.92	54.48	52.45	51.57	49.68	48.15	46.90
117.5	30.6	61.30	59.40	57.62	54.49	51.88	49.72	48.78	46.77	45.16	43.83
112.5	26.9	58.69	56.61	54.69	51.30	48.50	46.19	45.19	43.07	41.37	39.98
107.5	23.5	55.99	53.75	51.68	48.07	45.11	42.70	41.66	39.47	37.72	36.31
102.5	20.4	54.78	52.46	50.33	46.62	43.59	41.13	40.07	37.84	36.07	34.63
97.5	17.6	53.40	51.00	48.79	44.96	41.84	39.30	38.21	35.92	34.10	32.62
92.5	15.0	52.39	49.92	47.65	43.73	40.53	37.94	36.83	34.48	32.62	31.10
87.5	12.7	51.41	48.87	46.54	42.52	39.24	36.59	35.45	33.05	31.13	29.57
82.5	10.7	50.10	47.48	45.07	40.91	37.54	34.80	33.63	31.15	29.16	27.54
77.5	8.9	48.65	45.92	43.43	39.13	35.64	32.82	31.61	29.05	27.00	25.32
72.5	7.3	46.62	43.77	41.16	36.69	33.07	30.15	28.90	26.27	24.16	22.45
67.5	5.9	44.46	41.48	38.78	34.14	30.43	27.44	26.17	23.50	21.38	19.66
62.5	4.7	41.92	38.81	36.01	31.24	27.46	24.46	23.18	20.53	18.44	16.77
57.5	3.7	38.35	35.12	32.23	27.39	23.62	20.67	19.44	16.90	14.94	13.40
52.5	2.8	34.39	31.08	28.17	23.39	19.74	16.96	15.82	13.50	11.75	10.41
47.5	2.1	32.91	29.60	26.69	21.96	18.39	15.68	14.58	12.35	10.69	9.42
42.5	1.5	31.85	28.53	25.64	20.94	17.43	14.78	13.70	11.54	9.93	8.71
37.5	1.0	31.52	28.21	25.31	20.63	17.13	14.50	13.43	11.29	9.70	8.49
32.5	0.7	31.52	28.20	25.31	20.62	17.13	14.50	13.43	11.29	9.70	8.49

TABLE 6.—Estimates of average weight of catch (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

LONG LINERS											
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	59.30	57.92	56.63	54.33	52.38	50.73	50.00	48.41	47.10	46.00
117.5	30.6	57.53	56.05	54.68	52.23	50.16	48.41	47.63	45.96	44.57	43.41
112.5	26.9	55.76	54.18	52.71	50.11	47.91	46.05	45.23	43.45	41.97	40.74
107.5	23.5	54.18	52.51	50.96	48.20	45.87	43.90	43.03	41.14	39.58	38.26
102.5	20.4	52.88	51.13	49.50	46.61	44.16	42.09	41.18	39.19	37.53	36.13
97.5	17.6	52.31	50.51	48.85	45.89	43.38	41.25	40.31	38.26	36.55	35.11
92.5	15.0	51.85	50.02	48.32	45.30	42.74	40.56	39.60	37.49	35.72	34.23
87.5	12.7	51.33	49.46	47.72	44.62	41.98	39.74	38.74	36.55	34.71	33.14
82.5	10.7	50.84	48.93	47.15	43.98	41.27	38.95	37.92	35.65	33.73	32.09
77.5	8.9	50.61	48.68	46.88	43.66	40.91	38.56	37.50	35.19	33.22	31.54
72.5	7.3	50.39	48.44	46.61	43.35	40.56	38.16	37.09	34.72	32.70	30.96
67.5	5.9	50.30	48.34	46.51	43.23	40.41	38.00	36.91	34.52	32.47	30.70
62.5	4.7	50.28	48.31	46.48	43.19	40.37	37.94	36.86	34.45	32.40	30.62
57.5	3.7	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
52.5	2.8	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
47.5	2.1	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
42.5	1.5	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
37.5	1.0	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
32.5	0.7	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56

Figure 15. The values of F of large fish are relatively smaller than those estimated with the original growth curve.

Results of the yield-per-recruit calculations are shown in Table 7. The results indicate that if effort is held constant and size at recruitment is increased to the optimum, less than a 3% increase in yield per recruit would occur. If size at recruitment is constant and effort is doubled, yield per recruit would increase by about 28% which is considerably more than when the original growth curve is used. If size at recruitment is increased to 77.5 cm and effort doubled, a 44% increase in yield per recruit would occur.

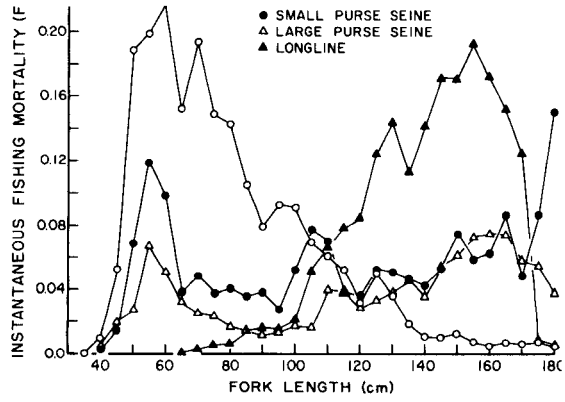

FIGURE 15.—Estimates of size-specific F when its initial value is 0.2 and using the modified growth curve.

TABLE 7.—Estimates of yield per recruit (kg) for the entire fishery when $M = 0.8$, initial $F = 0.2$, and hypothetical growth curve is used.

ENTIRE FISHERY											
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.80	1.48	2.06	2.99	3.70	4.24	4.47	4.95	5.32	5.61
117.5	30.6	0.84	1.55	2.15	3.12	3.85	4.41	4.65	5.13	5.50	5.79
112.5	26.9	0.88	1.62	2.25	3.25	4.00	4.58	4.82	5.30	5.67	5.97
107.5	23.5	0.92	1.70	2.35	3.39	4.15	4.74	4.98	5.46	5.83	6.11
102.5	20.4	0.96	1.76	2.43	3.49	4.27	4.85	5.09	5.57	5.93	6.21
97.5	17.6	0.98	1.80	2.49	3.56	4.35	4.93	5.17	5.64	5.99	6.25
92.5	15.0	1.00	1.84	2.53	3.62	4.40	4.98	5.21	5.68	6.01	6.26
87.5	12.7	1.02	1.87	2.57	3.66	4.44	5.01	5.24	5.69	6.01	6.25
82.5	10.7	1.04	1.89	2.60	3.69	4.47	5.03	5.25	5.69	5.99	6.21
77.5	8.9	1.05	1.92	2.63	3.72	4.48	5.03	5.24	5.65	5.93	6.12
72.5	7.3	1.07	1.94	2.66	3.74	4.48	5.01	5.21	5.59	5.84	6.01
67.5	5.9	1.08	1.96	2.68	3.74	4.47	4.96	5.15	5.49	5.70	5.83
62.5	4.7	1.09	1.98	2.69	3.74	4.44	4.91	5.08	5.39	5.57	5.66
57.5	3.7	1.11	1.99	2.69	3.71	4.37	4.80	4.95	5.20	5.32	5.37
52.5	2.8	1.11	1.99	2.69	3.67	4.28	4.66	4.79	4.98	5.05	5.05
47.5	2.1	1.12	1.99	2.68	3.63	4.21	4.55	4.66	4.81	4.84	4.81
42.5	1.5	1.12	1.99	2.67	3.62	4.18	4.51	4.61	4.75	4.77	4.73
37.5	1.0	1.12	1.99	2.67	3.61	4.18	4.50	4.60	4.73	4.75	4.71
32.5	0.7	1.12	1.99	2.67	3.61	4.17	4.50	4.60	4.73	4.75	4.70

Sensitivity of Results to Errors in Estimates of Natural Mortality

Size-specific values of F were estimated using values of M of 0.6 and 1.0 and an initial value of $F = 0.2$. The results are compared to size-specific F when $M = 0.8$ in Figure 16. Although the absolute values differ considerably, the same general trends appear in each curve. The ratio of F/M varies about threefold.

Results of yield-per-recruit calculations are shown in Tables 8 and 9 and Figures 17 and 18. There is a steeper horizontal gradient when $M = 1.0$ and a steeper vertical gradient when $M = 0.6$ than when $M = 0.8$. That is, yield per recruit is more sensitive to changes in effort

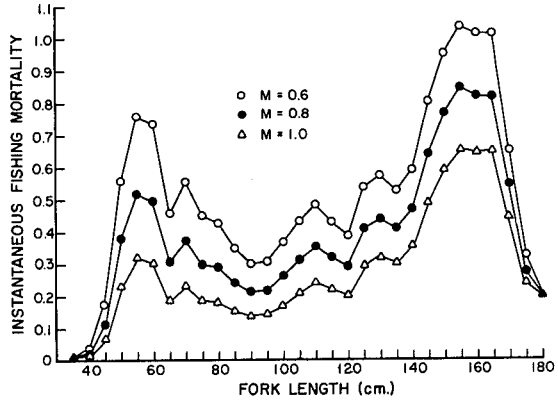

FIGURE 16.—Estimates of size-specific F when its initial value is 0.2 and using values for M of 0.6, 0.8, and 1.0.

TABLE 8.—Estimates of yield per recruit (kg) for the entire fishery when $M = 0.6$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

		ENTIRE FISHERY									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	3.52	5.82	7.34	9.07	9.93	10.39	10.55	10.81	10.98	11.10
117.5	30.6	3.61	5.94	7.47	9.18	10.00	10.43	10.58	10.81	10.95	11.04
112.5	26.9	3.70	6.06	7.58	9.26	10.04	10.44	10.56	10.76	10.86	10.92
107.5	23.5	3.79	6.16	7.68	9.30	10.03	10.38	10.48	10.63	10.70	10.72
102.5	20.4	3.85	6.24	7.74	9.31	9.98	10.28	10.36	10.47	10.49	10.48
97.5	17.6	3.90	6.28	7.77	9.28	9.91	10.16	10.22	10.28	10.27	10.22
92.5	15.0	3.93	6.31	7.77	9.24	9.82	10.03	10.07	10.09	10.04	9.97
87.5	12.7	3.95	6.33	7.77	9.18	9.70	9.87	9.90	9.87	9.79	9.68
82.5	10.7	3.97	6.33	7.74	9.09	9.55	9.66	9.66	9.58	9.45	9.31
77.5	8.9	3.99	6.33	7.70	8.95	9.33	9.38	9.35	9.20	9.01	8.82
72.5	7.3	4.00	6.31	7.63	8.79	9.08	9.06	8.99	8.78	8.54	8.30
67.5	5.9	4.01	6.27	7.53	8.57	8.75	8.64	8.54	8.25	7.94	7.65
62.5	4.7	4.01	6.23	7.44	8.37	8.47	8.29	8.16	7.80	7.45	7.13
57.5	3.7	4.00	6.15	7.28	8.05	8.01	7.73	7.55	7.11	6.70	6.33
52.5	2.8	3.98	6.06	7.10	7.70	7.54	7.16	6.95	6.43	5.97	5.56
47.5	2.1	3.96	5.99	6.96	7.45	7.20	6.75	6.52	5.95	5.46	5.04
42.5	1.5	3.95	5.96	6.92	7.37	7.09	6.62	6.38	5.80	5.30	4.87
37.5	1.0	3.95	5.96	6.90	7.35	7.06	6.59	6.35	5.77	5.26	4.83
32.5	0.7	3.95	5.96	6.90	7.34	7.06	6.59	6.34	5.76	5.26	4.83

TABLE 9.—Estimates of yield per recruit (kg) for the entire fishery when $M = 1.0$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

		ENTIRE FISHERY									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.66	1.18	1.62	2.26	2.72	3.06	3.19	3.47	3.67	3.84
117.5	30.6	0.69	1.24	1.68	2.36	2.83	3.18	3.32	3.60	3.81	3.98
112.5	26.9	0.72	1.29	1.76	2.45	2.94	3.30	3.45	3.74	3.96	4.13
107.5	23.5	0.75	1.35	1.83	2.55	3.06	3.42	3.57	3.87	4.09	4.27
102.5	20.4	0.77	1.39	1.89	2.63	3.15	3.52	3.67	3.97	4.20	4.37
97.5	17.6	0.79	1.43	1.93	2.69	3.21	3.59	3.74	4.04	4.27	4.44
92.5	15.0	0.81	1.45	1.97	2.73	3.26	3.64	3.79	4.09	4.31	4.48
87.5	12.7	0.82	1.47	1.99	2.76	3.29	3.67	3.82	4.12	4.34	4.50
82.5	10.7	0.83	1.49	2.02	2.79	3.32	3.70	3.85	4.14	4.35	4.51
77.5	8.9	0.85	1.51	2.05	2.82	3.35	3.72	3.86	4.14	4.34	4.49
72.5	7.3	0.86	1.53	2.07	2.84	3.36	3.72	3.86	4.13	4.32	4.45
67.5	5.9	0.87	1.55	2.09	2.86	3.37	3.72	3.85	4.10	4.27	4.38
62.5	4.7	0.88	1.56	2.10	2.86	3.36	3.70	3.82	4.06	4.21	4.31
57.5	3.7	0.89	1.57	2.11	2.86	3.34	3.65	3.76	3.97	4.09	4.16
52.5	2.8	0.90	1.58	2.11	2.84	3.30	3.58	3.68	3.85	3.94	3.99
47.5	2.1	0.90	1.58	2.11	2.82	3.26	3.52	3.61	3.76	3.83	3.85
42.5	1.5	0.90	1.58	2.10	2.81	3.24	3.50	3.59	3.73	3.79	3.80
37.5	1.0	0.90	1.58	2.10	2.81	3.24	3.50	3.58	3.72	3.78	3.79
32.5	0.7	0.90	1.58	2.10	2.81	3.24	3.50	3.58	3.72	3.78	3.79

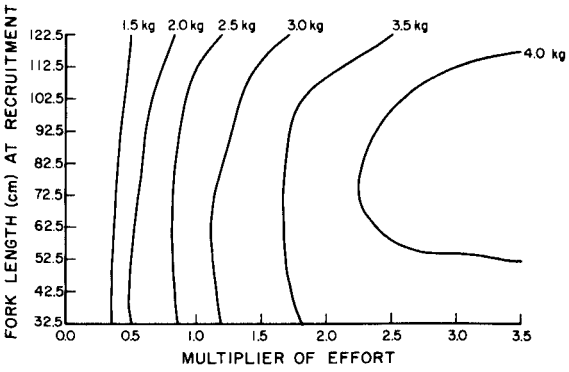

FIGURE 17.—Yield-per-recruit isopleths for the entire Atlantic yellowfin tuna fishery with $M = 1.0$.

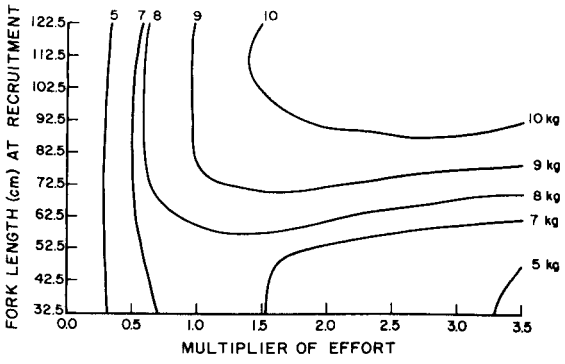

FIGURE 18.—Yield-per-recruit isopleths for the entire Atlantic yellowfin tuna fishery with $M = 0.6$.

when $M = 1.0$ and more sensitive to changes in size at recruitment when $M = 0.6$ than when $M = 0.8$. When $M = 1.0$ and effort is constant an increase in size at recruitment to 77.5 cm does not change yield per recruit. However, when $M = 0.6$, the same change in size at recruitment causes a 22% increase in yield per recruit. When $M = 1.0$ and size at recruitment is held constant, a doubling of effort causes a 29% increase in yield per recruit. When $M = 0.6$, the same change causes a 14% decrease in yield per recruit. When $M = 1.0$ and size at recruitment is increased to 77.5 cm, a doubling of effort causes a 39% increase in yield per recruit. When $M = 0.6$, the same changes cause a 27% increase in yield per recruit.

DISCUSSION

The use of results of our study must be based on three further assumptions: (1) the composition of the fleet will not change; (2) either the gear is currently dispersed so that all qualitative characteristics of the population are available to capture by each gear, or that the dispersal of gear as it now stands will not change; and (3) recruitment is constant.

Relation Between Composition of Fleet and Optimum Size at Recruitment

The preceding text has assumed that the composition of the fleet remains constant. The history of the fishery reveals that the composition has been a very dynamic process and there is no reason to believe that it will not continue to be. Since each fishing gear has a different curve of size-specific F, changes in the fleet composition will cause changes in size-specific F for the entire fleet. These changes will cause changes in the yield-per-recruit isopleths.

To illustrate the influence of changes in fleet composition on management strategy, the optimum size at recruitment was estimated for 441 combinations of baitboat and longline effort. For simplicity, effort of purse seiners is not included, i.e., we excluded two variables—small and large purse seiners. Multipliers of effort for each gear ranged from 0 to 2.0 with increments of 0.1.

The results (Table 10) show a considerable range in the estimates of optimum size at recruitment and that minimum size regulations must be adjusted to changes in the composition of the fleet to maintain maximum yield per recruit. As an example, with a 1.0 level of effort by both gears, the minimum size should be about 72.5 cm. If this were instituted as a minimum size regulation, the bait boat effort might decline to about 0.2 because of the extreme loss of catch. The minimum size, therefore, should be lowered to 67.5 cm. Now the longline effort might increase by about 80% due to the decrease in competition from bait boats—the minimum size should be increased to 77.5 cm. Finally, suppose an innovation occurs in bait fishing such that non-nominal effort again increases to about 0.7—the minimum size should be raised further to about 82.5 cm. These changes could occur slowly allowing for a smooth transition of the minimum size regulations. When economics are involved, however, the changes might be precipitous causing the confusion in the above example. If the possible changes in

TABLE 10.—Optimum size (cm) at recruitment for 441 combinations of multipliers of effort by bait boats and longliners.

Longline multiplier	Bait boat multiplier																				
	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0
0	32.5	32.5	32.5	32.5	32.5	32.5	37.5	37.5	42.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5
0.1	32.5	32.5	32.5	37.5	37.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5
0.2	32.5	37.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5
0.3	32.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5
0.4	32.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5
0.5	32.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5
0.6	32.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5
0.7	32.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5
0.8	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5
0.9	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5
1.0	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5
1.1	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5
1.2	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.3	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.4	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5
1.6	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5
1.7	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
1.8	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
1.9	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
2.0	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5

composition of both small and large purse seiners are included, the attempts to achieve some reason in the minimum size regulation based on maximum yield per recruit can become quite unwieldly.

Dispersion of Gear and Yield Per Recruit

The second assumption could be important. For example, in the eastern Pacific yellowfin tuna fishery effort has expanded farther offshore. Evidence suggests that larger fish were farther offshore and were not previously fully available to the fishery. A possible consequence of this phenomenon is a change in yield per recruit. Upon analysis of the data, the Inter-American Tropical Tuna Commission concluded, however, that the possible increase is minor (Joseph, pers. commun.). The surface gears have been fishing quite close to shore in the Atlantic. The possibility of offshore dispersal of the surface fleets and the effects of such a change on yield per recruit are unknown.

Interaction Between Minimum Size and Catch Quota Regulations

If recruitment is not constant, then the interaction between minimum size and catch quota regulations should be examined. Catch quotas are frequently based on assessments of the maximum sustainable average yield (MSAY), usually through a production model type analysis. The shape of the total yield curve, however, may be strongly dependent on the age at recruitment, t_r'. Therefore, the interaction between the two types of regulation should be examined before a singular action is taken. As an illustration, consider a population consisting of six age-groups with the growth curve and natural mortality coefficient ($M = 0.8$) similar to that of the Atlantic yellowfin tuna fishery, and assume also that recruitment is knife-edged at 19 mo. Figure 19 (lower curve) shows the total annual yield as a function of fishing mortality with an assumed arbitrary stock-recruitment function. Assume further that the fishery is operating at an $F = 1.0$. The yield per recruit at $F = 1.0$ and $t_r' = 19$ mo is 5.39, but the maximum yield per recruit is 6.11 at $t_r' = 27$ mo. If singular action were taken to increase t_r' to 27 mo, the upper total yield curve in Figure 19 would result. Not only did the yield per recruit increase, but so did the total yield at $F = 1.0$. In addition, the MSAY increased, but occurs at a much higher value for F. A phenomenon such as this may have occurred inadvertantly in the eastern tropical Pacific with the introduction of purse seiners which gave a better yield per recruit than the existing bait boats (Joseph, 1970).

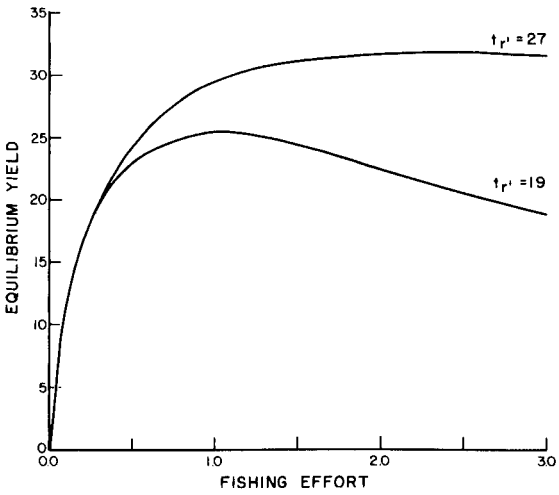

FIGURE 19.—Annual equilibrium yield as a function of fishing effort at two different ages at recruitment, t_r'.

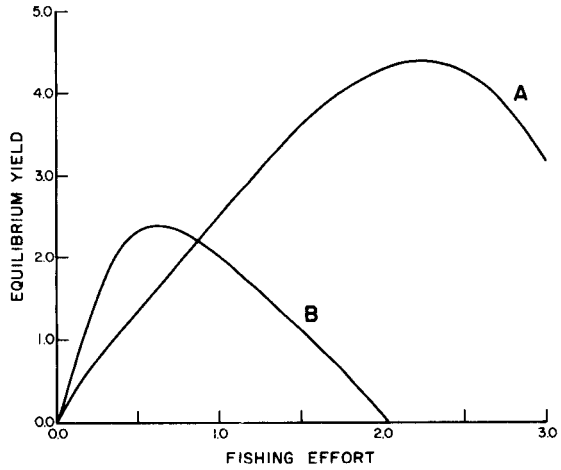

FIGURE 20.—Annual equilibrium yield as a function of fishing effort at two different ages at recruitment (see text).

The above result of singular action on the minimum size regulation resulted in a fortuitous increase in total yield and MSAY. This result may not always occur, however. Consider that if the fishery were operating with t_r' at 27 mo and $F = 0.2$, then the yield per recruit would be 2.77. The optimal yield per recruit is 3.02 at a t_r' of 19 mo. If singular action were taken to lower the t_r' to 19 mo, a slight loss of total yield would occur even with the improved yield per recruit. Even more disconcerting would be the loss in potential MSAY of 28%. The fishery would be suboptimized in a sense. Since the MSAY is usually estimated from a time series of catch and effort data, the actual potential which could have been realized had t_r' remained at 27 mo would likely be underestimated. It is likely that yield per recruit studies would continue as the fishery developed effort beyond $F = 0.2$, such that eventually the upper curve might be attained; this is because the optimal age at recruitment increases asymptotically as F increases. The low initial forecasts of MSAY, however, could hamper development of the fishery.

An even worse consequence of singular action on yield per recruit is illustrated in Figure 20. Assume the fishery is operating at about 0.6 unit of effort with an age at recruitment such to obtain curve A, but the yield per recruit is adjusted to maximal for the age at recruitment giving curve B. The actual MSAY of curve A might never be realized since the maximum equilibrium yield in curve B is also at 0.6 unit of fishing effort. This case represents true suboptimization.

CONCLUSIONS

Although there are some uncertainties in our knowledge of the parameters that enter into calculations of yield per recruit of yellowfin in the Atlantic, it is possible to come to some conclusions from our results.

The least amount of data and assumptions is involved in the simplified Beverton and Holt method. Results from this method (Table 1) show that, in all but a few extreme cases in a wide range of growth and mortality parameter values, an increase in the effective minimum size would result in an increase in yield per recruit. However, our most reasonable estimates of the parameters indicated that at the current level of fishing, an increase in the effective minimum size could only result in about an 8% increase in yield per recruit. We conclude that even if the quality of our data is poor an increase, probably minor, in yield per recruit of Atlantic yellowfin would occur if the effective minimum size is increased and if it is assumed that small yellowfin tuna were not dumped.

We next assumed that our most reasonable estimate of growth, constant Z, and effective minimum size are correct and constructed yield-per-recruit isopleths with the Ricker method for

several values of natural mortality. The results (Figures 1-3) indicated that yield per recruit would increase from 0 to 20% if effective minimum size is increased and effort remains constant. Again, our most reasonable estimate of the increase is only 8%. The results also indicate that little if any increase in yield per recruit would occur if fishing effort is doubled and effective minimum size is unchanged. However, if the effective minimum size is increased and effort is doubled, a modest (20 to 40%) increase in yield per recruit could occur. All these results again assume that there would be no dumping of small yellowfin tuna.

We finally assumed that the available data are accurate enough to also make reasonably accurate estimates of size-specific F. When using our most reasonable parameter estimates and holding effort constant, an increase in size at recruitment to 55 cm (3.2 kg) would obtain a 3.9% increase in yield per recruit and to 77.5 cm (8.9 kg) would cause less than a 10% increase in yield per recruit. Increasing the size at recruitment to 55 cm with $M = 0.6$ would cause a 7% increase in yield per recruit, but with $M = 1.0$ only a 1% increase would occur. Increasing the size at recruitment to 77.5 cm with $M = 0.6$ would increase yield per recruit by 22%, but with $M = 1.0$ no increase would occur. When size at recruitment is held constant and fishing effort is doubled, our best estimate of the change in yield per recruit is a 6% increase. Our estimates ranged from a 14% decrease to a 29% increase. It seems safe to agree with the report of the Abidjan meeting that if conditions remain constant, there is little to be gained on a yield-per-recruit basis from increases in fishing effort. With a doubling of fishing effort and an increase in size of recruitment to 55 cm, our most reasonable estimate is a 15% increase in yield per recruit, with a range of a 1% decrease to a 35% increase. When size at recruitment is increased to 77.5 cm and fishing effort is doubled, our most reasonable estimate of the change in yield per recruit is a 30% gain; however, the estimates range from 27 to 44%. Thus it appears that if it is possible to increase the size at recruitment, a doubling of effort would produce a modest increase in yield per recruit. These results, it must be noted, assume that small yellowfin tuna are not dumped.

It is interesting to note that the same general conclusions would be made using either the knife-edged recruitment or size-specific F approaches. The size-specific F approach, in addition, allows us to examine more precisely the effects of an absolute minimum size regulation and the effects on each gear. The general conclusions from both aspects of this study also agree fairly well with those of Joseph and Tomlinson (1972, see footnote 4). It is not surprising, however, that results from the size-specific F approach agree with theirs because they used similar methodology and data. Both estimates suggest that under present conditions the fishery is near the point of maximum yield per recruit.

Specifically addressing the recommendations outlined in the introduction section of this paper for considering a minimum size between 3.2 and 10 kg, we offer the following results based on our most reasonable parameter estimates:

1. Minimum size limit 55 cm (3.2 kg):
   a) Current levels of fishing mortality:
      i) No dumping results in a 4% increase in landed yield per recruit
      ii) 100% dumping results in a 3% decrease in landed yield per recruit
   b) Doubling fishing mortality:
      i) No dumping results in a 15% increase in landed yield per recruit
      ii) 100% dumping results in a 1% increase in landed yield per recruit

2. Minimum size limit 77.5 cm (8.9 kg):
   a) Current levels of fishing mortality:
      i) No dumping results in a 9% increase in landed yield per recruit
      ii) 100% dumping results in a 13% decrease in landed yield per recruit
   b. Doubling fishing mortality:
      i) No dumping results in a 31% increase in landed yield per recruit
      ii) 100% dumping results in a 16% decrease in landed yield per recruit.

The 55-cm (3.2 kg) minimum size limit would likely be of more benefit to the tuna fishery than the larger minimum size limit of 77.5 cm (8.9 kg) since less dumping would occur. Therefore, there would likely be, on the average, an increase in landed yield per recruit at the current or greater levels of fishing mortality; whereas, if a larger size limit were adopted, there would likely be, on the average, a decrease in landed yield per recruit at current levels of fishing

mortality and less of an increase (perhaps even a decrease) in landed yield per recruit than with the 55-cm (3.2 kg) minimum size and an increase in fishing mortality.

The results of this paper were obtained using reasonable assumptions and all available data on Atlantic yellowfin tuna. As we increased the number of assumptions we increased the number of conclusions. We think that it is unlikely that use of tecnhiques not used in this paper would result in conclusions that are significantly different from ours. That is, an increase in effective minimum size would result in a minor increase in yield per recruit, an increase in effort without increasing effective minimum size would not appreciably increase yield per recruit, and an increase in effective minimum size and effort would result in modest gains in yield per recruit. We wish to emphasize that these conclusions are based on a number of assumptions. We consider the assumptions reasonable, but because they are assumptions any management decisions, including the decision of taking no action, should be followed with careful evaluation of the results.

ACKNOWLEDGMENTS

We are indebted to James Joseph and Patrick Tomlinson of the Inter-American Tropical Tuna Commission for their useful comments on this paper. This study would not have been possible without the many valuable contributions of data and ideas by scientists of the nations that participate in the International Commission for the Conservation of Atlantic Tunas.

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SYSTEMATICS AND DISTRIBUTION OF THE FOUR SIBLING SPECIES COMPRISING THE GENUS *PONTELLINA* DANA (COPEPODA, CALANOIDA)

A. FLEMINGER AND K. HULSEMANN[1]

ABSTRACT

A global-scale study on systematics and distribution of the epipelagic copepod genus *Pontellina* (Family Pontellidae) was carried out on materials sorted from about 2,000 zooplankton samples collected at stations scattered throughout the circumglobal warm-water belt. Four distinctive species were found and described, three being new to science.

Each species was examined for evidence of conspicuous polytypy and geographical variation. Morphology and geographical distribution were utilized comparatively to perceive relationships that would shed light on the nature of selection pressures operating on external morphology. Morphology and distribution were also considered to determine phylogenetic relationships within the genus.

The geographic distribution of the four species was considered relative to major near-surface hydrographic features characterizing tropical and subtropical latitudes and especially the occurrence of eutrophic and oligotrophic areas in each ocean.

Sets of similarly collected, quantitative samples were used to determine the relative abundance of each species, and co-occurrences among the species were tested by recurrent group analysis. The trophic role of each species was considered and conclusions tested by a limited series of observations on stomach contents.

Geographical perspective, too often absent from studies on marine plankton, is a powerful tool for dealing with sibling species. Evidence of reproductively isolated populations that are morphologically similar in planktonic calanoids and other zooplankton as well has been presented in a number of studies combining geographical distribution and morphology (e.g., Schmaus, 1917; Johnson, 1935; Bowman, 1955, 1967; Brodsky, 1959; Foxton, 1961; Jones, 1966; Fontaine, 1967; Fleminger, 1967b; Frost and Fleminger, 1968; Mullin, 1969; Jaschnov, 1970). Our resolution of the sibling species comprising the genus *Pontellina* Dana is offered as an additional example.

In contrast to the 22 nominal species by our count comprising *Pontellopsis* Brady, the pontellid genus most similar in morphology, *Pontellina* has been universally regarded as monotypic since Giesbrecht's (1892) monumental review of planktonic marine copepods. Mori (1937) presented evidence of polytypy in *Pontellina* with his description of a unique male distinguished by an unusual chela. Apparently influenced by Sewell's views on copepod ontogeny (1929, 1932), Mori ascribed the specimen taken off Japan to *plumata*, suggesting that it represented the fully mature state and that previous descriptions of the *plumata* male were based on incompletely mature specimens. Our study was prompted by the appearance of other seemingly minor morphological features distinguishing adult individuals of both sexes that correlated with indications of distinctive geographical distributions among the observed forms.

In this paper we redefine the genus and describe its four species. The distribution of each species is considered in the context of our geographical records. Distribution is also discussed with respect to morphological similarities among the species and relationships to general oceanic circulation. Detailed considerations and views regarding environmental conditions that shape these distributions and the circumstances yielding the contemporary *Pontellina* speciation pattern will be presented separately elsewhere.

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MATERIALS AND METHODS

Materials

Plankton samples examined for the genus *Pontellina* in the course of this study were obtained from three major sources: the zooplankton collections of Scripps Institution of Oceanography, R. Scheltema's collection of Atlantic zooplankton maintained at the Woods Hole Oceanographic Institution, and quantitative sortings of *Pontellina* from the International Indian Ocean Expedition plankton collections, processed and furnished by the Indian Ocean Biological Centre, Cochin, India. Additional collections or specimens were obtained with the kind cooperation of the National Marine Fisheries Service; the U.S. Naval Oceanographic Office; T. K. S. Björnberg, University of São Paulo, Brazil; A. DeDecker, Division of Sea Fisheries, Cape Town, Republic of South Africa; B. Kimor, Israel Oceanographic and Limnological Research Ltd., Haifa, Israel; J. E. H. Legaré, Instituto Oceanográfico, Cumaná, Venezuela; D. J. Tranter, CSIRO, Cronulla, Australia.

Geographical distribution of the samples is shown in Figure 1a, and the localities yielding *Pontellina* are listed by species in Table 1. These collections broadly outline most major sectors of the Pacific, Indian, and Atlantic Oceans, the South Atlantic being the notable omission. Most of the samples were taken with open conical plankton nets ½ to 1 m in diameter at the mouth. Nets were towed obliquely, vertically, or horizontally between the surface and 200 m of depth. Stations were occupied irrespective of time of day or cloud cover.

Sample Analysis

Plankton samples were examined in rectangular plastic trays (5 × 7.5 × 1 cm) at 16 × magnification with the aid of a stereomicroscope. The entire sample was scanned if the settling volume did not exceed 20 cc. Otherwise volumetric subsamples were drawn, generally with the aid of a 10-cc piston pipette, after standardizing the total volume and stirring vigorously. Usually more than 2% of the total sample was examined, the actual percentage varying inversely with the size of the original sample.

Estimates of abundance and frequency of occurrence were obtained from particular sets of quantitative samples (Figure 1b) selected for homogeneity of sampling. In the case of Pacific zooplankton samples collecting procedures followed standard CalCOFI (California Cooperative Oceanic Fisheries Investigations) sampling practices (cf. Smith, 1971). The Indian Ocean samples (Figure 1b) are a composite of quantitative Indian Ocean Standard Net tows (Currie, 1963) obtained by various participants in the International Indian Ocean Expedition. Preliminary quantitative processing of these samples was carried out by the Indian Ocean Biological Centre, Cochin, India (Tranter, 1969). The Centre provided us with specimens of *Pontellina* sorted from known fractions of the original samples. Standard quantitative sampling from the Atlantic Ocean was unavailable to us.

Specimen Analysis

For routine examinations specimens were mounted loosely in a drop of glycerol. To enhance examination of fine denticles and spines, soft tissue was removed by warming specimens in a 10% aqueous solution of KOH at about 90°C for 1 to 2 h. After a brief rinse in distilled water the cuticle was transferred to 35% ethanol, then to 70% ethanol for 1 min and then stained in a solution of 1% Chlorazol Black E dissolved in 70% ethanol. Intensive staining usually requires not more than ½ min and should be followed immediately by a 1-min rinse in distilled water.

Examinations and dissections were carried out under stereomicroscopes at 12× to 100× magnification and under compound microscopes at various magnifications up to 600×. All drawings were made with the aid of a compound microscope equipped with a drawing attachment.

Several females and males of each species were studied under a scanning electron microscope after preparation by the critical point drying method (Cohen, Marlow, and Garner, 1968).

Measurements

For each species intact specimens with a reasonably straight urosome were chosen at random from localities scattered over the entire

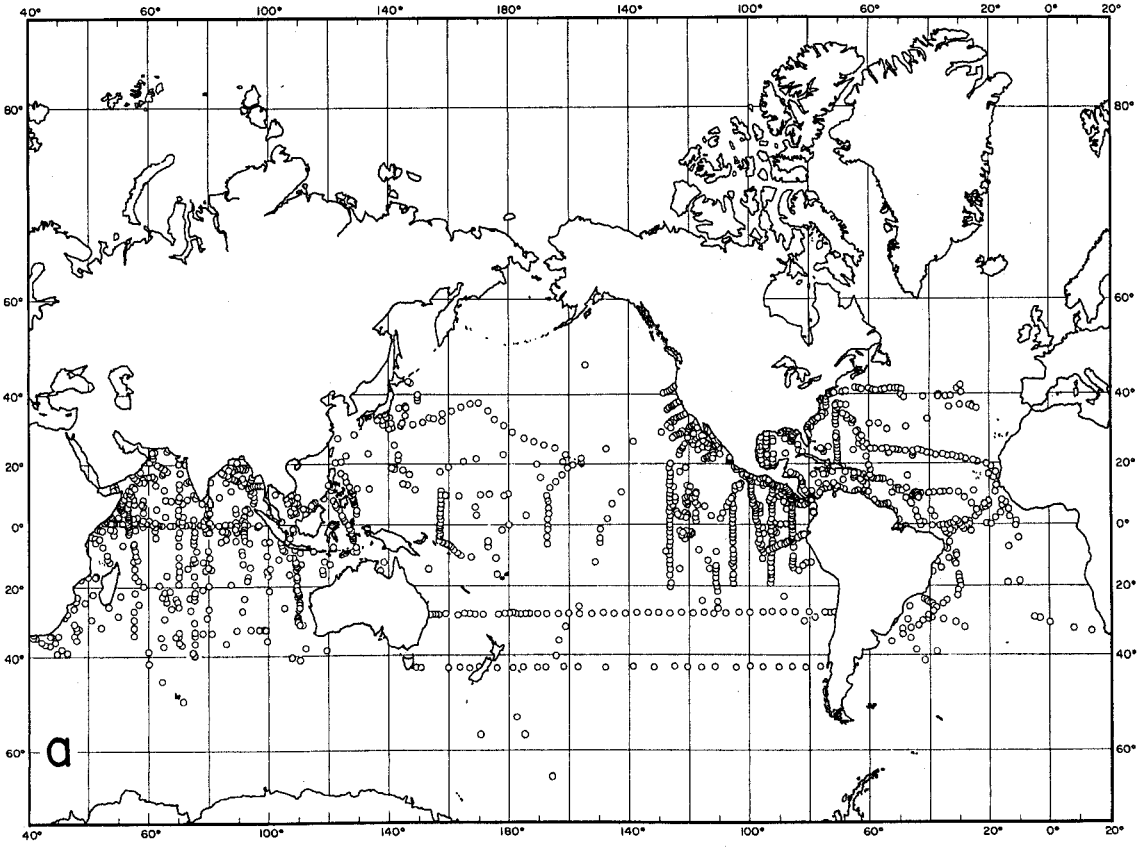

FIGURE 1a.—Geographical distribution of sampling stations. Each open circle represents one or more samples. Overlapping stations and replicate sampling are omitted for the purpose of clarity. Areas intensively surveyed are shown symbolically as evenly spaced grid.

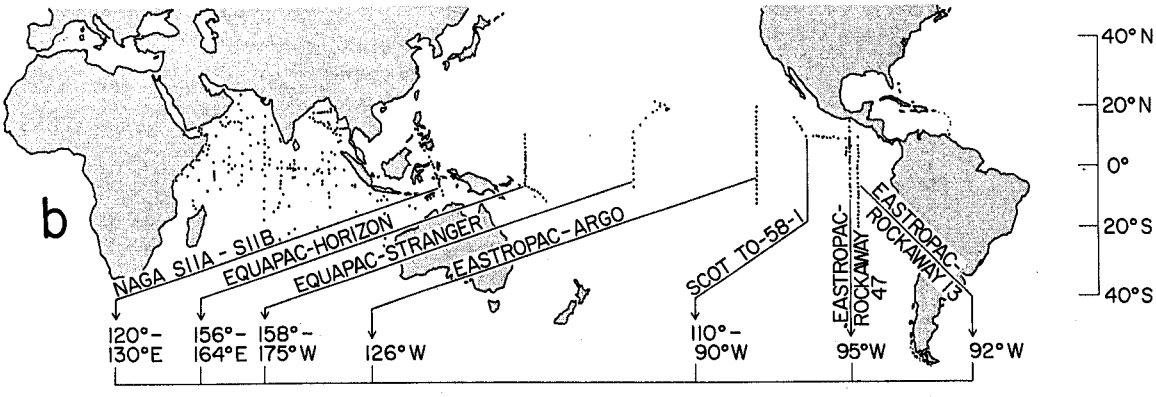

FIGURE 1b.—Distribution and identification of sets of quantitative zooplankton samples used to estimate the frequency of *Pontellina* in the Pacific Ocean. Sets were selected for similarity of sampling; i.e., each set obtained by the same procedures and stations occupied in a closely ordered sequence during the same cruise. Dots indicate the sampling localities. Indian Ocean localities represent Indian Ocean Standard Net samples collected during the International Indian Ocean Expedition that were examined quantitatively for *Pontellina* in the course of this study. See Table 14 for summary of sampling data and Materials and Methods for analytical details.

TABLE 1.—Localities yielding *Pontellina* listed by species.

Location and station		Source of collecting data[1]
PONTELLINA PLATYCHELA		
Atlantic Ocean:		
RV *Alaska* 4:	29, 46.	H
Amazon Exp.:	17, 19.	B
RV *Atlantis II*-20:	2, 6, 9, 10, 12, 14, 15, 16, 24, 25, 26, 27, 28, 29, 31, 34, 35, 38, 39, 42, 49, 50, 56, 60.	F
-31:	25, 38, 40, 41, 43, 47, 48, 49, 50, 54, 55, 56, 57.	
-32:	60, 61, 84, 85, 86, 88, 89, 90, 94A, 98, 108, 110, 112.	
Cato 6 Exp.:	34 (26°11'S 38°46'W), 46 (34°37'S 47°58'W).	
RV *Chain* 35:	19, 29, 33, 39, 43.	F
RV *Chain* 60:	13, 16.	
La Creuse Exp.:	4, 5, 7, 10.	B
Lusiad VII Exp.:	69 H-4, 73 H-5, 79 (00°56'N 11°29'W), 80 H-12, 81 H-13.	A
RV *Oregon:*	1289 (17°10'N 74°20'W), 1291 (17°50'N 72°00'W), 1292 (18°08'N 74°35'W), 1293 (19°55'N 74°10'W), 1294 (19°45'N 74°45'W).	
RV *Thomas Washington*:	8.	B
10°29'N 64°12'W (Cumaná, Venezuela).		
PONTELLINA PLUMATA		
Atlantic Ocean:		
RV *Alaska* 1:	29.	H
2:	46, 56.	
4:	10, 29, 40, 42, 46.	
5:	42.	
Amazon Exp:	19, 20.	B
RV *Atlantis II*-13:	9, 35, 44, 48.	F
-20:	2, 22.	
-31:	2, 5, 6, 7, 8, 9, 11, 13, 15, 17, 18, 21, 23, 24, 25, 26, 28, 29, 38, 44, 57.	
-32:	61, 62, 63, 64, 66, 67, 68, 72, 73, 74, 87, 118D, 119.	
Björnberg:	M 242 (11°24'S 33°19'W).	
Cato 6 Exp.:	33 (25°16'S 49°01'W), 34 (36°11'S 38°46'W), 36 (30°06'S 39°21'W), 39 (30°26'S 35°20'W), 40 (30°56'S 31°21'W), 41 (32°28'S 28°17'W), 48 (30°10'S 39°23'W), 49 (25°50'S 39°24'W), 50 (24°33'S 41°02'W).	
RV *Chain* 49:	3, 5, 8, 9, 10, 11, 14, 15, 16, 17, 19, 20, 21, 22, 23, 26, 27.	F
60:	17.	
Cyprus:	10-20 (off coast of Israel).	
RV *Delaware*:	7, 19, 20, 25.	
La Creuse Exp.:	3, 4, 5, 7, 10.	B
Lusiad VII Exp.:	21 (30°23'S 02°47'W), 24 (30°09'S 04°42'W), 52 (19°13'S 13°44'W).	
N-3 Cruise:	4 (30°55'N 79°21'W).	
RV *Oregon:*	1291 (17°50'N 72°00'W), 1292 (18°08'N 74°35'W), 1294 (19°45'N 74°45'W).	
RV *Theodore N. Gill* 2:	41.	G
5:	3, 4.	
7:	4, 5.	
8:	5, 9.	
Pacific Ocean:		
Aries I Exp.:	30 (09°20'S 127°05'W).	
Bonacca Exp.:	22.	A
CalCOFI Cruise		
5804:	80.110, 60.110, 100.80.	E
5810:	100.70, 120.90.	
5901:	100.70.	
Capricorn Exp.:	1, 2, 3, 28, 29, 30, 31, 32, 33, 35.	A
Circe I Exp.:	3, 4.	B
Circe II Exp.:	9, 11, 12, 13, 14.	
RV *David Starr Jordan* 57:	025 (10°30'N 119°43.5'W), 076 (03°20'N 119°42'W), 116 (7°30'N 119°43.5'W), 123 (07°00'N 120°40'W), 130 (09°31'N 120°39'W), 132 (09°45'N 120°12'W).	
60:	071 (02°00'N 117°17'W), 122 (04°00'N 116°41'W), 134 (07°05'N 116°58'W).	
EASTROPAC Exp.:		
RV *Argo* 11:	197, 215, 234, 242, 250, 266, 282, 287, 291, 299, 303, 308, 320, 328.	D
RV *David Starr Jordan* 12:	053, 059, 063.	D
RV *Rockaway* 13:	056.	D
EQUAPAC Exp.:		
RV *Horizon*:	19, 20, 21, 22, 23, 24, 25, 26, 27, 29, 30, 31, 32, 34, 35, 36, 37, 38, 39, 40, 41.	A
RV *Stranger:*	3, 5, 11, 15, 17, 19, 21, 23.	A
Monsoon Exp.:	1, 2, 3, 4, 5, 7, 35, 37, 38, 39, 40.	A
Muddauber Exp.:	TDS-86.	B
Naga Exp. S11A:	160, 164, 169, 169A.	B
S11B:	5, 10, 16, 17, 20, 24, 27, 29, 31, 36, 38, 41, 50, 58, 62, 66, 78, 86.	
NAVOCEANO RV *Hunt*		
1968:	12, 14.	B
1969 (Apr.):	8, 31-6.	
1969 (May):	9.	
1969 (Oct.):	3.	
1969 (A-14):	6, 16.	
NAVOCEANO RV *Silas Bent:*	1-10, 1-11, 1-12, 1-16, 1-20.	B
Piquero IV Exp.:	12, 16, 17.	B
V Exp.:	40D, 43D, 44, 45D, 46, 47N, 47D, 48, 49, 50D.	
Scan IV Exp.:	1, 2, 35D, 6.	B
V Exp.:	5.	
Scorpio II Exp.:	92, 96, 98, 112, 114, 118, 120, 122, 138, 140, 144, 146, 148, 152, 154, 160, 164, 166, 168, 170, 172, 174, 176, 180, 182.	B
Shellback Exp.:	47, 51, 103.	A
TO-58-1 Cruise (Scot):	27, 29, 37, 56B.	B
TO-60-2 Cruise (Step 1):	62.	B
RV *Townsend Cromwell* 51:	064 (03°30'S 120°45'W), 085 (02°29'N 120°49'W).	
TRANSPAC Exp.:	85A, 87A, 87B, 89A, 92A, 92B, 94A, 96A, 98A, 98B, 100A, 102A, 106A, 108A, 110A, 112A, 118A, 118B, 122A, 126A, 126B, 132A, 134A, 142A, 143A.	A
Troll Exp.:	24, 24A, 25, 25A, 27, 27A, 28, 28A, 29, 30A, 31, 31A, 32, 32A, 33, 35.	A
32°15'N 117°16'W (15-VIII-1962).		
Indian Ocean:		
Circe II Exp.:	Camera 3.	B
III Exp.:	22, 25, 27, 28, 29, 38.	
RV *Diamantina:*	3/93/63 (27°30'S 110°00'E).	
Dodo VI Exp.:	13, 65, 70, 74, 81.	A
RV *Gascoyne:*	G1/5/63 (27°30'S 110°00'E), G1/32/63 (28°55'S 110°00'E).	
International Indian Ocean Exp.		
RV *Anton Bruun*		
A:	6, 8, 9A, 11.	
1:	30, 33, 51, 53, 57, 58, 60, 67, 70, 78.	
2:	106, 108, 110, 111, 112, 116, 117, 118, 120, 121, 127, 134, 135, 137, 141, 142, 143.	
3:	149.	

TABLE 1.—*Continued*

Location and station		Source of collecting data[1]
4A:	189.	
5:	283, 284, 295, 302, 312, 315, 318, 320, 322, 324, 326A, 327B.	
6:	328, 333.	
7:	370, 371.	
8:	404, 413, 415.	
RV *Argo* (Lusiad Exp.):	3, 8, 9, 10, 12, 15, 17, 18, 20, 34, 40, 41, 44, 45, 46, 49, 55, 61, 65, 71, 81, 86, 96.	C
RV *Diamantina*		
2 (1962):	61, 100.	C
1 (1963):	4, 47.	
3 (1963):	113.	
2 (1964):	100A.	
5 (1964):	212.	
1 (1965):	60.	
RV *Discovery* 1:	5031, 5038.	C
RV *Discovery* 3:	5267A, 5269A, 5275, 5371A, 5387, 5400B, 5412A, 5437A, 5548.	
RV *Kagoshima Maru*		
3:	7, 15, 16, 24, 30.	C
RV *Kistna* 13:	296, 301.	C
RV *Koyo Maru*		
14:	19.	C
16:	20.	
RV *Meteor*:	90, 93B, 95B, 114, 116A, 116B, 126A, 130A, 137, 138, 144, 151, 157, 168, 173, 181.	C
RV *Oshoro Maru*		
1:	3, 17, 44, 45, 50.	C
7:	7, 8.	
11:	3, 10, 19, 23.	
RV *Umitaka Maru*		
23:	1-7.	C
24:	6303.	
RV *Varuna* 30:	1775.	C
RV *Vitiaz* 35:	5198A, 5198B, 5200, 5205, 5207, 5208, 5217, 5221, 5224, 5278.	C
36:	5336.	
Lusiad I Exp.:	2, 4.	A
II Exp.:	5, 8, 9, 10, 11, 12, 13, 15, 19, 20, 29, 39, 45, 51, 61, 62, 66, 76, 88, 96.	
V Exp.:	40, 42, 43, 45, 46, 47, 50, 59, 60, 64, 68, 73, 76, 78, 84, 92, 96, 100, 104.	
VI Exp.:	1, 8.	
Monsoon Exp.:	7, 10, 11, 12, 18, 19.	A
PONTELLINA MORII		
Pacific Ocean:		
Aries I Exp.:	30 (09°20'S 127°05'W).	
CalCOFI Cruise		
5810:	153.70.	E
Capricorn Exp.:	2, 4, 5, 35.	A
Circe II Exp.:	9, 11, 12, 14.	B
RV *David Starr Jordan*		
57:	116 (07°30'N 119°43.3'W), 123 (07°00'N 120°40'W).	
60:	122 (04°00'N 116°41'W), 134 (07°05'N 116°58'W).	
EASTROPAC Exp.		
RV *Argo* II:	197, 211, 234, 320, 328.	D
RV *Rockaway* 13:	071, 095, 099, 103.	
EQUAPAC Exp.:		
RV *Horizon*:	20, 21, 25, 30, 31, 32, 35.	D
RV *Stranger*:	11, 17, 19.	
RV *Islander VI* (CSIRO):	2/50/70 (15°47'S 137°28'E), 1/9/71 (12°24'S 138°11'E).	
La Pared Exp.:	17F.	B
Monsoon Exp.:	1, 3, 6.	A
Naga Exp. S11A:	83, 127A, 164, 169, 169A.	B
S11B:	5, 10, 16, 17, 20, 24, 27, 31, 36, 41, 46, 66, 78, 86.	
NAVOCEANO RV *Hunt*		
1968 :	14.	B
1969 (May):	9.	
1969 (Oct.):	2, 3.	
1969 (A-14):	7, 9.	
NAVOCEANO RV *Silas Bent*:	1-11, 1-12, 1-16, 1-17, 1-18, 1-20.	B
Piquero V Exp.:	40D, 45D, 48.	B
Scan IV Exp.:	1, 2, 3, 35D, HF 18, DSDP 17, 48D.	B
V Exp.:	4, 5.	
Scorpio II Exp.:	156.	B
Shellback Exp.:	100, 105.	A
TO-58-1 Cruise (Scot):	14.	B
TRANSPAC Exp.:	87B, 92A, 96A, 98B.	A
Troll Exp.:	24A, 25, 25A, 26, 27A, 28, 30, 30A, 31A, 32, 32A.	A
Indian Ocean:		
Circe III Exp.:	22, 23, 25, 26, 27, 29.	B
Dodo VI Exp.:	12, 70, 81, Mombasa Harbor.	A
International Indian Ocean Exp.		
RV *Anton Bruun*		
A:	6, 7, 10A, 11.	C
1:	25, 28, 29, 30, 32, 33, 34, 35, 36, 43, 51, 52, 53, 55, 56, 57, 58, 68, 69, 70, 71, 72, 73, 75, 76, 79.	
2:	106, 108, 109, 110, 111, 112, 113, 114, 120, 121, 123, 142.	
4A:	189, 198.	
5:	283, 284, 323, 287A, 323A, 327B, 327C.	
6:	328, 333, 336	
7:	358, 367, 371.	
8:	413, 414.	
RV *Argo* (Lusiad Exp.):	3, 12, 41, 46, 49, 55, 65, 71, 81, 85.	C
RV *Diamantina*		
2 (1962):	61.	
1 (1963):	47.	C
RV *Discovery*		
1:	5031, 5038.	C
3:	5267, 5269A, 5385, 5412A.	
RV *Kistna*:	296, 298, 301, 304, 514, 515.	C
RV *Meteor*:	90, 91, 93A, 93B, 95B, 96, 106, 114, 116A, 130A, 137, 138, 145, 151, 154, 157, 161B, 168, 186, 198.	C
RV *Natal* 6:	163, 174.	C
RV *Oshoro Maru* 11:	3, 13, 19.	C
RV *Pioneer* 442:	1, 35.	C
RV *Umitaka Maru* 23:	1-7.	C
RV *Varuna* 30:	1775.	C
104:	2007, 2009.	
106:	2041.	
RV *Vitiaz* 35:	5224.	C
Lusiad I Exp.:	2.	A
II Exp.:	1, 10, 11, 13, 14, 16, 27, 55, 62, 66, 90.	
V Exp.:	43, 45, 58, 60, 66, 68, 76, 78.	
VI Exp.:	1, 8.	
Monsoon Exp.:	7, 11, 14.	A
PONTELLINA SOBRINA		
Pacific Ocean:		
Bonacca Exp.:	27, 31, 32, 33, 34, 35, 36, 37, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58.	A
CalCOFI Cruise		
5801:	153.50.	E
5804:	Gulf of Panama.	
5807:	Gulf of Panama.	
5901:	157.10.	
6108:	BPT 14.	
Capricorn Exp.:	2, 4, 6, 35.	A

TABLE 1.—*Continued*

Location and station		Source of collecting data[1]
Circe II Exp.:	9, 11, 12, 14.	B
RV *David Starr Jordan*		
57:	002 (13°42'N 120°13'W), 012 (13°16'N 119°23'W), 025 (10°30'N 119°43.5'W), 064 (04°00'N 120°43'W), 076 (03°20'N 119°42'W), 108 (06°32'N 119°50'W), 132 (09°45'N 120°12'W).	
60:	056 (03°22'S 119°30'W), 067 (01°36'N 117°22'W), 071 (02°00'N 117°17'W), 122 (04°00'N 116°41'W), 132 (06°34"N 116°22.3'W), 134 (07°05'N 116°58'W), 148 (09°27.7'N 117°49'W), 156 (10°36'N 117°17'W).	
65:	170 (00°28'N 96°58'W).	
Dragon Exp.:	N-1.	B
EASTROPAC Exp.:		
RV *Argo* 11:	234, 291, 299.	D
RV *David Starr Jordan* 12:	033, 037, 041, 059, 063, 077, 100.	
RV *Rockaway* 13:	048, 056, 060, 064, 071, 075, 083.	
El Golfo II Exp.:	XVIII B1-D1, B2-D1, A6-D1, B1-N1.	B
Harpoon Exp.:	13 (16°00'N 95°12'W).	
La Creuse Exp.:	15, 16, 17, 18, 21, OT-1, OT-6, OT-12, OT-14.	B
Muddauber Exp.:	125-4, 126-1, TDS-86.	B
Piquero V Exp.:	40D, 43D, 44.	B
Shellback Exp.:	47, 51, 63, 67, 185.	A
RV *Townsend Cromwell*		
51:	051 (03°15'S 118°23'W), 061 (02°30'S 119°47'W), 064 (03°30'S 120°45'W), 076 (02°28'S 121°42'W), 079 (02°42'N 121°49'W).	
TO-58-1 Cruise (Scot):	16, 17, 27, 29, 31, 32, 33, 35, 36, 37, 38, 42, 45, 46, 48, 56.	B
TO-58-2 Cruise:	9, 16.	B

[1] A Snyder and Fleminger, 1965
B Snyder and Fleminger, 1972
C Anonymous, 1969
D Love, 1972
E Fleminger, 1967a
F Scheltema, 1971 (only chart)
G Anderson, Gehringer, and Cohen, 1956; Anderson and Gehringer, 1958, 1959a, 1959b
H Collier, Drummond and Austin, 1958

area of its geographical distribution. Total length (TL), prosome, i.e., cephalosome and thorax combined (P), and urosome (U) were measured with an ocular micrometer at 50× magnification under a stereoscopic microscope; smaller structures were measured under a compound microscope at 100 × to 400× magnification. The morphological terms and abbreviations in general follow those of Fleminger (1967b).

Measurements, drawings, and descriptions refer to the right side or to appendages from the right side unless stated otherwise. TL and the length of U were measured (Figure 2a) to the distal end of the right furcal ramus, without allowance for any telescoping of segments. The length and width of the furcal rami were measured in dorsal view. In the adult female, the right ramus is fused to the anal segment; the length was obtained from the distance between the medial notch indicating the place of fusion with the anal segment and the insertion of the second innermost furcal seta (Figure 2d). The length of the left furcal ramus was also measured from the medial junction with the anal segment to the insertion of the second innermost furcal seta from the median. In both males and immature females the lengths of the right and left furcal rami were measured from the lateral margin at the proximal end to the insertion of the second innermost seta at the distal end (Figure 2c). For all stages the right furcal ramus was measured across its maximum width (Figure 2c).

The segments of the fifth legs (P5) of the female were measured from the anterior side (Figure 2f). The length of the exopod (Re) was taken as extending from the junction with the second basal segment (B2) to the base of the longest distal seta; the endopod (Ri) was measured from the junction with B2 to the tip of the medial spine. The length of the point on the fifth thoracic segment (ThV) is taken in lateral view as the distance between its tip and its base where the point is delineated by a distinct step or turn to the posterior (Figure 2g). The length of the spermatophore sac was measured as the distance from the distal end to the outer margin of the proximal convolution taking care to position the spermatophore to avoid diminution by an oblique angle of view (Figure 2b). Measurements of segments 13-17 and the succeeding three free segments of the male right antennule (A1) were taken from intact specimens positioned in lateral view (Figure 2e). P5 of the male was measured from the posterior side: the length of the second free segment of the left leg extends from the junction with B2 to the distal margin near the seta (Figure 2h); the length and width of the proximal segment of the chela are, respectively, the shortest distance

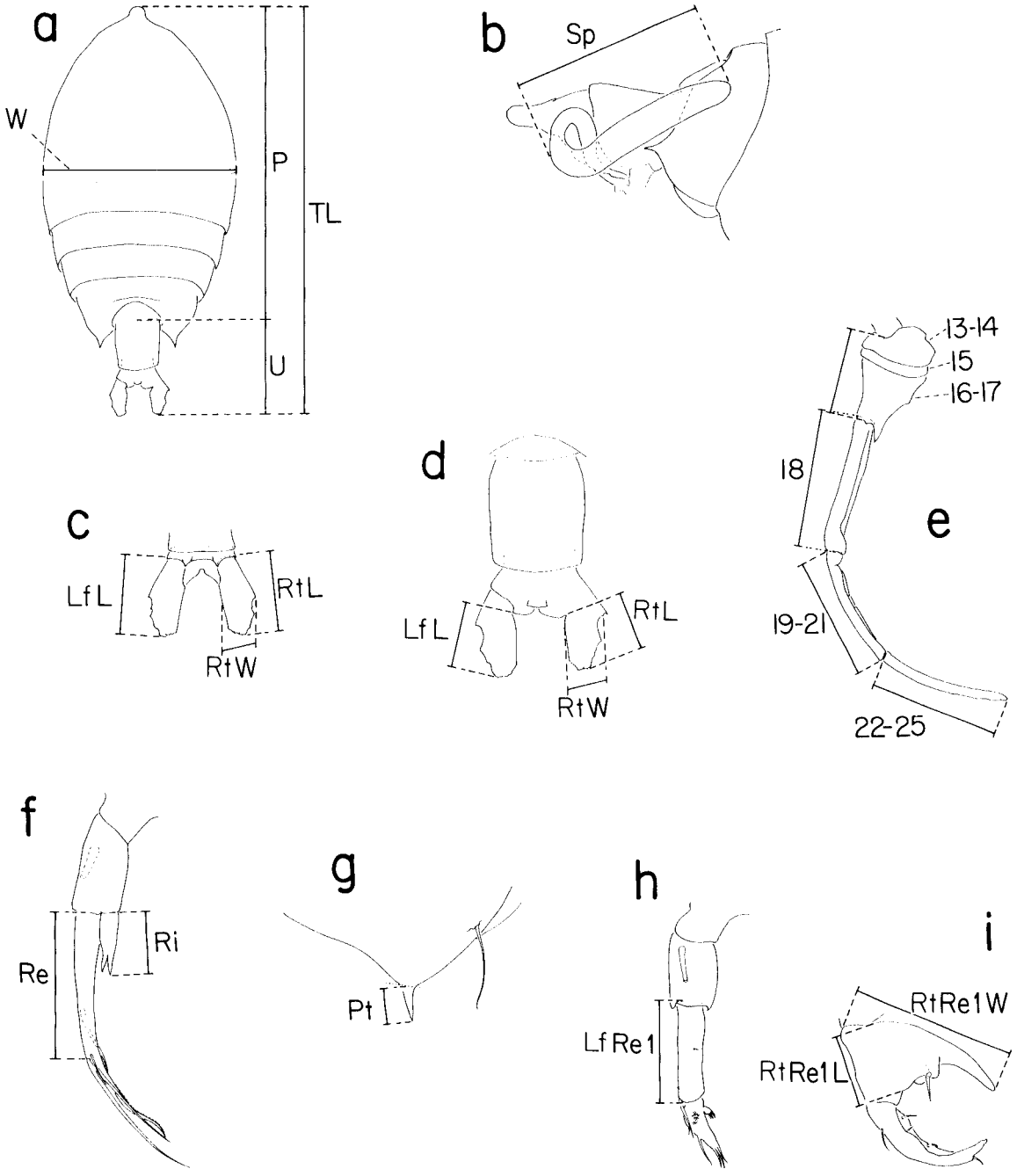

FIGURE 2.—Measurements taken from *Pontellina* specimens. **a**. dorsal view, female; **b**. abdomen with spermatophore, ThIV-V, lateral view, female; **c**. anal segment and furcal rami, dorsal view, male; **d**. urosome, dorsal view, female; **e**. right A1, segments 13-25 male; **f**. right P5, anterior view, female; **g**. spine on right ThIV-V, lateral view, female; **h**. left P5, posterior view, male; **i**. chela of right P5, posterior view, male. L = length; Lf = left; P = prosome length; Pt = spine; Re = exopod; Re1 = first exopodal segment; Ri = endopod; Rt = right; Sp = spermatophore; TL = total length; U = urosome length; W = prosome width.

between the shallow swelling in the proximal lateral corner and the distal margin, and the distance between the proximal medial corner and the tip of the large lateral prong (Figure 2i).

Types and reference specimens have been deposited with the Smithsonian Institution, U.S. National Museum, Washington, D.C.

GENUS *PONTELLINA* DANA

Pontella Dana, 1846 (in part), p. 184, type not designated; Dana, 1849, p. 26, type not designated.

Pontellina Dana, 1853 (in part), p. 1135, type not designated; Giesbrecht, 1889, p. 29, type by monotypy, *Pontellina plumata* (Dana); Giesbrecht, 1892, p. 73, 497; Giesbrecht and Schmeil, 1898, p. 149.

Calanops Claus, 1863, p. 211, type by monotypy, *Calanops messinensis* Claus = *Pontellina plumata* (Dana), Giesbrecht, 1889, p. 29.

Pseudopontia Claus, 1892, p. 861, 864, type by monotypy, *Pseudopontia plumata* (Dana) = *Pseudopontella plumata* (Dana), Claus, 1893, p. 278.

Pseudopontella Claus, 1893, p. 278, type by monotypy, *Pseudopontella plumata* (Dana) = *Pontellina plumata* (Dana), Giesbrecht and Schmeil, 1898, p. 149.

Not *Pontellina* Claus, 1892, p. 851; 1893, p. 272.

Diagnosis

Relatively small pontellids, less than 2 mm in TL. Prosome in dorsal view broadly oval, less than twice as long as maximum width; forehead lacking headhooks; ThIV-V corners symmetrical; rostrum proximally protuberant, bifurcate at base, and extending ventrad as slender, elongate, flexible filaments; in lateral view, filaments more than 10 times longer than wide at maximum width; ventral eye present but inconspicuous, scarcely produced, and lacking a distinctive lens. In A1 (except sexually modified right A1 of male) segments 13, 14, and 15 separate and about equal in length. A2 with Re about as long as Ri1, length of Ri1 less than 4 times maximum width.

Female lacking distinctive dorsal lenses in forehead. Furcal rami weakly asymmetrical, right ramus fused to anal segment. P5 with monomerous Re bearing 1 lateral and 3 terminal setae, in addition to one medial setiform process fused to Re and serrated along medial margin; Ri monomerous and terminating in one or two apical spines. A2 and mandible (Mnd) with elongate setae reaching beyond thorax when extended posteriad.

Male with one pair of dorsal lenses in forehead.

Additional Description

Both sexes with cephalic groove and agreeing in meristic features of all appendages except for those modified by sexual maturation. Nonsexually modified appendages agree with those of *Pontellina plumata* as shown by Giesbrecht (1892, pl. 25, fig. 1, 6, 7, 9, 12-14, 18, 20, 21, 23-25). Segmentation, setation, and spination of nonsexually influenced appendages are virtually identical among the four species and, except for A1, closely resemble those of *Pontellopsis*. They are as follows:

A1: 17 free segments; segments 2-5, 6-8, 24-25 fused, 9-11 partly fused.

A2: 2 basal segments; Re: 3 segments with 1, 4, 3 setae, respectively; Ri: 2 segments; Le: 6, Li: 6 + 2 setae.

Mnd: palpus 1 seta; Re: 5 segments with a total of 6 setae; Ri: 2 segments with 4 and 6 setae, respectively.

Mx1: Li1: 14 spines; Li2: 3 spinelike setae; Li3: small, 3 setae; B2: 3 + 2 setae; Ri: 4 + 1 setae; Re: 8 setae; Le: 1 + 8 setae.

Mx2: lobe 1: 3 + 1 setae; lobes 2-5: 2 + 1 setae each; Ri: 6 + 1 setae.

Mxp: 5-segmented, fingered lobe on B1 with 2, 2, 3 setae.

P1: trimerous Re: 1, 1, 4 Si; 1 St; 1, 1, 2 Se; trimerous Ri: 1, 2, 4 Se; 1 St; 0, 0, 1 Se.

P2 and P3: trimerous Re: 1, 1, 5 Si; 1 St; 1, 1, 3 Se; bimerous Ri: 3, 5, Si; 1 St; 0, 2 Se.

P4: trimerous Re: 1, 1, 5 Si; 1 St; 1, 1, 3 Se; bimerous Ri: 3, 4 Si; 1 St; 0, 2 Se.

Se of P1 smooth; Se of Re1 and Re2 of P2 with toothed medial margin; Se of Re3 with toothed medial and lateral margins; in Se of P3 and P4 also both margins toothed.

St of Re 3 of P1 to 4 with toothed lateral margin.

B1 of P1 to 4 with 1 Si; B2 ususally without setae.

Right A1 in male with segments 13-17 swollen, 13-14 and 16-17 fused; length of swollen section varies considerably due to either telescoping of segments or expansion of articulations. Distal three free segments slender and consisting of segment 18 followed by a compound segment formed by fusion of segments 19-21, and ending in a compound segment fusing segments 22-25.

Mandibular blade (Giesbrecht 1892, pl. 25, fig. 14) bearing a one-pointed apical (ventral) tooth, a two-pointed subapical tooth, two deeply cut two-pointed medial teeth, and three basal (dorsal) teeth; basal seta lacking; dorsal accessory bristles exceed teeth in length; patches of spinules appear on anterior side of blade.

P5 segmentation in both sexes typically pontellid; B2 of male bearing a large plumose seta on posterior surface, Ri lacking, Re bimerous; right leg with elongate B1, cheliform Re; left leg with reduced B1 fused to precoxa, distal segment of Re armed with four short setiform processes.

Spermatophore with relatively long neck bearing one full counterclockwise turn relative to proximal end, helix occurring between spermatophore sac and place of attachment located in a cement mass overlying genital pore of female. Elongate spermatophore neck may also be connected secondarily to right side of genital segment proximal to helix, thereby orienting sac dorsad or anterodorsad with helix and sac flanking right side of genital segment. When secondary lateral cementation absent, neck, helix, and sac hang free from ventral side of genital segment.

PONTELLINA PLUMATA (DANA)

(Figures 3 and 4)

Pontella plumata Dana, 1849, p. 27 (type locality not designated); Brady (in part), 1883, p. 92, pl. 37, fig. 1-10 only.

Pontella turgida Dana, 1849, p. 28 (type locality not designated).

Pontellina plumata: Dana, 1853, p. 1135; Dana, 1855, pl. 79, fig. 10; Giesbrecht, 1889, p. 29; Giesbrecht, 1892, p. 497, pl. 4, fig. 1, pl. 25, fig. 1, 4, 6, 7, 9, 12-14, 18, 20, 21, 23-26, 36, pl. 40, fig. 49-53; Mori (in part), 1937, p. 99, pl. 47, fig. 7-11 only; Grice, 1962, p. 240, pl. 34, fig. 11-15; Brodsky, 1962, p. 147, fig. 47; Park, 1968, p. 569, pl. 13, fig. 15-16.

Pontellina turgida: Dana, 1853, p. 1136; Dana, 1855, pl. 79, fig. 11, 12.

Calanops messinensis Claus, 1863, p. 212, pl. 2, fig. 11, pl. 36, fig. 13-16, pl. 37, fig. 10 (Messina).

Pontellopsis speciosus Brady, 1915, p. 138, pl. 10, fig. 1-8 (Durban Bay). NEW SYNONYMY.

Pontellopsis aequalis Mori, 1932, p. 172, 175, pl. 4, fig. 7-13 (25°20′50″N, 124°7′30″E).

not *Pontella plumata:* Brady (in part), 1883, p. 93, pl. 37, fig. 11 only.

not *Pontellina navalium* Oliveira, 1947, p. 472, fig. 12; Vervoort, 1965, p. 191.

Specimens seen: 1,259 adult females, 917 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean ($\bar{x}$)	*Range*	*Standard error* $s_{\bar{x}}$	*Specimens*
Female	1.69	1.44-1.94	0.0126	75
Male	1.51	1.34-1.92	0.0130	67

Prosome-urosome length ratio (PUR):

	Median	*Range*	*Specimens*
Female	3.28:1	2.92-3.72:1	75
Male	3.07:1	2.84-3.93:1	52

Diagnosis

Female

Posterior corner of ThIV-V in lateral view produced into conspicuous spiniform process of characteristic shape (Figure 3 a, b, d-g). Ventral margin of spine more or less continuous with ventral margin of ThIV-V, transition with dorsal margin abrupt and stepped; junction of distal end of spine and thicker basal portion usually set off by weak shoulder, spine extending posteriad, sometimes tilted weakly ventrad or dorsad. In dorsal view spine more or less continuous with posterior tapering of corner, shoulder or constriction sometimes present; spine usually directed posteriad and slightly laterad, sometimes straight or turned slightly mediad.

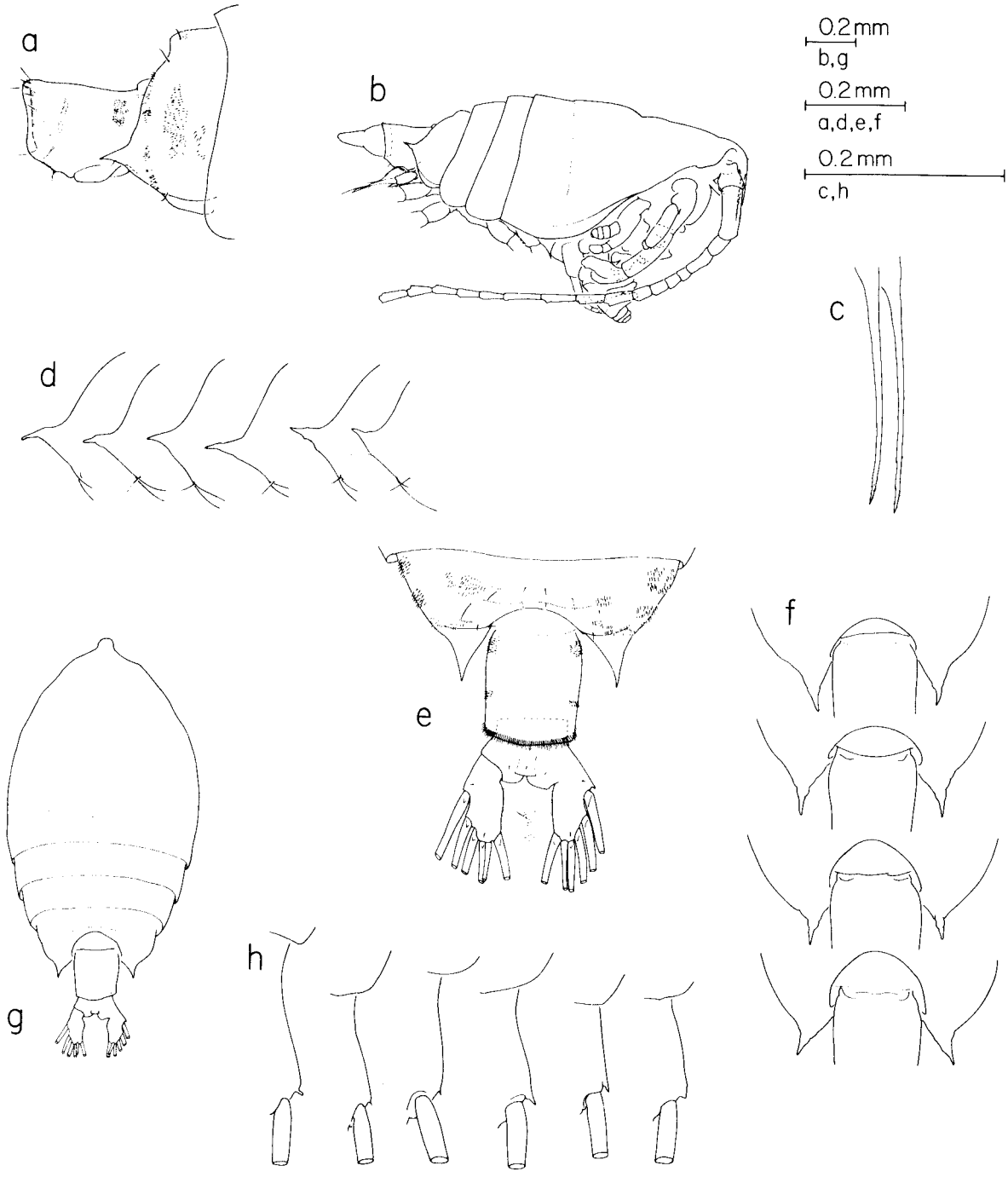

FIGURE 3.—*Pontellina plumata* s.str., adult female: **a**. ThIV-V, genital segment, lateral view (TRANSPAC 96A); **b**. habitus, lateral view, swimming legs incomplete (same station as **a**, different specimen); **c**. rostral filaments, lateral view (*Atlantis II*-31-2); **d**. range of variation observed in ThIV-V, lateral view (left to right: Lusiad VI-8; *Chain* 49-11; Lusiad II-66; *Chain* 49-11, different specimen; *Atlantis II*-31-73; same station, different specimen); **e**. ThIV-V, urosome, dorsal view (same specimen as **a**); **f**. range of variation observed in ThIV-V, dorsal view (top to bottom: Scorpio II-118; *Chain* 49-11; same station, different animal; *Chain* 49-20); **g**. habitus, dorsal view (same specimen as **b**); **h**. lateral margin of right furcal ramus of various specimens, dorsal view (left to right: *Atlantis II*-31-2; Troll 28A; *Atlantis II*-20-22; Dodo VI-65; Troll 25; Scorpio II-182).

Genital segment bearing anterolateral and posterolateral clusters of hairs on both sides of segment (Figure 3 a, e); anterior cluster larger, best seen in dorsal view. Posterior cluster less prominent, of similar or coarser hairs. A row of relatively long, fine hairs encircling segment near distal margin.

Male

In lateral view posterior corner of ThIV-V somewhat angular, apex usually bearing one minute denticle (Figure 4e-h). Chela of right P5 with proximal segment extending distolaterad as a relatively slender digitiform process opposing apex of distal falcate segment (Figure 4i); base of distolateral digitiform process flanked by small anterior process, triangular in lateral view, and small angular posterior process bearing a sensoriiform seta (Figure 4j); in lateral view posterior basal process and digitiform process with relatively straight margins intersecting at an angle greater than 70° (Figure 4j); in posterior view two basal processes overlapping, both extending toward center of lumen of chela; additional sensoriiform setae on proximal segment of chela: one anteromedial near articulation with distal segment; on distal segment: one proximomedial, one mediosubapical, and three lateral. Left P5 (Figure 4i) with proximal segment of Re (Re1) short relative to other three species below. Length of right furcal ramus exceeds left Re1 by 1.55-1.85 times, 46 specimens (see Figure 30).

Additional Description

Female

Right furcal ramus fused to anal segment, varying directly with prosome length, relatively longer than that in Indian and Pacific congeners described below (Figure 25); ratio of length to width highest in genus, usually 1.5 times longer than wide (median 1.56:1, range 1.28-1.74:1, 134 specimens), showing apparent overlap only with the equatorial Atlantic congener (see Figure 27); lateral margin of right furcal ramus with small pointed projection somewhat variable in shape and size just anterior to base of outermost seta (Figure 3e, h). Glandlike tissue within right furcal ramus with associated ductlike structure extending toward lateral point. Left furcal ramus not fused and appreciably longer than right ramus (see Figure 19).

P5 (Figure 4a, c, d) with inner margin of Re lacking hair, Ri polymorphic with one or two apical spines fused to segment, spines on left and right Ri may differ in number in same specimen (Figure 4b, Table 7); Re 2 to 3 times longer than Ri, median 2.37:1, range 1.97-3.08:1, 59 specimens, differing strongly from Indian and Pacific congeners (see Figure 29).

Attached spermatophore observed on four specimens (see Figure 33 a, b; Table 5), hanging free from single place of attachment in vicinity of genital pore, neck with small helical turn near place of attachment and larger helical turn at origin of sac.

Male

Right furcal ramus not fused to anal segment, about equal in length to left ramus (see Figure 19), varying directly with prosome length (see Figure 26); ratio of length to width relatively high (median 2.30:1, range 2.0-2.53:1, 44 specimens), but showing more overlap with congeners than found among females (see Figure 28).

Types

Unknown, presumed to be lost. Reference specimens from the Atlantic, Pacific, and Indian Oceans have been deposited in the U.S. National Museum, Smithsonian Institution.

Reference Specimens

4 ♂, 4 ♀, *Atlantis II*-31-5, lat. 39°13.0′N, long. 63°26.5′W, 14 Jan. 1967, ¾-m net, oblique tow, maximum cable out 200 m.

2 ♂, 2 ♀, Capricorn 31, lat. 06°31′N, long. 124°41′W, 13 Feb. 1953, 1-m net, oblique tow, maximum cable out 200 m.

2 ♂, 2 ♀, TRANSPAC 134A, lat. 23°26.3′N, long. 161°49.6′W, 17 Nov. 1953, 1-m net, oblique tow between surface and 129 m est.

2 ♂, 4 ♀, Lusiad V-76, lat. 02°01′S, long. 91°58′E, 24 Apr. 1963, 1-m net, oblique tow, maximum cable out 280 m.

2 ♂ Lusiad V-104, lat. 03°01′S, long. 52°58′E, 10 May 1963, 1-m net, oblique tow, maximum cable out 280 m.

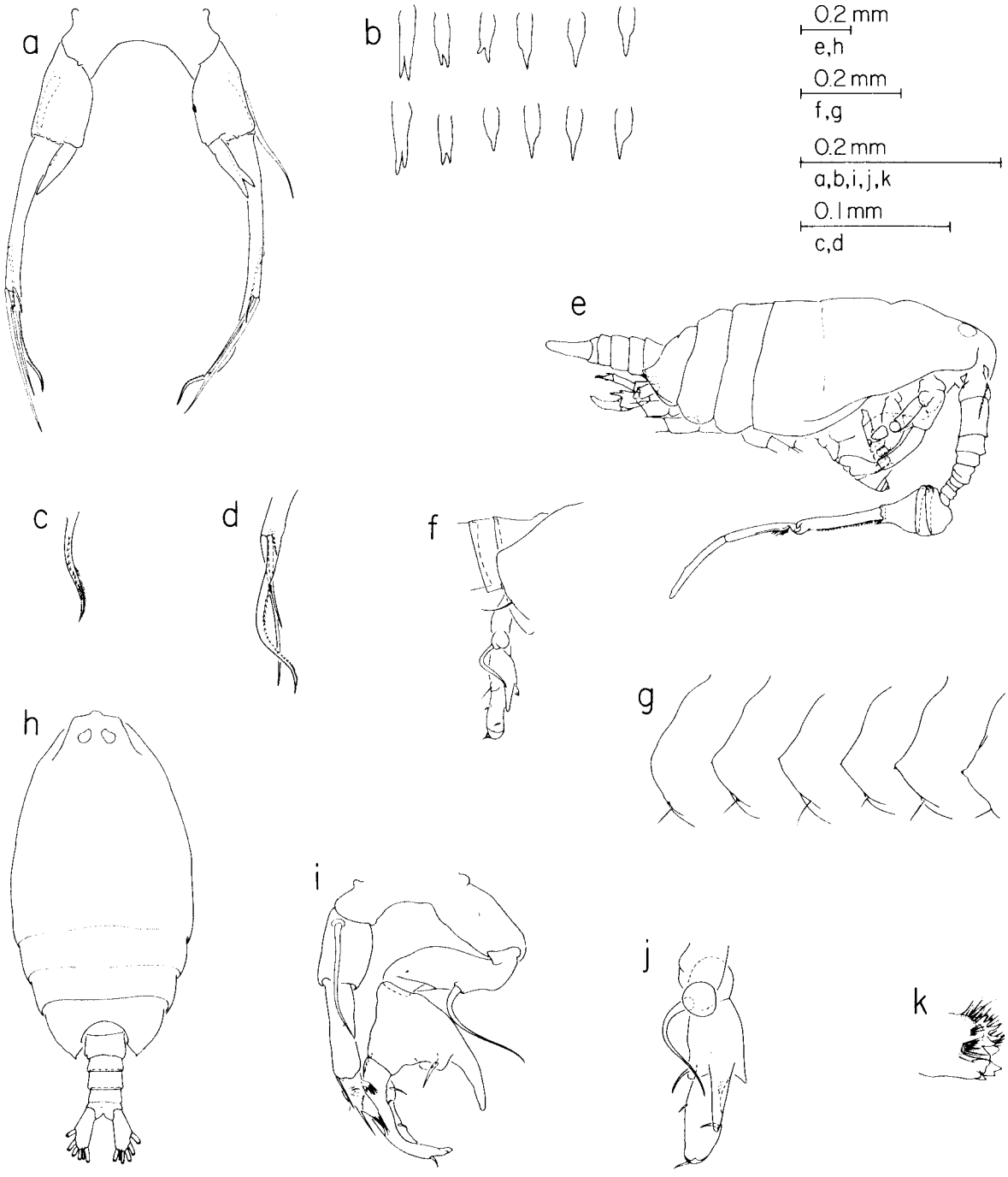

FIGURE 4.—*Pontellina plumata*, s.str. Adult female: **a.** P5 anterior view (TRANSPAC 96A); **b.** P5 Ri of other specimens, right side above, left side below (left to right: Scorpio II-146; Lusiad II-66; La Creuse 3; same station, different specimen; *Atlantis II*-31-6; Lusiad V-45); **c.** enlargement of P5 apex; **d.** enlargement of P5 Re distal process (TRANSPAC 96A). Adult male: **e.** habitus, lateral view (*Atlantis II*-31-28); **f.** ThIV-V, part of urosome, P5, lateral view (TRANSPAC 92B); **g.** variation observed in ThIV-V, lateral view (left to right: Dodo VI-70; *Gill* 8-9; La Creuse 7; *Gascoyne* G1/5/63; Circe NT-38; Monsoon 18). **h.** habitus, dorsal view (same as **e**); **i.** P5, posterior view (same as **f**); **j.** P5 chela, lateral view (same as **f**); **k.** mandible, gnathobase, lateral view.

Remarks on Synonymy and Variability

Dana (1849, 1853, 1855) described the male and female of *P. plumata* as separate species based on specimens obtained from several equatorial localities (in the Atlantic Ocean: lat. 08°30′N to 00°, long. 23° to 18°W; 00°15′N, 31°00′W; 01°00′ to 04°30′S, 17°30′ to 21°30′W; 04°30′S, 25°00′W). Our efforts to use his descriptions and illustrations to separate the two species in our Atlantic collections were fruitless. Moreover, Dana's specimens of *Pontellina* are apparently lost (T. E. Bowman, in litt.).

The present concept of *P. plumata* originates from Giesbrecht's (1892) redescription and synonymy which have been generally accepted. Hence we regard his description of the species as the basis for the type species of the genus.

Several authors have noted morphological variation in *plumata*, observations that may indicate that they had examined specimens of two or more of the four species we recognize in the genus. Thus, Dana (1853) reported that the furcal rami were relatively longer in males from the Cape of Good Hope region than in males from the Pacific Ocean. Giesbrecht (1892) found that the posterolateral corners of ThIV-V were longer in males from the Pacific than in those from waters off Naples. Tanaka (1964) mentions differences in the posterolateral corners of ThIV-V in both sexes of *plumata*. Mori (1937) believed the differences he encountered in specimens of *Pontellina* were a function of ontogeny. On the other hand, a number of authors have published illustrations which appear to be based solely on *plumata* specimens (e.g., Giesbrecht, 1892; Brodsky, 1962; Grice, 1962; Park, 1968).

Distribution

P. plumata exhibits a warm-water circumglobal distribution bounded in the north and south roughly by the subtropical convergence zones of each hemisphere (Figure 5). Adults were frequent in occurrence but relatively low in abundance. For example, in 131 zooplankton samples containing the species from the Indian and Pacific Oceans (Indian Ocean Standard Net and CalCOFI Standard Net zooplankton samples; tows through the epipelagic layer) abundance estimates ranged from 0.002 to 0.4 adults per m^3 water strained, the median being 0.02. In the sets of samples selected for quantitative analysis (Figure 1b) the species appeared infrequently and in minimal numbers in the eastern tropical Pacific. In the remainder of the equatorial Pacific and in the Indian Ocean *plumata* was found in about half of the samples examined.

Values of mean abundance in temporally and geographically related sets of samples usually exceeded 0.02 per m^3 of water strained (see Figure 35, Table 14). With regard to the Atlantic Ocean our impressions from the available nonquantitative collections is that the abundance of *plumata* is not appreciably different from that in the Indian and Pacific Oceans.

The widespread co-occurrence of three sibling species (described below) imposes serious reservations on the use of previously published records of *plumata*. It would be best to consider earlier records primarily as evidence of the occurrence of the genus, a useful attribute considering the virtual absence of the genus at latitudes above 40°.

PONTELLINA PLATYCHELA SP.N.

(Figures 6 and 7)

Specimens seen: 168 adult females, 466 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean ($\bar{x}$)	*Range*	*Standard error* $s_{\bar{x}}$	*Specimens*
Female	1.70	1.54-1.96	0.0173	30
Male	1.56	1.41-1.74	0.0089	57

Prosome-urosome length ratio (PUR):

	Median	*Range*	*Specimens*
Female	3.44:1	3.19-3.89:1	30
Male	3.22:1	2.86-3.55:1	49

Diagnosis

Female

Posterolateral corner of ThIV-V ending in a relatively minute dentiform process extending posteriad or weakly medioposteriad (Figure

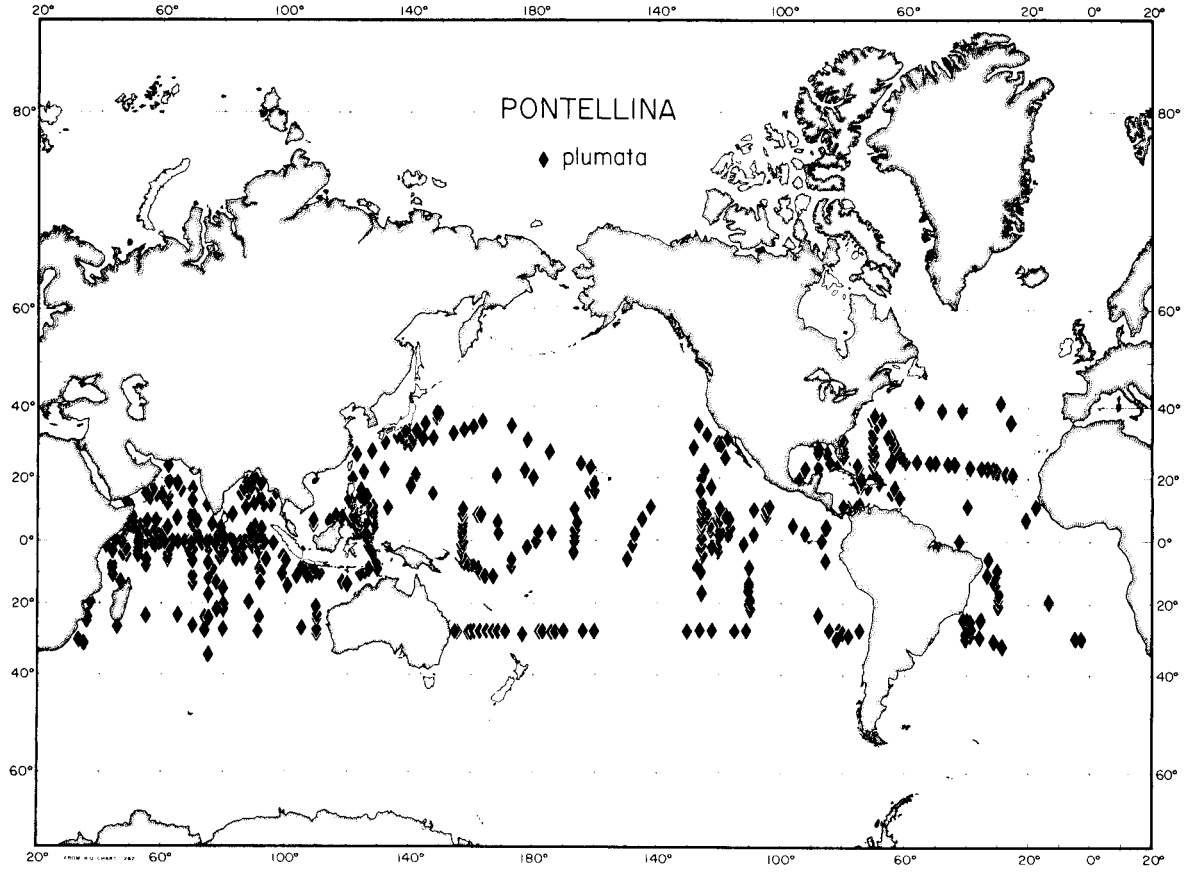

FIGURE 5.—*Pontellina plumata* s.str. Geographical distribution of captures recorded during the present study.

6a-c, f-h); in dorsal view denticle not sharply set off from tapering lateral margin of ThIV-V. Genital segment (Figure 6f, g) with several isolated lateral sensory hairs and line of slender hairs along distal margin, lacking lateral clusters of coarse hairs.

Male

Posterolateral corners of ThIV-V in lateral view tending to be rounded and lacking denticle (Figure 7c, d). Chela of P5 differing markedly from that in *plumata* due to strong antero-posterior expansion of both segments (Figure 7a, b); distal segment spatulate; in proximal segment base of laterodistal digitiform process greatly expanded; in posterior view posterior basal process barely differentiated but sensoriform seta present, anterior basal process relatively small, and extending toward center of lumen of chela. Left P5 (Figure 7a) with proximal segment of Re (Re1) somewhat longer than that in *plumata*, length of right furcal ramus exceeds Re1 by 1.3-1.5 times, 21 specimens (see Figure 30).

Etymology

The name *platychela* is derived from the Greek words platys (= broad) and chela (= crab's claw) and refers to the relatively large chela of the adult male.

Types

Holotype: Adult male, TL 1.52 mm, PUR 3.22:1; sorted from plankton sample taken at *Atlantis II*-31 stn. 48, lat. 00°56′N, long. 25°20′W, 12 Feb. 1967, ¾-m net, oblique tow, maximum cable out 200 m. USNM No. 141613.

Allotype: Adult female, TL 1.72 mm, PUR

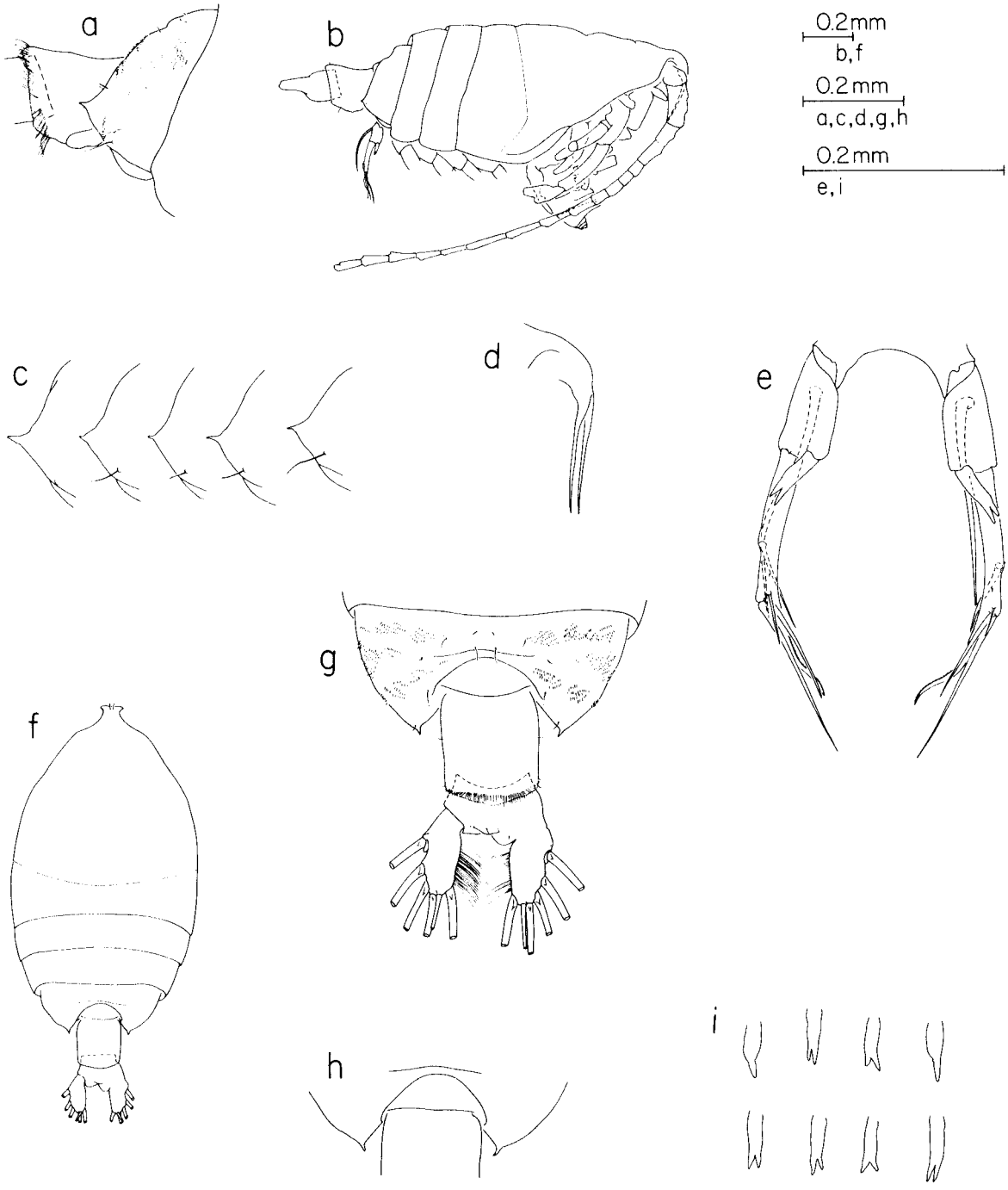

FIGURE 6.—*Pontellina platychela*, sp.n., adult female: **a.** ThIV-V, genital segment, lateral view (*Atlantis II*-20-28); **b.** habitus, lateral view (*Atlantis II*-20-2); **c.** range of variation in ThIV-V, lateral view (left to right: Lusiad VII-81 H13; *Atlantis II*-31-40; Lusiad VII-81 H13, different specimen; *Atlantis II*-20-31; same station, different specimen); **d.** rostrum, lateral view (same as **a**); **e.** P5, anterior view (same as **a**); **f.** habitus, dorsal view (same as **b**); **g.** ThIV-V, urosome, dorsal view (same as **a**); **h.** ThIV-V, dorsal view, another specimen (*Atlantis II*-20-31); **i.** P5 Ri of other specimens, right side above, left side below (all four specimens Lusiad VII-69 H4).

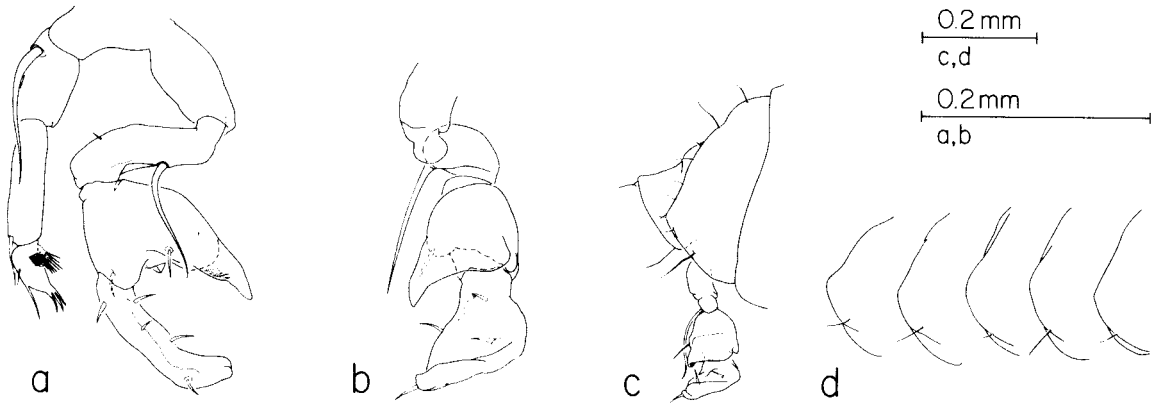

FIGURE 7.—*Pontellina platychela* sp.n., adult male: **a.** P5, posterior view (*Atlantis II*-20-24); **b.** P5 chela, lateral view (same as **a**); **c.** ThIV-V and P5, lateral view (*Atlantis* II-20-27); **d.** range of variation in ThIV-V (left to right: 3 specimens Amazon 17; La Creuse 7; *Oregon* 1293).

3.52:1; right furcal ramus length 0.110 mm, width 0.075 mm; from same sample as male. USNM No. 141614.

Paratypes: 3♂, 3♀ from same sample. USNM No. 141615.

Reference specimens: 5♂, 5♀, *Oregon* stn. 1293, lat. 19°55′N, long. 74°10′W, 23 Apr. 1955, G III net towed between surface and 2m. USNM No. 141616.

Distribution

P. platychela was found only in epipelagic tows taken in equatorial latitudes of the Atlantic Ocean (Figure 8). The species appeared regularly in samples collected between lat. 10°S and 10°N. The more extensive sampling available to us from north of the equator indicates that few *platychela* extend as far as lat. 21° or 22°N and that the species disappears abruptly at higher latitudes. We anticipate that in the vicinity of the Gulf Stream its northward occurrence may be extended somewhat by examination of additional samples, paralleling occurrences to the south in the Brazil Current.

Additional Description

Female

Right furcal ramus somewhat shorter than in *plumata* (see Figure 27), typically 1.4 times longer than wide (median 1.44:1, range 1.28-1.55:1, 35 specimens), lateral process anterior to proximal seta lacking, but interior of ramus with glandlike tissue and ductlike structure leading to lateral margin as in *plumata*.

P5 (Figure 6e) essentially as in *plumata* including proportional length relationship of Re and Ri, median 2.27:1, range 1.69-2.91:1, 49 specimens (see Figure 29); Ri polymorphic with one or two apical spines fused to segment, in same specimen spines on left and right Ri may differ in number as in *plumata* (Figure 6i, Table 7).

Attached spermatophore observed in one specimen (see Figure 33c-e, Table 5); neck cemented to ventral side of genital segment in vicinity of genital pore and buried within large irregular mound of cement extending across entire length of genital segment and right ventral side of anal segment, neck extending to right anterolateral side of anal segment along with continuation of cement fixing it to anal segment, large helical counterclockwise turn following emergence of neck from cement orienting succeeding sac anterodorsad.

Male

Right furcal ramus as in *plumata* (see Figures 19, 26), but relatively wider (see Figure 28), ratio of length to width typically 2:1 (median 2.06:1, range 1.91-2.34:1, 37 specimens).

Our impression from the available Atlantic

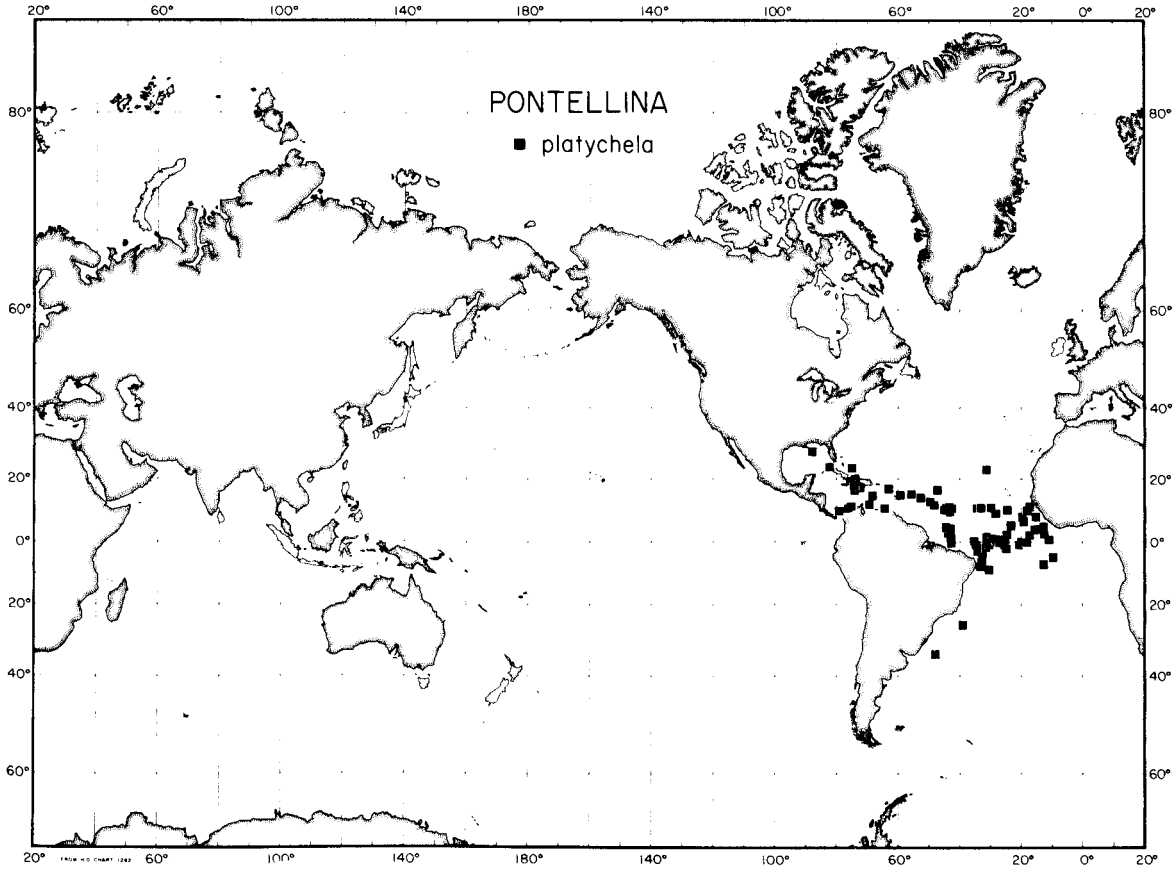

FIGURE 8.—*Pontellina platychela* sp.n. Geographical distribution of captures recorded during the present study.

collections is that the abundance of *platychela* is generally similar to the numbers of *Pontellina* in the Indian and Pacific Oceans (cf. Tables 14, 18), i.e., typically less than 0.2 adults per m^3 of water strained.

PONTELLINA MORII SP.N.

(Figures 9 and 11)

Pontellina plumata: Mori (in part), 1937, p. 99, pl. 48, fig. 1-12 only; Dakin and Colefax, 1940, p. 99, fig. 139. NEW SYNONYMY.

Specimens seen: 433 adult females, 284 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean ($\bar{x}$)	*Range*	*Standard error* $s_{\bar{x}}$	*Specimens*
Female	1.61	1.38-1.88	0.0145	54
Male	1.44	1.26-1.68	0.0100	58

Prosome-urosome length ratio (PUR):

	Median	*Range*	*Specimens*
Female	3.64:1	3.39-4.10:1	35
Male	3.34:1	2.87-3.73:1	50

Diagnosis

Female

Posterolateral corner of ThIV-V ending in a short spiniform process extending posteriad or somewhat medioposteriad; in contrast to *plumata* junction of spine and ThIV-V corner relatively

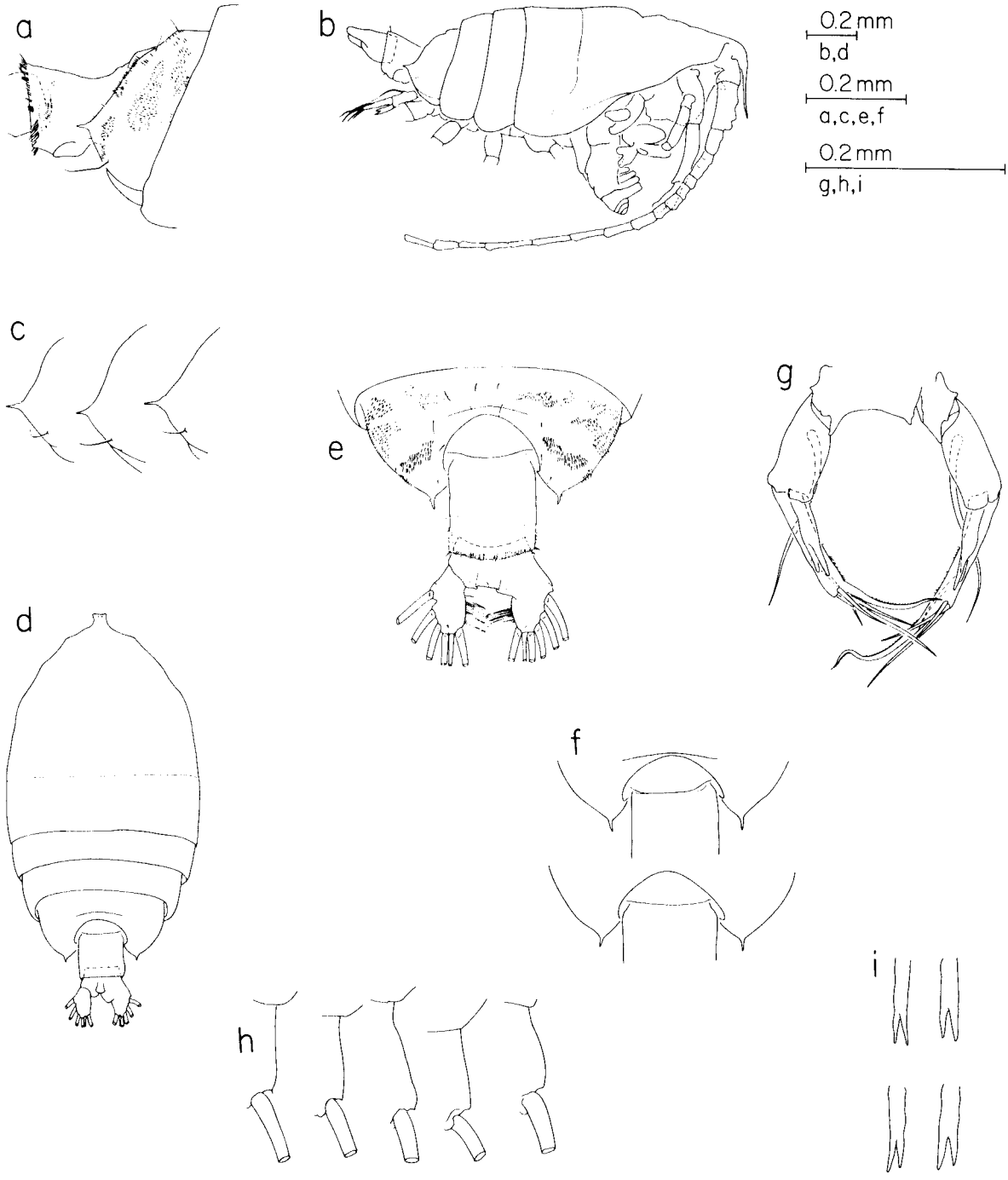

FIGURE 9.—*Pontellina morii* sp.n., adult female: **a.** ThIV-V and genital segment, lateral view (Lusiad V-66); **b.** habitus, lateral view (Circe III NT-27); **c.** variation in ThIV-V, lateral view (left to right: Troll 31A, 2 specimens Lusiad II-66); **d.** habitus, dorsal view (Circe III NT-26); **e.** ThIV-V and urosome, dorsal view (same as **a**); **f.** variation in ThIV-V, dorsal view (top: Troll 31A; bottom: Lusiad II-66); **g.** P5, anterior view (Lusiad V-66); **h.** variation observed in lateral margin of right furcal ramus, dorsal view [left to right: Scan IV-3; TO-58-1 (Scot) 14; Lusiad II-13; Lusiad II-10; Lusiad V-45]; **i.** P5 Ri in other specimens, right side above, left side below (left: Troll 30; right: Silas Bent 1-12).

abrupt in both dorsal and lateral views (Figure 9a-f), right and left sides symmetrical (Table 2), spine small, not exceeding 0.035 mm irrespective of TL (Figure 10), spine roughly one-half as long as that in its congener from the eastern equatorial Pacific described below. Genital segment with posterolateral cluster of coarse hairs on both sides, lacking anterolateral cluster found in *plumata* although several fine hairs may occur at this site (Figure 9a, e): posterior margin of segment bordered by fine, long hairs as in *plumata*.

Male

ThIV-V typically ending posteriorly in a small spiniform process (Figure 11b, c) similar to female. P5 with chela of *plumata*-type but both segments showing distinctive features; distal segment short, not reaching opposing disto-lateral digitiform process on proximal segment (Figure 11d), apex of distal segment with prominent triangular spur on posterior side (Figure 11d-f); proximal segment in lateral view with basal process posterior to digitiform process acuminate, intersection of posterior basal process and digitiform process usually in form of a deep angular notch; in posterior view proximal segment with axis of posterior basal process extending somewhat parallel to digitiform process and not overlapping anterior basal process, latter angled toward articulation between proximal and distal segments. Left P5 with Rel longer than that in *plumata* (see Figure 30).

Additional Description

Female

Right furcal ramus considerably shorter than in *plumata* relative to prosome (see Figure 25), right furcal ramus with median ratio of length to width 1.25:1, range 1.12-1.44:1, 46 specimens; lateral edge of right ramus with small point variable in shape just anterior to base of outermost seta (Figure 9e, h), glandular tissue within ramus as in *plumata*.

P5 with Re bearing hairs along median margin (Figure 9g); Ri relatively longer than that

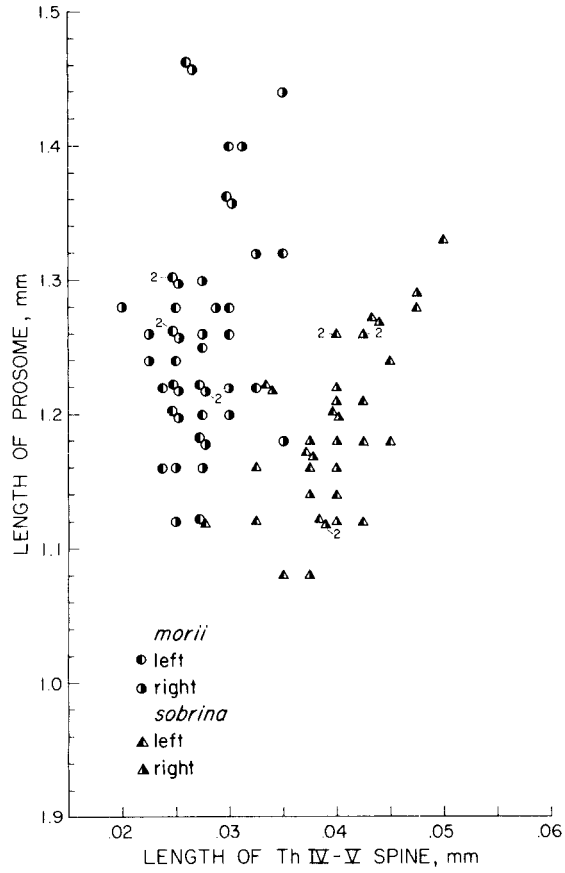

FIGURE 10.—Length of prosome (ordinate) plotted against length of ThIV-V spine (abscissa) for females of *Pontellina morii* and *P. sobrina*.

TABLE 2.—Length of posterior spine on thoracic segment IV-V in adult females of *Pontellina morii* and *P. sobrina*.

Species		$\bar{x}$ (mm)	Range (mm)	s	N
P. morii	left side	0.0263	0.018-0.035	0.0010	38
	right side	0.0275	0.020-0.035	0.0032	40
	combined	0.0269	0.018-0.035	0.0037	78
P. sobrina	left side	0.0409	0.033-0.050	0.0032	33
	right side	0.0404	0.028-0.049	0.0032	32
	combined	0.0407	0.028-0.050	0.0045	65

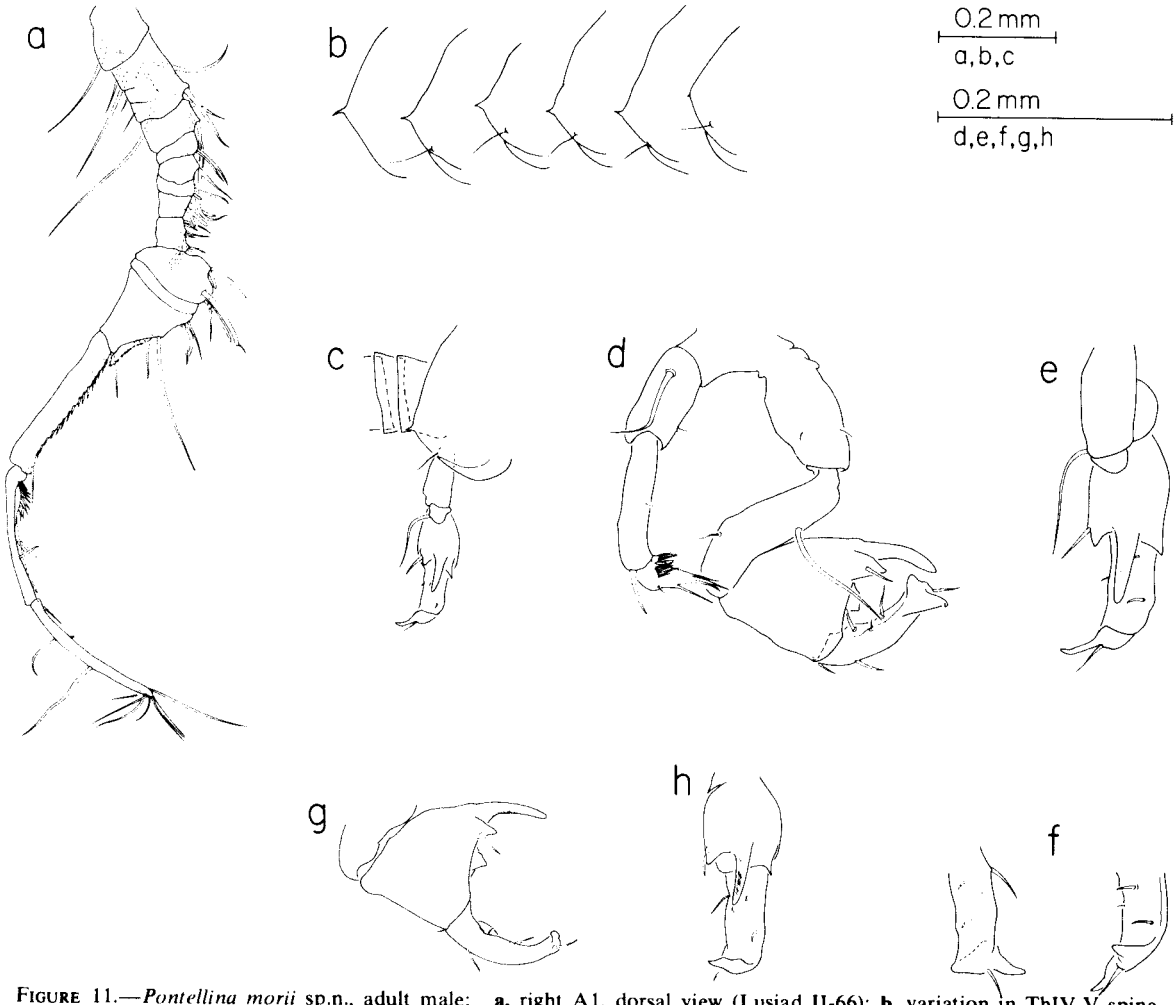

FIGURE 11.—*Pontellina morii* sp.n., adult male: **a.** right A1, dorsal view (Lusiad II-66); **b.** variation in ThIV-V spine, lateral view (left to right: Shellback 105; Troll 25; Lusiad II-55; Troll 32A; 2 specimens Monsoon 6); **c.** ThIV-V, P5 and first two segments of urosome, lateral view (Lusiad V-78); **d.** P5, posterior view (same as **a**); **e.** P5 chela, lateral view (same as **c**); **f.** apex of distal segment of P5 enlarged (same as **c**); **g.** aberrant chela showing a weakened subapical spur on distal segment, posterior view (*Anton Brunn I*-58); **h.** aberrant chela, lateral view (same as **g**).

in *plumata*, Re being less than 1.8 times longer than Ri, median 1.45:1, range 1.22-1.76:1, 55 specimens (see Figure 29); Ri typically with two relatively equal apical spines (Figure 9g, i; Table 7).

Attached spermatophore observed in four specimens (see Figure 33f-h, Table 5), appearance and orientation similar to that in *platychela* except for less cement on ventral side of urosome, especially on anal segment.

Male

Right furcal ramus differing from that in *plumata* in having a relatively shorter length (see Figure 26), median length-to-width ratio 1.93:1, range 1.80-2.07:1, 39 specimens, but overlapping extensively with its congener from the eastern equatorial Pacific (described below). Left P5 with Re1 considerably longer than that in *plumata:* in *morii* length of left P5 Re1 to length of right furcal ramus ranges from 1.08 to 1.26:1, 20 specimens (see Figure 30).

Etymology

This patronym commemorates the late

Takamochi Mori who first called attention to the distinctiveness of this species and for his pioneering contributions to our knowledge of Pacific Calanoida.

Types

Holotype: Adult male, TL 1.36 mm, PUR 3.25:1; sorted from plankton sample taken at Lusiad II stn. 66, lat. 01°54′N, long. 79°01′E, 30 Aug. 1962, 1-m net, oblique tow, maximum cable out 280 m, USNM No. 141621.

Allotype: Adult female, TL 1.56 mm, PUR 3.87:1, right furcal ramus length 0.090 mm, width 0.080 mm, from same sample as male. USNM NO. 141622.

Paratypes: 5♂, 5♀ from same sample. USNM No. 141623.

Reference specimens: 2♂, 2♀, Lusiad V stn. 76, lat. 02°01′S, long. 91°58′E, 24 Apr. 1963, 1-m net, oblique tow, maximum cable out 280 m. USNM No. 141625. 2♂, 2♀, Capricorn stn. 2, lat. 02°54′N, long. 168°40′E, 28 Nov. 1952, 1-m net, oblique tow, maximum cable out 200 m. USNM No. 141624.

Distribution

P. morii was found primarily at Indian and Pacific Ocean localities distributed in a zonal band lying roughly between lat. 20°N and 20°S (Figure 12). Occurrences at higher latitudes are few and mostly in the vicinity of western boundary currents; e.g., in the Kuroshio Current region just east of Japan and east of southern Africa in the region of the Mozambique and Agulhas Currents. In the eastern

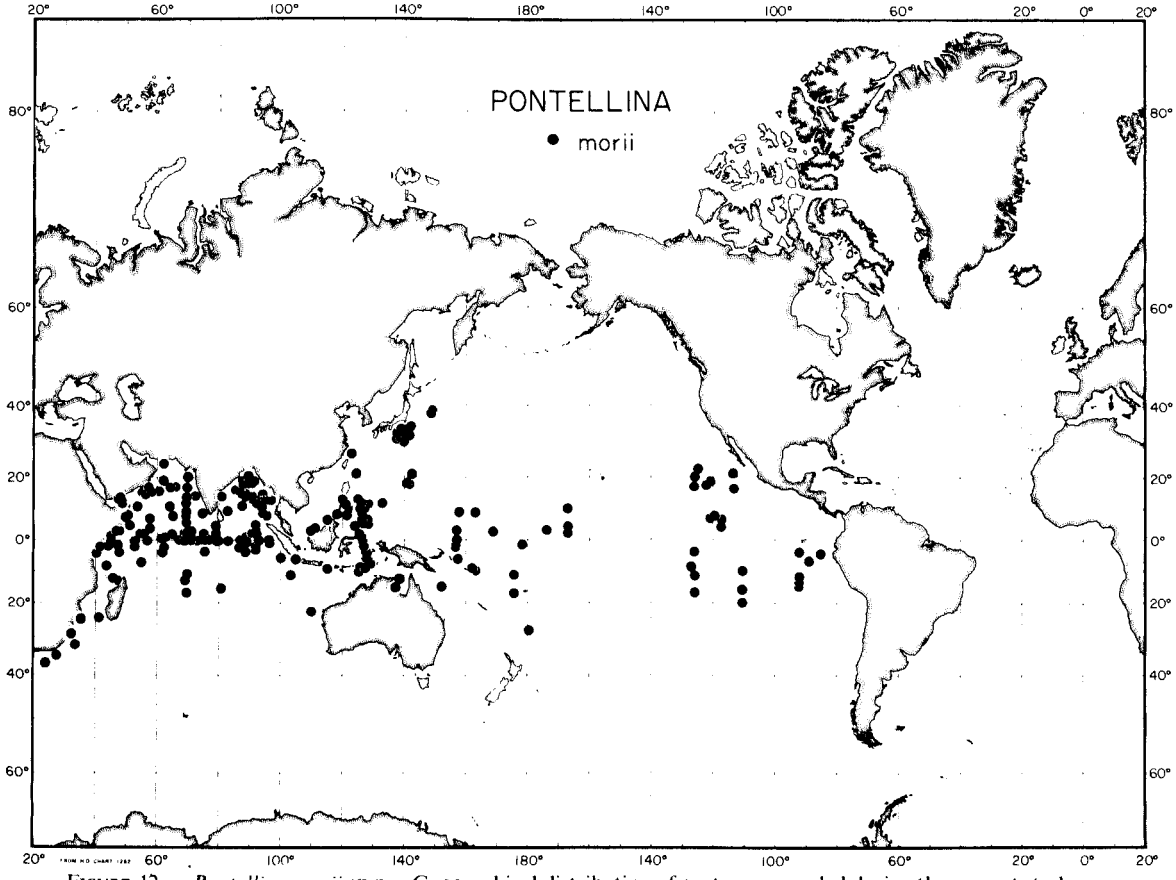

FIGURE 12.—*Pontellina morii* sp.n. Geographical distribution of captures recorded during the present study.

Pacific *morii* approached the Americas in the vicinity of Baja California and also at the latitudes of the Gulf of Guayaquil.

Among the 72 quantitatively analyzed samples containing *morii* estimates of abundance ranged from 0.003 to 0.5 individuals per m^3, the median being 0.01. In the sets of samples selected for quantitative analysis (Figure 1b) mean abundance in the Indian Ocean exceeded 0.04 individuals per m^3, 5 or more times higher than that found in sets of samples from the Pacific Ocean (Figure 35, Table 14); frequency of occurrence in the Indian Ocean (~30%) was also higher than in the Pacific Ocean (≤20%).

PONTELLINA SOBRINA SP.N.

(Figures 13 and 14)

Specimens seen: 421 adult females, 364 adult males.

Standard measurements: specimens randomly selected from locations spanning the observed geographical distribution.

Total length (TL), mm:

	Mean ($\bar{x}$)	*Range*	*Standard error* $s_{\bar{x}}$	*Specimens*
Female	1.57	1.42-1.78	0.0134	50
Male	1.41	1.18-1.64	0.0118	56

Prosome-urosome length ratio (PUR):

	Median	*Range*	*Specimens*
Female	3.73:1	3.17-4.16:1	33
Male	3.43:1	3.06-3.75:1	51

Diagnosis

Female

Most similar in appearance to *morii*. Spiniform process strongly demarcated from ThIV-V corner and typically symmetrical as in *morii*, but spine almost twice as long (Figure 10, Table 2); in dorsal view weakly curved spines extending posterolaterad (Figure 13g). Genital segment with two lateral clusters of hairs on both sides, anterior cluster consisting of fine hairs, posterior cluster consisting of coarse hairs (Figure 13 a, g); posterior margin of segment with border of long fine hairs as in all preceding species.

Male

ThIV-V (Figure 14a, b) as in female. P5 (Figure 14c, d) most similar to that in *morii* with notable differences present in chela. Distal segment of chela relatively long, apex extending beyond apex of laterodistal digitiform process of proximal segment. Moreover, distal segment lacking subapical spur (Figure 14c, d); in lateral view posterior basal process and digitiform process of proximal segment separated by rounded notch (Figure 14d); proximal segment in posterior view as in *morii*. Left P5 with Rel longer than that in *plumata* (see Figure 30).

Additional Description

Female

Right furcal ramus somewhat shorter relative to its width as well as to length of prosome (see Figures 25, 27), median ratio of right furcal ramus length to width 1.12:1, range 1.02-1.31:1, 66 specimens; lateral edge of right ramus usually with broad point immediately anterior to base of outermost seta (Figure 13h), glandular tissue within ramus as in *plumata*.

P5 (Figure 13i) similar to that in *morii* except that ratio of lengths of exopod to endopod tends to be smaller, median 1.29:1, range 1.07-1.50:1, 52 specimens (see Figure 29); Ri typically with two relatively equal apical spines (see Table 7).

Attached spermatophore observed in 27 specimens (see Table 5), not differing appreciably in general features from those observed in *morii*.

Male

Right furcal ramus similar to that in *morii* in both relative length (see Figure 26) and in proportion of length to width, median 1.88:1, range 1.71-2.07:1, 40 specimens (see Figure 28); Rel of left P5, compared to length of right furcal ramus, relatively longer than that in *morii* (see Figure 30), this ratio in *sobrina* ranging from 0.96-1.17:1, 21 specimens.

Etymology

The name *sobrina*, Latin for cousin, was chosen to acknowledge the close morphological relationship to *morii*.

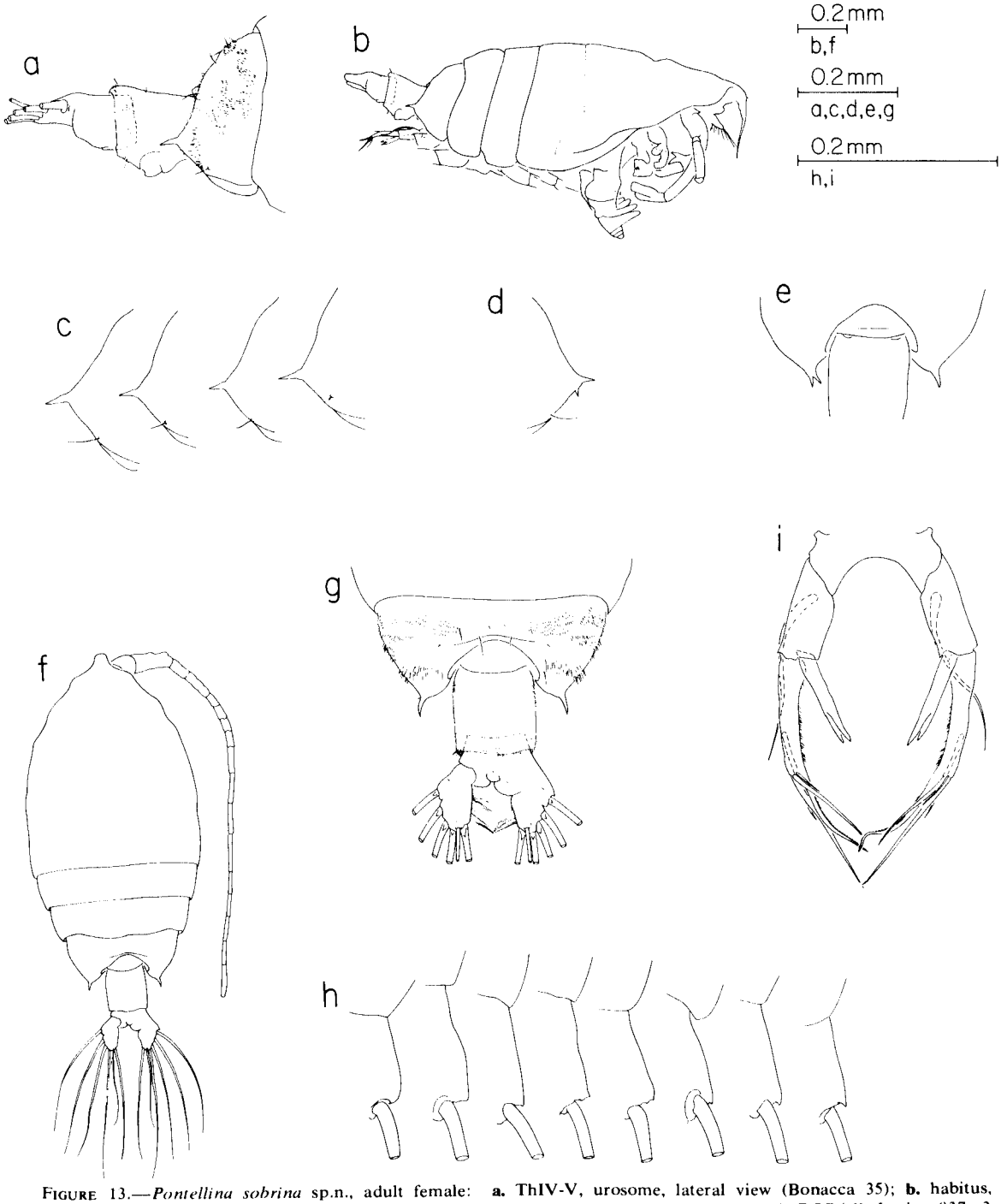

FIGURE 13.—*Pontellina sobrina* sp.n., adult female: **a.** ThIV-V, urosome, lateral view (Bonacca 35); **b.** habitus, lateral view (same as **a**); **c.** variation in ThIV-V spine, lateral view (left to right: EASTROPAC *Jordan* 037; 2 specimens Bonacca 31, Shellback 51); **d.** variation in left ThIV-V, lateral view, specimen with two spines (Bonacca 50); **e.** variation in left ThIV-V, dorsal view (La Creuse OT-6); **f.** habitus, dorsal view (same as **a**); **g.** ThIV-V and urosome, dorsal view (same as **a**); **h.** variation in lateral margin of right furcal ramus, dorsal view (left to right: La Creuse OT-6; La Creuse 18; La Creuse OT-14; La Creuse 17; La Creuse OT-14, different specimen; 2 specimens La Creuse 18; Bonacca 33); **i.** P5, anterior view (same as **a**).

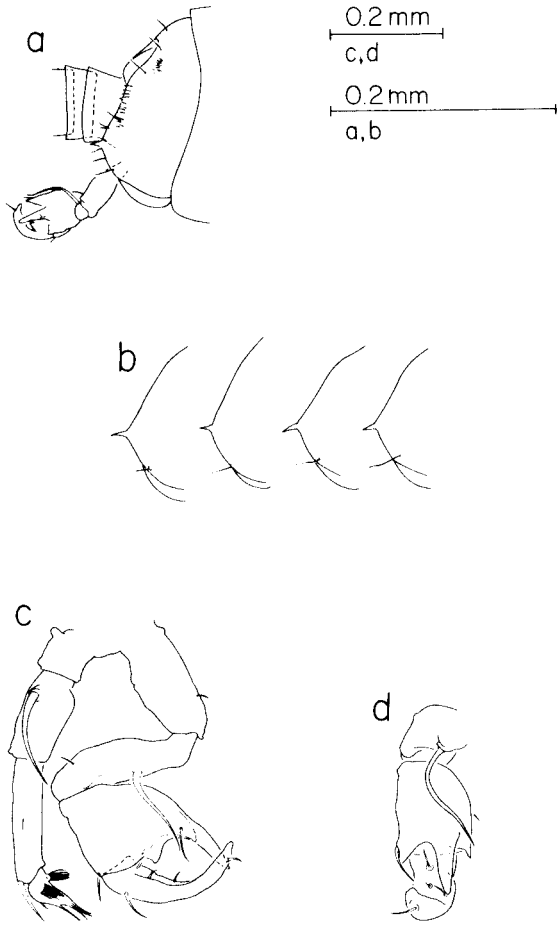

FIGURE 14.—*Pontellina sobrina* sp.n., adult male: **a.** ThIV-V, part of urosome and P5, lateral view [TO-58-1 (Scot) 33]; **b.** variation observed in ThIV-V spine, lateral view (left to right: Bonacca 55; Bonacca 43; 2 specimens Bonacca 51); **c.** P5, posterior view (La Creuse 21); **d.** chela P5, lateral view (Shellback 51).

Types

Holotype: Adult male, TL 1.42 mm, PUR 3.44:1, sorted from plankton sample taken at Bonacca stn. 51, lat. 13°44′N, long. 90°51′W, 19 Aug. 1963, ½-m net, oblique tow, maximum cable out 200 m. USNM No. 141617.

Allotype: Adult female, TL 1.52 mm, PUR 3.75:1, right furcal ramus length 0.080 mm, width 0.075 mm, from same sample as male. USNM No. 141618.

Paratypes: 5♂, 5♀ from same sample. USNM No. 141619.

Reference specimens: 5♂, 5♀, La Creuse stn. 15, lat. 08°41.2′N, long. 79°31.2′W, 4 May 1962, GV net towed between 0 and 4 m. USNM No. 141620.

Distribution

P. sobrina is obviously indigenous to the eastern tropical Pacific Ocean (Figure 15). The species was found only at Pacific stations east of long. 130°W. Occurrences at latitudes higher than 20° were restricted to a few samples taken near the mouth of the Gulf of California. Thus, the apparent boundaries coincide in general with the North and South Equatorial Currents, and its westernmost limits lie in the path of the Equatorial Countercurrent.

In 31 quantitative samples containing *sobrina* abundance varied from 0.01 to 0.66 individuals per m^3, the median being 0.04. In the sets of samples selected for quantitative analysis (Figure 1b) *sobrina* showed mean abundance values (ranging from 0.02 to 0.09 individuals per m^3) similar to those of *morii* in the Indian Ocean and to *plumata* outside of the eastern tropical Pacific (see Figure 35, Table 18).

DEVELOPMENTAL STAGES AND BREEDING

Immature specimens of *Pontellina* were sorted routinely together with adults. They were neither as abundant nor as frequent as the adults, a difference that is at least partially attributable to escapement of younger stages through the relatively coarse mesh (~0.5 mm) of most of the nets used to obtain our samples. General *Pontellina* habitus characteristics such as appearance of the prosome in dorsal view, rostrum, strong Mx2, and relatively long setae on A2 and Mnd served to distinguish the specimens. The number of swimming legs and body segments as well as total body length were used to determine their ontogenetic stage. Identification to species was reasonably certain only for stage V copepodids; details are presented below. Specimens of stages III and IV were tentatively assigned to species on the basis of their geographical origin. The following

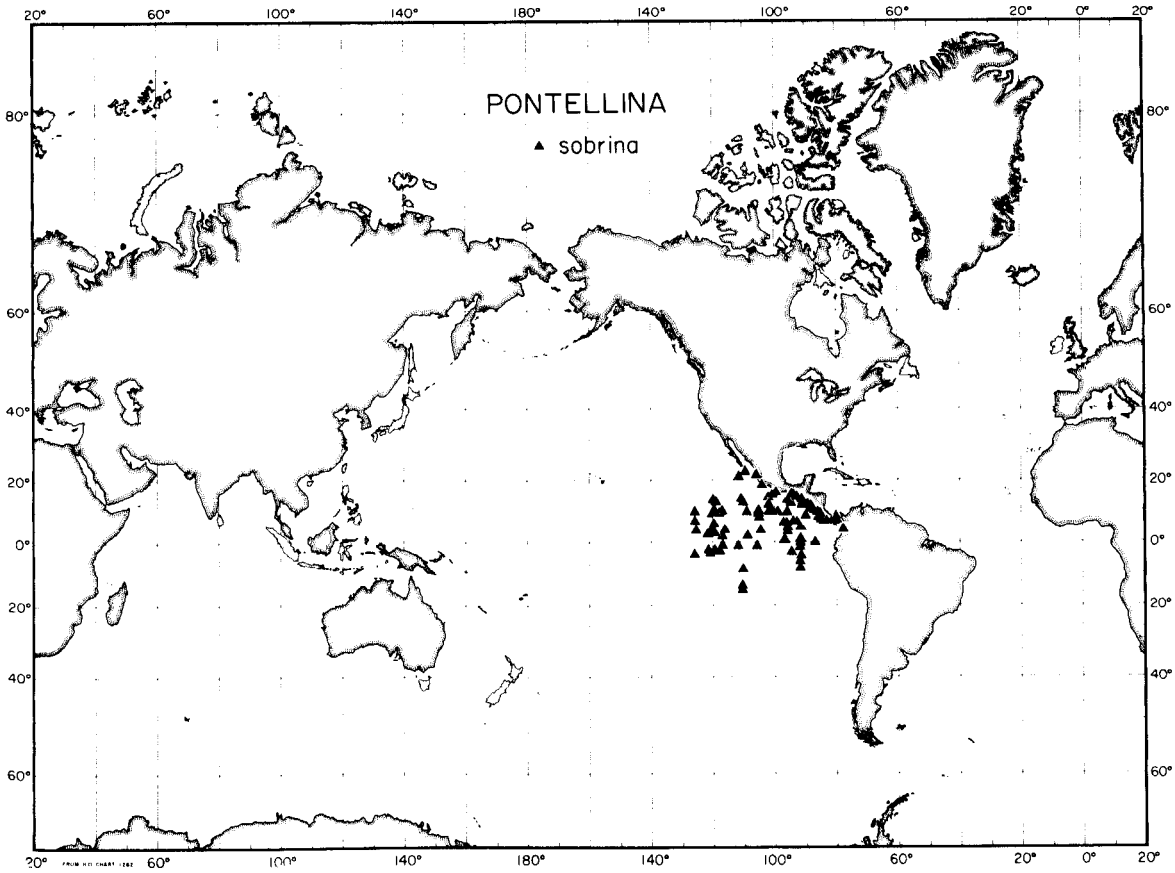

FIGURE 15.—*Pontellina sobrina* sp.n. Geographical distribution of captures recorded during the present study.

notes and Table 3 summarize ontogenetic characteristics of stages II through V prevailing in the genus.

Stage II

TL 0.72-0.76 mm (5 specimens). Rostral filaments and dorsal ocelli-like structures present; prosome with 4 free segments, urosome with 2 segments. Re of P1 and P2 bimerous, Ri of P1 and P2 and both rami of P3 unimerous, P4 consisting of a pad with folds, short setae and an incipient Ri; P5 lacking.

Stage III

(Figure 16c)

TL 0.82-0.88 mm (20 specimens). Neither sexes nor species distinguishable. Prosome with 5 segments, urosome with 2 segments. Re of P3 bimerous, Ri of P3 as well as both rami of P4 unimerous. P5 lobiform, bearing one apical seta.

Stage IV Female

(Figure 16a)

TL 0.90-1.10 mm (22 specimens, probably including all four species). Urosome with 3 segments. Re of P3 and P4 bimerous, Ri unimerous. Re of P5 unimerous; right Re and elongate seta on mediodistal corner of Re slightly larger than those of left P5; Ri lobiform, incompletely separated from B2.

Stage IV Male

(Figure 16b)

TL 0.95-1.10 mm (22 specimens, probably including all four species). Male resembles

TABLE 3.—Ontogenetic development in copepodite stages of *Pontellina*.

	II	III	IV♂	IV♀	V♂	V♀
Thoracic segments	4	5	5	5	5	5
Free abdominal segments	2	2	3	3	4	3
Rostral filaments	present	present	present	present	present	present
Dorsal ocelli	present	present	present	present	present	present
Right A1					segments 13-16 swollen	
P1 Re segments	2	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P2 Re segments	2	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P3 Re segments	1	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P4 Re segments	lobe, 1 seta	1	2	2	3	3
Ri segments	lobe, 1 seta	1	1	1	2	2
P5 Re segments	absent	lobe, 1 seta	1 right leg slightly larger than left	1 right leg slightly larger than left	2 right leg larger than left	1 right leg with 5 setae, left leg with 6 setae
Ri segments	absent	absent	rudimentary	1	absent	1

corresponding stage of female, but P5 with Ri absent or appearing as a small distal swelling on B2. Right Re also slightly larger than left.

Stage V Female

(Figure 17a-l)

TL 1.18-1.48 mm (40 specimens, all species represented). ThIV and V almost completely separated. Urosome with 3 segments, genital segment largest and with weak ventral swelling. Furcal rami incompletely separated from anal segment. Lateral margin of right furcal ramus proximal to first seta lacking protrusion. Left and right A1 symmetrical. Re of P3 and P4 trimerous, Ri bimerous. P5 with proportions of Re and Ri showing similarity to those of adult. Re unimerous with 5 setae on right leg, 6 setae on left leg; proximal Si of left side notable for its size and curved shape, an asymmetry lacking in the adult.

Stage V Male

(Figure 18a-q)

TL 1.20-1.44 mm (40 specimens, all species represented). ThIV and V almost completely separated. Urosome with 4 segments. Furcal rami incompletely separated from anal segment.

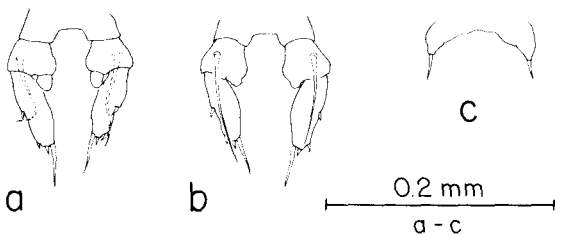

FIGURE 16.—*Pontellina* sp. copepodite stages: **a.** stage IV female, P5, anterior view; **b.** stage IV male, P5, posterior view; **c.** stage III copepodid, P5.

Right A1 with segments 13-16 slightly swollen, segments distal to swelling partly fused. P5 trimerous, slightly curved medially; right leg longer than left leg, Ri not developed.

In other genera of Pontellidae, as well as in a number of other heterarthrandrid families (Diaptomidae, Temoridae, Centropagidae, Pseudodiaptomidae) we note that fusion of urosomal segments I and II in the female first appears in the stage V copepodid (Gurney, 1931; Johnson, 1935; Crisafi, 1960; Lawson and Grice, 1970; Grice, 1971). Morphological features of the genital plate, antrum, and internal structures such as the seminal receptacles (Fahrenbach, 1962; Frost and Fleminger, 1968) are lacking in the stage V female. We also note that in most amphascandrid families (e.g., Calanidae, Para-

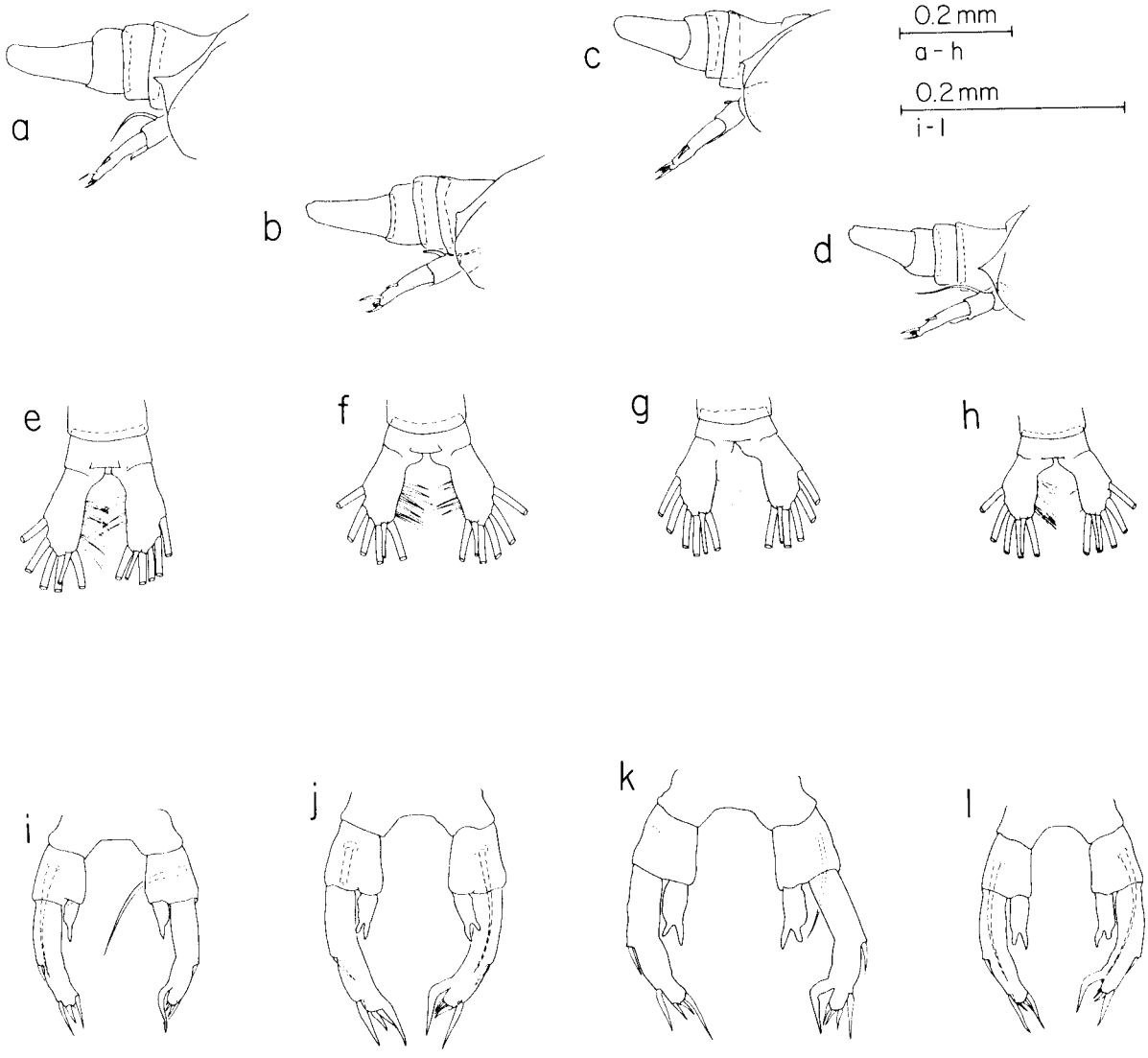

FIGURE 17.—Copepodite stage V, females: **a-d.** ThIV-V, right P5 and urosome, lateral view; **e-h.** anal segment, furcal rami, dorsal view; **i-l.** P5, anterior view. *Pontellina plumata:* **a, e** (*Atlantis II*-31-1); **i** (Lusiad V-60). *P. platychela:* **b, f, j** (*Atlantis II*-20-42). *P. morii:* **c, g, k** (Dodo VI, near Mombasa Harbor). *P. sobrina:* **d, h, l** [TO-58-1 (Scot) 56].

calanidae, Pseudocalanidae, Aetideidae, Euchaetidae, Phaennidae, Scolecithricidae) but not in Eucalanidae (Johnson, 1937; Sewell, 1929; Björnberg, 1967; and our unpublished observations of all species) fusion of urosomal segments I and II seems to be delayed until the appearance of the sexually mature female. This pattern has been documented by a number of ontogenetic studies on individual species (With, 1915; Nicholls, 1934; Campbell, 1934; Marshall and Orr, 1955; Matthews, 1964; and our unpublished observations).

Notes on Individual Species

Pontellina plumata
(Figures 17a, e, i; 18a, e, i, m, p)

Copepodite stage V female: TL $\bar{x}$ 1.38 mm, range 1.26-1.48 mm, 10 specimens. Posterolateral corner of ThV (Figure 17a) produced into a strong point similar to the adult. Furcal rami symmetrical (Figures 17e, 19), length of right ramus relative to width greater than that in *morii* (Figure 20). P5 Ri shorter than in *morii*

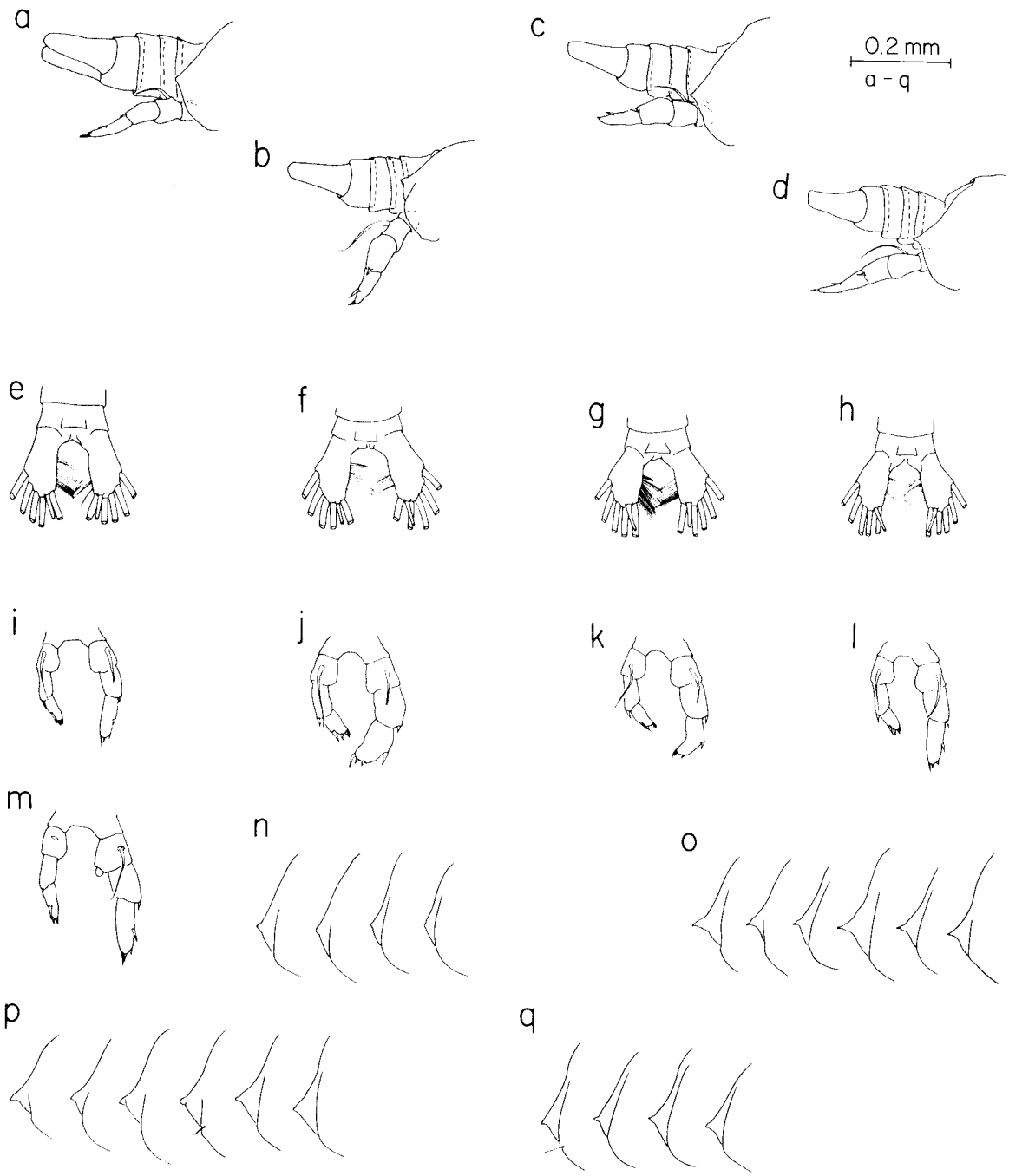

FIGURE 18.—Copepodite stage V, males: **a-d.** ThIV-V, right P5 and urosome, lateral view; **e-h.** anal segment, furcal rami, dorsal view; **i-m.** P5, posterior view; **n-q.** range of variation in ThIV-V, lateral view. *Pontellina plumata:* **a, e, i** (Lusiad V-43); **m** (Monsoon 2, atypical P5 with Ri); **p** (left to right: *Atlantis II*-31-74; *Atlantis II*-31-7; *Atlantis II*-31-28; *Atlantis II*-31-23; *Gascoyne* G1/32/63; Troll 25A). *P. platychela:* **b** (*Atlantis II*-31-60); **f, j** (*Atlantis II*-31-15); **n** (left to right: *Oregon* 1289; *Atlantis II*-31-50; *Atlantis II*-20-42; *Atlantis II*-31-57). *P. morii:* **c, g, k** (Lusiad V-43); **q** (left to right: EQUAPAC *Horizon* 31; Lusiad V-68; *Anton Bruun II*-58; *Anton Bruun I*-60). *P. sobrina:* **d, h, l**: La Creuse 18); **o** [left to right: EASTROPAC *Rockaway* 064; TO-58-1 (Scot) 29; TO-58-1 (Scot) 38; EASTROPAC *Rockaway* 071; TO-58-1 (Scot) 36; EASTROPAC *Rockaway* 056].

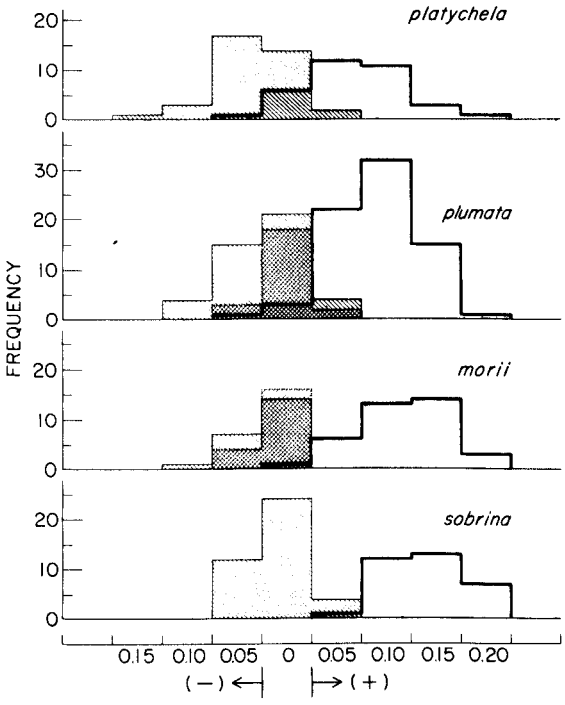

FIGURE 19.—Frequency distribution of differences in length of left furcal ramus and right furcal ramus for the four species of *Pontellina*. Gray with heavy outline = adult females; left-diagonal hatch with light outline = adult males; right-diagonal hatch with dotted outline = stage V females.

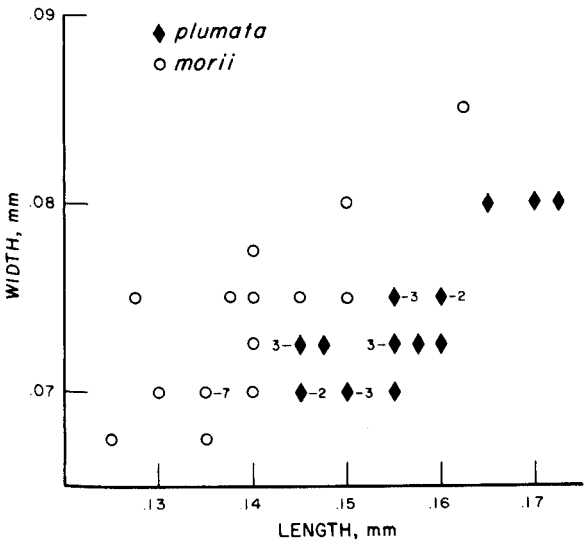

FIGURE 20.—Width of right furca (ordinate) plotted against length (abscissa) for female stage V copepodids of *Pontellina plumata* and *P. morii*.

relative to length of right furcal ramus (Figure 21). Re to Ri length ratio, median 3.0:1, range 2.3-3.5:1, 19 specimens (Figure 22); left P5 with medialmost seta on Re small and gently curved (Figure 17i) relative to that in *morii* (Figure 17k).

Copepodite stage V male: TL $\bar{x}$ 1.30 mm, range 1.20-1.44 mm, 10 specimens. Posterolateral corner of ThV ending in a broad point (Figure 18a, p). Terminal segment of right P5 about 3.1 times longer than wide (Figure 18i), endopod rarely present (Figure 18m). Furcal rami (Figure 18e) similar in relative length and width to those of female.

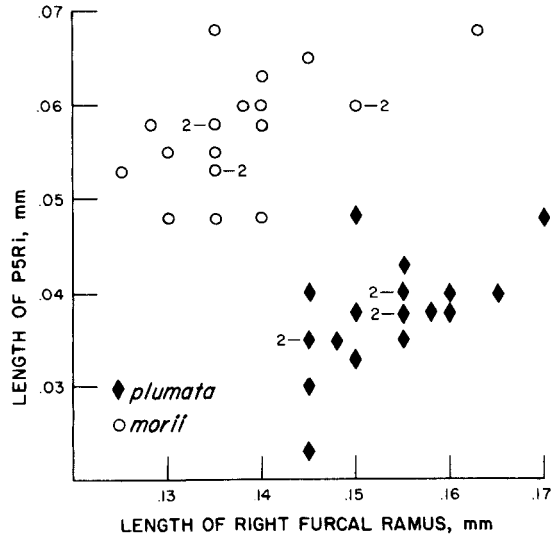

FIGURE 21.—Length of P5 Ri (ordinate) plotted against length of right furcal ramus (abscissa) for female stage V copepodids of *Pontellina plumata* and *P. morii*.

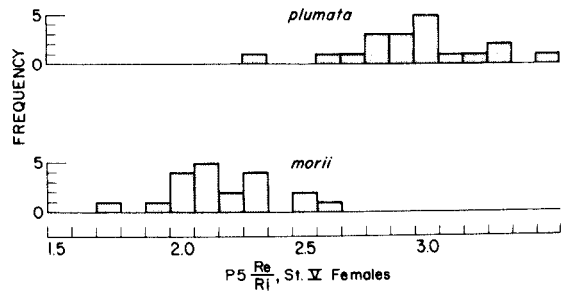

FIGURE 22.—Frequency distribution of P5 Re:Ri ratio for female stage V copepodids of *Pontellina plumata* and *P. morii*.

Pontellina platychela
(Figures 17b, f, j; 18b, f, j, n)

Copepodite stage V female: TL $\bar{x}$ 1.37 mm, range 1.18-1.46 mm, 10 specimens. ThV posterolateral corners rounded and ending in a small denticle (Figure 17b) as in adult. Furcal rami (Figure 17f) and P5 (Figure 17j) resembling those of *plumata*.

Copepodite stage V male: TL $\bar{x}$ 1.30 mm, range 1.24-1.36 mm, 10 specimens. Margin of posterolateral corner of ThV with weak denticle (Figure 18b, n). P5 with distinctive right leg (Figure 18j), Re considerably broader than in the other three species, about 1.6 times as long as wide. Furcal rami (Figure 18f) as in *plumata*.

Pontellina morii
(Figures 17c, g, k; 18c, g, k, q)

(Notes based on specimens from localities in the Indian Ocean.)

Copepodite stage V female: TL $\bar{x}$ 1.28 mm, range 1.18-1.36 mm, 10 specimens. ThV corner typically with a small spiniform point (Figure 17c) resembling that in the adult. Ri of P5 (Figure 17k) longer than in *plumata* (Figure 21), typically with 2 spines; Re:Ri length ratio considerably less (median 2.1:1, range 1.7-2.6:1, 20 specimens) than in *plumata* (Figure 22). Furcal rami symmetrical (Figure 19), shorter than those in *plumata* (Figure 20), as in sexually mature stages. Medial setalike process of Re of left P5 (Figure 17k) more abruptly bent (~90°) than that of the other three species (Figure 17i).

Copepodite stage V male: TL $\bar{x}$ 1.21 mm, range 1.12-1.32 mm, 10 specimens. Posterolateral corner of ThV ending in a relatively short spiniform point (Figure 18c, q) about one-half the length of that in *sobrina* (Figure 18d, o) and much less robust than that in *plumata* (Figure 18a, p). Distal segment of right P5 distinctly bent mediad (Figure 18k). Furcal rami (Figure 18g) similar in relative length and width to those in female.

Pontellina sobrina
(Figures 17d, h, l; 18d, h, l, o)

(Notes based on juvenile specimens from easternmost Pacific localities which were accompanied by large numbers of adults; the localities are relatively distant from those yielding *morii*.)

Copepodite stage V female: TL $\bar{x}$ 1.25 mm, range 1.18-1.34 mm, 10 specimens. Differences between sexually immature *sobrina* and *morii* females are relatively weak, e.g., greater length of the ThV point (Figure 17d) and the weaker bend of the medial setalike process on the left Re of P5 (Figure 17l), appear to be useful, but lack confirmation by measurements from a geographically representative series of specimens.

Copepodite stage V male: TL $\bar{x}$ 1.25 mm, range 1.12-1.38 mm, 10 specimens. Posterolateral corner of ThV produced into a relatively long slender point (Figure 18d, o). Right P5 with straight distal segment resembling that in *plumata*, but all segments in P5 of *sobrina* appear slightly wider.

Sex Ratios

In laboratory-reared populations sex ratios among adult copepods of several families have been found to vary widely (for recent comments see Heinle, 1970; Katona, 1970; Paffenhöfer, 1970). In natural populations, however, late immature copepodids have been found to produce males and females in about equal numbers (Marshall, 1949). Among randomly sorted, sexually mature adults of the four species of *Pontellina* females consistently outnumbered males by roughly 1.3:1 (Table 4).

Assuming that the sexes are genetically one to one, the observed male-to-female ratios in *Pontellina* could be readily accounted for if females live longer than males, a likelihood suggested by many authors for various amphascandrid copepod genera. In a small series of rearing experiments on *Labidocera trispinosa*, A. Barnett (pers. comm., 1972) has found that following the adult moult females live 2 to 3 wk and males about 1 wk.

TABLE 4.—Frequency of sexually mature individuals and sex ratios in *Pontellina*.

Species	♀ N	♀ %	♂ N	♂ %	♀:♂	No. samples
platychela	[1]159	54	[1]137	46	1.16	72
plumata	1,259	58	917	42	1.37	531
morii	433	60	284	40	1.52	240
sobrina	421	54	364	46	1.16	113

[1] One sample, i.e., *Atlantis II* 20-42, was omitted because it provided the extremely disproportionate capture of 327 males and 10 females.

REMARKS ON SEASONAL OCCURRENCE AND BREEDING

Capture records alone do not necessarily disclose the distribution of the optimal habitat of a planktonic species (Fleminger, 1972), i.e., the region in which reproduction is usual, typically successful, and from which the progeny is likely to become entrained in a circulation system that ultimately provides new breeding stocks with suitable conditions for their offspring. Our sampling of *Pontellina* is incomplete for critical assessment of the impact of seasonal change on occurrence, geographical distribution, or reproduction. Moreover, as a consequence of the relatively large mesh sizes of the nets (see Table 15) sampling of most juvenile stages was not representative. Thus spermatophore occurrence on females is the only source of breeding information available to us.

In *Calanus*, spermatophores constitute evidence of mating within the past 48 h (Marshall and Orr, 1955). In other copepods, spermatophores are lost or shed soon after attachment; in *Labidocera trispinosa* discarding of the spermatophore has been observed to occur just prior to egg laying (G. Theilacker, pers. comm., 1970).

Few spermatophores were observed in *Pontellina* (Table 5) suggesting that as in *Calanus* they are not retained for an appreciable time after attachment. The 27 records of *sobrina* females bearing a spermatophore afford a glimpse of breeding patterns in that species. Spermatophore-bearing females appeared in February, May, and August samples. The localities span most of the latitudinal extent of *sobrina* captures on record, but all lie to the east of long. 98°W, and most are relatively close to the mid-American coast. In contrast, the few records of *morii* and *plumata* bearing spermatophores are widespread, suggesting that both species breed over a more extensive range in accordance with their more extensive geographical distributions.

PHYLOGENETIC RELATIONSHIPS AMONG THE *PONTELLINA* SIBLINGS

Dobzhansky (1972) stressed the heuristic value of sibling species when he pointed out " . . . sibling species permit the dissection of the process of speciation into studiable components." *Pontellina* appears especially well suited to explore the question of speciation in the planktonic biotope. Restriction to shallow tropical and subtropical oceanic waters apparently limits opportunities for complex diversity in planktonic calanoids (Fleminger and Hulsemann, 1973). The four species of *Pontellina* satisfy the number of suitable ranges that appear to be available within these biogeographical limits.

Three of these ranges reflect the geographically limited and relatively shallow lenses of Tropical Surface Water (Wyrtki, 1966, 1967) described from the eastern equatorial Pacific but also known on the basis of similar general features to prevail in the equatorial Atlantic Ocean (Muromtsev, 1963) and in the equatorial Indian Ocean (Wyrtki, 1971). The fourth range consists of the series of deeper lenses of warm water beyond Tropical Surface Waters and lying between the subtropical convergences in the Atlantic, Indian, and Pacific Oceans.

Pontellina's position as a distinctive genus is unchallenged, being strongly separated from its closest relative, *Pontellopsis*, in both morphology and habitat. Compelling evidence favoring consideration of the four populations of *Pontellina* as separate species is furnished by the morphological distinctions of each, their independent geographical distributions, and the morphological integrity of their diagnostic features. That is, despite widespread regions of geographical overlap where two or three of the species may be captured in the same net tow, no evidence of intergradation or hybridization has been observed.

Evidence of strongly regionalized habitat adaptation may be inferred from the apparent failure of each species to colonize areas occupied by its adjacent congener. Failure to colonize must be regarded as significant. All four species occur in surface layers (Wilson, 1942; Heinrich, 1961; Vinogradov and Voronina, 1964; Fleminger and Hulsemann, unpublished data) where air-sea interactions provide opportunity for dispersal and advection with neighboring circulation systems, but the distribution of each species overlaps at most only a portion of the range of its neighboring congeners.

TABLE 5.—Adult female specimens of *Pontellina* bearing a spermatophore.

Species	Sampling date	Latitude	Longitude	Station	Total length (mm)	Sac length (mm)
P. platychela	III-8-66	00°08'S	18°31'W	*Atlantis II*-20-42	1.66	0.490
P. plumata	VI-15-69	33°49'N	139°10'E	Scan IV-1	1.66	0.460
					1.76	0.460
	VI-6-52	01°00'S	112°24'W	Shellback 47	1.50	0.425
	III-30-69	21°54'S	110°02'W	Piquero V-49	1.56	0.365
P. morii	IV-19-68	05°11'N	123°58'E	Circe II-NT 11	1.58	0.420
	VII-2-52	05°18'S	85°04'W	Shellback 105	1.86	0.440
P. sobrina	II-12-67	00°28'N	92°02'W	EASTROPAC *Rockaway* 060	1.68	0.390
	V-12-58	07°22'N	92°47'W	Scot 46	1.56	0.360
					1.70	0.395
	V-4-62	08°41'N	79°31'W	La Creuse 15	1.40	0.340
					1.44	0.385
					1.46	0.370
					1.42	0.355
	V-7-58	09°45'N	96°04'W	Scot 35	1.62	0.410
	VIII-16-63	09°51'N	85°43'W	Bonacca 42	1.48	0.385
					1.46	0.320
	V-17-62	13°07'N	91°34'W	La Creuse OT-6	1.48	0.330
					1.50	0.355
	VIII-18-63	13°29'N	90°09'W	Bonacca 50	1.50	0.320
					1.62	0.360
					1.52	0.340
					1.48	0.340
	VIII-19-63	13°44'N	90°51'W	Bonacca 51	1.50	0.390
					1.52	0.340
	VIII-20-63	13°57'N	92°02'W	Bonacca 58*	1.54	0.390
					1.56	0.415
					1.48	0.355
					1.56	0.365
					1.50	0.375
					1.50	0.380
					1.52	0.395
					1.50	0.385

* One additional specimen was observed in this sample with a damaged spermatophore.

Morphology and distribution also support our conclusion that the four species are phylogenetically close and, in fact, comprise a monophyletic unit—or holophyletic in Ashlock's (1971) terminology—appearing to have been recently derived from a single tropical-subtropical epiplanktonic precursor (in preparation).

Our objective in this section is to examine the degree of similarity among the siblings as a basis for determining phylogenetic relationships. In the absence of a fossil record, inferences drawn from comparative morphology, geographical distribution, and essential habitat adaptation may provide a relative historical perspective for judging phylogeny within a taxon.

Phylogenetic relationships within *Pontellina* were judged both intuitively and objectively on the basis of characters that showed a cohesive pattern of similarity or dissimilarity. We concur with the rebuttals of Throckmorton (1965, 1968) and Voris (1971) to the views of orthodox numerical taxonomy in defense of the weighting of taxonomic characters: i.e., characters differ in their taxonomic usefulness, and the adaptive significance of these differences is not beyond logic and comprehension.

Throckmorton and Voris show empirically that characters are decidedly not equal in their content of phylogenetic information. Their operational method for character selection rests upon the direct and assumption-free advantages of *a posteriori* weighting of correlated sets of derived characters.

Judging from the numerous articles in Systematic Zoology, numerical taxonomic phylogenies derived from large numbers of unweighted characters do not vary from phylogenies implicitly or explicitly arranged by experienced workers employing sets of correlated adaptive characters.

Body Dimensions and Proportions

Total Length (TL)

Intraspecific sexual differences in TL are greater than interspecific differences; males are about 10% shorter than females (Table 6, Figure 23). In both sexes *morii* and *sobrina* are smaller than *platychela* and *plumata*. The difference between the mean TL of males or females of species belonging to the same pair is not significant. However, the difference between the mean TL of either species of one pair with that of either species in the other pair is highly significant in both sexes (Student's *t*-test). The overall difference is produced largely by the distance between the rostrum and the cephalic groove and the length of the furca (see below).

Prosome-Urosome Length Ratio (PUR)

In both sexes *morii* and *sobrina* occur at the high end of the PUR distribution (Table 6, Figure 24). In males, *morii* and *sobrina* have similar distributions at the high end of the

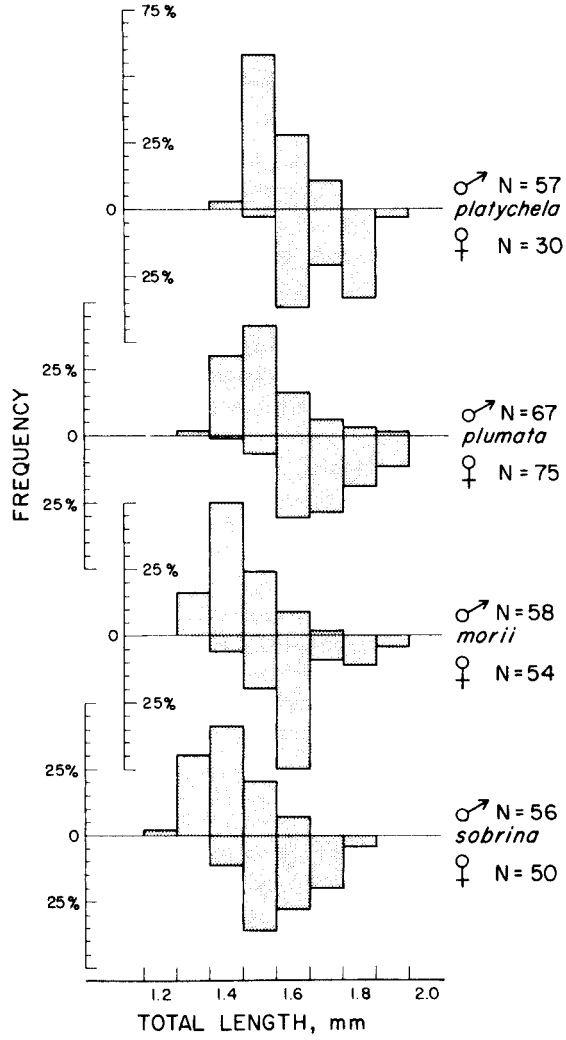

FIGURE 23.—Frequency distribution of total length for both sexes of the four species of *Pontellina*.

TABLE 6.—Total length (TL) and prosome-urosome length ratio (PUR) of *Pontellina* spp. adults; data from various geographical localities combined.

	TL (mm)				PUR			
Species	$\bar{x}$	Range	$s_{\bar{x}}$	*N*	$\bar{x}$	Range	$s_{\bar{x}}$	*N*
Males:								
P. platychela	1.699	1.54-1.96	0.0173	30	3.438:1	3.19-3.89:1	0.0362	30
P. plumata	1.692	1.44-1.94	0.0126	75	3.282:1	2.92-3.72:1	0.0179	75
P. morii	1.608	1.38-1.88	0.0145	54	3.643:1	3.39-4.10:1	0.0360	35
P. sobrina	1.570	1.42-1.78	0.0134	50	3.732:1	3.17-4.16:1	0.0417	33
Females:								
P. platychela	1.556	1.41-1.74	0.0089	57	3.223:1	2.86-3.55:1	0.0228	49
P. plumata	1.511	1.34-1.92	0.0130	67	3.066:1	2.84-3.93:1	0.0243	52
P. morii	1.435	1.26-1.68	0.0100	58	3.339:1	2.87-3.73:1	0.0245	50
P. sobrina	1.406	1.18-1.64	0.0118	56	3.426:1	3.06-3.75:1	0.0235	51

range, *platychela* being intermediate and *plumata* occupying the low end. Females follow the same general pattern, but *morii* and *sobrina* show considerably less overlap.

Length of Furcal Rami

The length of both rami is directly related to prosome length as well as TL. Shortening and fusion of the right ramus in adult females introduces asymmetry but the change does not alter the essential relationship to body length. In the female sex (Figure 25) *morii* and *sobrina* occupy one side of the overall distribution of length of the right ramus, *platychela* and *plumata* the other with virtually no overlap between the two pairs of species. Males show more scatter (Figure 26) and apparent differences in allometry; *sobrina* and *morii* tend to diverge with respect to furcal length while *plumata* and *platychela* tend to diverge with respect to prosome length.

Examination of furcal length relative to furcal width increases separation of the three equatorial species. It also enhances separation of *platychela* and the Atlantic samples of *plumata* as well as separation of *morii* and the Indo-Pacific samples of *plumata* (Figure 27). A generally similar pattern is seen in the males (Figure 28) except that *morii* and *sobrina* overlap freely with respect to the furcal length: width ratio.

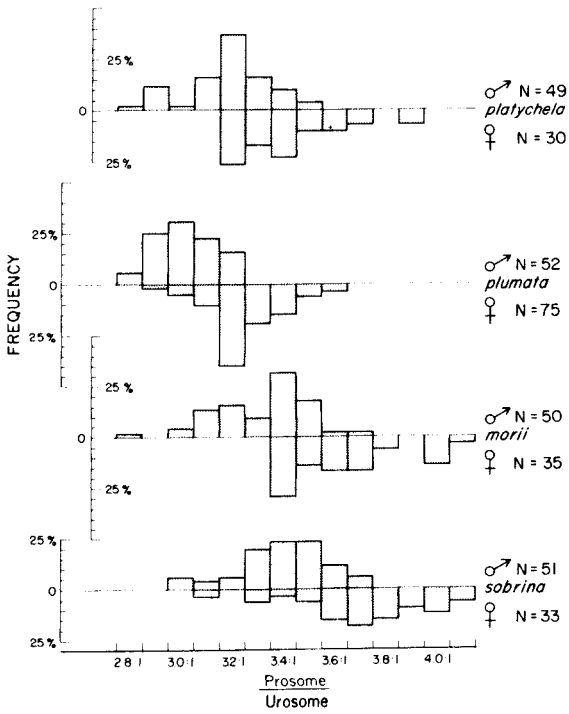

FIGURE 24.—Frequency distribution of P:U ratio for both sexes of the four species of *Pontellina*.

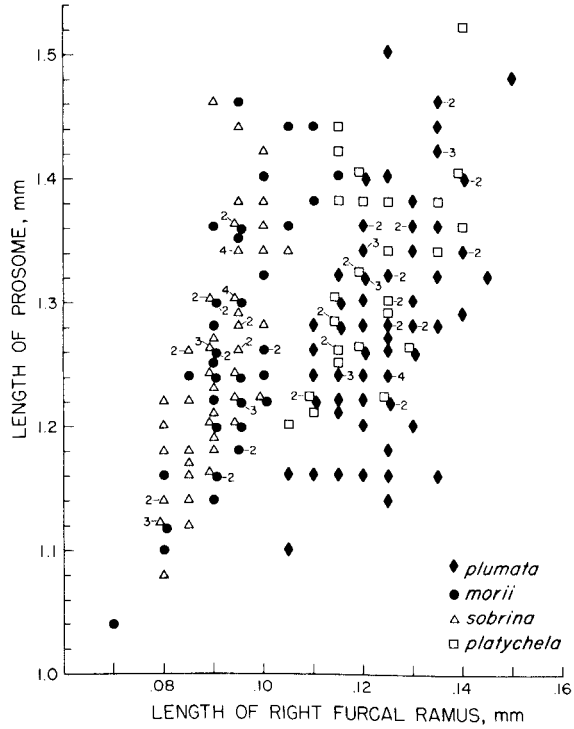

FIGURE 25.—Length of P (ordinate) plotted against length of right furcal ramus (abscissa) for females of the four species of *Pontellina*.

ThIV-V Posterior Spine

Strong sexual dimorphism appears in adults. Among the females, *plumata* is unique; the base of the posteriorly directed spine rises roughly at the level of the proximal margin of the genital segment, the spine is robust and broadly triangular in both dorsal and lateral views (Figure 3a, d-f). The spines in the three equatorial species are similar to each other in being diminutive and needlelike or dentiform. They differ primarily with respect to relative length of the spine (Figures 6a, c, g, h; 9a, c, e, f; 11; 13a, c, g).

The ThIV-V spine in males appears in three states: *plumata* exhibits a minute denticle that

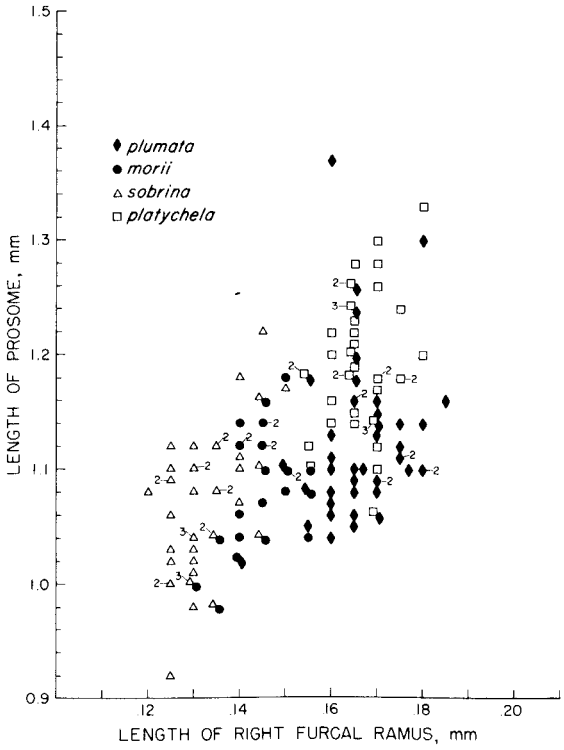

FIGURE 26.—Length of P (ordinate) plotted against length of right furcal ramus (abscissa) for males of the four species of *Pontellina*.

may be borne on a weakly produced boss; *morii* and *sobrina* bear a small spine resembling that found in the female of the species; *platychela* has no outgrowth whatsoever.

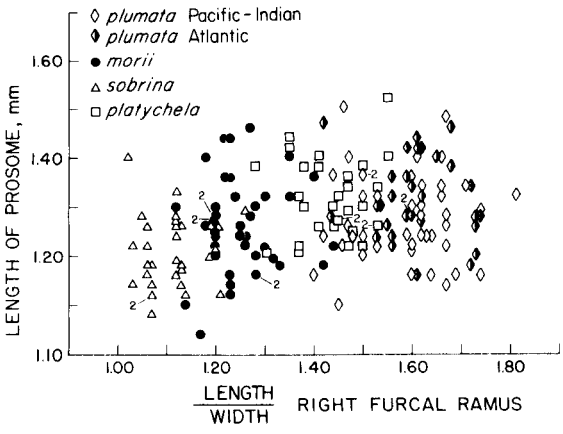

FIGURE 27.—Length of P (ordinate) plotted against length: width ratio of right furcal ramus (abscissa) for females of the four species of *Pontellina*.

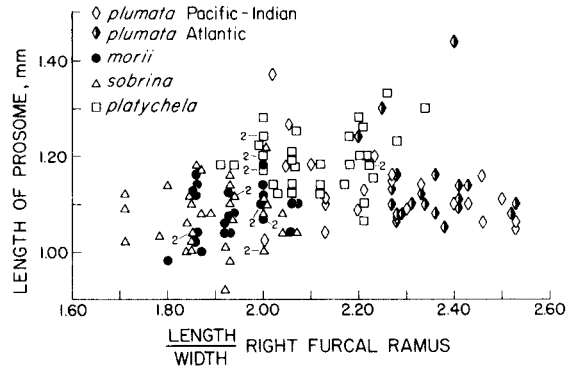

FIGURE 28.—Length of P (ordinate) plotted against length: width ratio of right furcal ramus (abscissa) for males of the four species of *Pontellina*.

Female Genital Segment

The distribution of lateral clusters of spinules provides the basis for distinguishing the different character states. Two species, *sobrina* and *plumata*, are similar in having two clusters on each side; *morii* has one cluster and *platychela* has none. There is preliminary evidence from examination with the scanning electron microscope (SEM), however, that the similarity of *plumata* with *sobrina* may in fact be superficial. Cluster size and spinule size differ even under the light microscope, and the SEM indicates the presence of fine sensoriiform filaments in *sobrina* and *morii*, but not in *plumata* or *platychela*. The SEM also revealed a second cluster consisting of minute denticles in *morii* anterior to the one visible with the aid of a light microscope (in preparation).

Female Fifth Pair of Swimming Legs

The two characters found in P5 that provide diagnostic information, i.e., the Re:Ri length ratio (Figure 29) and the distribution of spines on the endopod (Table 7) agree in showing strong similarity between *morii* and *sobrina* on the one hand and between *platychela* and *plumata* (all geographical sectors combined) on the other. It should be noted, however, that the similarity between *platychela* and *plumata* is weakened when the comparison is restricted to Atlantic Ocean samples of *plumata* (in preparation).

The distribution of the spines on the endopod is also noteworthy by virtue of the compelling

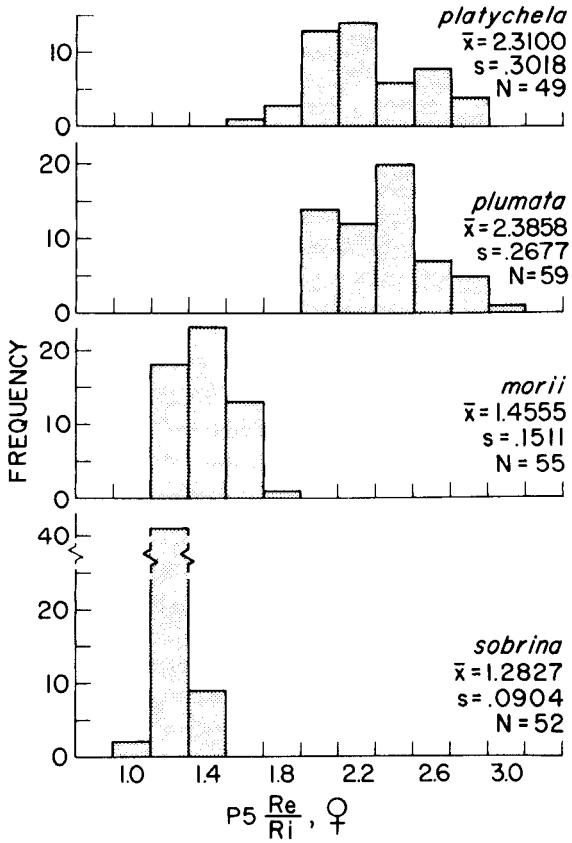

FIGURE 29.—Frequency distribution of P5 Re:Ri ratio for females of the four species of *Pontellina*.

evidence it provides in support of our judgment that the four siblings are valid species recently derived from the same parent species. The frequencies and widespread geographical occurrence of phenotypes are evidence of simple Mendelian inheritance and indicative of balanced polymorphism. Another pontellid, *Labidocera diandra*, has also been shown to be polymorphic (Fleminger, 1967b). In both *Pontellina* and *Labidocera* the apparent polymorphism affects a sexually modified appendage before the onset of maturity, the phenotypes being distinguishable in copepodite stage V. However, within its species group, only *L. diandra* displays the polymorphism which is visible in the male sex.

Male Fifth Legs and Right First Antenna

Segment lengths of sexually modified appendages that we examined tend to vary directly with prosome length. We chose the length of the right furcal ramus (Figure 25) instead of the prosome as our standard body length reference for comparing morphometry of sexual appendages because the furcal ramus length yielded graphic presentations with considerably less scatter within each sample.

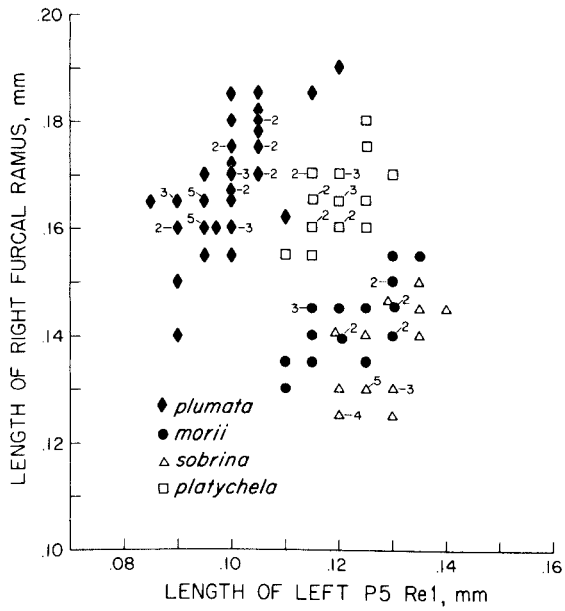

FIGURE 30.—Length of right furcal ramus (ordinate) plotted against length of left P5 Re1 (abscissa) for males of the four species of *Pontellina*.

TABLE 7.—Frequencies (%) of phenotypes varying in the number of spines on the endopod of the fifth pair of swimming legs in *Pontellina* spp. females.

Species (*N*)	Left leg: 1 spine Right leg: 1 spine	1 spine 2 spines	2 spines 1 spine	2 spines 2 spines
platychela (100)	34	16	12	38
plumata (300)	37	12	16	34
morii (200)	1	2	1	96
sobrina (100)	0	1	0	99

TABLE 8.—Dimensions of selected segments of sexually modified appendages of *Pontellina* spp. adult males.

Segments and species	$\bar{x}$(mm)	s	N	Range (mm)
Left P5 Re1 length:				
platychela	0.1193	0.0048	21	0.110-0.130
plumata	0.0988	0.0067	48	0.085-0.120
morii	0.1221	0.0079	19	0.110-0.130
sobrina	0.1269	0.0060	21	0.120-0.140
Right P5 Re1 width:				
platychela	0.1895	0.0109	20	0.170-0.210
plumata	0.1647	0.0112	47	0.140-0.195
morii	0.1960	0.0091	20	0.180-0.215
sobrina	0.1814	0.0098	21	0.165-0.200
A1 segment 18 length:				
platychela	0.3417	0.0152	26	0.300-0.365
plumata	0.3364	0.0220	32	0.285-0.400
morii	0.3063	0.0159	31	0.280-0.340
sobrina	0.3014	0.0137	29	0.280-0.335

Length of Left First Exopodal Segment

This segment is much shorter in *plumata* than in the other three species (Figure 30, Table 8). Small differences appear among the three equatorial species but they are inconspicuous in comparison to their distribution as a group relative to that of *plumata*.

Width of Right First Exopodal Segment

As in the section above on the left, Re1, the distributions of the three equatorial species broadly overlap, but *plumata* tends to be appreciably smaller (Figure 31, Table 8).

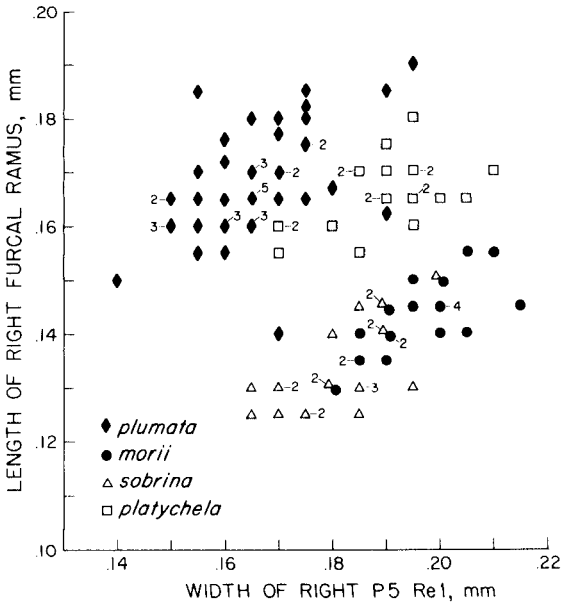

FIGURE 31.—Length of right furcal ramus (ordinate) plotted against width of right P5 Re1 (abscissa) for males of the four species of *Pontellina*.

Morphology of Right First Exopodal Segment

The proximal segment of the chela appears in three essential states: the swollen condition of *platychela* (Figure 7a, b), the slender condition of *plumata* (Figure 4i, j) and the slender condition characterized by a more distal position of the posterolateral outgrowth shared by *morii* and *sobrina* (Figures 11d, e; 14c, d).

Morphology of Right Second and Third Exopodal Segments

The distal segment of the chela appears in three states: the swollen condition of *platychela* (Figure 7b), the shortened, spurred condition of *morii* (Figure 11d, f) and the simple attenuated condition shared by *plumata* and *sobrina* (Figures 4j, 14d).

Length of Segment 18, Right First Antenna

Two siblings, *plumata* and *platychela*, broadly overlap and occupy the upper half of the overall distribution; the other two, *morii* and *sobrina*, broadly overlap in the lower half of the distribution (Figure 32, Table 8).

Spermatophore Attachment

(Figures 33, 34)

The three equatorial species agree in having

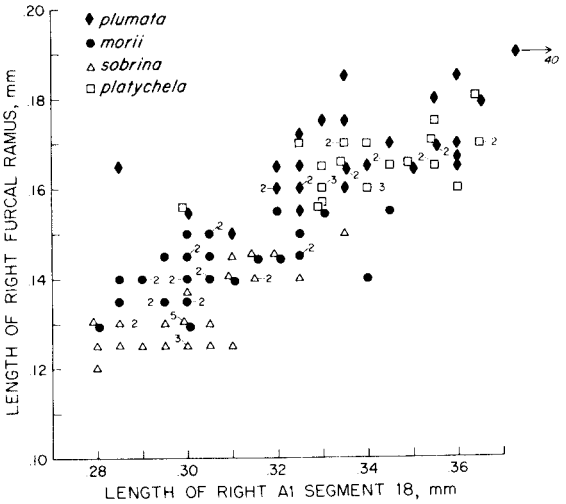

FIGURE 32.—Length of right furcal ramus (ordinate) plotted against length of segment 18 of right A1 (abscissa) for males of the four species of *Pontellina*.

the proximal end of the sac cemented to the right side of the genital segment, *morii* and *sobrina* in a virtually identical fashion, differing somewhat from the condition found in *platychela*. In *plumata*, however, attachment is restricted to the proximal end of the neck, the remainder of the neck and the entire sac hanging free from the body but showing helical convolutions similar to those present in the other congeners.

Geographical Occurrence

Three of the species, *morii*, *sobrina*, and *platychela*, were found primarily in low latitudes between 20°N and 20°S (Figures 8, 12, 15). The three species are essentially allopatric to one another, each predominating in a geographically different segment of equatorial circulation in the world's oceans (see Table 20). Relatively high frequencies of abundance or occurrence coincided with eutrophic equatorial regions characterized by a shallow O_2 minimum layer (≤ 1 ml/liter) lying at or near the permanent thermocline. The three species tend to concentrate in the uppermost 20 to 30 m of depth and virtually disappear below 50 m (in preparation).

The fourth sibling, *plumata*, is widespread in subtropical latitudes (Figure 5) and may be locally abundant in tropical regions downstream from areas of persistent upwelling. It is the only species of the genus with a circumglobal range but tends to be infrequent to absent in tropical areas dominated by its equatorial cognates (see Table 20). Its vertical distribution appears to encompass the surface to 200-m depth in subtropical latitudes, the lower limit shoaling to about 100 m in tropical latitudes (in preparation).

Summation of Phylogenetic Similarities

Thus within the framework of the 17 characters considered above, *morii* and *sobrina* show the highest frequency of similar character states. In practice their overall morphological similarity is sufficient to require routinely close inspection at appreciable magnifications for reliable separation. Though the next most frequently linked pairing, *plumata* and *platychela*, show similarity in about 60% of the features in Table 9, at low magnifications under a stereomicroscope they are almost as distinct from one another as each is from *morii* or *sobrina*.

As noted in the calanoid genera, *Labidocera* and *Clausocalanus* (Fleminger 1967b; Frost and Fleminger, 1968), the distinguishing features of the sibling species in *Pontellina* are limited to sexually modified characters, i.e., the fifth legs, the genital segment, the posterior corner of ThIV-V, the male right A1, and the caudal furca.

There is reason to regard *plumata* as retaining the strongest similarity to the *Pontellina* ancestral stock. This view rests upon two features: the slightly stronger resemblance of sexually modified structures in *plumata*, especially the ThIV-V spine in the female, to those of *Pontellopsis* and of the more eurytopic circumglobal distribution of *plumata* in comparison to the restricted distributions of its equatorial congeners.

To examine the statistical significance of the phylogenetic relationships inferred from the characters given in Table 9 we have utilized a computer program that detects significant levels of co-occurrence among sets of overlapping functions. The program has been informative in the detection of communities as well as in systematic classifications of flexibacteria (Fager, 1969).

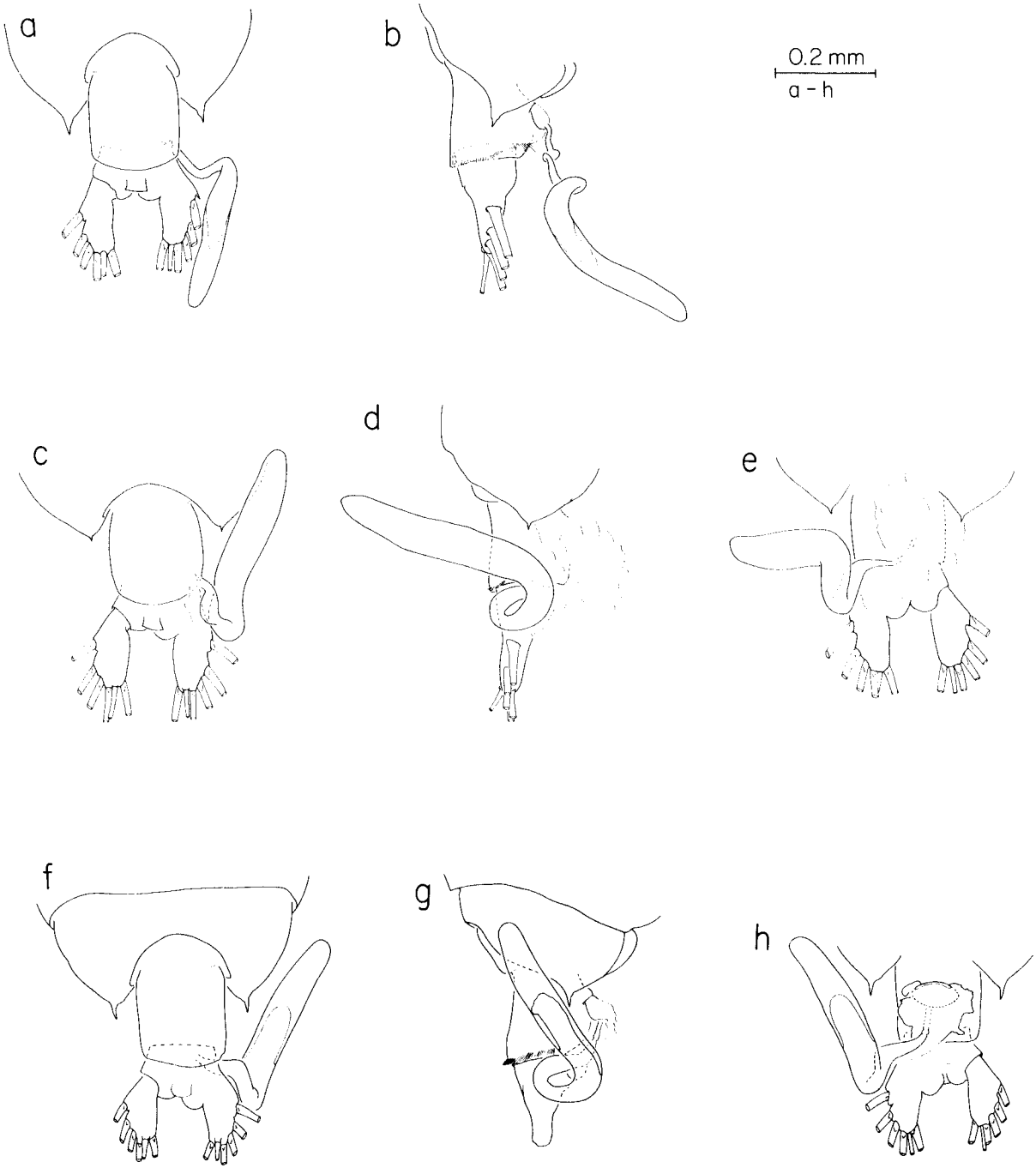

FIGURE 33.—ThIV-V and urosome of female with attached spermatophore. **a, b.** *Pontellina plumata*. **c-e.** *P. platychela*. **f-h.** *P. morii*. **a, c, f** dorsal view; **b, d, g** lateral view; **e, h** ventral view.

TABLE 9.—Shared character states among species of *Pontellina*.

Character	No. of states	Species sharing same state	Species with unique character state	Remarks
1. $\bar{x}$TL ♀	2	*morii* and *sobrina*; *plumata* and *platychela*		Significant differences produced by furcal ramus length
♂	2	*morii* and *sobrina*; *plumata* and *platychela*		
2. PUR ♀	2	*morii* and *sobrina*; *plumata* and *platychela*		Significant differences produced by furcal ramus length
♂	2	*morii* and *sobrina*; *plumata* and *platychela*		
3. Furcal ramus length ♀	2	*morii* and *sobrina*; *plumata* and *platychela*		
♂	2	*morii* and *sobrina*; *plumata* and *platychela*		
4. Furcal ramus length:width ratio ♀	2	*morii* and *sobrina*; *plumata* and *platychela*		
♂	2	*morii* and *sobrina*; *plumata* and *platychela*		
5. Th IV-V ♀	2	*morii*, *sobrina*, and *platychela*	*plumata*	
6. Th IV-V ♂	2	*morii* and *sobrina*; *plumata* and *platychela*		Minor differences between *plumata* and *platychela* ignored
7. Genital segment ♀	3	*plumata* and *sobrina*	*platychela*; *morii*	SEM results ignored
8. P5 ♀, Re:Ri ratio	2	*morii* and *sobrina*; *plumata* and *platychela*		
9. P5 ♀, Ri spines	4	*morii* and *sobrina*; *plumata* and *platychela*		
10. P5♂, left Re1 length	2	*morii*, *sobrina*, and *platychela*	*plumata*	
11. P5♂, right Re1 width	2	*morii*, *sobrina*, and *platychela*	*plumata*	
12. P5♂, right Re1 morphology	3	*morii* and *sobrina*	*plumata*; *platychela*	
13. P5♂, right Re 2-3 morphology	3	*plumata* and *sobrina*	*morii*; *platychela*	
14. A1 ♂ right seg. 18 length	2	*morii* and *sobrina*; *plumata* and *platychela*		
15. Spermatophore attachment	3	*morii* and *sobrina*	*plumata*; *platychela*	
16. Geographical distribution	4		*plumata*; *platychela*; *morii*; *sobrina*	
17. Latitude and depth distribution	2	*morii*, *sobrina*, and *platychela*	*plumata*	

Frequency of similarities in 17 characters:

morii and *sobrina* linked in 15 instances or 82%.
platychela linked with *morii* and *sobrina* in 4 instances or 24%.
plumata and *platychela* linked in 10 instances or 59%.
plumata and *sobrina* linked in 1 instance or 6%.
plumata unique in 7 instances or 41%.
platychela unique in 5 instances or 29%.
morii unique in 3 instances or 18%.
sobrina unique in 1 instance or 6%.

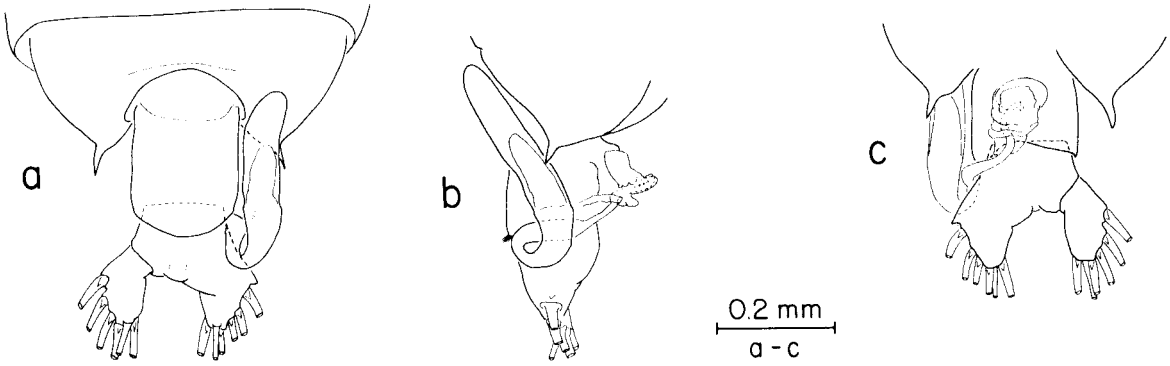

FIGURE 34.—ThIV-V and urosome of female *Pontellina sobrina* with attached spermatophore: **a.** dorsal view; **b.** lateral view; **c.** ventral view.

The program calculates an index of affinity for all possible pairs of species as the geometric mean of the proportion of common character states corrected for the number of characters used in the analysis: i.e., $J/\sqrt{A \times B} - \frac{1}{2}\sqrt{B}$, where A and B are the total number of characters recorded for the two species, $B \geqslant A$, and J is the number of shared character states. Values of the index above 0.5 have been found empirically to provide objective repeatable groupings of related sets of values.

A number of characters listed in Table 9 were omitted from the recurrent group analysis to avoid biasing the computations with redundant information. Characters 1, 2, and 4 were not scored since their morphometric states are determined largely by the value of character 3. Characters 11 and 14 were deleted since they parallel character 10 in showing a direct relationship to TL and to furcal length. In the absence of a fossil record the distributional characters 16 and 17 were not scored on the intuitive grounds that they are complex derivatives of both 1) overall genetic adaptation and 2) fortuitous abiotic historical events that might obscure essential phylogenetic patterns. All of the scored characters were weighted equally and disregard the preliminary results from SEM observations.

The recurrent group analysis reveals only one grouping with an index higher than 0.5, that of *morii* and *sobrina* (Table 10). Similarity between *plumata* and *platychela* falls well below the acceptable level of significance. The other possible pairings are dissimilar in most to virtually all of the 10 characters used in the analysis. Assuming equal rates of evolution the results indicate that the divergence of *plumata*, *platychela*, and the *morii-sobrina* lineage are likely to be divisions of greater age than that of *morii* and *sobrina*.

GEOGRAPHICAL VARIATION AND SYMPATRY

In the course of this study two conspicuous and parallel instances of geographical variation were encountered in the fifth legs of *plumata* females. This variation was expressed in the number of spines at the distal end of the endopod and the length of the exopod relative to that of the endopod.

As noted above the number of spines on the endopod of the female's fifth leg is polymorphic throughout *Pontellina*. The bilateral two-spined morph is overwhelmingly dominant in *morii* and *sobrina*. However, four morphs are common in *platychela* and *plumata*. Comparison of randomly selected samples of Atlantic specimens of *plumata* with specimens from the Indian and Pacific Oceans indicate significant differences

TABLE 10.—Values of the recurrent group affinity index (Fager, 1969) and the probability of obtaining this or higher values by chance for all possible pairs of *Pontellina* spp. Further discussion in text.

Species pair	Affinity index	*p*
morii and *sobrina*	0.642	<0.001
platychela and *plumata*	0.242	>.4
platychela and *morii*	0.042	>.8
platychela and *sobrina*	0.042	>.8
plumata and *sobrina*	0.042	>.8
plumata and *morii*	0	—

in the frequency of the four morphs (Table 11). The bilateral one-spined morph is much more frequent than the bilateral two-spined morph in the Atlantic Ocean whereas in the Indian and Pacific Oceans the frequencies of the two morphs are more alike and the differences are not significant.

Notably, the frequencies of the morphs in *platychela* differ significantly from those of the *plumata* sample from the Atlantic but not from those of the Indian and Pacific samples of *plumata*. Of the pairs of species sharing common boundaries only *morii* and *sobrina* do not appear to have appreciably different morph frequencies (Table 11).

In the ratio exopod to endopod length for the fifth legs in females, the distribution of the Atlantic sample of *plumata* differed significantly from those of the Indian and Pacific Oceans (Table 12). As in the case of the endopodal spines, pairs of species with common boundaries showed significantly different distributions of the exopod-endopod ratios.

Extrapolating from the similarity of Indian and Pacific Ocean samples, differences between Atlantic and Indian-Pacific populations of *plumata* appear to be geographically abrupt. Thus they may be viewed as reflecting 1) local pressures on *plumata* within each geographical population, 2) restricted gene flow between the Indian and Atlantic Ocean populations, 3) or both. *P. plumata* showed the highest frequency of unique character states in *Pontellina* (Table 9). Furthermore it tends to occupy a conspicuously peripheral position relative to the other three species in its dimensions of sexually modified appendages in both sexes (e.g., Figures 27, 28, 30, 31). It is also the only species of the genus sharing common boundaries with the other three species of *Pontellina*. Therefore, the geographical differences between Atlantic and Indian-Pacific populations of *plumata* parallel the extensive character divergence (Mayr, 1970: 51-53) otherwise distinguishing the species. Considering the fact that all morphological structures involved are sexually modified it would appear that we are witnessing reinforcement of premating barriers (Dobzhansky, 1970:376-382).

Similar disjunct morphological differences distinguishing Atlantic from Indian and Pacific populations of epipelagic calanoids have been reviewed (Fleminger and Hulsemann, 1973) and the number of examples increased (Fleminger and Hulsemann, 1973; Fleminger, 1973). Similar patterns in the strength of divergence in secondary sexual characters relative to

TABLE 11.—X^2 test of homogeneity in the distribution of spines on the endopod of the fifth legs in adult females.

	Number of spines on endopod (left leg-right leg):				
	2-2	1-2	2-1	1-1	
Population	Number of specimens				Total
platychela, Atlantic Ocean	38	16	12	34	100
plumata, Atlantic Ocean	22	11	16	51	100
plumata, Pacific Ocean	39	14	15	32	100
plumata, Indian Ocean	41	11	18	30	100
morii, Indian Ocean	94	2	1	3	100
morii, Pacific Ocean	98	0	2	0	100
sobrina, eastern tropical Pacific Ocean	99	1	0	0	100

	X^2	d.f.	p
plumata Atl. vs. *plumata* Pac.	9.48	3	<0.025 p >0.01
plumata Atl. vs. *plumata* Ind.	11.3	3	0.01
plumata Pac. vs. *plumata* Ind.	0.76	3	<0.9 p >0.75
platychela vs. *plumata* Atl.	9.14	3	<0.05 p >0.025
platychela vs. *plumata* Pac.	3.61	3	<0.5 p >0.25
platychela vs. *plumata* Ind.	2.5	3	<0.75 p >0.5
morii Pac. vs. *sobrina*	3.01	3	<0.5 p >0.25
morii Ind. and Pac. vs. *plumata* Ind. and Pac.	146.84	3	<0.001
sobrina vs. *plumata* Pac.	84.34	3	<0.001

buildup of anaerobic conditions. Division of tank bottoms into sundry tunnels and levels was created by specific placement of bricks and clay drain tiles.

AERATION STUDY

Aeration provided by jetting streams of filtered seawater into respective tanks was compared to aeration supplied by bubbling air through airstones into tanks in which water was continuously added with no agitation of the water column for an 8-week period. Two airstones were placed in each tank and valve-regulated air lines controlled the pressure at approximately 4 psi. Oxygen levels were monitored periodically and used along with survival rates as a basis for evaluation of replicate groups aerated by each method.

STOCKING DENSITY STUDY

Survival data were compared among triplicate tanks stocked at 10, 20, and 40 shrimp per m^2 for an 8-week period. These densities of approximately 40, 80, and 160 g/m^2 were chosen on the basis of data provided in pond and laboratory culture of penaeid shrimp (Broom, 1969; Subrahmanyam and Oppenheimer, 1969).

PRELIMINARY NUTRITIONAL STUDY

Triplicate groups of ten 4 g brown shrimp (*P. aztecus*) were fed a series of pelleted diets. Growth data (biomass increase) was used as a means of evaluation. Diets examined consisted of those patterned after Japanese purified diets (i.e., diets containing only chemical ingredients) (Table 1, Group I) (Diet 1 was conducted for 5 weeks and Diets 2, 3, and 4 for 11 weeks each); a second group of semipurified diets (i.e., containing defined chemical ingredients but containing one or more natural products) providing four combinations of levels of protein, fat, shrimp, and fish meal (Group II) (conducted for 11 weeks); and a third group designed to compare the nutritional value of casein, yeast, and soy hydrolysates (Group III) (conducted for 6 weeks). All of these groups were fed at 5% of their respective biomass daily. In addition, Diet 6 was fed at 5, 10, and 15% of biomass (Group IV) (conducted for 6 weeks).

TABLE 2.—Percent of pellet dissolved over time and at at three concentrations of binder. (Values are means and standard deviation on two replicates with Diet 1.)

Percent binder (collagen) added	Hours		
	6	12	24
1			
3	13 ± 1.2	14 ± 0.9	18 ± 1.7
5	11 ± 0.8	10 ± 0.6	10 ± 0.6
10	10 ± 0.6	10 ± 1.1	10 ± 1.0

Combined environmental factors which produced best survival in each of the environmental experiments (i.e., culture conditions consisting of bare fiber glass tank bottoms, supplied aeration, and a stocking density of approximately 40 g/m^2) were used in all nutritional studies. This combination offered a maximum potential for an increase in biomass and therefore allowed accurate evaluation of differences among diets tested. Although survival in bare fiber glass tanks was not significantly different from sand substrates, the fact that bare tanks were simpler to maintain dictated that they be used for the nutritional studies.

Prior to starting nutritional studies, the physical properties of pelleted diets were evaluated for acceptability as shrimp food. Pellet consistency was determined according to its ability to resist dissolution over a given period of time, and texture and size were chosen according to animal performance when presented several choices. Collagen[4] proved to be a suitable binding agent. Using an experimental design with time and collagen levels as variables, a pellet with 5% collagen added as a binder was found to offer optimum consistency over a 24-hr immersion in salt water (Table 2). Percent dissolution was measured by taking dry weights after 6, 12, and 24 hr of immersion (no shattering of pellets was observed, and all loss of weight was therefore assumed to be from dissolution). Animals were observed to feed most readily on

[4] Supplied on an experimental basis by the Hides and Leather Division of the U.S. Department of Agriculture Eastern Utilization Laboratory in Philadelphia, Pa.

pellets 0.3 cm in diameter by approximately 1.5 cm in length and which sink in water, and hence, pellets having these characteristics were used in both environmental and nutritional experiments.

RESULTS AND DISCUSSION

SUBSTRATE STUDY

A survival rate of 80% was obtained after 5 weeks in tanks without substrate, 80 to 90% survival was maintained over much of the duration of the experiment among both treatments having sand-shell substrates, and less than 60% survival occurred among tanks having brick subdivisions (Figure 1). Although *P. setiferus* is reported to burrow less than either *P. duorarum* or *P. aztecus* (Anderson, 1966; Pérez Farfante, 1969), it apparently was able to avoid predation, especially during the highly vulnerable moulting period, quite successfully with or without a sand substrate, since 5-week survival data among the two sand-shell treatments and the bare tank bottom treatment were not significantly different ($P < 0.05$) (Duncan, 1955). If the type of shelter is a factor in increased survival for penaeids maintained under culture conditions, the brick subdivisions should have enhanced survival. However, the markedly high mortality rate among this group, significantly different from the other three treatments ($P < 0.05$), may have resulted from either failure of the shrimp to behaviorally segregate and thus fully utilize this protection or from physical abrasion against the sharp and coarse brick surface. Although there may have been toxic substances in the brick materials, the bricks were carefully washed and assumed to be otherwise inert in any chemical effect they may have had on the animals. Although differences in volume of water caused by placing various substrates in their respective treatments was not controlled for, it was felt that these differences in a running water system were not critical to the survival of shrimp. Differences in bottom area among the treatments caused by placement of different types of substrate were neither controlled for nor measured but were also thought to be negligible compared to differences found among treatment groups. The high degree of cannibalism noted by Subrahmanyam and Oppenheimer (1969) in tanks without substrate was not observed in any groups.

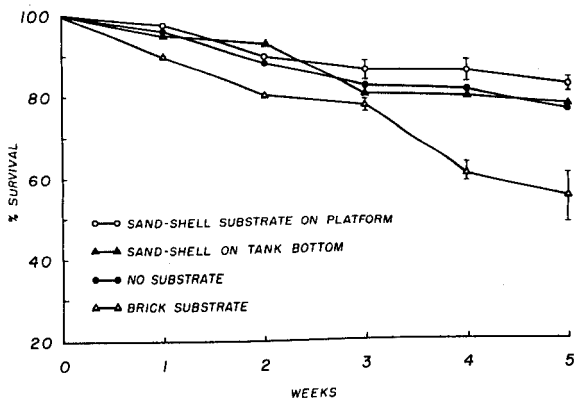

FIGURE 1.—Mean and standard error for percentage of animals surviving after 5 weeks of growth on four different substrates.

AERATION STUDY

The group having oxygen supplied by injecting air through airstones had significantly higher survival rates ($P < 0.05$) when compared with a treatment aerated by agitation of the water column (Figure 2). Although the average oxygen levels were similar between the two treatments (3.4-6.8 ppm), such levels in tanks aerated by high-pressure nozzles often dropped for short intervals due to clogging of the nozzles with silt and biological debris. Electrical power failures which affected water flow but not the compressed air supply (equipped with stand-by DC power) also caused intermittent drops in oxygen levels. Such short-term irregularities may have been more critical to shrimp tolerances than is indicated from reference to average oxygen level values, per se. Also, at the relatively high temperatures maintained throughout the study, short drops in oxygen levels could have been very critical. Decreased survival in tanks with agitation of the 0.75-m water column may also have resulted from physical agitation of the animals.

TABLE 14.—Mean abundance (No./m³) and frequency of occurrence of adult *Pontellina* in sets of samples forming meridional transects crossing the Equator. *Vertical tows with Indian Ocean Standard Net (~200-0 M). ** Oblique tows with CalCOFI Standard Net (~200-0 m or less).

					plumata		*morii*		*sobrina*		*platychela*	
Region	Longitude	Latitude	No. of Samples	Sampling dates	$\bar{x}$ No./m³	Percentage occurrence	$\bar{x}$ No./m³	Percentage occurrence	$\bar{x}$ No./m³	Percentage occurrence	$\bar{x}$ No./m³	Percentage occurrence
Indian Ocean	40°E-80°E	35°S-25°N	233*	Jan.-Dec. 1962-65	0.0741 ± .028	33	0.0678 ± .019	29	0	0	0	0
	80°E-110°E	27°S-18°N	107*	Jan.-Dec. 1962-64	0.0438 ± .034	48	0.0425 ± .020	37	0	0	0	0
Austral-Asian Seas Pacific Ocean	120°E-130°E	12°S-12°N	23**	Mar.-May 1961	0.0395 ± .015	83	0.0200 ± .010	65	0	0	0	0
	156°E-164°E	12°S-12°N	23**	Aug.-Sep. 1956	0.0182 ± .008	83	0.0045 ± .004	22	0	0	0	0
	174°W-160°W	06°S-21°N	15**	Aug.-Sep. 1956	0.0313 ± .030	40	0.0033 ± .005	20	0	0	0	0
	126°W	12°S-20°N	22**	Feb.-Mar. 1967	0.0710 ± .037	77	0.0034 ± .003	18	0	0	0	0
	124°W-112°W	14°S-17°N	13**	Feb. 1953	0.0938 ± .090	46	0	0	0	0	0	0
	113°W- 86°W	05°N-16°N	23**	Apr.-May 1958	0.0008 ± .0001	4	0.0004 ± .0001	4	0.0243 ± .021	43	0	0
	95°W	10°S-15°N	19**	Sep. 1967	0.0058 ± .006	21	0.0031 ± .005	11	0.0863 ± .072	79	0	0
	92°W	20°S-10°N	22**	Feb.-Mar. 1967	0.0077 ± .007	18	0.0095 ± .013	23	0.0186 ± .014	36	0	0

TABLE 15.—Above: Maximum linear dimensions of *Pontellina* cephalothorax. Dorso-ventral height taken in lateral view includes Mx2 with setal fan closed, width across trunk taken in dorsal view (mm).
Below: Mesh width of nets listed in Table 14.

Copepodite stage	II	III	IV	V		Adult	
Sex	—	—	—	♂	♀	♂	♀
Typical specimen	0.30 × 0.28	0.38 × 0.34	0.48 × 0.44	0.61 × 0.56	0.62 × 0.60	0.70 × 0.66	0.90 × 0.75
Small specimen	0.28 × 0.26	0.36 × 0.34	0.46 × 0.42	0.58 × 0.54	0.56 × 0.56	0.62 × 0.60	0.75 × 0.64
Nets[1]	Juday net	IOSN		CalCOFI SN		POFI SN	
Mesh widths (mm)	0.18	0.33		0.55/0.25 (silk) 0.505/0.28 (nylon)		0.66/0.31	

[1] IOSN = Indian Ocean Standard Net
CalCOFI SN = California Cooperative Oceanic Fisheries Investigations Standard Net.
POFI SN = Pacific Oceanic Fisheries Investigation Standard Net.

TABLE 16.—Comparison by Student-*t* test of mean abundance in day (0601 to 1800 h local time) and night (1801 to 0600 h local time) collections. Samples of each set selected for similarity of geographical origin, collecting procedures and the presence of the species, i.e., samples negative for the species omitted. Samples derived primarily from those listed in Table 14.

Species	Source of samples	Day mean/m³	s^2	N	Night mean/m³	s^2	N	t	p
plumata	Indian Ocean	0.0945	2.7318	70	0.1048	1.7640	48	0.0370	>0.9
	Austral-Asian Seas	0.0483	0.1488	12	0.0413	0.0784	7	0.6000	>0.9
	Pacific Ocean	0.0770	1.2224	43	0.0405	0.1720	41	0.1986	>0.8
	Atlantic Ocean	0.0857	2.7429	7	0.0133	0.0033	3	1.0251	>0.3
morii	Indian Ocean	0.1504	3.7540	56	0.1550	5.1996	41	0.0107	>0.9
	Austral-Asian Seas	0.0300	0.0400	12	0.0400	0.1040	6	0.0081	>0.9
	Pacific Ocean	0.0332	0.0804	22	0.0462	0.4721	24	0.0881	>0.9
sobrina	Pacific Ocean	0.0307	0.0858	16	0.0914	2.8169	35	0.1423	>0.8

TABLE 17.—Occurrence of *Pontellina* spp. in day (0601 to 1800 h local time) and night (1801 to 0600 h local time) samples. + present, − absent.

	Day		Night			
	+	−	+	−	χ^2	p
Atlantic Ocean:						
plumata	25	16	13	22	3.389	$0.1 > p > 0.05$
platychela	23	18	23	12	0.383	$0.75 > p > 0.5$
Eastern Pacific Ocean:						
plumata	15	19	13	49	4.360	$0.05 > p > 0.025$
morii	6	28	13	49	0.015	$0.9 > p > 0.75$
sobrina	9	25	26	36	1.648	$0.25 > p > 0.1$
Indian-Western Pacific Ocean:						
plumata	108	30	87	31	0.491	$0.5 > p > 0.25$
morii	80	58	66	52	0.040	$0.9 > p > 0.75$

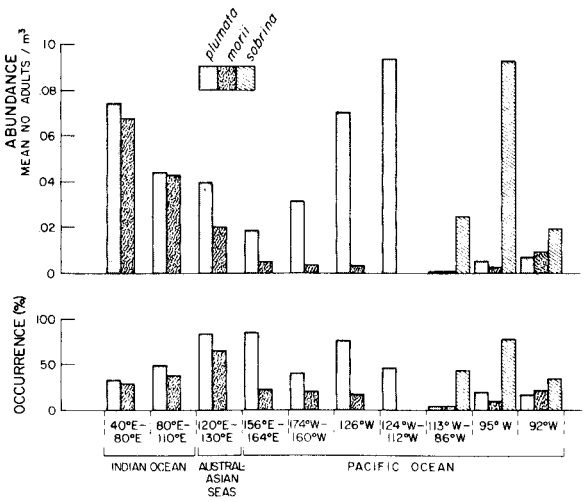

FIGURE 35.—Mean abundance (No. adults/m³) and percentage frequency of occurrence in sets of samples shown in Figures 1b and 38 and listed in Table 14. Confidence limits of the means shown in Table 14. Further discussion in text.

The appearance of *sobrina* is restricted to the eastern tropical Pacific where its abundance and occurrence resemble the values for *morii* and *plumata* in their regions of dominance, respectively.

Quantitative data on *Pontellina* in the Atlantic Ocean are few. In six quantitative samples from the western Atlantic *plumata* abundance ranged from 0.01 to 0.46 adults per m³. Two samples containing *platychela* provided estimates of 0.001 and 0.08 adults per m³.

Extremely high values of *plumata* s.l., however, have been reported from the Atlantic. Judging from their geographical origin, the northeastern Gulf of Guinea, these abundance estimates (Mahnken, Jossi, and McCabe, 1968) are probably referrable to *platychela*. Mahnken and his co-workers record the species at 18 of 63 sampled localities scattered offshore from the Bight of Benin west to Cape Palmas. They indicate areal abundance of the species by contouring selected class intervals of number per 1,000 m³ water strained. In lieu of the actual estimates per sample we used midpoints of each contoured interval to calculate the mean abundance. The yield is a surprisingly high mean of 1.01 individuals per m³, an order of magnitude higher than our highest mean values from the Pacific and Indian Oceans. Aside from possible bias introduced by our extrapolations several factors may be responsible for these unusually high values: e.g., count of immature as well as adult specimens, use of nets with smaller mesh width (0.281 mm), use of surface tows in a region relatively rich in zooplankton presumably concentrated in the very shallow layer of tropical surface water above the permanent thermocline, etc.

Summing our mean values of *plumata*, *morii*, and *sobrina* in each meridional set of samples, we find remarkably good agreement between our abundance estimates and those derived by previous studies of *plumata* s.l. in the Pacific Ocean (Table 18). We normalized the published data to conform to the units employed in the present study. Normalization was simplified by the following assumptions:

a. we assumed 100% filtration efficiency;
b. we assumed that *Pontellina* occurs only above 200 m and, in calculating volume of water strained by the net, omitted segments extending below 200 m;
c. in sets of vertically stratified tows we considered the overall estimate of abundance as if it were from a continuous tow sampling between 200 m and the surface;
d. we assumed that previous studies on *Pantellina* failed to discriminate among the different species; the published values were regarded as representing a combined estimate of the abundance of all species of the genus found in the region.

Estimates obtained from Heinrich (1968) and Vinogradov and Voronina (1963) are about one order of magnitude higher than other middle and west Pacific estimates. These higher values may be accounted for by two factors, namely that the counts include immature copepodids and that the samples were taken with nets of 0.18-mm mesh, small enough to retain *Pontellina* copepodids of stage II and possibly of stage I as well (Table 15). Sherman's (1963, 1964) counts appear to have been derived from adult specimens, partly by inference from his text and partly from the relatively wide mesh comprising most of the filtering cone in the POFI (Pacific Oceanic Fisheries Investigation) Standard Net (0.66 mm).

TABLE 18.—Mean abundance (No./m³) of *Pontellina* spp. in meridional transects crossing the Equator.

Region	Longitude	Latitude	Source of data	$\bar{x}$ no. adults	$\bar{x}$ no. adults and juveniles	Number of samples	Sampling months	Depth, tow, net
Indian Ocean (west)	40°E-80°E	35°S-25°N	present study	0.1419	—	233	Jan.-Dec. (1962-65)	200-0 m, vert., IOSN[1]
Indian Ocean (east)	80°E-110°E	27°S-18°N	present study	0.0863	—	107	Jan.-Dec. (1962-64)	200-0 m, vert., IOSN[1]
Austral-Asian Seas	125°E-135°E	12°S-12°N	present study	0.0596	—	23	Mar.-May (1961)	150-0 m, obl., CalCOFI SN[2] (silk)
Pacific Ocean	156°E-164°E	12°S-12°N	present study	0.0230	—	23	Aug.-Sept. (1956)	150-0 m, obl., CalCOFI SN[2] (silk)
	160°E	04°S-16°30′N	Vinogradov and Voronina, 1963	—	0.1023	17	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	176°W	14°S-13°N	Vinogradov and Voronina, 1963	—	0.3790	21	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	120°E-175°W	04°S-30°N	Heinrich, 1968	—	0.1910	91	W of 160°E Jul.-Aug. (1957)	500-0 m, vert., Juday 80 cm
							E of 160°E Nov.-Feb. (1957-58)	
	168°E-155°W	20°S-20°N	Sherman, 1964	0.1379	—	59	Jan.-Apr. (1962)	Surface, POFI SN[3]
	174°W-160°W	06°S-21°N	present study	0.0346	—	15	Aug.-Sep. (1956)	150-0 m, obl., CalCOFI SN[2] (silk)
	158°W	07°S-21°N	Sherman, 1963	0.0438	—	13	June-July (1961)	Surface, POFI SN[3]
	154°W	13°S-13°N	Vinogradov and Voronina, 1963	—	0.1172	18	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	140°W	18°S-17°30′N	Vinogradov and Voronina, 1963	—	0.1600	29	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	126°W	12°S-20°N	present study	0.0744	—	22	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN[2] (nylon)
	95°W	10°S-15°N	present study	0.0952	—	19	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN[2] (nylon)
	92°W	20°S-10°N	present study	0.0358	—	22	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN[2] (nylon)

[1] IOSN = Indian Ocean Standard Net.
[2] CalCOFI SN = California Cooperative Oceanic Fisheries Investigations Standard Net.
[3] POFI SN = Pacific Oceanic Fisheries Investigation Standard Net.

Disregarding collecting and sample enumerating procedures as well as differences among the individual species, estimates of mean abundance of *Pontellina* across the Pacific (Table 18) vary from 0.023 to 0.379 with a median of 0.1 individuals per m³. For epipelagic copepods this appears to be a rather low and remarkably uniform set of values that varies within the unusually narrow range of one order of magnitude. Summing the abundance of the three species produces a notable lack of any pronounced geographical trend though the mean abundance shows moderate, irregular undulations along the equatorial belt crossing the Indian and Pacific Oceans.

Low abundance and relatively uniform dispersion throughout the geographical region occupied by each species suggests that the species of *Pontellina* are high-order predators. This impression is supported for adults at least by the exclusive presence of animal remains in their stomach and the predominance of copepod

fragments (Table 19). Though all of the species appear to be similarly predaceous within their respective epiplanktonic communities, we must conclude that appreciable differences in the abundance and occurrence of the sibling species are indicative of real changes in habitat conditions and real differences in the adaptive optima for each species.

Remarks on Geographical Distribution

This discussion hinges upon inferences drawn from the evidence presented in the preceding sections. Chief among them are the validity of the four sibling species of *Pontellina* as separate noninterbreeding populations. Based on morphological homogeneity each population appears to be closely adapted genetically to prevailing environmental conditions in the geographically limited hydrographic systems comprising its particular habitat. Except for differences between Atlantic and Indian-Pacific populations of *plumata* morphological indications are that panmixis prevails in each species.

The three tropical species, *morii*, *sobrina*, and *platychela*, occupy eutrophic waters characterized by equatorial upwelling and a shallow, steeply graded, permanent thermocline. The mixed layer overlying the thermocline is relatively homogeneous in temperature and has been referred to as Tropical Surface Waters (Wyrtki, 1966, 1967). In our use of this term, Tropical Surface Waters are restricted to the surface layer in regions where the permanent thermocline has a temperature gradient of $\geqslant 0.1°C$ per m and encompasses an overall decrease in temperature from about 24° ± 1°C at the top to about 15° ± 1°C at the bottom. These pools of warm water are subjected to seasonally repetitive changes in the strength of the equatorial Trade Winds (Wyrtki, 1966, 1967; Taft, 1971). The seasonal changes produce monsoonlike reverses in the circulation of the equatorial segment inhabited by each species. This phenomenon apparently provides a sufficiently closed hydrographic circulation to maintain breeding stocks in proximity to suitable nursery grounds and thus ensures continual success of each species.

The equatorial distributions of the tropical species of *Pontellina* are not without precedence. The tropical Atlantic has previously been characterized in faunistic terms, for example, by a number of mesopelagic fishes (Backus et al., 1970) as well as by a sergestid shrimp

TABLE 19.—List of identified particles from microscopic analysis of stomach contents in adult female *Pontellina*.

Species	Specimen number	Copepod parts	"Oncaea" parts	"Paracalanus" parts	Crustacean parts	Algal parts	Source of specimen: Ocean	Station
plumata	1	x	x				Atlantic	La Creuse 5
	2	x					Indian	Dodo VI-81
	3	x	x				Pacific	Scorpio II-146
	4	x	x				Indian	Lusiad V-45
	5	x	x				Pacific	*Jordan* 57-076
	Percentage no. with ingested particles in midgut: 71%							
platychela	1	x		x			Atlantic	*Atlantis II* 20-28
	2	x	x				Atlantic	La Creuse 5
	3	x					Atlantic	*Atlantis II* 31-40
	4				x		Atlantic	*Atlantis II* 31-54
	5		x				Atlantic	*Oregon* 1289
	Percentage no. with ingested particles in midgut: 63%							
morii	1	x	x				Pacific	Troll 30
	2	x					Pacific	TRANSPAC 98B
	3	x	x				Pacific	EQUAPAC H-31
	4	x					Indian	Lusiad V-45
	5	x					Indian	Lusiad II-14
	Percentage no. with ingested particles in midgut: 63%							
sobrina	1	x	x				Pacific	Bonacca 35
	2	x					Pacific	CalCOFI 5801: 153.50
	3	x	x				Pacific	Scot 45
	4	x	x				Pacific	*Jordan* 60-056
	5	x	x				Pacific	Bonacca 31
	Percentage no. with ingested particles in midgut: 83%							

(Judkins, 1972). Among the Atlantic Foraminifera listed by Bé and Tolderlund (1971) as tropical species only *Candeina nitida* shows a geographical distribution similar to that of *P. platychela*.

In general species characterizing the eastern tropical Pacific, unlike *sobrina*, tend to follow the coastline of the Americas from about lat. 30°N to 20°S and extend westward to long. 160° to 180°W: e.g., *Euphausia distinguenda*, (Johnson and Brinton, 1963), *Eucalanus inermis*, (Lang, 1967), *Melamphaes spinifer*, (Ebeling, 1962), *Stomias colubrinus*, (Gibbs, 1969).

These distributions are meridionally and zonally more extensive than the limited dispersion observed in *P. sobrina* and others like *Pontella danae*, *P. agassizi*, and *Pontellopsis lubbockii* (Heinrich, 1964; Fleminger, 1967b; and unpublished records). The dissimilarities probably relate to differences in depth range, the more widespread forms having access to subsurface currents flowing northward (Wooster and Jones, 1970) and southward (Wooster and Gilmartin, 1961) under the eastern boundary currents as well as westward in the tongue of low oxygen water accompanying the North Equatorial Current which is traceable to the Philippines (Reid, 1965; Wyrtki, 1966; Tsuchiya, 1968).

Distributions of epipelagic species in the equatorial Indian and Pacific Oceans resembling that of *morii* include a number of other copepods, e.g., several species of *Eucalanus*, (Fleminger and Hulsemann, 1973; Fleminger, 1973); *Clausocalanus minor*, (Frost and Fleminger, 1968); several euphausiids such as *Euphausia diomediae*, *E. paragibba*, and *Stylocheiron microphthalma*, (Brinton, 1962); and fishes such as *Scopelogadus unispinus*, (Ebeling and Weed, 1963) and *Stomias affinis*, (Gibbs, 1969) though the lattermost is also considered to inhabit the tropical Atlantic.

Although the ubiquitous *plumata* overlaps geographically with each of the tropical species, *plumata*'s overall range lies mostly in the enormous basin of oligotrophic waters spreading across the tropics and subtropics of each ocean, waters markedly different in vertical thermal structure from those of its tropical congeners. The almost mutually exclusive distributions of *plumata* and its more localized congeners, *platychela* in the equatorial Atlantic and *sobrina* in the eastern tropical Pacific, are evidence of relatively intensive environmental gradients and the adaptive response to appreciably different environmental optima, which separate the distributions of these pairs of species.

For example, *morii* has been found at the edge of the south Atlantic as well as the edge of the eastern tropical Pacific; concomitantly *sobrina* occurs in the North Equatorial Current, but successfully extends only a few degrees of longitude to the west of its habitat; *platychela* is adjacent to but fails to establish itself in the Sargasso Sea; finally *plumata*, despite apparent circumglobal distribution, does not appear in large numbers where its equatorial congeners abound. Thus, the optimum habitats appear to be regionally distributed and those that are contiguous are sufficiently different to prevent colonization by expatriated congeners transported to the margin of the habitat. The possibility of interference among the species is open but in the light of available knowledge of calanoids it seems intuitively to be most unlikely.

Thus, the two classes of epipelagic warm-water distributions found in *Pontellina* suggest a fundamental dichotomy in the circumglobal warm-water belt. The three tropical species correlate with geographically separated shallow lenses of eutrophic water. Each lens is known to overlie regions of intense temperature and oxygen gradients and to be partially bounded by the similarly intense tropical convergences (Neumann and Pierson, 1966).

P. plumata, however, correlates with the circumglobal warm-water pool that is largely oligotrophic. The oligotrophic pool tends to be deep, the permanent thermocline often exceeding 200 m in depth. Temperature gradients in the thermocline and along its margins at the subtropical convergence are relatively weak, and oxygen is generally at or near saturation (Neumann and Pierson, 1966). Evidence that the Atlantic pool may be at least partially isolated with respect to *Pontellina* whereas the Indian and Pacific pools are confluent is suggested by morphological differences in the *plumata* populations reported above.

The circulation systems and physical conditions known to maintain these lenses of eutrophic tropical water and the pools of oligotrophic tropical-subtropical waters are the obvious mechanisms sustaining the geographical dis-

tribution of the four species of *Pontellina*. This is apparent in the relationship between the distribution of each species and the location of prevailing near-surface isotherms that locate the hydrographic limits of these bodies of water. The localities for the tropical species are largely enveloped by the mean winter season position of the 24°C isotherm at 10 m (Figure 36), the lower thermal limit of Tropical Surface Water. The 10-m depth was chosen to reduce the influence of diurnal fluctuations. The localities for *plumata*, however, vary broadly between the position of the 20° and 15°C mean winter season isotherms (Figure 37). Factors confining the distributions to the observed limits, however, are not obvious; more data on depth range, vertical migratory behavior, and depth of food organisms would probably be enlightening.

Notably, more than three-quarters of the samples (77.5%) containing *Pontellina* yielded specimens of only one species. To examine joint occurrences of *Pontellina* congeners more closely, all capture records of a species were tallied by ocean and grouped with respect to the presence or absence of other congeners in the same sample (Table 20). Comparison of singular and joint occurrences for all possible pairings indicates that the latter are relatively infrequent. In no case of joint occurrences did the index of affinity (Fager and McGowan, 1963) reach a positive value. No two species within the genus would appear to occupy the same spatial habitat or, in other words, be members of the same community. Thus, the extensive overlapping of *morii* and *plumata* in the equatorial Indian and Pacific Oceans may be viewed as a function of intermingling due to the spatial proximity of the two habitats and perhaps also due to a greater number of similarities shared by these two habitats than between those of the other possible pairings within the genus.

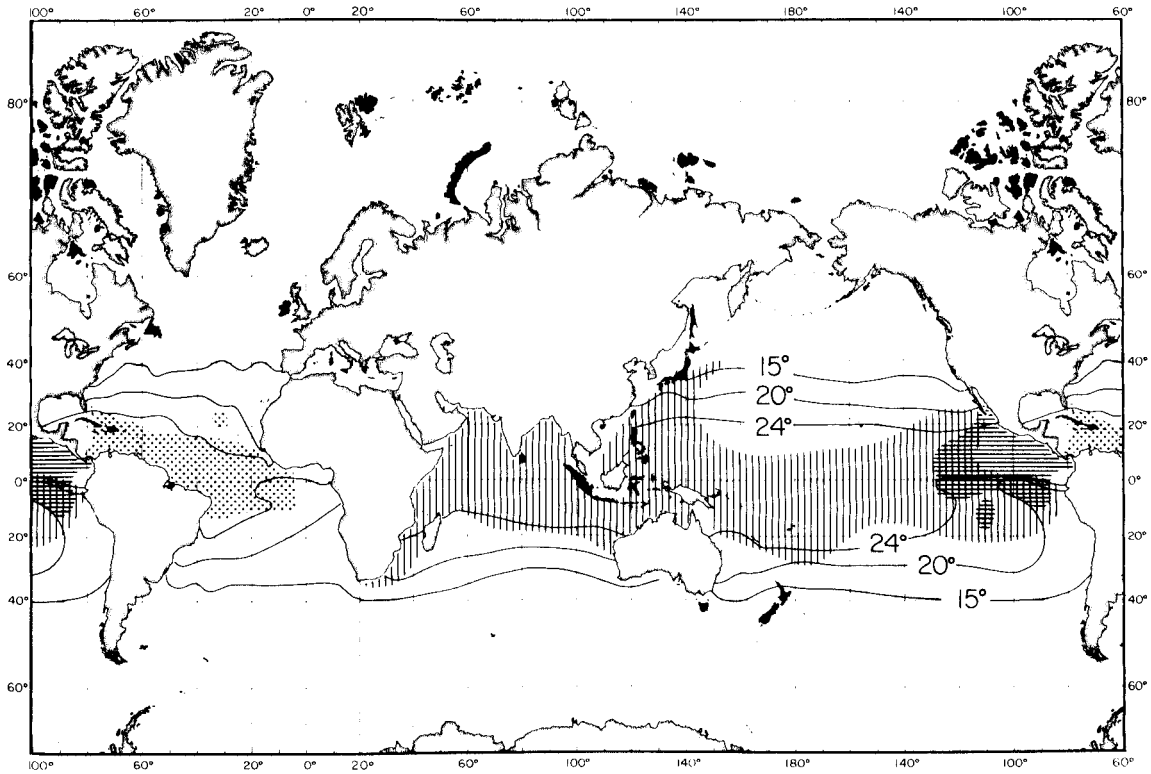

FIGURE 36.—Comparison of geographical area enveloping all capture records of tropical species of *Pontellina* with selected mean isotherms at 10 m for winter season of each hemisphere. Data from Muromtsev (1958, 1963) and Wyrtki (1971). Dotted shading outlines capture records of *P. platychela* shown in Figure 8; horizontal shading outlines capture records of *P. sobrina* shown in Figure 15; vertical shading encloses the capture records of *P. morii* shown in Figure 12.

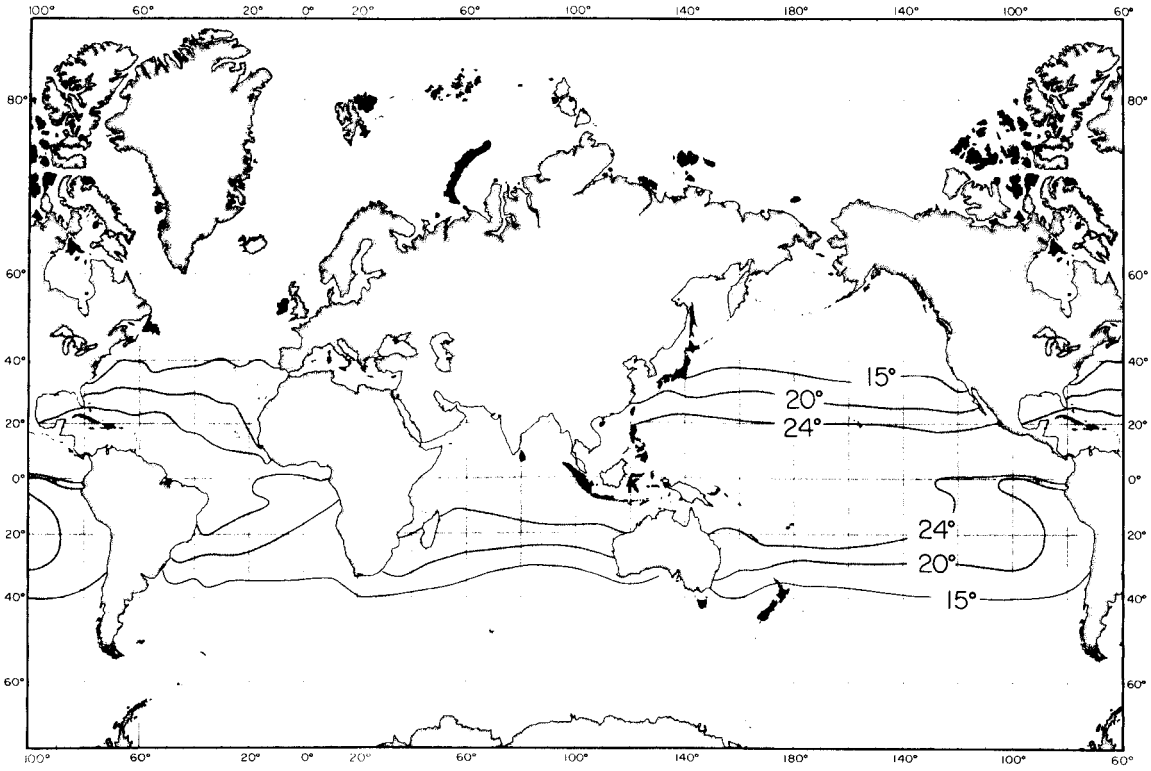

FIGURE 37.—Comparison of shaded area enveloping all capture records of *Pontellina plumata*, shown in Figure 5 with selected mean isotherms at 10 m for winter season of each hemisphere. Data from Muromtsev (1958, 1963) and Wyrtki (1971). Further discussion in text.

TABLE 20.—Separate and joint occurrences among species of *Pontellina*. Values in parentheses are the index of affinity; a value greater than 0.5 suggests joint membership in the same communal assemblage of species.

	plumata	*morii*	*sobrina*	*platychela*	Total
Indian Ocean and Australasian Seas:					
plumata	129	96 (-7.01)	0	0	225
morii		78	0	0	78
sobrina			0	0	0
platychela				0	0
Total	129	174	0	0	303
Pacific Ocean:					
plumata	136	46 (-3.77)	23 (-5.20)	0	205
morii		23	6 (-2.69)	0	29
sobrina			85	0	85
platychela				0	0
Total	136	69	114	0	319
Atlantic Ocean:					
plumata	80	0	0	14 (-3.93)	94
morii		0	0	0	0
sobrina			0	0	0
platychela				58	58
Total	80	0	0	72	152
All records combined:					
plumata	345	137	18	4	514
morii		101	1	0	102
sobrina			85	0	85
platychela				58	58
Totals	345	238	104	72	759

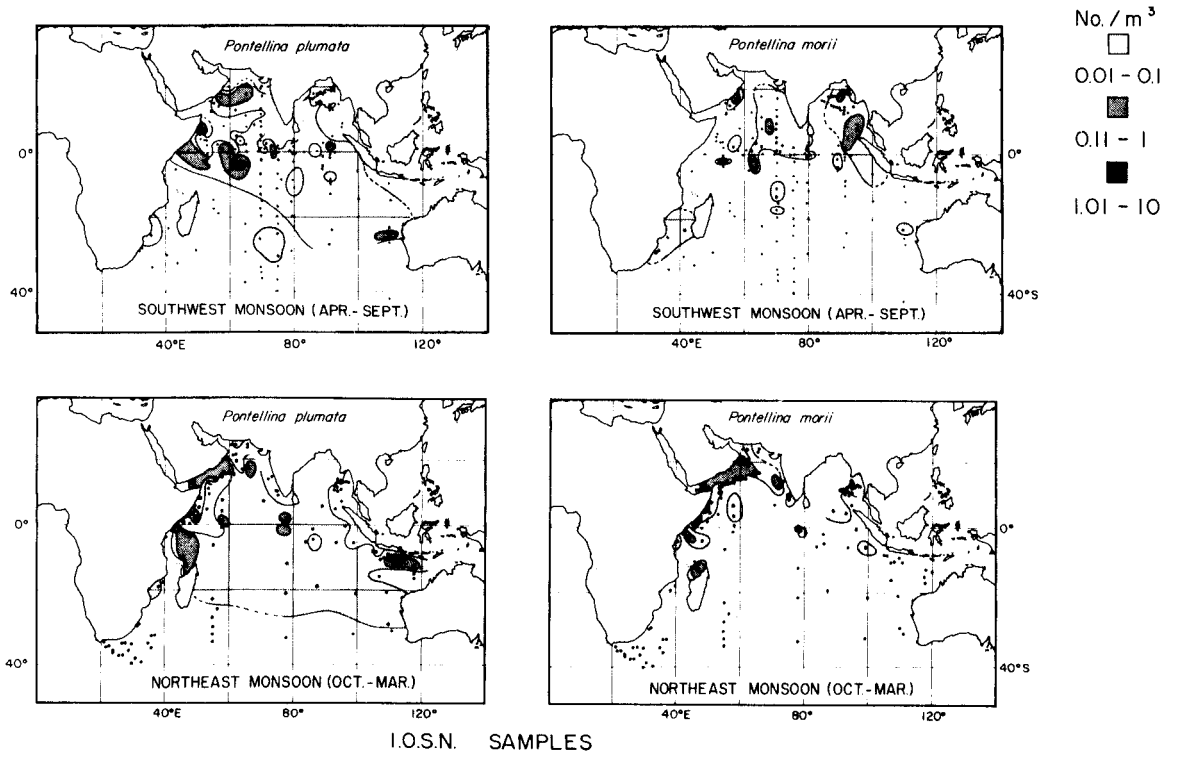

FIGURE 38.—Abundance of *Pontellina morii* and *P. plumata* in Indian Ocean Standard Net (IOSN) collections. Samples collected during southwest and northeast monsoon seasons. Dots represent localities sampled. Abundance values are estimated number of adults per m³ water strained.

P. morii and *plumata* exhibit distinctive distributions in both monsoon seasons (Figure 38) as well as general zonal separation (Figure 39), differences that are blurred in charts prepared without regard for seasonal variation (e.g., Figures 5, 12). During the southwest monsoon, *plumata* appeared in large numbers off the Somali coast and near the Seychelles whereas *morii* was much more frequent in the eastern Arabian Sea and the eastern Bay of Bengal. In the northeast monsoon both species were abundant in the Somali Current. However, only *morii* appeared to be common in and about the Andaman Sea whereas an indication of large numbers of *plumata* appeared just south of Java.

Morphological relationships analyzed above indicate the species have common ancestry that produced three main lines of descent represented respectively by *plumata*, *platychela*, and the Indian-Pacific tropical pair of siblings, *morii* and *sobrina*. Ample evidence of co-occurrence

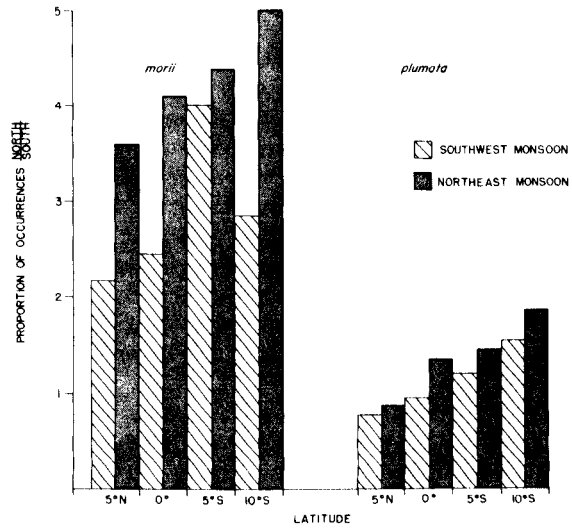

FIGURE 39.—Frequency of occurrence of *Pontellina plumata* and *P. morii* in the Indian Ocean north of selected latitudes compared to that south of the same latitudes.

without intergradation between *morii* and *sobrina* support the conclusion that both are valid species that have evolved relatively recently.

Morphological-geographical patterns provide inferential evidence that sympatry among subsets of the four species have led to modifications of secondary sexual features, presumably in the course of developing premating barriers to hybridization. Obvious examples of this emerge from comparison of pairs of species which have extensive contiguous boundaries: e.g., *plumata* and *platychela* in the Atlantic and *plumata* and *morii* in the Indian and Pacific Oceans. In each pair of species the chela on the male fifth leg in the tropical congener is broadened in contrast to the slender chela found in *plumata*. In the females of each pair the hair patches on the genital segment are either missing or reduced to one pair in the tropical species while *plumata* maintains two prominent pairs. Another source of evidence lies in the geographical variations in the female fifth legs of *plumata* which follows a pattern indicative of character displacement.

CONCLUSIONS

1. The genus *Pontellina* represented by four species is epipelagic and occupies oceanic sectors of the circumglobal warm-water belt.

2. Three of the species occur chiefly in eutrophic sectors of equatorial latitudes where the layer above the thermocline is relatively homogeneous; the distinctiveness of this layer was noted by Wyrtki who refers to it as Tropical Surface Water. One species, *platychela*, occupies the tropical Atlantic; *sobrina* is in the eastern tropical Pacific; and *morii* is found in the tropical Indian and tropical Pacific Oceans.

3. The fourth species, *plumata* s.str., occurs most frequently in oceanic, oligotrophic regions in tropical and subtropical latitudes.

4. Morphological differences among the species are subtle and restricted to secondary sexual structures.

5. The four species comprise a monophyletic complex showing three basic derivatives, *plumata*, *platychela*, and a third that underwent a subsequent episode of speciation to produce *morii* and *sobrina*.

6. The female fifth leg is polymorphic and represented by four phenotypes or morphs. Geographical variation in the frequency of morphs in *plumata* distinguishes Atlantic from Indian and Pacific populations; relationships with *platychela* in the Atlantic and *morii* and *sobrina* elsewhere suggest the variation is the result of character displacement. Three of the four morphs in *morii* and *sobrina* appear to be extremely rare.

7. Each species exhibits a distinctive geographic range independent of the other three. Absence of conspicuous geographical variation indicates sufficient transport and advection to maintain panmixis within each species except the Atlantic and Indian-Pacific populations of *plumata*.

8. Abundance of all four species is low despite relatively frequent occurrence within the limits of the distribution. These indications of high-order predation are supported by examination of gut contents in sexually mature adults in which the remains consisted primarily of particles from small copepods.

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STOCK COMPOSITION, GROWTH, MORTALITY, AND AVAILABILITY OF PACIFIC SAURY, *COLOLABIS SAIRA*, OF THE NORTHEASTERN PACIFIC OCEAN

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ABSTRACT

Recent international interest in the Pacific saury *(Cololabis saira)* resource of the northeastern Pacific Ocean prompted studies to determine the stock's composition, structure, growth, mortality, and availability.

During August-September 1969-71, data were obtained from more than 5,000 fish sampled from 19 individual schools captured between southern California and Vancouver Island, B.C. Length and age frequency distributions indicate fish grow to 340 mm in length during their 6-year lifespan. Larger fish apparently migrate farthest north and consequently age at full recruitment off Washington is III or IV, and II off Oregon. Spawning is extended over most of the year and the stock is believed homogeneous. First maturity appears to be reached during the second year. Numbers of males and females were nearly equal until age IV when females began to predominate. Length-weight regressions are presented by sex. Bertalanffy growth parameters were calculated: $K = 0.42$, $L_\infty = 342$ mm, and $t_0 = -0.72$ years. The total instantaneous mortality coefficient was estimated at 1.25-2.20.

Data on distribution and availability suggest a viable domestic fishery on this species is unlikely.

In 1969, an investigation of the distribution, availability, and biology of Pacific saury, *Cololabis saira*, in the northeastern Pacific Ocean was begun by our laboratory. This study was a direct result of a tenfold decrease in combined Japanese and Soviet landings of the species in the northwestern Pacific Ocean since 1958. Unusually high market demand created international interest in the unexploited stock in the eatern Pacific Ocean.

Initial studies were concerned primarily with the development of sampling and harvesting gears (Ellis and Hughes, 1971). This paper contains results of research on the biology and availability of saury, except for parasite studies which were treated separately (Hughes, 1973). The purpose of the paper is to provide initial information on stock composition, growth, and mortality and to supplement previous studies of distribution and abundance. Data were obtained during research vessel surveys, conducted primarily during August and September 1969 off the California coast, and during August and September 1970 and 1971 off the Washington and Oregon coasts.

STATUS OF KNOWLEDGE

Parin (1960) reported that the Pacific saury inhabits the northern Pacific pelagic zone and has a continuous range from Asia to North America. Sokolovskii (1969) inferred from studies of parasites and biological and morphometric characteristics of the species that there exist within its total range, stocks distinguishable from one another—western (Asian), central (Aleutian), and eastern (American)—that there is no clear boundary between these stocks, and that there are rather wide zones of mixture of the stocks. The eastern stock ranges from Baja California to the Gulf of Alaska (Ahlstrom and Casey, 1956; Clemens and Wilby, 1961). Novikov and Kulikov (1966) found that in the eastern Pacific Ocean, saury occupied an extensive coastal region 50-70 miles wide between lat. 41° and 48°N during August-October, but that major concentrations were irregularly distributed. Their survey indicated the most dense aggregations occurred off southern Oregon during August, October,

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and November in water temperatures of 12.5 to 13.5°C. Data obtained from night-light station observations off California indicated that in the California Cooperative Oceanic Fisheries Investigations area saury occurred most frequently in waters north of San Francisco in a band 40-120 miles offshore (Smith, Ahlstrom, and Casey, 1970). Peak availability occurred during November. Results of egg surveys suggested peak spawning activity occurs off California during April, May, and June and that the standing stock in the eastern North Pacific Ocean was at least 450,000 to 500,000 tons (Ahlstrom, 1968; Smith et al., 1970).

METHODS

The method of finding schools of Pacific saury was similar to procedures employed by commercial Japanese saury vessels. The Japanese technique has been reviewed by Inoue and Hughes (1971). The Japanese use artificial lights during hours of darkness to visually locate schools near the surface and to attract the fish alongside the vessel for eventual capture. Sonar was also used to assist in detecting concentrations during 1970 and 1971. Our surveys were generally restricted to areas where surface water temperatures were between 13° and 17°C. Typically, they were conducted along a zig-zag track designed to cross boundaries between warm and cold water masses. Once detected and concentrated under the vessel's alluring lights, the total weight of each school was derived by estimating the percentage of the school captured, weighing our catch, and then computing the weight of the remaining fish.

During 1969, surveying was confined to waters off California and fishing was conducted with a Japanese-style boke-ami (Andreev, 1962). Operations were conducted off the Washington and Oregon coasts in 1970 and extended to include waters off Vancouver Island, B.C., during 1971. During those periods fishing was conducted with a small purse seine designed for capturing saury (Ellis and Hughes, 1971).

Table 1 summarizes times and locations where fishing was conducted and samples retained for biological studies. Catches were randomly subsampled aboard ship. All samples collected were returned to the laboratory for processing. Samples taken in 1969 were iced, whereas those collected in 1970 and 1971 were frozen. Only length frequency data were taken from the 1969 samples. Biological data from individual fish obtained during 1970 and 1971 included knob length[2] measured to the nearest millimeter, body weight to the nearest gram, sex, and maturity. Scales were removed for later examination.

TABLE 1.—Fishing areas and number of Pacific saury collected, 1969-1971.

Date	Coastal area	Location W Long	Location N Lat	Sample size
Aug 1969	Calif.	124°03′	37°49′	220
Aug 1969	Calif.	124°03′	37°51′	222
Aug 1969	Calif.	124°03′	37°53′	143
Aug 1969	Calif.	123°59′	37°55′	52
Aug 1969	Calif.	123°48′	37°58′	31
Sept 1969	Calif.	122°23′	36°10′	160
Sept 1970	Oreg.	125°50′	45°03′	299
Sept 1970	Oreg.	125°11′	44°33′	300
Sept 1970	Oreg.	125°08′	44°30′	300
Sept 1970	Wash.	126°02′	47°43′	284
Sept 1970	Wash.	125°58′	47°41′	192
Sept 1970	Wash.	126°00′	47°39′	191
*July 1971	Calif.	120°00′	33°00′	98
Aug 1971	Van. Isl.	127°06′	49°16′	105
Aug 1971	Wash.	126°04′	48°21′	512
Sept 1971	Oreg.	125°01′	44°01′	506
Sept 1971	Oreg.	124°59′	43°55′	508
Sept 1971	Oreg.	125°00′	43°54′	508
Sept 1971	Oreg.	125°02′	44°02′	268
Sept 1971	Oreg.	125°04′	43°58′	419
			Total	5,248

* Sample captured with variable mesh gillnet. This sample used only in the growth analysis.

Sex determination of fish measuring less than 230 mm was generally difficult. When gross examination of gonads proved inadequate, samples were further subsampled—the gonads cross-sectioned and examined for the presence of a lumen under 10× binocular microscopes.

Age was determined from plastic impressions of scales (Clutter and Whitesel, 1956) examined with a microprojector device (Mosher, 1950). Age determination of Pacific saury has long been a point of contention between Soviet and Japanese scientists working in the western Pacific (Kotova, 1958; Hotta, 1960). Details of assessment criteria by which ages were determined for this report have been documented by Mosher.[3]

[2] Knob length (Kimura, 1956)—the distance between the tip of the lower jaw and the posterior end of the muscular knob on the caudal base—has been accepted internationally as the unit of length measurement for saury.

[3] K. H. Mosher. Age determination of eastern Pacific saury using scales. Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash. Unpubl. manuscr.

Preliminary scale studies indicated that the samples might be of two races of fish with different growth patterns—those with a wide zone of initial growth (distance between the focus and first annulus) and those with a much narrower zone of initial growth. Similar growth patterns have been detected by Japanese scientists on scales of fish of the western stock of Pacific saury and interpreted as distinct spring- and autumn-born "subpopulations" (Hotta, 1960). Accordingly, fish were classified as being either spring-born, autumn-born, or intermediate type by examining the initial growth zone of the scale. Length-weight regressions and von Bertalanffy growth in length parameters were determined for fish of the spring- and autumn-born scale types and compared statistically. In addition, electrophoretic techniques (Utter, Hodgins, and Johnson, 1972) were employed to test for significant inter-area heterogeneity as well as heterogeneity of fish with spring- and autumn-born scale features.

STOCK COMPOSITION

Temporal and spacial variations in length, age, sex, and maturity are treated in this section. In analyzing the sex ratio and age frequency data, fish of the spring- and autumn-born scale types were treated separately.

Size and Age Composition

There was a trend toward increasing length and average age with increasing latitude. Mean lengths in the California, Oregon, and Washington-Vancouver Island areas were 201 mm, 238 mm, and 277 mm, respectively (Figure 1). Length frequency histograms (Figure 2) show there was an absence of fish <160 mm off Washington-Vancouver Island which were represented off Oregon and relatively abundant off California. Conversely, fish >300 mm were absent off California, represented off Oregon, and relatively abundant off Washington-Vancouver Island.

Samples taken off California exhibited an unusual quadra-modal length-frequency distribution believed to be a sampling artifact rather than fluctuation in year-class strength. [Three of six schools sampled were schooled by size (Figure 1) which produced the minimum length mode at 165 mm and the maximum length mode at 270 mm.]

More symmetrical length distributions were produced from the three schools sampled in 1970 and five schools sampled in 1971 off Oregon. Lengths ranged from 159 mm to 293 mm in 1970 and 158 to 330 mm in 1971. Length distributions for both years are similar, being moderately skewed to the right with a mode at 210 mm in 1970 and 235 mm in 1971.

The three schools sampled off Washington in 1970 and two schools off Washington-Vancouver Island in 1971 showed more variation between years than the Oregon samples. A bimodal distribution was more apparent in 1971, modes at 245 and 305 mm, than the moderately asymmetrical distribution in 1970 with mode at 260 mm. Lengths ranged from 160 to 334 mm in 1970, and 161 to 340 mm in 1971. The upper limit of this latter range may exceed the previously known maximum length of the species in the eastern North Pacific Ocean. Clemens and Wilby (1961) reported lengths to 14 inches (356 mm); however, it is unclear whether this is standard or total length. The two saury measuring 340 mm knob length were ripe females measuring 363 and 364 mm in total length and weighing 180 and 190 grams respectively.

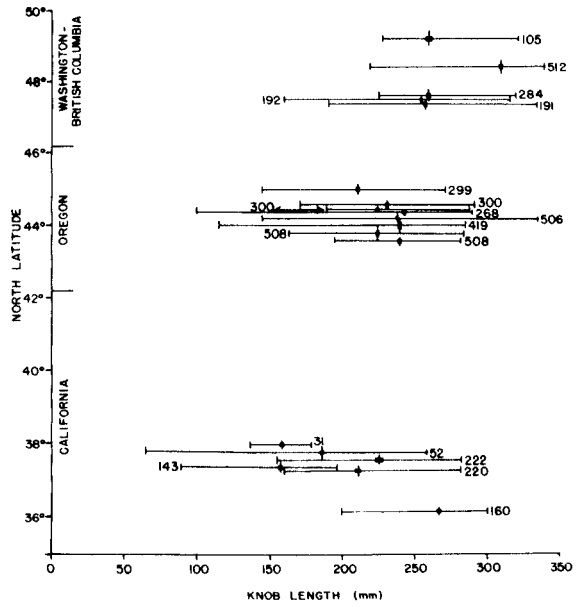

FIGURE 1.—Lengths (mean, range and S.D. of mean) of eastern Pacific saury plotted against latitude of capture. Numbers indicate sample size per school.

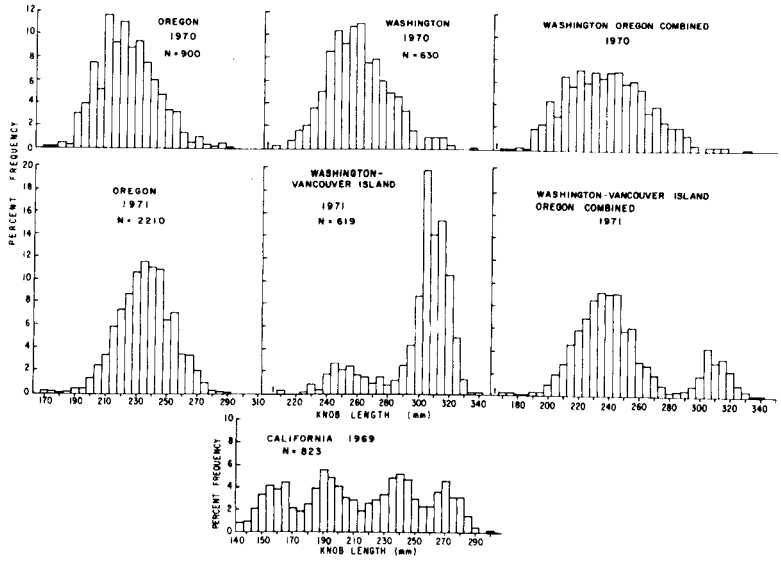

FIGURE 2.—Length frequency distributions of eastern Pacific saury captured off the Pacific coast of North America during August-September 1970-71.

Figure 2 also shows length-frequency distributions for combined Washington-Oregon samples in 1970 and Washington-Vancouver Island samples in 1971. A bimodal distribution is not apparent in 1970 but is distinct in 1971. Little variation in modes is noted between years.

Age frequency was determined from the 13 saury schools sampled off the Oregon-Washington-Vancouver Island coasts during 1970-71. Figure 3 histograms indicate the percentage of age groups by area, year, and areas combined within year.

Variations in age composition by latitude followed the expected trend established by size composition. Oregon fish were predominantly 1- and 2-year-olds while Washington-Vancouver Island fish were predominantly 2-, 3-, 4-, and 5-year-olds. Age composition of Oregon samples indicated little variation between 1970 and 1971 with age groups 1 and 2 representing 89% of the 1970 fish and 92% of the 1971 fish. In contrast, Washington fish showed considerable variation between years. In 1970, 93% of the fish were 2- and 3-year-olds while 54% were 4-year-olds in 1971. Sampling deficiencies probably account for the decline in the relative abundance of the 1968 year class between 1970 (2-year-old fish) and 1971 (3-year-olds). Fish aged as 6-year-olds were represented in 1970 and 1971 Washington samples, but it appears few fish survive beyond the age of 5.

Fish of the spring-born scale type consistently dominated all schools sampled (Figure 4) and also dominated most age groups. The greatest variation occurred at Oregon latitudes where fish of the autumn-born scale type comprised 27% of the 1970 samples and 12% in 1971. Washington samples were comprised of 21% autumn-born type in 1970 and 22% in 1971.

Sex Ratio and Maturity

The sex ratio was examined by age group for variation between area, year, and scale type.

Area differences in age composition and difficulties in determining sex of young fish hampered some comparisons; however, numbers of males and females were about equal through age 3 with females becoming predominant at age 4 and beyond. For more meaningful analysis, ages 1-3 and 4-6 were pooled for each area-year category. The sex ratio of saury of autumn- and spring-born scale types were next examined and found so similar that statistical treatment was unnecessary. Sex ratios of area-year-age group categories are presented in Table 2. While the sex ratio was age-dependent, sex composition differences in 1-3 year-olds of Washington vs Oregon catches in both 1970 and 1971 and 4-6 year-olds of Washington vs Oregon catches in 1971 were nonsignificant (0.05 level).

Size and age at first maturity could not be

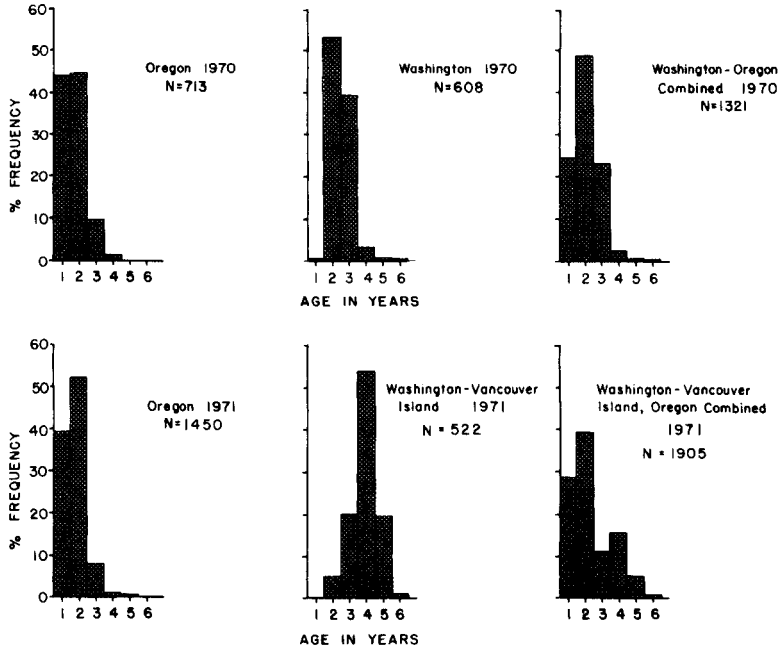

FIGURE 3.—Age frequency distributions of eastern Pacific saury captured off the Pacific coast of North American during August-September 1970-71.

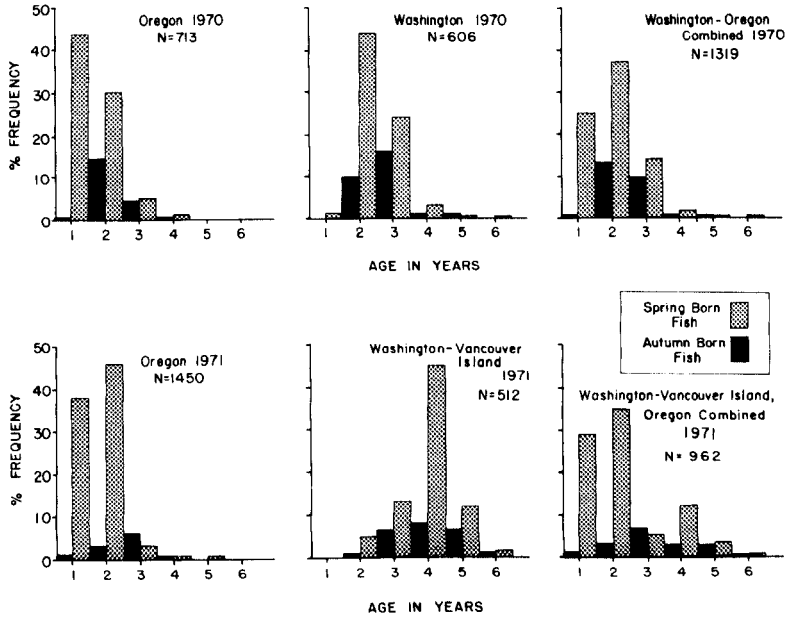

FIGURE 4.—Age frequency distributions of eastern Pacific saury showing age groups separated into spring- and autumn-born fish.

TABLE 2.—Sex ratios of age groups sampled in areas off the Pacific coast, 1970-1971.

Year-area category	Age group	Total no. fish examined	No. fish used for sex ratio	Sex ratio (% males)
1970				
Wash.	1-3	578	253	49.4
Oreg.	1-3	702	143	43.4
Wash.	4-6	28	26	30.8
Oreg.	4-6	10	10	0.0
1971				
Wash.-B.C.	1-3	179	100	54.0
Oreg.	1-3	1,365	1,024	56.1
Wash.-B.C.	4-6	391	388	37.6
Oreg.	4-6	8	6	33.3

directly determined from my samples since all but the very large fish were sexually inactive or immature upon collection. However, egg measurements obtained for ten 300-330 mm females collected off Washington in 1971 showed there were three distinct size groups of eggs: 0.1—0.4 mm, 0.8—1.5 mm, and the mature mode of 1.7—2.0 mm. Eleven smaller specimens collected off California by MacGregor[4] in March 1951 and 1954 ranged from 196 to 204 mm and contained eggs with a similar range (0.84—1.9 mm) indicating that saury are capable of reaching first maturity at lengths near 200 mm. Such fish would probably range from 1.1 to 1.4 yrs. old (Table 3).

Eighteen of the 19 schools sampled were composed principally of apparently mature fish in a resting state. The remaining school was predominantly 4-year-olds with females outnumbering males 1 to 0.73, and 96% of these were in spawning condition. Fish displaying both spring-born and fall-born growth patterns of scales were found in this school.

LENGTH-WEIGHT RELATION

The length-weight relation of saury captured in 1970 and 1971 was determined by fitting the logarithmic form of the equation $W = qL^d$, where W is weight in grams and L is knob length in millimeters, to mean emperical weights in each 5-mm length interval.

Separate relationships were determined for each hypothesized race and area-year category by sex. Using an analysis of covariance (Dixon and Massey, 1969), no significant difference in the L-W relation was detected between years, areas, or scale type, but there was a significant difference (0.05 level) between males and females.

A total of 1,170 males and 1,642 females representing immature, mature resting, and ripe saury were included in the length-weight regressions presented in Figure 5. The equation for males was $W = 3.293 \times 10^{-6} L^{3.050}$ and for females $W = 2.077 \times 10^{-6} L^{3.132}$. Females were slightly lighter than males at lengths <225 mm and heavier than males at lengths >280 mm.

GROWTH

Interpretation of growth was complicated because of the possible racial aspect and extended spawning season. Growth was determined for sexes combined because of the high probability of error in determining the sex of young fish. It was assumed that growth in length is asymptotic and that the von Bertalanffy (1938) growth equation adequately represents such growth.

Following methods of Stevens (1951), average lengths (observed and calculated from weight at age) were fitted to the equation $lt = L_\infty [1 - e^{-K(t-t_0)}]$.

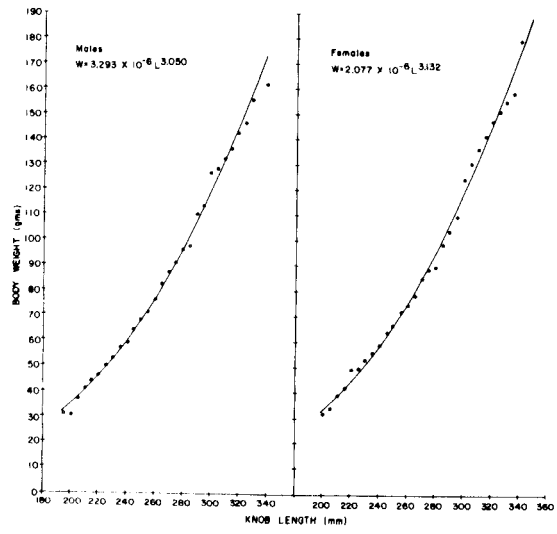

FIGURE 5.—Length-weight relation of male and female saury. The curve is fitted to mean-observed weight per 5-mm length interval.

[4] J. MacGregor, Fishery Biologist, Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Southwest Fish. Center, La Jolla, Calif., personal commun.

TABLE 3.—Average observed length at age, lengths calculated from weight at age and estimated von Bertalanffy growth parameters of hypothesized spring- and autumn-born fish.

Spring born fish			Autumn born fish		
Age (years)	Average observed length at age (mm)	Length calculated from weight at age[1] (mm)	Age (years)	Average observed length at age (mm)	Length calculated from weight at age[2] (mm)
1.10	183.9	182.5	0.75	142.8	151.2
1.40	219.0	223.6	1.00	178.7	182.1
2.40	245.5	249.3	2.00	232.1	235.8
3.40	268.8	272.7	3.00	256.8	260.6
4.40	308.6	312.5	4.00	297.0	303.0
5.40	319.8	321.4	5.00	314.5	316.8
6.40	319.9	323.0			
	L_∞ = 351.43	L_∞ = 360.23		L_∞ = 353.45	L_∞ = 348.50
	K = 0.34	K = 0.36		K = 0.38	K = 0.38
	t_0 = −1.19	t_0 = −0.83		t_0 = −0.72	t_0 = −1.02

1 $W = 1.497 \times 10^{-6} L^{3.189}$
2 $W = 1.809 \times 10^{-6} L^{3.155}$

Growth was first compared between fish of the autumn- and spring-born scale type. Table 3 summarizes the respective sets of length at age data and presents growth parameters. Little difference is noted between respective sets of length at age data for the two groups of fish. Although there is no consistent advantage in using lengths derived from weights at age, it should be noted that estimated t_0 values are sensitive to the method chosen. Regardless of method, no significant differences in growth parameters L_∞ and e^{-K} existed between fish of spring- and autumn-born scale types. Their graphic similarity is shown in Figure 6 where observed lengths at age and fitted curves are presented. Lack of significant differences in growth patterns between fish of spring- and autumn-born type suggested that respective data sets be pooled and that a single growth curve be presented (Figure 7). The resulting estimated parameters were L_∞ = 342.36, K = 0.41, and t_0 = −0.72. The calculated L_∞ is close to the maximum observed length of 340 mm. The estimated age at 95% growth completion was 6.5 years.

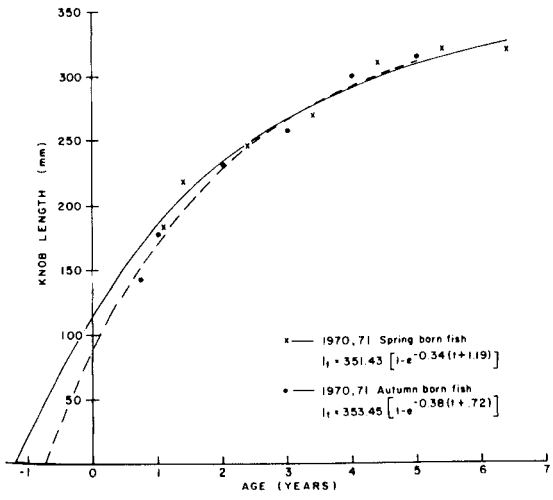

FIGURE 6.—Average observed length at age and fitted growth curves of spring- and autumn-born saury captured in offshore waters from southern California north to Vancouver, British Columbia 1970-71.

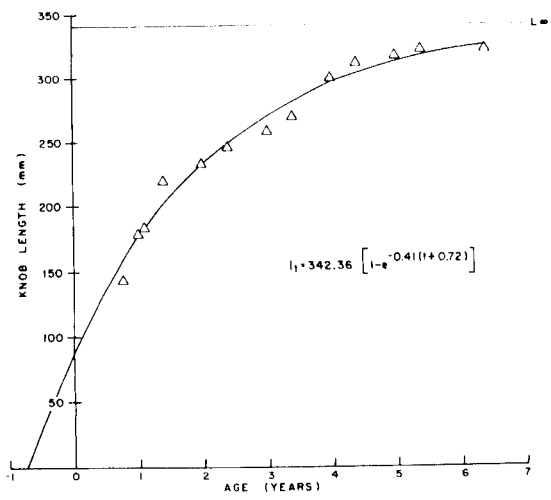

FIGURE 7.—Average observed length at age and fitted growth curve of eastern Pacific saury after pooling data from spring- and autumn-born fish.

MORTALITY

There are several limitations to the data used for estimating natural mortality: (1) Sampling was conducted during a period of apparent migration which caused the stock along the Pacific coast to become stratified in size and age composition, (2) sampling was limited and not conducted throughout the stock's entire geographical range, and (3) age frequency data indicate possible variations in annual recruitment and/or survival rate. Thus, one or more basic assumptions underlying traditional mortality models are violated to some degree. Realizing the above limitations and considering this an initial study of the adult stock, I have generated a range of estimates using several independent techniques.

A catch curve analysis (Robson and Chapman, 1961) was applied to the 1970 data since equal sampling occurred off Washington and Oregon, the only areas sampled, during that period.

Age	Coded age	No. of fish in catch
II	0	$N_0 = 644$
III	1	$N_1 = 313$
IV	2	$N_2 = 32$
V	3	$N_3 = 7$
VI	4	$N_4 = 1$
		$n = 997$

Annual survival rate estimate:

$$\hat{S} = .2876$$
$$\text{Var}(s) = 0.00017$$
$$\text{SE}(s) = 0.013$$
$$95\%\ \text{CI}(s) = .2876 + 2(0.013)$$
$$= (.2616, .3136)$$

When the above data were converted to a total annual instantaneous mortality rate, $Z = 1.25$ and 95% CI, $Z = (1.16, 1.34)$.

The raw age data were also converted to natural log form and treated by simple linear regression. The result was a significant linear relationship with $Z = 1.67$ and 95% CI, $Z = (1.41, 1.93)$.

Beverton and Holt's (1956) formula using length frequency data was also applied to the 1970 data. While this technique was designed primarily for exploited populations, its use generated another independent estimate and enabled the use of substantial numbers of fish which could not be aged.

The Beverton and Holt formula $Z = \frac{K(L_\infty - L)}{(L - L_r)}$ where L is the average length of the fish in the catch that are as large as, or larger than, the first fully recruited length L_r, estimated $Z = 1.41$ when $L_\infty = 342$ mm, $K = 0.41$, $L = 248$ mm, and $L_r = 220$ mm.

Survival rates were generated for each of the four area-year categories by subjecting respective sets of age frequency data to Jackson's (1939) technique:

$$S = \frac{N_2 + N_3 + \cdots + N_r}{N_1 + N_2 + \cdots + N_r - 1}.$$

The analysis yielded the following estimates:

Oregon, 1970; $Z = 1.58$,
Oregon, 1971; $Z = 1.80$,
Washington, 1970; $Z = 2.20$,
Washington-Vancouver Island, 1971; $Z = 1.27$.

The seven individual estimates obtained indicate a possible range of Z from 1.25 to 2.20 and an overall average Z of 1.60.

AVAILABILITY OF FISHABLE CONCENTRATIONS

Fishable concentrations of saury (>¾ ton) were usually located in waters of 15°-17°C near areas of upwelling. Surface temperatures strongly influence distribution and migration patterns of western Pacific saury (Fukushima, 1956 and 1962) as they appear to in the eastern Pacific (Ellis and Hughes, 1971). All studies indicate sharp thermal fronts affect and often dictate patterns of migration and areas where temporary concentrations may form.

Throughout the surveys, high density areas capable of sustaining productive fishing operations were rarely encountered. Most encounters were single schools (1-3 tons) or loose aggregations of fish dispersed over large areas of surface waters. The average probability of locating at least one fishable concentration during a night's operation (averaging 8 hr of searching effort and 70 miles of tracklines) was about 0.3. The relative densities decreased slightly with increasing latitudes, but large saury, which are currently in greatest commercial demand, were

more available in the northern portion of the study area.

Low availability has evidently hampered Japanese attempts to establish new fishing grounds in the eastern Pacific. Operations by about 15 Japanese saury vessels in 1970 and 19 vessels in 1971 met financial failure. Consequently, major fishery firms such as Nihon Suisan, Hoko Suisan, and Nichiro have reportedly abandoned attempts to exploit the eastern Pacific saury resource.[5]

DISCUSSION

It seems pertinent to propose some general hypotheses about the life history of the eastern Pacific saury based on information presented here and in papers by Ahlstrom and Casey (1956), Ahlstrom (1968), and Smith et al. (1970).

The coastal stratification of saury by size and age composition during at least August-September is probably due to a northerly migration by many adults from California waters. Sea surface temperatures and position of warm-cold fronts strongly influence migration patterns and rates of movement of saury in the western North Pacific Ocean (Fukushima, 1956, 1962). Several factors indicate a similar situation exists in the eastern Pacific Ocean. Our surveys indicated eastern Pacific saury display narrow limits of thermal preference and are found most often near areas of upwelling. Furthermore, there is an excellent correlation between the apparent spacial and temporal distribution of saury and average month-by-month sea-surface temperature data. Using Johnson's (1961) 12-year monthly means and a thermal preference range of 14.0° to 17.0°C, it is apparent that large quantities of saury would not begin a northerly migration from California waters before June. Migration into northern Oregon and Washington waters would not be expected to occur before July. Rapid warming during July and August produces a favorable temperature regime along the coasts of Washington, Vancouver Island, and into Queen Charlotte Sound. While temperature conditions remain favorable in September, seasonal cooling occurs off Vancouver Island and Washington during October and continues through Oregon and northern California waters in November. Thus, it appears that in addition to influencing the time and patterns of saury migration, temperature conditions could also restrict the bulk of the stock to oceanic areas between Baja California and Queen Charlotte Sound or the southern Gulf of Alaska.

From the data presented, the degree of migration appears to be dependent on size and age of fish, and many young adults and juveniles apparently remain in California waters throughout the year.

Fish exceeding 300 mm in length (primarily ages 4, 5, and 6) reach maturity during the migration in August and release their mature mode of eggs (1.8-2.0 mm) in late August or September. Since Hatanaka's (1956) work on maturity in the western North Pacific Ocean (three modes of eggs, 0.6, 1.1, and 1.9 mm) is in close agreement with this study, it seems reasonable that eastern Pacific saury release modes of eggs at about the same intervals—2 months between the first and middle mode. Thus, the second spawning of large fish would probably take place in October or November and the third spawning during the winter while off California. Younger adults, sexually inactive during August-September, probably mature and spawn during the following winter and spring while in more southerly waters, primarily off California. It is not known whether 2- and 3-year-old fish spawn more than one mode of eggs per year.

The above hypothesis would account for the reported low abundance of eggs in California waters during August-September (Smith et al., 1970) when most spawning saury occupy a northerly regime. The spawning of younger age groups coincides with peak egg abundance in California during April, May, and June. Such an extended spawning season would account for spring-born, autumn-born, and some intermediate growth patterns detected from scale samples, as well as the fact that three-quarters of the samples displayed the spring-born growth characteristic.

There seems to be little likelihood that spring- and fall-born fish constitute different races, since both types were observed spawning together in the same school. Furthermore, statistical comparisons of length-weight and

[5] J. H. Shohara (Compiler). 1972. 12 Japanese vessels licensed for distant-water saury fishing [Excerpted from Shin Suisan Shimbun Sokuho, July 18 and July 29, 1972]. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Foreign Fish. Inf. Release 72-27, p. 3. (Processed.)

growth parameters failed to disclose any significant differences between these groups. These results are in line with unpublished results of Utter whose biochemical gene frequency studies gave no indication of heterogeneity between spring-born and fall-born saury.[6] Biochemical techniques also indicated intra-area homogeneity of fish in waters between southern California and Vancouver Island. Additional samples would have been desirable for a more complete racial study; however, results of this initial study strongly suggest the eastern Pacific saury stock is basically represented by a single gene pool.

Growth, maturity, and mortality studies indicate that saury (1) display rapid growth during the first year of life, (2) are capable of attaining maturity during the second year, and (3) probably do not survive beyond 6 years of age. Results indicate the total mortality coefficient (Z) is between 1.25 and 2.20. Since fishing mortality has remained insignificant, Z would be a result of natural mortality (M), assuming migration during the sampling period has not significantly confounded the situation. Intuitively, it seems Z is a reasonable approximation of M since sampling was conducted over a wide geographical area during the middle of the migratory period. No previous estimates of natural mortality have been published for the eastern Pacific saury stock; however, Novikov (1969) reports natural mortality in the western Pacific to be about 50%. Converting to instantaneous mortality for direct comparison, his estimate would be about 0.70.

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HEAVY METALS IN THE NORTHERN FUR SEAL, *CALLORHINUS URSINUS*, AND HARBOR SEAL, *PHOCA VITULINA RICHARDI*

RAYMOND E. ANAS[1]

ABSTRACT

Samples of liver, muscle, and kidney from fur seal, *Callorhinus ursinus*, and liver from harbor seal, *Phoca vitulina richardi*, were analyzed for total mercury. Liver and kidney of fur seals were analyzed for lead, cadmium, and arsenic. Fur seals were from the Pribilof Islands, Alaska, and from off the Washington coast. Harbor seals were from the waters of southern California, Oregon, Washington, and the Bering Sea. All of the samples, including a fetus taken 3 mo before birth, contained mercury, lead, and cadmium. Arsenic was not detected. Mercury was highest in liver, followed by kidney, then muscle. The maximum concentration of mercury in liver was about 700 ppm in a southern California harbor seal and 170 ppm in a fur seal taken off the Washington coast. Concentrations of cadmium and lead were highest in the kidney (maximums of 1.8 ppm lead and 15.6 ppm cadmium) of fur seals. Concentrations of mercury did not correlate with age in muscle or kidney ($P > 0.05$) but did correlate significantly with age in liver ($P < 0.01$). Concentrations of cadmium and lead in liver and kidney did not correlate with age ($P > 0.05$). In samples of liver collected from harbor seals, the highest concentrations of mercury were from southern California seals.

Heavy metals are persistent contaminants that ultimately end up in the oceans. Little is known of the sublethal effects of these contaminants on living marine resources, but some heavy metals are known to be harmful. One ppb (part per billion) of four commonly used organomercurial fungicides reduced the photosynthetic rate of a marine diatom (Harriss, White, and MacFarlane, 1970). Skerfving, Hansson, and Lindsten (1970) reported chromosome breakage in humans who ate fish containing 1-7 ppm (parts per million) methylmercury.

Heavy metals are added to the sea by land erosion, volcanic activity, and man. A committee of experts selected mercury, lead, cadmium, and arsenic as the four inorganic pollutants most threatening to the marine environment (Food and Agriculture Organization of the United Nations, 1971). The same elements were selected for this study. Average levels of the four most critical heavy metals in the ocean are about 0.00003 ppm (mg/l) mercury, 0.08 ppm cadmium, 0.00003 ppm lead, and 0.003 ppm arsenic (U.S. Senate, 1970). Williams and Weiss (1973) found 0.00027 ppm mercury at 10-m depth and 0.000029-0.000096 ppm from 100- to 4,080-m depth in water samples taken 430 km southeast of San Diego, Calif.

Amounts of contaminants in seals provide us with data at this time in a marine species near the top of the food web in the ocean. Up to 172 ppm mercury in liver of northern fur seals, *Callorhinus ursinus* (Anas, 1970a); 66 ppm in liver of gray seals, *Halichoerus grypus* (Jones, Jones, and Stewart, 1972); and 24 ppm mercury in liver of short-finned pilot whales, *Globicephala scammoni* (Hall, Gilmartin, and Mattsson, 1971) have been reported. Buhler[2] reported 60 ppm cadmium in the kidney, 6 ppm cadmium in the liver, and 225 ppm mercury in the liver of California sea lions, *Zalophus californianus*. This report documents the amounts of mercury, lead, cadmium, and arsenic in northern fur seals and of mercury in harbor seals, *Phoca vitulina richardi*.

Northern fur seals are a migratory species that breed each summer mainly on the Pribilof Islands, Alaska, and on the Commander Islands

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[2] D. R. Buhler, Environmental Health Sciences Center, Oregon State University, Corvallis, Oregon 97331, personal communication.

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and Robben Island, USSR. Small breeding colonies are found in the Kurile Islands, Japan, and on San Miguel Island, Calif. During winter and spring, fur seals are pelagic and migrate as far south as southern California and Japan. Fur seals feed principally on fishes and squids in offshore areas.

Harbor seals are a nonmigratory species found in the northern hemisphere in both the Pacific and Atlantic Oceans. Those collected for this study (subspecies *richardi*) are found from Mexico to the Bering Sea. Harbor seals feed principally on fishes, squids, and octopuses near coastlines.

METHODS

The liver and kidneys were selected as the principal tissues for this study because heavy metals tend to accumulate in these organs (DuBois and Geiling, 1959; Curry, 1969). Samples of muscle were collected from fur seals but not from harbor seals.

Collection of Samples

In general, the sampling was conducted as follows: From a seal liver weighing about 1.8 kg, a kidney weighing about 0.5 kg, or muscle from the shoulder area, a sample of about 75 g was placed in a new unwashed glass bottle or polyethylene bag and stored at −23°C. Analyses were made about 5 mo after initial sampling.

Samples included liver and muscle from 3-mo-old pups and 2- and 3-yr-old male fur seals from the Pribilof Islands; liver, muscle, and kidney from fur seals (mostly adult females) from Washington; and liver from harbor seals from California, Oregon, Washington, and the Bering Sea. Tissues from fur seals taken on the Pribilof Islands were kept in polyethylene bags; all other tissues were kept in new glass bottles.

Analyses of Samples

For the analysis of mercury, four replicate 20-mg samples were taken from a piece of tissue in the sample bottle and analyzed. The mean of these four replicates was taken as representative of the particular tissue for that analysis. The analytical procedure for mercury involves introduction of the weighed sample into a tubular furnace from which the products of combustion and vaporized mercury are drawn. After scrubbing and filtering to remove interfering components, the mercury vapor is passed through a cell and read by atomic absorption spectrophotometry.[3]

For lead, cadmium, and arsenic analyses, a separate 2-g sample was taken for each metal. The lead analysis was carried out by digesting the sample in a 5:2 nitric-sulfuric acid mixture followed by dry ashing in a muffle furnace at 550°C until all organic material was removed. Following dissolution in 5 ml of hydrochloric acid, lead content was determined by the double extraction, mixed color dithizone method (Committee on Chemical Procedures of the Occupational Health Section, American Public Health Association, 1955).

For cadmium, the sample was wet ashed in a 2:1 nitric-perchloric acid mixture, and the resultant solution diluted to a known volume with water. The cadmium was extracted into methyl isobutyl ketone (MIBK) by means of chelation with sodium diethyldithiocarbamate (NDDC) and measured by atomic absorption (Berman, 1967).

For arsenic, the sample was wet ashed in an 8:4:1 nitric-perchloric-sulfuric acid mixture to oxidize organic matter and release organically bound arsenic. Following digestion, the sample was diluted to 25 ml volume with water and arsenic determined by the silver diethyldithiocarbamate method (American Public Health Association, 1971).

Detection limits of the analyses were 1 ppb for mercury, 0.1 ppm for lead, 0.01 ppm for cadmium, and 0.2 ppm for arsenic. Recoveries were over 90% for mercury and cadmium where mercury was added as elemental mercury dissolved in nitric acid and cadmium was added as cadmium sulfate. Lead and arsenic recoveries were over 95% with lead added as lead nitrate and arsenic added as arsenic trioxide.

All of the tissue samples were analyzed by Environmental Health Laboratories Inc.,

[3] Hermann, W. J., Jr., J. W. Butler, and R. G. Smith. 1968. A dynamic system for the rapid microdetermination of mercury in undigested biological materials. Presented at Applied Seminar on Laboratory Diagnosis of Diseases Caused by Toxic Agents, Washington, D.C., Nov. 8-9, 1968. Wayne State Univ., Detroit, Mich., Dep. Med., 14 p., 1 fig. (Processed.)

Farmington, Mich.[4] A sample of paper lid liners from the glass bottles was analyzed by the use of neutron activation by Battelle Pacific Northwest Laboratories, Richland, Wash., to determine amounts of mercury, lead, cadmium, and arsenic.

Age Determinations

Ages were assigned to fur seals by counting layers of dentine in sectioned upper canine teeth (Scheffer, 1950; Fiscus, Baines, and Wilke, 1964). Errors in assigning ages to fur seals are small in young seals but increase sharply in animals older than 7 yr (Anas, 1970b). Most errors in older animals, however, are only of a magnitude of ± 2 yr. Although canine teeth of harbor seals have layers of dentine, it is not known if these layers accurately portray age. Ages were not assigned to harbor seals, but body lengths were taken.

RESULTS

Heavy Metals in Fur Seal Tissues

Amounts of total mercury were higher in liver than in muscle or kidney of fur seals (Table 1). Mercury in liver ranged from 0.4 ppm in a fetus taken 3 mo before birth (the liver of the 11-yr-old mother had 86 ppm), to 0.1-0.3 ppm in 10 pups, 3-19 ppm in 30 young males, 7-78 ppm in two young females, and 19-172 ppm in 36 adult females. For muscle, 0.1 ppm was found in five pups, 0.1-0.4 ppm in 29 young males, and 0.2-0.4 ppm in 10 adult females. Mercury in kidney ranged from 0.2 ppm in a fetus (the mother had 1 ppm), to 0.7 ppm in a young male, and 0.6-1.6 ppm in eight females, 1 to 20 yr old.

A wide range of mercury was found only in the liver, so variability due to sampling is more important for liver than for muscle or kidney. The 95% confidence limits of within-sample variability for the 20-mg samples of liver were ± 11% of the mean values. The average variability between seals within ages was 55 times greater than the variability within the 20-mg samples. Thus, to increase accuracy, larger samples of seals are more important than additional 20-mg samples from each piece of liver.

Methylmercury was not determined in this study. However, in samples of liver from California sea lions, about 2% of the total mercury was methylmercury (Buhler, see Footnote 2).

On the average, amounts of lead and cadmium were higher in kidney than in liver (Table 2). Arsenic was not detected in any of the samples. Lead in liver ranged from 0.8 ppm in a fetus (the mother also had 0.8 ppm), to 0.2 ppm in a young male, and 0.4-0.8 ppm in eight females. Lead in kidney ranged from 0.3 ppm in a fetus (0.8 ppm in the mother), to 1.8 ppm in a young male, and 0.8-1.2 ppm in eight females. Cadmium in liver ranged from 0.5 ppm in a fetus (4.6 ppm in the mother), to 0.6 ppm in a young

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1. — Parts per million mercury on a wet weight basis in liver, muscle, and kidney of fur seals taken off Washington and on the Pribilof Islands, 1970-71.

Age (years)	Sex	Area	Year collected	Number of seals	Tissue	Mercury	
0.3 (Pups)	Mixed	Pribilof	1970	10	Liver	0.1	0.3
		Islands	1970	5	Muscle	0.1	
2-3	Male	Pribilof	1970	29	Liver	3.0	19.0
		Islands	1970	29	Muscle	0.1	0.4
5-19	Female	Washington	1970	29	Liver	19.0	172.0
		Coast	1970	10	Muscle	0.2	0.4
Fetus	Male	Washington	1971	1	Liver	0.4	
		Coast	1971	1	Kidney	0.2	
1	Male	Washington	1971	1	Liver	3.7	
		Coast	1971	1	Kidney	0.7	
1-20	Female	Washington	1971	8	Liver	7.1	132.0
		Coast	1971	8	Kidney	0.6	1.6

TABLE 2. — Parts per million cadmium and lead on a wet weight basis in kidney and liver of fur seals taken off Washington, 1971.[1]

Age (years) of specimens	Sex of specimens	Kidney		Liver	
		Cadmium	Lead	Cadmium	Lead
Fetus	M	0.1	0.3	0.5	0.8
1	M	1.7	1.8	0.6	0.2
1	F	6.9	0.8	0.9	0.6
3	F	4.3	0.8	2.2	0.6
6	F	15.6	1.2	2.6	0.6
8	F	0.2	0.9	1.2	0.5
11	F	6.2	0.8	4.6	0.8
15	F	9.6	0.9	1.1	0.4
16	F	1.0	1.0	1.7	0.5
20	F	6.8	0.8	1.7	0.7

[1] Arsenic was not found above the limit of detection of 0.2 ppm (mg/kg) in either kidney or liver in any of the samples.

male, and 0.9-4.6 ppm in eight females. Cadmium in kidney ranged from 0.1 ppm in a fetus (6.2 ppm in the mother), to 1.7 ppm in a young male, and 0.2-15.6 ppm in eight females.

Lid liners from new glass bottles had 1.1 ppm mercury and 0.4 ppm arsenic. Lead and cadmium were not detected. The tissues and lid liners were never in direct contact, but some transfer of mercury from the lid liners and glass bottles could have occurred. However, the maximum contribution from the lid liners would have been 0.004 ppm mercury, so the data were not adjusted.

Heavy Metal — Age Comparisons in Fur Seals

Regression equations were computed for samples from fur seals collected in 1970 and 1971 to determine if mercury in liver, muscle, and kidney and if lead and cadmium in liver and kidney were correlated with age. Significant correlations for mercury have been reported for fur seal liver (Anas, 1970a) and whole fishes (Bache, Gutenmann, and Lisk, 1971). Untransformed data were used here because log transformations did not significantly improve the correlations. Fetuses and pups were not included in the calculations. Only liver tissues were collected both in 1970 and 1971. The correlation coefficients in the two years for mercury in liver were common ($P > 0.05$), so the data were pooled. Mercury in liver had a significant positive correlation with age ($P < 0.001$, $r = +0.84$). The data indicate that mercury accumulates in liver. Mercury in muscle and kidney did not correlate with age ($P > 0.05$, $r = +0.05$ and $+0.51$, respectively). Also, lead and cadmium in liver and kidney did not correlate with age ($P > 0.05$, $r = +0.19$ and -0.45 for lead and $r = +0.17$ and $+0.04$ for cadmium in liver and kidney, respectively). Sample sizes were 67 for mercury in liver, 39 for mercury in muscle, and 9 for cadmium and lead in liver and kidney.

Mercury in Harbor Seal Livers

Harbor seals are nonmigratory, so levels of contaminants in this species are useful for locating geographical concentrations of contaminants, provided that the food species do not migrate long distances. Studies suggest that the principal food species of harbor seals do not migrate far (Scheffer and Sperry, 1931; Spalding, 1964; Kenyon, 1965). The highest levels of mercury were found in harbor seals from San Miguel Island (Table 3). One harbor seal from San Miguel Island had 700 ppm mercury in the liver. The amount of mercury in this sample is so much higher than the amounts found in the other seals that the possibility of contamination of the sample should be considered. However, as far as is known, this sample was treated no differently than the other samples. The sample size is small and the ages are not known, but the concentrations of

TABLE 3. — Parts per million mercury on a wet weight basis in liver of harbor seals taken in the eastern Pacific Ocean, 1970-71.

Location	Date collected	Sex	Length (cm)	Mercury
San Miguel Is., Calif.	2 June 1971	F	161	700
	2 June 1971	F	153	81
	4 June 1971	M	176	124
	5 June 1971	F	156	171
Columbia R., Oregon	May 1971	M	—	0.3
	do	M	112	3.2
	do	F	126	68
Washington Coast	2 Sept. 1971	F	84	1.3
Puget Sound, Washington	24 Nov. 1970	M	—	60
	21 June 1971	M	95	12
Pribilof Is., Alaska	17 Aug. 1971	M	135	0.6
	do	F	140	3.2
	do	M	175	8.9

mercury in San Miguel Island seals appear to differ significantly from those from the Pribilof Islands. Except for the one seal with 700 ppm mercury, the amounts of mercury found in harbor seals from all areas studied are within the range of those found in livers of fur seals.

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BIOECONOMIC CONTRIBUTION OF COLUMBIA RIVER HATCHERY COHO SALMON, 1965 AND 1966 BROODS, TO THE PACIFIC SALMON FISHERIES

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ABSTRACT

Marked coho salmon, *Oncorhynchus kisutch*, smolts of the 1965 and 1966 broods were released from 20 hatcheries on four sections of the Columbia River and tributaries. Commercial and sport fisheries in marine waters from Pelican, Alaska, to Avila Beach, Calif., and on the Columbia River were sampled during 1967-69 for marks.

The net value of the estimated total catch of hatchery fish was calculated after adjusting for the effects of marking. Also estimated for each brood were the total costs of rearing including amortized capital outlay. Total benefits of $8.58 million for the 1965 brood and $9.11 million for the 1966 brood were estimated as applicable to normal production years when no marking takes place. Corresponding costs were estimated as $1.29 million for the 1965 brood and $1.23 million for the 1966 brood. Estimated benefit/cost ratios for the 20 Columbia River coho salmon hatcheries, as operated under production regimes prevailing during the study, may prove useful in decisions affecting management policies. The ratios are 6.6/1 for the 1965 brood, 7.4/1 for the 1966 brood, and 7.0/1 for both broods combined.

Use of the Columbia River has expanded tremendously in the past 30 years through Federally financed and/or licensed water use projects. This expansion has depleted valuable stocks of Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, through the loss and deterioration of natural stream habitat. Therefore, mitigative measures—hatcheries, fish ladders, and spawning channels—to supplement the declining natural production of Columbia River salmon and steelhead trout have been Federally funded.

To counteract the severe loss of salmon and steelhead trout environment in the Columbia River basin, the U.S. Government began financing the Columbia River Development Program in 1949. The Program is a cooperative effort of the fish management agencies of the states of Oregon, Washington, and Idaho and the Federal Government. The Columbia Fisheries Program Office, National Marine Fisheries Service, Portland, Oreg., administers the Program, which is designed to increase production of salmon and steelhead in the Columbia River. The Program's major thrust has been to improve the runs of salmon and steelhead by protecting and improving stream environment and by production of fish in hatcheries. The main accomplishment is the construction or modernization of 21 salmon and steelhead hatcheries on the lower Columbia River and tributaries.

There are two major reasons for the concentration of effort on salmon and steelhead trout. First, their life histories allow successful hatchery propagation. Second, these species are historically and economically important to the United States. Annual catches of Pacific salmon have ranked first or second for the past 3 decades in landed value of commercial finfishes to United States fishermen. Chinook salmon, *O. tshawytscha*, and coho salmon, *O. kisutch*, landings have accounted for 35% of the 6-yr average (1966-71) commercial value ($70 million) for salmon—$12.5 million for chinook and $11.9

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for coho (Lyles, 1968, 1969; National Marine Fisheries Service, 1971; Riley, 1970, 1971; Wheeland, 1972). In addition, the net economic value of marine and freshwater sport fishing for salmon in the U.S. in 1970 was estimated at $77.7 million. This fishery was made up of 64% coho and 32% chinook.[3]

In 1950 five salmon hatcheries, representing the entire Columbia River production of hatchery coho salmon, released about 1 million juveniles typified by a short rearing period, poor nutrition, and low survival. In contrast, the number of hatcheries rearing coho increased to 20 by 1966-67, and annual releases averaged 20 million smolts. These salmon benefited from advances in fish culture, especially nutrition, applied during the early 1960's and were characteristically large and healthy with a high survival potential (Cleaver, 1969a).

In 1962 the Columbia Fisheries Program Office started a marking study to estimate the contribution of Columbia River hatchery-reared fall chinook salmon to the Pacific coast fisheries. In 1965 this study was expanded to include coho salmon. Accordingly, representative (10%) samples from all Columbia River hatcheries rearing 1965- and 1966-brood coho salmon were marked. Sampling for these marked coho took place from 1967 through 1969 in the sport and commercial fisheries from Alaska to California. A contribution study of this magnitude had never before been undertaken. The information to be gained from this study was critically needed to determine if increased Federal funding for Columbia River hatcheries was economically justified.

The objectives of this report are to (1) describe the design and operations of marking and release procedures, (2) estimate the contribution (catch) to Pacific salmon fisheries during 1967, 1968, and 1969 for the 1965-66 brood coho salmon hatchery releases, and (3) develop benefit/cost ratios for these two broods.

BIOLOGICAL EVALUATION

Experimental Design

Procedures were basically the same as described by Worlund, Wahle, and Zimmer (1969) for the fall chinook salmon study but will be summarized here. The Columbia River was divided into four sections. These sections will be defined later. Releases of marked fish were intended to identify and estimate the catches from each section. Execution of the plan depended, as for the evaluation of fall chinook salmon hatcheries, on the cooperation of many people in the following agencies:

Alaska Department of Fish and Game
Fisheries Research Board of Canada
Washington Department of Fisheries
Fish Commission of Oregon
Oregon State Game Commission
California Department of Fish and Game
National Marine Fisheries Service
Bureau of Sport Fisheries and Wildlife

The basic plan was to mark the same proportion of juvenile coho salmon released at each hatchery and to sample for marks in commercial and sport fisheries. Total catches of fish from all hatcheries then could be estimated from (1) fractions of marked fish in each release, (2) numbers of each type of mark actually recovered, (3) fractions of the total catches sampled for marks by time and area in each fishery, and (4) information on any bias associated with application or detection of marks.

Allocation of Marks

The 20 hatcheries involved in this study are distributed over much of the mainstem Columbia River accessible to anadromous fish (Figure 1). Klaskanine River Salmon Hatchery, the lowermost station, and Leavenworth National Fish Hatchery, the uppermost, are on tributaries about 25 km and 800 km (15 and 500 miles), respectively, above the Columbia River mouth. Some hatcheries (Bonneville, Cascade, OxBow, and Little White Salmon) are adjacent to the main Columbia River and release their fish almost directly into it. In contrast, fish released at the Toutle River station must travel 65 km (40 miles) to reach the Columbia River.

Four different marks were available (from the Pacific Marine Fisheries Commission) for the 1965 brood of coho salmon. The Columbia River was therefore divided into four sections—Lower River, Middle River, Upper River, and Uppermost River—and one mark was assigned to each (Table 1). The adipose-right maxillary

[3] George K. Tanonaka. 1972. A general comparison of the commercial and sport salmon fisheries of the United States, 1940-70. Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash. (Unpubl. manuscr.) 15 p., 7 tables, 4 fig., App. A-B.

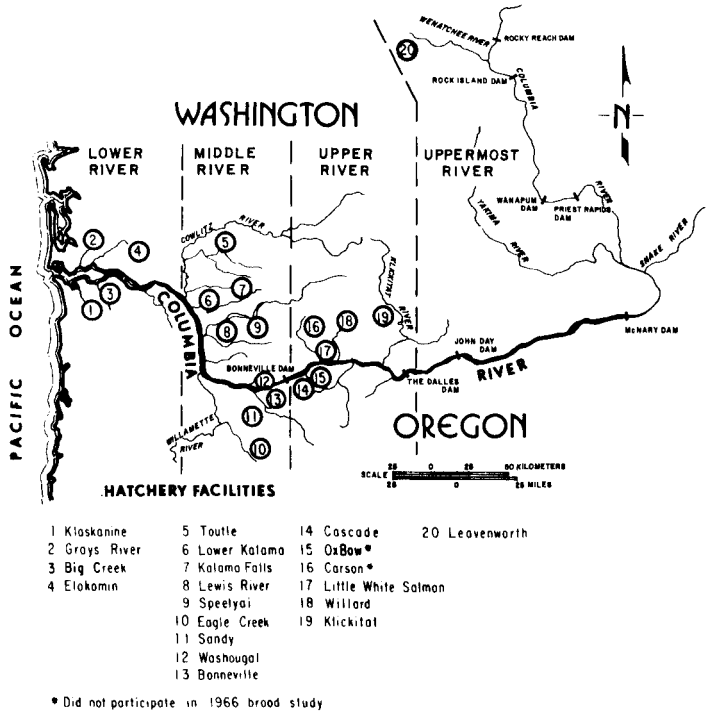

FIGURE 1.—Location and grouping by river section of Columbia River hatcheries participating in this study.

mark (Ad-RM) was used for hatcheries in the Lower River section—Columbia River mouth to Cowlitz River. The adipose-only finclip (Ad) was allotted to hatcheries in the Middle River section—the Cowlitz River to Bonneville Dam. Hatcheries in the Upper River section—Bonneville Dam to The Dalles Dam—were issued the adipose-left maxillary mark (Ad-LM). Leavenworth National Fish Hatchery, the only study hatchery in the Uppermost River section—above The Dalles Dam—was assigned the dorsal-adipose finclip (D-Ad).

The same marks were used for the 1966 brood with one exception; at Leavenworth National Fish Hatchery, maxillary marks were added to the D-Ad finclip. Juveniles with D-Ad-RM marks were released at the hatchery and those with D-Ad-LM were trucked downstream and released below Bonneville Dam. The purpose of the two marks and release sites was to examine differential mortality due to passage through dams; results will be treated in a subsequent report.

Sources of Variation and Error

To evaluate variations between broods and river sections, two broods (1965-66) of coho salmon were included in the study, and each river section was allotted a specific mark. Mortality due to marking, the most important source of error, was evaluated by comparing marked/unmarked ratios in hatchery releases and returns. To evaluate the dilution effect of returning wild fish on the marked/unmarked ratio at study hatcheries, oxytetracycline (TM-50) was added to the diet of both broods of coho salmon reared at Big Creek (Ad-RM mark) and Eagle Creek (Ad finclip) hatcheries. Tetracycline deposits a permanent mark on the bone structure of feeding juvenile salmon and, at spawning, this mark is readily detected on coho vertebrae under ultraviolet light (Weber and Ridgway, 1967). Thus, wild coho were identifiable and were subtracted from the total unmarked returns to Big Creek and Eagle Creek hatcheries.

Marked fish were held at Klickitat State Salmon Hatchery to evaluate the degree of mark regeneration. Markers at all participating hatcheries were asked to record naturally missing fins and maxillary bones. Catch samplers were alerted to possible regeneration so they could look for malformed fins.

Rearing techniques at different hatcheries varied within as well as between river sections.

The limited number of marks available precluded individual hatchery comparisons as made from data of the fall chinook salmon study (Cleaver, 1969b; Worlund, Wahle, and Zimmer, 1969; Lander, 1970; Henry, 1971). The size of fish at release reflects partially the differences in rearing techniques. In both wild and hatchery salmon stocks, it is well known that large smolts survive better and contribute more to catches, other factors being reasonably equal, than do small smolts (Ricker, 1962; Fredin, 1964; Johnson, 1970). The average size of fish in releases varied considerably between hatcheries, somewhat between river sections, and slightly between broods. Again, the limited number of marks prevented evaluation of the effect of size at release on contribution, but average weights are included to complete the data record (Appendix Tables 1a and 1b).

Estimating Procedures

Simple numerical examples explain the basic estimating procedures. A more formal account was reported in the chinook salmon study (Worlund, Wahle, and Zimmer, 1969).

The first quantities to be estimated were the numbers of marked and unmarked fish in hatchery releases. This was done with data from a 10-part sampler (see "Marking and Release Procedures"). The device was precalibrated from a number of trials with known numbers of fish to find the average number and percentage retained by a single closed pocket. The following example illustrates the fish enumeration procedure. Suppose a precalibrated pocket is found to remove a 10.1% sample. Also, suppose after passing all the fish in a pond through the sampler, the number of fish retained by the

TABLE 1.—Grouping of Columbia River hatcheries participating in study and type of mark assigned to each group.

River section and hatchery[1]	Hatchery location	Mark[2]
Lower River (Columbia River mouth to Cowlitz River)		
Klaskanine (FCO)	Klaskanine River	Ad-RM
Grays River (WDF)	Grays River	" "
Big Creek (FCO)	Big Creek, Columbia River	" "
Elokomin (WDF)	Elokomin River	" "
Middle River (Cowlitz River to Bonneville Dam)		
Toutle (WDF)	Green River, Toutle River	Ad only
Lower Kalama (WDF)	Hatchery Creek, Kalama River	" "
Kalama Falls (WDF)	Kalama River	" "
Lewis River (WDF)	Lewis River	" "
Speelyai (WDF)	Speelyai Creek, Lewis River	" "
Sandy (FCO)	Cedar Creek, Sandy River	" "
Eagle Creek (FCO)	Eagle Creek, Clackamas River	" "
Washougal (WDF)	Washougal River	" "
Bonneville (FCO)	Tanner Creek, Columbia River	" "
Upper River (Bonneville Dam to The Dalles Dam)		
Cascade (FCO)	Eagle Creek, Columbia River	Ad-LM
OxBow (FCO)	Herman Creek, Columbia River	" "
Carson (BSFW)	Tyee Springs, Wind River	" "
Little White Salmon (BSFW)	Little White Salmon River	" "
Willard (BSFW)	Little White Salmon River	" "
Klickitat (WDF)	Klickitat River	" "
Uppermost River (above The Dalles Dam)		
Leavenworth (BSFW)	Icicle Creek, Wenatchee River	D-Ad D-Ad-LM D-Ad-RM

1/ Acronyms designate the following agencies: FCO = Fish Commission of Oregon, WDF = Washington Department of Fisheries, and BSFW = Bureau of Sport Fisheries and Wildlife.

2/ Ad = adipose finclip, D = dorsal finclip, LM = left maxillary bone clip, and RM = right maxillary clip.

closed pocket is found to be 6,060. The total number of fish in that pond is then estimated as 6,060/0.101 = 60,000. Suppose further that of the 6,060 fish retained by the pocket, 606 fish are found to be marked. Then 606/6,060 = 10% of the estimated 60,000 fish in the pond, or 6,000 fish are estimated to be marked and 54,000 unmarked. The total release, numbers marked and unmarked, and proportion marked were estimated for a hatchery by summing data from all ponds. Finally, estimates of the foregoing quantities for all fish released into a given river section were obtained by summing the estimates for appropriate hatcheries.

To estimate actual recoveries with a certain mark during a specific sampling period in a given fishery, the total catch (of marked and unmarked fish) during that period was multiplied by the fraction of sampled fish observed with that mark during the same period. For example, 16 Ad-RM marks were detected during June 1-30, 1968, from 9,827 coho salmon examined at Crescent City, Calif., in a catch of 31,082 from the commercial troll fishery. Thus, 16/9,827 (approximately 0.2%) of the sample had Ad-RM marks. The total marked catch for that period and landing port was estimated to be about 0.2% of the 31,082 fish caught or 62 Ad-RM marks (actual calculations were carried to eight places to avoid rounding errors). Similar calculations were made for each period. The results then were summed for all periods and appropriate landing locations to estimate the seasonal recovery of a certain mark in the given fishery (e.g., Ad-RM marks in the California troll fishery during 1968).

The catch of unmarked hatchery fish for each ocean sport and commercial fishery, and the Columbia River fisheries, was estimated for each year and brood by dividing the estimated catch of fish having a specific mark by the expected marked/unmarked ratio. The latter was calculated from the ratio at release and the estimated relative survival of marked fish. Suppose an estimated 2,000 1965-brood Ad-RM marks were recovered in 1968 in the California ocean sport fishery, the marked/unmarked ratio was 0.1 for all hatcheries where Ad-RM marks were released, and the survival of marked fish was estimated to be 80% that of unmarked fish; then the estimated catch of unmarked fish would be $(2{,}000)/(0.1 \times 0.80) = 25{,}000$ fish.

The catch of hatchery fish released from a given river section was estimated by summing estimates for marked and unmarked hatchery fish from each type of fishery. Nondetection of certain marks in ocean fisheries complicated the estimation of the hatchery contribution.

The relative survival of marked fish was estimated by comparing marked/unmarked ratios at release and return, as noted earlier for tetracycline (internal) and finclip (external) marking at the Big Creek and Eagle Creek stations. At the Big Creek station for the 1965 brood, for example, the pond sampling procedures just described gave an estimated marked/unmarked ratio at release of 0.12083 (for the Ad-RM finclip). Enumeration at the hatchery of all internally- and externally-marked returns ("jacks" or age 2 males in 1967 plus age 3 males and females in 1968) gave a marked/unmarked ratio of 0.09885. The survival of marked fish between the time of release and at return to the hatchery was therefore estimated to be 0.09885/0.12083 = 0.8181 that of unmarked fish.

With estimates of all these quantities at hand, it remained only to estimate the average weight and unit value of fish caught to calculate their total economic value. Weight data were collected from a predetermined number of fish throughout the season at different landing locations from which a given fishery operated. Resulting means were assumed to be representative.

Assumptions

The foregoing method of estimating catches of hatchery fish requires certain assumptions. These are considered after presentation of the data (see "Bias Associated with Marks" and "SUMMARY"). The main assumptions are:

1. A marked fish is identifiable as a marked fish throughout life.
2. All fish detected and reported with the kind of mark applied are hatchery fish.
3. All coho salmon sampled in ocean fisheries are in their third and final year of life.
4. Marked and unmarked fish have the same maturity schedules.
5. The same proportion of releases is marked at each hatchery in a given river section.
6. Marked and unmarked fish from a given river section are equally vulnerable to capture

(i.e., have the same distribution by time and area).

Field Operations

Marking and Release Procedures

Artificial propagation procedures were similar at all coho salmon hatcheries during the study period. Adults normally returned to the hatcheries during September-November and were spawned during October-November. Fry generally reach the free-swimming stage in March. The fish were released as smolts 13 mo later at an average length of 12-15 cm (4.5-6 inches) and were available during the following year to the fisheries from central British Columbia to central California.

The marking phase of this study began in May 1966 and ended in June 1967. About 10% of the 1965- and 1966-brood coho salmon were marked. A modified sampling tool (Worlund, Wahle, and Zimmer, 1969) was used to obtain a random sample for marking. The "10-part sampler" consisted of a cylindrical liner containing a circular metal frame divided into 10 equal pie-shaped sections with a zipper-bottomed net pocket hung from each section. When a 10% sample was to be taken, the zippers on all but one of the pockets were opened, the frame and liner were placed in a water-filled tub, and about 18 kg (40 pounds) of fish were placed into the liner. The closed net pocket retained the desired sample when the line and frame were lifted. The fish that passed through the open net pockets remained in the tub and were placed into another pond. This procedure was followed until all the coho in each pond were processed.

Fish to be marked were anesthetized with MS-222[4] (tricaine methanesulfonate). The fins and maxillary bones were clipped with bent-nosed scissors. Marked fish were held in hatchery troughs until they recovered from the anesthetic, then returned to the group from which they came. To insure that fins and maxillary bones were actually removed, quality control of marking was maintained by periodic random sampling of the marked fish throughout the marking operation.

[4] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

The entire coho salmon production of each hatchery was sampled to estimate the proportion and numbers of marked fish released. The "10%" samples removed initially by the calibrated pocket were set aside then resampled to obtain a "1%" sample which was sorted into marked and unmarked groups, counted, and weighed. The counts together with an estimate of the proportion removed by the particular pocket of the sampler were used to estimate the numbers of marked and unmarked fish released.

In Table 2, the estimated numbers of marked and unmarked fish released and the percentages marked are summarized for each mark type and brood year. Detailed data for each hatchery are given in Appendix Tables 1a and 1b. Over 40 million coho salmon of both broods were released from the study hatcheries. The number of marked fish released by section for the 1965- and 1966-brood years combined were Lower River, 0.9 million; Middle River, 1.7 million; Upper River, 1.3 million; and Uppermost River, 0.2 million. A total of 39.1 million coho from both broods was released from the study hatcheries in the Lower, Middle, and Upper River sections. Of these, 9.8% were marked. About 0.9 million coho were released from the Uppermost River section, of which 21.1% were marked.

Recovery of Marks in Fisheries

The mark-sampling phase of this study was designed in 1963 for fall chinook salmon and was expanded to include coho in 1967, 1 year before the 1965-brood coho were expected to appear in great numbers in the fishery. This advanced sampling was done for two reasons: (1) to locate the sampling problem areas and correct any deficiencies before the major appearance of the 1965-brood coho in the fisheries and (2) to assist the Washington Department of Fisheries in recovering their marked 1964-brood Puget Sound coho. This phase of the investigation ended in 1969. Catch sampling covered major ocean fisheries from Pelican, Alaska, southward to Avila Beach, Calif., and Columbia River fisheries. Sampling for marks in each area consisted of recording numbers of fish examined for marks and the recoveries of each type of mark detected. Lengths and weights of marked coho salmon from both broods were recorded also. The sampling sea-

TABLE 2.—Estimated numbers, percentage marked, and marked to unmarked ratios of 1965- and 1966-brood coho salmon released from evaluation hatcheries by river sections.

Brood year	River section and (in parentheses) mark	Marked released	Unmarked released	Total released	Proportion marked	Marked/ unmarked
1965	Lower River (Ad-RM)	508,294	4,670,794	5,179,088	0.0981	0.1088
	Middle River (Ad)	845,674	7,895,360	8,741,034	0.0967	0.1071
	Upper River (Ad-LM)	837,829	7,670,539	8,508,368	0.0985	0.1092
	Uppermost River (D-Ad)	101,734	402,272	504,006	0.2018	0.2529
	Subtotal 1965 brood	2,293,531	20,638,965	22,932,496	0.1000	0.1111
1966	Lower River (Ad-RM)	385,630	3,569,807	3,955,437	0.0975	0.1080
	Middle River (Ad)	764,262	6,965,703	7,729,965	0.0989	0.1097
	Upper River (Ad-LM)	493,110	4,544,676	5,037,786	0.0979	0.1085
	Uppermost River (D-Ad-LM)[1/]	96,643	466	97,109	0.9952	207.3884
	Uppermost River (D-Ad-RM)	78,092	269,355	347,447	0.2248	0.2899
	Subtotal 1966 brood	1,817,737	15,350,007	17,167,744	0.1059	0.1184
	TOTAL BOTH BROODS	4,111,268	35,988,972	40,100,240	0.1025	0.1142

1/ Released below Bonneville Dam.

sons were stratified into relatively small time units (usually 2-wk periods).

The main fisheries sampled were ocean sport and commercial, Columbia River sport and commercial, and Puget Sound fisheries. The ocean fisheries were stratified further by port of landing. The Alaska and British Columbia troll, purse seine, and gillnet fisheries; Columbia River commercial and sport fisheries; and Puget Sound sport and commercial fisheries were stratified by area of catch. The specific fisheries sampled are listed in Table 3 and shown in Figure 2.

Catch data for each time-location stratum were provided by management agencies. The catch of coho salmon in numbers of fish was an estimate for most fisheries. Commercial catches were estimated either from (1) the total weight of landings and an estimate of average fish size or (2) total salmon landings (numbers) and an estimate of species composition. Estimates of sport catches were from measures of total effort and catch per unit of effort or from salmon punch cards together with independent sampling by the management agency.

About 20% of each time-location stratum was sampled for marks. Table 4 gives the annual total catch of both broods of coho salmon by year and number sampled for marks each year. During the 3 years of sampling, 15.4% of the total catch of 21.1 million coho were examined for marks. The actual mark sampling percentages were 18.3, 13.5, and 14.3% for 1967, 1968, and 1969, respectively.

Enumeration of Returns to Hatcheries

An estimate of the numbers returning to hatcheries was required to measure the total hatchery output and marking mortality. All returns to most hatcheries were examined for marks; at some hatcheries, the numbers marked and unmarked were calculated after a known percentage of the total return was sampled for marks. A breakdown of the returns to each of the study hatcheries is in Appendix Tables 2a and 2b.

Estimation of Total Catch from Hatcheries

Actual Recoveries

Tables 5a and 5b summarize marked recoveries by brood year, mark, year of recovery,

TABLE 3.—Areas where catches were examined for marked coho salmon of Columbia River origin by port or zone of landing and type of fishery.

Area sampled	Type of fishery				
	Sport	Commercial			
	Rod and reel	Troll	Gill net	Dip net	Purse seine
British Columbia		Alaska area, Zones 29, 40-43, and Area C.[1]	Zones 29, 40-43		Zones 40-43.
Washington ocean	Sekiu	Seattle	Grays Harbor.		
	Neah Bay	Neah Bay	Willapa Bay.		
	LaPush	LaPush.			
	Westport	Westport.			
	Ilwaco	Ilwaco.			
Puget Sound and Juan de Fuca Strait	Zones 6-12		Zones 1-15		Zones 1-12.
Oregon ocean	Warrenton	Astoria.			
	Tillamook	Tillamook.			
	Pacific City	Pacific City.			
	Depoe Bay	Depoe Bay.			
	Newport	Newport.			
	Florence	Florence.			
	Winchester Bay	Winchester Bay.			
	Coos Bay	Coos Bay.			
	Gold Beach	Bandon.			
	Brookings	Port Orford.			
		Gold Beach.			
		Brookings.			
California ocean	Crescent City	Crescent City.			
	Trinidad	Trinidad.			
	Eureka	Eureka.			
	Shelter Cove	Fort Bragg.			
	Fort Bragg	Albion.			
	Albion	Point Arena.			
	Bodega Bay	Bodega Bay.			
	San Francisco	Point Reyes.			
	Half Moon Bay	San Francisco.			
	Santa Cruz	Half Moon Bay.			
	Monterey	Moss Landing.			
	Morro Bay	Monterey.			
	Avila	Morro Bay.			
		Avila.			
Columbia River and tributaries	Zones 1-6		Zones 1-7	Klickitat River.	
	Cowlitz River.				
	Kalama River.				
	Lewis River.				
	Toutle River.				
	Washougal River.				

1/ Canadian catch 3-12 miles off Washington, Oregon, and California.

river section of origin, and fishery. All marks from the Uppermost River section (Leavenworth Hatchery in Appendix Table 4) are combined as D-Ad marks in Table 5b. During the 3 years of sampling, 37,632 marked coho salmon were recovered. More marked 1965- than 1966-brood coho were caught, but more were released from the 1965 brood. Carson National Fish Hatchery and OxBow Salmon Hatchery, while participating in the study for the 1965 brood, did not do so for the 1966 brood (Table 2). The fraction of marked releases actually recovered for the 1965 brood, 0.0089, was slightly less than for the 1966 brood, 0.0093 (Tables 2, 5a, and 5b).

Estimated Recoveries

As explained under "Estimating Procedures," the total catch of fish with a particular mark was estimated for each stratum (fishery, port of landing or area of capture, and time period) from actual mark recoveries and the sampling fraction. It was assumed that a random sample of coho salmon was examined in each stratum and that in each sample all the marked fish were inspected. The total catch for each mark in each fishery was estimated by summing over the time periods and appropriate ports of landing or areas of capture.

The estimated catches and hatchery returns

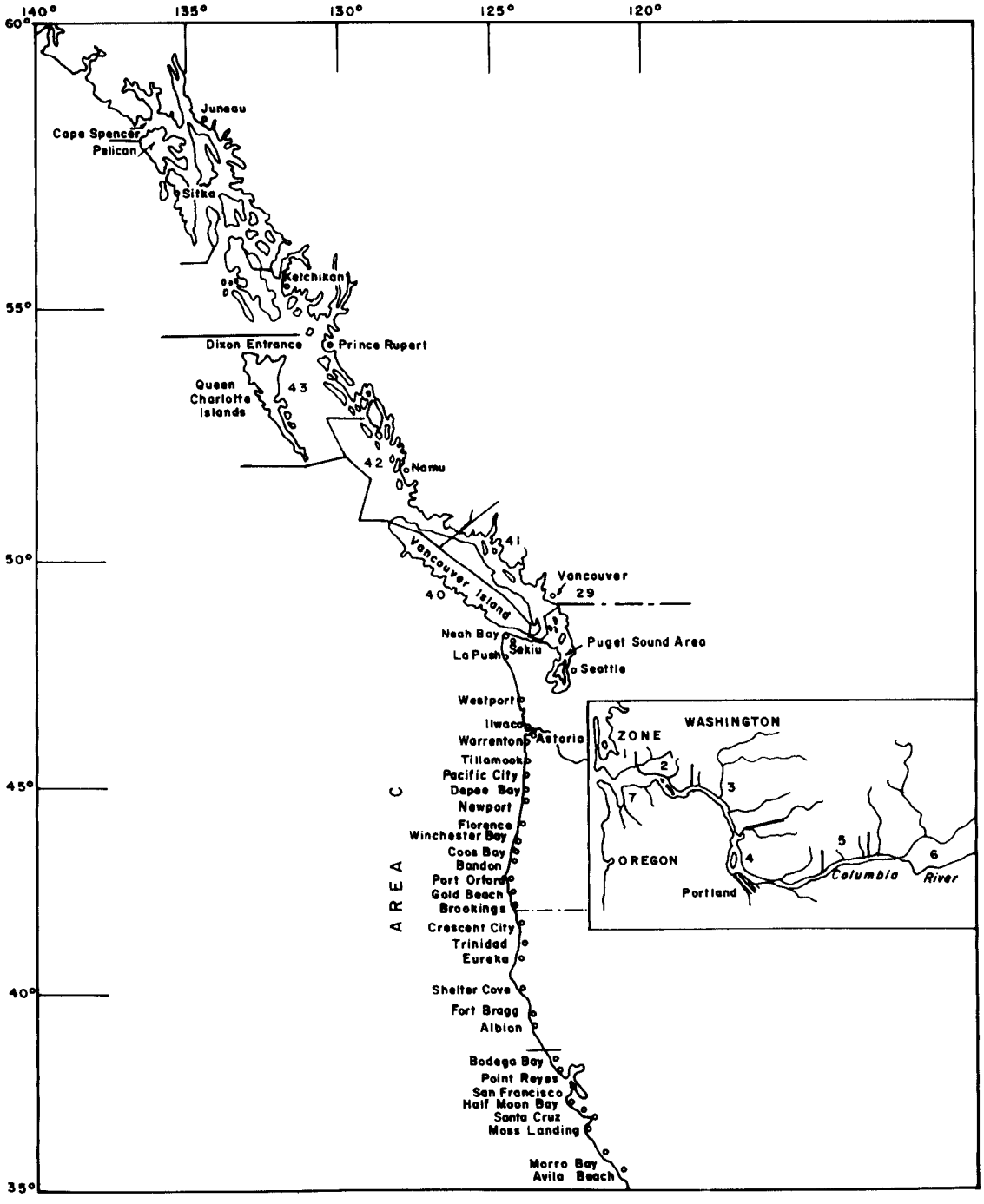

FIGURE 2.—Ports and zones sampled for marked coho salmon of Columbia River origin.

of marked fish are summarized in Tables 6a and 6b by region of recovery, fishery, brood year, and mark. The marks from the Uppermost River section (Appendix Table 5a) are combined in Table 6b. The total estimated catch of marked fish from both broods was 179,096. A total of 33,910 marked coho salmon returned to the study hatcheries during the 3 yr of sampling.

Bias Associated with Marks

To proceed from the estimated catch of marked fish to the total catch of hatchery fish, we must be sure that our assumptions (see "EXPERIMENTAL DESIGN") are satisfied. Some elements (e.g., loss of maxillary bones due to hooking, loss of fins due to injury) cannot be evaluated; others (e.g., mark regeneration, natural marks, relative survival of marked fish) can be appraised more adequately.

Mark Regeneration (Assumption 1) and Quality of Marking

We have three indications of the permanence of fin and maxillary marks. First, about 550 marked coho salmon of the 1966 brood were held for 2 yr at the Klickitat station for fin regeneration studies. We examined these fish periodically throughout the retention period and observed no adipose regeneration. However, we noted a 4.5% complete maxillary regeneration. Second, the appearance of D-Ad marks in the releases of the 1966-brood coho from Leavenworth National Fish Hatchery indicated maxillary regeneration; the maxillary bone was clipped from all 1966-brood Leavenworth coho marked, yet 5% of the marked coho released had only a D-Ad finclip. During marking of the Leavenworth coho, 100 marked fish per marker were examined at irregular periods each day to check mark quality. No unclipped maxillaries were observed. This caused us to disregard failure to clip maxillaries as a reason for the appearance of the D-Ad marks. Therefore, we believe the D-Ad marks occurred mainly because of maxillary regeneration. Finally, the percentage of D-Ad-only marks in the 1969 lower Columbia River commercial catch of 1966-brood Leavenworth Hatchery marked fish was 6.5%. This is very close to the percentage of D-Ad-only marks in the release. Because of these indications, we are assuming that mark regeneration caused little bias in this study.

Natural Marks (Assumption 2)

The catch of hatchery fish would be overestimated if marks identical to those used in this study occurred naturally. To ensure that no natural marks existed in hatchery stocks, coho salmon returns at most Columbia River and some Puget Sound hatcheries were examined for 2 yr before the study. Approximately 35,000 returns were examined and no marks identical to those we planned to use were observed. Also, fish markers at all participating hatcheries examined approximately 3.5 million coho for naturally missing fins and maxillary bones. Only 26 were found to have naturally missing adipose fins and none had naturally missing dorsal fins or maxillary bones.

The possible occurrence of natural marks from other river systems is more difficult to evaluate. Comparisons of the percentage of each mark caught in the lower Columbia River

TABLE 4.—Estimated catches of coho salmon and number of fish examined for marks, 1967-69.[1]

Year	Catch of coho salmon			Sampled for marks
	1965 brood	1966 brood	All ages	
1967	22,946	0	7,539,255	1,381,255
1968	8,587,969	20,457	8,608,426	1,158,932
1969	0	4,933,706	4,966,589	710,753
Total	8,610,915	4,954,163	21,114,270	3,250,940

1/ From all areas sampled (Table 3).

TABLE 5a.—Number of marked 1965-brood Columbia River coho salmon by release section recovered in the fisheries by year, region of capture, and type of fishery, 1967-68.

River section and (in parentheses) mark	Year	California		Oregon		Washington (without Puget Sound)		Puget Sound		British Columbia	S. E. Alaska	Columbia River				TOTALS
												Sport		Commercial		
		Sport	Commercial	Sport	Commercial	Sport	Commercial	Sport	Commercial	Commercial	Commercial	Main	Trib.	Gill net	Dip net	
Lower River (Ad-RM)	1967	0	0	0	0	0	0	0	0	0	0	1	0	15	0	16
	1968	101	491	135	1,049	212	401	0	5	72	*	0	3	107	5	2,581
Middle River (Ad)	1967	0	0	0	0	0	0	0	0	0	0	4	20	1	0	25
	1968	156	968	1,822	5,106	2,187	3,339	0	67	790	*	2	41	778	1	15,257
Upper River (Ad-LM)	1967	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1968	16	131	77	697	324	489	0	1	65	*	0	0	180	65	2,045
Uppermost River (D-Ad)	1967	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
	1968	6	23	52	194	119	144	0	0	9	*	0	0	67	0	614
TOTALS	1967	0	0	0	0	0	0	0	0	0	0	5	20	18	0	43
	1968	279	1,613	2,086	7,046	2,842	4,373	0	73	936	*	2	44	1,132	71	20,497

*No sampling.

TABLE 5b.—Number of marked 1966-brood Columbia River coho salmon by release section recovered in the fisheries by year, region of capture, and type of fishery, 1968-69.

River section and (in parentheses) mark	Year	California		Oregon		Washington (without Puget Sound)		Puget Sound		British Columbia	S. E. Alaska	Columbia River				TOTALS
												Sport		Commercial		
		Sport	Commercial	Sport	Commercial	Sport	Commercial	Sport	Commercial	Commercial	Commercial	Main	Trib.	Gill net	Dip net	
Lower River (Ad-RM)	1968	0	0	0	0	0	0	0	0	0	*	1	2	6	0	9
	1969	22	158	107	911	482	432	0	1	32	*	0	1	158	3	2,307
Middle River (Ad)	1968	0	0	0	0	0	0	0	0	0	*	17	34	12	0	63
	1969	191	905	1,578	4,479	2,120	1,865	2	15	312	*	1	33	759	18	12,278
Upper River (Ad-LM)	1968	0	0	0	0	0	0	0	0	0	*	2	1	6	16	25
	1969	14	102	86	662	525	356	0	1	9	*	0	1	233	53	2,042
Uppermost River (D-Ad)	1968	0	0	0	0	0	0	0	0	0	*	0	0	3	0	3
	1969	6	40	31	118	52	67	0	0	1	*	0	0	50	0	365
TOTALS	1968	0	0	0	0	0	0	0	0	0	*	20	37	27	16	100
	1969	233	1,205	1,802	6,170	3,179	2,720	2	17	354	*	1	35	1,200	74	16,992

*No sampling.

commercial fishery with the percentage of each mark caught in each ocean fishery give an indication of the occurrence of natural marks. After making these comparisons, we noted a preponderance of Ad-only marks especially in the Oregon sport fishery for the 1965 brood and the California sport and commercial fisheries for the 1966 brood. In these fisheries, we observed

TABLE 6a.—Estimated number of marked 1965-brood coho salmon in catches and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1967-68.

Region	Fishery type	D-Ad		Ad-LM		Ad		Ad-RM		Total	
		1967	1968	1967	1968	1967	1968	1967	1968	1967	1968
Ocean fisheries:											
British Columbia.....	Commercial...	0	46	0	459	0	6,339	0	581	0	7,425
Washington.....	Sport.....	0	677	0	1,809	0	11,490	0	1,206	0	15,182
	Commercial...	0	636	0	2,051	0	14,382	0	1,716	0	18,785
Oregon.....	Sport.....	0	226	0	265	0	7,944	0	420	0	8,855
	Commercial...	0	736	0	2,530	0	17,821	0	3,564	0	24,651
California.....	Sport.....	0	18	0	30	0	299	0	331	0	678
	Commercial...	0	109	0	789	0	5,554	0	2,617	0	9,069
Subtotal.....	Sport.....	0	921	0	2,104	0	19,733	0	1,957	0	24,715
	Commercial...	0	1,527	0	5,829	0	44,096	0	8,478	0	59,930
Freshwater fisheries:											
Columbia River.....	Sport.....	0	0	0	0	344	290	25	16	369	306
	Commercial...	7	238	0	846	2	4,907	130	825	139	6,816
Total.....	All fisheries	7	2,686	0	8,779	346	69,026	155	11,276	508	91,767
Columbia River escapement:											
Study hatcheries.....		38	138	1,125	1,882	4,391	9,399	1,568	1,864	7,122	13,283

TABLE 6b.—Estimated number of marked 1966-brood coho salmon in catches and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1968-69.

Region	Fishery type	D-Ad		Ad-LM		Ad		Ad-RM		Total	
		1968	1969	1968	1969	1968	1969	1968	1969	1968	1969
Ocean fisheries:											
British Columbia.....	Commercial...	0	7	0	77	0	2,970	0	278	0	3,332
Washington.....	Sport.....	0	242	0	2,333	0	9,324	0	2,178	0	14,077
	Commercial...	0	281	0	1,456	0	7,782	0	1,807	0	11,326
Oregon.....	Sport.....	0	148	0	392	0	7,304	0	492	0	8,336
	Commercial...	0	645	0	2,930	0	19,952	0	4,261	0	27,788
California.....	Sport.....	0	23	0	38	0	611	0	58	0	730
	Commercial...	0	224	0	465	0	6,024	0	728	0	7,441
Subtotal.....	Sport.....	0	413	0	2,763	0	17,239	0	2,728	0	23,143
	Commercial...	0	1,157	0	4,928	0	36,728	0	7,074	0	49,887
Freshwater fisheries:											
Columbia River.....	Sport.....	0	0	45	35	541	397	31	20	617	452
	Commercial...	6	283	58	2,470	125	8,104	57	1,619	246	12,476
Total.....	All fisheries	6	1,853	103	10,196	666	62,468	88	11,441	863	85,958
Columbia River escapement:											
Study hatcheries.....		8	0	624	1,075	2,191	5,769	2,067	1,771	4,890	8,615

samplers recording partially regenerated Ad-LM and Ad-RM as Ad-only marks. We attribute the preponderance of Ad-only marks in the above mentioned fisheries to the reluctance of samplers to distinguish between partially regenerated maxillaries and maxillaries lost through injury.

Age and Maturity Schedules (Assumptions 3 and 4)

Godfrey (1965) noted that ocean catches of coho salmon in the regions sampled in this study are all, or nearly all, age 3 adults. Johnson (1970) estimated that the ocean catch of

marked 1964-brood coho from Big Creek Hatchery (Figure 1) contained only 3% age 2 coho. This available evidence indicates that Assumption 3 (all coho in ocean fisheries are in their third and final year of life) is reasonably satisfied.

A comparison was made of marked and unmarked returns (Appendix Tables 2a and 2b) to hatcheries in the same river section where released to test Assumption 4 (marked and unmarked fish have the same maturity schedules). Appendix Table 3 shows the percent of 2-yr-old coho salmon in the marked and unmarked returns by river section and brood year. Unmarked strays to other river sections could not be identified by origin, so it was necessary to assume that straying was the same for marked and unmarked returns. The D-Ad comparison (Leavenworth Hatchery) was not made because passage difficulties at John Day Dam in 1969 led to no returns of adults to Leavenworth Hatchery. The nearly equal percentages of 2-yr-olds in the marked and unmarked returns by river section and brood year indicate that Assumption 4 is satisfied.

Marked Proportions at Release and Capture (Assumptions 5 and 6)

Inspection of mark proportion data in Appendix Tables 1a and 1b shows the variability between hatcheries to be small enough to consider Assumption 5 (same proportion of releases marked at each hatchery in a given river section) reasonably well satisfied. At present, no data exist to support Assumption 6 (equal vulnerability to capture for marked and unmarked fish from a given river section), but it is intuitively satisfied. Fish marked by clipping maxillary bones and/or the adipose fin would not seem to be more vulnerable to capture by fishing gear than unmarked fish.

Relative Survival of Marked Fish

Worlund, Wahle, and Zimmer (1969) found that marked fall chinook salmon did not survive as well as unmarked chinook. We also found this for coho salmon. To determine the unmarked catch of hatchery fish, we must account for the lower survival of marked fish. The relative survival values for both broods and each mark type of coho were calculated as explained under "Estimating Procedures." Oxytetracycline (TM-50) was used to mark both broods of coho at Eagle Creek and Big Creek hatcheries to obtain survival values for Ad and Ad-RM marked coho, respectively. Returns to three hatcheries, Little White Salmon, Cascade, and Klaskanine, on streams having no wild spawning populations were used to obtain relative survival values for both broods of Ad-LM and Ad-RM marked coho. Finally, the marked to unmarked ratios at release and return for each river section were combined to obtain survival values for each mark type in both brood years.

The relative survival estimates are in Appendix Table 6. Marked coho salmon that strayed to sections other than where they were released (Appendix Tables 2a and 2b) were excluded from the marked returns in computing relative survival (see "Bias Associated with Marks"). Therefore, the median value for each of the mark types for both brood years combined was arbitrarily used to obtain reasonable approximations for relative survival. The same value was used for Ad-LM and Ad-RM marked coho. The median values for the Ad-only and Ad-maxillary marked coho were 89 and 72%, respectively.

The relative survival of D-Ad marked 1965-brood coho salmon from Leavenworth National Fish Hatchery (Uppermost section) was obtained from TM-50 marking data. In 1967 and 1968, a total of 174 D-Ad-TM-50 marked and 1,305 TM-50-only marked 1965-brood coho returned to Leavenworth. From these values, the marked to unmarked relative survival of 1965-brood D-Ad marked coho was calculated to be 53%. Few hatchery returns of 1966-brood Leavenworth coho were obtained because of passage difficulties at John Day Dam due to construction of fish ladders and mortalities caused by trapping at Priest Rapids Dam. Hence, a relative survival estimate for the D-Ad-RM and D-Ad-LM marks could not be calculated. The value for the D-Ad marked 1965-brood coho (53%) was therefore used to estimate the 1966-brood Leavenworth catch of unmarked fish.

Final Estimates Corrected for Marking

One marked fish represented about 9 unmarked ones at release but about 11-20 (depending on the mark) at return (Tables 2, 6a, and 6b). The foregoing estimates of relative survival for unmarked fish were applied (see "Estimating

Procedures") to estimate the catch of unmarked hatchery fish, then marked fish were added to estimate the total catch.

An additional calculation was required before estimating the unmarked catch associated with the marked 1966-brood Leavenworth Hatchery fish because of the recovery of 1966 brood D-Ad-only marks. The recovery was due to either regeneration or nondetection of D-Ad-maxillary marks (see "Bias Associated with Marks"). Therefore the estimated catch of 1966 brood D-Ad marks had to be apportioned between the estimated catches of D-Ad-RM and D-Ad-LM marks before calculating the catch of unmarked 1966-brood fish. The D-Ad marks were apportioned by the ratio of their occurrence at the time of release. At Leavenworth Hatchery, 5,081 D-Ad marks were estimated to have been released with the D-Ad-RM marks. Below Bonneville Dam, 4,393 D-Ad marks were estimated to have been released with the D-Ad-LM marks. This is a total release of 9,474 D-Ad marks of which 54% (5,081/9,474) came from D-Ad-RM marks and 46% (4,393/9,474) came from D-Ad-LM marks. These ratios were used to apportion the estimated catch of 666 D-Ad marks (Appendix Table 5a) between the D-Ad-RM and D-Ad-LM marked fish in each of the fisheries. For example, 88 D-Ad marked coho (Appendix Table 5a) were estimated to have been caught in the Washington sport fisheries in 1969. Using the occurrence percentages of the D-Ad marks at release, $88 \times 0.54 = 48$ were calculated to be from D-Ad-RM marks and $88 \times 0.46 = 40$ were calculated to be from D-Ad-LM marks. This apportioning was done for each fishery and results are in Appendix Table 4b.

The estimated catches of marked fish used to calculate the catches of unmarked hatchery fish are in (1) Table 6a for the estimated 1965 brood D-Ad, Ad-LM, Ad, and Ad-RM marks captured in the ocean and Columbia River fisheries; (2) Table 6b for the estimated ocean and Columbia River catches of 1966 brood Ad-LM, Ad, and Ad-RM marked fish; and (3) Appendix Table 5b for the catches of marked 1966-brood Leavenworth coho salmon. Appendix Table 7 presents the resulting estimated catches of unmarked hatchery fish.

The estimated total catch of Columbia River hatchery fish (Appendix Table 8) was obtained by adding the estimated catch of marked fish (Tables 6a and 6b) to the estimated unmarked catches (Appendix Table 7). The resulting catch estimates may affect management decisions in years when no marking studies take place. Therefore, as a final step, we divided the estimated catch of each mark in each fishery (Tables 6a and 6b) by the estimated relative survival for that mark (see "Relative Survival of Marked Fish") to obtain a theoretical catch of marked fish assuming no marking mortality. The results were then added to the estimated unmarked catch (Appendix Table 7) to obtain a theoretical total catch of Columbia River hatchery coho salmon. The results are in Table 7 by region of recovery, type of fishery, and year of capture. The table includes the estimated sport catches of hatchery fish in Columbia River tributaries where no creel census took place. This is broken down in detail by year of capture, brood, and stream in Appendix Table 9.

An estimated total of 2,188,172 Columbia River hatchery coho would have been caught during the 3 years of sampling had no marking taken place. This is about 16% of the total catch in areas sampled (Table 3) of 1965- and 1966-brood coho caught during 1967-69 (Table 4)—13% for the 1965 brood and 21% for the 1966 brood. Another useful statistic is the catch/1,000 fish released. For the combined 1965 and 1966 broods, this was 55/1,000—50/1,000 for the 1965 brood and 61/1,000 for the 1966 brood (Tables 2 and 7).

ECONOMIC EVALUATION

A main purpose of this paper is to develop benefit/cost ratios for the 1965 and 1966 broods of coho salmon from Columbia River hatcheries. To develop these ratios, estimates must be made of (1) the costs of rearing the 40.1 million smolts released (Table 2) and (2) the value of the theoretical catch of 2,188,172 coho (Table 7). The rearing costs will be presented first.

Cost Accounting

Production costs are broken down into two categories: (1) amortized construction costs or capital costs and (2) operational costs.

Capital

The "annual imputed capital charge" for each hatchery was computed by amortizing the capital expenditures at each hatchery into 30 equal

TABLE 7.—Theoretical catch of 1965- and 1966-brood hatchery coho salmon by region of recovery, type of fishery, and year of capture, 1967-1969.[1]

Region	Fishery type	1965 brood			1966 brood		
		1967	1968	Total	1968	1969	Total
Ocean fisheries:							
British Columbia.....	Commercial...	0	88,755	88,755	0	38,824	38,824
Washington.....	Sport.....	0	182,372	182,372	0	171,035	171,035
	Commercial...	0	226,212	226,212	0	136,016	136,016
Oregon.....	Sport.....	0	104,063	104,063	0	96,371	96,371
	Commercial...	0	300,004	300,004	0	332,075	332,075
California.....	Sport.....	0	8,750	8,750	0	8,393	8,393
	Commercial...	0	113,700	113,700	0	86,573	86,573
Subtotal.....	Sport.....	0	295,185	295,185	0	275,799	275,799
	Commercial...	0	728,671	728,671	0	593,488	593,488
Freshwater fisheries:							
Columbia River.....	Sport.....	18,739	10,627	29,366	15,584	10,855	26,439
	Commercial...	1,929	82,831	84,760	3,087	151,377	154,464
Total.....	All fisheries	20,668	1,117,314	1,137,982	18,671	1,031,519	1,050,190

1/ Corrected for differential finclip mortality and assuming no marking had taken place.

annual payments using an interest rate of 3.5%.[5] This rate was the average 3- to 5-yr government bond interest rate weighted by the total annual capital outlay at all hatcheries from 1949 (inception of Columbia River Development Program) through 1970. All outlays prior to this period are assumed to be depreciated out completely. The imputed capital charge for each study hatchery was apportioned among the broods and species present by using the percentage of time spent caring for each group of fish. The total annual imputed capital charges for the 1965- and 1966-brood coho salmon are $271,600 and $235,600, respectively.

Operation

The operation and maintenance costs at each hatchery are divided into two categories. They are fish food and drugs and other operational costs. The cost of fish food and drugs is apportioned between each brood and species according to the pounds of each brood and species produced. The operational costs other than food and drugs include costs for labor, personal services, travel, transportation of items, communication services, equipment, supplies and materials, and administration. These costs are allocated to each brood and species in the same manner as the capital costs. The operational costs apportioned to the 1965- and 1966-brood coho are $1,020,700 and $991,000, respectively. The total costs applicable to rearing the 1965- and 1966-brood coho are then $1,292,300 and $1,226,600, respectively.

Benefits

To determine the benefit provided by hatchery releases of 1965- and 1966-brood coho salmon to the commercial and sport fisheries, an estimate of the net economic value to these fisheries must be made. Additional information is critically needed to improve the basis for estimating values for fishery resources; however, the values used in this report are based on the best information now available and the limitations of these values are discussed.

Commercial

Ex-vessel market prices have been used to represent estimated net values for commercially caught fish. There are two quite different reasons why this method can provide satisfactory estimates.

The Columbia River salmon production from hatcheries included in this study provide only a portion of the total salmon production. Use of the ex-vessel price in the standard benefit-cost technique would require the deduction of all associated costs. However, excess capacity typically exists in the fishing sector, so little or

[5] The "annual imputed capital charge" is the estimated cost of government funds over the life of the project.

no additional fishing effort would be needed to land the production from these hatcheries. While this provides an adequate reason to omit fishing costs for hatchery fish, this would not be true for total salmon production.

A stronger basis for omitting costs necessary to land fish and using the ex-vessel price, results from current fishery management policies. Regulated inefficiency has been used in salmon fisheries to prevent overharvest thus excluding efficient fishing methods. This process probably results in dissipation of at least 75% of potential net benefits and may be as high as 95% (Richards, 1969).[6] Since the market prices used result from normal market activities and thus represent the market value of the fish resource to users, this potential benefit could be realized if society elects to change management methods and reduce fishing costs.

Several inadequacies exist in the use of the ex-vessel price as a representation of the net value for commercially caught fish. The first inadequacy is that the ex-vessel market price fails to completely measure market value. Gear or supplies furnished by processors and bonuses paid are examples of values that are not included in estimated market values. A second inadequacy exists since ex-vessel values fail to completely measure potential production. For example, a large share of the catch is now taken on troll gear and many sublegal size fish are caught. In the removal from the gear and release of these sublegal fish, many sustain injuries that result in death or reduced growth. This wastage significantly reduces the total production from the resource to society. Also, estimated market values do not include other types of benefits. For example, ex-vessel prices may not always be determined in markets with adequate competition to indicate total benefits, resulting in a producer surplus (i.e., additional profits to fish buyers). Benefits due to employment and income generated for coastal communities and the regional and national economy are not included. Consumer surplus or benefits to consumers that are not included in market prices are also omitted.

These factors indicate that using the ex-vessel price for commercially caught fish is a reasonable estimate of benefits that could be realized. If all factors were included, this could prove to be a quite conservative estimate of total benefits.

Tables 8a and 8b present the net value of commercially caught 1965- and 1966-brood coho salmon by ocean regions and Columbia River commercial fisheries. Two calculations were required to obtain the net value. The theoretical commercial catch was multiplied by the average Ad marked coho weight to obtain the total pounds of Columbia River coho caught by region. The total pounds were then multiplied by the average ex-vessel price paid in each region to obtain the net value of the coho catch to that region.

Sport

The net value for salmon and steelhead sport fishing is estimated to be $20 per day of fishing. This value results from reconciling the existing research that is closely related to estimated net economic values of Columbia River sport caught salmon. The maximum potential benefits from sport fishing at a single market price is predicted at $20 per fishing day by Brown, Singh, and Richards (1972).[7] A single market price is intended to be comparable with typical conditions that underlie normal market price determination. The original data for this report were from a 1962 survey in Oregon with results published in 1964. The net value that resulted in maximum benefits was estimated at $8 per day of fishing in the original analysis (Brown, Singh, and Castle, 1964). However, Brown and Nawas (in press) developed research techniques that more efficiently utilize available information. When these techniques were used in an analysis of the 1962 survey data, an estimated value of $20 per day was derived. This is the estimated value used in this report.

Two other reports support the revised Oregon results. The estimated net economic value for the 1967 sport salmon fisheries of Washington resulted in a recommended value of $28 per day of fishing (Mathews and Brown, 1970). An evaluation of the net economic values for the Idaho sport fisheries, based on a 1968 survey, resulted

[6] Jack A. Richards. 1969. An economic evaluation of Columbia River anadromous fish programs. U.S. Dep. Int., Fish Wildl. Serv., Bur. Commer. Fish., Working paper 17, 274 p. (Processed.)

[7] William G. Brown, Ashok K. Singh, and Jack A. Richards. 1972. Influence of improved estimating techniques on predicted net economic values for salmon and steelhead. (Oreg. State Univ., Corvallis), Agric. Exp. Stn. unpubl. manuscr., 26 p. (Typescript.)

TABLE 8a.—Estimated value of the theoretical catch of 1965-brood coho salmon from Columbia River hatcheries.

Region	Fishery type	Age	Fish	Sample size	Average weight 1/		Total weight		Value per unit catch 2/ 3/	Total value
			Number	Number of fish	Lbs.	Kg.	Lbs.	Kg.	Dollars	Dollars
Ocean fisheries:										
British Columbia.....	Commercial...	3	88,755	143	5.5	2.5	488,152	221,888	0.45	$ 219,668
Washington.....	Sport.....	3	182,372	----	----	----	----	----	15.82	2,885,125
	Commercial...	3	226,212	--5/	5.5	2.5	1,244,166	565,530	0.45	559,875
Oregon.....	Sport.....	3	104,063	----	----	----	----	----	20.53	2,136,413
	Commercial...	3	300,004	386	5.6	2.5	1,680,022	750,010	0.45	756,010
California.....	Sport.....	3	8,750	----	----	----	----	----	19.01	166,338
	Commercial...	3	113,700	272	6.3	2.9	716,310	329,730	0.45	322,340
Subtotal.....	Sport.....	3	295,185	----	----	----	----	----	----	5,187,876
	Commercial...	3	728,671	----	----	----	4,128,650	1,867,158	-----	1,857,893
Freshwater fisheries:										
Columbia River.....	Sport.....	2	18,739	----	----	----	----	----	42.02	787,412
		3	10,627	----	----	----	----	----	46.51	494,262
Zones 1-5 & 7.....	Commercial...	2	1,883	--6/	3.0	1.4	5,649	2,636	0.26	1,469
		3	78,825	385	7.8	3.5	614,835	275,888	0.28	172,154
Indian fisheries 4/.....	Commercial...	2	46	--6/	3.0	1.4	138	64	0.18	25
		3	4,006	--7/	7.8	3.5	31,247	14,021	0.24	7,499
Subtotal.....	Sport.....	2&3	29,366	----	----	----	----	----	----	1,281,674
	Commercial...	2&3	84,760	----	----	----	651,869	292,609	-----	181,147
Total.....	All fisheries		1,137,982	----	----	----	----	----	----	8,508,590

1/ Weights for ocean commercial fisheries are dressed weights and those for Columbia River fisheries are round weights. Original weights are in pounds for Ad marked fish.

2/ Entries for Washington and Columbia River fisheries (dollars per pound) were obtained from Dale Ward, Washington State Department of Fisheries (personal communication). Washington price was used for British Columbia and Oregon commercial fisheries. Entry for California was obtained from Pat O'Brien, California Department of Fish and Game (personal communication).

3/ The value of a sport caught coho is based on a value of $20.00 per angler day divided by the catch per angler.

4/ Columbia River set net and dip net fisheries and Klickitat River dip net fishery.

5/ No sampling for weight was done in the Washington commercial fisheries. Average weight obtained from Sam Wright, Washington Department of Fisheries (personal communication).

6/ Catches of Ad marked fish were too small to obtain an adequate sample for average weight. Average weight obtained from Paul Hirose, Fish Commission of Oregon (personal communication).

7/ Catches of Ad marked fish were too small to obtain an adequate sample for average weight. Average weight from zones 1-5 used.

TABLE 8b.—Estimated value of the theoretical catch of 1966-brood coho salmon from Columbia River hatcheries.

Region	Fishery type	Age	Fish	Sample size	Average weight 1/		Total weight		Value per unit catch 2/ 3/	Total value
			Number	Number of fish	Lbs.	Kg.	Lbs.	Kg.	Dollars	Dollars
Ocean fisheries:										
British Columbia.....	Commercial...	3	38,824	100	5.8	2.6	225,179	100,942	0.48	$ 108,086
Washington.....	Sport.....	3	171,035	----------					18.05	3,087,182
	Commercial...	3	136,016	--5/	6.2	2.8	843,299	380,845	0.48	404,784
Oregon.....	Sport.....	3	96,371	----------					24.94	2,403,493
	Commercial...	3	332,075	331	5.7	2.6	1,892,828	863,395	0.48	908,557
California.....	Sport.....	3	8,393	----------					19.92	167,189
	Commercial...	3	86,573	92	6.3	2.9	545,410	251,062	0.48	261,797
Subtotal.....	Sport.....	3	275,799	----------						5,657,864
	Commercial...	3	593,488	----------			3,506,716	1,596,244	-----	1,683,224
Freshwater fisheries:										
Columbia River.....	Sport.....	2	15,584	----------					46.51	724,812
		3	10,855	----------					49.63	538,734
Zones 1-5 & 7.....	Commercial...	2	2,580	--6/	3.6	1.6	9,288	4,128	0.28	2,601
		3	145,242	329	8.7	4.0	1,263,605	580,968	0.35	442,262
Indian fisheries 4/.....	Commercial...	2	508	--6/	3.6	1.6	1,829	813	0.24	439
		3	6,134	--7/	8.7	4.0	53,366	24,536	0.29	15,476
Subtotal.....	Sport.....	2&3	26,439	----------						1,263,546
	Commercial...	2&3	154,464	----------			1,328,088	610,445	-----	460,778
Total.....	All fisheries		1,050,190	----------						9,065,579

1/ Weights for ocean commercial fisheries are dressed weights and those for Columbia River fisheries are round weights. Original weights are in pounds for Ad marked fish.

2/ Entries for Washington and Columbia River fisheries (dollars per pound) were obtained from Dale Ward, Washington State Department of Fisheries (personal communication). Washington price was used for British Columbia and Oregon commercial fisheries. Entry for California was obtained from Pat O'Brien, California Department of Fish and Game (personal communication).

3/ The value of a sport caught coho is based on a value of $20.00 per angler day divided by the catch per angler.

4/ Columbia River set net and dip net fisheries and Klickitat River dip net fishery.

5/ No sampling for weight was done in the Washington commercial fisheries. Average weight obtained from Sam Wright, Washington Department of Fisheries (personal communication).

6/ Catches of Ad marked fish were too small to obtain an adequate sample for average weight. Average weight obtained from Paul Hirose, Fish Commission of Oregon (personal communication).

7/ Catches of Ad marked fish were too small to obtain an adequate sample for average weight. Average weight from zones 1-5 used.

in estimates comparable to those originally reported for the 1962 Oregon survey (Gordon, n.d.).[8]

The value of $20 per day is believed to be a reasonable estimate based on existing research information. However, limitations associated with this estimated value should be recognized. A range of values is needed for sport-caught fish that reflect differences in quality variables such as distance from metropolitan areas, environmental conditions, species involved, and success level. The reports mentioned here not only indicate an average value for these different variables but involve different time periods, geographic areas, and research methods. This is also an estimated market value and does not include other values such as consumer surplus (i.e., benefits to consumers that are not measured by market prices), benefits due to employment and income generated in local communities and the regional and national economy, and benefits to nonusers who may not fish but may want fishing preserved and available.

Since the value per fishing day is an average of various quality factors, no values by species are estimated directly. The only method presently available to determine values for fish is by success levels. This requires careful interpretations; for example, greater success results in lower values per fish. This means that higher total values would result with poorer success since the number of fish involved at the estimated market price is not fully taken into account. For this report, success is assumed to be estimated at an average of the total landings of all species. This is probably reasonable since mostly ocean fishing and entire seasons are involved.

Limitations of estimated sport and commercial values need to be emphasized. The estimated market price of $20 per fishing day excludes consumer surplus whereas the estimated number of fishing days does not. Consequently, multiplying market prices by actual participation is not comparable with the ex-vessel prices used for values of commercially caught fish since these values do not contain consumer surplus. Therefore extreme caution should be observed in comparing values between fish species or total values of sport and commercial fishing.

[8] Douglas Gordon. (n.d.). An economic analysis of Idaho sport fisheries. Univ. Idaho, Coll. Forestry, Wildl. and Range Sci., Idaho Coop. Fish. Unit., Review draft, 60 p. (Processed.)

To obtain values for the 1965- and 1966-brood sport-caught coho salmon, the estimated market value of $20 per day of fishing is divided by the success level in each region. This value per fish is then multiplied by the number of coho taken in each region. The results are presented in Tables 8a and 8b.

Benefit/Cost

The total net economic values of the 1965- and 1966-brood coho salmon were $8,508,590 and $9,065,579, respectively. Benefits were also derived from the sale of excess 1965- and 1966-brood coho carcasses at the study hatcheries. The revenue from carcass sales is used to purchase additional fish food. This allows additional fish to be reared, thus providing future benefits to society.

Coho carcasses were sold at Fish Commission of Oregon and Washington Department of Fisheries hatcheries. The values of the 1965- and 1966-brood coho carcasses sold are $75,035 and $40,973, respectively. When these values are added to the net economic values, total benefits of $8,583,625 for the 1965 brood and $9,106,552 for the 1966 brood are obtained. The benefit to cost ratios are then $8,583,625/$1,292,300 or 6.6/1 and $9,106,552/$1,226,600 or 7.4/1 for the 1965 and 1966 broods, respectively. The average benefit to cost ratio is 7.0/1.

SUMMARY

When this marking study was designed, four marks were available from the Pacific Marine Fisheries Commission. The Columbia River was divided into four sections. Each section was assigned a specific mark. All study hatcheries within a given section (except Leavenworth station in the Uppermost River section) marked approximately 10% of their coho salmon production with the assigned mark (Table 2). Two broods, 1965 and 1966, of coho salmon were included in the study. During the 2-year marking phase, 4.1 million of the 40.1 million total coho production were marked (Table 2). Approximately 22.9 million 1965-brood and 17.2 million 1966-brood coho were released (Table 2).

Sampling for marks was conducted in most coho salmon fisheries, with few exceptions, from Avila Beach, Calif., to Pelican, Alaska (Figure

2 and Table 3). During 1968 and 1969, there was no sampling done in the southeast Alaska troll and gillnet fisheries. During the 3 yr of mark sampling, an average of 15.4% of the coho catch was examined for marks (Table 4). A total of 37,632 marked coho was recovered from 1967 through 1969 (Tables 5a and 5b).

The appropriateness of the estimating procedures used to determine hatchery contribution is dependent on the validity of six assumptions. Additional studies and data collections previously described were incorporated into the marking experiment to help test the assumptions. The first assumption, permanence of fin marks, was tested by holding marked fish in fresh water over a period of months. Little total regeneration occurred, but maxillary regeneration caused confusion between maxillary-adipose and adipose-only marked coho salmon. The second assumption, origin of fish marked with hatchery marks, was tested by examining returning adult coho prior to the marking study and coho fingerlings at the time of marking for natural marks. No noteworthy numbers of naturally missing adipose fins or maxillary bones were observed. Prior to this study, a number of age studies have supported that Assumption 3, all adult coho are 3 yr old, is valid (Godfrey, 1965). The mark sampling data (Appendix Tables 2a and 2b) indicate that the fourth assumption, same maturity schedule for marked and unmarked fish, is valid. Appendix Tables 1a and 1b show the validity of Assumption 5, hatcheries in a given section have the same proportion of marked releases. Assumption 6, equality of ocean distribution could not be tested because regeneration and nondetection of maxillary marks distorted the picture.

A total of 179,096 marked 1965- and 1966-brood coho salmon were estimated to have been caught. An additional 33,910 marked coho returned to study hatcheries to spawn (Tables 6a and 6b). The theoretical estimated catch assuming no marking had taken place was 2,188,172 coho and comprised about 16.1% of the total catch of 1965-66 brood coho in the fisheries sampled (Table 7).

The estimated costs of rearing the 1965 and 1966 broods of coho salmon are $1,292,300 and $1,226,600, respectively. The estimated benefits, including carcass sales, received from the harvest of these two broods of coho are $8,583,625 and $9,106,552, respectively. The benefit to cost ratios are then 6.6 to 1 for the 1965 brood and 7.4 to 1 for the 1966 brood.

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APPENDIX TABLE 1a.—Estimated numbers, percent marked, and mean weights of 1965-brood coho salmon released from study hatcheries.

Hatchery group and (in parentheses) mark	Number of fish			Percent marked	Mean weight 1/
	Marked	Unmarked	Total		
Lower River (Ad-RM)					
Elokomin	118,137	1,170,725	1,288,862	0.0917	14
Big Creek	164,759	1,363,618	1,528,377	0.1078	29
Grays River	106,986	946,441	1,053,427	0.1016	23
Klaskanine	118,412	1,190,010	1,308,422	0.0905	33
Total Ad-RM	508,294	4,670,794	5,179,088	0.0981	25
Middle River (Ad)					
Bonneville	81,402	786,425	867,827	0.0938	22
Washougal	245,489	2,152,336	2,397,825	0.1024	24
Sandy	85,871	868,250	954,121	0.0900	27
Eagle Creek 2/	69,988	610,113	680,101	0.1029	16
Lewis 3/	65,453	649,490	714,943	0.0915	28
Kalama Falls	148,242	1,434,022	1,582,264	0.0937	27
Lower Kalama	37,069	315,463	352,532	0.1052	27
Toutle	112,160	1,079,261	1,191,421	0.0941	25
Total Ad	845,674	7,895,360	8,741,034	0.0967	19
Upper River (Ad-LM)					
Klickitat	146,123	1,365,134	1,511,257	0.0967	16
Little White Salmon 4/	357,407	3,290,348	3,647,755	0.0980	15
Willard	--	--	--	--	19
Carson	158,868	1,477,931	1,636,799	0.0971	15
OxBow 2/	47,578	424,892	472,470	0.1007	29
Cascade	127,853	1,112,234	1,240,087	0.1031	26
Total Ad-LM	837,829	7,670,539	8,508,368	0.0985	19
Uppermost River (D-Ad)					
Leavenworth	101,734	402,272	504,006	0.2018	25
TOTAL ALL HATCHERIES	2,293,531	20,638,965	22,932,496	0.1000	--

1/ Mean weights in grams per fish. Values in total lines are averages weighted by total release at each hatchery in that river section.
2/ Additional 70,198 fish released with LM mark.
3/ Includes release from Speelyai hatchery.
4/ Includes release from Willard hatchery.
5/ Released from Bonneville hatchery.

APPENDIX TABLE 1b.—Estimated numbers, percent marked, and mean weights of 1966-brood coho salmon released from study hatcheries.

Hatchery group and (in parentheses) mark	Number of fish			Percent marked	Mean weight[1]
	Marked	Unmarked	Total		
Lower River (Ad-RM)					
Elokomin	85,319	761,349	846,668	0.1008	28
Big Creek	122,552	1,159,780	1,282,332	0.0956	23
Grays River	60,852	530,173	591,025	0.1030	27
Klaskanine	116,907	1,118,505	1,235,412	0.0946	28
Total Ad-RM	385,630	3,569,807	3,955,437	0.0975	26
Middle River (Ad)					
Bonneville	146,457	1,361,388	1,507,845	0.0971	24
Washougal	85,741	769,789	855,530	0.1002	25
Sandy	98,702	920,106	1,018,808	0.0969	22
Eagle Creek[2]	130,384	1,028,499	1,158,883	0.1125	20
Lewis[3]	85,442	882,958	968,400	0.0882	27
Kalama Falls	85,022	789,515	874,537	0.0972	28
Lower Kalama	38,792	357,123	395,915	0.0980	27
Toutle	93,722	856,325	950,047	0.0986	24
Total Ad	764,262	6,965,703	7,729,965	0.0989	24
Upper River (Ad-LM)					
Klickitat	79,864	770,023	849,887	0.0940	28
Little White Salmon[4]	369,935	3,339,807	3,709,742	0.0997	20
Willard	--	--	--	--	17
Carson[5]	--	--	--	--	--
OxBow[5]	--	--	--	--	--
Cascade	43,311	434,846	478,157	0.0905	23
Total Ad-LM	493,110	4,544,676	5,037,786	0.0979	20
Uppermost River (D-Ad-RM, D-Ad-LM[6])					
Leavenworth	78,092	269,355	347,447	0.2248	23
Leavenworth[6]	96,643	466	97,109	0.9952	23
TOTAL ALL HATCHERIES	1,817,737	15,350,007	17,167,744	0.1059	--

1/ Mean weights in grams per fish. Values in total lines are averages weighted by total release at each hatchery in that river section.
2/ Additional 126,323 fish released with LM mark, 87,733 released with An mark, and 127,514 released with RM mark.
3/ Includes release from Speelyai hatchery.
4/ Includes releases from Willard hatchery.
5/ Nonparticipating for 1966 brood.
6/ Released below Bonneville Dam.

APPENDIX TABLE 2a.—Number of marked and unmarked 1965-brood coho salmon recovered at hatcheries in each section of the Columbia River in 1967 and 1968.

Recovery location, by hatchery	Marked and unmarked	Origin	Year of return 1967	1968
Middle River--Continued				
Lewis River	Unmarked	--	1,072	1,894
	Ad-LM	Upper river	0	0
	Ad	Lewis	88	235
	Ad-RM	Lower river	0	0
Kalama Falls	Unmarked	--	1,176	10,451
	Ad-LM	Upper river	0	0
	Ad	Kalama Falls	107	865
	Ad-RM	Lower river	0	0
Lower Kalama	Unmarked	--	524	1,915
	Ad-LM	Upper river	0	0
	Ad	Lower Kalama	89	227
	Ad-RM	Lower river	0	0
Toutle	Unmarked	--	4,417	24,931
	Ad-LM	Upper river	0	0
	Ad	Toutle	416	2,030
	Ad-RM	Lower river	0	0
Upper River				
Klickitat	Unmarked	--	916	1,398
	Ad-LM	Klickitat	41	117
	Ad	Mid river	6	27
	Ad-RM	Lower river	0	0
Little White Salmon	Unmarked	--	1,044	5,403
	Ad-LM	Little White Salmon	46	419
	Ad	Mid river	8	58
	Ad-RM	Lower river	0	0
OxBow	Unmarked	--	(*)	103
	Ad-LM	OxBow	(*)	3
	Ad	Mid river	(*)	2
Cascade	Unmarked	--	7,247	7,227
	Ad-LM	Cascade	549	576
	Ad	Mid river	44	104
	Ad-RM	Lower river	5	21
Uppermost River				
Leavenworth	Unmarked	--	310	1,849
	D-Ad	Leavenworth	38	138

*Returns not examined.

APPENDIX TABLE 2a.—Continued.

Recovery location, by hatchery	Marked and unmarked	Origin	Year of return 1968	Year of return 1969
Middle River--Continued				
Lewis River	Unmarked	--	1,911	2,945
	Ad-LM	Upper river	0	0
	Ad	Lewis River	233	302
	Ad-RM	Lower river	0	0
Kalama Falls	Unmarked	--	1,592	10,696
	Ad-LM	Upper river	0	0
	Ad	Kalama Falls	148	888
	Ad-RM	Lower river	0	1
Lower Kalama	Unmarked	--	1,887	2,739
	Ad-LM	Upper river	0	1
	Ad	Lower Kalama	192	263
	Ad-RM	Lower river	0	1
Toutle	Unmarked	--	2,546	23,664
	Ad-LM	Upper river	0	0
	Ad	Toutle	200	2,093
	Ad-RM	Lower river	0	0
Upper River				
Klickitat	Unmarked	--	181	1,347
	Ad-LM	Klickitat	15	163
	Ad	Mid river	2	13
	Ad-RM	Lower river	0	0
Little White Salmon	Unmarked	--	5,036	8,131
	Ad-LM	Little White Salmon	341	666
	Ad	Mid river	44	105
	Ad-RM	Lower river	1	2
Cascade	Unmarked	--	2,144	1,374
	Ad-LM	Cascade	146	83
	Ad	Mid river	41	22
	Ad-RM	Lower river	3	14
Uppermost River				
Leavenworth	Unmarked	--	69	32
	D-Ad	Leavenworth	1	0
	D-Ad-LM	Leavenworth	7	0
	D-Ad-RM	Leavenworth	0	0

APPENDIX TABLE 2b.—Number of marked and unmarked 1966-brood coho salmon recovered at hatcheries in each section of the Columbia River in 1968 and 1969.

Recovery location, by hatchery	Marked and unmarked	Origin	Year of return 1968	1969
wer River				
Elokomin	Unmarked	--	4,527	6,316
	Ad-LM	Upper river	3	1
	Ad	Mid river	2	10
	Ad-RM	Elokomin	280	532
Big Creek	Unmarked	--	5,682	7,719
	Ad-LM	Upper river	0	0
	Ad	Mid river	0	5
	Ad-RM	Big Creek	430	489
Grays River	Unmarked	--	5,375	5,310
	Ad-LM	Upper river	0	2
	Ad	Mid river	0	10
	Ad-RM	Grays River	518	516
Klaskanine	Unmarked	--	10,473	2,623
	Ad-LM	Upper river	0	0
	Ad	Mid river	0	0
	Ad-RM	Klaskanine	788	172
ddle River				
Bonneville	Unmarked	--	7,034	3,115
	Ad-LM	OxBow	90	148
	Ad	Bonneville	585	567
	Ad-RM	Lower river	26	24
Washougal	Unmarked	--	2,204	9,060
	Ad-LM	Upper river	0	0
	Ad	Washougal	237	1,033
	Ad-RM	Lower river	0	7
Sandy	Unmarked	--	4,134	3,079
	Ad-LM	Upper river	27	11
	Ad	Sandy	422	267
	Ad-RM	Lower river	20	13
Eagle Creek	Unmarked	--	929	1,799
	Ad-LM	Upper river	2	0
	Ad	Eagle Creek	85	191
	Ad-RM	Lower river	1	0
	LM	Eagle Creek	77	221

APPENDIX TABLE 2b.—Continued.

Recovery location, by hatchery	Marked and unmarked	Origin	Year of return 1967	1968
ower River				
Elokomin	Unmarked	--	533	1,616
	Ad-LM	Upper river	0	0
	Ad	Mid river	0	3
	Ad-RM	Elokomin	41	105
Big Creek	Unmarked	--	10,540	10,573
	Ad-LM	Upper river	0	0
	Ad	Mid river	26	5
	Ad-RM	Big Creek	936	1,079
Grays River	Unmarked	--	1,363	2,651
	Ad-LM	Upper river	3	0
	Ad	Mid river	41	0
	Ad-RM	Grays River	40	213
Klaskanine	Unmarked	--	7,201	4,151
	Ad-LM	Upper river	0	0
	Ad	Mid river	0	1
	Ad-RM	Klaskanine	527	365
iddle River				
Bonneville	Unmarked	--	7,401	16,602
	Ad-LM	OxBow	468	735
	Ad	Bonneville	188	787
	Ad-RM	Lower river	5	44
Washougal	Unmarked	--	22,098	43,264
	Ad-LM	Upper river	0	3
	Ad	Washougal	2,651	4,316
	Ad-RM	Lower river	0	3
Sandy	Unmarked	--	6,021	5,222
	Ad-LM	Upper river	18	24
	Ad	Sandy	664	517
	Ad-RM	Lower river	14	32
Eagle Creek	Unmarked	--	593	2,371
	Ad-LM	Upper river	0	5
	Ad	Eagle Creek	63	222
	Ad-RM	Lower river	0	2
	LM	Eagle Creek	58	215

APPENDIX TABLE 3.—Percentage of two-year-old coho salmon in the marked and unmarked returns to Columbia River hatcheries by river section and brood year, 1965-66.

River section and (in parentheses) mark	Brood	Percent of 2-year-olds	
		Marked	Unmarked
Lower (Ad-RM)	1965	47	51
	1966	54	54
Middle (Ad)	1965	32	29
	1966	27	28
Upper (Ad-LM)	1965	36	40
	1966	36	40

APPENDIX TABLE 4.—Actual number of marked coho salmon of the 1966 brood from Leavenworth National Fish Hatchery recovered—by type of mark, year of recovery, region of capture, and type of fishery, 1968-69.

Region	Fishery type	D-Ad		D-Ad-RM		D-Ad-LM 1/		Total	
		1968	1969	1968	1969	1968	1969	1968	1969
British Columbia.....	Commercial.....	0	0	0	0	0	1	0	1
Washington.....	Sport.....	0	18	0	5	0	29	0	52
	Commercial.....	0	30	0	7	0	30	0	67
Oregon.....	Sport.....	0	20	0	5	0	6	0	31
	Commercial.....	0	34	0	32	0	52	0	118
California.....	Sport.....	0	2	0	1	0	3	0	6
	Commercial.....	0	19	0	8	0	13	0	40
Columbia River.....	Sport.....	0	0	0	0	0	0	0	0
	Commercial.....	3	2	0	15	0	33	3	50
Total.....	All fisheries..	3	125	0	73	0	167	3	365

1/ Released below Bonneville Dam.

APPENDIX TABLE 5a.—Estimated number of marked coho salmon of the 1966 brood from Leavenworth National Fish Hatchery recovered—by type of mark, year of recovery, region of capture, and type of fishery, 1968-69.

Region	Fishery type	D-Ad		D-Ad-RM		D-Ad-LM 1/		Total	
		1968	1969	1968	1969	1968	1969	1968	1969
British Columbia.....	Commercial.....	0	0	0	0	0	7	0	7
Washington.....	Sport.....	0	88	0	23	0	131	0	242
	Commercial.....	0	123	0	30	0	128	0	281
Oregon.....	Sport.....	0	114	0	15	0	19	0	148
	Commercial.....	0	184	0	176	0	285	0	645
California.....	Sport.....	0	7	0	2	0	14	0	23
	Commercial.....	0	137	0	35	0	52	0	224
Columbia River.....	Sport.....	0	0	0	0	0	0	0	0
	Commercial.....	6	7	0	90	0	186	6	283
Total.....	All fisheries..	6	660	0	371	0	822	6	1,853

1/ Released below Bonneville Dam.

APPENDIX TABLE 5b.—Estimated recovery of D-Ad-RM and D-Ad-LM marked 1966-brood coho salmon from Leavenworth National Fish Hatchery after redistribution of the D-Ad-only marks.

Region	Fishery type	D-Ad-RM		D-Ad-LM 1/		Total	
		1968	1969	1968	1969	1968	1969
British Columbia.....	Commercial.....	0	0	0	7	0	7
Washington.....	Sport.....	0	71	0	171	0	242
	Commercial.....	0	96	0	185	0	281
Oregon.....	Sport.....	0	77	0	71	0	148
	Commercial.....	0	275	0	370	0	645
California.....	Sport.....	0	6	0	17	0	23
	Commercial.....	0	109	0	115	0	224
Columbia River.....	Sport.....	0	0	0	0	0	0
	Commercial.....	3	94	3	189	6	283
Total.....	All fisheries..	3	728	3	1,125	6	1,853

1/ Released below Bonneville Dam.

APPENDIX TABLE 6.—Relative survival of marked 1965- and 1966-brood coho salmon by mark type and hatchery groups.

Brood	Mark	Tetracycline group	Cascade, Little White, Klaskanine	All hatcheries
1965	Ad-LM	--	.69 3/	.69 5/
	Ad	.89 1/	--	.92 6/
	Ad-RM	.82 2/	.79 4/	.79
1966	Ad-LM	--	.68 3/	.72
	Ad	.83 1/	--	.89 6/
	Ad-RM	.68 2/	.70 4/	.72

1/ Eagle Creek National Fish Hatchery.
2/ Big Creek Salmon Hatchery.
3/ Cascade Salmon Hatchery, Little White Salmon National Fish Hatchery.
4/ Klaskanine River Salmon Hatchery.
5/ Klickitat State Salmon Hatchery, Cascade Salmon Hatchery, Little White Salmon National Fish Hatchery.
6/ Bonneville Salmon Hatchery returns not included in calculations.

APPENDIX TABLE 7.—Estimated catch of unmarked 1965- and 1966-brood hatchery coho salmon by region, fishery type, brood year, and year of capture.

Region	Fishery type	1965 brood			1966 brood		
		1967	1968	Total	1968	1969	Total
Ocean fisheries:							
British Columbia.....	Commercial...	0	80,101	80,101	0	34,981	34,981
Washington.....	Sport.....	0	163,997	163,997	0	153,837	153,837
	Commercial...	0	203,620	203,620	0	122,210	122,210
Oregon.....	Sport.....	0	93,759	93,759	0	86,658	86,658
	Commercial...	0	270,127	270,127	0	298,453	298,453
California.....	Sport.....	0	7,878	7,878	0	7,529	7,529
	Commercial...	0	102,523	102,523	0	77,724	77,724
Subtotal.....	Sport.....	0	265,634	265,634	0	248,024	248,024
	Commercial...	0	656,371	656,371	0	533,368	533,368
Freshwater fisheries:							
Columbia River.....	Sport.....	3,928	3,246	7,174	6,516	4,771	11,287
	Commercial...	1,733	74,548	76,281	2,775	136,057	138,832
Total.....	All fisheries	5,661	999,799	1,005,460	9,291	922,220	931,511

APPENDIX TABLE 8.—Estimated total catch of 1965- and 1966-brood hatchery coho salmon by region, fishery type, brood year, and year of capture.

Region	Fishery type	1965 brood			1966 brood		
		1967	1968	Total	1968	1969	Total
Ocean fisheries:							
British Columbia.....	Commercial...	0	87,526	87,526	0	38,313	38,313
Washington.....	Sport.....	0	179,179	179,179	0	167,914	167,914
	Commercial...	0	222,405	222,405	0	133,536	133,536
Oregon.....	Sport.....	0	102,614	102,614	0	94,994	94,994
	Commercial...	0	294,778	294,778	0	326,241	326,241
California.....	Sport.....	0	8,556	8,556	0	8,259	8,259
	Commercial...	0	111,592	111,592	0	85,165	85,165
Subtotal.....	Sport.....	0	290,349	290,349	0	271,167	271,167
	Commercial...	0	716,301	716,301	0	583,255	583,255
Freshwater fisheries:							
Columbia River.....	Sport.....	4,297	3,552	7,849	7,133	5,223	12,356
	Commercial...	1,872	81,364	83,236	3,021	148,533	151,554
Total.....	All fisheries	6,169	1,091,566	1,097,735	10,154	1,008,178	1,018,332

APPENDIX TABLE 9.—Estimated 1967-69 sport catch in Columbia River tributaries (where no creel census was made) of 1965- and 1966-brood hatchery coho salmon.

Stream	1965 brood			1966 brood			Estimation method
	1967	1968	Total	1968	1969	Total	
Icicle River	50	15	65	10	10	20	1/
Klickitat River	5	6	11	5	0	5	2/ 3/ 4/
Little White Salmon R.	111	8	119	7	2	9	2/ 3/ 5/
Wind River	2	0	2	--	--	--	2/ 3/ 4/
Washougal River (upper)	10,382	2,048	12,430	2,493	872	3,365	1/ 3/ 5/
(lower)	1,385	273	1,658	332	116	448	1/ 3/ 4/
Elokomin River	59	75	134	92	115	207	2/ 3/ 4/
Grays River	10	218	228	265	213	478	2/ 3/ 4/
Sandy River	513	944	1,457	1,457	1,198	2,655	3/ 4/ 6/
Eagle Creek (Clackamas)	928	1,709	2,637	1,744	1,433	3,177	3/ 4/ 6/
Big Creek	410	754	1,164	603	496	1,099	3/ 4/ 6/
Klaskanine River	534	983	1,517	1,346	1,106	2,452	3/ 5/ 6/
TOTAL	14,389	7,033	21,422	8,354	5,561	13,915	

1/ Estimates from discussions with Gene Nye, Washington Department of Fisheries, and local fishery personnel.
2/ Catches from Washington Department of Fisheries punch card returns 1967-1969.
3/ Age groups broken down by using jack to adult ratios obtained in creel census on Lewis, Kalama, Cowlitz, and Toutle Rivers.
4/ 70% of catch apportioned to hatchery production.
5/ Entire catch assumed hatchery.
6/ Catches from Oregon State Game Commission punch card returns 1967-1969.

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ABILITY OF MALE KING CRAB, *PARALITHODES CAMTSCHATICA*, TO MATE REPEATEDLY, KODIAK, ALASKA, 1973

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ABSTRACT

An experiment to test abilities of male king crab to mate repeatedly in an environment approximating natural conditions was conducted during the spring of 1970. Twenty-four males of varying size and shell age were placed into separate undersea compartments for intervals up to 56 days with 222 females. The ability of males to mate repeatedly was determined by introducing females in mating condition to males at the rate of one every 5 days.

No difference in mating capabilities of males of different types was evident until after exposure to seven females. At this point egg fertility and relative fullness of brood chamber of the females mated to the small old-shell males decreased significantly. Large new-shell males showed a marked decline in mating ability after the ninth mating. One small new-shell male mated with 13 females.

Owing to declining stocks within the Kodiak Island fishery, commercial harvest of king crab has declined from 96 to 11 million pounds over the past seven years, 1965-1971. To determine the level of king crab brood stocks necessary for perpetuation of a maximum sustained yield fishery, the reproductive capabilities of the king crab are being studied in detail.

In 1964, biologists of the Alaska Department of Fish & Game determined experimentally that recently-molted sublegal (smaller than 146 mm carapace length) male king crabs were capable of mating. Eleven males ranging from 120 to 144 mm carapace length mated 51 females in 16 days (Powell and Nickerson, 1965). Observations on individual males were not obtained. In 1971, males as small as 85 mm carapace length were found to be capable of mating (Powell, Shafford, and Jones, 1972). Of 3,402 males observed mating in nature from 1963 to 1971, however, only two were smaller than 100 mm (Powell, Rothschild, and Buss[4]).

Several authors have reported old-shell males congregated with adult females during the mating season and indicated they may be capable breeders because new-shell males were separate from the females at the time (Gray and Powell, 1966; Miyahara and Shippen, 1965).

Currently the reproductive success or failure of any particular brood year is not readily apparent until approximately 8 yr later when males are entering the fishery. At this late date, it is doubtful that we can, with any precision, evaluate the degree to which each of the limiting factors contributes to the success or failure; consequently we are unable to determine if resultant abundance levels are attributable to initial magnitude of egg production, environment, or effects of commercial fishing.

Prior to 1970, managers assumed that any level of harvest of males was acceptable as long as the 7-inch size limit (carapace width outside spines) was observed.

In recent years, we observed that the proportion of adult females without eggs and with partial broods had increased and that some of the female population was not being serviced (unpublished Alaska Department of Fish & Game data). Large adult females have approximately nine times more eggs than small ones (Haynes, 1968) and initial examination of unpublished Department of Fish & Game data reveals that the incidence of adults without eggs and with partial broods is greater among the

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[4] Powell, Guy C., Brian J. Rothschild, and James A. Buss. 1972. A study of king, *Paralithodes camtschatica* (Tilesius) brook stocks, Kodiak Island, Alaska, 1963-1971. 30 p. (Processed)

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larger individuals. In order to place more males on the mating grounds and to stabilize annual harvests, a quota system was initiated in 1970.

It is important to know whether that segment of the male population harvested by the commercial fishery, i.e., large males and old-shell males (Nickerson, Ossiander, and Powell, 1966) possess greater mating capabilities than smaller protected males which molt during the mating season. Also of significance is the question of whether undersized males would be adequate in numbers and ability to mate all females if larger males were removed by the fishery. Recent increases in the numbers of adult females with broods of reduced size appear related to simultaneous increased exploitation rates and may result from matings with males which had mated several times previously. Our experiment was designed to gain insight into these phenomena and to obtain more complete data for individual males, especially comparative data on mating ability for old-shell males and recently molted new-shell males.

In this paper, mating refers to the actual fertilization of the eggs. Hence, the term "mating capability" refers to the ability of the male to fertilize the eggs of the females to which he is exposed.

METHODS AND MATERIALS

Experimental Equipment and Location

The experiment was conducted in undersea pens, the sides and top of which were covered with nylon mesh; the bottoms were open to allow crabs to dig in the substrate as they would do in nature. Each pen was 8′ × 8′ × 4′ and each divided into four equal sized compartments. Compartments were numbered 1 through 28 and situated in 40 ft of water on a level stretch of muddy-sand bottom east of Near Island adjacent to an area where king crabs normally mate. The study location is one mile from the city of Kodiak, Alaska. Pens were designed and located to simulate natural conditions. Environmental factors such as daily tidal currents, pressures, light intensities, temperatures, and salinities were considered important in that they might influence mating. For this reason, undersea pens were considered superior to aquaria.

The mating study was conducted in compartments 1 through 24 while 25 through 28 were used to store crabs. Females were held in storage prior to and after the completion of mating.

Fishery biologists and trained technicians utilizing scuba observed the crabs underwater every day. Individual crabs were identified by tagging with permanent "isthmus" loop tags (Gray, 1965) prior to being placed in the pens.

Experimental Procedures

The experiment was designed to compare mating capabilities of four size shell-age classes of male king crabs (small new-shell, small old-shell, large new-shell, and large old-shell) by studying the effects of repeated matings on the ability of these males to mate successfully with additional females. A 5-mm range, 145-149, was used as a dividing point between small and large males at the juncture of legal and undersize crabs. Those 144 mm or less (commercially undersize males) were classified as small while those 150 mm or larger were classified as large (Table 1). Small males averaged 140 mm, large males 167.

Most males used in the experiment were captured by scuba divers. A few of the males of required size, however, were not available by diving (the preferred method of collecting) and therefore were taken from the catches of commercial pots and trawls.

All females used in the study were in premolt condition and were in the pre-copulatory embrace (Powell and Nickerson, 1965): i.e., they had already been selected for mating by males in the natural environment. The use of these females (called "graspees") was our method of insuring that females were ready to mate with males when introduced into the pens. Females from natural mating areas near the pens were captured by scuba divers a day or two before they were needed and ranged in length from 104 to 181 mm, with an average size of 134 mm.

TABLE 1.—Size relationships of experimental crabs.

Male king crabs		No. of female partners	Carapace length (mm)			
			Range		Mean	
Class	Number		Male	Female	Male	Female
Small old-shell	4	29	136-144	107-181	142	133
Large old-shell	9	82	156-193	114-175	178	134
Small new-shell	4	35	136-142	115-150	139	135
Large new-shell	10	76	150-168	104-160	158	134
Total	27[1]	222				

[1] Three extra males replaced three original males which died.

Females were separated from the males which held them and placed in storage ready for use in the experiment. The average length of females increased as the study progressed because older females mate later in the season.[5] Females captured 15 March through 15 April averaged 128 mm, while those captured 20 April to 20 May averaged 140.

Twenty-four females were paired randomly with the 24 males in the pens at the beginning of each of the 14 separate 5-day periods beginning 16 March and continuing through 24 May. On days when a complete set of 24 females could not be captured, those which had been were introduced to males which previously had had the largest number of female partners. Incomplete sets of females exist for early and late spawning periods—1, 2, 3, 12, 13, and 14—when mating crabs were relatively scarce. In addition, 12 females escaped from six compartments on 9 May when two pens were accidentally lifted; as many as three females were lost from a single compartment. During the middle of the mating season, 31 March through 5 May, females were abundant; consequently each male received a female for each of the eight consecutive periods within this interval. Females were introduced to males as soon after capture as possible; none were held more than two days and many were introduced the same day.

Females were left with males until mating was completed and eggs were known to be fertilized; consequently males commonly shared their compartments with several females at a time. Approximately 10 days after eggs were deposited on the pleopods, a sample of approximately 1,000 was obtained from each female to determine success of fertilization. Each sample consisted of several separate groups of eggs taken from scattered locations within the egg mass. Samples were preserved in Bouin's solution. Fertilized eggs developing for 7 to 10 days at approximately 37°F showed cleavage when viewed microscopically. When eggs were known to be fertilized (i.e., advanced cleavage stages observed), females were separated from their experimental male partners and placed in storage compartments 25-28.

Divers made observations at daily intervals recording data on underwater slates. Observations included collecting and measuring shed exoskeletons to determine day of molting, examining recently-molted females to determine relative fullness of the brood chamber, and recording activities of mating and feeding.

RESULTS

Relative success of male copulation was measured in two ways. First, relative fullness of brood chamber was determined subjectively by visually deciding what proportion of the brood chamber was filled with eggs and recording same on a scale of zero to one hundred (Table 2). The second, percent of eggs fertilized, was determined in two steps; (1) a prompt microscopic viewing of several hundred eggs to obtain quick estimates, followed later by (2) a careful microscopic examination of 100 eggs (Table 3).

Both measures of mating success provided compatible results and revealed that infertile eggs are scattered throughout the egg mass rather than being grouped separately from fertile eggs.

The raw data, y, for each of the two measurement variables were transformed so that they would be more normally distributed, using the formula:[6]

$$z = \sqrt{n + 1/2}\,\sin \sqrt[-1]{\frac{y + 3/8^*}{n + 3/4}}$$

In this case, n is equal to 100, since both methods of measurement are based on a scale of 100.

A covariance analysis was performed relating z to x, the number of females mated. This analysis fits a least squares regression line $z = a_i + b_i x$ for each of the four groups, where a_i, b_i represent the intercept and slope respectively for the ith group. The results of this analysis are presented in Table 4. Slopes for each group appear to be significantly different from zero, except for percent of eggs fertilized in large old-shell and small new-shell males. The more negative the slope of the regression line, the less the

[5] Determined from 3,402 observations of grasping pairs of king crabs captured over a 9-year period, 1963-1971. See page 257 National Geographic Magazine, Vol. 139, No. 2, Feb. 1971 for photograph of grasping pairs.

[6] Thoni, H. Transformation of variables used in the analysis of experimental and observational data, a review. Technical Report No. 7, Statistical Laboratory, Iowa State University, Ames, Iowa, July 1967.

TABLE 2.—Success of each mating as determined by the relative fullness of the brood chamber (percent).

Male class	Male carapace length (mm)	Number of successive matings: 1	2	3	4	5	6	7	8	9	10	11	12	13	14
		Relative fullness of brood chamber (percent)													
Small old-shell	144	100	100	100	90	—	—	—	—	—					
	136	100	100	100	0	80	80	50	0	0					
	144	100	100	100	100	80	85	60	50	0					
	142	100	90	90	10	85	90	100	—	—					
No. of observations	4	4	4	4	4	3	3	3	2	2					
Average	141.5	100	97.5	97.5	50	81.7	85.0	70.0	25.0	0					
Large old-shell	164	100	100	90	100	80	90	80	75	80					
	156	80	100	90	100	100	100	90	20	80	30	—	—	—	—
	163	100	90	100	100	100	100	—	—	—	—	—	—	—	—
	190	100	100	100	100	90	100	100	90	90	75	80	90	5	35
	184	100	100	70	100	100	90	90	100	—	—	—	—	—	—
	193	100	90	95	100	50	100	90	60	80	0	—	—	—	—
	181	100	85	100	100	90	100	100	—	—	—	—	—	—	—
	180	100	100	100	100	100	100	90	75	20	85	—	—	—	—
	189	90	90	100	90	90	75	20	90	—	—	—	—		—
No. of observations	9	9	9	9	9	9	9	8	7	5	4	1	1	1	1
Average	177.8	96.7	95.0	93.9	98.9	88.9	95.0	82.5	72.9	70.0	47.5	80	90	5	35
Small new-shell	140	60	100	100	80	100	100	90	100	100	100	60	60	50	—
	136	100	75	80	100	75	60	—	—	—	—	—	—	—	—
	142	100	80	60	90	75	90	50	75	25	—	—	—	—	—
	138	100	100	90	100	100	90	90							
No. of observations	4	4	4	4	4	4	4	3	2	2	1	1	1	1	
Average	139.0	90	88.8	82.5	92.5	87.5	85.0	76.7	87.5	62.5	100	60	60	50	
Large new-shell	150	75	100	100	100	90	90								
	160	100	100	100	70	100	0	90	90	90	70	0	0		
	165	10	100	100	10	100	75	80	70	90	100	80	—		
	163	100	90	100	100	90	60	90	50	60	—	—	—		
	168	100	90	90	100	100	100	100	10	80	75	—	—		
	161	100	100	100	100	90	75	60	—	—	—	—	—		
	160	100	100	90	80	35	—	—	—	—	—	—	—		
	153	100	—	—	—	—	—	—	—	—	—	—	—		
	151	100	70	70	100	90	90	80	50	60	60	0	—		
	151	100	85	80	100		—	—	—	—	—	—	—		
No. of observations	10	10	9	9	9	8	7	6	5	5	4	3	1		
Average	158.2	88.5	92.8	92.2	84.4	86.9	70.0	83.3	54.0	76.0	76.2	26.7	0		

TABLE 3.—Success of each mating as determined by percent of egg mass fertilized.

Male class	Male carapace length (mm)	Number of successive matings: 1	2	3	4	5	6	7	8	9	10	11	12	13	14
		Percent of eggs fertilized													
Small old-shell	136	100	100	100	0	97	79	99	0	0					
	142	100	100	100	87	96	90	99	—	—					
	144	100	100	100	100	100	100	82[2]	99[2]	0					
	144	100	100	100	90	—	—	—	—						
No. of observations		4	4	4	4	4	3	3	3	2	2				
Average		141.5	100	100	100	69.3	97.7	89.7	93.3	44.5	0				
Large old-shell	164	100	100	90	100	100	100	100	99	100	—	—	—	—	—
	156	100	100	95	100	100	100	99	91	100	92	—	—	—	—
	163	100	99	100	100	100	100	—	—	—	—	—	—	—	—
	190[1]	100	100	100	100	100	97	98	100	100	100	100	100	[1]	[1]
	184	100	100	100	100	99	100	100	100	—	—	—	—	—	—
	193	99	98	97	100	100	100	99	100	100	0	—	—	—	—
	181	98	100	100	100	100	100	99	—	—	—	—	—	—	—
	180	99	99	100	100	100	100	100	100	100	100	—	—	—	—
	189	100	100	100	100	100	100	100	100	—	—	—	—	—	—
No. of obersvations		9	9	9	9	9	9	9	8	7	5	4	1	1	1	1
Average		177.8	99.6	99.6	98.0	100	99.9	99.7	99.4	98.6	100	73	100	100	[1]	[1]
Small new-shell	140	100[2]	100	100	100	100	100	100[2]	100	98[2]	95[2]	100	97	100[2]	—
	136	98	100	91[2]	94[2]	98[2]	86	—	—	—	—	—	—	—	—
	142	100	100	98	99	100	89	100	99[2]	99[2]	—	—	—	—	—
	138	100	100	100	100	100	100	100[2]		—	—	—	—	—	—
No. of observations		4	4	4	4	4	4	4	3	2	2	1	1	1	1
Average		139.0	99.5	100	97.2	98.2	99.5	93.8	100	99.5	98.5	95	100	97	100
Large new-shell	150	100	100	100	100	100	100	—	—	—	—	—	—		
	160	100	100	100	100	100	0	97	100	100	91	0	0		
	165	100	100	100	100	98	99	87	97	0	99	59	—		
	163	100	100	100	100	100	100	100	98	100	—	—	—		
	168	100	100	38	100	98	94	97	95	100	35	—	—		
	161	100	100	100	100	99	98	100	—	—	—	—	—		
	160	100	99	99	100	95	—	—	—	—	—	—	—		
	153	100	—	—	—	—	—	—	—	—	—	—	—		
	151	100	100	100	100	100	100	100	99	100	100[2]	0	—		
	151	100	98	100	100	—	—	—	—	—	—	—	—		
No. of observations		10	10	9	9	9	8	7	6	5	5	4	3	1	
Average		158.2	100	99.7	93	100	98.8	84.4	96.8	97.8	80.0	81.2	19.7	0	

[1] The last 2 females ovulated but escaped before egg samples were taken.
[2] Female larger than male.

TABLE 4.—Comparison of king crab mating ability, slopes and slope contrasts for relative fullness of brood chamber and percent of eggs fertilized.

	Relative fullness of brood chamber			Percent of eggs fertilized		
Male class	Slope	Standard deviation of slope	F Value for Test of slope = 0	Slope	Standard deviation of slope	F Value for Test of slope = 0
Small old-shell	b_1 = -1.416	0.234	F = 36.5 P < .0001	b_1 = -1.171	0.202	F = 33.5 P < 0.0001
Large old-shell	b_2 = -0.616	0.112	F = 30.3 P < .0005	b_2 = -0.087	0.107	F = .7 P = .32
Small new-shell	b_3 = -0.328	0.164	F = 3.9 P = .05	b_3 = -0.036	0.142	F = .1 P = .75
Large new-shell	b_4 = -0.677	0.116	F = 33.9 P < .0001	b_4 = -0.637	0.100	F = 40.4 P < .0001
Test for equality of slopes $b_1 = b_2 = b_3 = b_4$			F = 4.07, P = 0.01			F = 11.74, P = .0001

	Slope Contrasts					
	Contrast estimate	Standard deviation of estimate	F Value for test of contrast = 0	Contrast estimate	Standard deviation of contrast	F Value for test of contrast = 0
Old-shell vs. new-shell $b_1 + b_2 - b_3 - b_4$	-1.028	0.329	F = 9.80 P = 0.001	-0.585	0.287	F = 4.1 P = 0.04
Large vs. small $b_1 + b_3 - b_2 - b_4$	-0.450	0.329	F = 1.9 P = 0.17	-0.482	0.287	F = 2.8 P = 0.10

mating ability of the males in that particular group. A test of the hypothesis of equality of slopes ($b_1 = b_2 = b_3 = b_4$) yields an F ratio of 4.1 for relative fullness of brood chamber and 11.7 for percent of eggs fertilized, significant at the 1 and 0.01 percent level respectively. In order to determine the significance of the size shell-age classifications, contrasts of old-shell versus new-shell and small versus large were computed as shown in Table 4. These contrasts indicate that the major contribution to the inequality in slopes comes from the difference in shell age. Size did not appear to be a significant factor as is indicated by P values of 0.17 and 0.10 respectively for relative fullness of brood chamber and percent of eggs fertilized. Within the shell-age contrast, the small old-shell males contribute the most in the form of a more negative slope, indicating that these males have much less mating ability than the other three groups.

The data presented thus far give a comparison of the mating abilities of the four size shell-age groups. A linear approximation was assumed for each group and, although this procedure is not exact, it is sufficiently close for comparative purposes. Graphs of the curves for mating ability versus number of matings indicate that small old-shell and large new-shell males have the least linear relationship of the four groups. The points plotted in Figures 1 and 2 are the means of the transformed variables for each successive mating. A point may represent as few as one or as many as ten observations, as shown in Tables 2 and 3. The original 0 to 100 scale is attached to the graphs to make them easier to read; thus after the means are computed, they are transformed back to the original scale.

The slopes of the functions were approximated by computing the means of the transformed measurement variables for each x and fitting empirical curves to the data points. Figures 1 and 2 show the relationship between percent of eggs fertilized and relative fullness of brood chamber respectively and are presented primarily as an aid to fisheries management. The results, however, are quite consistent with those given in Table 4. The graphs show a marked decline in the mating ability of small old-shell males after approximately the seventh mating and a decline in the ability of large new-shell males after the tenth mating. Figure 2 indicates that partial clutches result from mating with small old-shell and large new-shell males which had mated several times previously.

The least squares regression lines for large old-shell males and small new-shell males are also plotted in Figures 1 and 2. These groups show little decrease in mating ability as the number of matings increases, particularly for the percent of eggs fertilized. The slope of the

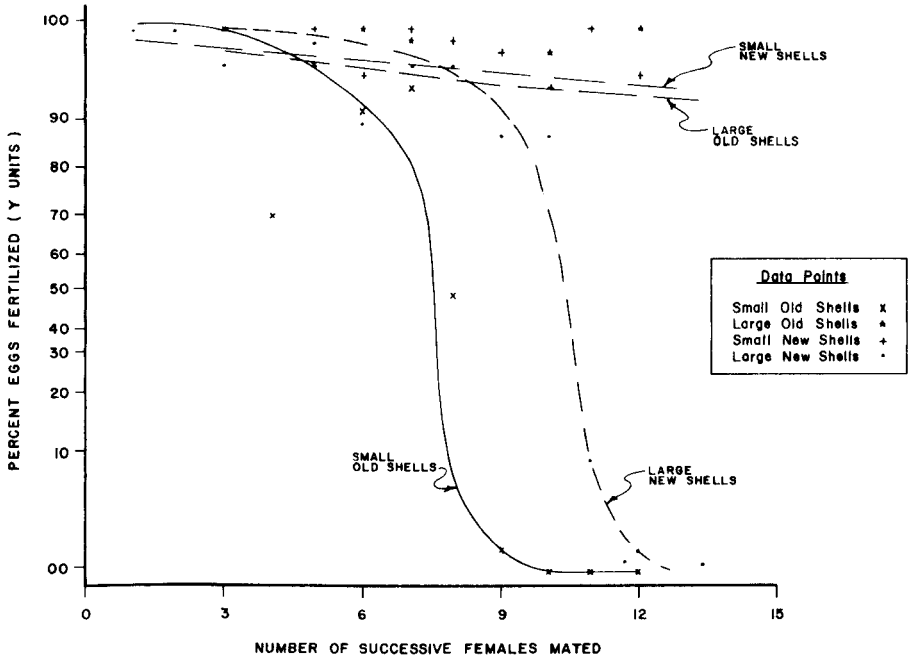

FIGURE 1.—Mating ability of male king crabs expressed as percentage of eggs fertilized.

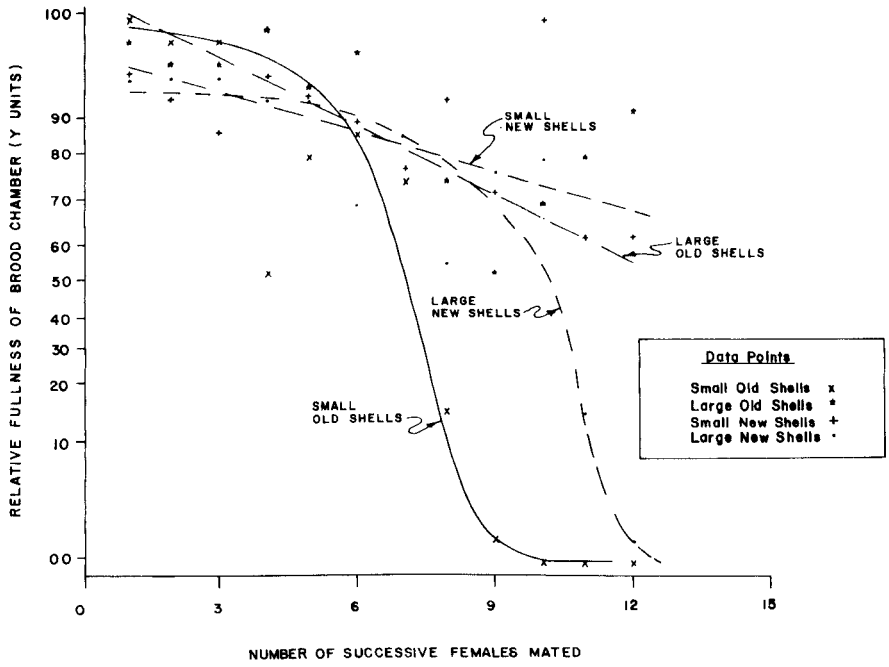

FIGURE 2.—Mating ability of male king crabs expressed as relative fullness of brood chamber of mated females.

regression line for large old-shell males for relative fullness of brood chamber is quite steep (-0.616) and nearly approaches the slope for large new-shell males (-0.677); however, there are no points in the vicinity of zero to indicate that mating ability for large old-shell males drops off suddenly after a certain number of matings. Furthermore, the other measurement variable indicates that the mating ability of large old-shell crabs does not decline at a significant rate when exposed to a maximum of 13 females.

DISCUSSION

This study indicates that all classes of males tested possessed considerable ability to mate repeatedly at the approximate rate of one female every 5 days. Mating ability of small old-shell and large new-shell male king crabs decreases markedly after approximately the seventh to ninth mating. The decline for large old-shells and small new-shells is not as noticeable.

Although the analysis of covariance for this experiment does not indicate significant differences in mating ability attributable to size, one should be hesitant in saying categorically that size is not a relevant factor. By examining the individual slopes in the graphs, it is evident that certain combinations of age and size have a marked effect on mating ability and one must realize that when a given factor is examined, the other factor is averaged out.

The knowledge obtained as a result of this investigation represents just a beginning in the understanding of the mating of king crabs. To what extent these findings are applicable to mating in nature remain uncertain. The effects of holding experimental crabs in undersea pens must be understood before realizing full application of the data to practical management of the fishery.

Holding males in pens could adversely affect mating ability of some classes, particularly later matings after prolonged captivity, while simultaneously enhancing ability of others by forcing partners into constant close association with one another. Larger females used later in the experiment may also have affected results.

Even though size does not appear to be a significant factor in mating ability as far as the number of repeated matings is concerned, and even though small males appear to be capable breeders, it remains a possibility that in some instances in nature small males may not serve adequately as brood stock. Measurements of 6,804 king crabs captured by divers as mating pairs, 1963-1971, reveal that small young females are the first to mate each season followed three months later by large old females (Powell, Rothschild, and Buss, 1972). Further, males mating in nature with "pubescent" females (i.e., those mating for the first time and therefore the smallest found) are older and larger, averaging 42 mm more than females, with grasping observed as early as January 9 (Powell, Shafford, and Jones, 1972).

Apparently male size and male-female ratios are not the only factors affecting mating in nature. The presence in recent years of high incidence of adult females without eggs and with partial clutches within certain locations of the Kodiak fishery seem to be fishery-related because they occur only in areas of intense fishing (Powell, 1969[7]).

Adult female king crabs form mating congregations in shallow water from January through April and these congregations are intermittently distributed throughout the thousands of square miles of shallow habitat. For mating to be successful in each congregation, adequate numbers of capable males must be present during the relatively brief matable period following female ecdysis, otherwise delayed mating may adversely affect the success of ovulation and subsequent fertilization (Kurata, 1961; McMullen, 1969; and Wallace, Pertuit, and Hvatum, 1958).

The ratio of males to females necessary for complete mating success in nature appears dependent upon factors other than just numbers alone. The rate at which females molt and spatial distribution and size differences of adults inhabiting the location are also believed important. The greater the rate of female molting, the greater the number of males required. Male crabs select partners as early as 16 days prior to mating and continually grasp them until copulation occurs soon after female ecdysis (Powell, Rothschild, and Buss, 1972). Because of premating "grasping" behavior, it is possible that females molt without male partners though a

[7] Powell, Guy C. 1969. Some aspects of king crab biology. Proc. Am. Fish. Soc., West. Div. Meeting, Jackson Hole, WY, June 1969. (Processed)

favorable male-female ratio exists, because all males are either preoccupied grasping other females or resting between subsequent matings.

King crabs segregate to varying degrees according to size, sex, age, and time of year. Commercial fishing is concentrated in areas inhabited by large males with total effort varying according to factors such as accessibility. Thus cropping of males may be excessive in one area but not in another. Incidence of nonovigerous adult females is lowest in areas where sublegal sized males are abundant, but is often high in exploited areas with few adult males (unpublished, Alaska Dept. Fish & Game).

Size differences between partners, presence of competing males, and time of year also must be considered in evaluating the reproductive potential of mating populations.

It is conceivable that even with many young adult males present, a population of large old females may be inadequately serviced partly because the few surviving large males may, through aggressive behavior, keep smaller males away. To what extent competitive behavior exists is presently unknown but large old males commonly are found mating small young females in nature. Of the 14 matings in this experiment, where females were larger than males, 79 percent produced partial clutches.

Small males probably produce less reproductive material (sperm) than large males, and as a result, may be less capable of fertilizing the greater masses of eggs of large females.

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AN EVALUATION OF MID-WATER ARTIFICIAL STRUCTURES FOR ATTRACTING COASTAL PELAGIC FISHES[1]

DONALD A. WICKHAM AND GARY M. RUSSELL[2]

ABSTRACT

Mid-water artificial structures positioned off Panama City, Fla. during August 1970 were evaluated to determine their ability to attract coastal pelagic fishes. Quantitative and qualitative experimental results were obtained using scuba divers and purse seine catches. The feasibility of using artificial structures to facilitate the commercial harvest of coastal pelagic fishes with purse seines was established and the methods described. Average catch values of 398 kg (875 lb) per structure were obtained during a period when coastal pelagic fishes were unavailable to the local fishery. A greater total production was obtained from structures fished daily compared with those allowed to soak for 3 days before being fished. Experimental purse seine collections established that fish leave the structures at night with new recruitment occurring daily. No significant differences were obtained from preliminary experiments to evaluate the effects of structure size and color on attraction effectiveness. A working hypothesis is presented to describe apparent behavioral mechanisms involved in the attraction of some species of coastal pelagic schooling fish to objects in the sea. This study indicates that artificial-structure fish-attraction has potential for development as a technique to facilitate the harvest of the latent coastal pelagic fishery resources in the Gulf of Mexico.

Artificial structures have been shown to be effective for attracting concentrations of pelagic fishes (Hunter and Mitchell, 1968). Klima and Wickham (1971) visually evaluated the species and number of coastal pelagic fishes attracted to experimental artificial structures in the northeastern Gulf of Mexico. These observations established the feasibility of attracting large numbers of coastal pelagic fishes with artificial structures; however, many questions concerning structure attraction characteristics and dynamics as well as their actual usefulness in augmenting conventional harvesting methods for these species still remained unanswered.

Studies were conducted during August 1970, in 5 to 10 fathoms (9 to 18 m) of water offshore of Shell Island, Panama City, Fla. to obtain quantitative samples for evaluating the validity of scuba-diver estimates of structure-attracted fish aggregations, to evaluate methods for using a conventional purse seine for capturing structure-attracted fish, and to obtain catch-production values for single structures. We also evaluated effects of structure soak time and size-color differences on attraction effectiveness. Day and night samples, plus scuba-diver observations of fish behavior, provided additional clues to the dynamics of the coastal pelagic fish aggregations attracted to artificial structures.

MATERIALS AND METHODS

Our fish attraction devices were three-dimensional structures. Each structure was constructed from vinyl-cloth covered, wood and wire frame panels. Two panels were fastened along one side, permitting the structure to be stored flat, but opened into a three-dimensional right prism when deployed for fish attraction. Two sizes of structures were used. The small structure panels were 0.9 × 1.5 m (3 × 5 ft) in size and the large structures, with twice the surface area of the smaller structures, were 1.8 × 1.5 m (6 × 5 ft). All structures were white except those painted for specific experiments.

Structures were positioned 4-6 m (15-20 ft) beneath the surface. The structure design and mooring arrangement are illustrated in Figure 1. Structures were spaced at approximately 0.8-km

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(0.5-mile) intervals. Their arrangement in the experimental site is shown in Figure 2. The eight structure mooring locations were used with different structures as required for specific experiments.

The 15-m (49-ft) single boat-rig bait purse seiner, *Gulf Ranger*, was chartered to make quantitative collections at selected artificial structures using a tom-weight type purse seine, 22 m (12 fathoms) deep and 110 m (60 fathoms) in length, with 3.2 cm (1¼-inch) stretched mesh webbing. A 6-m (20-ft) inboard-outdrive power boat was used as a diving platform and for picking up and resetting structures sampled by the purse seine.

Daily visual estimates of the number and species of fish present at each structure were made independently by scuba divers. We obtained quantitative data from selected structures by collecting all the fish around these structures with the purse seine. Diver estimates and purse seine catch data are given in Table 1.

Scuba divers made visual estimates of the fish aggregation at a structure prior to beginning the purse seine set. The structure anchor was picked up by the divers as soon as the seiner began setting its net. When pursing was half completed, the structure counterweight was retrieved to prevent its being tangled in the purse line. After the purse rings were up, the dive boat would take the structure aboard, pass over the cork-line, and reset the structure clear of the net.

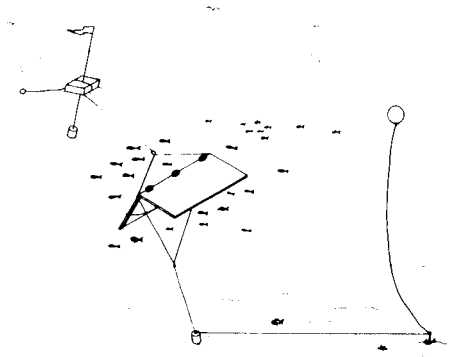

FIGURE 1.—Artificial structure design and mooring arrangement.

The captain of the *Gulf Ranger* estimated the catch weight after each purse seine set and the biologist aboard sampled each catch to provide

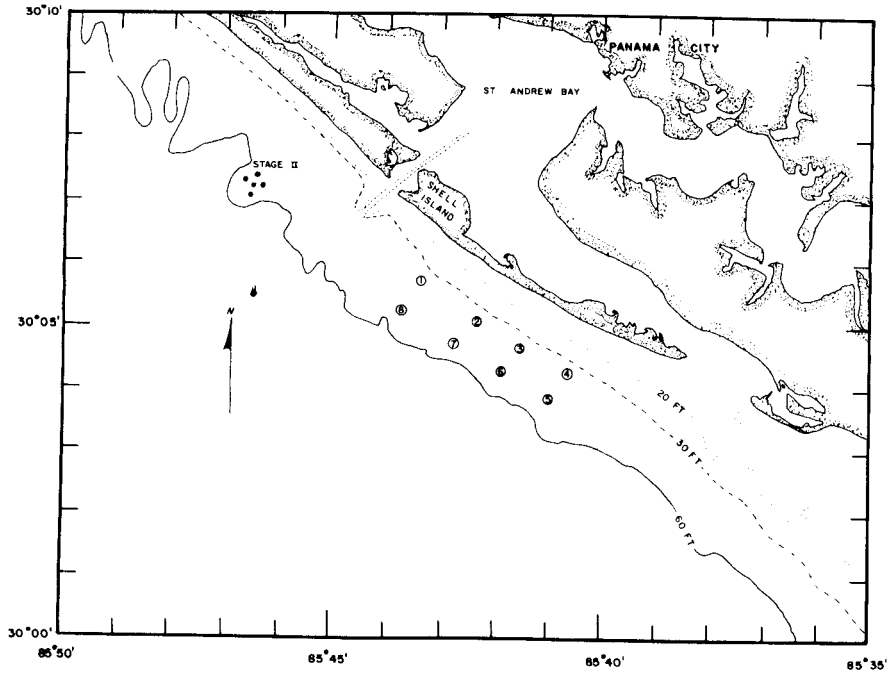

FIGURE 2.—Map of experimental site with numbered circles illustrating positions where artificial structures were deployed. Stage II is a Navy research platform west of the study area.

TABLE 1.—Diver estimates and purse seine catches.

Structure position		1		2		3		4		5		6		7		8	
Structure type		Large white		Small white		Large white		Small white		Large white		Small white		Large white		Small white	
Date 1970	Sample type	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)
July																	
12	Diver 1	1330	227	1415	22	1531	681	1557	227	1635	136	1702	136	1726	454	Lost-No observations	
	Diver 2		272		68		681		136		318		227		454		
	Average		250		45		681		181		227		181		454	—	—
13	Diver 1	1010	136	1034	454	1110	136	1133	136	1200	454	1235	136	1300	454	—	—
	Diver 2		227		227		136		136		272		90		227		—
	Average		181		340		136		136		363		113		340		—
14	Diver 2	1037	136	1100	227	1125	227	1215	227	1150	227	1241	136	1309	227	—	—
	Diver 3		227		136		136		227		90		363		227		—
	Average		181		181		181		227		159		250		227		—
15	Diver 2	1045	227	1130	454	1215	681	1240	454	1305	681	1345	454		Lost-No observations		
	Diver 3		227		454		909		454		909		454		—	—	—
	Average		227		454		795		454		795		454		—		—
16	Diver 1	0945	681	1015	318	1045	454	1110	454	1137	681	1207	90	—	—	—	—
	Diver 3		454		454		909		318		909		90		—		—
	Average		568		386		681		386		795		90		—		—
17	Diver 1	1202	227	1227	227	1255	136	1316	90	1356	136	1418	136	—	—	—	—
	Diver 2		227		454		227		136		136		136		—		—
	Average		227		340		181		113		136		136		—		—
18	Diver 1	0947	136	1013	227	1045	318	1105	136	1130	45	1200	136	—	—	—	—
	Diver 2		227		227		227		136		45		454		—		—
	Average		181		227		272		136		45		295		—		—
20	Diver 2	0945	136	1300	45	1010	136	1245	227	1150	136	1135	136	1315	909	1045	136
	Diver 3		90		681		136		181		90		227		909		136
	Average		113		363		136		204		113		181		909		136
	Purse seine	0945	90	1600	90	—	—	—	—	—	—	—	—	1403	1,363	1105	45
August																	
17	Diver 1	0953	454	1533	45	1031	68	1100	454	1325	1,136	1346	90	1406	454	1121	454
	Diver 3		227		136		136		454		909		90		227		454
	Average		340		90		102		454		1,022		90		340		454
	Purse seine	1100	363	1730	363	—	—	—	—	—	—	—	—	1630	681	1400	818
18	Diver 2	0940	45	1320	454	1255	454	1020	909	1130	454	1200	454	1220	363	1050	227
	Diver 3		22		454		454		2,272		454		2,272		454		90
	Average		34		454		454		1,590		454		1,363		409		159
	Purse seine	1000	90	1350	318	—	—	—	—	—	—	—	—	1230	454	1105	227
19	Diver 2	0915	90	1250	45	1415	454	1650	909	1600	227	1505	272	1140	363	1050	227
	Diver 3		136		227		454		909		227		227		227		136
	Average		113		136		454		909		227		250		295		181
	Purse seine	0830	68	1400	454	1500	454	1715	909	1620	454	1540	272	1245	681	1130	545
20	Diver 1	1225	136	1515	454	1715	454	1700	681	1630	681	1610	681	1430	363	1335	136
	Diver 2		227		454		454		454		1,136		909		454		227
	Average		181		454		454		568		909		795		409		181
	Purse seine	1300	409	1550	363	2145	45	2040	45	2305	9	2230	45	1445	454	1350	272
21	Diver 2	1240	36	1425	227	—	No observation	1700	454	1635	1,363	1620	454	1555	363	1340	227
	Diver 3		22		318		—		681		1,136		681		363		90
	Average		34		272		—		568		1,250		568		363		159
	Purse seine	1300	90	1500	45	—	—	2030	45	2115	9	2220	11	1600	454	1355	363
22	Diver 1	1243	136	1347	227	1406	454	1425	227	1505	681	1443	454	1326	227	1306	363
	Diver 3		136		454		363		227		1,363		909		363		318
	Average		136		340		409		227		1,022		681		295		340

TABLE 1.—Diver estimates and purse seine catches.—Continued.

Structure position		1-4		1-4		1-4		1-4		5		6		7	
Structure type		Small white		Small blue		Small green		Small yellow		Large white		Large white		Large white	
Date 1970	Sample type	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)	Sample time	Weight (kg)
August															
24	Diver 2	1300	136	1335	227	1430	272	1535	454	—	—	—	—	—	—
	Diver 3		136		363		227		454		—		—		—
	Average		136		295		250		454		—		—		—
	Purse seine	1305	113	1400	454	1505	272	1615	318	—	—	—	—		
25	Diver 2	1500	454	1245	227	1625	454	1430	136	1725	818	1705	681	1600	909
	Diver 3		454		22		363		227		909		909		909
	Average		454		125		409		181		863		795		909
	Purse seine	1530	363	1245	113	1630	363	1430	272	1730	272	2200	13	2245	[1]454
26	Diver 1	1212	909	1455	909	1132	318	1330	136	1600	681	1437	1,363	1538	227
	Diver 3		909		909		454		227		909		1,363		909
	Average		909		909		386		181		795		1,363		568
	Purse seine	1255	409	1515	68	1145	113	1405	113	1610	363	—	—	—	—
27	Diver 1	1440	454	1345	227	1245	454	1140	454	1540	454	1420	454	1530	1,363
	Diver 2		1,363		454		454		909		909		454		909
	Average		909		340		454		681		681		454		1,136
	Purse seine	1500	90	1400	272	1300	113	1200	227	1600	181	1700	[2]1,363	—	—

[1] Set around nightlight.
[2] 1,136 kilograms little tunny.

data on species composition. It was not practical to totally weigh each catch as it came aboard or to keep the fish from individual sets separated for later weighing; consequently the captain's catch weight estimates had to serve as our quantitative standard. The accuracy of the captain's estimates was established by comparing the daily total of his estimates with the daily fish house landing records for the *Gulf Ranger* (Table 2). We believed the accuracy of these estimates ($r^2 = 0.97$) justified our utilizing them for evaluating diver estimates and for quantifying experimental data (Figure 3).

RESULTS

Diver Estimates

The validity of scuba-diver observations was evaluated by comparing the divers' estimates of the total number and species composition of fish present at a structure with data obtained from the purse seine catch at that structure. Numerical estimates obtained by the divers for coastal pelagic school fish were converted to weight, utilizing a catch average of approximately 22 fish per kilogram to permit comparison with purse seine catch data.

The comparison of diver estimates with the captain's estimates for the corresponding purse seine catches are plotted in Figure 4 for data collected 17-21 August 1970 (Table 1). Data from 24 August to 27 August were not included in this comparison because schools of little tunny (*Euthynnus alletteratus*) began following the purse seiner and were occasionally observed attacking and scattering the structure-attracted fish schools before the purse seine set was completed. A linear regression analysis of the mean for each set of paired diver estimates ($Y = 76.5 + 0.56X$; $r^2 = 0.68$) indicates that although considerable variation does exist, fish schools less than 182 kg (400 lb) tend to be slightly overestimated while the larger schools are increasingly underestimated. A linear regression analysis was also calculated for each diver's individual estimates and these calculations indicated that estimates made by diver 2 tend to be more accurate than the more conservative estimates made by divers 1 and 3.

The purse seine catch sample data indicated scuba divers were able to identify the major

TABLE 2.—Diver estimates, purse seiner captain's estimates, and fish house landing totals for daily catches from artificial structures.

Date 1970	No. daytime sets	Total average diver estimates for structures sampled	Total purse seiner captain's daily catch estimates	Fish house landings	Fish house landings by species	
					Round scad	Spanish sardine
		kilograms				
August						
17	4	1,227	2,227	2,193	830	1,363
18	4	1,057	1,091	909	614	295
19	8	2,568	3,841	4,045	1,830	2,215
20	4	1,227	1,500	1,545	727	818
21	4	830	955	852	432	420
Total	24	6,909	9,614	9,544	4,433	5,111
[1]21	4	1,136	1,159	1,034	761	273
[1]25	5	2,034	1,386	1,682	716	966
[1]26	5	3,182	1,068	693	443	250
[1]27	6	3,523	1,114	1,194	489	705
Total	20	9,875	4,727	4,603	2,409	2,194
9-day total	44	16,784	14,341	14,147	6,842	7,305

[1] Data not used for scuba-diver estimates-purse seiner catch comparisons.

species attracted to the structures. They were not, however, able to determine accurately the percent species composition for the schools of mixed coastal pelagic fishes. These mixed schools contributed over 95% of the catch weight taken from each structure. The mixed coastal pelagic school fish consisted of round scad (*Decapterus punctatus*) and Spanish sardine (*Sardinella anchovia*). The bait fish occurred at each structure in mixed schools of varying percent species composition. The difficulty encountered by the divers in obtaining accurate percent species composition data for this group was probably the result of behavioral differences between the species. Round scad usually approached closer to the divers than Spanish sardine, which tended to concentrate on the side of the school farthest away from the divers.

Jacks usually represented less than 5% of the total catch weight and consisted primarily of small 15-cm (6-inch) blue runner (*Caranx crysos*), crevalle jack (*C. hippos*), and bar jack (*C. ruber*). Among the species which comprised the major components of Klima and Wickham's (1971) jack group, amberjack (*Seriola* sp.) were only occasionally observed and rainbow runner (*Elagatis bipinnulata*) were notable by their absence in this series of experiments. The jacks are not treated separately in our paper because of their minor contribution to the total number and weight of the structure-attracted fish aggregations.

Comparison of diver estimates and purse seine catch data indicates that although purse seine data are quantitatively superior both sampling techniques are complementary and, combined, provide a more complete picture of the experimental environment than either singularly. Where diver estimates provided the only available data they are considered sufficient to permit rough evaluation of the experimental results in terms of their commercial significance.

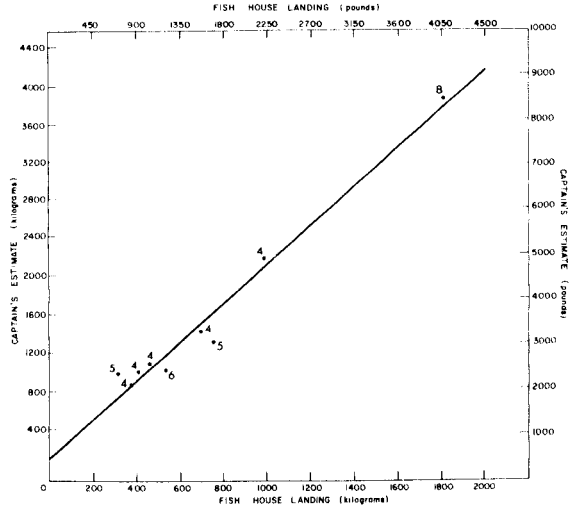

FIGURE 3.—Relationship between the daily total of the *Gulf Ranger* captain's estimates of structure-purse seine catches and the daily fish house landing records. Statistical evaluation of this data by linear regression analysis yields $Y = 216.4 + 0.876X$; $r^2 = 0.97$. N = number of set estimates in each daily total.

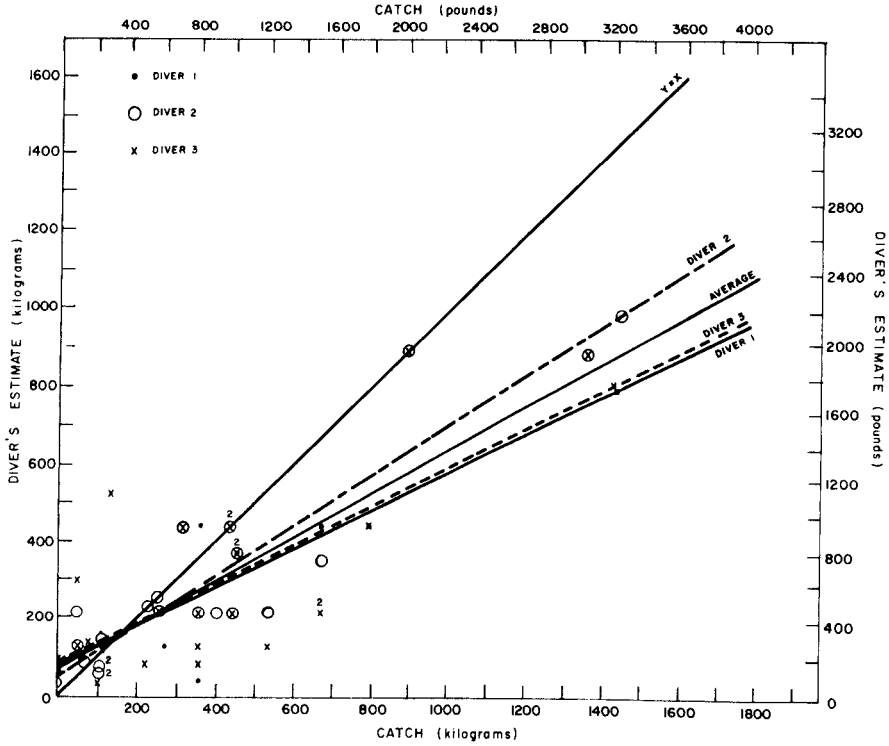

FIGURE 4.—Relationship between divers' estimates of bait fish school size and the captain's estimate of the purse seine catch at each structure. A linear regression analysis of the average paired diver estimates yields $Y = 76.5 + 0.56X$; $R^2 = 0.684$. A linear regression analysis of the estimates made by each diver yields $Y = 77.6 + 0.504X$; $r^2 = 0.285$ for diver one; $Y = 55.3 + 0.683X$; $r^2 = 0.704$ for diver two; and $Y = 98.4 + 0.501X$; $r^2 = 0.42$ for diver three.

Recruitment Patterns and Production

Our observations indicate a rapid recruitment with fish being observed at structures the day following placement. To obtain estimates of production and recruitment of bait fish to the structures, we made daily diver estimates and purse seine collections at four selected structures. Four other structures, also observed daily by divers, were set on after being in position for 3 days. During this period (17-21 August 1970), our structures produced an average of 398 kg (875 lb) per set. These catch rates are not extremely large, but they were made when bait fish were not seasonally available to the local beach seine fishery. No bait was being landed, except for fish captured around our structures. The total daily diver estimates and purse seine collections are plotted in Figure 5, along with the 3-day accumulative totals, to allow comparison of production between the four structures fished daily and the four structures set on once, following the 3-day soak period. Our day 3 catch results indicate no significant advantage in catch size was realized by allowing the structures to soak for 3 days. The potential total catch, assuming daily sets had been made on the 3-day soak structures, indicated from our consistently conservative diver estimates was three times larger than the actual catch after 3 days' soaking. The total accumulative catch from the four structures set on daily was also approximately three times larger than the actual catch from the four 3-day soak structures even though diver estimates indicated smaller total fish concentrations were present at the structures set on daily. These results show that a greater total production was obtained by making daily sets. This high rate of daily attraction and the apparent lack of fish accumulation provided further indications

that fish were being attracted to the structures on a daily basis.

Comparison of Day and Night Collections

A series of day and night sets were conducted to determine whether fish leave the structures at night. Divers estimated the quantities of fish at four selected structures which were then set on during daylight hours. The quantity of fish at four other structures was estimated by divers just before dark and fish around these structures were collected after dark. Diver estimates, and day and night catch results, are plotted in Figure 6. The diver estimates were conservative for structures set on during the day, with estimates for both days being less than the actual catch for three of the four structures. The divers frequently estimated that concentrations of fish present at the structures fished at night were larger than at the structures fished in the daylight. Nighttime collections however, consistently produced only 45.5 kg (100 lb) or less of mixed species. These results provided further evidence that bait fish leave the structures at night and that new recruitment was occurring daily. The nighttime sets were made during the new moon and we lack data on whether bait fish also leave the structures at night during the full moon.

Size and Color Evaluation

The success of bait fish attraction with artificial structures appeared to be dependent upon the visibility of the structure. We evaluated two sizes of structures to determine whether doubling the structure size would increase the number of fish attracted. An analysis of variance for purse seine capture data ($F = 0.75 < F_{0.90(1,5)} = 4.06$) and diver estimates revealed no significant difference in attraction by structure size.

Structure attraction was also evaluated in terms of color visibility. We compared a white structure with ones painted fluorescent green, blue, and yellow since Kinney (1970) reported that fluorescent paints provide greater visibility under water. Structure position was rotated daily so that a structure of each color occupied each of the four positions. An analysis of variance for catch data ($F = 0.026 < F_{0.90(3,9)} = 2.8$) and diver estimates revealed no significant

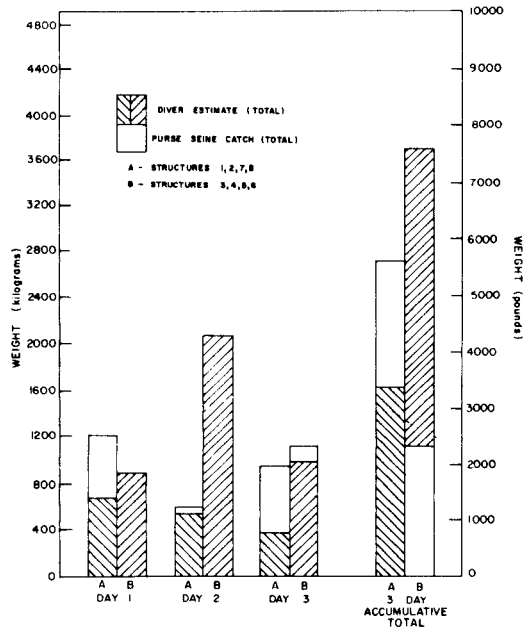

FIGURE 5.—Total of daily average diver estimates and purse seine catch weights, 17-19 August 1970. (A) Structures estimated by divers and fished daily by purse seine. (B) Structures estimated daily by divers but fished by purse seine only on day three.

difference in the number of fish attracted to the structures on the basis of color. During these color evaluation studies, the bait fish schools were occasionally scattered by little tunny. These predator attacks may have affected the catch data; however our diver estimates were not affected and also indicate no significant color preference.

Divers reported the experimental changes in size and color extended the visible range of a single structure less than 2.1 m (6 ft) which apparently was not sufficient to significantly improve the structures' attraction capabilities.

Structure placement (Figure 3) in relation to the distance offshore (water depth) or to the along-shore current direction tended to have some effect on the number of fish attracted, with larger numbers of fish being attracted to structures positioned offshore than to those positioned inshore. Structures positioned on the eastern end of the experimental area also tended to attract more fish than those on the western end. These general patterns probably vary with seasonal changes in water temperature and prevailing current direction. Our experiment was

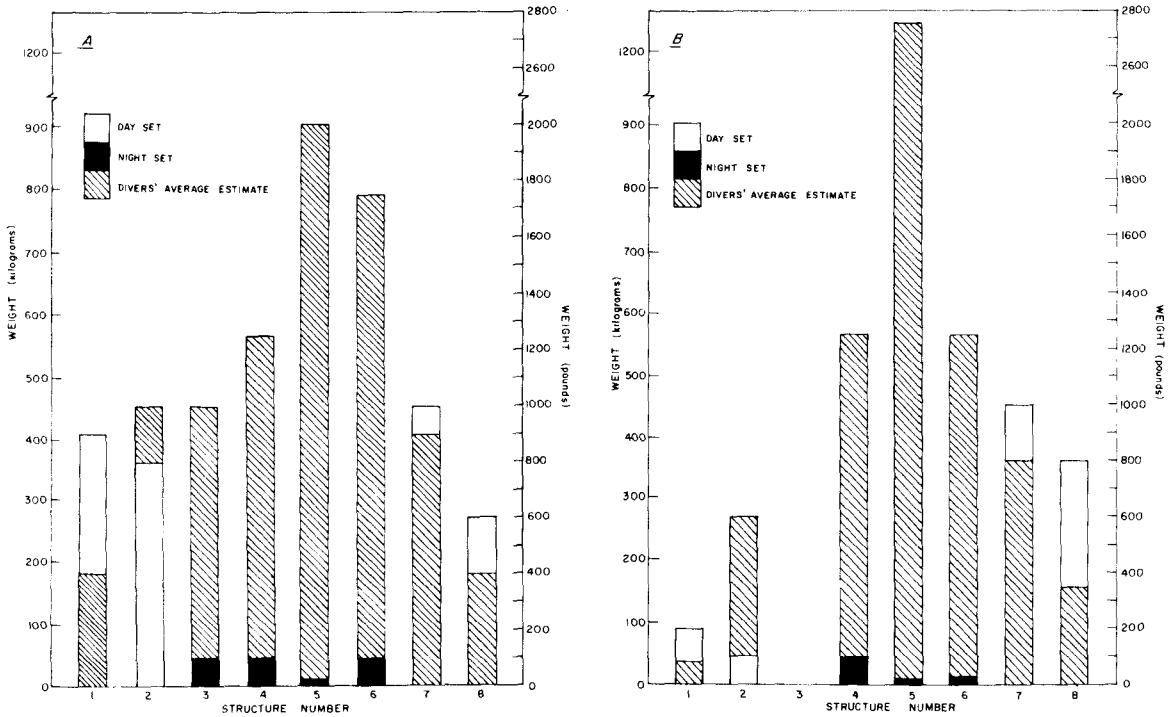

FIGURE 6.—Average diver estimates and day and night purse seine catch weights for each structure on (A) August 20, and (B) August 21, 1970. No diver observations or purse seine sets were made at structure three on August 21 due to an afternoon squall.

not designed to evaluate the effects of structure placement on fish attraction and further studies would be necessary to meaningfully evaluate these effects.

Responses to Moving Structures

A bait fish school was observed by Klima and Wickham (1971) to have remained with a free drifting artificial structure moving slower than the current. One of our structures (Structure No. 8, 19 August 1970), with a school of bait fish in attendance, was also observed dragging its anchor and moving slowly with the current. This structure was towed for 20 min at a speed of approximately 2 knots against a 0.5 knot current for a distance of approximately 0.8 km (0.5 mile) in order to return it to its experimental mooring location. The structure moved up to the surface while being towed, but the fish swam along with it, trailing out behind when the towing speed was increased. After the structure was reanchored in position, the fish school began swimming around it in the usual manner. Divers estimated that over half the original number of fish remained around the structure after towing. A purse seine set made on this structure after repositioning produced 545 kg (1,200 lb) of fish.

Behavior Observations at Structures

Our observation of bait-fish-school behavior at the structures is in general accordance with the behavior described by Klima and Wickham (1971). The bait-fish schools normally maintained a position up-current from the structures and were observed continuously feeding on crab larvae and other particulate material in the water. During very slow or zero current conditions, the bait fish would often mill about in a loose aggregation (Figure 7) or form long streaming schools making large looping passes out and around the structures in all directions. The schools would frequently swim beyond the divers' range of visibility, remaining out of sight for periods up to 3 min or longer before streaming back in and around the structures from a different direction.

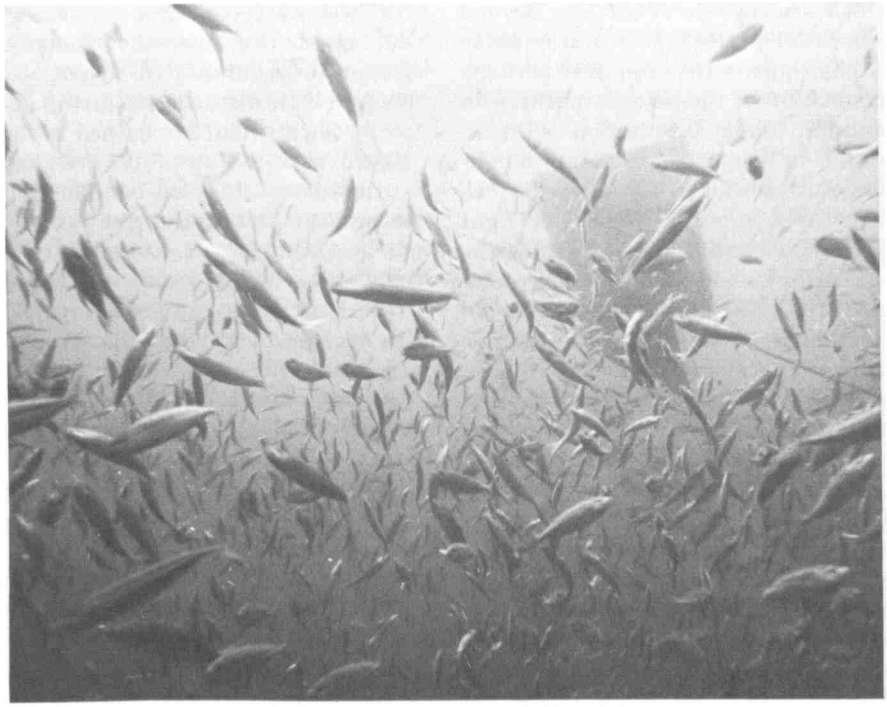

FIGURE 7.—Underwater photograph of a mixed school of round scad *(Decapterus punctatus)* and Spanish sardine *(Sardinella anchovia)* swimming past an artificial structure.

A different pattern of behavior was observed by the divers when the bait-fish schools were threatened by the presence of feeding predators, i.e., Spanish mackerel (*Scomberomorus maculatus*), king mackerel (*S. cavalla*), little tunny (*E. alletteratus*), and bluefish (*Pomatomus saltatrix*). On these occasions, relatively small bait-fish schools, i.e., 100 kg (220 lb) or less, would form a milling ring with the structure in the center or swirl in a tight group in quick passes close to the structure as the predators made darting attacks on the school. Larger schools would usually be split by the attacking predators with one group of bait fish moving to the structure and circling it as described above while the remaining fish moved off in tight, fast-darting groups.

Behavioral Mechanisms

Different sizes and species of fish apparently associate with objects in the sea for different reasons involving different behavioral mechanisms. Hypotheses advanced to explain the association of fishes with floating objects were reviewed by Gooding and Magnuson (1967). The initial attraction of pelagic fishes to objects probably results from their visually detecting the object in the optical void of the pelagic environment, since fish beyond the visual range of a structure or structure-attracted fish school are not attracted (Hunter and Mitchell, 1967). Significantly improving the visual characteristics of an object apparently increases the rate and number of fish it attracts (Hunter and Mitchell, 1967; Klima and Wickham, 1971). Objects, however, must serve a meaningful function beyond that involved in the initial visual attraction in order for pelagic fish to remain in association with them. To tentatively explain this behavior in mixed schools of round scad *(D. punctatus)* and Spanish sardine *(S. anchovia)* around artificial structures, Klima and Wickham (1971) proposed the hypothesis: "Floating objects and underwater structures provide spatial references around which fish can orient in the otherwise unstructured pelagic environment." This tentative hypothesis was given some support by our study, but it must be modified and expanded to account for our additional behavioral observations. Our studies indicate that although coastal

pelagic bait fish are capable of ranging beyond sight of an object for periods of several minutes or longer, they apparently require periodic visual reconfirmation of the object's position in order to maintain their orientation with it. This assumption is supported by our observations that structure-attracted fish aggregations leave the structures at night when low light levels inhibit visual contact. Our observations of coastal pelagic bait-fish behavior around artificial structures also indicate that the structures can apparently be useful to these species for predator avoidance. Schools of bait fish associated with an artificial structure have been observed to be immediately attacked by predators upon removal of the structure from the water. Bait-fish schools threatened by the presence of feeding predators were observed to form a tight ball or ring around the structure or swirl in tightly packed formation making quick darting passes near the structure. On several occasions, we have observed the attack behavior of a predator to be interrupted at the moment the bait fish darted past the structure. Mitchell and Hunter (1970) describe laboratory experiments in which splitnose rockfish *(Sebastes diploproa)* and opaleye *(Girella nigricans)* were pursued more often, for longer periods, and captured more frequently by ocean whitefish *(Caulolatilus princeps)* in an aquarium when kelp was absent than when it was present.

Our present supposition as to the possible mechanisms involved in the association of some species of coastal pelagic schooling fish with objects in the sea are summarized in the following working hypothesis: "Objects in the sea provide visual stimuli which attract certain species of pelagic schooling fish and are used in conjunction with natural optomotor responses to provide a spatial reference for orientation in the otherwise relatively unstructured pelagic environment; however, in the presence of feeding predators stimulus priorities are restructured such that the objects become useful for predator avoidance." An increasing body of subjective evidence is available to support much of this conjecture, but its verification lacks the requisite quantitative experimental evidence.

Purse Seine Operations

The feasibility of harvesting structure-attracted coastal pelagic bait fish with conventional tom-weight type purse seines was evaluated during our development of the quantitative collection procedures. Fish aggregations normally showed little disturbance during purse seine sets while the structure remained in the water. Fish stayed with the structure even when it floated at the surface after the counterweight was lifted to prevent its tangling the purse line. The fish showed distress and attempted to escape the net only when the structure was removed from the water and the diving boat prepared to pass over the corkline and reset the structure. The only deviation from this pattern was observed when bait fish were attacked by predators, i.e., little tunny *(E. alletteratus)*, which on several occasions were following the seiner. On these occasions, the predators scattered the bait fish during the set and then escaped before the net was completely closed.

During our experimental collections, we utilized an additional small boat and several men to handle the structures during the purse seine operations. Sets have been made, however, using only the seine skiff and its operator to retrieve and reset the structures. These trials indicate that in a commercial fishing operation using artificial structures, fishing procedures can be modified so that additional men and equipment should not be required. The applicability of structure-attraction techniques for augmenting purse seining during commercial fishing operations, although technically feasible, remains dependent upon the production potential of structures and their recruitment characteristics in the geographical area under consideration.

SUMMARY AND CONCLUSIONS

An evaluation of our diver estimates and purse seine catch data indicates that a combination of these techniques provides a more complete description of the artificial structure experimental environment than either singularly. Our comparative results support the contention by Klima and Wickham (1971) that quantitative diver estimates tend to be conservative where large fish schools are involved. Our divers were able to qualitatively determine the major species present at a structure, but were unable to reliably establish the percent species composition in mixed species schools.

The quantity of fish attracted to the structures during our study was not as large as the schools reported by Klima and Wickham (1971). Coastal pelagic school fish, however, were seasonally unavailable to the local fishery during the study period and the fish captured around our structures were the only bait fish being landed.

The rapid rate of recruitment during our study was similar to the pattern of recruitment reported by Klima and Wickham (1971) with fish being observed at the structures the day following placement. Our experimental results indicated that the fish were recruited to the structures daily and no significant accumulation in the fish population was observed when the structures were allowed to soak for 3 days. Consequently, a greater total production was obtained from the structures by making daily sets. Comparative day and night sets provided further evidence that fish schools dispersed from structures at night during the new moon and new fish were being recruited each day.

We were unable to significantly improve the rate or number of fish attracted to a structure either by doubling its size in relation to our standard structure, or by painting it with fluorescent colors. The experimental changes in size and color apparently did not extend the visible range of a structure sufficiently to significantly increase the number of fish attracted. Further study is required to determine whether multiple structure units might be successful as a means for significantly improving the effective range of structure attraction.

The feasibility of harvesting structure-attracted coastal pelagic bait-fish schools with conventional tom-weight purse seines was established by the success of our quantitative collection procedures. The incidence of successful purse seine sets was greatly improved using the artificial structure techniques since the coastal pelagic fish schools remained in association with the structures during the sets and made no attempt to escape.

Our experience during this study indicates that artificial-structure fish attraction techniques can be developed to facilitate the harvest of the latent coastal pelagic resources in the Gulf of Mexico. Artificial-structure fish attraction techniques may also have sport fishing applications, potential for development as a method for providing ground truth for fishery survey remote sensor evaluation and as a method for monitoring fish movements and relative changes in abundance in certain geographical areas. These potential applications for artificial-structure fish attraction techniques will be the subject of future investigations.

ACKNOWLEDGMENTS

We would like to thank John W. Watson, Jr. for his contributions during all phases of the field work, especially for his assistance as a diver. Charles Roithmayr and Wayne Adkison provided valuable assistance by obtaining purse-seine catch samples and recording data aboard the chartered purse seiner *Gulf Ranger*.

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THE AGE COMPOSITION OF STRIPED BASS CATCHES IN VIRGINIA RIVERS, 1967-1971, AND A DESCRIPTION OF THE FISHERY[1]

GEORGE C. GRANT[2]

ABSTRACT

The age composition of Virginia catches of the striped bass, *Morone saxatilis*, is being monitored as one of the parameters important in rational management of the species. Catches of pound nets and fyke nets, relatively nonselective gear types used in estimates of age structure, were sampled semimonthly in three Virginia rivers from July 1967 through June 1971.

Seasonal changes in age composition are slight with older, migratory striped bass occurring more frequently in winter and spring catches. Young fish are not caught by these nets in significant numbers until the spring following the year of their hatch. An age group that is dominant in summer usually continues its dominance through the spring of the following year.

Differences in age composition of striped bass catches among rivers and years occur as a result of variable year class strength. Although one-year-olds normally dominate catches, two-year-olds may predominate either through local failure of a year class or by continued dominance of a relatively strong year class.

A brief description of the striped bass fishery in Virginia is included.

Closer management of anadromous fish stocks may become necessary as a protective response to increasing human populations along the Atlantic coast of the United States. Because of their reproductive migrations into river systems, these anadromous fishes may be most directly affected by the expanding megalopolis of the east coast and the increased pollution of coastal waters.

One valuable anadromous species is the striped bass, *Morone saxatilis* (Walbaum). Although the biology and habits of striped bass are fairly well studied (Raney, 1952), effective management of the stocks has been hampered by the absence of data on population parameters such as age composition and mortality.

An investigation of striped bass in Virginia[3] was initiated in 1967 after a review of results from the Chesapeake Bay Cooperative Striped Bass Program (Lewis, 1961; Mansueti, 1961; Massmann and Pacheco, 1961) and follows the suggestions of Sykes (1961) for further research on striped bass. This paper considers the age composition of striped bass catches in Virginia and briefly describes the fishery.

DESCRIPTION OF THE FISHERY

The coastal Virginia fishery for striped bass is scattered and diverse. It includes trawlers, pound nets, fyke nets, haul seines, gill nets and sport fishing gear.

In the commercial fishery, pound nets are fished at permanent locations and are most consistently in use. They are lifted only during brief periods for cleaning, to prevent possible ice damage, or because of nuisance factors such as abundant jellyfish. Fyke nets, hung and fished much like small pound nets in Virginia waters, are usually located farther upriver than the pound nets. Catches are relatively small and the gear is employed more sporadically than pound nets. Trawlers are limited to offshore fishing by law. Therefore striped bass are available to this gear only in winter months, when they are migrating along the coast. Striped bass availability to trawlers increases during severe winters when the river populations migrate to the warmer coastal waters (Grant et al., 1970). Gill net mesh size and manner of fishing vary with the season in the striped bass fishery. Small mesh "spot and perch nets"

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[2] Virginia Institute of Marine Science, Gloucester Pt., VA 23062.

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(2⅞ - 3½" stretch mesh) are anchored in the summer and staked from late fall to winter. Large mesh "shad nets" (5½" stretch mesh) are staked or drifted in late winter and spring. Haul seines are used sporadically throughout the warmer months, but most effectively in the spring.

Sport fishing for striped bass is intensive in the lower Chesapeake Bay, especially along the Chesapeake Bay Bridge-Tunnel in spring and fall. The sport fishery extends from the mouth of the Bay to the freshwater regions of major river systems from March through December. Attraction of small striped bass to the numerous lighted piers extends sport fishing well beyond daylight hours.

Commercial landings of striped bass in Virginia[4] for the 40-yr period 1930-1969 show a ninefold increase from a low of 0.3 million pounds in 1934 to 2.8 million pounds in 1966 (Figure 1). The overall trend in landings (and striped bass populations) has been rising during this period. Two definite peaks of abundance are evident, one in the late 1940's and the other in the 1960's. Not included in these landings are sport catches, which have increased to as much as 50 percent of the total catch in certain areas (Grant, unpublished data). Averaged commercial landings in the most recent years have declined; continuation or reversal of this decline depends on contributions to subsequent catches by successful year classes such as those of 1966 and 1970 (Grant and Joseph, 1969; Grant, Burrell, and Kriete, 1971).

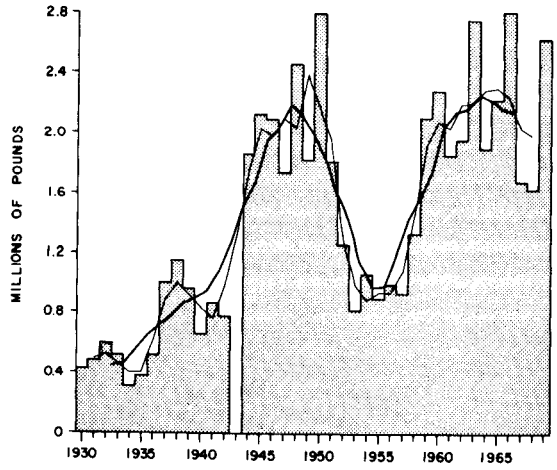

FIGURE 1.—Annual landings of striped bass in Virginia, 1930-69. Moving averages (indicated by heavy line for 6-yr average and light line for 3-yr average) incorporate an interpolated value of 1,321,000 pounds for 1943.

AGE COMPOSITION

Methods and Materials

Pound nets and fyke nets trap striped bass over their entire size range, except for the young-of-the-year which are incompletely recruited to the gear. These two gear types were, therefore, considered to be essentially nonselective (allowing for escapement of Age 0 fish) and were sampled for estimates of the age composition of striped bass stocks residing in the James, York, and Rappahannock rivers. Although differences in the age composition of catches by pound and fyke nets did occur, no consistency was evident in these differences, so catches were pooled for analysis. Rappahannock River samples were taken from pound nets only.

The scale method was used for age determinations. Scales were first used in age analysis of striped bass populations by Scofield (1931); this method was fully developed and validated for striped bass by Merriman (1941). Samples of approximately 50 striped bass were obtained from each river system semimonthly. Scales were removed from individual fish at the site specified by Merriman (1941). Cellulose acetate impressions of scale sculpturing were prepared using five or six scales from each fish. Annuli were counted at a magnification of 15× with all scales being read at least twice and instances of disagreement re-examined.

Annuli on the scales of Virginia striped bass form between April and June, coincident with the spawning season and hatch of a new year class. The growth year of local populations, therefore, may be considered to extend from July to June. Young-of-the-year do not become Age I fish until late spring of the year following their hatch. In this paper, July 1 is designated as the start of each year so that a member of the 1966 year class caught between 1 July 1967 and 30 June 1968 would be called Age I. Seasonal designations are used as follows: winter (Jan.-Mar.), spring (Apr.-June), summer (July-Sept.), fall (Oct.-Dec.); these quarterly periods

[4] Data from Koo (1970) and from annual summaries of regional fisheries statistics published by the Bureau of Commercial Fisheries.

were chosen on the basis of water temperatures and are more meaningful in the present context than terrestrial seasons.

Seasonal Age Composition

James River

Catches in the James River (Table 1) typify the seasonal pattern observed in all three rivers. The age group that dominated July-September catches generally continued to dominate through the following June, i.e., for a complete sampling year that began in July.

Striped bass older than Age III were present throughout the 1967-1968 sampling year and were most abundant in spring. In other years, these mature fish appeared in April; some remained in the river through summer, but none were taken during the fall and winter. Young-of-the-year were generally absent from catches, except for the appearance of the 1969 year class in spring months of 1970.

York River

The general pattern of dominance observed in the James River was repeated in the York (Table 2). An exception occurred in winter months of 1970, when icing of the river severely reduced catches and the small sample consisted mostly of older fish. A more notable exception was the dominance of young-of-the-year striped bass in spring months of 1971.

Mature striped bass older than Age III rarely appeared during warmer months in the York River. Seventy-eight percent of these older individuals were taken in winter and spring months, 7.5% in the summer quarter.

Rappahannock River

Only one seasonal shift in age group dominance occurred in Rappahannock River catches of striped bass during the four-year sampling period. Older fish dominated in winter months of 1970 (Table 3), as observed in the York River.

TABLE 1.—Age composition of striped bass caught by nonselective fishing gear in the James River within quarterly periods, July 1967-June 1971.

	Number in Age Group								
Quarterly Period	0	I	II	III	IV	V	VI	≥VII	*N*
(1967) July-Sept	—	—	35	24	1	1	1	1	63
Oct-Dec	1	19	122	10	2	—	3	—	157
(1968) Jan-Mar	—	9	8	4	—	1	—	4	26
Apr-June	—	22	39	34	8	2	8	26	139
% Subtotal	0.3	13.0	53.0	18.7	2.9	1.0	3.1	8.1	
July-Sept	—	70	189	94	27	4	1	3	388
Oct-Dec	—	97	89	13	—	—	—	—	199
(1969) Jan-Mar	(no samples)								0
Apr-June	—	154	108	16	19	10	8	12	327
% Subtotal	0	35.1	42.2	13.5	5.0	1.5	1.0	1.6	
July-Sept	—	31	235	58	3	4	—	3	334
Oct-Dec	—	8	85	13	—	—	—	—	106
(1970) Jan-Mar	—	1	3	2					6
Apr-June	19	33	81	29	10	3	2	14	191
% Subtotal	3.0	11.5	63.4	16.0	2.0	1.1	0.3	2.2	
July-Sept	1	98	57	64	12	1	1	1	235
Oct-Dec	—	33	8	6	—	—	—	—	47
(1971) Jan-Mar	(no samples)								0
Apr-June	(no samples)								0
% Subtotal	0.4	46.5	23.0	24.8	4.3	0.4	0.4	0.4	
							Total Number Aged		2,218

TABLE 2.—Age composition of striped bass caught by nonselective fishing gear in the York River within quarterly periods, July 1967-June 1971.

Quarterly Period	Number in Age Goup								
	0	I	II	III	IV	V	VI	≥VII	N
(1967) July-Sept	—	317	22	4	—	—	—	—	343
Oct-Dec	—	112	20	1	—	—	—	—	133
(1968) Jan-Mar	—	16	13	11	—	—	—	—	40
Apr-June	2	119	21	2	—	—	—	2	146
% Subtotal	0.3	85.2	11.5	2.7	0	0	0	0.3	
July-Sept	—	84	126	5	—	1	—	2	218
Oct-Dec	1	274	210	27	4	—	—	—	516
(1969) Jan-Mar	1	178	151	40	14	4	1	1	390
Apr-June	11	191	75	15	3	3	1	6	305
% Subtotal	0.9	50.9	39.3	6.1	1.5	0.6	0.1	0.6	
July-Sept	—	221	149	13	2	2	—	—	387
Oct-Dec	8	225	200	47	11	2	1	3	497
(1970) Jan-Mar	—	1	4	6	1	—	—	—	12
Apr-June	41	84	33	10	2	3	2	—	175
% Subtotal	4.6	49.6	36.0	7.1	1.5	0.7	0.3	0.3	
July-Sept	—	223	48	2	—	—	—	—	273
Oct-Dec	13	425	65	16	6	—	—	—	525
(1971) Jan-Mar	13	82	13	8	1	1	—	3	121
Apr-June	145	131	9	12	7	—	2	2	308
%Subtotal	13.9	70.2	11.0	3.1	1.1	0.1	0.2	0.4	
								Total Number Aged	4,389

Seasonal occurrence of striped bass older than Age III was similar to that observed in the York. Eighty-three percent of these individuals were taken in winter and spring months, 11.2% in the summer months.

Young-of-the-year first appeared in fall catches, but significant numbers were not taken until the following spring. This seasonal pattern was similar to observations from the York River.

Differences in Age Composition between Years and Rivers

Differences between both years and rivers in the age structure of Virginia striped bass catches are shown in Figure 2, where age composition data have been combined into sampling year totals within river systems. James River catches were dominated by Age II striped bass in three of the four sampling years, and by Age I fish (1969 year class) in 1970-1971. Rappahannock River catches, on the other hand, were dominated by Age I striped bass in three of the four years, and by Age II fish in 1968-69. Age I fish dominated York River catches in all four years. Except for the continued domination of Rappahannock River catches by the 1966 year class during the 1968-69 sampling year, age composition in the York and Rappahannock rivers was similar.

Among the 1965-1969 year classes which progressed through the fishery as Age I and II fish during the four-year sampling period, the 1966 year class appears to have contributed most heavily to the York and Rappahannock river catches. The 1967 year class was strongest in the James River. Dominance of year classes in the various years and river systems is summarized in Table 4.

TABLE 3.—Age composition of striped bass caught by nonselective fishing gear in the Rappahannock River within quarterly periods, July 1967-June 1971.

Quarterly Period	Number in Age Group								
	0	I	II	III	IV	V	VI	≥VII	N
(1967) July-Sept	—	124	11	2	—	—	—	—	137
Oct-Dec	2	280	48	11	2	—	—	1	344
(1968) Jan-Mar	—	84	25	17	4	6	19	23	178
Apr-June	6	217	12	2	—	1	—	1	239
% Subtotal	0.9	78.5	10.7	3.6	0.7	0.8	2.1	2.8	
July-Sept	—	81	220	1	2	—	—	—	304
Oct-Dec	4	124	256	8	1	—	—	—	393
(1969) Jan-Mar	—	36	139	14	4	1	—	3	197
Apr-June	30	121	146	8	—	1	—	11	317
% Subtotal	2.8	29.9	62.8	2.6	0.6	0.2	0	1.2	
July-Sept	—	156	110	47	3	3	—	—	319
Oct-Dec	—	152	113	32	3	—	—	—	300
(1970) Jan-Mar	—	17	35	40	2	1	—	4	99
Apr-June	28	142	20	44	4	5	1	10	254
% Subtotal	2.9	48.0	28.6	16.8	1.2	0.9	0.1	1.4	
July-Sept	—	123	87	7	10	1	—	—	228
Oct-Dec	8	200	86	4	1	—	1	—	300
(1971) Jan-Mar	3	127	64	16	14	1	4	1	230
Apr-June	86	149	30	7	14	1	1	5	293
% Subtotal	9.2	57.0	25.4	3.2	3.7	0.3	0.6	0.6	
							Total Number Aged		4,132

DISCUSSION

Seasonal and Annual Age Composition of River Catches

Seasonal variation in the age composition of striped bass catches is slight (Tables 1-3) when viewed over a sampling year begun in July. Most of the seasonal variation occurs among subdominant age groups, specifically the appearance of young-of-the-year in the fall and the annual return of older, mature stocks in winter and spring. A year class that is dominant in summer tends to remain dominant through the following spring. Changes in year class dominance from one year to another usually occur in summer, so *age group* dominance tends to remain constant.

Annual differences in age composition, on the other hand, can be striking. Although Age I striped bass are expected to predominate in pound net and fyke net catches, strong year classes may continue to dominate catches a second year as Age II individuals. This occurred in the Rappahannock River as a result of the strong 1966 year class (Figure 2).

The predominance of Age II striped bass catches from the James River during three of the four sampling years differs from the age composition observed in the York and Rappahannock rivers. Partial explanations are available for two of these cases: 1) the 1965 year class dominated 1967-68 catches because of the local failure of the 1966 year class (Grant and Joseph, 1969); 2) the 1966 year class dominated 1968-1969 catches after entering the James from other rivers where it was an unusually successful year class.

The Virginia Fishery and Cycles of Abundance

The appearance of a dominant year class of striped bass in Chesapeake Bay waters is reflected in subsequent catches within the Bay

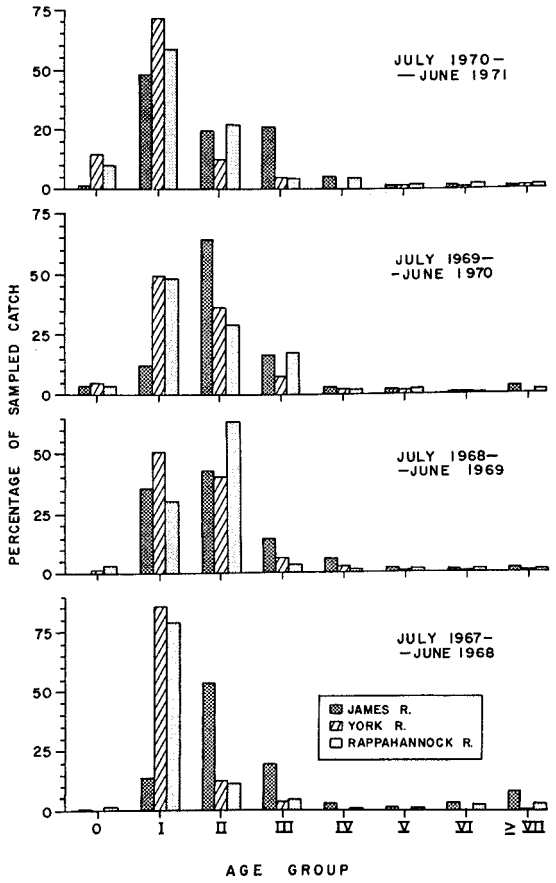

FIGURE 2.—Age composition of sampled pound and fyke net catches in the James, York, and Rappahannock rivers, July 1967-June 1971.

(Tiller, 1950; Vladykov and Wallace, 1952; Murphy, 1960; Shearer, Ritchie, and Frisbie, 1962) and along the migration route in coastal states from Virginia to New England (Merriman, 1941; Schaefer, 1968). Schaefer (1968) concluded that Chesapeake Bay is the primary source of striped bass caught in the surf of Long Island, and that Hudson River stocks may significantly contribute to these populations only when dominant year classes from Chesapeake Bay are unavailable. Yet it is generally believed, although still debatable, that only a small proportion of those striped bass originating in Chesapeake Bay enter the coastal migration (Vladykov and Wallace, 1952; Mansueti, 1961; Massmann and Pacheco, 1961; Grant et al., 1970).

Koo (1970) has shown an apparent six-year

TABLE 4.—Summary of the year classes of striped bass that dominated catches in Virginia rivers, 1967-1971.

River	Sampling Year (July through June)			
	1967-68	1968-69	1969-70	1970-71
James	1965	1966	1967	1969
York	1966	1967	1968	1969
Rappahannock	1966	1966	1968	1969

TABLE 5—Contribution of age groups I-III to pound net and fyke net catches of striped bass in three Virginia rivers, 1967-1971.

Sampling Year (July-June)	Percentage of Sampled Catch in Age Groups I-III		
	James	York	Rappahannock
1967-1968	84.7	99.4	92.8
1968-1969	90.8	96.3	95.3
1969-1970	90.9	92.7	93.4
1970-1971	94.3	84.3	85.6

cycle of abundance in Maryland. Such a cycle could result from the appearance of a dominant year class every six years, followed by three years of high catches (Ages I-III), then three of relatively low catches. The younger age groups (I to III) contribute most to Virginia pound net and fyke net catches of striped bass (Table 5), as expected for nonselective fishing gear. Over 90% of sampled individuals were from age groups I to III, except: 1) 84.7% in the James River during the first year of sampling due to catches of large numbers of older fish, particularly the 1958 year class; 2) 84.3% in the York River in the 1970-1971 sampling year; and 3) 85.6% in the Rappahannock River in the same year. The last two exceptions occurred because of contributions by the latest dominant year class (1970—then Age 0).

Although the age composition of Virginia catches would seem to conform to Koo's (1970) six-year cycle, no such cycle is apparent in Virginia landings (Figure 1), even though the dominant year classes mentioned by Koo (1970) were also successful ones in Virginia. The difference between Maryland and Virginia landings, relative to this six-year cycle, might stem from local successes of year classes interspersed among those appearing at six-year intervals. In addition to the 1958, 1964 and 1970 cyclically dominant year classes, certain Virginia rivers have produced large hatches of striped bass in 1961 and 1966 (Grant and Joseph, 1969; Grant, Burrell, and Kriete, 1971). Catches of these aperiodically strong year clas-

es tend to obscure, or even eliminate, peaks in landings contributed by Koo's Chesapeake-wide dominant year classes. Thus only long-term trends in abundance remain evident (Figure 1).

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LARVAL FISHES OF YAQUINA BAY, OREGON: A NURSERY GROUND FOR MARINE FISHES?

WILLIAM G. PEARCY AND SHARON S. MYERS[1]

ABSTRACT

Based on a survey of planktonic fish larvae, the Yaquina Bay estuary appears important as a spawning or rearing ground only for *Clupea harengus pallasi* (Pacific herring) and a variety of small cottids, gobies, and stichaeids. Other investigators, however, have found an abundance of juvenile *Parophrys vetulus* (English sole), *Citharichthys stigmaeus* (sanddab), *Hypomesus pretiosus* (surf smelt), *Platichthys stellatus* (starry flounder) and embiotocids (surf perches), indicating that the bay is an important nursery area for these species.

Of the 44 types of larval fishes found in the bay, *C. h. pallasi* and *Lepidogobius lepidus* (bay goby) were co-dominants each year, 1960-1970, comprising 90% of all larvae collected. There was no evidence of trends in abundances or species composition during the 11-yr study.

Maxima of planktonic fish eggs and *L. gobius* larvae occurred in the summer; maxima of all larvae combined and most species of larvae occurred in the winter and spring. High densities of larval herring were found in February and March, and peak numbers appeared earlier in the lower than the upper estuary.

Larvae of *C. h. pallasi*, *L. lepidus*, and *Cottus asper* were common at all stations from 0.5 to 8 nautical miles up the estuary, but not in the adjacent open ocean. Larvae of many species that were found in the estuary in small numbers were more abundant in offshore waters. Although English sole and sanddab were rare in the bay as larvae, juveniles were numerous.

This is a study of the species composition, relative abundance, seasonal and annual occurrence and distribution of larval fishes in an Oregon estuary. It was undertaken to increase the extremely limited knowledge of fish larvae in estuaries of the Pacific Northwest and to evaluate the role of these estuaries as spawning and nursery grounds.

According to Clark (1967) and McHugh (1966, 1967) the young of up to 70% of the economically important Atlantic species of fishes inhabit estuaries during part of their early life. Many species spawn offshore and young stages subsequently move into brackish estuaries. Although the Pacific coast is known for its runs of anadromous salmonids which migrate through estuaries, "There is no counterpart on the Pacific coast of the mass inshore movement of larvae and young of offshore-spawning nektonic species into brackish nursery grounds that is such a striking feature of the ecology of most Atlantic coast and Gulf of Mexico estuaries." (McHugh, 1967). Thus the number of species that are dependent on estuaries may not be as great on the Pacific as the Atlantic coast.

Oregon's estuaries are few in number and include but a small area. For this reason man's infringement on them for recreation, land development, harbors, agriculture, and waste disposal will be intense. This study evaluates some long-term trends of the relative abundance of larval fishes. Hopefully it will facilitate future comparisons of faunal changes within this estuarine habitat.

THE ESTUARY

Yaquina Bay (Figure 1) is a small tidal estuary on the central Oregon Coast. It extends inland about 37 km and has an area of about 11.6 km^2. A channel is dredged to a depth of 7.9 m to McLean Point and to 3.7 m to the town of Toledo. Tides are mixed, semidiurnal with a mean tidal range of 1.7 m (Kulm and Byrne, 1967). According to Zimmerman (1972) the bay has an exchange ratio of 52% and a flushing time of 13.3 tidal cycles during the summer. The estuary is well-mixed with little vertical stratification in the summer when freshwater runoff is low, and is partially mixed (4-19‰ salinity

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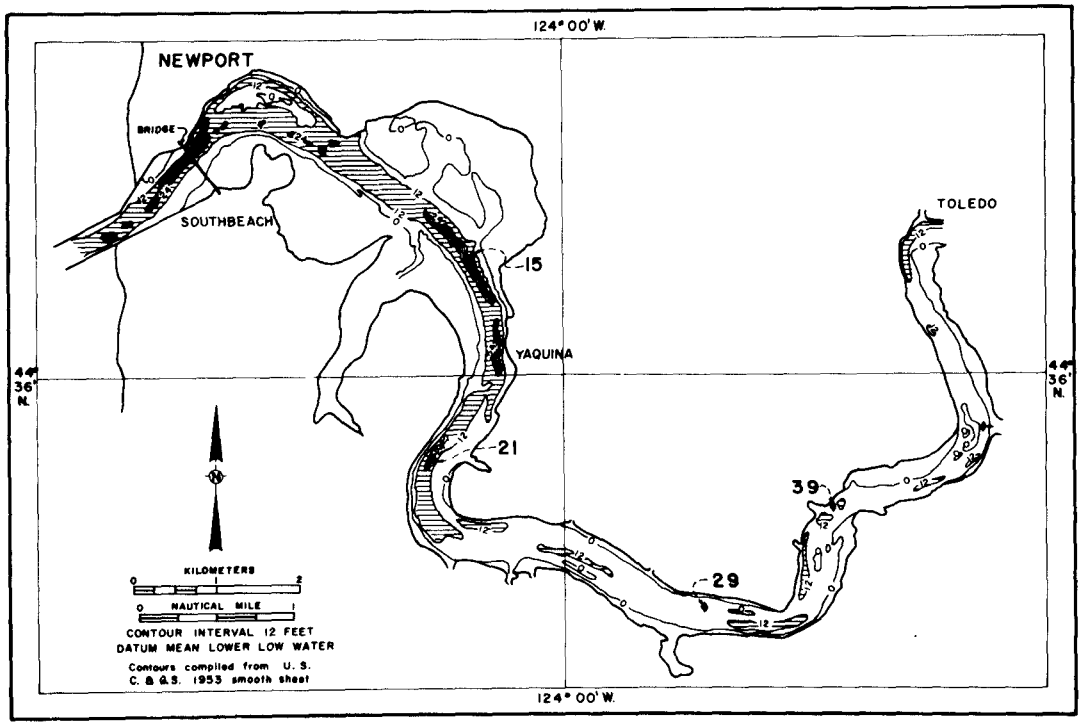

FIGURE 1.—Yaquina Bay estuary, showing location of stations: Bridge, Buoy 15, 21, 29, and 39.

difference from surface to bottom) during other seasons (Burt and McAlister, 1959; Kulm and Byrne, 1967; Zimmerman, 1972). Salinity is lowest and also most variable during the winter period of high precipitation. Temperatures, however, are most variable during the summer, owing to periodic advection of cold upwelled waters into the bay and to local heating (Frolander, 1964; Frolander et al., 1973).

SAMPLING METHODS

A 12.5 cm diameter Clarke-Bumpus (CB) Sampler with nylon (Nitex®)[2] net of 0.233 mm mesh aperture was used to collect 393 plankton samples from January 1960 to December 1970 and to provide a long time series for analysis at one station (Buoy 21) located in Yaquina Bay about 4.3 nautical miles from the ocean (Figure 1). In addition, both the CB and a 20.2 cm diameter nonclosing Bongo Sampler were towed together at five stations (Bridge and Buoys 15, 21, 29, and 39) from June 1969 to June 1970 (223 tows). The bongo had nylon nets with 0.233 mesh on one side and a 0.571 mesh on the other and was attached 1 m below the CB on the same towing cable. The CB net was 61.6 cm long with the filtering area of the mesh to mouth area ratio of 6.2:1. The bongo nets were cylindrical-conical, 177 and 161 cm long for the 0.233 and 0.571 mesh nets respectively. Both bongo nets had a filtering area to mouth area ratio of 10.5:1.

Samples were collected from small boats, generally at weekly intervals during the sampling period. Oblique-step tows were made at 2 knots. At the three deep stations (Bridge, Buoys 15 and 21) the net was towed horizontally at each of three depths for 4 min: about 1 m above the bottom, at mid-depth and 1 m below the surface. At the two shallow stations in the upper estuary the nets were towed at each of two depths for 6 min: 1 m above the bottom and 1 m below the surface. Tows were made during daylight, in mid-channel, against tidal currents, and did not coincide with any particular tidal stage. However, several 24-h series of CB tows (123 tows) were made during the 11-yr period to assess diel and tidal variations at single stations.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

Samples were also collected with the bongo nets (0.233 and 0.571 mm mesh) in the open ocean off Yaquina Bay from June 1969 to June 1970, often within a day of the bay sampling. A total of 113 step oblique tows was made at four stations 1, 3, 5, and 10 miles from the coast.

Volume of water filtered during each tow was estimated by flowmeters in the mouth of the nets. TSK meters were mounted on the inside wall of the bongo frames. Meters were calibrated periodically by towing them over a measured distance. Samples were preserved in the field with Formalin. In the laboratory entire samples were sorted for fish larvae with the aid of 2¼-power illuminated magnifier. Fish eggs were sorted from the 1960-1968 CB samples.

SPECIES COMPOSITION

Larval fishes representing 17 families were found in Yaquina Bay during the 11-yr studies. These included 45 distinct types of larvae, 22 of which were identified to species (Table 1). Most families were represented by only one or two species or types. The family Cottidae, however, was represented by 14 different larval types, by far the most for any family. The family with the next largest number of types was Pleuronectidae with 6 identified species.

TABLE 1.—Species composition of fish larvae from Yaquina Bay from all samples examined, 1960-1970.

Clupeidae
Clupea harengus pallasi
Engraulidae
Engraulis mordax
Osmeridae
Hypomesus pretiosus
Gobiesocidae
Gobiesox meandricus
Gadidae
Microgadus proximus
Gasterosteidae
Aulorhynchus flavidus
Syngnathidae
Syngnathus griseolineatus
Stichaeidae
Lumpenus sagitta
Anoplarchus sp.
Chirolophis sp.
2 unknown types
Pholidae
Pholis ornata
Ammodytidae
Ammodytes hexapterus
Gobiidae
Lepidogobius lepidus
1 unknown type
Scorpanenidae
Sebastes spp.
Hexagrammidae
Hexagrammos sp.
Ophiodon elongatus
Cottidae
Leptocottus armatus
Cottus asper
Scorpaenichthys marmoratus
Enophrys bison
Hemilepidotus spp.
9 unknown types
Agonidae
2 unknown types
Cyclopteridae
3 unknown types
Bothidae
Citharichthys sp.
Pleuronectidae
Psettichthys melanostictus
Platichthys stellatus
Glytocephalus zachirus
Isopsetta isolepis
Parophrys vetulus
Lyopsetta exilis

THE 11-YR SERIES

Relative Abundances

Table 2 summarizes the occurrence and average density of different fish larvae collected during the 11-yr CB series at Buoy 21. Two species, *Clupea harengus pallasi* (Pacific herring) and *Lepidogobius lepidus* (bay goby), were clearly the most abundant larvae. Combined they accounted for 90% of all the fish larvae collected in the 393 samples.

These two species were consistently the codominants during all years of the sudy (Table 3). *C. h. pallasi* ranked first in abundance during 8 yr. *L. lepidus* ranked first in 3 yr and second in the 8 yr that *C. h. pallasi* was dominant. *Cottus asper* (prickly sculpin) ranked third in abundance. *Leptocottus armatus* (Pacific staghorn sculpin), Gobiidae type 1, and *Hypomesus pretiosus* (surf smelt) alternated in the fourth, fifth, and sixth positions. Average number of these larvae per m^3 varied from year to year, but no obvious long-term trends in the relative abundance of these species suggested environmental changes or species succession. (Similarly, Frolander et al. [in press] found no evidence for persistent changes of zooplankton abundances in Yaquina Bay over the same time period.)

In order to learn if all six of the common species were more abundant in some years than others, rank correlations were calculated from annual abundances in Table 3. *Clupea h. pallasi* and *L. lepidus* were both caught in large numbers in 1967, but the Coefficient of Concordance, W, (Tate and Clelland, 1957) indicated little agreement among ranking of years ($P > 0.2$). In other words, there was no

TABLE 2.—Fish larvae collected in Clarke-Bumpus nets during 1960-1970 at Buoy 21, ranked by abundance.

Item	No. of Tows occurred in out of 393	Total No. collected	Total No. larvae ÷ total volume of water filtered $m^3 \times 10^3$	Months of occurrence
Clupea harengus pallasi	76	2,174	510	I-V
Lepidogobius lepidus	98	1,287	302	IV-X
Cottus asper	47	129	30	I-V
Leptocottus armatus	42	53	12	VIII-III
Gobiidae type 1	27	49	11	VII-III, VI
Hypomesus pretiosus	23	39	9.1	VIII-IX, XI-IV
Lumpenus sagitta	8	29	6.8	I-II
Enophrys bison	12	20	4.7	I-III
Ammodytes hexapterus	10	15	3.5	I-III
Anoplarchus sp.	10	12	2.8	II-III
Cottidae type 1	8	10	2.3	II-III, VI-VII
Engraulis mordax	6	7	1.6	VII-IX
Pholis ornata	7	7	1.6	I-III
Parophrys vetulus	4	6	1.4	II-III
Platichthys stellatus	3	3	0.7	V-VI
Cyclopteridae type 1	3	3	0.7	VI, VII, XII
Cottidae type 10A	3	3	0.7	II, XI
Cottidae type 5	3	3	0.7	VIII, IX
Citharichthys sp.	2	2	0.5	II-III
Cyclopteridae type 2	2	2	0.5	VI-VII
Sygnathus griseolineatus	2	2	0.5	VII-VIII
Cottidae type 10B	1	1	0.2	I
Cottidae type 11	1	1	0.2	III
Sebastes spp.	1	1	0.2	I
Hexagrammidae	1	1	0.2	II

evidence that "good" or "bad" years occurred simultaneously for different species of larvae.

SEASONAL VARIATIONS

Total Eggs and Larvae

The average monthly catch of pelagic fish eggs at Buoy 21 was highest in the summer, with highest values ($>2/m^3$) from July to October (Figure 2). Eggs of the northern anchovy (*Engraulis mordax*) were sometimes abundant during this season. Numbers of fish larvae, on the other hand, peaked early in the year, from February to June, and few larvae were taken after June. *C. h. pallasi* and *L. lepidus* larvae were the main contributors to these large larval catches. These two species, and many others found in the estuary, have demersal eggs.

This seasonal maximum of fish larvae in the first half of the year in Yaquina Bay is similar to the seasonality reported in the Straits of Georgia, British Columbia by Parsons, LeBrasseur, and Barraclough (1970).

Individual Species

The seasonal occurrence of larvae collected at Buoy 21 is summarized in Table 2. The majority of the larval species were most common in the winter or spring, including *C. h. pallasi*, *Cottus asper*, *Hypomesus pretiosus*, *Parophrys vetulus*, *Ammodytes hexapterus*, *Lumpenus sagitta*, *Anoplarchus* sp., *Pholis ornata*, and *Enophrys bison*. *L. lepidus* was

TABLE 3.—Average abundance of the six most common fish larvae by year, 1960-1970, Clarke-Bumpus samples, Buoy 21.

Item	Average number of larvae per $10^3 m^3$ water filtered										
	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970
Clupea harengus pallasi	174	542	278	279	1,230	335	273	1,136	961	526	506
Lepidogobius lepidus	312	230	37	114	326	402	161	1,169	471	74	132
Cottus asper	17	35	24	38	41	48	35	68	5	20	14
Gobiidae type 1	11	1	2	50	24	0	0	11	0	34	14
Leptocottus armatus	17	6	12	34	12	7	18	17	5	10	2
Hypomesus pretiosus	5	7	0	23	4	4	18	3	0	44	7

the only common species with a distinct peak of larval abundance in the summer (April-September). Several species were collected most months of the year: considering all years together, larvae of *Hypomesus pretiosus* were found every month but May, June, July and October, *L. armatus* every month except April-July, and Gobiidae type 1 every month but April, May and July.

Pacific Herring

Catches of *C. h. pallasi* larvae during each January-June period, 1960-1970, are illustrated for Buoy 21 in Figure 3. Herring larvae were common from February-April, with peak numbers usually in February and March. Though sampling variability and the limited number of samples precluded annual comparisons of abundance, no obvious long-term trends, such as decreasing catches, are evident during this 11-yr period, nor is there good evidence for large fluctuations in larval numbers. This suggests a fairly stable population of spawning herring over this time period.

The initial occurrence of larval herring varied among years, from January to March, suggesting annual differences in time of spawning or hatching times (e.g., contrast 1969 and 1970 with 1961-1963). This variability may be related to water temperature. The surface temperature of first larval occurrence varied from 7.3°C to 10.5°C (average = 9.0°C). To estimate date of first spawning, incubation time was calculated from a curve of incubation times vs. temperature (Outram, 1955; Taylor, 1971; Steinfeld, 1972). Incubation was estimated to range between 12 and 17 days for the first herring larvae caught during these years using surface water temperatures at Buoy 21. (Because herring spawn in shallow water, often intertidally [Steinfield, 1972; Taylor, 1971; Hardwick, 1973], surface temperatures were used.) Surface temperatures averaged for the date of first herring larval occurrence and the previous 17 days (2-3 observations) were plotted against time of first larval occurrence after January 1 (Figure 4). This revealed a surprising relationship: Years of earliest occurrence of larvae (i.e., 1969 and 1970) had lowest water temperatures (< 8°C) preceding first catches, and most years of latest occurrence (i.e. 1961, 1963, 1965, 1966) had highest temperatures (>9.2°C) during

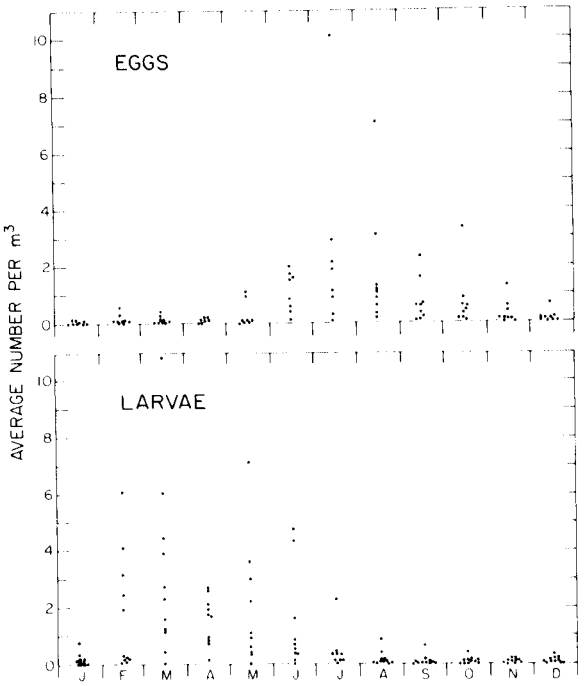

FIGURE 2.—Average monthly catches of fish eggs and larvae in Clarke-Bumpus samples at Buoy 21. Each point represents a monthly average for fish eggs each year, 1960-1968, and for fish larvae each year, 1969-1970. No samples were available from April-July 1966.

incubation of the first hatch. Thus, factors other than water temperature appear to be important in determining the time of the initial spawning of herring in Yaquina Bay.

Steinfeld (1972) observed from egg surveys in Yaquina Bay that herring had four major spawnings during February and March 1970. These occurred at about 2-wk intervals starting in early February, the most intensive spawnings coinciding with highest tides. Newly hatched larvae would therefore be expected in most of the catches throughout the larval periods. Measurements of larvae contributing to early and late peaks in 1964 and 1967 showed that recently hatched larvae (6-8 mm) were indeed present in April, but as expected, the percentage of small larvae was lower later in the year.

HORIZONTAL VARIATIONS

The average number of larvae collected at the different stations in both the estuary and the open ocean are listed in Table 4, permitting comparison of horizontal variations of relative abundance at nine stations from 8 miles up the

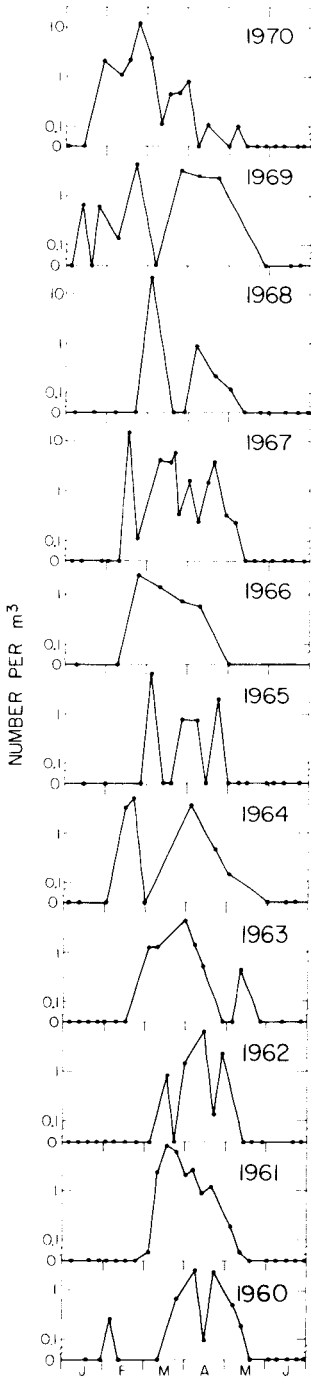

FIGURE 3.—Number of Pacific herring larvae per m³ caught in Clarke-Bumpus nets at Buoy 21 during January-June periods, 1960-1970.

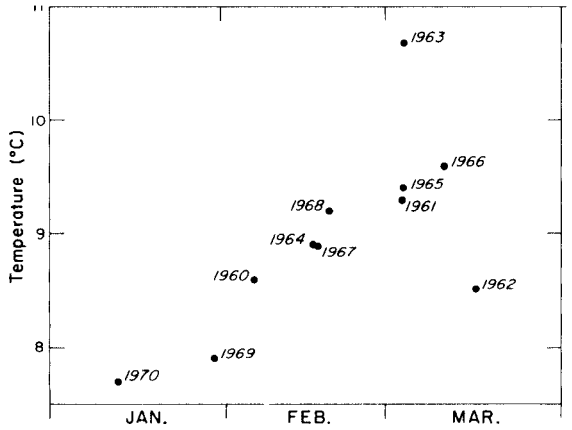

FIGURE 4.—Average surface temperature at Buoy 21 during and 14-17 days prior to first catches of herring larvae vs. date of first catches of herring larvae, 1960-1970.

estuary to 10 miles off the coast. Within the estuary, larvae of *C. h. pallasi*, *L. lepidus*, and *Cottus asper* usually ranked first, second, and third respectively in the catches at all five stations, from 0.5 to 8 nautical miles up the estuary. *L. lepidus* was the only common species restricted to the bay; it was most numerous in the upper estuary. Larvae of *C. h. pallasi* were abundant in the bay and rare outside the bay. Some of the other species that are considered to be primarily bay forms are *Cottus asper*, found in greatest numbers in the upper estuary, and *Enophrys bison*, *Leptocottus armatus* and *Pholis ornata*, found mainly in the lower estuary.

Many of the larvae found in the bay were found in greater numbers offshore. Larvae of the surf smelt, *H. pretiosus*, were sometimes abundant in the lower estuary where juvenile *H. pretiosus* were also numerous. Osmerids were most abundant 1 mile offshore. We assume that these were mainly *H. pretiosus*, a species known to spawn in the surf zone. Consequently, the surf smelt larvae found in the bay may be carried there by tidal exchange. Larvae of *A. hexapterus*, *Sebastes* spp., pleuronectids, gadids, and cyclopterids were all found in higher numbers offshore than in the bay. *Parophrys vetulus* was only found offshore.

Engraulis mordax larvae were found throughout the bay and to 3 miles offshore. They were not found 5 or 10 miles offshore. This larval distribution, and the large numbers of anchovy

TABLE 4.—Average number of larvae per $10^3 m^3$ filtered in bongo nets (mesh 0.233 and 0.571 mm combined) calculated from total number of specimens collected ÷ total volume filtered for entire year. Only species represented by five or more larvae are listed. June 1969-June 1970.

	BAY					OFFSHORE (mi)			
	39	29	21	15	BR	1	3	5	10
A. BAY ONLY									
Lepidogobius lepidus	106.0	340.5	113.4	92.9	6.4	0	0	0	0
Lumpenus sagitta	0	0	0.5	1.1	1.3	0	0	0	0
Anoplarchus spp.	0	0.6	0.7	1.1	1.0	0	0	0	0
B. PRIMARILY BAY									
Clupea h. pallasi	509.2	428.2	442.6	556.0	183.3	0.3	0.5	0	0
Gobiidae type 1	0.5	0.9	13.7	5.3	1.3	0.6	0.3	0	0
Cottus asper	40.7	42.3	21.0	10.1	9.2	0.6	0	0	0
Enophrys bison	0	0	2.3	9.6	18.8	0.3	0	0	0
Leptocottus armatus	0.7	1.6	10.0	7.2	3.8	0.3	0	0	0
Cottidae Type 1	0	0	0.5	1.3	1.3	0.6	0.5	1.0	0.3
Pholis ornata	0	0	0.8	1.3	1.3	0.3	0.5	0	0
C. PRIMARILY OFFSHORE									
Engraulis mordax	0.5	1.0	0.5	0.3	0.2	2.1	1.1	0	0
Hypomesus pretiosus-Osmerids	1.0	0.6	3.0	15.7	27.2	100.9	18.6	4.6	0.3
Gadidae	0	0	0.5	0	0.2	0.6	4.5	0.7	1.1
Ammodytes hexapterus	0	0	0	0.5	0.5	1.8	13.0	2.0	2.5
Sebastes spp.	0	0	0	0.5	0.8	6.9	4.2	1.5	19.6
Ophiodon elongatus	0	0	0	0.3	0	0.6	0.8	0.7	0
Hemilepidotus	0	0	0	0	0.2	1.5	2.9	0	1.2
Cottidae type 12	0	0	0	0.3	0.5	0.9	0	0	0
Agonidae	0	0	0	0	1.0	0.3	0.5	0.2	0
Cyclopteridae	0	0	0.2	0.3	0.2	0.6	3.2	0.2	0.5
Psettichthys melanostictus	0.2	0	0.5	0	0.5	5.1	31.1	3.4	0.5
Isopsetta isolepis	0	0	0	0	0.2	0.6	36.1	5.1	1.1
Lyopsetta exilis	0.2	0	0	0	0	0	9.0	0	0.3
Citharichthys sp.	0	0	0	0.5	0.5	1.0	0	0	0
D. OFFSHORE ONLY									
Stenobrachius leucopsarus	0	0	0	0	0	0.3	0.5	1.0	1.6
Cottidae type 16	0	0	0	0	0	0	2.4	0	0.3
Cottidae unident. spp.	0	0	0	0	0	1.8	9.6	7.1	0.6
Parophrys vetulus	0	0	0	0	0	1.2	9.0	11.9	8.9
Blennoids	0	0	0	0	0	3.3	4.5	0	0

eggs within the bay, is peculiar since Richardson (1973) reported that anchovy larvae were abundant well offshore, usually in Columbia River plume waters, and not near the coast.

Pacific Herring

Abundance

Herring larvae were abundant at all five stations during February and March 1970 (Figure 5). A peak in catches occurred in late January at the three stations closest to the ocean, and conversely, higher numbers occurred later (April and May) at the upper estuarine stations. These trends suggest earlier spawning near the mouth and later spawning in the upper estuary. Based on intertidal surveys, Steinfeld (1972) found herring eggs near the mouth from February 5 to 20, 1970, and in the upper estuary above Buoy 21 from March 8 to 24, 1970. The trend for earlier spawning near the mouth of the estuary was therefore found in both larval and egg surveys. However, the fact that Steinfeld did not find any spawn before February 5 while we collected many larvae between January 23 and February 10 indicates that intertidal surveys may miss substantial areas of eggs, perhaps from subtidal spawning.

Comparison of Nets

Catches of herring larvae in the three types of nets (CB and bongo with 0.233 mm mesh and bongo with 0.571 mm mesh) were usually similar on a m^3 basis, especially at high densities of larvae (Figure 5). The type of net catching the highest or the lowest number of larvae alternated among tows. We had not expected catches by the CB to compare favorably with the bongo in view of the known avoidance capability of Atlantic herring larvae (Bridger, 1956; Tibbo et al., 1958).

The percentage of herring larvae of different

sizes caught at Buoy 29 in the three nets during the 1970 larval season is shown in Figure 6. Little difference is apparent in the proportion of different sizes of larvae in the different nets. All curves show that the number of larvae caught between 6 and 8 mm was less than between 8 and 10 mm. This is probably explained by hatching of some larvae at lengths over 8 mm, and hence is a true reflection of relative abundance, rather than lack of retention of the smallest larvae by the nets. Larvae larger than 20 mm were not caught at all in the CB samples, presumably because of the capability of large larvae to avoid this gear.

TIDAL-DIEL VARIATIONS

Figure 7 illustrates the variations in CB catches of fish eggs and larvae during several diel sampling periods at Buoy 21. In Figure 7A, peaks in both egg and larval abundance occurred during periods of low water (Mann-Whitney U test, $P < 0.01$). Similarly, highest catches of herring larvae coincided with times of low water in Figure 7B ($P = 0.06$). In neither of these figures is a day-night difference evident ($P > 0.2$). In Figure 7C, however, catches of herring larvae were not correlated with tidal stage ($P > 0.2$), but highest catches coincided with darkness ($P < 0.01$); all but one of the 9 nighttime catches exceeded the 14 daytime catches.

Therefore, both tidal and diel factors may influence catches. We believe the high catches associated with low water were caused by tidal excursion of water with high density of eggs or larvae. In other words, the center of abundance of *L. lepidus* larvae and fish eggs (Figure 7A) and *C. h. pallasi* (Figure 7B) was up the estuary from Buoy 21 at high tide. The ability of larger larvae to avoid plankton nets during the daytime (see Figure 6; Tibbo et al., 1958; Bridger, 1956; and Colton, Honey, and Temple, 1961) was thought to explain the high catches after dark in Figure 7C, but this interpretation was not supported by the similar size-frequency distributions of day- and night-caught larvae.

THE ESTUARY AS A NURSERY

The results of this study on the planktonic fish larvae tentatively support McHugh's (1966,

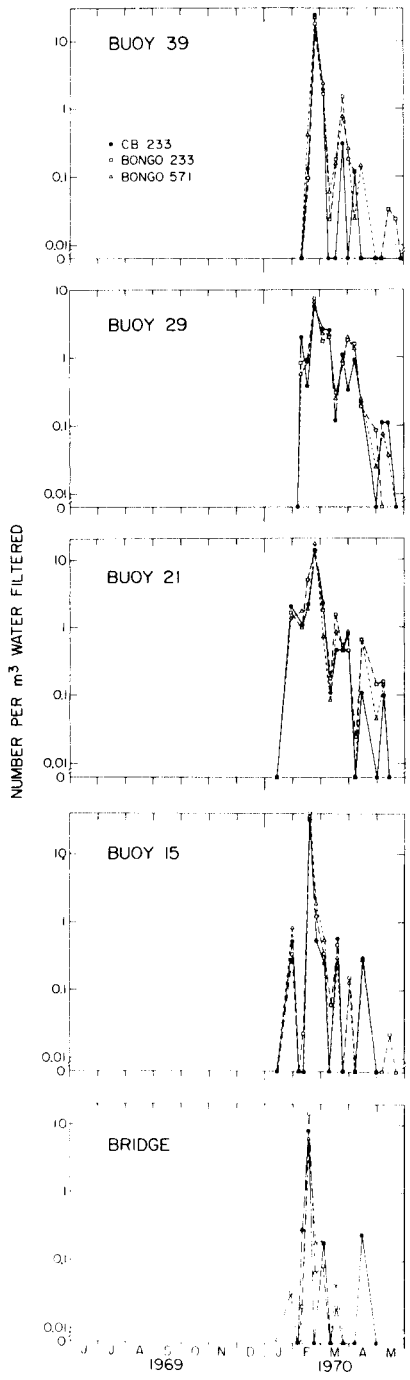

FIGURE 5.—Number of Pacific herring per m³ caught in Clarke-Bumpus nets with 0.233 mm mesh, the bongo net with 0.233 mm mesh and the bongo net with 0.571 mm mesh at five stations in Yaquina Bay, June 1969-June 1970.

1967) contention that estuaries of the Pacific coast may be less important as nursery grounds than eastern seaboard estuaries. But such a conclusion is unwarranted without a comparison of larval abundances within the estuary with those in adjoining open ocean to learn if larvae are restricted to or concentrated in estuaries. High numbers of larvae within the estuary are not necessarily proof of estuarine dependance, as they may be more abundant in the ocean. Conversely, low densities of a species inside the estuary may indicate importance if it is absent elsewhere. A comparison of larval catches in Yaquina Bay with the open ocean is possible since we collected fish larvae at stations 1, 3, 5, and 10 miles off Yaquina Bay, using the same bongo nets during the same sampling period as the bay sampling. The results of this comparison (Table 4) corroborate our earlier suggestion: with the exception of the Pacific herring the estuary does not appear to be important to the pelagic larvae of commercial fishes. Most of the larvae that were restricted to or were most common in the estuary were of small, non-food species of cottids, stichaeids, and gobies. Larvae of all the pleuronectids collected were more common offshore than inside the estuary.

Thus the Pacific herring was the only species of commercial interest that appeared to use the estuary extensively as both a spawning and a nursery ground. In California, herring spawn in bays and estuaries (Hardwick, 1973). Since Pacific herring are known to comprise more or less distinct populations with adults returning to the same bay to spawn (Stevenson, 1955; Rounsefell, 1930), estuaries may be vital to the maintenance of herring along some portions of the west coast.

Feeding conditions for herring are undoubtedly related to their use of estuaries as nurseries. Russell (1964) found that Yaquina Bay is used as a feeding ground for 1 to 4 yr-old herring which fed mainly on the copepods *Acartia clausii* and *Pseudocalanus* sp., both abundant within the bay. *A. clausii*, which is thought to maintain indigenous populations in Yaquina Bay, is especially abundant in the upper estuary (Buoys 21 and 29) early in the spring when densities of adults and immatures exceed 30,000m^3 (Zimmerman, 1972 Frolander et al., 1973). The numbers of copepod eggs, nauplii, and copepodites, important food for Atlantic herring larvae, probably exceed this

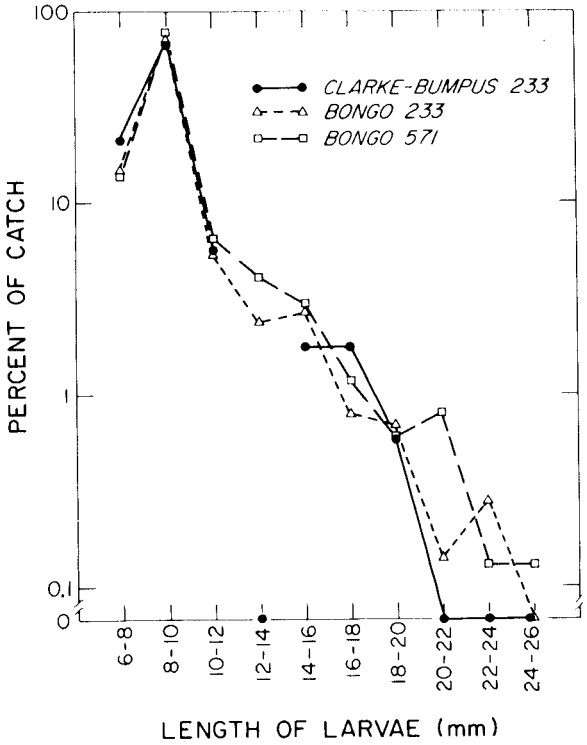

FIGURE 6.— Catches of different lengths of herring larvae at Buoy 29 expressed as a percentage of the total catch for each of the Clarke-Bumpus and bongo nets with 0.233 mm mesh and the bongo net with 0.571 mm mesh, February 10-March 13, 1970.

density during the early spring and provide adequate food for larval herring (Blaxter, 1965; Bainbridge and Forsyth, 1971; Sherman and Honey, 1971).

Our planktonic survey of fish larvae was not adequate to assess completely the estuary as a nursery ground. First, plankton nets are selective and only weakly swimming pelagic larvae were effectively sampled. Other young stages may not have been fully susceptible to capture because they actively avoid the nets. Secondly, the young of some species may have been present but simply unavailable for sampling because of their distributions. These may include young that migrate into the estuary after metamorphosis, benthic forms, or young that reside in shallow areas of the estuary.

For example, viviparous embiotocids (*Phanerodon furcatus*, *Rhacochilus vacca*, and *Embiotoca lateralis*) are common species in Yaquina Bay. Mature females of all these species are numerous in the middle and upper estuary

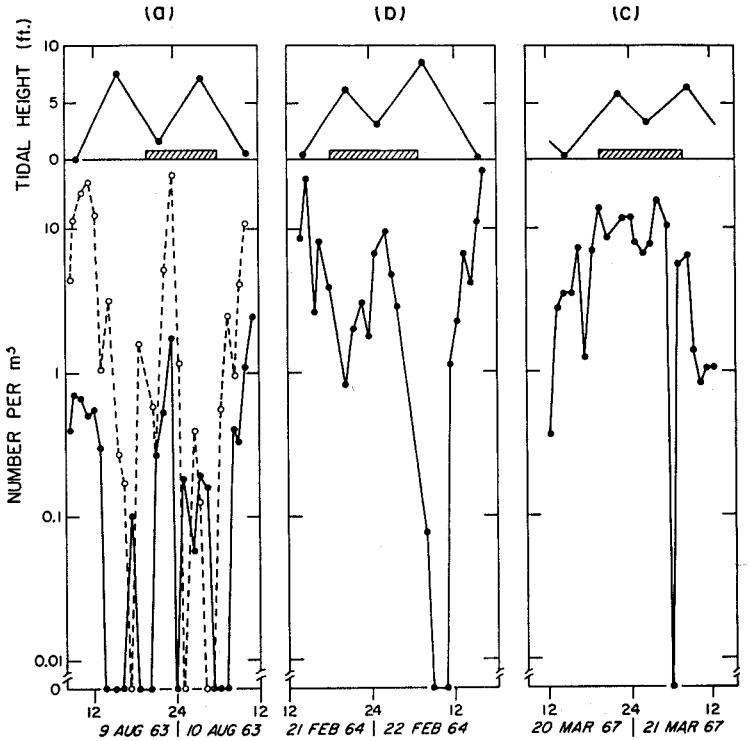

FIGURE 7.—Diel variations in the CB catches at Buoy 21: A. 9-10 August 1963; solid line=fish larvae; dashed line=fish eggs. B. 21-22 February 1964; solid line=herring larvae. C. 20-21 March 1967; solid line=herring larvae. The tidal height above mean lower-low water and period of darkness (hatched bar) are shown above each figure. Dates and noon and midnight are indicated below each figure.

during the spring when they give birth to young which use the estuary as a nursery (Beardsley, 1969; Wares, 1971). Because of their pelagic nature and swimming abilities, young embiotocids are not readily captured in small plankton nets or trawls. Beardsley (1969) and Westrheim (1955) also found many juvenile starry flounder (*Platichthys stellatus*) in Yaquina Bay, and Haertel and Osterberg (1967) concluded that the starry flounder use the upper Columbia River estuary as a nursery ground.

A trawl survey of juvenile fishes of Yaquina Bay by Wm. Johnson (pers. comm.), conducted during the same period and at the same stations as our plankton survey, provided useful information on the juvenile fishes caught in mid-channel of the estuary near the bottom. Relative abundances of the young fishes caught are shown in Table 5. Three species were dominant: *Hypomesus pretiosus*, *Parophrys vetulus*, and *Citharichthys stigmaeus*. They comprised 79% of the total number of fishes collected. Of these, only the abundant *H. pretiosus* was also common in plankton collections (Tables 2, 3, and 4). *Lepidogobius lepidus*, *Cottus asper*, and *Leptocottus armatus*, though presumbly benthic as juveniles, were not abundant in the trawl collections despite their abundance as pelagic larve. Johnson (pers. comm.) caught large numbers of juvenile *L. armatus* in shoal areas of Yaquina Bay with a beach seine, indicating that juveniles of some species may reside mainly in shallow water.

Young of both *Parophrys vetulus* and *Citharichthys stigmaeus* were abundant within Yaquina Bay, indicating that the bay provides a nursery for these species. Peak numbers of *P. vetulus* (15-45 mm) were found between April and June at Buoy 21, but young were captured at all stations from Buoy 15 to 39.

Citharichthys stigmaeus (30-80 mm) were concentrated in the lower estuary and were rarely captured up-estuary of Buoy 21. They were most common in May and June. *Hypomesus pretiosus* (35-50 mm) were abundant at all trawling stations, but only in January and February (Johnson, pers. comm.).

The importance of estuaries as nursery grounds for flounder, and especially for *Parophrys vetulus*, has been emphasized by others. Westrheim (1955) reported appreciable numbers of small *Parophrys vetulus*, *Citharichthys sordidus*[3] and *Platichthys stellatus* (starry flounder) in Yaquina Bay. Sand sole (*Psettichthys melanostictus*) were also encountered frequently. Although no adults of the commercially important English sole were caught, juveniles (20-180 mm) were common until autumn when most emigrated from the bay. Olsen and Pratt (1973) also reported that juvenile English sole were abundant in lower Yaquina Bay from April to September 1971, emigrating to offshore areas in October. Based on the incidence of a parasitic infection, apparently acquired only in estuaries, they concluded that estuaries are likely to be the exclusive nursery grounds for *Parophrys vetulus* on the Oregon coast, a conclusion that is supported by the absence of 0-age English sole in Demory's (1971) ocean trawling survey off the Oregon-Washington coast. Misitano (1970) and Eldridge (1970) found large numbers of English sole in Humboldt Bay, California. Villadolid (1927, as cited in Misitano, 1970) captured 0-age English sole by trawling in San Francisco Bay but found none off the coast. Shallow protected waters along the indented British Columbia coastline also provide nursery grounds for this species (Ketchen, 1956). Bays and estuaries are therefore vital as nursery areas for *P. vetulus* in their first year of life, perhaps because the sediments in these protected waters provide an ideal feeding habitat for the young as opposed to coarse sand sediments at similar depths along the open coast.

Sexually mature (ripe) *P. vetulus* were not caught in Humboldt or Yaquina Bay but are known to spawn offshore (Westrheim, 1955; Harry, 1959; Jow, 1969). Young larvae were uncommon in plankton collections from these bays (Eldridge, 1970; Misitano, 1970). In our study *P. vetulus* larvae were common offshore but were absent or rare in Yaquina Bay (Table 4). Therefore young English sole must be transported into the bay from offshore waters as late larval stages or migrate in as juveniles. In Humboldt Bay, Misitano (1970) captured metamorphosing English sole (average length, 23 mm) by midwater trawling, especially after dark. These larvae were active swimmers in aquaria but usually resided on the bottom. As a result they would be relatively inaccessible to daytime plankton collections.

The question remains, however, how these larvae enter estuaries. Currents off the northern Pacific coast during the winter and spring are largely inshore and northerly (Burt and Wyatt, 1964; Wyatt, Burt, and Pattullo, 1972) and would transport buoyant fish eggs such as those of English sole (Budd, 1940; Ketchen, 1956; Alderdice and Forrester, 1968) toward and then along the coast. Retention in estuaries would seem to require active behaviorial responses by the larvae, such as a change in depth distribution to enhance transport into and reduce advection out of estuaries. Since a two-layered transport system prevails in Yaquina Bay during the winter (Kulm and Byrne, 1967; Burt

TABLE 5.—Relative abundance (%) of juvenile fishes collected at four stations in Yaquina Bay (Bridge to Buoy 29) in a 1.8-m beam trawl (1.5 mm stretch mesh), January-June, 1970 (courtesy Wm. Johnson).

Hypomesus pretiosus	36.2
Parophrys vetulus	24.6
Citharichthys stigmaeus	18.2
Enophrys bison	4.1
Clupea h. pallasi	3.6
Ammodytes hexapterus	2.5
Leptocottus armatus	2.3
Hexagrammos decagrammus	1.1
Pholis ornata	1.0
Raja binoculata	0.7
Platichthys stellatus	0.7
Hemilepidotus hemilepidotus	0.7
Lumpenus sagitta	0.7
Engraulis mordax	0.6
Lepidogobius lepidus	0.5
Cymatogaster aggregata	0.5
Sebastes melanops	0.4
Artedius fenestralis	0.4
Psettichthys melanostictus	0.4
Ophiodon elongatus	0.3
Sygnathus griseolineatus	0.3
Pallasina barbata	0.1
Symphurus atricauda	<0.1
Artedius harringtoni	<0.1
Anoplarchus purpurescens	<0.1
Phanerodon furcatus	<0.1
Embiotoca lateralis	<0.1
Occella verrucosa	<0.1
Gobiesox maeandricus	<0.1

[3] Probably *C. stigmaeus*, the species usually found by others in Yaquina Bay.

and McAlister, 1959) and since Kulm and Byrne (1967) found that marine sand was transported by strong currents 6 miles up the Yaquina Bay estuary during the winter, the season when *P. vetulus* enter the estuary, then descent of larvae into deep water, where net transport exists up the estuary, may result in transport into and retention within estuaries of English sole and other species, as found for other larval fish (Pearcy, 1960; Pearcy and Richards, 1962; and Graham, 1972).

In conclusion, Yaquina Bay, like many east coast estuaries, is an important nursery for the young of several species of marine fishes. This was not apparent from a survey of planktonic larvae, however. Only the larvae of Pacific herring, a species that spawns in bays, were abundant in our plankton collections in Yaquina Bay. Although the pelagic larvae of flatfishes were much more common in offshore than estuarine waters, the juveniles of several species move into the estuary in large numbers.

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CALANOID COPEPODS OF THE GENUS *AETIDEUS* FROM THE GULF OF MEXICO[1]

TAISOO PARK[2]

ABSTRACT

The copepod population known previously as belonging to *Aetideus armatus* (Boeck) in the Gulf of Mexico and Caribbean Sea is recognized as a separate species. The males of *Aetideus acutus* Farran and *Aetideus giesbrechti* Cleve are fully redescribed with figures.

The genus *Aetideus* Brady, 1883, comprised four species (*A. armatus*, *A. bradyi*, *A. acutus*, and *A. giesbrechti*) when Sars (1925) established the genus *Euaetideus* to distinguish the last three species from the first. A new species has since been added to each genus, *A. pacificus* and *E. australis*. Bradford (1971) reviewed the genera *Aetideus* and *Euaetideus* on the basis of specimens from the Atlantic and Pacific Oceans. Having found a close similarity between the males, she proposed the merging of the two genera. In agreement with her proposal, the name *Euaetideus* is considered here as a junior synonym of *Aetideus*.

In the Gulf of Mexico, three species of *Aetideus* (*A. armatus*, *A. acutus*, and *A. giesbrechti*) have been recorded (Owre and Foyo, 1967; Park, 1970). During the examination of plankton samples obtained from the Gulf of Mexico by the RV *Alaminos* in September 1971, all of these species were found, including the males.

A. armatus had been known to have worldwide distribution (Vervoort, 1957) until Bradford (1971) recognized a population in the Southern Hemisphere and two in the North Pacific as separate species. Bradford also noted differences between the northern and southern forms of *A. armatus* in the Atlantic, but the differences were not considered as taxonomically significant. When examined in detail in the light of Bradford's findings, the Gulf of Mexico population of *A. armatus*, however, was found to be significantly different from either the northern or southern Atlantic form of the species, or from any other known species of the genus. Therefore, it is described here as a new species.

A. acutus and *A. giesbrechti* found in this study were in agreement with the descriptions by Grice (1962) and Park (1968) for the Pacific forms. The males of these species have not been fully described, except for brief descriptions by Giesbrecht (1892) and Bradford (1971).

AETIDEUS MEXICANUS, NEW SPECIES

Type.—Holotype female, U.S. National Museum No. 143777; allotype male USNM No. 143778; 30 female and 7 male paratypes, USNM No. 143779. Type locality, lat. 25°15′N, long. 89°11′W, in the Gulf of Mexico (sampling depth, about 500-0 m).

Female.—Body lengths of 31 type specimens, 1.66-1.84 mm. Proportional lengths of prosome and urosome about 78:22. Viewed dorsally, body slender, with a round, slightly produced forehead (Figure 1A). Laterally, dorsal margin of forehead broadly vaulted at level of mouth (Figures 1B, D). Two rostral rami separated by a U-shaped notch (Figure 1G). Distance between tips of rostral rami exceeding depth of notch (1.07-1.15:1). Metasomal process extending straight backward; although variable in length, generally reaching about distal end of genital segment. Dorsally, genital segment (Figure 1H) wider than long, with its widest part close to its proximal end. Shape of spermatheca (Figures 1C, F) similar to *A. armatus* as described by Bradford (1971), with short wide neck connecting proximal and distal sacs; space between two sacs slightly

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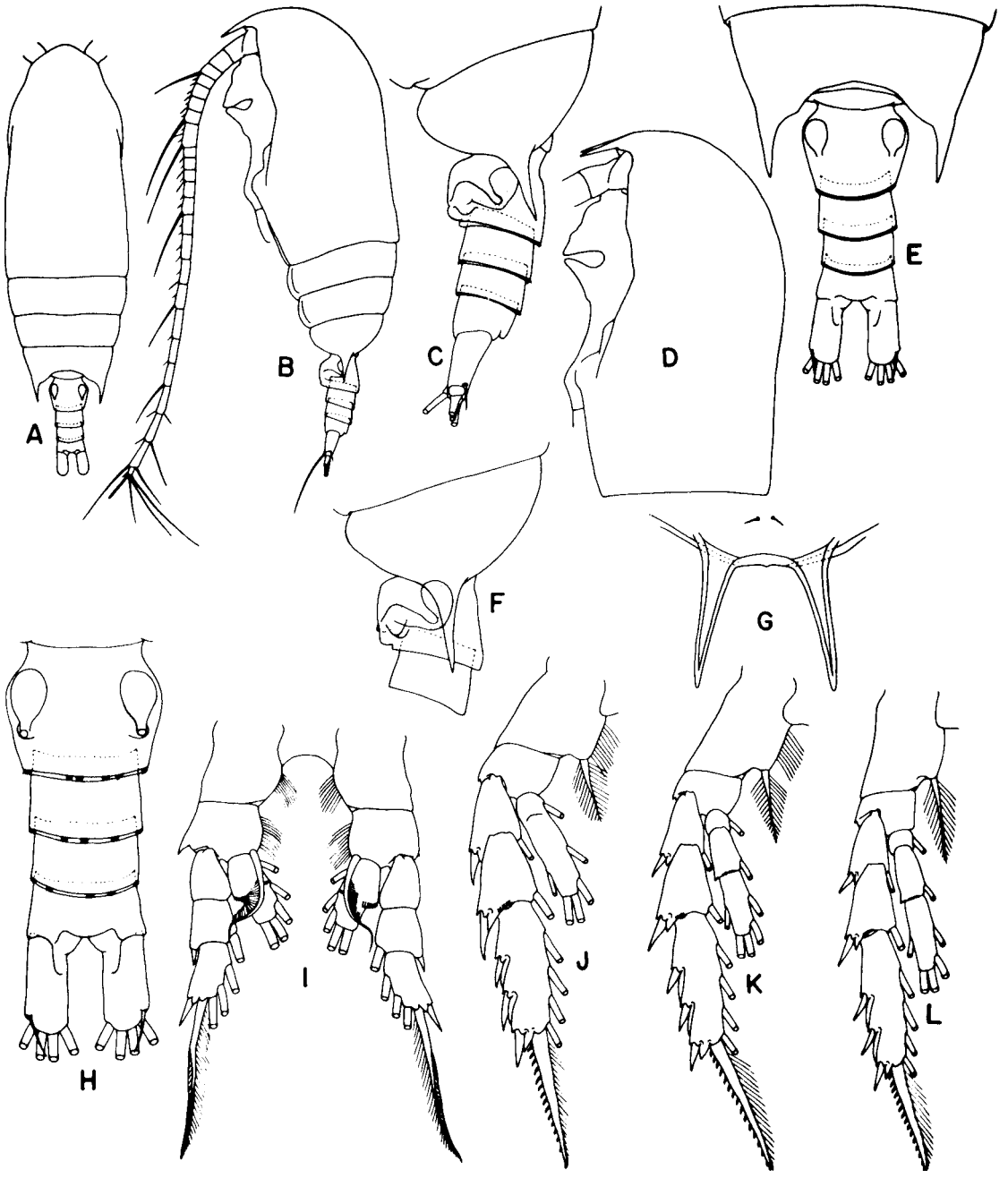

FIGURE 1.—*Aetideus mexicanus*, new species. Female: A, habitus, dorsal; B, habitus, lateral; C, posterior part of body, lateral; D, forehead, lateral; E, posterior part of body, dorsal; F, last metasomal and first two urosomal segments of another specimen, lateral; G, rostrum, anterior; H, urosome, dorsal; I, first pair of legs, anterior; J, second leg, anterior; K, third leg, anterior; L, fourth leg, anterior.

wider than connecting neck. Caudal ramus about 2.4 times as long as wide.

Antennules extending beyond distal end of caudal ramus by last two segments. Other cephalic appendages as in *A. pacificus* as described by Park (1968). In most of the specimens dissected the first pair of legs were asymmetrical, with the external margin of the right

basis produced distally into a large tooth-like process (Figure 1I). Second to fourth legs (Figures 1J-L) similar to *A. pacificus*, but coxa of fourth leg without spinules at base of internal seta. Terminal exopodal spines of second to fourth legs with 15-17 teeth.

Male.—Body lengths of eight type specimens, 1.58-1.68 mm. Proportional lengths of prosome and urosome about 75:25. Body slender, with forehead slightly produced (Figure 2A). Rostrum reduced. Metasomal process pointing straight backward, reaching about distal end of genital segment (Figures 2D, E). Second to fourth urosomal segments and caudal rami (Figure 2E) with width:length ratios of 1:0.98-1.05, 1:1.08-1.15, 1:1.12-1.19, and 1:1.82-2.00, respectively. Antennules reaching about distal end of fourth urosomal segment, nineteenth and longest segment (Figure 2G) with width:length ratio of 1:4.9-5.1. On second leg (Figure 2M), endopod reaching distal end of second exopodal segment. On second and third legs (Figure 2N), terminal exopodal spines longer than third exopodal segments, with about 29 and 23 teeth, respectively. Second to fourth segments of fifth leg (Figure 2O) with width:length ratios of 1:3.7-4.2, 1:8.3-8.7, and 1:9.0-9.7, respectively.

Remarks.—The female of *A. mexicanus* is distinguished from *A. armatus* by the slender body, long antennules which extend beyond the caudal rami by two segments and, particularly, the fourth leg which lacks spinules at the base of the coxal seta found in all other species of the genus (Bradford, 1971). The male of *A. mexicanus* is very close to that of *A. armatus* as described by Bradford but seems to differ from it in the proportions of the caudal rami and of the second to fourth segments of the fifth legs. However, the importance of these characters in the distinction between the two species is yet to be determined.

Distribution.—*A. mexicanus* was found in a number of plankton samples taken from the upper 500 m in the Gulf of Mexico by the RV *Alaminos* in September 1971. *A. armatus* recorded from the Caribbean Sea by Park (1970) belongs to this new species.

AETIDEUS ACUTUS FARRAN, 1929

Male.—Body length, 1.22-1.36 mm according to 48 randomly selected specimens. Proportional lengths of prosome and urosome about 79:21. Dorsally, forehead (Figure 3B) more produced than in *A. mexicanus*. Rostrum reduced. Metasomal process with wide base, distinctly curved downward when viewed laterally (Figure 3E) and slightly curved inward in dorsal view (Figure 3D). Second to fourth urosomal segments and caudal rami with width: length ratios of 1:0.83-0.88, 1:0.75-0.81, 1:0.78-0.81, and 1:1.64-1.83, respectively.

Antennules reaching about distal end of third urosomal segment, nineteenth and longest segment (Figure 3F) with width:length ratio of 1:3.31-3.52. Other cephalic appendages similar to *A. mexicanus*. On second leg (Figure 3L), endopod reaching distal end of second exopodal segment. Terminal exopodal spines of second and third legs (Figure 3M) longer than their third exopodal segments, with about 23 and 18 teeth, respectively. Terminal exopodal spines of fourth legs (Figure 3N) shorter than their third exopodal segments, with about 16 teeth. Second to fourth segments of fifth leg (Figure 3O) with width:length ratios of 1:3.41-3.78, 1:6.72-7.33, and 1:6.00-6.60, respectively.

Remarks.—The male of *A. acutus* was first described very briefly by Bradford (1971). The present specimens seem to be in agreement with her descriptions. The male of *A. acutus* is easily distinguished from those of *A. mexicanus* and *A. giesbrechti* by its considerably smaller size. In the shape of the forehead, metasomal process, and antennule, it is closely related to *A. giesbrechti*, but differs from this species in the relative lengths of the urosomal segments and caudal rami.

The female specimens of *A. acutus* in the present study (1.48-1.62 mm in body length according to 80 randomly selected specimens) are identical with the specimens described by Park (1968) from the Pacific, and can be readily recognized by the shape of the spermatheca (Figure 3A). The appendages are similar to those of *A. pacificus* as described by Park (1968), except that the maxillule carries 3+3+6 setae on the endopod.

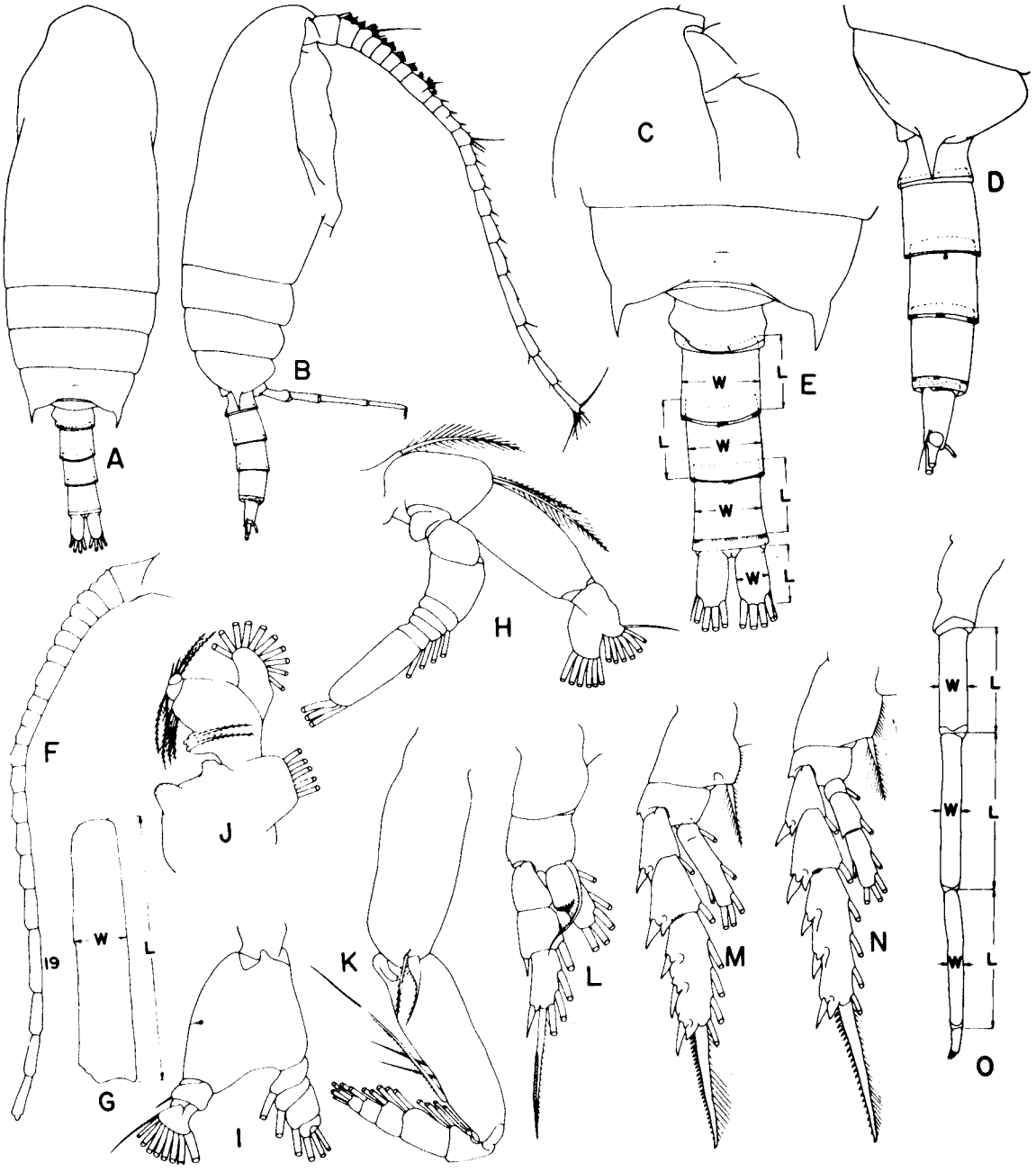

FIGURE 2.—*Actideus mexicanus*, new species. Male: A, habitus, dorsal; B, habitus, lateral; C, forehead, lateral; D, posterior part of body, lateral; E, posterior part of body, dorsal; F, antennule, setae omitted; G, 19th segment of antennule; H, antenna; I, mandible; J, maxillule; K, maxilliped; L, first leg, anterior; M, second leg, anterior; N, third leg, anterior; O, fifth leg, anterior. (L and W, length and width of segment.)

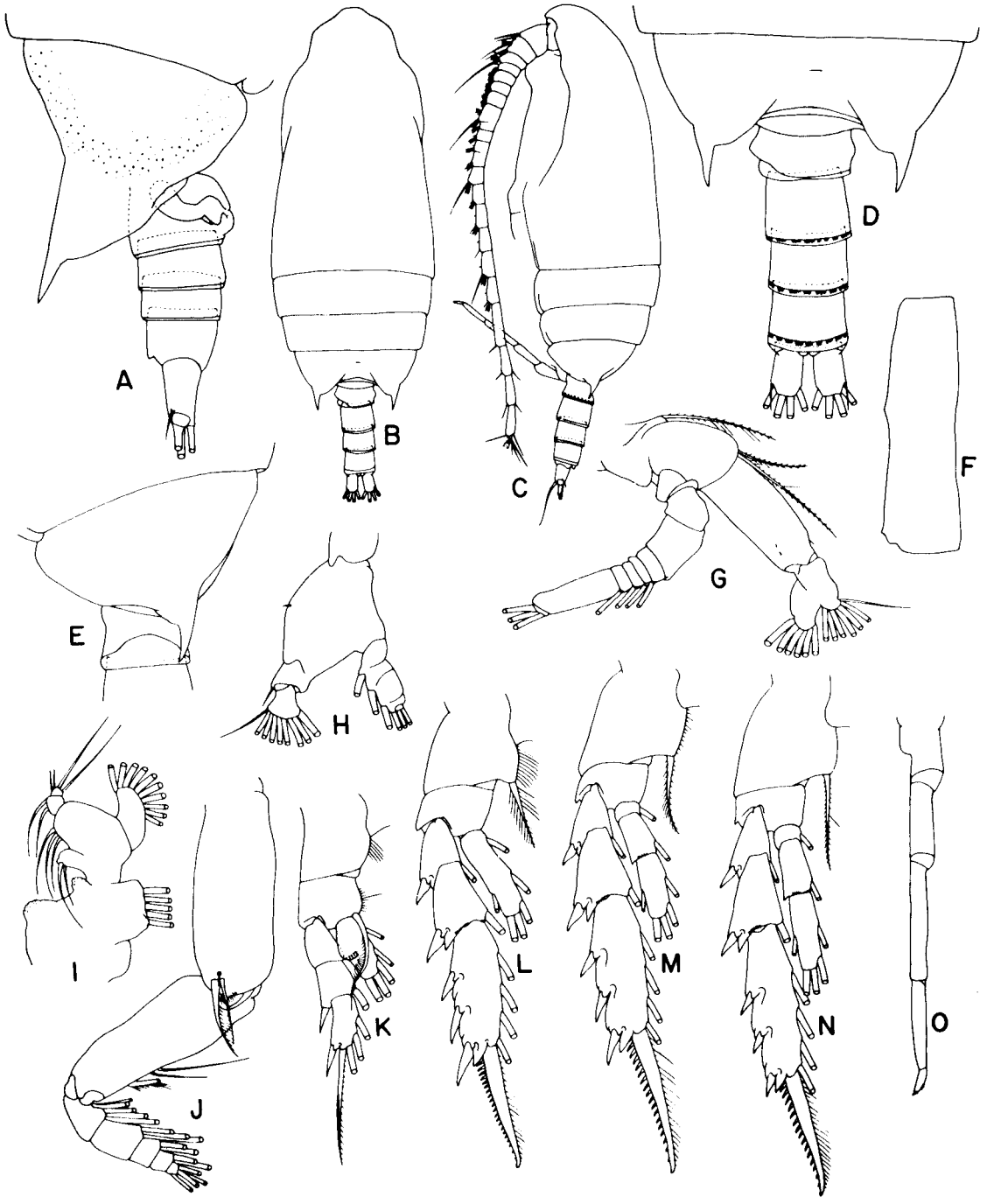

FIGURE 3.—*Aetideus acutus*. Female: A, posterior part of body, lateral. Male: B, habitus, dorsal; C, habitus, lateral; D, posterior part of body, dorsal; E, last metasomal and genital segments, lateral; F, 19th segment of antennule; G, antenna; H, mandible; I, maxillule; J, maxilliped; K, first leg, anterior; L, second leg, anterior; M, third leg, anterior; N, fourth leg, anterior; O, fifth leg, anterior.

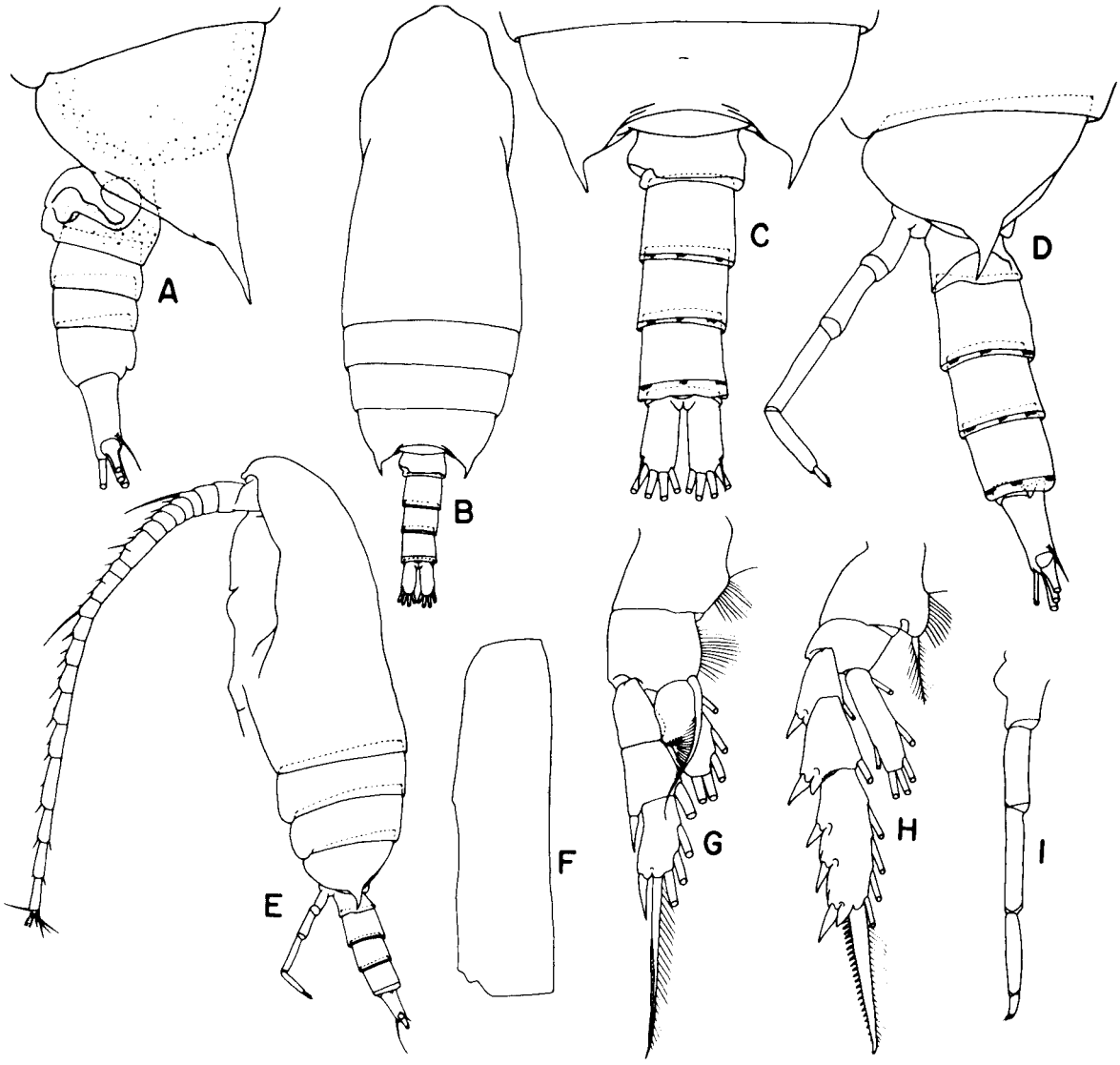

FIGURE 4.—*Aetideus giesbrechti*. Female: A, posterior part of body, lateral. Male: B, habitus, dorsal; C, posterior part of body, dorsal; D, posterior part of body, lateral; E, habitus, lateral; F, 19th segment of antennule; G, first leg, anterior; H, second leg, anterior; I, fifth leg, anterior.

Distribution.—*A. acutus* was originally described from off New Zealand (Farran, 1929). The species has so far been known to occur on the Great Barrier Reef (Farran, 1936), in the Malay Archipelago (Vervoort, 1957), off the Pacific coast of Middle Japan (Tanaka, 1957; Tanaka and Omori, 1970), in the tropical Pacific (Grice, 1962), the northwestern Pacific (Brodsky, 1962), the central North Pacific (Park, 1968), the northeast Atlantic (Grice and Hulsemann, 1965), the Caribbean Sea and Gulf of Mexico (Park, 1970), and in the western Indian Ocean (De Decker and Mombeck, 1965; Grice and Hulsemann, 1967). In the Gulf of Mexico, *A. acutus* is the most common of all three *Aetideus* species so far known to occur, and it is mainly found in the upper 500 m.

AETIDEUS GIESBRECHTI CLEVE, 1904

Male.—Body length, 1.52-1.60 mm according to 50 randomly selected specimens. Propor-

tional lengths of prosome and urosome about 77:23. Dorsally, forehead (Figure 4B) produced as in *A. acutus*. Rostrum reduced. Metasomal process (Figures 4C, D) as in *A. acutus*. Second to fourth urosomal segments and caudal rami with width:length ratios of 1:0.93-0.95, 1:0.85-0.86, 1:0.88-0.89, and 1:2.27-2.38, respectively.

Antennules reaching about distal end of third urosomal segment, nineteenth and longest segment (Figure 4F) with width:length ratio of 1:3.75-3.86. Other cephalic appendages as in *A. acutus*. On second leg (Figure 4H), endopod extending beyond distal end of second exopodal segment. Terminal expodal spine longer than third exopodal segment, with about 24 teeth. Second to fourth segments of fifth leg (Figure 4I) with width:length ratios of 1:3.34-4.00, 1:6.00-6.25, and 1:5.00-6.65, respectively.

Remarks.—The male of *A. giesbrechti* is close to *A. mexicanus* in size but can be distinguished from it by the more produced forehead, wide and curved metasomal process, relatively short urosomal segments, wide nineteenth segment of the antennule, and long endopod of the second leg.

A. giesbrechti, including the male, was first described with figures by Giesbrecht (1892) under the name of *A. armatus*. Although the female has been reported by many authors, the male has since been found only by Bradford (1971). The female specimens found in the present study (1.84-2.08 mm in body length according to 76 randomly selected specimens) are in agreement with the descriptions given by Grice (1962) for the Pacific specimens. The appendages are identical with those of *A. acutus*, but the females of the two species are different in the form of spermatheca (Figure 4A).

Distribution.—As reviewed by Vervoort (1957), *A. giesbrechti* has been found throughout the world's oceans, except for the high latitudes. In the Gulf of Mexico the species is quite common in the upper 500 m.

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NORMAL POSTMORTEM CHANGES IN THE BROWN SHRIMP, *PENAEUS AZTECUS*[1]

DONALD V. LIGHTNER[2]

ABSTRACT

A study was carried out to determine the normal rates and patterns of gross and histologic postmortem changes in the brown shrimp (*Penaeus aztecus* Ives). Experimental shrimp were held at 10°, 20°, or 30°C in water-saturated air or in seawater at a salinity of 30‰. Observations were made at 0, 2, 4, 8, 12, 24, 48, and 72 h postmortem.

The first change observed grossly was the onset of a rigorlike stiffening of the abdominal musculature. This stiffening was noted at 2 h postmortem at 30°C, but disappeared by 12 h postmortem. The condition appeared later and persisted longer at the lower temperatures.

Histologically, the tubule epithelium of the hepatopancreas was the first tissue to show autolytic change. The autolysis in the remaining tissues examined occurred in the following order: foregut and midgut epithelium, heart, neurons and nerve fibers, antennal gland epithelium, gill epithelium, epidermis, muscle, and lastly connective and cuticular tissue elements. In all tissues the rate of autolysis was temperature-dependent.

Shrimp from the Gulf of Mexico represent one of the most valuable fishery products of the United States. Their popularity as a food item and for use as sportfishing bait in some coastal areas has resulted in recent studies aimed at developing methods of artificially culturing these animals. Despite the enormous value of shrimp as a seafood, little is known about their histology and the rates and patterns of postmortem change.

Postmortem biochemical changes in the muscle of brown shrimp (*Penaeus aztecus* Ives) were reported by Flick and Lovell (1972). They reported that the compounds ATP, ADP, AMP, IMP, and glycogen decreased with time postmortem, while inosine, hypoxanthene, and lactic acid increased. The latter compounds were suggested as being partly responsible for flavor deterioration of ice-stored shrimp. Tissue pH values increased from 7.4 to 8.2 after 10 days in ice-stored shrimp (0°C), and, according to these authors, even with advanced bacterial spoilage, increases in pH are usually observed in fish and shellfish. Shrimp tails remained tender and soft during the entire storage period of 10 days (at 0°C) and did not exhibit any of the characteristics commonly associated with rigor mortis (Flick and Lovell, 1972).

In the only histologic study of postmortem change in an invertebrate animal, Sparks and Pauley (1964) reported the normal postmortem changes in the oyster, *Crassostrea gigas*. The digestive tubules of the oyster underwent the most rapid autolytic change in dead oysters held at 14°-16°C, while the Leydig tissue, gut, stomach, mantle, gill and palps autolyzed somewhat less rapidly. The gonads were the most resistant of all oyster tissue to autolysis with ova and sperm appearing relatively normal even after all other tissues had undergone extensive autolysis.

There are certainly a number of factors which influence the rate of autolysis in a dead animal. Some of these factors include water temperature, dissolved oxygen concentration, pH, bacterial flora of the water and of the animal, and the physiological condition of the animal at the time of death. It has been demonstrated in man and other animals that postmortem changes occur in a regular and irreversible pattern and at a relatively constant rate from one individual to another when factors causing variation in the rate and pattern are considered (Sparks and Pauley, 1964). Differentiation of histological changes due to disease from those due to postmortem autolysis or poor fixation is possible once the normal rates and patterns

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of postmortem changes under various conditions are known.

The present study was undertaken to determine the normal rates and patterns of postmortem change in penaeid shrimp as an aid in distinguishing gross and histologic changes due to autolysis from changes due to disease.

MATERIALS AND METHODS

Juvenile brown shrimp averaging 50 mm in total length (tip of rostrum to tip of telson) were obtained live from a commercial bait dealer and were held in 500-liter fiberglass tanks for several days prior to being killed. Control shrimp were killed by immersion in fixative. The remaining shrimp were killed by placing the shrimp between wet towels in an enamel tray for 30 min. The shrimp were removed after 30 min and placed into 100-ml glass jars. Two groups at three temperatures (10°, 20°, and 30°C) were studied: one in air and the other in seawater. Shrimp held in air were introduced wet into test jars and the jars were sealed. Shrimp held in water were introduced into the test jars and enough Instant Ocean[3] artificial seawater (at 30 ‰ salinity) was added to fill the jars. Jars were held in wire baskets at midlevel in constant temperature baths.

Samples for antemortem examination were taken at 0 h while those for postmortem examination were taken at 2, 4, 8, 12, 24, 48, and 72 h. Four control shrimp were taken for study and two shrimp (one from seawater and one from air) were taken from the 10°, 20°, and 30°C baths at each of the remaining sampling times.

General appearance, color, odor, and condition of the hepatopancreas were noted at each sampling period. Tissues for microscopic examination were preserved in 10% buffered Formalin, prepared for microscopy with standard paraffin embedding and sectioning methods, and stained with hematoxylin and eosin.

RESULTS

Gross Observations

The first change observed was the onset of a rigorlike condition of the abdomen which appeared at about 2 h after death at 30°C and at 4 and 24 h at 20° and 10°C, respectively. The abdomen became flaccid at 12 and 48 h after death in shrimp held at 30° and 20°C, but at 10°C the abdomen remained rigid at 72 h after death (Table 1).

TABLE 1.—Time of onset of a rigor-like stiffening of shrimp abdominal musculature at 10°, 20°, and 30°C in air and seawater.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	–	–	–	–	–	–
2	–	–	+	–	+	+
4	–	–	+	–	+	+
8	–	–	+	+	+	+
12	–	+	–	+	–	–
24	+	+	+	+	–	–
48	+	+	–	–	–	–
72	+	+	–	–	–	–

+ = stiff
– = flaccid

Color change and the appearance of spoilage odor were first observed at 4 h after death at 30°C. The general appearance of the shrimp changed from the usual semitransparent to a whitish-opaque at about the same time the first trace of odor was detected (Tables 2 and 3). At 20° and 10°C the first color change and appearance of odor were noted at 12 h and 24 h, respectively. At all three temperatures the color of the shrimp changed from opaque to an orange-red and finally to red with some blackened areas (Table 2). The intensity of spoilage odor increased along with the color change (Tables 2 and 3).

Fluid leakage from the hepatopancreas was first observed at 4 h at 30°C and at about 8 and 12 h postmortem at 20° and 10°C. Enzymatic digestion of hepatopancreas and surrounding tissues was grossly evident at 12 h at 30°C as

TABLE 2.—Times of postmortem color change of whole shrimp at 10°, 20°, and 30°C in air and seawater.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	–	–	–	–	–	–
2	–	–	–	–	–	–
4	–	–	–	–	0	0
8	–	–	–	–	0	0
12	0	–	–	0	LR	LR
24	LR	0	LR	LR	Rb	Rb
48	LR	LR	R	Rb	Rb	R
72	Rb	R	Rb	R	Rb	Rb

– = normal
0 = opaque
LR = orange to light red
R = red
Rb = red with blackened edges of cuticle or blackened appendages

[3] Reference to trade names in this publication does not imply endorsement of commercial product.

TABLE 3.—Time of appearance of postmortem spoilage odor in whole shrimp held at 10°, 20°, and 30°C in air and seawater.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	−	−	−	−	−	−
2	−	−	−	−	−	−
4	−	−	+	−	+	+
8	−	−	+ +	−	+	+
12	−	−	+ +	−	+ +	+ +
24	+	+	+ +	+ +	+ +	+ +
48	+ +	+	+ + +	+ + +	+ + +	+ + +
72	+ +	+ +	+ + +	+ + +	+ + +	+ + +

− = normal
+ = odor

indicated by a loosening of the junction of the cephalothorax and abdomen. By 48 h the junction was very loose and by 72 h the tissues of the junction appeared mostly liquified. At 10° and 20°C the same process was observed but at a proportionately slower rate.

Histological Observations

Since the same patterns of autolysis were seen in shrimp held at all three temperatures, the differences being a function of time (Table 4), only the histological results from the 30°C portion will be presented in the text. The only significant histological differences between groups held in air and water noted were the more rapid tissue decomposition due to increased bacterial action in animals held submerged in seawater.

Digestive Tract

According to Roberts (1966), the digestive tract in shrimp is composed of three divisions: (1) the foregut, which includes the mouth, esophagus, stomach, and associated glands; (2) the midgut and hepatopancreas; and (3) the hindgut. Of these organs the hepatopancreas, the foregut, and midgut were studied in detail. The hindgut was not studied.

Hepatopancreas

The glandular hepatopancreas is the first organ to undergo autolytic change (Figure 1a). This organ is a compound tubularacinar exocrine gland composed of tubules which end in blind sacs or acini. The tubules and acini are lined with a simple low to high columnar epithelium (Figure 1b). Autolysis of the epithelium of this

TABLE 4.—Rate of postmortem histologic change in shrimp held in air or seawater at three temperatures.

a. Hepatopancreas.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	0*	0	0	0	0	0
2	2.5*	2.5	2.5	2.5	3	3.5
4	4	4	4	4	4	4
8	4	3.5	4.5	5	4.5	4.5
12	3.5	4	—	—	5	5
24	5	4	5	5	5	5
48	5	5	5	5	5	5
72	5	5	5	5	5	5

b. Midgut epithelium.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	0*	0	0	0	0	0
2	1*	1	1	1	1-2	1
4	2	1	1-2	1-2	—	2
8	4	—	4-5	—	3	4
12	—	3	2	4	5	4
24	5	4	—	5	5	—
48	5	5	5	5	—	5
72	5	5	5	5	5	5

c. Abdominal muscle.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	0*	0	0	0	0	0
2	0	0	0	0	0	0
4	1	1	2	1	1.5	1
8	0	1	2	2	2	2
12	1	1	2.5	2.5	3	3
24	3	3	3.5	3	3.5	3.5
48	2.5	3	4	4	3.5	4.5
72	4	3.5	4.5	4	4.5	4

d. Epidermis.

H postmortem	Temperature (°C)					
	10°C		20°C		30°C	
	Air	Water	Air	Water	Air	Water
0	0*	0	0	0	0	0
1	0	0	0	0	0	0
2	0	0	0	0	0	0
4	0	1	—	—	2	2
8	1	1	—	2	3	3
12	2	2	3	3	4	4
24	3	3	3	3	4	—
48	3	3	4	4	5	5
72	5	5	5	5	5	5

— No observation made.
* Average assigned values from a scale of 0 to 5 denoting the general histological appearance of the tissue or organ.
0 = Normal histologic appearance, like the control, no postmortem change.
1 = Slight change, scattered pyknotic nuclei, slight staining differences.
2 = More advanced cellular change with increases in nuclear pyknosis, karyrhexis, karyolysis, some cytolysis; loss of normal appearance or structure of the tissue or organ.
3 = Further advanced change with no normal appearing areas.
4 = Advanced autolytic change, tissue or organ represented by cellular debris or by its fibrous or cuticular stroma.
5 = Complete autolysis, tissue or organ no longer demonstrable.

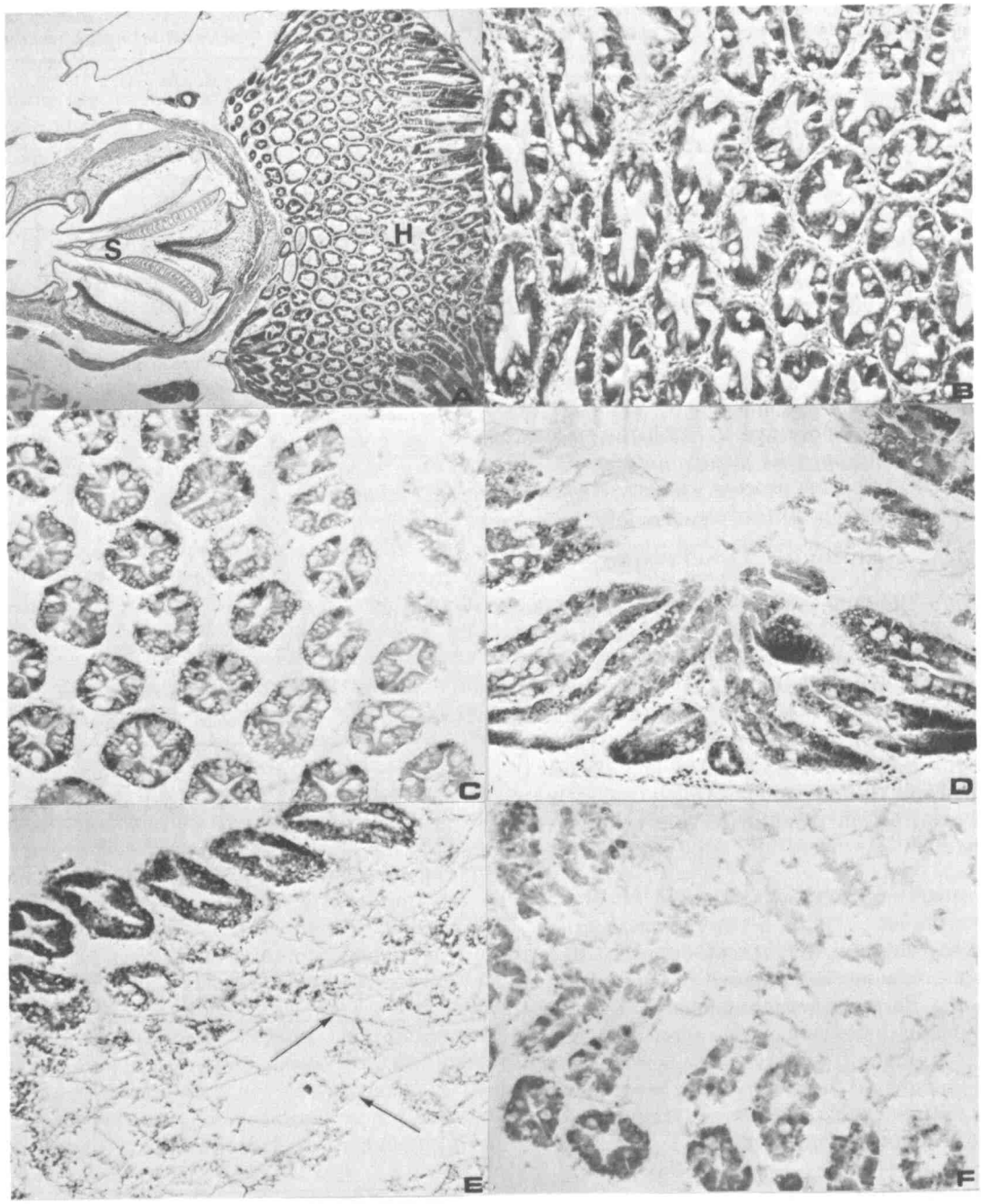

FIGURE 1.—**a.** Normal stomach (S) and hepatopancreas (H). 25×. **b.** Normal hepatopancreas. 120×. **c.** Hepatopancreas at 2 h postmortem showing edematous swelling between adjacent tubules. Autolysis is more advanced nearer the center of the organ (upper right) than at the periphery (left). 110×. **d.** Hepatopancreas at 4 h postmortem showing tubules on longitudinal section. Note the progression of autolytic change in the tubules from the periphery of the organ (bottom) to the autolyzed center (top). 110×. **e.** Hepatopancreas showing near complete autolysis (4 h postmortem). Note network of connective tissue stroma (arrows) remaining after autolysis of tubule epithelium. 120×. **f.** Hepatopancreas at 8 h postmortem showing advanced autolysis. Intensely pyknotic nuclei are present in the remaining epithelial cells near the periphery of the organ. Tissue debris and remnants of the connective tissue stroma are present nearer the organ's center (upper right). 120×.

organ proceeds so rapidly that by 2 to 4 h postmortem, the epithelium of tubules near the center of the organ showed advanced autolysis. These tubules showed desquamation and cytolysis of the lining epithelium and replacement with eosinophilic debris (Figures 1c and 1d). Nearer the periphery of the organ, the condition of the tubules and tubule epithelium appeared progressively more normal, with the most normal appearing tubules and acini at the periphery (Figures 1c and 1d). In the band of tissues between the normal appearing periphery and the lysed core, all stages of cell death were observed. A thin band of tissue in this area contained tubules whose epithelial cells possessed scattered pyknotic nuclei and had slight cytoplasmic staining differences (Figure 1e). Deeper to this layer the epithelial cells of tubules and acini possessed scattered pyknotic nuclei and had slight cytoplasmic staining differences (Figure 1e). The cytoplasm of these cells was highly vacuolated and stained variably with hematoxylin and eosin but generally much less basophilicily than normal (Figure 1c). At this time the spaces between adjacent tubules and acini had become swollen (Figures 1c and 1d). Slightly deeper to this layer epithelial cell nuclei had undergone karyorrhexis or karyolysis and disappeared. Many of the cells of this area had lysed and the cellular debris stained red with eosin. The supportive stroma of the hepatopancreatic tubules remained intact in some areas after the epithelium had autolyzed, thereby masking the former site of the hepatopancreatic tubules (Figure 1e).

By 8-12 h postmortem even the tubules and acini at the periphery of the organ showed advanced autolytic change, and the tissue debris and remnants of supportive stroma in the center of the organ were liquified (Figure 1f). The connective tissue capsule of the organ had become ruptured and few recognizable tubules were present. Past 12 h no trace of the hepatopancreas was present, and surrounding tissues had also been partially or completely digested, presumably by enzymes released from the autolyzed hepatopancreas.

Foregut and Midgut

Autolytic changes in the foregut, particularly the epithelium of the stomach (Figure 1a), proceeded at approximately the same rate as changes in the hepatopancreas. Nuclear changes within epithelial cells were observed at 2 h postmortem with considerable change by 4 h. By 8 to 12 h the epithelium of the stomach had undergone nearly complete autolysis and had disappeared, leaving only the cuticular elements of the stomach lining intact. The cuticular elements of the esophagus and stomach persisted for the duration of the study (72 h).

The midgut extends from the pyloric stomach to the sixth abdominal segment where it joins with the hindgut (Roberts, 1966). It is without a lining cuticle. The first autolytic change in the midgut was observed in the lining epithelium at 2 to 4 h, when the epithelial cells began to show changes such as scattered pyknotic nuclei, changes in staining reaction from a pale basophilic reaction to a more eosinophilic one, and the "blebing" of the apical ends of epithelial cells into the gut lumen (Figure 2a). The epithelium usually remained attached to the basement membrane at 2 h, but in some areas portions of the midgut epithelium had been sloughed into the gut lumen (Figures 2b and 2c). Sloughed epithelial cells were rounded and had intensely pyknotic nuclei and a uniform eosinophilic cytoplasm. At this time the gut lumen usually contained a fibrous, eosinophilic coagulum (Figure 2b). The gut wall basal to the lining epithelium showed no appreciable changes by 4 h.

By 8 to 12 h the midgut epithelium had been sloughed into the gut lumen (Figure 2d). The epithelial cells in the gut lumen were rounded, and some had pyknotic nuclei, but they were mostly anucleate. Many of the epithelial cells had lysed and left behind amorphous masses of eosinophilic debris (Figure 2d). Changes in the cellular elements of the wall of the midgut became apparent by 8-12 h. These changes consisted primarily of a decrease in nuclear number in the muscle and connective tissue cells present and pyknosis of those nuclei remaining (Figure 2d). In general, the cytoplasm of the cells present showed increased eosinophilia.

No trace of the lining epithelium was present after 24 h (Figure 2e). The coagulum, which was present in the gut lumen of some animals at 2-8 h, was still present. Also present in the gut lumen were large numbers of bacteria (Figure 2e). No nuclei were present in the gut wall, and the cellular elements remaining stained intensely with eosin.

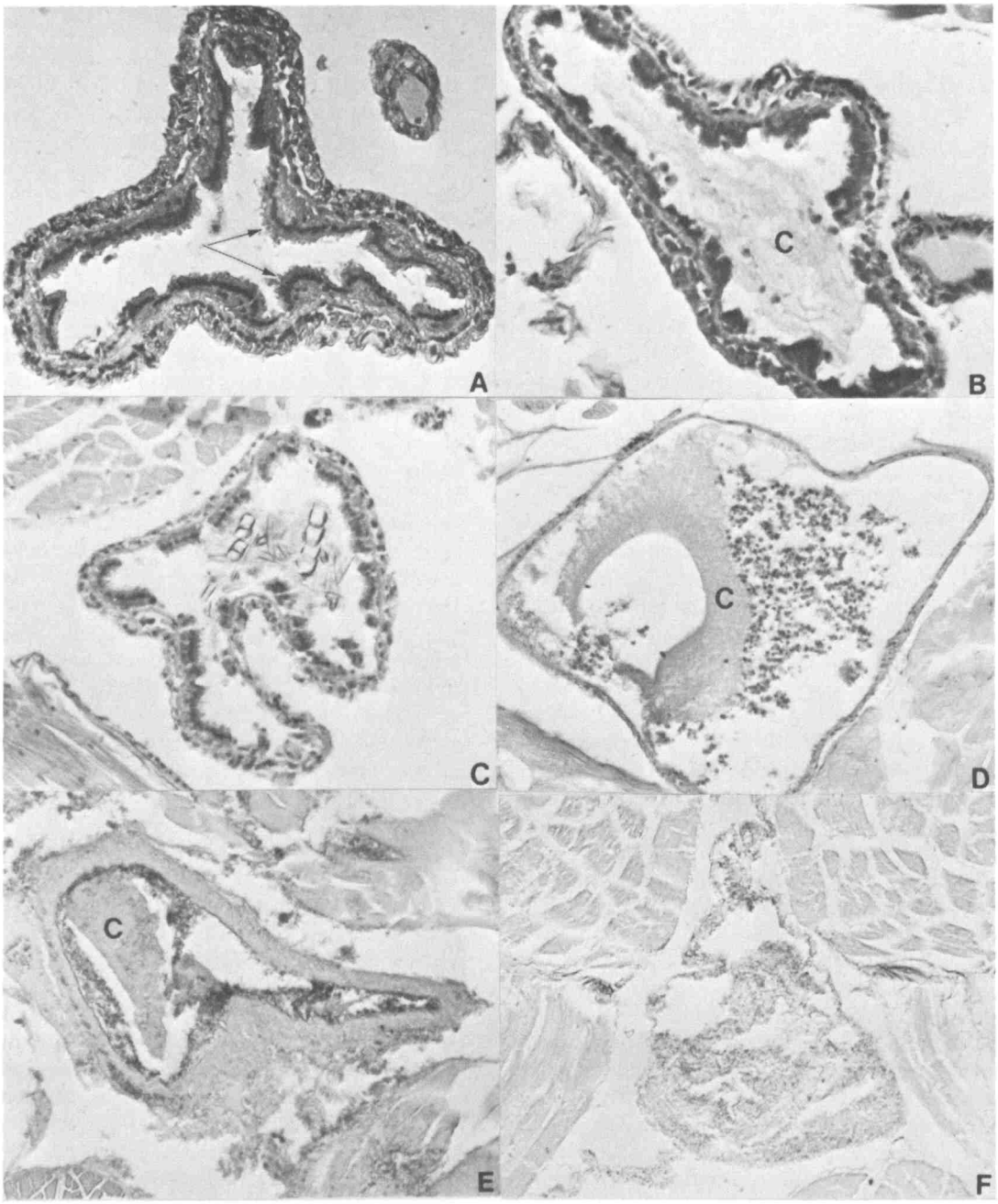

FIGURE 2.—**a.** Cross section of midgut at 2 h postmortem. The appearance is near normal except for the "blebing" of the apical ends of some of the epithelial cells (arrows) and a few pyknotic nuclei. 250×. **b.** Midgut showing more advanced autolytic change at 2 h postmortem. Some epithelial cells have been sloughed into the gut lumen where an eosinophilic coagulum (C) has formed. 240×. **c.** Midgut at 4 h postmortem. Most of the epithelial cells possess pyknotic nuclei, and some of the cells have been sloughed into the gut lumen. 210×. **d.** Midgut at 8 h postmortem. Sloughed epithelial cells are rounded and are either anucleate or have pyknotic nuclei. An eosinophilic coagulum is present. 160×. **e.** Midgut at 24 h postmortem. An eosinophilic coagulum is present in the gut lumen as are numerous bacteria. No trace of the gut epithelium remains. The muscle and fibrocyte cells of the gut wall are anucleate. 190×. **f.** Site of midgut at 48 h postmortem. Bacteria and debris have filled the gut lumen. Only fibrous elements of the gut wall remain. 150×.

By 48 h, the gut wall had become thin and was frequently interrupted. The gut lumen was filled with bacteria and other debris (Figure 2f). By 72 h, all traces of the gut, including the gut wall, had disappeared leaving the former site of the gut marked only by masses of bacteria and amorphous eosinophilic cellular debris.

Heart and Major Vessels

In shrimp the heart lies immediately dorsal and slightly caudad to the large hepatopancreas. Only the thin connective tissue coverings of the two organs separate them. Hence, autolysis of the hepatopancreas and release of its proteolytic enzymes results in a rapid destruction of the rather loose tissues of the shrimp heart (Figure 3a). The hepatopancreas showed considerable autolytic change by 4 h postmortem leaving the heart barely recognizable (Figure 3b). By 8 h the heart was not distinguishable from the other tissue debris present at the heart's former location in the cephalothorax. Vessels in the vicinity of the hepatopancreas and heart also disappeared by 4-8 h, but vessels elsewhere, such as in the abdomen, persisted much longer, some still recognizable after 24 h. However, by 48 h vessels were not usually demonstrable anywhere in the body of a shrimp.

Musculature

Shrimp locomotory muscle is striated and presents a histologic appearance that is similar to that of vertebrate striated muscle (Figure 4a). The muscles of the cephalothorax in the vicinity of the hepatopancreas underwent rapid autolytic change, apparently due to digestion by enzymes released on lysis of the hepatopancreas. Further from the hepatopancreas, the rate of autolytic change in the muscle was much slower. The earliest observed postmortem change in the muscle was at 4 h when some individual muscle fibers had a slightly "frayed" appearance. There was a pronounced swelling, presumably edematous, between adjacent muscle fibers (Figure 4b). By 8-12 h, muscle cell nuclei had become pyknotic. After 24 h muscle cells had become anucleate, highly eosinophilic, and the edematous swelling between adjacent muscle cells had decreased. Cross striations within muscle fibers were especially evident (Figures 4d, 4e, and 4f).

In some, but not all, of the shrimp studied, bacterial growth was evident between muscle bundles, especially in the vicinity of the gut. The presence of large numbers of bacteria greatly increased the rate of tissue deterioration (Figure 4c), while muscle not heavily invaded by bacteria remained recognizable as muscle tissue at 72 h (Figure 4f).

Integument

The integument, consisting of epidermis and an overlying cuticle, underwent rapid degeneration in the area of the cephalothorax that surrounds the hepatopancreas, leaving only

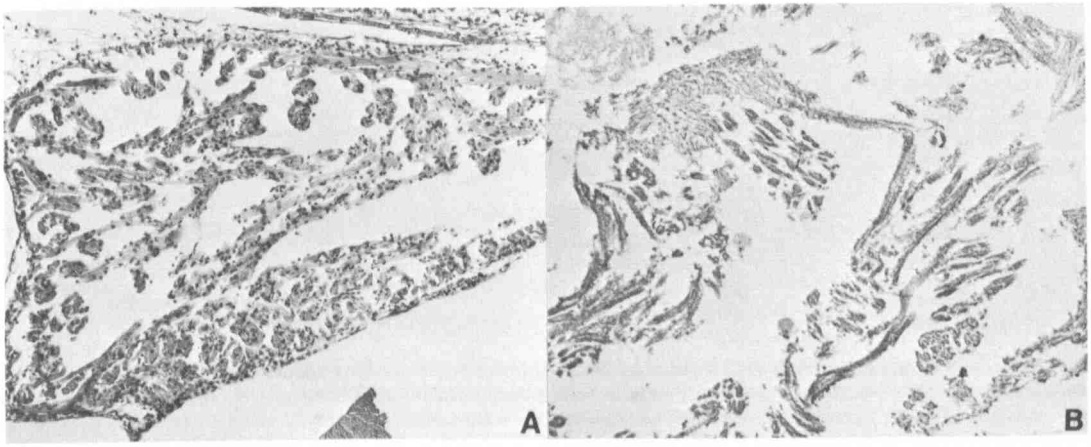

FIGURE 3.—**a.** Normal heart. 110×. **b.** Heart at 4 h postmortem showing considerable autolytic change and loss of structural detail. 100×.

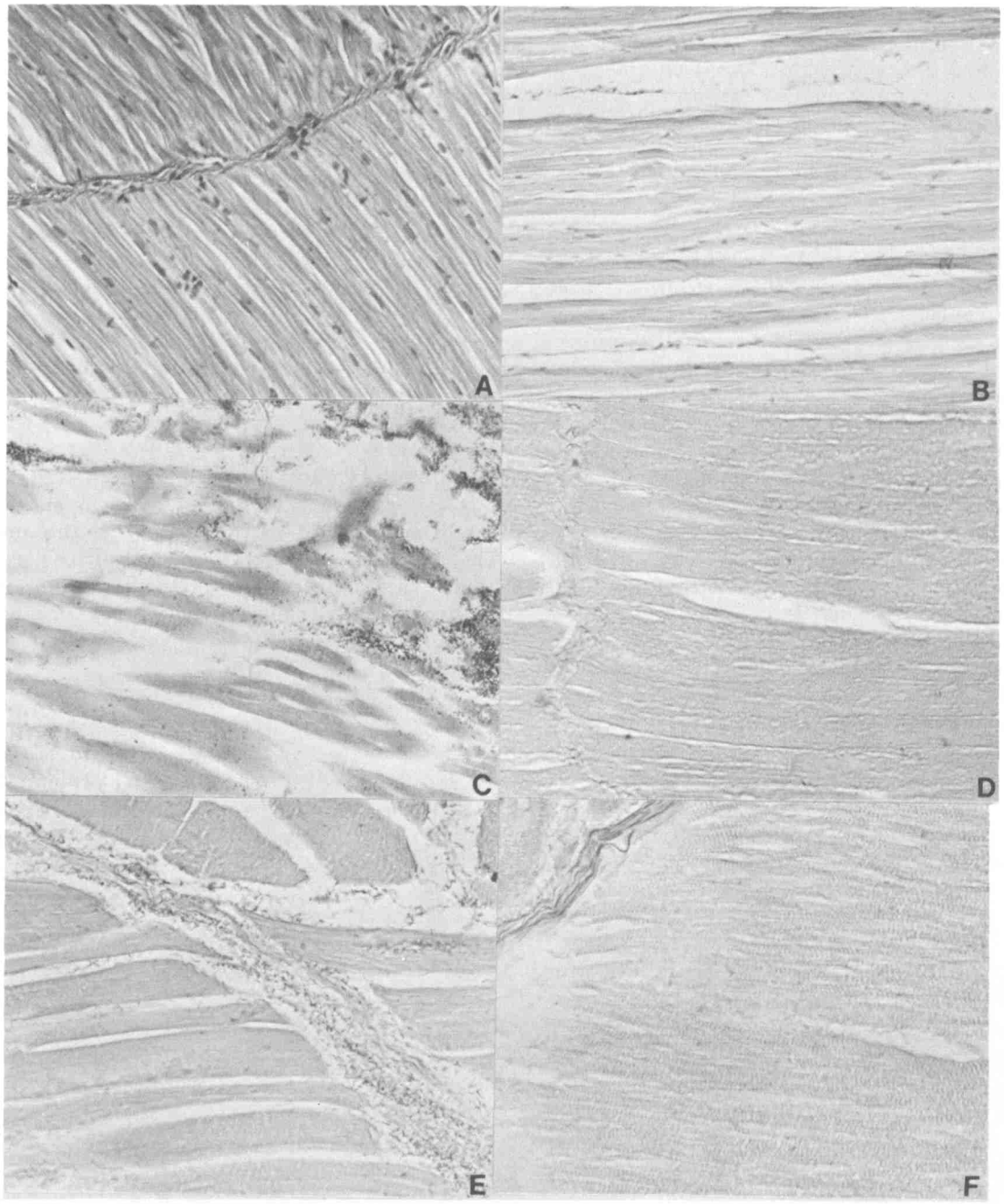

FIGURE 4.—**a.** Normal abdominal muscle. 220×. **b.** Muscle at 4 h postmortem showing edematous swelling between muscle bers. Sarcoplasmic staining reaction is more eosinophilic than normal and there has been a decrease in the number of nuclei although few pyknotic nuclei are shown. 150×. **c.** Muscle showing advanced autolytic change due to the presence of large amounts of bacteria (12 h postmortem). 190×. **d.** Muscle at 24 h postmortem. Edematous swelling has decreased, but the muscle fibers have become anucleate. Note the prominence of cross striations. 240×. **e.** Muscle at 48 h postmortem. 240×. **f.** Muscle fibers with prominent cross striations are still recognizable at 72 h postmortem. 250×.

the cuticle remaining by 4 h. Distant from the hepatopancreas, the epidermis showed pyknotic nuclei and cell rounding by 4 to 8 h (Figures 5a and 5b). A slight hemocytic response was present at this time in the subepidermal tissue layers representing the only inflammatory-like response observed in the study.

The epidermis had frequently become detached from the overlying cuticle by 12 to 24 h postmortem and many of the epidermal cells had lysed, with those remaining having pyknotic nuclei (Figure 5c). By 24 to 48 h nearly all traces of the epidermis had been lost and in some animals examined only cellular debris or clumps of bacteria marked its former location (Figure 5d). Though usually interrupted, the cuticle was the most resistant structure to autolytic change and showed only slight histological change by 72 h.

Gills

The shrimp respiratory system consists of paired gills in the branchial chambers of the cephalothorax. The structure of the gills is dendrobranchiate (Barnes, 1963). The gills are covered by a thin cuticle underlain by a thin epithelium and other supportive cells (Figure 6a).

A peritrichous ciliated protozoan (Figure 6b), presumably a commensal on shrimp (especially common on the gills but also found elsewhere on

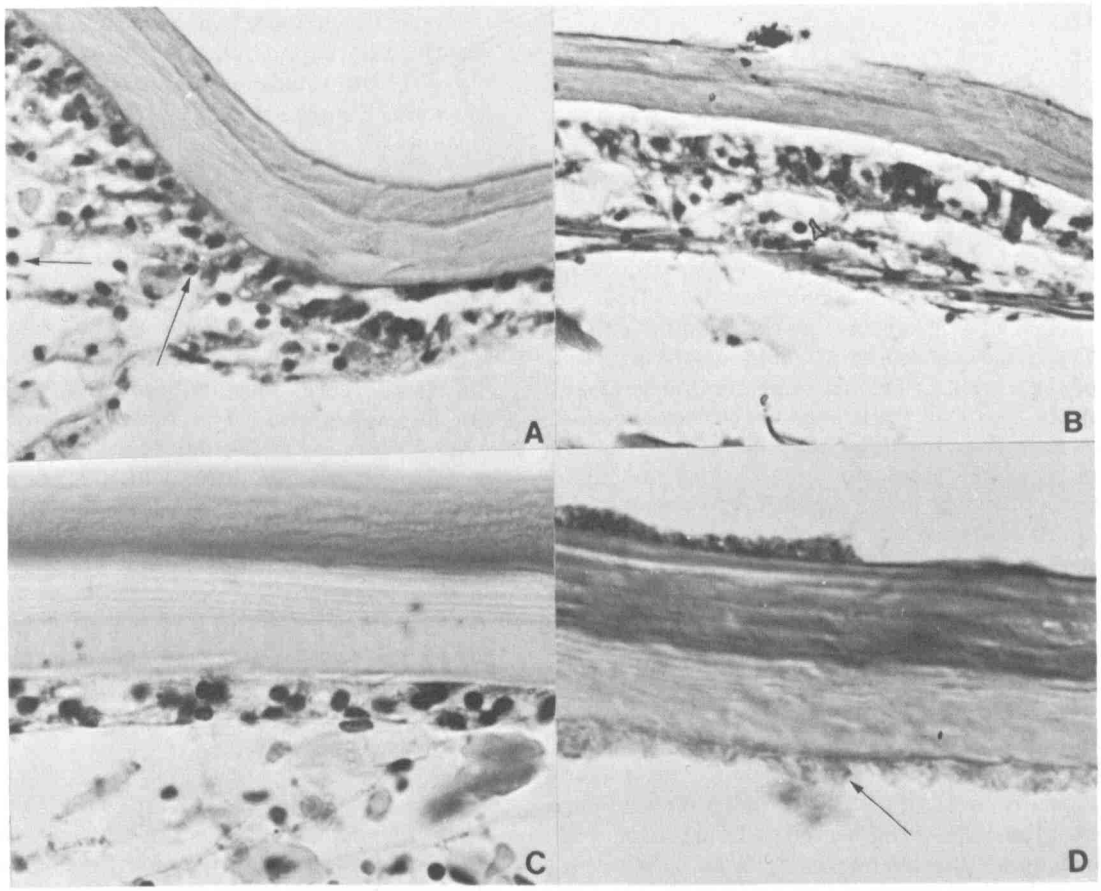

FIGURE 5.—**a.** Integument consisting of epidermis and overlying cuticle at 4 h postmortem. Some of the epidermal cells possess pyknotic nuclei. A few hemocytes are present in the subepidermal tissues (arrows). 480×. **b.** Integument at 8 h postmortem. Inflammatory cells are present in the subepidermal tissue. There is an increase in nuclear pyknosis in the epidermis and in the subepidermal tissue. 300×. **c.** Epidermis and cuticle at 24 h postmortem. All of the epidermal cells have intensely pyknotic nuclei, as does all the subepithelial tissue. 600×. **d.** Integument at 48 h postmortem. The cuticle is present, but the epidermis is represented by debris (arrows). 750×.

the body surface), increased rapidly in numbers for 2 to 4 h after death of the shrimp. They were absent by 8 h postmortem.

The cellular elements of the gills underwent fairly rapid autolytic change. By 8-12 h scattered pyknotic nuclei were present (Figure 6c). By 24 h the cellular elements of the gills were for the most part anucleate, with some portions of the gills having only eosinophilic debris within the lamellar cuticle (Figure 6d). By 48 h the thin cuticle of gill lamellae had begun to deteriorate and hence the gill lamellae sectioned transversely began to lose their typical "dumbbell" appearance (Figure 6e). By 72 h the gills were usually no longer demonstrable histologically, but in one of four animals examined portions of the gills were still evident (Figure 6f).

Nerve Tissue

The nervous system of shrimp is composed of a large ventral nerve cord and segmental ganglia from which smaller nerve branches originate to innervate the tissues. At the anterior end of the ventral nerve tract is the supraesophageal ganglion, which anteriorly receives the large optic nerve tracts.

Neuron perikaryons in the ganglia (Figure 7a) underwent the most rapid autolytic change of the various elements of shrimp nerve tissue. After 2 to 4 h, these cells showed considerable rounding, pyknotic or karyolytic nuclei, and a change in cytoplasmic staining from highly basophilic to a lesser basophilic to almost eosinophilic (Figure 7b). By 8 h no trace of neuron perikaryons was evident.

The nerve tracts of the ventral nerve, its branches, and the optic nerves autolyzed less rapidly than did neuronal perikaryons. However, nerve cell processes (axons and dendrites) within the nerve tract autolyzed more rapidly than did the supportive neurolemmal and glial cells, and were no longer demonstrable histologically by 12 to 24 h (Figure 7c). The supportive glial cells of the nerve tracts persisted without noticeable change to 8 to 12 h, but these cells became anucleate or underwent autolysis after 24 h, and their former presence was represented only by debris and an occasional pyknotic nucleus (Figure 7d).

After 24 h postmortem, the basic structural arrangement of the nerve tract remained recognizable due to the persistence of neurolemmal fibers (Figures 7d and 7e), which persisted to 72 h at the sites of the optic nerve and ventral nerve tracts.

Antennal Gland

The antennal gland of crustaceans had been demonstrated to be important in ion regulation (Robertson, 1959). The antennal or hemocoelic excretory gland in shrimp is located in the cephalothorax above the supraesophageal ganglion (Young, 1959). The gland is composed of a collection of tubules and a bladder (Figures 8a and 8b). By 4 h some sloughing of tubule epithelium was evident (Figure 8b), but for the most part the histologic appearance of the organ remained normal. At 12 h, however, most of the nuclei of the tubule epithelium were intensely pyknotic (Figure 8c), and by 24 h the organ had disappeared or had become difficult to recognize (Figure 8d). No trace of the gland was found after 48 h postmortem.

Gonadal Tissue

Since the animals used in this study were immature juvenile shrimp, the gonads were small, poorly differentiated and were located in the cephalothorax lateral and slightly caudad to the hepatopancreas. The terminal ampule of male shrimp was poorly developed and in female shrimp the ovarian lobe, which extends into the abdomen in older shrimp, had not yet developed.

The rate of autolysis in the gonads of the shrimp studied was rapid, due to their close proximity to the hepatopancreas. Gonadal tissue was not recognizable histologically after 4 to 8 h postmortem.

DISCUSSION

The rigorlike stiffening observed in this study may represent true rigor mortis. Sparks (1972) postulated that rigor mortis or a similar phenomenon may occur in some invertebrates with well organized skeletal systems and associated skeletal muscles. He based his opinion on the observation that many arthropods, which are flaccid after somatic death, subsequently

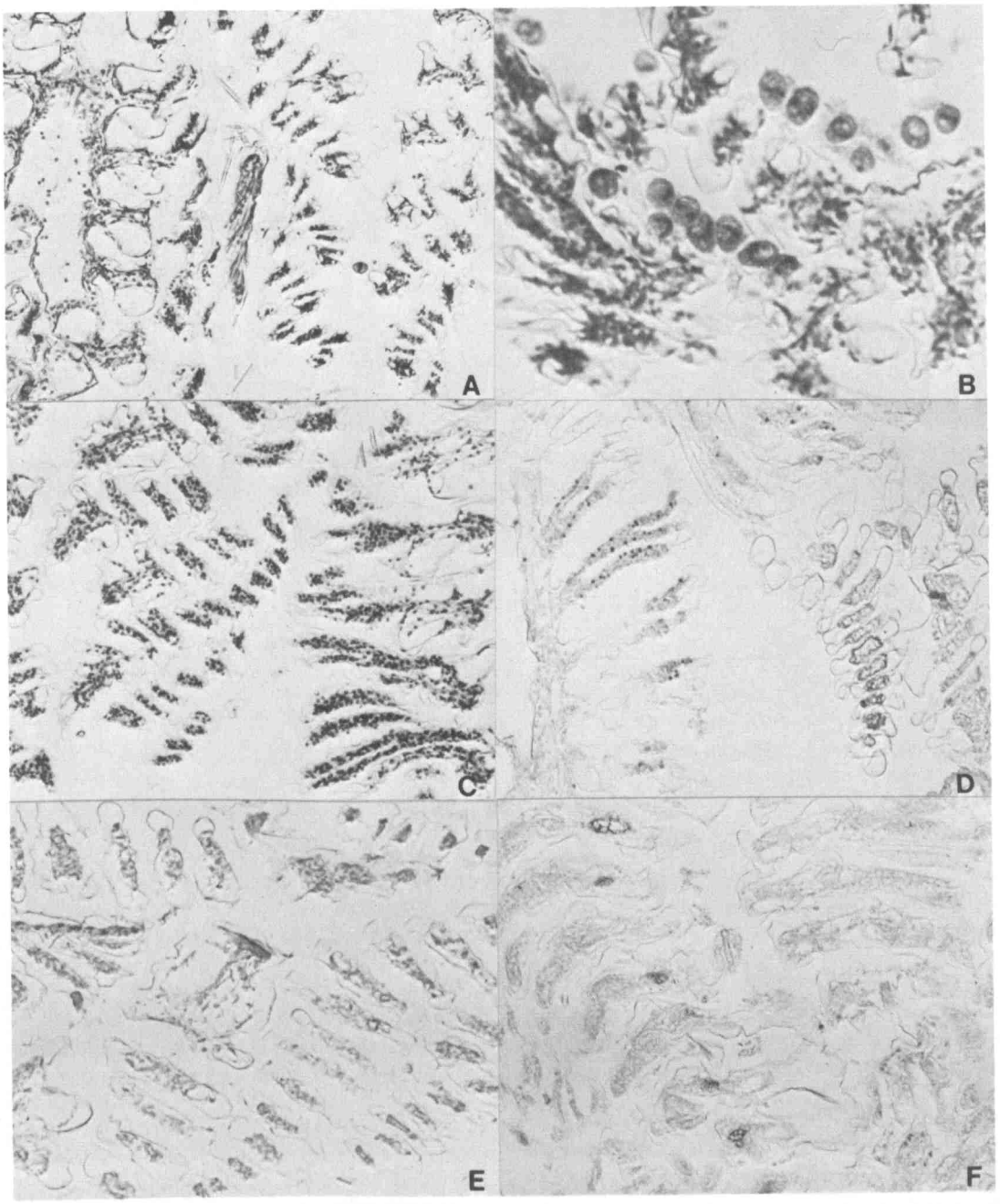

FIGURE 6.—**a.** Normal gills. 120×. **b.** An unidentified ciliated protozoan abundant on the gills at 4 h postmortem. 240×. **c.** Gills at 12 h postmortem. Note the absence of the protozoan and the presence of pyknotic nuclei in the cellular elements. 130×. **d.** Gills at 24 h postmortem. Except for a few pyknotic nuclei only the cuticle and cellular debris remain. 160×. **e.** Gills at 48 h postmortem. The tissue is still recognizable as gills; however, the lamellae are losing their usual "dumbbell" appearance and contain only eosinophilic cellular debris. 190×. **f.** Gills at 72 h postmortem. Gills were recognizable histologically only from this one of four animals examined. 120×.

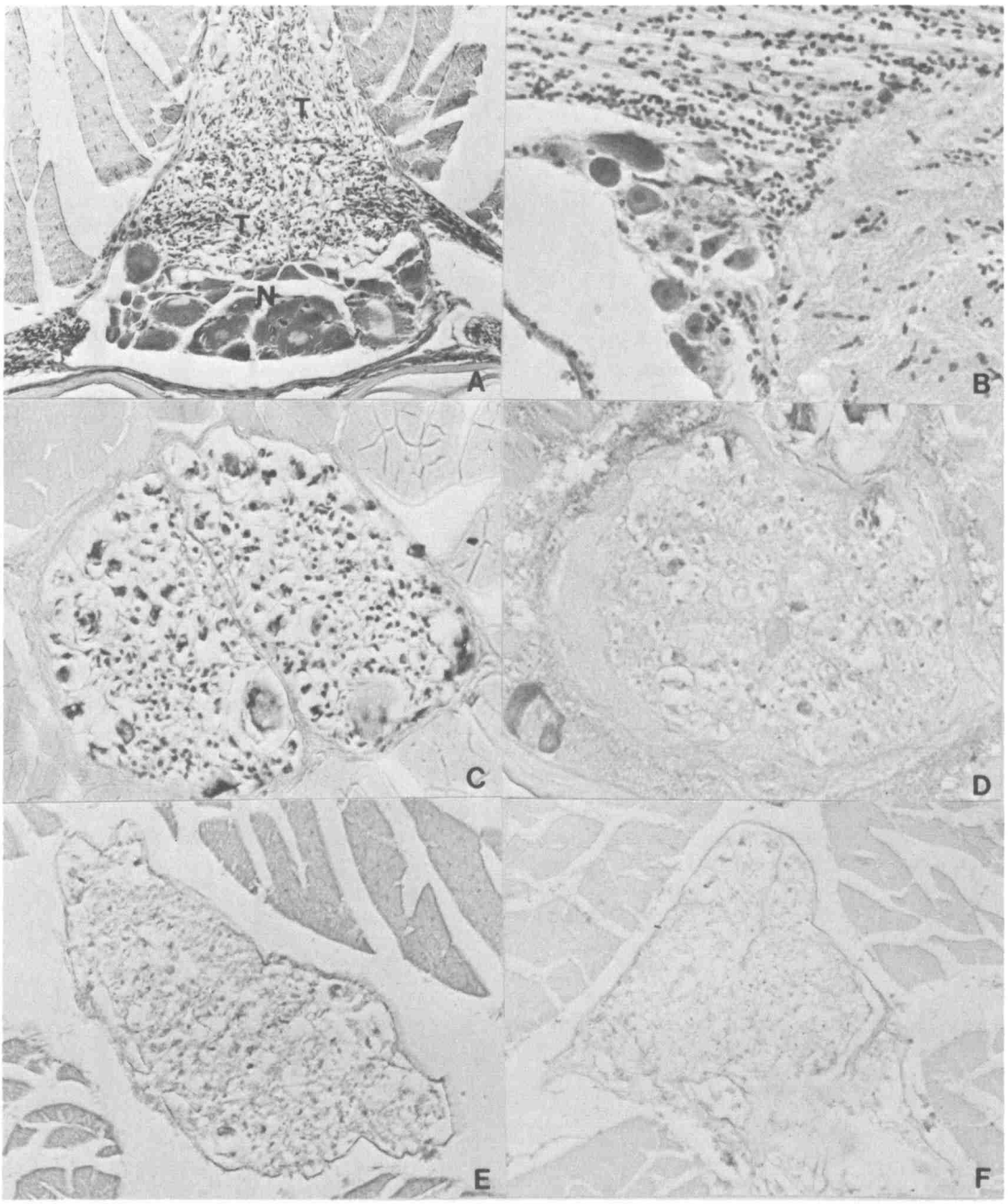

FIGURE 7.—**a.** Cross section of an abdominal segment ganglion on the ventral nerve (0 h control). Neuron perikaryons (N) are present ventral to the large ventral nerve tract (T). 110×. **b.** Sagittal section of an abdominal segment ganglion at 4 h postmortem. The neuron perikaryons are rounded and have pyknotic nuclei. Nerve cell processes, neurolemmal and glial cells in the nerve tract show no apparent autolysis. 220×. **c.** Cross section of the ventral nerve at 12 h postmortem. Nerve cell processes are not evident and neurolemmal and glial cells possess pyknotic nuclei. 200×. **d.** Cross section of the ventral nerve at 24 h postmortem. Only supportive fibrous tissue elements and eosinophilic debris remain. 190×. **e.** Cross section of ventral nerve at 48 h postmortem. Fibrous elements are still present. 200×. **f.** Ventral nerve in cross section at 72 h postmortem. The fibrous elements of the nerve are still present. 120×.

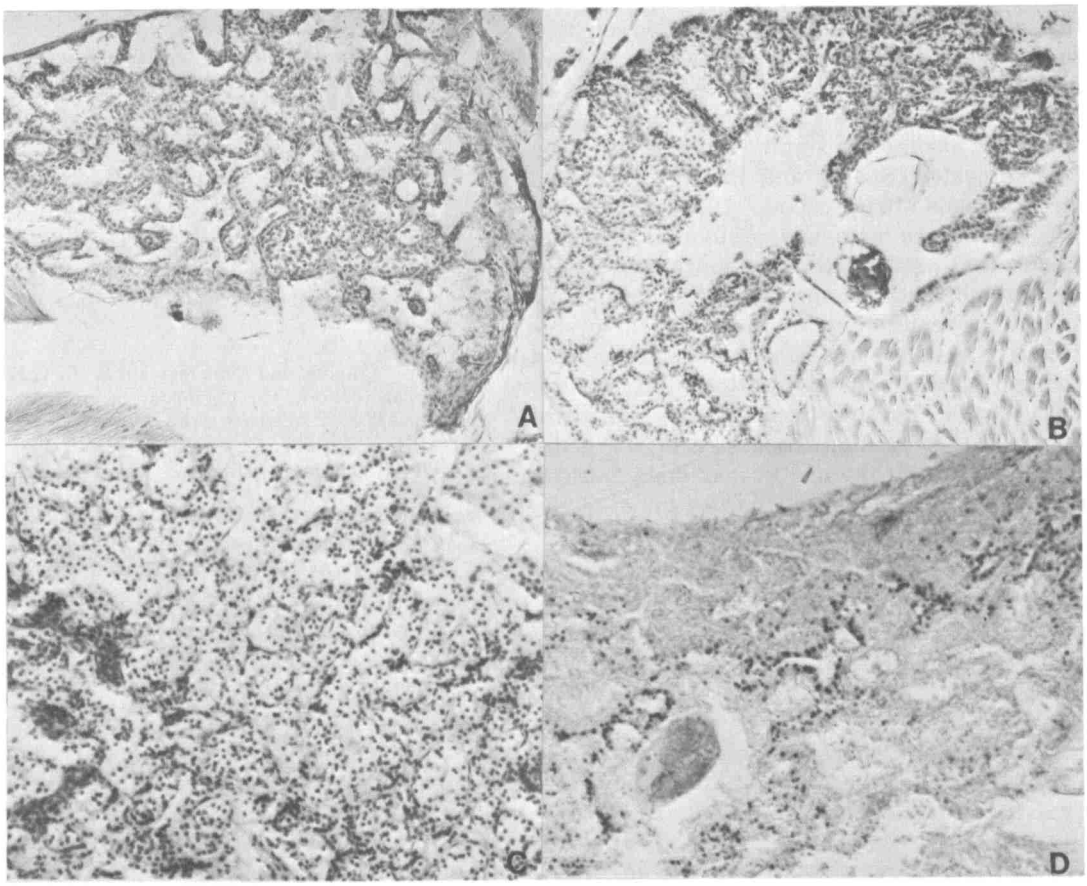

FIGURE 8.—**a.** Normal antennal gland. 100×. **b.** Antennal gland at 4 h postmortem. A few epithelial cells have been sloughed into the tubule lumens. 100×. **c.** The tubule epithelium of the antennal gland at 12 h postmortem showing intense nuclear pyknosis. 150×. **d.** Antennal gland at 24 h postmortem. The tubule epithelium has lysed filling the tubule lumens with eosinophilic debris and nuclear remnants. 150×.

become rigid. Whether this was due to desiccation of the tissues or actual rigor of the muscles was not determined. In the present study, freshly killed juvenile shrimp became rigid in sealed glass jars containing water-saturated air and when totally submerged in water. Desiccation was not possible. The time of onset of rigidity was, as in vertebrates, temperature-dependent, occurring earlier at higher temperatures than at lower temperatures.

Flick and Lovell (1972) in studying postmortem biochemical changes in penaeid shrimp reported that shrimp tails remained soft and did not exhibit any of the characteristics commonly associated with rigor mortis during a storage period of 10 days at 0°C. Perhaps the effect of freezing or near-freezing temperature on shrimp muscle either masks or inhibits the onset of physical rigor.

The rate of autolysis of the hepatopancreas is extremely rapid. The organ is a large, multifunctional organ believed to produce the bulk of enzymes used in the digestive process in shrimp and to have some absorptive and storage function. The hepatopancreas connects to the midgut near its origin from the pyloric stomach. The gut is a short, nearly straight tube, and, hence, enzymatic digestion must occur as rapidly as possible if the shrimp is to utilize its food efficiently. Even careful handling of shrimp to avoid stress before fixation, opening of the cuticle over the hepatopancreas, or excision and bisection of the gland to enhance fixation, frequently failed to provide adequate penetration and fixation of the organ when Formalin fixatives were used. The remaining tissues of shrimp are generally adequately fixed for light microscopy with Formalin, provided

that small pieces of tissue are used or that the cuticle is opened on smaller shrimp that are fixed whole.

The relative rates and patterns of postmortem change in shrimp are similar to those described for the oyster (Sparks and Pauley, 1964) and for mammals (Cruickshank, 1912; Smith and Jones, 1966). In mammals, oysters, and shrimp, tissues that produce large amounts of proteolytic enzymes such as the mammalian pancreas and lining epithelium of the stomach, oyster digestive tubules, and shrimp hepatopancreas and gut epithelium autolyze the most rapidly. Tissues that autolyze nearly as rapidly are high lipid containing tissues such as nerve tissue. In the shrimp and in mammals, muscle, connective, and epidermal tissues undergo the least rapid autolysis.

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BOTHUS THOMPSONI (FOWLER) 1923, A VALID SPECIES OF FLATFISH (PISCES:BOTHIDAE) FROM THE HAWAIIAN ISLANDS

PAUL STRUHSAKER AND ROBERT M. MONCRIEF[1]

ABSTRACT

Bothus thompsoni (Fowler) 1923 is resurrected from the synonymy of *B. bleekeri* Steindachner and redescribed. *B. thompsoni* differs from all other recognized species of the genus in possessing 11-17 gill rakers on the lower limb of the first gill arch and 115-147 lateral line scales. *B. thompsoni* is endemic to the Hawaiian Islands where it inhabits the outer shelf in depths of 70-115 m.

Fowler (1923) proposed *Platophrys thompsoni* on the basis of a single specimen obtained by John W. Thompson. Although no exact locality data were given, we assume the specimen was from the Honolulu market. *Platophrys* is now considered a synonym of *Bothus*, while Norman (1934), without comment, relegated *Bothus thompsoni* to the synonymy of *B. bleekeri* Steindachner. Gosline and Brock (1960) followed Norman in listing *B. bleekeri* from the Hawaiian Islands. Previously, only the holotype of *B. thompsoni* was available for study. Our examination of numerous specimens collected by the National Marine Fisheries Service (NMFS) during recent bottom trawling surveys in the 60-700 m depth range of the Hawaiian Islands demonstrates that *B. thompsoni* should be recognized as a valid species.

MATERIAL AND METHODS

All specimens were collected with 12.5-m (headrope) shrimp trawls during bottom trawling surveys in the Hawaiian Islands with the NMFS RV *Townsend Cromwell*. Sampling effort and general ichthyological results of these surveys are given by Struhsaker (1973). Most specimens examined (one exception from Maui) were from the north coast of the island of Oahu.

The following description is based on a series of 29 male (55.8-114.4 mm SL) and 31 female (39.1-103.7 mm SL) specimens all of which are housed in the National Museum of Natural History (USNM) and Bernice P. Bishop Museum (BPBM). Additionally, 33 uncatalogued specimens cleared and stained by the method described by Taylor (1967) were utilized in vertebral and gill raker counts, and more uncatalogued specimens were examined, obtaining supplementary dorsal, anal, and caudal ray counts.

Measurements and counts are usually as defined by Norman (1934), Hubbs and Lagler (1958), and Gutherz (1967). Standard length was taken from tip of snout to end of hypural plate on the blind side. Horizontal eye diameter was taken between edges of the bony orbits. Snout to axis of greatest depth was taken from the snout to a vertical line at the greatest body depth. The last two dorsal and anal rays are each associated with pterygiophores and are counted as two. Lateral line scale rows just above the lateral line and pored lateral line scales were counted. Vertebral counts were taken from radiographs and from cleared and stained specimens. Gill rakers were counted as discussed below.

To evaluate morphometric characters, measurements in original units and as percent of standard length were plotted as functions of standard lengths.

RESULTS

Description

Although a figure of *B. thompsoni* did not accompany the original description, Fowler (1928), in listing the species for Oceania, provided a figure of the type (Pl. IV, C) which is

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housed in the BPBM (3398). Measurements of the 106.8 mm SL male holotype (Fowler gave an undefined length of 134 mm) expressed as percent of standard length are given in Table 1. We obtained the following counts on this specimen: dorsal rays 86; anal rays 62; caudal rays 16; pectoral rays (both sides) 12; lateral-line scale rows 130; pored lateral-line scales 83; gill rakers 19 (5 + 14). Fowler (1923) gave counts of 132 scale rows and 20 gill rakers (6 + 14). Otherwise, our counts agree with his.

Photographs of recently collected female (106.4 mm SL) and male (114.4 mm SL) specimens (both BPBM 14102) are shown in Figures 1 and 2.

Counts

Dorsal and anal ray counts, expressed as bivariate relations, for 101 specimens are given in Table 2. Dorsal rays ranged from 84 to 95 ($\bar{X}$ = 87.9) and anal rays ranged from 64 to 70 ($\bar{X}$ = 66.3). Although the dorsal ray counts are skewed to the right, the distribution does not deviate significantly from a normal distribution ($P > 0.2$; Kolomogorov-Smirnov test for goodness of fit, D = 0.0702).

There were considerably fewer pored lateral-line scales (Table 3) ($\bar{X}$ = 80.9) than the number of vertical scale rows above the lateral line ($\bar{X}$ = 131.6).

There was a tendency towards more pectoral rays (Table 3) on the ocular side ($\bar{X}$ = 12.24) than on the blind side ($\bar{X}$ = 11.49). The upper pectoral ray on the ocular side is reduced and sometimes inconspicuous. The upper pectoral ray on the blind side is also reduced, but easily visible.

Bothus thompsoni appears to be unique among species of *Bothus* in usually possessing 16 caudal rays. Of 163 specimens examined (Table 3), 2 (1.2%) had 15 rays, 157 (96.3%) had 16 rays, and 4 (2.5%) had 17 rays. The caudal rays are usually associated with the four hypural elements. Of 31 cleared and stained specimens having 16 rays, 11 had a caudal ray formula of 4-4-4-4 (dorsal element counted first). Other formulae obtained and number of specimens are as follows (rays articulating between elements are enclosed by parentheses): 4-4-3-(1)-4, (6 specimens); 4-4-3-5, (5 specimens); 3-(1)-4-4-4, (4 specimens); 3-(1)-4-3-(1)-4, (2 specimens); 3-(1)-4-3-5, (1 specimen); 3-(1)-4-3-5, (1 specimen); 4-4-3-5, (1 specimen). Two specimens with 15 rays had formulae of 4-4-3-4 and 3-(1)-4-4-3.

None of the caudal rays of *B. thompsoni* was associated with the neural and haemal spines of the penultimate vertebra or articulated in the space between the spines and hypural elements. Thus, *B. thompsoni* differs from certain other species of *Bothus* which have rays associated with the neural and haemal spines of the penultimate vertebra or which occur in the interspace between the spines and hypural elements. Gutherz (1970) gives a formula of 1-4-4-3-4-1 for larval *Bothus* (species not determined) from the western North Atlantic. We obtained the same formula for 12 cleared and stained specimens of *B. pantherinus* (Rüppell) from the Hawaiian Islands. In these specimens the first and last rays most often articulated in the interspace between the spines and hypural elements. These

TABLE 1.—*Bothus thompsoni*: Measurements of 13 characters for holotype, 29 males, and 31 females expressed as percent of standard length. Holotype excluded from regression statistics (a = ordinate intercept, b = regression coefficient).

Characters measured	Holotype BPBM 3398 percent of standard length	Range percent standard length for males	a	b	r^2	Range percent standard length for females	a	b	r^2
Head length	28.5	25.7-29.5	0.646	0.270	0.965	26.0-29.6	1.100	0.264	0.983
Snout length: to upper eye	23.9	14.0-21.5	−5.865	0.252	0.961	13.0-16.6	−1.022	0.162	0.968
to lower eye	6.3	4.4- 6.2	0.315	0.048	0.821	4.8- 6.8	−0.171	0.569	0.857
Orbit diameter: upper	11.6	9.1-12.6	2.255	0.084	0.828	8.2-12.4	1.656	0.087	0.896
lower	9.6	7.6-10.9	2.222	0.071	0.811	8.0-11.5	2.263	0.067	0.874
Interorbital distance	14.9	7.7-13.5	−5.856	0.182	0.958	5.1- 8.6	−1.112	0.088	0.949
Length of upper jaw	10.3	8.0-10.6	1.102	0.081	0.856	8.2-10.4	0.770	0.084	0.943
Greatest body depth	60.8	57.7-66.0	−1.046	0.629	0.968	57.0-67.3	−0.057	0.632	0.973
Least depth caudal peduncle	11.2	9.7-11.4	0.042	0.107	0.970	9.2-11.6	0.195	0.104	0.981
Length of pectoral fin: ocular side	21.7	19.0-24.7	4.661	0.159	0.912	18.8-24.9	4.925	0.153	0.924
blind side	18.4	15.3-18.7	2.294	0.141	0.928	14.0-18.5	0.826	0.155	0.930
Length of anal fin base	75.2	73.4-77.4	2.373	0.734	0.958	71.9-84.8	−3.634	0.814	0.966
Snout to greatest body depth	46.3	41.6-48.6	−4.156	0.497	0.959	41.4-50.0	0.341	0.452	0.961

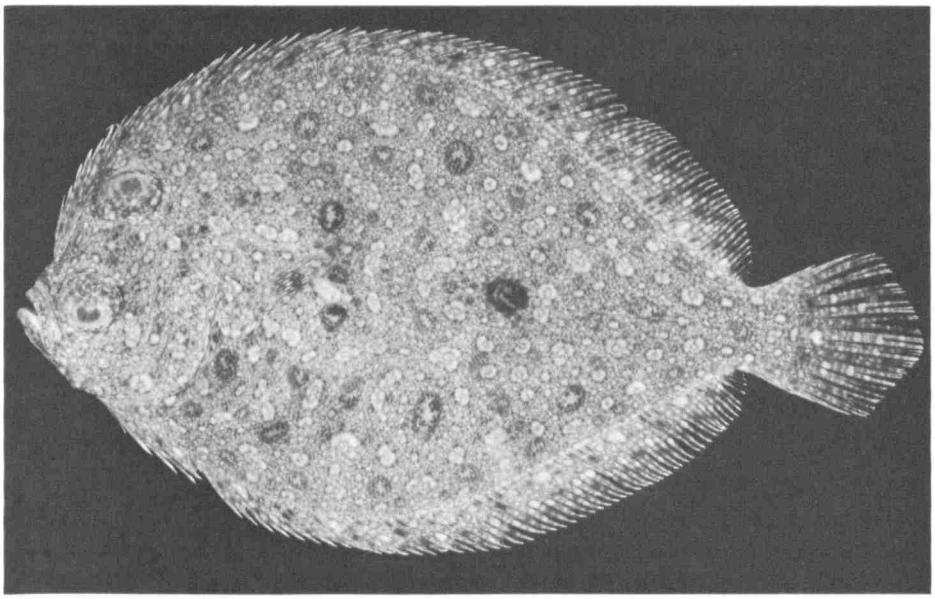


FIGURE 1.—A 106.4 mm SL female *Bothus thompsoni*.

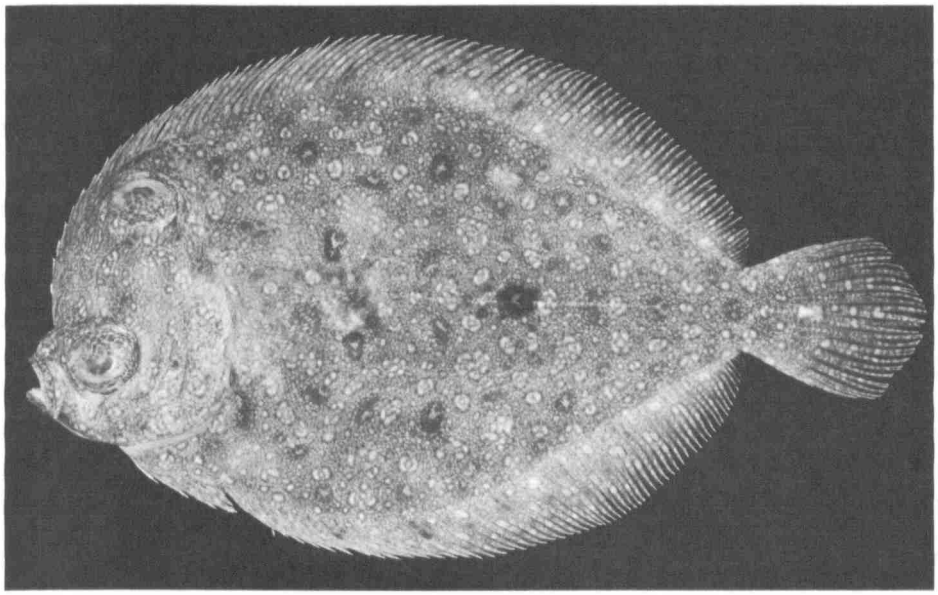


FIGURE 2.—A 114.4 mm SL male *Bothus thompsoni*.

data indicate that *B. thompsoni* exhibits a more variable caudal ray formula than *B. pantherinus*.

The first two and last two caudal rays of *B. thompsoni* are usually simple. Of a sample of 20 specimens, only 2 (10%) had either the second or penultimate ray divided.

The arrangement of gill rakers in *B. thompsoni* is shown in Figure 3, and counts are given in Table 3. There are 3-9 reduced gill rakers associated with the epibranchial and 1-4 reduced gill rakers associated with the hypobranchial. A series of 9-14 well-developed gill rakers is principally associated with the ceratobranchial. The reduced gill rakers associated with the epibranchial comprise the counts for the upper limb of the gill arch. The first well-developed

TABLE 2.—Dorsal and anal ray counts for 101 specimens of *Bothus thompsoni*.

Number of anal rays	Number of dorsal rays 84	85	86	87	88	89	90	91	92	93	94	95	Total number of specimens
70							1					1	2
69						1		1					2
68					1	3	1	4	1				10
67			2	5	7	7	5	3	1				30
66		3	7	3	9	8							30
65	2		8	7	3								20
64	2	1	2	1	1								7
Total number of specimens	4	4	19	16	21	19	7	8	2			1	101

raker occurs at the angle of the arch and is included in the counts for the lower limb, although stained material reveals this raker to be more closely associated with the epibranchial. The last one or two well-developed rakers are associated with the hypobranchial.

The number of gill rakers in the size range examined is apparently independent of size. A regression coefficient calculated for 28 females was not significant ($P > 0.4$).

Vertebral counts were obtained from 96 specimens. There are usually 10 abdominal vertebra (94 specimens), but two individuals had 11 (28 caudal vertebrae in both cases). Counts of caudal vertebrae (including urostyle) were 27 (7), 28 (69), and 29 (18), while total vertebral counts were 37 (7), 38 (69), and 39 (20).

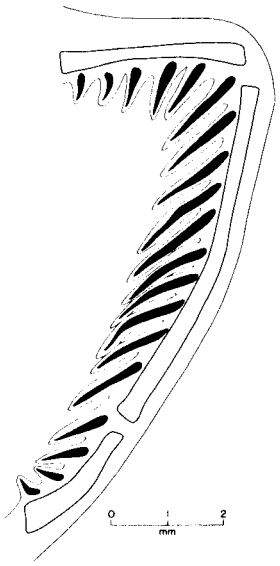


FIGURE 3.—A typical first gill arch from the ocular side of *Bothus thompsoni*.

Measurements

The measurements obtained from 29 male and 31 female specimens for 13 characters are summarized in Table 1. Linear regressions were calculated in original units of measurement (mm) with standard length as the independent

TABLE 3.—*Bothus thompsoni*: Counts for eight characters.

Characters	Frequency of occurrence 3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	N	$\bar{X}$
Caudal rays	-	-	-	-	-	-	-	-	-	-	-	-	2	157	4	-	-	-	-	-	-	-	163	16.01
Pectoral rays (ocular side)	-	-	-	-	-	-	-	1	7	32	22	1	-	-	-	-	-	-	-	-	-	-	63	12.24
Pectoral rays (blind side)	-	-	-	-	-	-	-	2	29	31	1	-	-	-	-	-	-	-	-	-	-	-	63	11.49
Gill rakers (upper limb)	1	5	29	29	21	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	91	5.92
Gill rakers (lower limb)	-	-	-	-	-	-	-	-	1	3	21	22	27	13	4	-	-	-	-	-	-	-	91	14.38
Gill rakers (total)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	11	13	24	9	17	6	5	91	20.30
	70-71	72-73	74-75	76	78	80	82	84	86	88	90-91	92-93												
Pored lateral line scales	1	-	-	5	6	8	3	4	2	1	-	1											31	80.9
	114-115	116-117	118-119	120-121	122-123	124	126	128	130	132	134	136	138	140	142	144	146-147							
Lateral line scale rows	1	-	-	-	4	2	6	6	17	5	6	8	5	-	1	-	2						63	131.6

variable. Plots of all regressions are linear and exhibit high r^2 values.

The regressions obtained for the 13 measured characters were subjected to analysis of covariance to test for sexual dimorphism. Highly significant differences ($P<0.001$) were found between the regression coefficients for two characters (which are related): interorbital distance (Figure 4) and snout to upper eye. Juvenile and adult male specimens of *B. thompsoni* are similar to many *Bothus* spp. males in possessing a much greater interorbital distance than females of the same species. Male *B. thompsoni* exhibit positive allometric growth of the interorbital distance, this measurement being about 7.5%-9.0% of standard length at a length of 50-60 mm and about 12%-14% of standard length at a length of 100-115 mm. In female specimens longer than 50 mm the interorbital distances were 6.0%-8.6% of standard length. Interorbital distances of 5.3% and 5.1% of standard length were noted in two specimens 39 mm and 48 mm long. As expected, male *B. thompsoni* exhibited positive allometric growth of the snout to upper eye distance.

Among the remaining 11 characters subjected to analysis of covariance, there were no significant differences between regression coefficients. There were significant differences ($P<0.05$) in the elevations of the regressions between sexes for four characters. Both the upper and lower orbit diameters of males tend to be larger than for females; the differences in adjusted means for the two characters are 0.35 and 0.40 mm, respectively. Females tend to have a greater body depth and a greater snout to greatest body depth distance. The differences in adjusted means for these two characters are 1.1 and 1.0 mm, respectively.

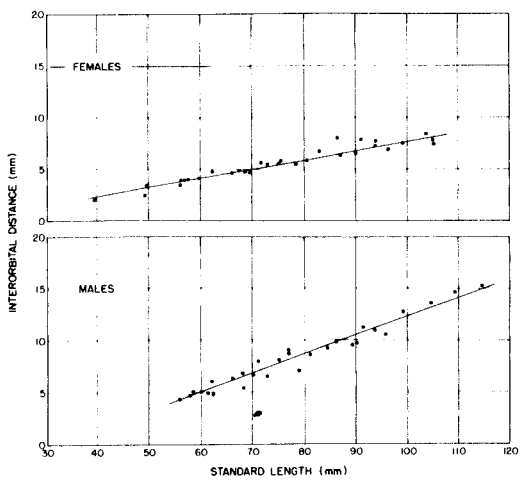


FIGURE 4.—Plots of the interorbital distance of 29 male and 31 female specimens of *Bothus thompsoni*.

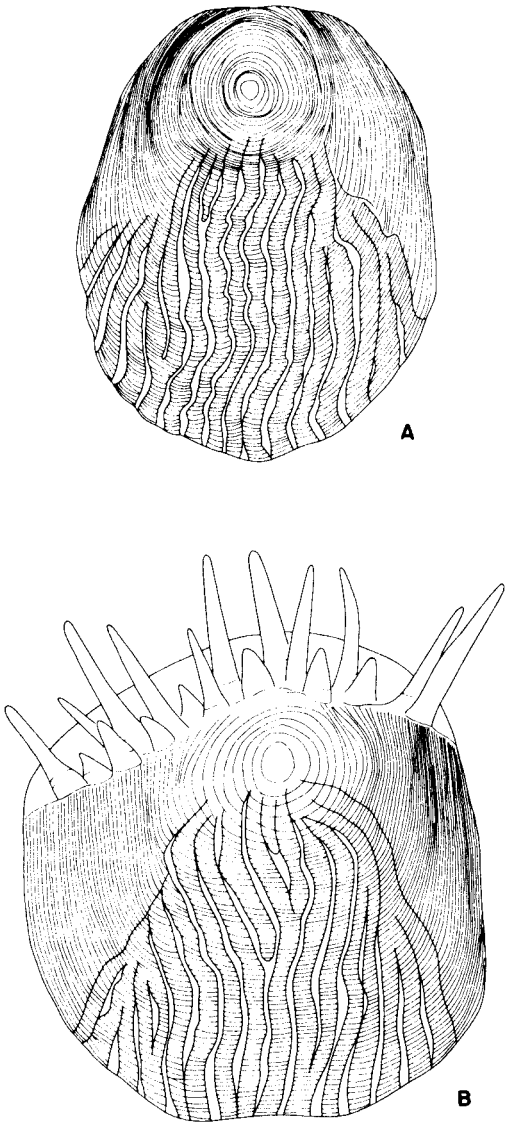
In both sexes, the pectoral fins of the ocular side tend to be longer than those of the blind side (Table 1). The pectoral fins of both sexes exhibit negative allometric growth. This is most pronounced on the ocular size where the pectoral length is about 24%-25% of standard length at 40-60 mm and about 18%-21% of standard length at a length of 100-115 mm. There is only slight negative allometric growth of the pectoral fin on the blind side where this structure varies from 14.0% to 18.7% of standard length.

All other morphometric characters examined exhibited approximately isometric growth.

Two of the measurements we obtained for the holotype (Table 1) do not fall within the ranges we obtained from our study series: interorbital distance and snout to upper eye.

Other morphological characters

Bothus thompsoni has cycloid scales on the blind side and on most of the ocular side (Figure 5A). Ctenoid scales occur on the proximal portions of the dorsal and anal rays. There are 2-3 rows of ctenoid scales at the bases of the dorsal and anal fins (Figure 5B). Fowler (1923) stated that the holotype had ctenoid scales on the cheeks and postorbital region. In addition, we find that there is a patch of about 15 ctenoid scales below the curved portion of the lateral line in the holotype. A scale from this region is shown in Figure 5C. The occurrence of ctenoid scales on the cheek and in the vicinity of the curved portion of the lateral line is a variable character. Of 25 specimens (67.5-106.4 mm SL) from our study series, six had ctenoid cheek scales, three had ctenoid scales on the cheek and near the lateral line, and one had ctenoid scales near the lateral line only. The presence of ctenoid scales in these two regions does not appear to be related to size or sex. The cycloid scales are small and nonimbricated, but the ctenoid scales at the dorsal and anal fin bases overlap to a slight degree. The ctenii of the ctenoid scales generally occur in two rows: a primary row of well-developed ctenii and a secondary row of smaller ctenii basal to the



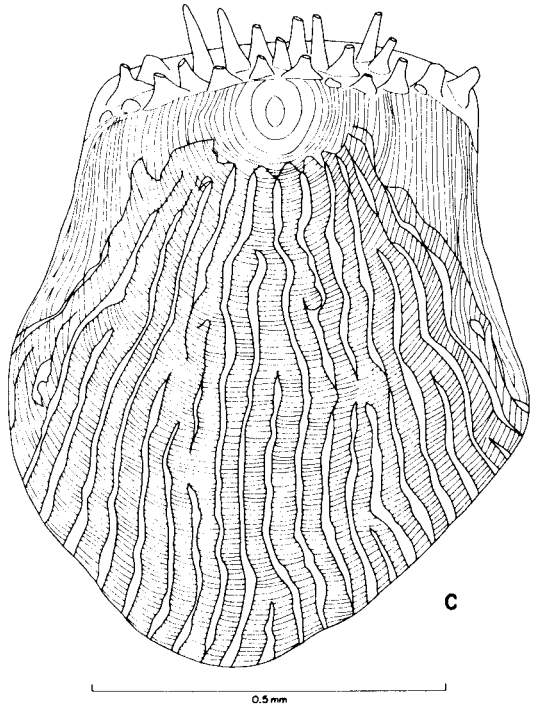


FIGURE 5.—Scales of *Bothus thompsoni*: A, cycloid scale from above the lateral line; B, ctenoid scale from near the dorsal fin base; and C, ctenoid scale from below the curved portion of the lateral line in the holotype.

primary row (Figure 5B and C). The number of ctenii on cheek scales varies from 5 to 8, while scales from the dorsal and anal fin bases at the greatest body depth have 15 to 25 ctenii.

The general arrangement of teeth in the upper and lower jaws is shown in Figure 6. There are usually three rows of teeth. The outer row consists of a few, stout conical teeth in the anterior portion of the jaws. The middle row consists of more numerous, but less stout, conical teeth. The inner row consists of depressed, poorly ossified conical teeth subequal in number to those in the middle row (except on the blind side of the upper jaw). The inner row of teeth are movable, being held in place by flesh and not inserted in the jaw bones.

The number of outer teeth, and, to a lesser extent, the middle teeth, vary according to jaw bone and size of specimen. This is illustrated in Figure 7 where the number of teeth are plotted by standard length for 10 females 49.2-106.4 mm SL and 10 males 55.8-114.5 mm SL. The increase in number of outer teeth with size is apparent for all jaw bones except the dentary on the ocular side. There also appear to be more outer teeth in the premaxillary of the ocular side of the males.

The teeth in the middle row also exhibit a general, but less well-defined, increase in numbers with size.

There are no fleshy papillae along the edges of the eyes such as reported for male *B. pantherinus* (Norman, 1934). There is a single prominent, blunt protuberance on the snout of males greater than 60 mm SL. This structure is represented in females by a small knob. The anterior edge of the lower orbit tends to be more developed and rugose in males than in females.

Coloration of fresh specimens

The blind side of both sexes is white, but tending to dusky white in males greater than about 80 mm SL, especially on the cheek and above the cheek. The ground color of the ocular side is light olive green. There is a single prominent dark spot on the lateral line posteriad about 60% of the standard length. There are two secondary dark ocelli near the pectoral fin. There are 14-15 olive green ocelli broadly distributed along the dorsal and ventral borders of the trunk. There are numerous light blue ocelli and spots distributed over the trunk, head, and dorsal, anal, caudal, and ventral fins. The pectoral fins are almost clear. In males, the light blue spots are more numerous and elongated along the anterior profile and between the eyes.

Comparison with Other Species of *Bothus*

A definitive discussion of the relation of *B. thompsoni* to other species of *Bothus* must await further study of the genus on a worldwide basis. *B. thompsoni* differs from all recognized species of *Bothus* (Fowler, 1933; Norman, 1934; Chabanaud, 1942; Stauch, 1966; Gutherz, 1967; Amaoka, 1969; Topp and Hoff, 1972) in possessing 11-17 gill rakers on the lower limb of the first arch (11 or fewer in other species) and 115-147 scale rows above the lateral line (apparently 100 or fewer in other species: Norman, 1934). It may also be unique in that it usually has only 16 caudal rays as opposed to 17 in other species. This character, however, apparently has been examined only rarely by earlier authors and few data on the numbers and arrangements of the caudal rays are available (Chabanaud, 1942; Amaoka, 1969; Gutherz, 1970). The figures given by Norman (1934) for *B. leopardinus* (Günther) and *B. bleekeri* indicate

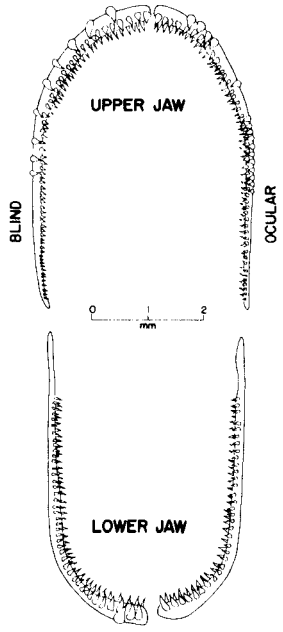


FIGURE 6.—The arrangement of teeth in *Bothus thompsoni*.

caudal ray counts of 16. However, a count of 16 is also indicated for *B. ovalis* (Regan) which Amaoka (1964) has shown to be the young of *B. myriaster* (Temminck and Schlegel). *B. myriaster* has 17 caudal rays (Amaoka, 1969). Chabanaud (1942) described *B. budkeri* from the Red Sea and gave caudal ray counts of 16 for the holotype and 17 for the two paratypes. A sample of 368 adult and larval specimens of *B. pantherinus* from the Hawaiian Islands had the following caudal ray counts: 16 (2.7%), 17 (95.7%), 18 (1.6%). Further examination of this character is required.

We have not examined specimens of *B. bleekeri*, and we separate this species from *B. thompsoni* on the basis of the description given by Norman (1934). In addition to the differences in gill raker and lateral line scale row counts discussed above, *B. thompsoni* has more pectoral rays on the ocular side (10-14 vs. 8-9). Adult male specimens of *B. thompsoni* do not have elongated pectoral rays (ocular side), whereas male *B. bleekeri* have elongated pectoral rays.

Two other species of *Bothus*, *B. pantherinus* and *B. mancus* (Broussonet), occur in the Hawaiian Islands. Adult specimens of *B. thompsoni* may be separated from similar life history stages of the former two species on the basis of body profile alone. Other useful characters for

distinguishing *B. thompsoni* from *B. pantherinus* and *B. mancus* (in addition to counts of the lateral line scale rows, lower gill rakers, and caudal rays) are as follows. Cycloid scales are present on the ocular side of *B. thompsoni* (except at the bases of the dorsal and anal fin, and occasionally on the cheeks and in the vicinity of the lateral line) as opposed to ctenoid scales on the ocular side for *B. pantherinus* and *B. mancus*. Adult males of the latter two species have elongated pectoral fin rays on the ocular side, while male specimens of *B. thompsoni* do not. *Bothus mancus* possess more dorsal and anal fin rays than do *B. thompsoni* and *B. pantherinus* (97-102 vs. 84-96 and 77-82 vs. 64-74, respectively; Hawaiian Island

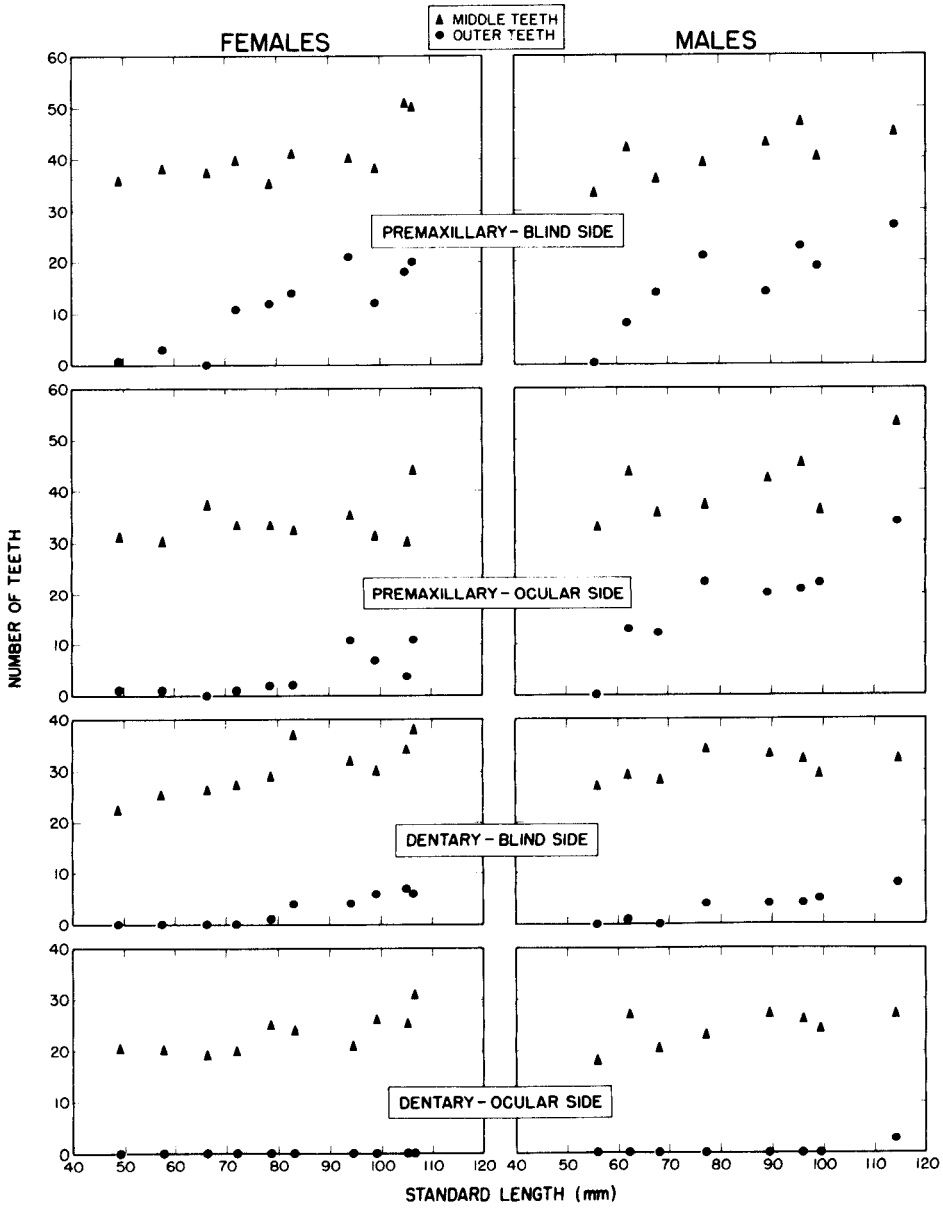


FIGURE 7.—Numbers of teeth in the outer and middle tooth rows in *Bothus thompsoni*.

specimens). *Bothus thompsoni* has 10-14 pectoral rays, whereas this count is 9-11 for both *B. pantherinus* and *B. mancus*.

With regard to other Indo-Pacific species recognized by Norman (1934), *B. thompsoni* differs from *B. myriaster* in that the pectoral fins of males are not elongated in the former species. The combination of cycloid and ctenoid scales on the ocular side of *B. thompsoni* differentiates it from *B. assimilis* (Günther) which has only cycloid scales and from *B. leopardinus* (Günther) which has only ctenoid scales on the ocular side (Norman, 1934). Norman (1934) considers also that *B. constellatus* (Jordan, *in* Jordan and Goss) is very doubtfully distinct from *B. leopardinus*.

Although no illustration was given of *B. budkeri* (Chabanaud, 1942) from the Red Sea, it differs from *B. thompsoni* in having a lesser body depth, fewer dorsal and anal rays, fewer gill rakers on the lower limb of the first arch, and only ctenoid scales on the ocular side.

Fowler (1933) described five species of *Bothus* from the Philippines and China Sea. The generic placement of several of these species is questionable. At any rate, none of them could be confused with *B. thompsoni*.

Ecology

With the exception of one specimen caught at a depth of 72 m off Maui, all specimens of *B. thompsoni* taken to date have come from depths of 90-113 m off the north coast of Oahu where bottom temperatures ranged from 24.5° to 26.0°C. About 580 specimens (32-107 mm SL) have been obtained at 13 stations where catches ranged up to 275 individuals per haul. An analysis of dispersion for this species (Struhsaker, 1973) shows it to have a highly clumped distribution. The type of bottom in the area of capture is primarily muddy sand interspersed with patches of sponge, broken shell, and rubble. *Bothus thompsoni* was often taken with 20-30 other species of fishes; it usually comprised less than 8% of the total catch, but occasionally ranged up to 30%. Numerically dominant species taken with *B. thompsoni* include *Trachinocephalus myops*, *Priacanthus* spp., *Antigonia eos*, *Parupeneus chrysonemus*, and *Lagocephalus hypselogeneion*. Struhsaker and Higgins (manuscr.[2]) have shown that *B. thompsoni* is the third most abundant larval flatfish (after *Engyprosopon xenandrus* Gilbert and *B. pantherinus*) taken in offshore midwater hauls near Oahu. They also presented evidence that *B. thompsoni* may spawn throughout the year.

ACKNOWLEDGMENTS

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MATERIAL EXAMINED

USNM 208494: TC-33-52 (R/V *Townsend Cromwell*, cruise 33, station 52); 1 male (109.2 mm SL); lat. 19°58.3′ N, long. 156°28.5′ W; depth 72 m, 13 Nov. 1967. USNM 208495: TC-36-15; 4 females (93.7-99.1 mm SL); lat. 21°37.7′ N, long. 158°08.8′ W; depth 113 m, 2 May 1968. USNM 208496: TC-36-20; 7 females (39.5-72.8 mm SL), 12 males (55.8-81.2 mm SL); lat. 21°36.8′ N, long. 158°12.5′ W; depth 110 m, 3 May 1968. USNM 208497: TC-40-115; 10 females (56.9-87.3 mm SL), 5 males (70.0-84.5 mm SL); lat. 21°36.8′ N, long. 158°08.2′ W; depth 102 m, 8 Nov. 1968. USNM 208498: TC-40-116; 4 females (56.0-105.4 mm SL), 3 males (58.6-104.5 mm SL); lat. 21°36.8′ N, long. 158°11.6′ W; depth 112 m, 1 Dec. 1968. USNM 208499: TC-40-119; 5 females (78.6-91.2 mm SL), 7 males (86.2-99.2 mm SL); lat. 21°36.8′ N, long. 158°11.2′ W; depth 96 m, 1 Dec. 1968. BPBM 14102: TC-40-125; 1 female (106.4 mm SL), 1 male (114.4 mm SL); lat. 21°36.8′ N, long. 158°11.6′ W; depth 102 m, 10 Nov. 1968.

[2] Struhsaker, P., and B. E. Higgins. Unpubl. manuscr. Post-larval flatfishes (Pisces:Pleuronectiformes): Observations on the identity and ecology of 11 Hawaiian species. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812.

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NOTE

DEVELOPMENT OF EGGS AND EMBRYOS OF THE SURF CLAM, *SPISULA SOLIDISSIMA*, IN SYNTHETIC SEAWATER

The eggs of the surf clam, *Spisula solidissima*, have been used extensively for investigations of egg structure and embryonic development of bivalves. Allen (1951) has pointed out the advantages of the use of surf clam eggs for research of this nature. These studies have been limited, however, to areas where natural seawater was readily available, due to the unsuitability of most synthetic seawaters for supporting the embryonic development of bivalves (David A. Nelson, NMFS, Milford, Connecticut and Gerald Zaroogian, Environmental Protection Agency Laboratory, West Kingston, Rhode Island, pers. comm.).

Experimental Observations

We recently reared *Spisula solidissima* embryos in a synthetic seawater formulation developed by Zaroogian, Pesch, and Morrison (1969) as a culture medium in which to rear oyster embryos. Our observations were made in salinities of 25 and 30 ‰ at 10°, 15°, and 20°C water temperatures. Within these ranges we found 20°C to be the optimum temperature for development, allowing us to rear eggs to the 5-day-old stage (early veliger) with almost 100% survival and no signs of larval abnormalities. At 20°C polar body formation occurs in about 45 min and the two-cell stage in about 90 min. The early veliger, or straight-hinge stage, is reached in less than 24 h. At 15°C all stages of development are normal but somewhat delayed, with development to the straight-hinge stage requiring more than 24 h. At 10°C the rate of development of all stages is greatly retarded and many abnormal embryos are present. The majority of fertilized eggs held at 10°C requires more than 96 h to develop to the straight-hinge stage.

At 20°C we found that development of fertilized eggs in synthetic seawater was comparable to the best development observed in natural seawater.

This study did not involve testing embryonic development of *S. solidissima* in synthetic seawater over a wide range of salinities, but was limited to those salinities currently in use in other research programs within this laboratory. It appeared that there was no difference in survival and development of eggs to the 5-day-old stage at salinities of 25 and 30 ‰, the only salinities tested. In earlier work, however, Stickney (in Yancey and Welch, 1968) reported that *S. solidissima* eggs failed to develop under experimental conditions in salinities of less than 23 ‰ in natural seawater.

Since the synthetic seawater formulation developed by Zaroogian, Pesch, and Morrison (1969) can be readily prepared, its general acceptance could lead to a wider utilization of surf clam eggs by embryologists and cytologists with standardization of techniques and comparability of results not always possible when natural seawaters from different locations are used.

LaRoche, Eisler, and Tarzwell (1970), in studies of bioassay procedures for oil and oil dispersant toxicity evaluation, suggested the use of Zaroogian's seawater as a standard testing medium in place of natural seawater, the composition of which varies, especially in regard to the presence of trace metals, dissolved organics, and particulate matter. They recommended the use of Zaroogian's seawater because of its ability to support spawning adults and larvae of the American oyster, *Crassostrea virginica*, for at least 48 h without visible adverse effects, and adult mummichog, *Fundulus heteroclitus*, grass shrimp, *Palaemonetes vulgaris*, and sandworm, *Nereis virens*, for extended periods. Thus, when sufficient research has been performed in this area, it may be possible not only to hold adult animals but also to rear the eggs and larvae of these animals in the same synthetic seawater. This would be an obvious advantage in assessing comparative tolerances to pollutants of different life stages.

Collection and Maintenance of Surf Clams in the Laboratory

Although some information on the collection and maintenance of surf clams in the laboratory and their reproductive cycle has been published (Loosanoff and Davis, 1963; Ropes, 1968; Yancey and Welch, 1968), we feel it pertinent to this paper that it be reviewed and our own observations added.

Adult surf clams can be purchased from biological supply houses or collected in their natural habitat. The range of *S. solidissima* is along the Atlantic Coast of North America, from the Gulf of St. Lawrence to Cape Hatteras (Yancey and Welch, 1968). South of Cape Hatteras the surf clam is represented by *Spisula solidissima raveneli*, similar to *S. solidissima* but a smaller species. *S. solidissima* is found in sandy bottoms from the low-tide line to depths of 500 ft in waters of oceanic salinity. They are present in shallow water beds, at various points along their range, and are easily hand-gathered along the coasts of Delaware, New Jersey, Long Island (New York), Rhode Island, and Massachusetts. Our collections have come mainly from Little Narragansett Bay and the area of Point Judith, in Rhode Island.

Surf clams can also be obtained from commercial clam boats working the beds, but our observations have shown that hand-gathered clams are more suitable for laboratory purposes; those obtained from commercial sources are often damaged by the action of the hydraulic dredge used in harvesting. They suffer high mortalities soon after introduction into the laboratory and long-term survival of those remaining also seems inferior to that of hand-gathered stocks.

We feel that the best working size for laboratory animals to be used as a source of gametes is 4 to 5 inches. Larger ones require more space and do not survive as well in crowded tanks. Smaller animals are more difficult to spawn, even though we have found some specimens as small as 5 cm to have viable sex products.

Ropes (1968), in a study of the reproductive cycle of offshore surf clam populations, found a biannual cycle during 3 years of the 4-year period covered by his study. This biannual cycle was characterized by a major mid-year spawning and a minor late-year spawning. He found ripe clams as early as May and as late as October during 3 years of the study. This pattern of ripeness may vary between inshore and offshore populations, depending on local temperature conditions. We found ripe clams only from June to August in inshore Rhode Island waters.

Surf clams can be collected prior to their natural spawning period and conditioned to ripeness in the laboratory. Conditioning refers to a procedure of gradually raising the water temperatures at which bivalves are maintained as a means of achieving gonad ripeness prior to the time one would expect to find ripe animals in the field (Loosanoff, 1954).

We have collected animals with unripe gametes from early winter through late spring (December to May) and conditioned them at 15°C. This temperature equals or exceeds that at which gametogenesis takes place in natural populations (Ropes, 1968). Such animals collected in early winter and conditioned in the laboratory have been spawned as early as March.

Ripe surf clams held in the laboratory at 15°C have never spawned spontaneously; thus, the spawning threshold of this animal in the laboratory would appear to be higher than 15°C. We do feel, however, even though we, as yet, lack quantitative data to substantiate it, that ripe animals held at 15°C tend to resorb their gametes more quickly than those held at a lower temperature following conditioning. Ripe animals collected in June and held at 10°C contained viable sex products in December.

Ropes (1968) reported that offshore populations spawn at lower temperatures than we found in our laboratory populations. He also noted that abrupt rises in water temperature were not clearly a cause of spawning in natural populations. A rapid increase in temperature is certainly an important factor in stimulating spawning in the laboratory. Clams conditioned at 15°C spawned when the temperature was raised quickly to 18-20°C. However, these clams were less responsive than those held in damp refrigeration (approximately 2°C, covered with a wet towel to prevent drying) overnight prior to exposure to 18-20°C. Refrigerated clams normally spawned within an hour after exposure to 18-20°C, while those conditioned at 15°C and exposed to water at 18-20°C did not.

Eggs and sperm can also be obtained by stripping the sex products from the gonads using a

method described by Costello et al. (1957). This involves removing one shell and gill, exposing the visceral mass, and slicing into the gonad which overlays the digestive glands and viscera. Care should be taken to avoid cutting into the underlying intestines and digestive glands, as the presence of body fluids in the cultures of eggs appears to be detrimental to embryonic development. The eggs and sperm are washed into separate collecting containers. Most of the tissue and debris collected along with the gametes can be removed by selective screening.

Stripped eggs tend to be more irregular in shape than naturally spawned eggs but soon become spherical. Previous investigators (Loosanoff and Davis, 1963) have reported the diameter of spawned mature eggs to average 56.5 μ. Our measurements of rounded stripped eggs from ripe clams have agreed with this.

To fertilize the eggs a small quantity of sperm suspension is added to the egg suspension and mixed by rapid stirring; care must be taken to add only a small quantity of sperm as *Spisula* eggs are quite susceptible to polyspermy at high sperm concentrations (Allen, 1951). Following fertilization the germinal vesicle breaks down and a thin membrane forms a short distance above the surface of the egg.

In conclusion we would like to point out that this is the first time to our knowledge that *Spisula solidissima* embryos have been reared in synthetic seawater, although they have been previously reared in the laboratory in natural seawater. Not all synthetic seawaters currently available are suitable for this purpose but that developed by Zaroogian, Pesch, and Morrison has consistently given us good results. We feel that the ability to rear these embryos in synthetic seawater will enhance the value of surf clam eggs and embryos in embryological and cytological research by offering a standardized rearing medium and a comparability of results not always possible when natural seawaters from different locations are used, as well as making possible the use of these organisms in bioassay procedures where the composition of the seawater must be known.

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ERRATUM

Fishery Bulletin, Vol. 71, No. 3

PAUL, A. J., AND HOWARD M. FEDER, "Growth, recruitment, and distribution of the littleneck clam, *Protothaca staminea*, in Galena Bay, Prince William Sound, Alaska," p. 665-677.

1) Page 665, left column, first paragraph. The last sentence should read:

"Feder and Paul (1973) and R. Nickeron (Alaska Department of Fish and Game, pers. comm.) suggested that a small clam fishery is feasible in Prince William Sound since paralytic shellfish poison (P.S.P.) does not seem to be a problem there, and many beaches with sizable populations of *P. staminea* and the butter clam, *Saxidomus giganteus*, occur in the area."

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ACOUSTIC TELEMETRY FROM FISH

JOHN KANWISHER,[1] KENNETH LAWSON,[1] AND GUNNAR SUNDNES[2]

ABSTRACT

Methods are described for monitoring physiological parameters such as temperature and electrocardiogram from free swimming fish. Information is telemetered as sound radiating from an acoustic transmitter implanted on the fish. Limitations of the technique and construction details of representative devices are covered. Uses in both behavior and physiology are considered.

Acoustic telemetry allows an investigator to study the behavior and physiology of fish under conditions which approximate their natural state. Improvements in electronic techniques permit construction of devices the size of one's little finger; these devices can transmit data such as heartbeat and temperature over ranges of several hundred meters for as long as a month. We describe here the use and constraints on sound as a means of transmitting these data. We then discuss, in detail sufficient for duplication, the construction of sample devices for transmitting, receiving, and interpreting the data. Finally, we show how these devices have been applied to specific experimental problems, and discuss the results we have obtained.

SOUND AS A TELEMETRY MEDIUM

For ranges beyond a few meters through water, sound is the only practical form of energy for telemetry. It travels with little loss, whereas radio waves and light are rapidly absorbed. Several properties of sound in water are important. For example greater ranges are possible in fresh water than salt (one rarely has a choice in this). Low frequencies transmit further than high. For ranges up to several hundred meters, any frequency below 100 kHz is suitable. If a range of several kilometers is needed, the frequency should be less than 20 kHz. Low frequencies, however, involve longer wave lengths which implies larger transducers. In the small devices necessary for fish work these are difficult to use. Thus we most frequently employ frequencies between 40 and 80 kHz. Only in large tuna could we use a transmitter big enough to work efficiently at 20 kHz. It had an open sea range of 8 km.

The interfering background noise, which tends to obscure the signal, varies greatly at different places. In general, the shallow water tropics are noisiest. At Coconut Island in Hawaii the natural acoustic energy may be 100 times greater than that at Friday Harbor in Puget Sound. Most of the noise appears to be from bottom animals such as snapping shrimp. Man-made noise, like that from boat motors, can also be troublesome.

Relative motion between a sound source and the receiver produces a Doppler shift in the apparent frequency such that

$$\frac{\Delta f}{f} = \frac{\text{relative velocity}}{\text{velocity of sound in water}}$$

The velocity of sound in water is 1,500 m/s. A relative velocity of 1 knot shifts frequency 0.03%. This is only significant when frequency is interpreted critically, as in the depth transmitter to be described.

Additional complications arise from the interference effects due to multiple sound paths between transmitter and receiver. These are frequently troublesome in small enclosures where sound reflects from the walls. Nulls in the sound field are produced which represent momentary loss of signal. The ear has little trouble interpreting periodic signals such as electrocardiogram (EKG), but in a transcribed record these effects can be confusing (see Figure 2).

These remarks are meant to make one's ambitions more modest when considering acoustic

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telemetry, particularly for work in the open sea. It is not possible to send across oceans with a miniscule device. But almost any small amount of energy will work in laboratory tanks. The low power transmitters described here are useful at distances of at least 100 m.

CONSTRUCTION

Heartbeat Transmitters

The cylindrical form of our devices is dictated by the transducers and batteries, both of which are round. A stainless steel tube is chosen into which the battery fits. The electronics are then packaged to this inside diameter. They are cast in epoxy resin in one end of the tube, with the heartbeat lead or thermistor coming out of the plastic. The tubular transducer is fit either inside or outside the tube, and similarly embedded in plastic to assure electrical insulation. The battery is held in place with a watertight cap on the other end. The metal case forms the indifferent reference electrode to the one placed near the heart. With the exception of the transducers (Penn Engineering & Manufacturing Co. Inc., % Aquadyne, Inc., Falmouth, Mass.) parts used in these devices are routine. Parts for a heartbeat transmitter cost about $15.00.

Large Heartbeat Transmitter

A vertebrate heart produces an electric field when it beats. A millivolt level signal from an electrode near the heart is amplified by Q_1 in the schematic of Figure 1. The larger voltage is used to vary the frequency of an oscillator (Q_2 and Q_3). Another amplifier (Q_4 to Q_7) after the oscillator drives a transducer at this frequency producing

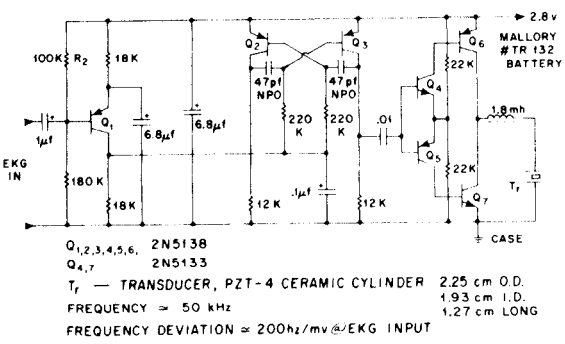

FIGURE 1.—Large heartbeat transmitter.

sound in the water. With a carrier frequency of 50 kHz the typical excursions are a few hundred hertz. Thus the EKG voltage is transformed into variations of the sound frequency. Another gain stage before the heartbeat amplifier can make the transmitter sufficiently sensitive to send signals of 100 μv or less. In this way we have been able to follow the electromyograms in the red and white muscles of fish. Figure 2 is an example of an EKG recorded from free swimming Atlantic cod, *Gadus morhua,* and Atlantic salmon, *Salmo salar.* The various sequential details of the heartbeat are clearly shown. The transmitter is 2 cm in diameter and 8 cm long.

Small Heartbeat Transmitter

Similar performance at the cost of greater effort at miniaturization can be had with the simpler and smaller transmitter shown in Figure 3, which is 1.5 cm by 7 cm. Reduced power consumption allows the same battery life (3 wk) as the larger transmitter. Be replacing R_2 in either transmitter with a thermistor, temperature will control the carrier frequency. The heartbeat can still be transmitted as variations around this changing frequency.

Depth Transmitter

The depth of a fish has been a difficult variable to transmit because of the lack of practical pressure sensors. Some information about depth has been discerned from water temperature. The recent appearance of small sensitive silicon pressure sensors has made direct measurement of depth feasible. We have built a depth transmitter around such a device (Figure 4).

The DC output voltage from the pressure sensor is increased by an operational amplifer, A. These larger voltage excursions control the frequency of an oscillator in the same way as amplified heartbeat signals. The thermistor in Q_1 compensates the oscillator against frequency variations due to temperature. The resistor in parallel with this thermistor must be empirically chosen to optimize this compensation. This allows the received frequency to be interpreted as pressure. The frequency change is 1000 Hz/m of depth. A 20°C change in temperature causes an equivalent pressure error equal to 5 cm of water. The circuit is a voltage controlled oscillator, useful with any millivolt-level DC signals. This instru-

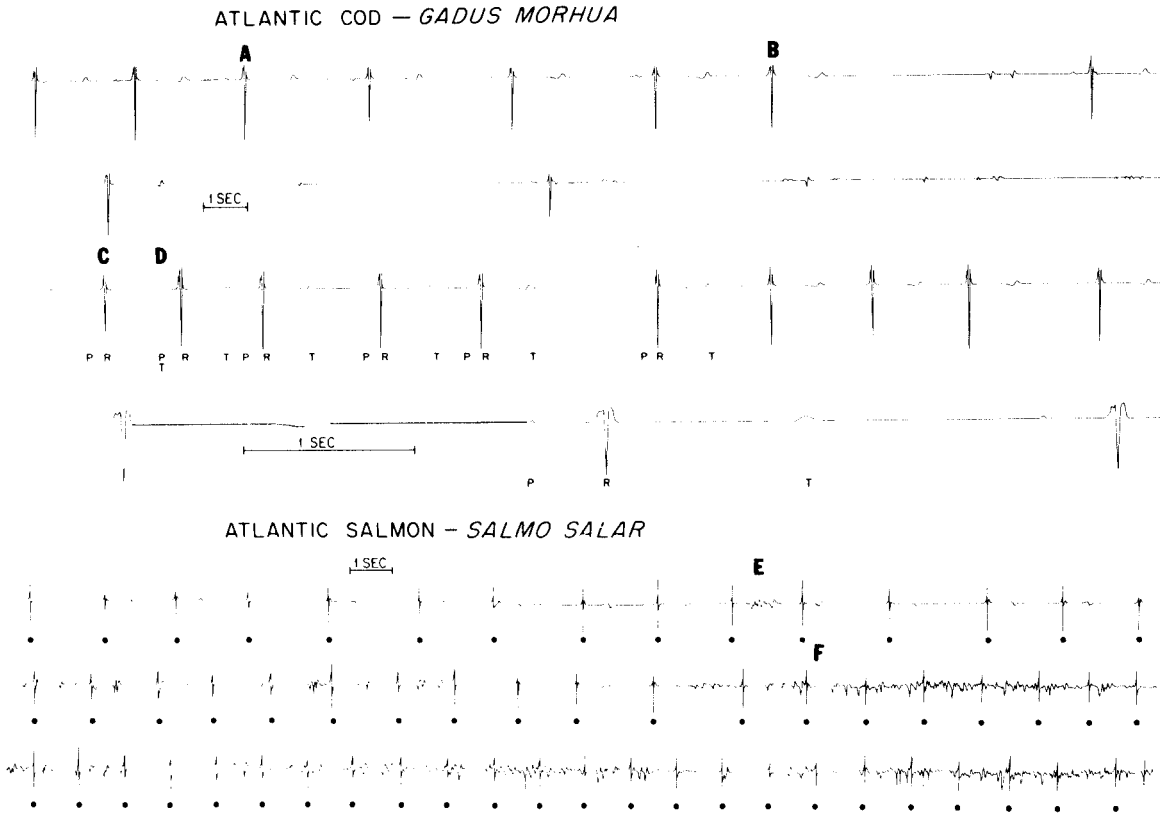

FIGURE 2.—Examples of electrocardiogram from free swimming Atlantic cod and Atlantic salmon. The experimenter approached the aquarium at A and looked over at B, slowing the heart rate. When he went away the heart started at the maximum rate at C, since the T wave is piled on the next P wave at D. The Atlantic salmon also showed a slowing at E from the same source. It was chased at F, resulting in a quickly accelerating heart rate from exercise. Noise while swimming is an acoustic artifact from reflections in the tank.

ment has an operating life of 1 wk. We are using it to study gas pressure in swim bladders. With a less sensitive sensor we can determine pressures at depths equal to 1,000 m.

Receiver

Much of our work has been done with tunable superheterodyne receivers. These employ a mechanical filter to set bandpass. Nearly equivalent results can be had from the simpler circuit of Figure 5. The hydrophone contains a frequency selective preamplifer with a voltage gain of 100. Amplification within the hydrophone is important to eliminate interference from motor ignition and radio stations. Power for this preamplifer comes down the same wire that carries signals to the receiver.

The preamplified signal is amplified another 100 times in A_1 (½ of a 1437 dual operational amplifier). Its output is mixed with a local oscillator in Q_3 to produce a signal at the audio difference frequency. This is amplified 10 times in A_2 and used to drive headphones. A 1-μv signal at the receiving hydrophone is clearly audible.

RESULTS

General

We originally developed our telemetry so it could be used with ease for human cardiac monitoring. Work with fish only required miniaturization. The usual method is to have the receiver output played through a speaker in the laboratory. This allows one to notice occasional events of interest. Such more or less casual monitoring has greatly reduced the need for observational patience. In this way we have obtained cues related to feeding and behavioral in-

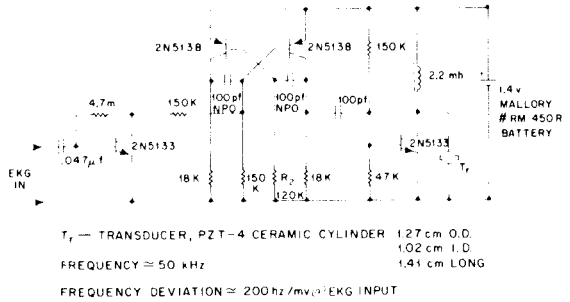

FIGURE 3.—Small heart beat transmitter.

teraction. At such times we could direct our attention more intently. Generally we have found that heart rate changes are related to specific details of a fish's physiology and also its behavior.

The transmitter can usually be carried in the stomach of the fish. It is readily inserted into an animal which has been anaesthetized with MS-222.[3] The EKG lead is brought out under the last gill arch. It is pushed under the skin immediately over the heart. The receiving hydrophone is placed against the fish so the transmitter can be monitored. There is no difficulty in interpreting when the lead placement for optimum EKG signal has been reached. The lead is then sutured in place.

The gills can now be flushed with anaesthetic-free water and the fish soon released. The entire operation takes 3 or 4 min. The fish will have been under anaerobic stress because no water has been flowing over the gills. Most specimens appear to fully recover in a few hours.

If drag is not important the transmitter can be sutured to the outside of the fish. This method has allowed us to work with plaice, *Pleuronectes platessa,* whose stomachs were too small. It was also convenient for some Atlantic cod and Atlantic salmon that repeatedly threw up a stomach tag.

Physiological Response

When a fish is swimming we find an expected increase in heart rate, reflecting the increased oxygen transport of the cardiovascular system. In an Atlantic cod this is a measure of both the instantaneous exertion, and also of any previously incurred oxygen debt (Wardle and Kanwisher, In press). Chasing a fish to maximum fatigue can result in an increased heart rate for as long as 10 to 20 h while this debt is being repaid. Thus one gets a substantiation of the already recognized biochemical changes in muscle glycogen and lactic acid. When remote monitoring shows a rapid heart rate one cannot tell if the fish is swimming at that moment or is reflecting a previous exhaustion.

Behavior

We were not prepared for the large component of behavioral response observed in the heart rate of all fish. Cardiac arrest is a well known response in conditioning. We found it to occur with the subtlest of cues, once the fish had recovered from initial handling. This can best be described by two anecdotes.

A plaice, which had not eaten for many months, had settled into the sand on the bottom of a 60-ft circular laboratory aquarium. It was mid-winter with low water temperatures and the fish appeared to be doing the equivalent of hibernating. In spite of this outward lethargy it responded to doors opening, relays clicking, and to any other sort of human activity in the vicinity.

It was, not unexpectedly, most sensitive to visual cues. We gradually reduced these to smaller objects moved in the visual field of the fish. The most sensitive response came early in the morning before local laboratory activity had started. At this time we could come quietly up to the tank and push a pencil a few centimeters over the edge. The plaice, 1½ m below responded by stopping its heart for 8 or 9 s.

Another incident concerned a venerable cod of more than a year in captivity. It had been re-

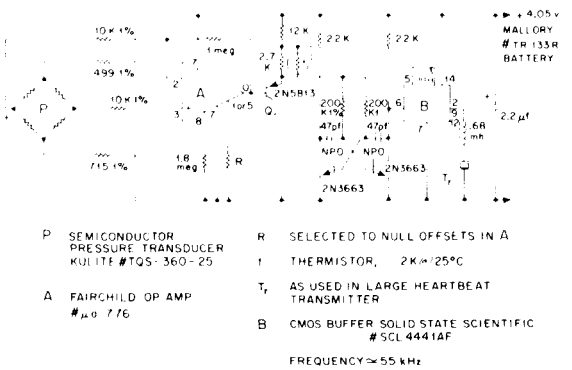

FIGURE 4.—Pressure transmitter.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

peatedly handled for blood samples and had largely accommodated to the presence of people. Its heart slowed only when the fish was physically touched.

At one point we started toward the fish with a dip net. This was one which the fish had never seen. It stopped swimming, faced the approaching strange net, and extended its fins in what we had come to recognize as a fright response. Its heart stopped for 19 s.

We detail these because we feel that such acoustic telemetry will be a valuable adjunct to behavior and sensory studies. When we have monitored three fish simultaneously some elements of social interaction showed in their variable heart rate. In particular, competition for food was easily discerned after a few simultaneous observations of feeding and listening to the EKG. In this manner we hope to build up a behavioral repertoire which will allow us to interpret data from a fish swimming free in the ocean where it cannot be observed.

The potential effect of behavior on such physiology as oxygen consumption had been previously shown by erratic increases when a fish was confined in a respirometer (Sundnes, 1957a, b). This could be overcome by keeping cod in a laboratory aquarium for many weeks, while it became used to people and capture. Veteran fish were found to increase their O_2 consumption and also showed immediate color changes whenever strangers were in the laboratory. We were reluctant to accept the respiratory data until substantiated by simultaneous observations of cardiac response.

Some species are difficult to acclimate to captivity. Atlantic salmon were brought directly from a fish farm and wired for EKG transmitting. They swam for several weeks at the maximum sustainable speed until they died. From this we could only learn the maximum heart rate. A 5-kg salmon showed 60 to 62 beats/min.

Later we have had fish which were hand fed in a laboratory tank for over a year. When these fish were tagged they were immediately returned to familiar surroundings. They soon joined in feeding frenzy and showed cardiac arrest when frightened. When they were chased the heart rate quickly increased, as shown in Figure 2. Resting rates below 30 beats/min were common.

This approach was not successful with skipjack tuna, *Katsuwonus pelamis*, in Hawaii. These

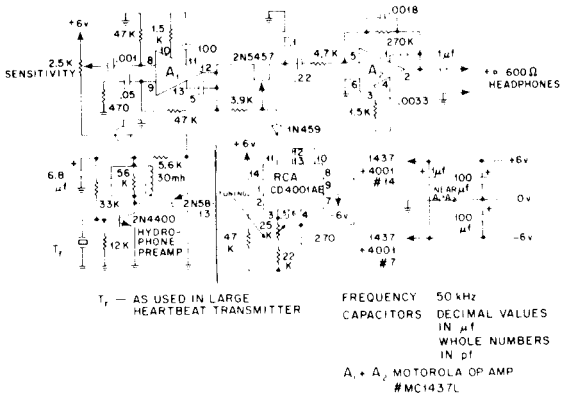

FIGURE 5.—Simple beat frequency oscillator receiver.

fast, probably warm-blooded fish were able to either get rid of our transmitter, or died in the effort. Their heart rates, however, were from 80 to 240 beats/min. This reflects their near mammallike metabolic rate. They recovered from fatigue in less than 1 h, much like man. We have used a new miniature tag (7 mm diameter × 35 mm long) successfully on mackerel, *Scomber japonicus*.

CONCLUSIONS

We have tried to outline the possibilities and methods of acoustic telemetry from fish. It is a valuable adjunct in both laboratory and open water studies. In many cases, such as monitoring the body temperatures of a free-swimming tuna, it is the only way to get the desired data (Carey and Lawson, 1973). The burgeoning solid state technology promises a rapid advancement in methodology beyond the relatively simple elements we have presented here.

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ABUNDANCE OF PELAGIC FISH DURING THE 19TH AND 20TH CENTURIES AS RECORDED IN ANAEROBIC SEDIMENT OFF THE CALIFORNIAS

ANDREW SOUTAR AND JOHN D. ISAACS[1]

ABSTRACT

Anaerobic sediment preserves a chronographic record of the bioclimatological conditions in coastal seas. Of the myriad elements within this record, the accumulation of pelagic-fish debris is of particular interest. The deposition of scales of the Pacific sardine, the northern anchovy, the Pacific hake, the Pacific saury, and the Pacific mackerel in the sediment of the Santa Barbara Basin, Alta California, and the Soledad Basin, Baja California, is generally in accord with available population estimates. The relation between scale deposition and population, when applied to the sedimentary record over the past 150 yr, suggests that major pelagic-fish productivity between 1925 and 1970 was substantially below pre-1925 levels.

Man in his search for an environmental perspective has unearthed a number of natural chronographic records. These include the well-known growth rings of trees (Fritts, 1972), the deposition of annual strata in the snowfields of Greenland and Antarctica (Murozumi et al., 1969), the incremental growth of coral and stromatolites (Knutson et al., 1972; Panella et al., 1968), and the formation of annual layers in certain lacustrine and marine sediments (Seibold, 1958).

Perhaps no richer records exist than those finely laminated deposits encountered beneath the sea in regions of anaerobic sedimentation. A web of circumstance involving productivity and topography serves to produce and protect such records, but no factor can be more important than the exclusion of burrowing animals from the sediment by a persistently low dissolved oxygen concentration in the bottom water. Here such diverse and informative fragments of the air-sea-land system as the tests of the microplankton, skeletal and integument debris from the nekton, air- and river-borne detritus, natural radioisotopes, and more recently, anthropogenic products fall in sequential association to a common resting place. Undisturbed, these threads of information accumulate to form a remarkable sedimentary chronicle combining the rhythmic pulse of the seasons with the vagaries, trends, and inconsistencies of ocean life, chemistry, and currents.

Of the myriad elements within the anaerobic sediment record, the temporal framework and the distribution of pelagic fish scales at depth in the sediment in the Santa Barbara Basin, Alta California (Figure 1a), and in the Soledad Basin, Baja California (Figure 1b), compose a particularly relevant set—relevant not only in relation to the continuing importance of pelagic fish as a resource off the Californias, but also as a potential indicator of long-term productivity and change. Such knowledge of ocean conditions within the broader context of the North Pacific gyre and the Northern Hemisphere climate can aid man in his search for a rational interaction with his environment, guide him toward a wise stewardship of marine resources, and aid him in discriminating between those changes that he produces by his interventions and those that are a part of the natural order.

Time in the laminated sediment of the Santa Barbara Basin can be estimated through the serial assignment of the year of deposition to each laminae pair (Figure 2a). It was suggested that the regular alternation of sediment density is a direct response to the monsoonal climate affecting southern California (Emery, 1960). Confirmation of this and the laminae pair sequence as a yearly depositional record has come through the correlation of regional rainfall and sediment-laminae patterns.[2] As indicated (Figure 3), the essentially random pattern of southern California seasonal

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[2]Soutar, A., J. D. Isaacs, P. A. Crill. Recent paleoclimatology and paleoecology of the Santa Barbara Basin. Unpubl. manuscr.

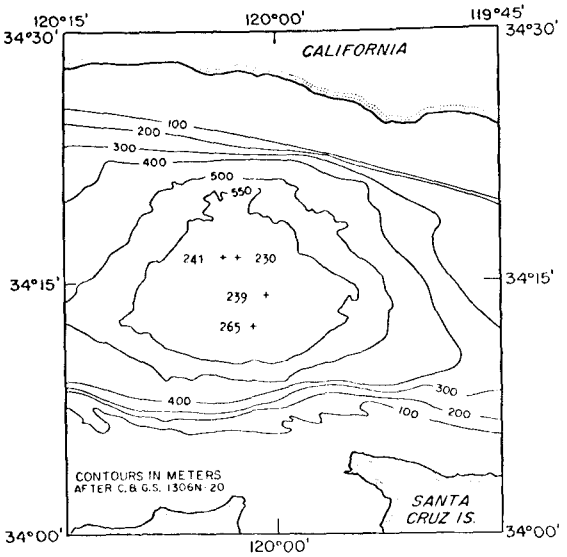


FIGURE 1a.—Santa Barbara Basin, California. The basin lies under the Santa Barbara Channel and reaches a maximum depth of 589 m (Hülsemann and Emery, 1961). Pertinent box-core locations (230,241,239, and 265) are shown.

rainfall can be simply transformed into a clear reflection of the serial pattern of varve thickness. This transformation corresponds to factors such as upstream aggradation (Schumm, 1969) which could cause a considerable delay in basin sedimentation.

Further development of the anaerobic-sediment chronology has been possible through the close agreement of Pb-210 and Th-228/Th-232 radiometric ages and the varve-sequence year (Koide et al., 1972, 1973; Krishnaswami, 1973) (see Figure 4a, b). These relatively short-term radiochronologic tools can be used to considerable advantage in the Soledad Basin sediment. Though this basin is morphologically and oceanographically similar to the Santa Barbara Basin in that there is virtually no dissolved oxygen in the bottom water, the absence of consistent seasonal rainfall inhibits the formation of distinct sequential varves (Figure 2b). Nevertheless, a reasonable time framework can be estimated for the near-surface sediment of the Soledad Basin from the measurement of Pb-210 and the Th-228/Th-232 ratio at depth (Koide et al., 1973) (see Figure 4c, d).

The distribution of pelagic fish-scale debris can be determined within the time-sediment framework. Specifically, large (20 × 20 cm) cores were frozen, then cut into longitudinal sections measuring 5 × 15 × ~40 cm. X-radiograph representations were obtained for each of the sections, and by means of recognizable stratigraphic patterns 5-yr block templates were drawn. In the case of the Santa Barbara Basin sediment, specific laminae can be identified within cores and between cores as to the year of deposition; therefore, precise templates can be constructed. This is particularly so for the time period 1860-1970 in which the laminae are well defined. The period from some time before 1810 to 1860 is partly obscured by bioperturbation apparently supported by a marginal increase in bottom-water dissolved oxygen. Only general sedimentation rates are available for the Soledad Basin sediment; therefore linear estimates of the 5-yr blocks were made for the core slab from which the radiometric ages were obtained. These estimates were carried out to the 90-yr limit of the Pb-210 method and were transferred by available stratigraphic markers to the other core sections. Furthermore, these linear estimates were continued to the bottom of the core, an additional 80 estimated years. It should be noted that the Th-228/Th-232 method permits age estimates in the uppermost sediment of the Soledad Basin that are comparable in accuracy to those in the Santa Barbara Basin. The templates

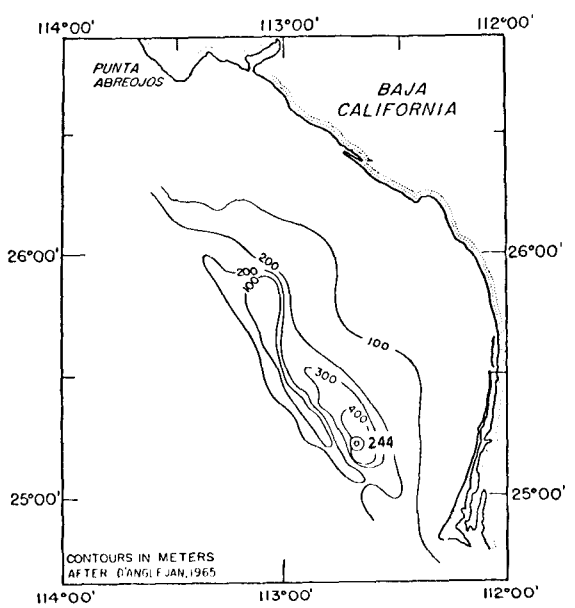


FIGURE 1b.—Soledad Basin, Baja California. This basin lies in a trough trending northwest from Cabo San Lazaro. The maximum depth is nearly 520 m and it occurs in the vicinity of core 244.

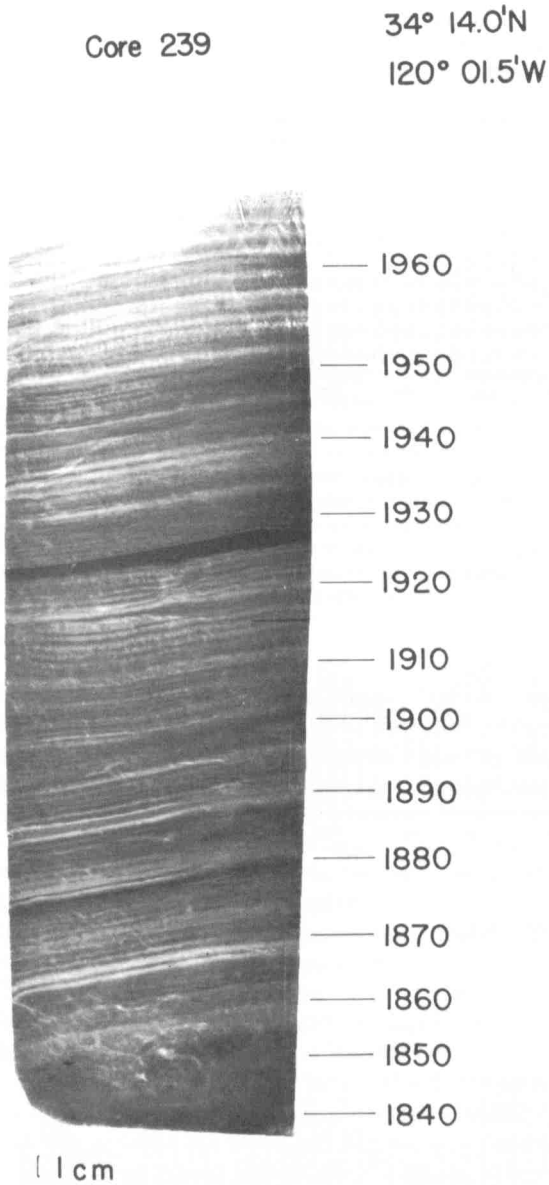


FIGURE 2a.—Radiograph of core 239, Santa Barbara Basin. The radiograph was obtained from a frozen core slab approximately 2 cm thick. The darker laminae are the more dense (negative print of radiograph transparency). Each pair of laminae are considered to be a single year with the denser sediment representing detritus brought in by winter rains (Soutar et al, in prep.).

so constructed were fitted to the frozen core sections by means of morphologic and stratigraphic markers, and the sections were split into the 5-yr blocks. These sediment blocks were subsequently treated with a buffered dilute H_2O_2 solution and gently washed on a 500μ screen. The retained coarse fraction was transferred to vials and stored wet with ethanol as a preservative. Identification and enumeration of the material was carried out at low magnification.

The presence of fish scales in contemporary laminated sediment should not be unexpected, particularly to those acquainted with the stratified diatomite of the Monterey Formation cropping out along the Coastal Range of California (David, 1943). In some instances whole or partial skeletons of fish are present in these deposits.

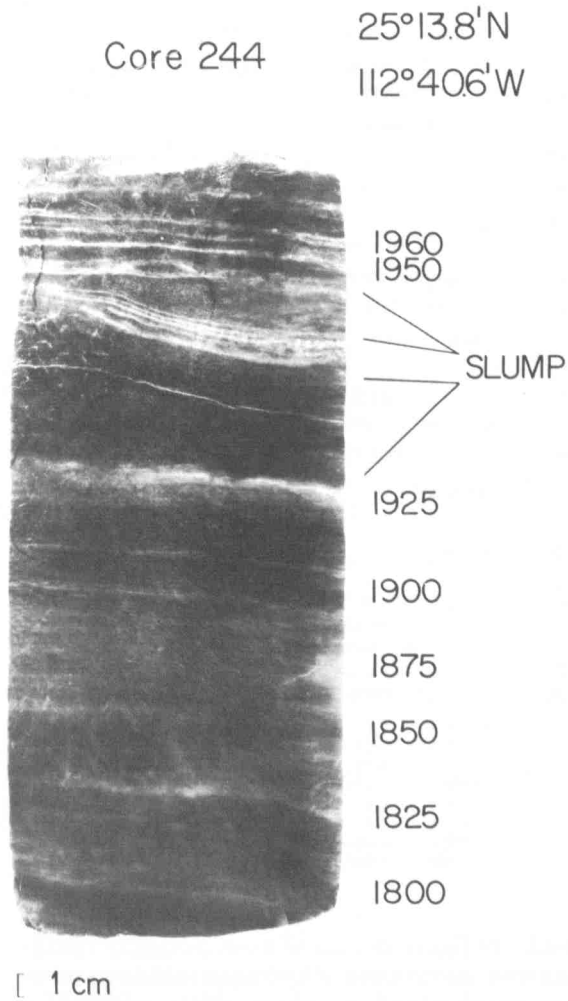
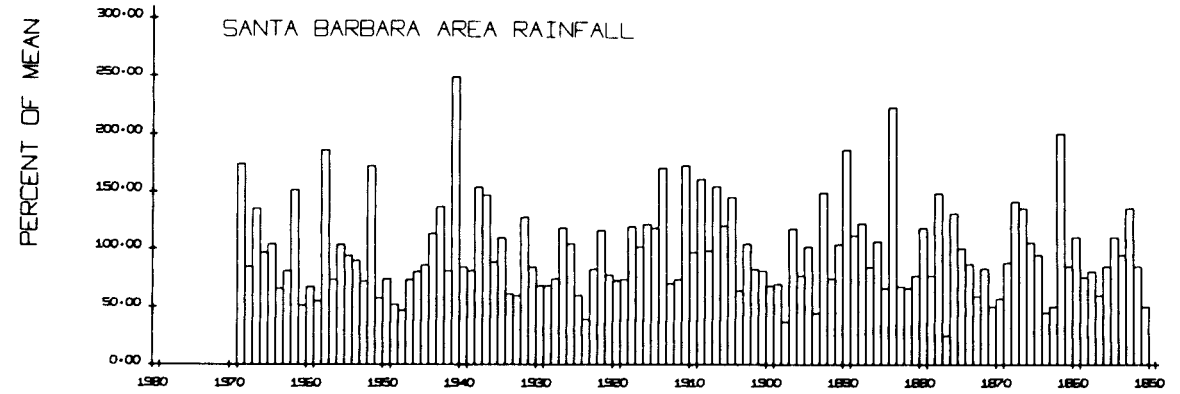
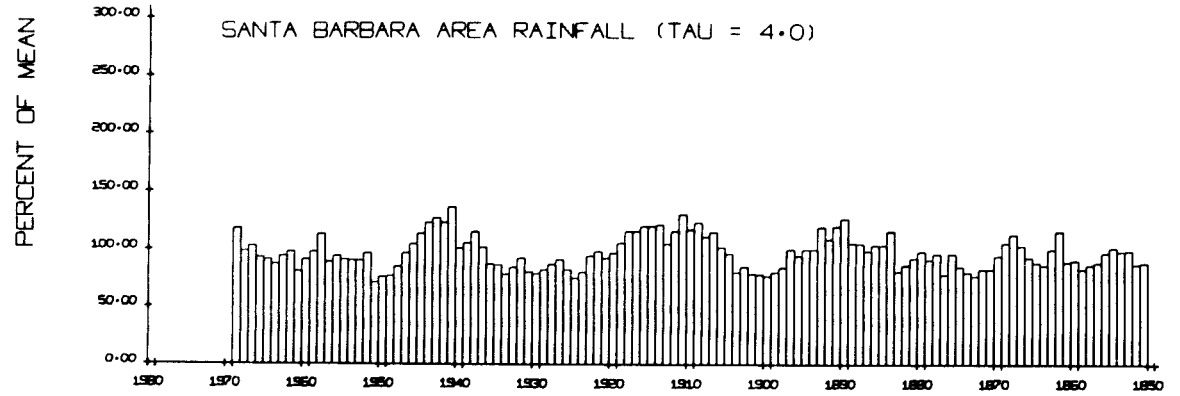
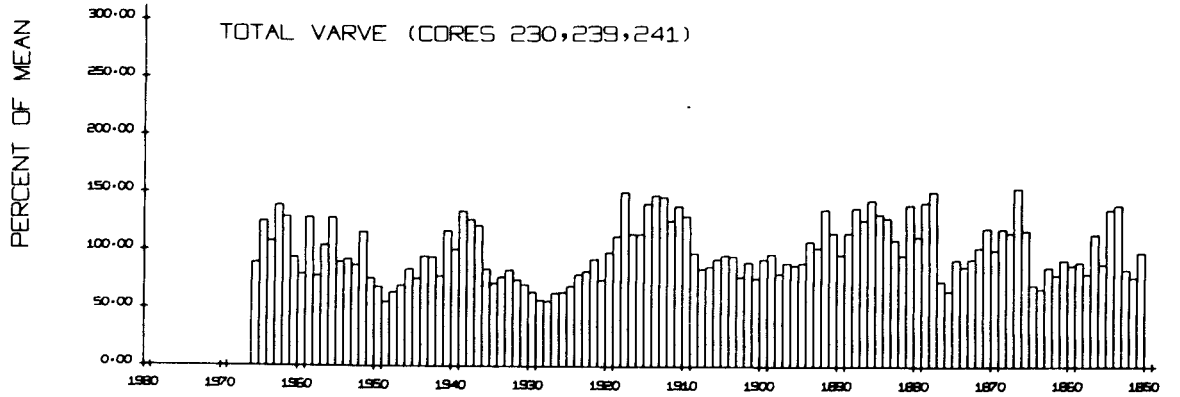


FIGURE 2b.—Radiography of core 244, Soledad Basin. Although laminae are present there are no consistent patterns that would suggest varves. There is, however, enough information to physically correlate between slabs and to identify irregular sedimentation events.







Such are likely victims of mass mortality resulting from an invasion of hydrogen sulfide water or red water situations which, while reported in Walvis Bay, South Africa (Brongersma-Sanders, 1957), do not seem characteristic of the present coastal waters off the Californias. On the other hand, the occurrence of separate scales is likely the incidental result of serious if not fatal trophic interactions. Previous investigation has indicated that, with few exceptions, fish scales are deposited in Santa Barbara Basin as individual events (Soutar, 1967).

Interstitial-water measurements (Sholkovitz, 1973) indicate an increase of dissolved phosphate within the anaerobic sediment from 20 μmoles $PO_4^{\equiv}$ near the surface to levels in excess of 100

FIGURE 3.—Comparison of Santa Barbara regional rainfall, smoothed Santa Barbara regional rainfall, and total varve thickness. Spearman rank-correlation coefficient between Santa Barbara regional rainfall and total varve thickness is 0.26 (P = 0.02, n = 99). The highly variable pattern of seasonal rainfall is smoothed by the filter:

$$Y_t = \sum_{i=1}^{t} \frac{Ri}{\tau} \quad (1 - \frac{1}{\tau})_{t-i}$$

where Y_t = smoothed seasonal rainfall at year t; R_t = actual seasonal rainfall at year t; and τ = a time constant (years). Thus Y_t is the sum of $\frac{1}{\tau}$ of year t rainfall and exponentially decreasing portions of previous year's rainfall. The function tends to dampen rapid oscillations and lag slower oscillations at a slightly lower amplitude. The value of τ is derived by multiple regression analysis. Varve thickness at year t is the dependent variable and rainfall at year t, year t-1, year t-2, etc. are the independent variables. τ is found by fitting a log linear line to the regression coefficients. The Spearman rank-correlation coefficient between the filtered rainfall and the total varve thickness is 0.50 (n = 99). Due to the autocorrelation induced by the filter, no probability is assigned. Mean Santa Barbara regional rainfall is 42.2 cm, and mean varve thickness is 1.74 mm (at 60% water by weight).

μmoles at depth. Since the composition of fish scales is essentially an intermixture of microcrystalline apatite and a collagen-ichthylepidin matrix (Wallin, 1957), a potential for the degradation of the scale record is present. However, ichthylepidin, an albuminoid approaching keratin in composition, is unlikely to be degraded in an anaerobic environment (Kaplan and Rittenberg, 1963). Thus the organic matrix may contribute significantly toward the preservation of scales. The distinctly higher frequencies of scales at core depths in excess of 2 m further suggest a nondegraded record (Soutar and Isaacs, 1969).

The record of scale deposition in the Santa Barbara Basin (16 subcore-sample mean, 1810-1970) and the Soledad Basin (4 subcore-sample mean, 1780-1970) is in part presented (Figure 5a, b) and statistically summarized (Table 1) for: *Sardinops caerulea* (Pacific sardine), *Engraulis mordax* (northern anchovy), *Merluccius productus* (Pacific hake), *Colalabis saira* (Pacific saury), and *Scomber japonicus* (Pacific mackerel).

Of particular interest are those portions of the scale record covering the past few decades for which population estimates exist. Considerable attention has been directed towards the elucidation of the historical population levels of the Pacific sardine. Estimates of the population (fish 2 yr and older) derived from the solution of a fishery catch equation extend from 1930 up to 1959 (Murphy, 1966). These biomass estimates presented in single- and 5-yr averages (Figure 6) document the historical decline of the fishery and the population. Comparison of the 5-yr averages of the biomass and the scale-deposition rate in the Santa Barbara Basin sediment indicates a parallel but offset decline. The derived age frequency of the sedimented scales (Table 2) indicates that most (92%) of the contributing fish were less than 2 yr old, suggesting a relatively fast response on the part of the sediment to particular year-class sizes. Comparison of the 5-yr averages of the year-class size (numbers of 2-yr-old fish entering the fishery) and the scale-deposition rate indicates a direct proportional relationship (Figure 7 and Table 3).

Population estimates for the central, southern, and total populations of the northern anchovy for the years 1951 to 1966 have been made (Smith, 1972). The estimates of the total spawning population presented in single- and 5-yr averages, and the 5-yr averages for the subpopulations, record the recent ascendancy of the anchovy. Comparison is made of these population estimates with the northern anchovy scale-deposition rate in the Santa Barbara and Soledad Basin sediments (Figure 8 and Table 4). In the three 5-yr intervals having sufficient information, the scale deposition is proportional to the spawning biomass. The direct relation to spawning biomass may be associated with the relatively rapid mat-

Table 1.—Statistical summary of scale deposition (numbers/10^3cm^2/yr) for Santa Barbara Basin sediment, 1810-1970, and Soledad Basin sediment, 1780-1970.[1]

Sediment	Mean	Median	Variance	Maximum	Minimum
Santa Barbara Basin (N=32)					
Pacfic sardine	3.6	2.8	13.6	15.2	0
Northern anchovy	10.0	9.8	27.8	19.4	2.0
Pacific hake	24.8	21.8	310.1	73.0	5.5
Pacific saury	0.8	0.3	3.2	8.4	0
Pacific mackerel	0.3	0.2	0.2	1.9	0
Other	8.5	8.1	24.3	17.8	0
Total	48.1	44.7	532.6	108.1	21.0
Soledad Basin (N=38)					
Pacific sardine	0.4	0.2	0.4	3.0	0
Northern anchovy	9.2	7.5	43.5	26.4	0.6
Pacific hake	6.1	6.1	8.3	12.0	1.3
Pacific saury	0.3	0	0.8	3.9	0
Pacific mackerel	0.3	0	0.3	1.6	0
Other	2.9	2.2	4.0	6.8	0
Total	19.2	17.9	52.4	39.0	5.6

[1]In the case of the Santa Barbara sediment, the statistics are drawn from a 16 subcore set representing a combined area of 980 cm^2. The statistics for the Soledad Basin are drawn from a 4 subcore set having a combined area of 260 cm^2.

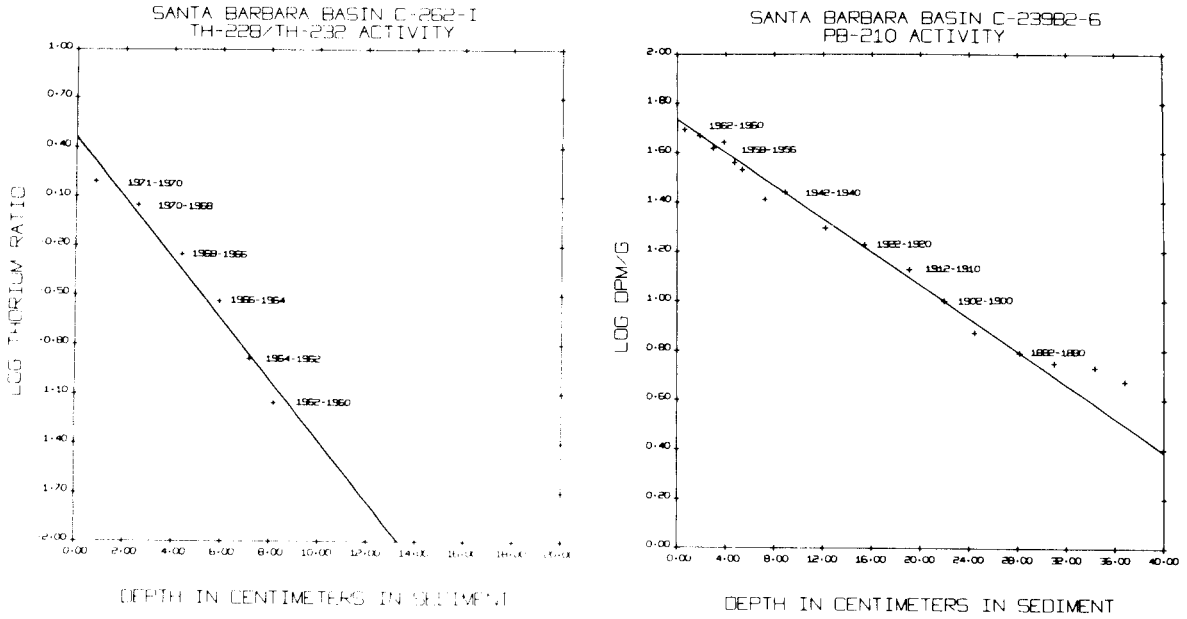


FIGURE 4a,b.—Santa Barbara Basin Th-228/Th-232 activity and Pb-210 activity at sediment depth. An excess of both the thorium isotopic ratio Th-228/Th-232 and the lead isotope Pb-210 are present in coastal surface sediments (Koide et al, 1972, 1973). In the case of Pb-210 (22.3 yr half life), the varve age estimate and the radiometric age estimate may be directly compared. The thorium ratio on the other hand cannot be directly estimated as function of time but may be calibrated against the accepted varve age.

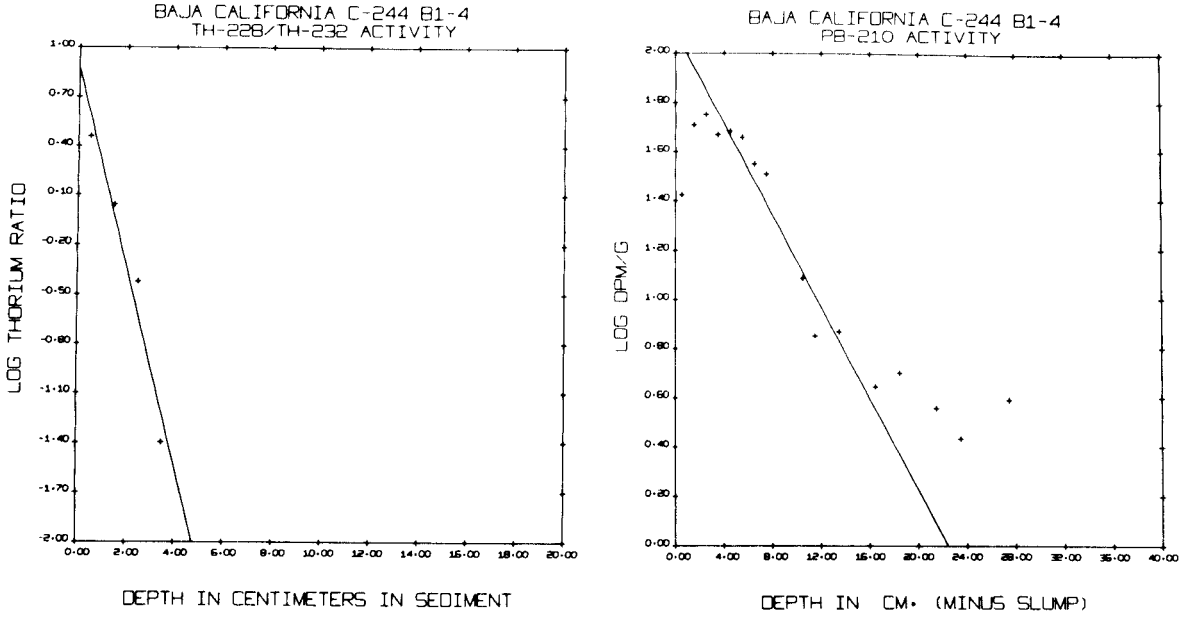


FIGURE 4c,d.—Soledad Basin Th-228/Th-232 activity and Pb-210 activity at sediment depth. The information gained from the study of these radiometric tools in the Santa Barbara sediment may be applied to the anaerobic sediment of the Soledad Basin. Here, despite the absence of consistent laminae, the radiometric ages provide the basis for a time framework. It should be noted that the scatter of Pb-210 points at the lower end (circa 1880) signals the merging with the supported background activity (U-238 series).

Table 2.—Derived-age[1] frequency of Pacific sardine, northern anchovy, and Pacific hake scales in sediment of the Santa Barbara and Soledad Basins.

Sediment	Age in years						
	0	1	2	3	4	5	6+
Santa Barbara Basin							
Pacific sardine	163	46	9	8	7	2	7
Northern Anchovy	62	110	78	48	18	1	9
Pacific hake	685	592	15	3	0	1	0
Soledad Basin							
Pacific sardine	13	1	1	0	0	0	0
Northern anchovy	139	16	12	36	(older than 3 yr)		
Pacific hake	208	22	1	1	0	1	0

[1]The derived age is an estimate of age based on the measurement of scale width. The scale width is a more reliable feature of sedimented scales than is the scale length as, for example, in the case of the sardine the exposed "wing" of the scale is often separated. The scale width is converted to an estimate of standard length and the estimate of standard length is converted to an age estimate by the growth curve.

uration of the northern anchovy. Considering that 50% of the anchovy mature in 2 to 3 yr (Clark and Phillips, 1952), then the derived-age frequency of the anchovy scales (Table 2) suggests that for Santa Barbara 35% and for Soledad 24% of the contributing anchovy are mature.

No direct population estimates are available for the Pacific hake; however, larval abundances thought to be proportional to the adult biomass have been provided.[3] In view of the estimate that 54% or more of the scale information in the sediment is derived from hake less than one year old, a proportional relationship between larval abundance and scale deposition might be anticipated. However, this comparison for the inshore region of southern California and southern Baja California from 1950 to 1965 indicates a non-systematic relationship (Table 5). One explanation of the inconsistency may be that between 1950 and 1965 the inshore larval populations were generally low and had no strong trend. It should also be noted that the inshore and total abundances are in themselves not entirely consistent, and, in fact, the total larval abundances tend toward an inverse relationship with the scale-deposition rate.

Information on the spawning population of the Pacific saury for the period 1950 to 1966 has been reported (Smith et al., 1970). Comparison of the spawning biomass and the scale-deposition rate (Table 6) indicates a sparse but sensible relation.

Egg abundances and catch information for the Pacific mackerel which could reflect the population are available, but the extremely low rate of scale deposition for this species limits an evaluation (Table 7).

The generally consistent relationships between the available estimates of pelagic fish populations and scale deposition provide an entree into the past. Such relationships are perhaps not unreasonable considering the strategic location of the basins adjacent to major spawning grounds. The short time over which population estimates and scale-deposition rates may be compared in the case of the anchovy, hake, saury, and mackerel is presently a limitation; nevertheless, relative measures of high and low spawning biomass may be made from the sedimentary information. The record for the Pacific sardine, however, should be amenable to direct interpretation in terms of year-class size and projected biomass, with the exception perhaps of those times when scale deposition far exceeds our experience.

Consideration of the scale record (Figure 5) as a population record affords a fascinating look into the flow of ocean life at the higher trophic level. The historical decline of the sardine, seen in perspective, appears as a subdued finale to a movement that had begun in 1890, thirty years before the inception of the fishery, and this movement in turn belongs to a theme extending into the millennia (Soutar and Isaacs, 1969). Levels of year-class success in excess of 10^{10} fish occurring in the late 1930's, which are historically considered impressive, appear in broader context to be at most moderate. Even higher levels of success suggested by the sedimentary record between 1855 and 1865 afforded insufficient reserve against a precipitous and natural decline. Nor can the virtual absence of the sardine from the waters off Alta California be

Table 3.—Comparison of Pacific sardine population (Murphy, 1966) and scale-deposition rate in the Santa Barbara Basin sediment.[1]

Year interval	2 yr and older annual biomass (10^6 metric tons)	2 yr old year annual class in year spawned (10^9)	Scale-deposition rate (no./10^3cm^2/yr)
1959-55	0.25	1.7	0
1954-50	0.63	2.1	0
1949-45	0.64	3.3	0.4
1944-40	1.84	3.5	0.5
1939-35	1.71	9.1	3.1
1934-30	[2]3.52	6.8	2.0

[1]The Spearman rank-correlation coefficient between the 2-yr and older biomass and the scale-deposition rate is 0.81, $n = 6$; and for the 2-yr-old year class and the scale-deposition rate is 0.99, $n = 6$. While these are highly suggestive of a significant relationship, no probabilities are assigned due to inherent autocorrelation in these series.
[2]Incomplete data.

[3]Smith, P.E. CalCOFI—the first twenty-five years. Unpubl. manuscr.

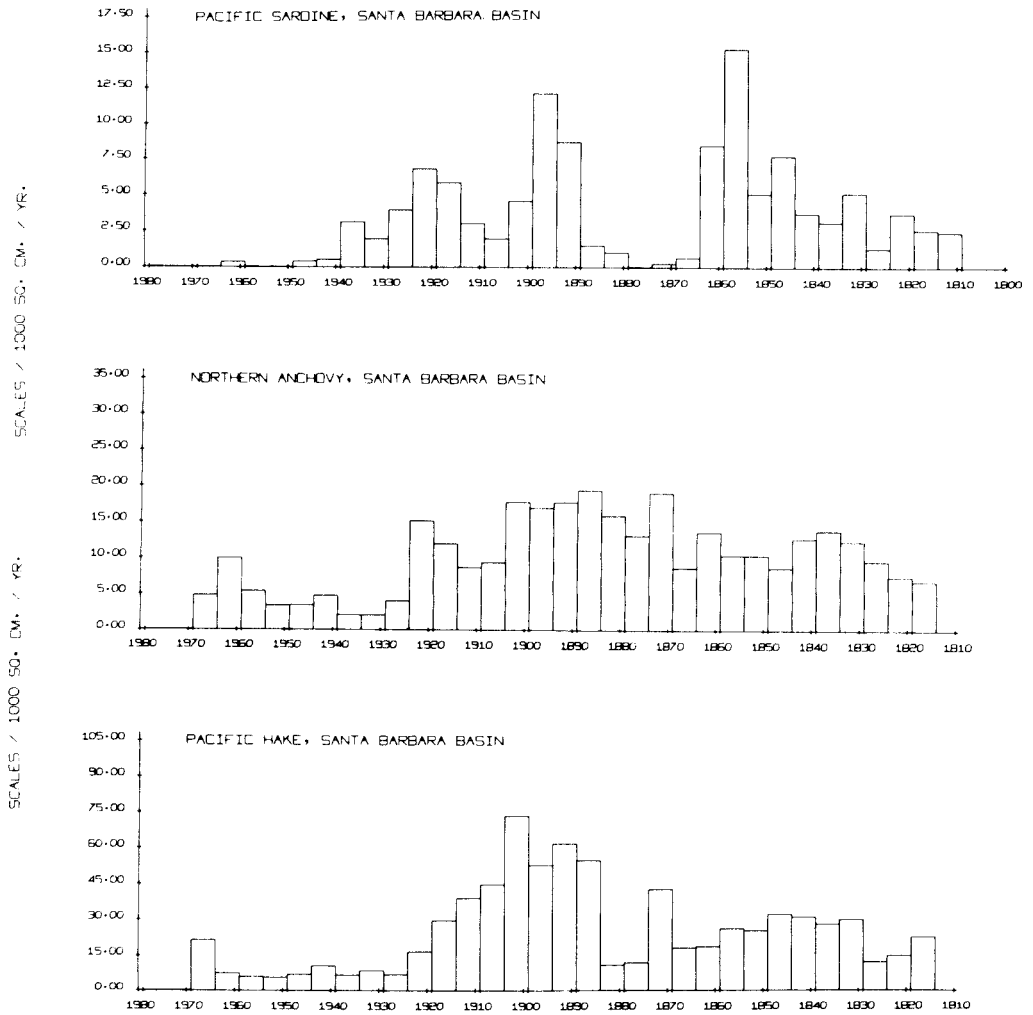


FIGURE 5a.—Histogram plot of the scale-deposition rate of the Pacific sardine, the northern anchovy, and the Pacific hake in sediment of Santa Barbara Basin, 1810 to 1969.

considered an unnatural circumstance. The levels of year-class success between 1865 and 1880 were likely as low as those estimated after 1940. It may be argued that in the previous period the sardine had moved offshore or migrated southward, thereby causing a decline in scale deposition. However, abandonment by a substantial population of a major spawning ground would seem problematic, and in regard to a southern immigration it can be said that during the apparent year-class failures from 1865 to 1880 no substantial sardine population occupied the southern waters near the Soledad Basin, Baja California. Indeed, the only time the sardine appears even moderately influential in these waters is the period 1920 to 1935, coincidental with the development of the fishery to the north. While the evidence from previous decades makes it impossible to accuse the sardine of avoidance, the coincidence may nevertheless underline the naturally intermittent occurrences of abundant sardine populations in California waters.

As in the case of the sardine, one's view of the distribution of the anchovy through time is colored by perspective. The sediments in both the Santa Barbara and Soledad Basins have responded to the recent increase in the anchovy population. This response appears as part of a

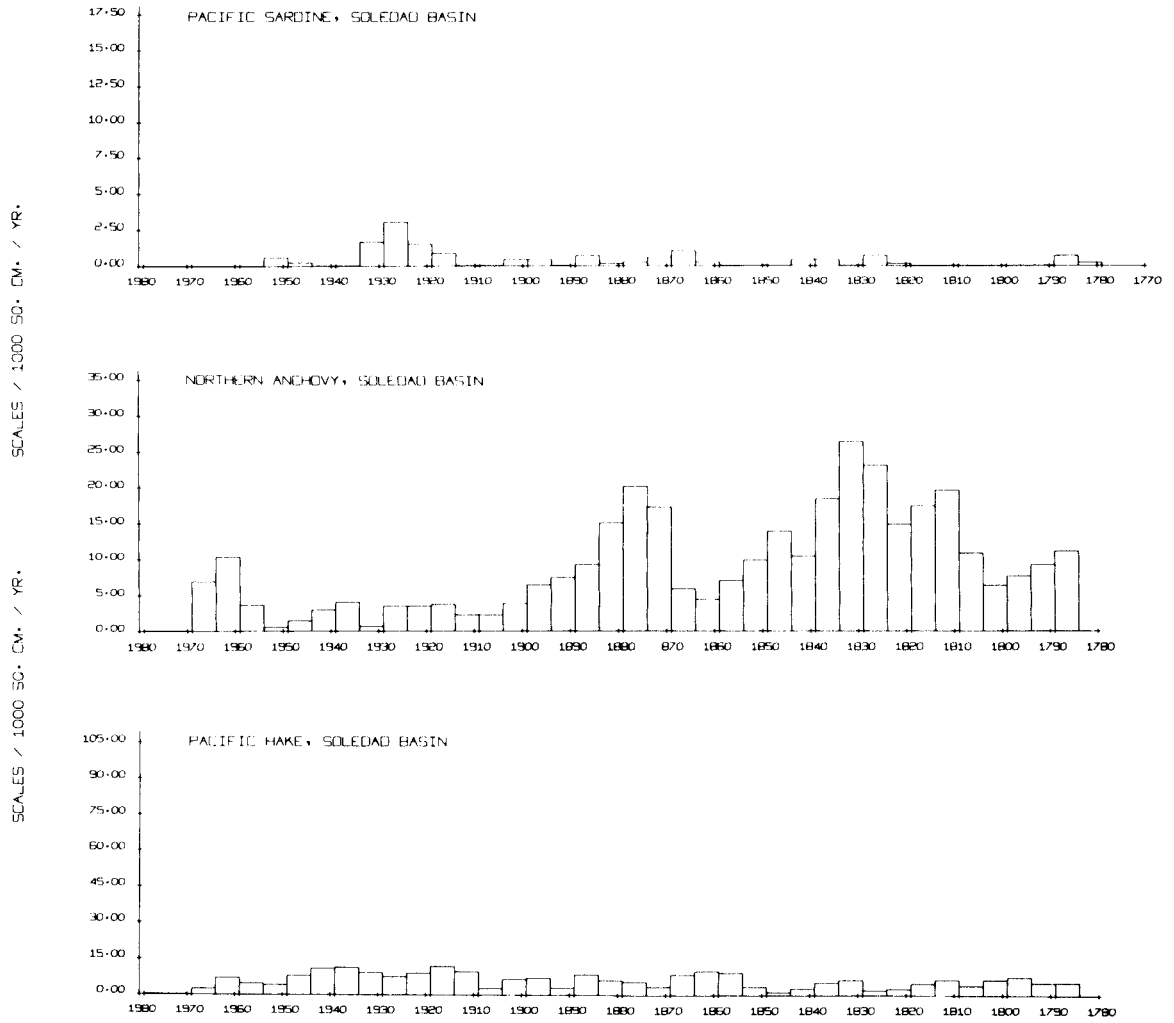


FIGURE 5b.—Histogram plot of the scale deposition rate of the Pacific sardine, the northern anchovy, and the Pacific hake in sediment of the Soledad Basin from about 1780 to 1969.

significant pattern of similarity in scale deposition (Table 8). The recorded increase in the anchovy population, while substantially above recent historical levels, when compared to the inferred population reached in most of the 19th and the early part of the 20th centuries, appears moderate. Furthermore, in contrast to the sardine, the population of the anchovy has been of comparable density in the waters of the Californias over the past two centuries. This then supports contemporary observations that the northern anchovy is regionally adapted and is capable of successful population responses covering at least the southern half of the California Current.

The inferred distribution of the Pacific hake, although made tenuous by the lack of clearly supportive population information, is, in the case of Santa Barbara Basin, strongly suggestive of the anchovy with an indication of a recent increase from low levels between 1920 and 1965 and with substantially higher levels before 1920 (Table 8, Figure 5). The inferred hake population in the water near Soledad Basin corresponds with the levels inferred for Santa Barbara back to the 1930's and in this regard is consistent with recent observations of essentially equal larval abundance in both areas. However, levels of inferred population before 1930 at Santa Barbara are considerably above those of Soledad, the latter showing a consistent level over the past 200 years.

TABLE 4.–Comparison of the northern anchovy population (Smith, 1972) and the scale–deposition rate in the Santa Barbara and Soledad Basin sediment.[1]

Year interval	Central subpopulation 5-yr average spawning biomass (10^6 metric tons)	Southern subpopulation 5-yr average spawning biomass (10^6 metric tons)	Total population 5-yr average spawning biomass (10^6 metric tons)	Scale-deposition rate, Santa Barbara Basin no./10^3cm^2/yr	Scale-deposition rate, Soledad Basin no./10^3cm^2/yr
1969-1965	[2]4.70	[2]0.92	[2]5.02	4.9	[2]7.0
1964-1960	2.95	1.18	4.29	10.0	10.3
1959-1955	1.34	0.37	1.85	5.4	3.6
1954-1950	0.54	0.47	1.04	3.3	0.6
1949-1945	—	—	—	3.4	1.5
1944-1940	—	—	[2]2.37	4.7	3.0

[1]As defined (Vrooman and Smith, 1971) the central subpopulation area includes southern Alta California inshore, offshore, and seaward and Baja California inshore, offshore, and seaward. The southern subpopulation area includes southern Baja California inshore, offshore, and seaward. Inshore includes 0–80 miles; offshore includes 80–160 miles; and seaward includes 160–280 miles.
[2]Incomplete data.

TABLE 5.—Comparison of Pacific hake larval abundance (Ahlstrom, 1969; Smith, in prep.) and scale–deposition rate in Santa Barbara and Soledad Basin sediment.

Year interval	California coastal inshore area (5-yr average)	Southern Baja coastal inshore area (5-yr average)	Total (inshore and offshore) (5-yr average)	Scale-deposition rate Soledad Basin no./10^3cm^2/yr	Scale-deposition rate Santa Barbara Basin no./10^3cm^2/yr
1969-1965	[1]3,500	[1]880	[1]10,360	[1]21.3	[1]2.5
1964-1960	480	590	3,810	7.3	6.9
1959-1955	600	420	11,850	5.8	4.6
1954-1950	540	880	12,660	5.5	4.0

[1]Incomplete data.

Consideration of the relationships of the three major species provides further insight into the distribution of pelagic fish through time. Most if not all investigators have found the hypothesis that the Pacific sardine and the northern anchovy are direct competitors unavoidable. This hypothesis is not supported by the less-than-significant positive correlation between the scale deposition of the two species in the Santa Barbara sediment (Table 8). However, fluctuations in relative abundance of even closely competitive species in the marine environment may follow quite different rules than mere abundance or autecologic correlation. The abundance of species may be directly related to advantageous conditions. However, whenever an advantageous or disadvantageous series of years is of critical duration (determined by specific differences in life history) the abundances may be inversely related. In this context the apparent decline and subsequent recovery of the sardine population between 1865 and 1890 from levels which appear substantially above historical experience, in the presence of what also appears to be substantial anchovy populations, may not be entirely enigmatic.

The associations of the anchovy, hake, and sardine in the Santa Barbara sediment (Table 8) is further suggestive of periods favorable or unfavorable to these three species. This is in contrast to the Soledad sediment from which it may be inferred the anchovy alone is able to maintain high population levels. Some idea of the total pelagic-fish productivity off the Californias may be gained by combining the inferred populations of the anchovy, hake, and sardine into a total spawning biomass estimate (Figure 9). This biomass estimate suggests that the central California and presumably the northern Baja California regions can become a dominant center of pelagic fish productivity. Even though significant densities of northern anchovy have been present in the water above Soledad Basin, available information (Table 4) suggests these represent a relatively smaller southern subpopulation. The

Table 6.—Comparison of the Pacific saury population (Smith et al., 1970) and the scale–deposition rate in the Santa Barbara and Soledad Basin sediments.

Year interval	Total population spawning biomass CalCOFI area (10^6 metric tons)	Total scale-deposition rate, Santa Barbara Basin no./10^3 cm^2/yr	Total scale-deposition rate, Soledad Basin no./10^3 cm^2/yr
1969-1965	[1]0.21	[1]1.1	[1]0.0
1964-1960	0.12	0.3	0.0
1959-1955	0.18	1.1	0.0
1954-1950	0.23	2.2	0.6

[1]Incomplete data.

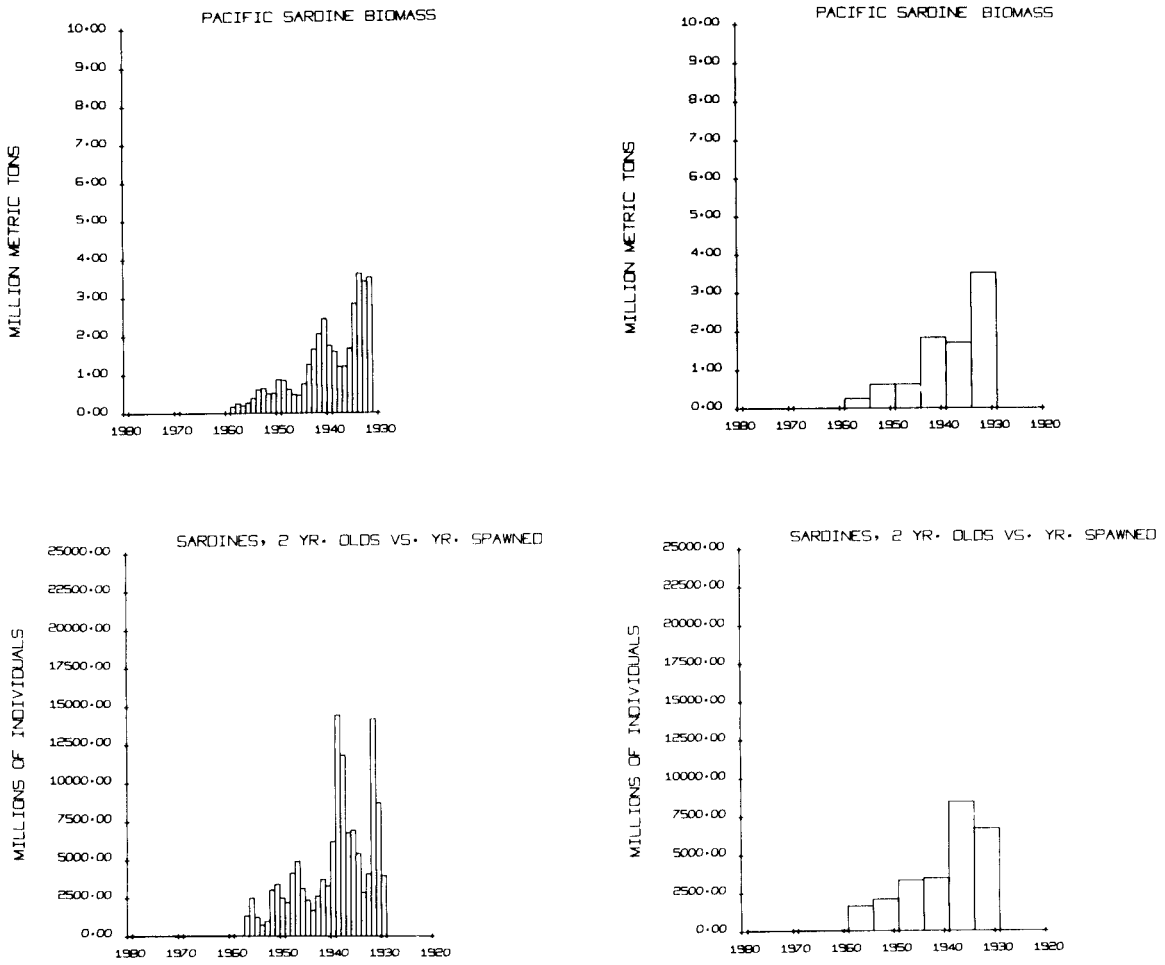


FIGURE 6.—Yearly estimates of Pacific sardine biomass 2-yr and older and year class size at 2 yr old (after Murphy, 1966). The yearly population estimates (left) are grouped into 5-yr block averages (right) that correspond to the sampling intervals in the sediment.

TABLE 7.—Comparison of Pacific mackerel larval abundance (Ahlstrom, 1969; Smith, in prep.), fishery landings (Fitch, 1952),[1] and scale-deposition rate in Santa Barbara and Soledad Basin sediment.

Year interval	Southern California coastal inshore area (5-yr average)	Southern Baja coastal inshore area (5-yr average)	Total (inshore and offshore) (5-yr average)	Southern California landings (5-yr average) (metric tons)	Scale-deposition rate, Santa Barbara Basin no./10^3cm^2/yr	Scale-deposition rate, Soledad Basin no./10^3cm^2/yr
1969-1965	[2]	[2]	[2]	1,660	[2]0	[2]0
1964-1960	560	21,000	38,600	17,830	0	0
1959-1955	1,260	3,060	16,100	18,390	0.2	0
1954-1950	650	10,100	19,000	10,780	0.2	0.8
1949-1945	—	—	—	21,660	0.6	0
1944-1940	—	—	—	35,020	0.4	1.6
1939-1935	—	—	—	45,430	0.2	1.6
1934-1930	—	—	—	—	1.6	0.8

[1]Also subsequent Cal. Dept. Fish and Game landing statistics.
[2]Incomplete data.

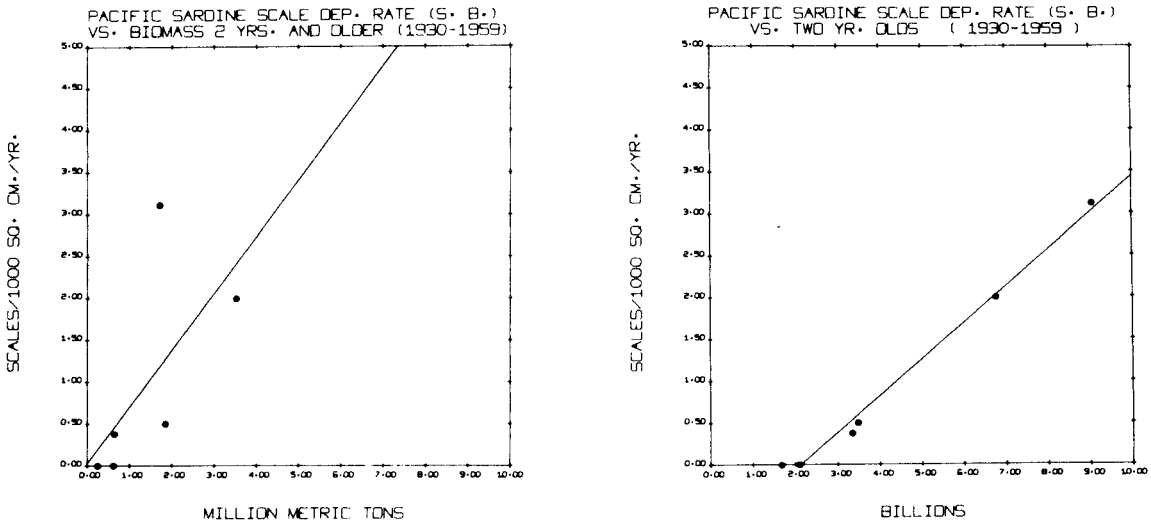


FIGURE 7a,b.—Scatterplot of the 5-yr averages of the Pacific sardine biomass (after Murphy, 1966) and the scale-deposition rate in Santa Barbara sediment, 1930 to 1959. The plot of biomass versus scale deposition though indicating a significant relationship (Spearman rank-correlation coefficient is 0.81, n = 6) shows considerable scatter. If, on the other hand, the year-class size at 2 yr of age is plotted against the scale-deposition rate in the year spawned, the scatter is markedly reduced and a highly significant relationship emerges (Spearman rank-correlation coefficient is 0.99, n = 6). The reduction in scatter can be explained through the observation that most of the scales encountered in the sediment were derived from younger fish.

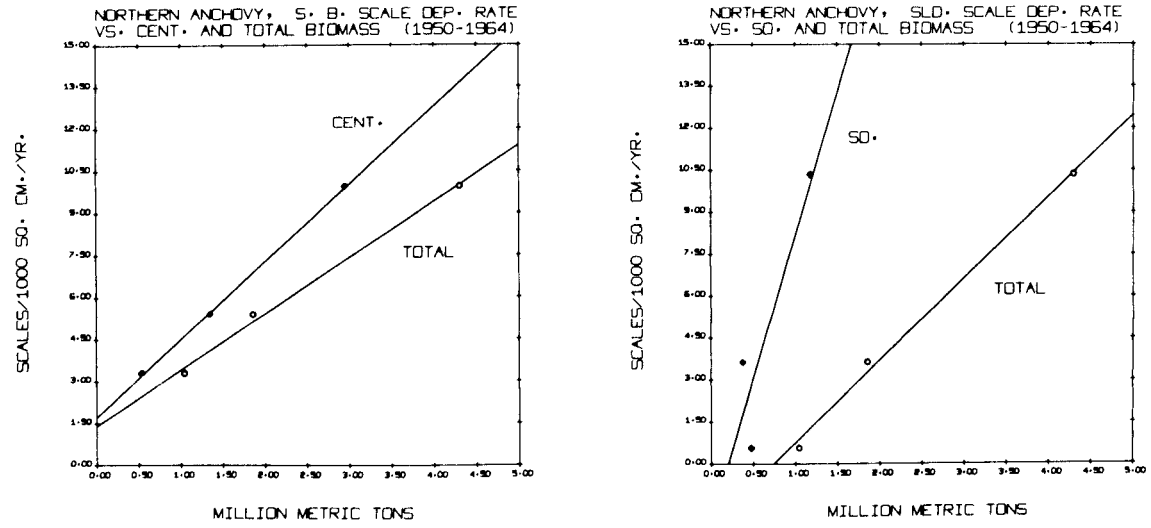


FIGURE 7c,d.—Scatterplot of the 5-yr averages of the northern anchovy spawning population estimates (after Smith, 1972) and the scale-deposition rates in Santa Barbara and Soledad Basin sediment, 1950 to 1965. The scale-deposition rates in both the basins vary directly with increasing population estimates of the northern anchovy. The relatively steep slope of the southern subpopulation (S) relative to the central subpopulation (CNT) reflects the smaller southern population.

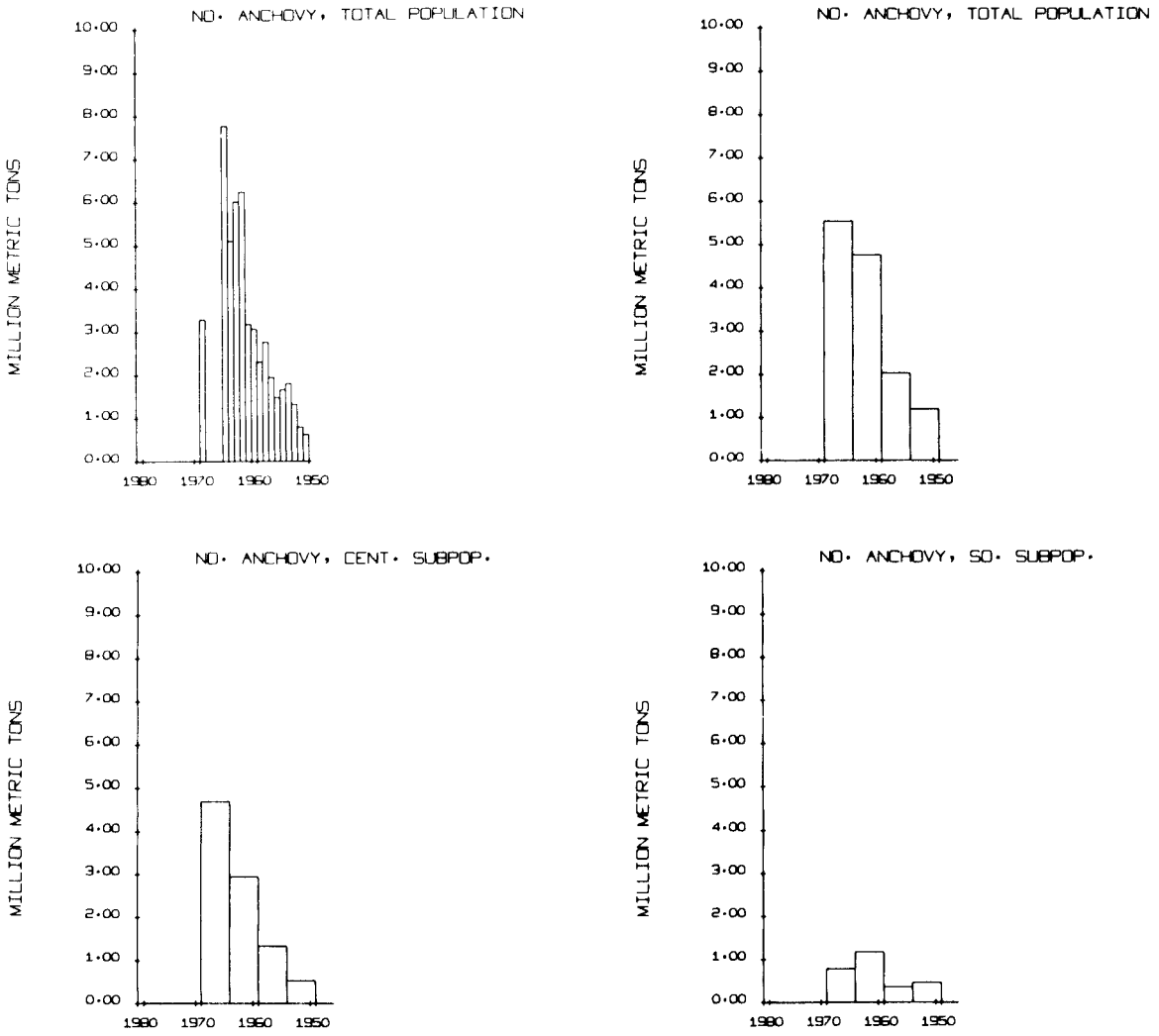


FIGURE 8.—Yearly estimates of the northern anchovy biomass (after Smith, 1972). The yearly total population estimates (upper left) are grouped into 5-yr block averages (upper right). Also given are the central and southern subpopulation 5-yr block averages (lower).

Table 8.—Rank-correlation coefficients[1] between the scale occurrences of the Pacific sardine, the northern anchovy, and the Pacific hake in sediment of Santa Barbara and Soledad Basins (n = 32).

	Pacific sardine		Northern anchovy		Pacific hake	
	Santa Barbara	Soledad	Santa Barbara	Soledad	Santa Barbara	Soledad
Pacific sardine						
Santa Barbara		−0.02	0.34	0.05	0.49	0.19
Soledad			0.20	−0.19	−0.09	0.20
Northern anchovy						
Santa Barbara				0.37	0.65	−0.08
Soledad					0.26	−0.46
Pacific hake						
Santa Barbara						0.17
Soledad						

[1]While the correlation coefficients above 0.35 appear significant, nevertheless due to autocorrelation inherent in these time series the probabilities associated with these coefficients are likely to be greater than if the series were internally independent.

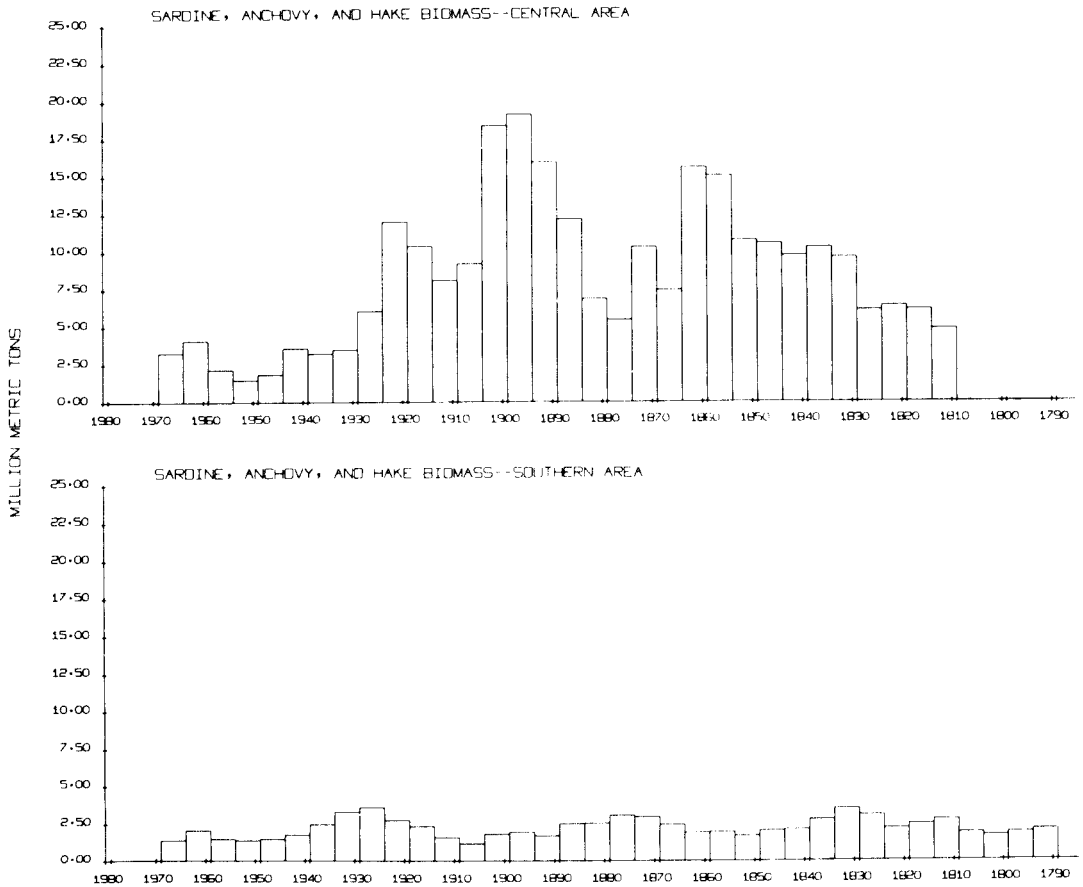


FIGURE 9.—Combined biomass estimate for the Pacific sardine, the northern anchovy, and the Pacific hake in Alta California and southern Baja California waters, 1810 to 1969. The biomass estimates are derived directly from the information in Tables 3, 4, and 5. In the case of the hake the average population level for the years 1950-1965 was assumed to be 0.9×10^6 metric tons (P.E. Smith, pers. comm.). One half of this population has been assigned to the central region; the other half has been assigned to the southern region. The actual relations used in the biomass calculation are as follows:

Sardine—Santa Barbara (central population) and Soledad (southern population): since $N_t = 2.27S_{t-2} + 2.15$ and $B_t = 0.38N_t - 0.40$ (Spearman rank-correlation coefficient is 0.97, $n = 6$; see also Sette, 1969); then $B_t = 0.85S_{t-2} + 0.40$

Anchovy—Santa Barbara: $B_t = 0.36S_t - 0.64$; and Soledad: $B_t = 0.08S_t + 0.29$

Hake—Santa Barbara and Soledad: $B_t = 0.08S_t$

where N is number of 2-yr olds, B is annual spawning biomass, S is scale deposition rate, and subscript t refers to year. The mean spawning biomass estimates for the sardine, anchovy, and hake are 3.5, 3.0, and 2.0 million tons for the central population and 0.7, 1.0, and 0.5 for the southern area.

importance of the central region would also likely extend to the north through the seasonal migration of these fish.

The projected mean biomass level for the three main species off California over the past 30 years is roughly 2 million metric tons and over the past 150 yr is 8 million metric tons. Thus the recent rise of the anchovy population may simply be a return to reasonably productive conditions. It is ironic that most of man's experience in the waters off the Californias appears to be associated with low pelagic-fish productivity. Conceding a significant effect of the fishery on the Pacific sardine does not mitigate the synchronous low population levels of the anchovy and the hake. As a matter of perspective, it should be emphasized that most of the understanding regarding the California Current system and pelagic fish, particularly that from

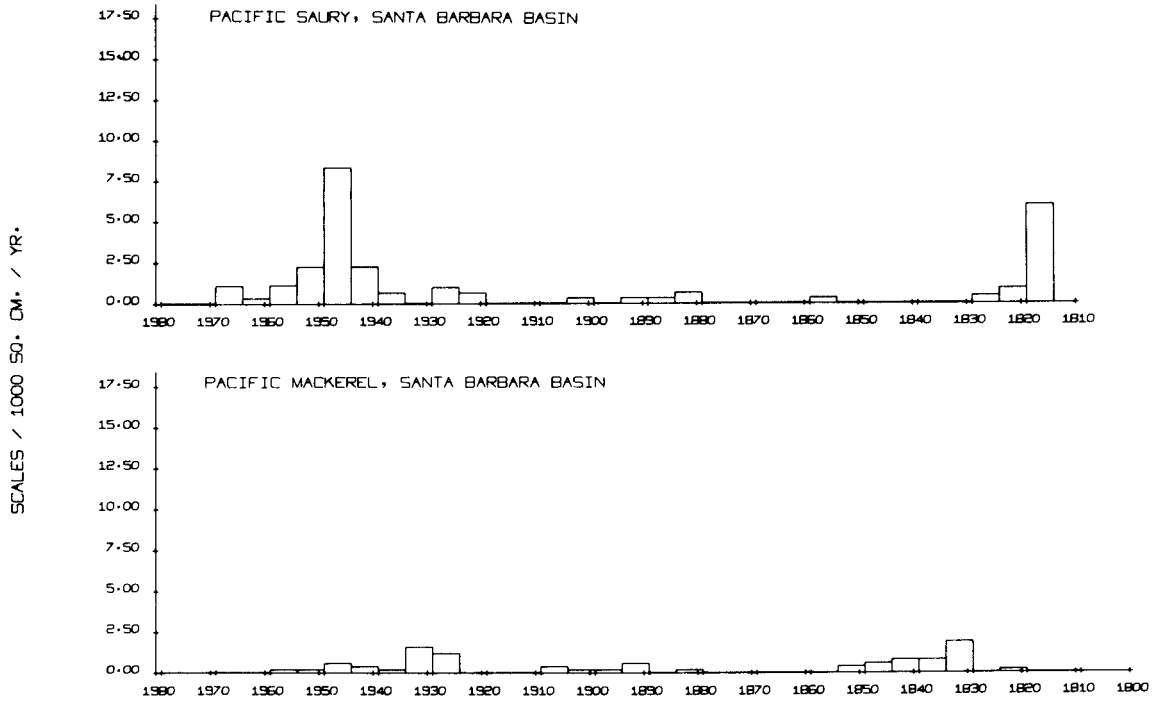


FIGURE 10a,b.—Histogram plot of the scale-deposition rate of Pacific saury and Pacific mackerel in sediment of the Santa Barbara Basin, 1810 to 1969.

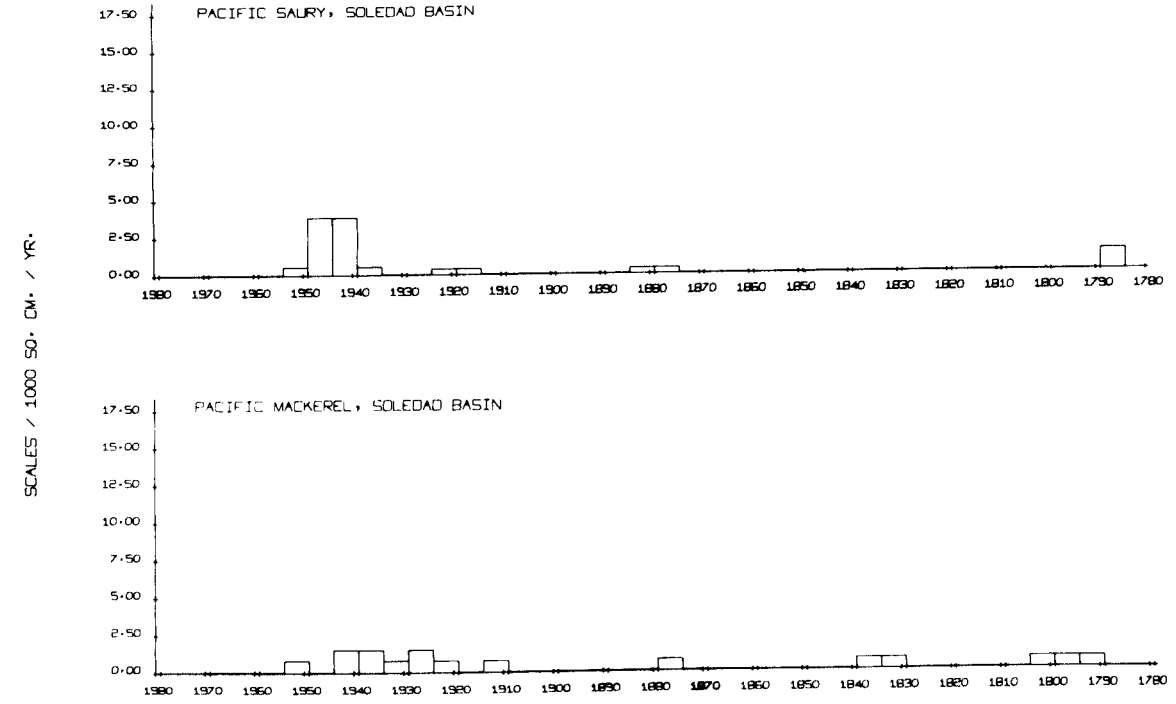


FIGURE 10c,d.—Histogram plot of the scale-deposition rate of Pacific saury and Pacific mackerel in sediment of the Soledad Basin from about 1780 to 1969.

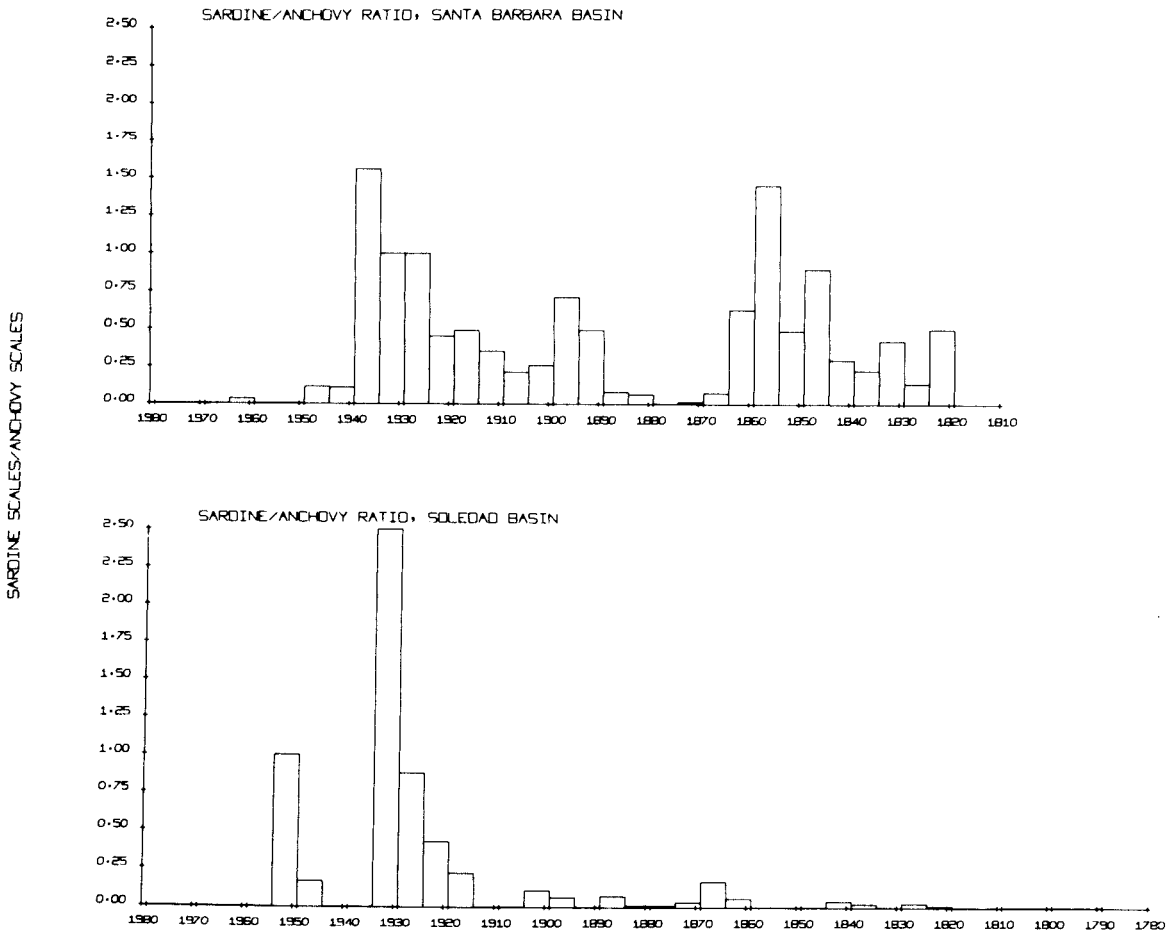


FIGURE 11.—The ratio of Pacific sardine scales to northern anchovy scales in the sediments of the Santa Barbara and Soledad Basins.

intensive efforts over the past 20 yr, has been gleaned from unproductive times, and there is yet limited appreciation of the capacity of the system. In regard to this point, a level of 15 million metric tons is suggested for the 1890's.

The scale records of two other pelagic fish serve to underscore the preceding observations. The record of the Pacific saury (Figure 10a, c) indicates an intrusion by this fish during the 1940's into the coastal waters. It would appear the saury found these waters attractive in the anomalous paucity of the more regular inhabitants. Although the information in the case of the Pacific mackerel is meager, the scale record (Figure 10b, d) resembles that of the saury in that the higher scale occurrences are near the ends of the record.

The records preserved in the sediments display a panorama of pelagic-fish abundance in the California Current over the past 150 yr. Interpretations of these records in the limited light of present knowledge point in both disturbing and exciting directions: disturbing, in revealing the magnitude and duration of the effort needed to encompass such a system; exciting, in the temporal glimmer of its flow and potential. The character of pelagic-fish abundance in California Current waters is perhaps best summarized in graphic form (Figure 11). The records of the two critical species, the Pacific sardine and the northern anchovy, when treated as a simple ratio exhibit a marked cyclical distribution (Santa Barbara) and a unique-event distribution (Soledad). The basic factors which gave rise to these distributions are most likely interspecific and autecologic. The

former is susceptible to scrutiny through the analysis of the projected fish populations through time. The latter is no less susceptible, for the sediments contain a rich record of fossil microplankton which promises to further define oceanic conditions off the Californias in relation to pelagic-fish productivity.

ACKNOWLEDGMENTS

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CHANGES IN THE AMOUNT AND PROPORTIONS OF DDT AND ITS METABOLITES, DDE AND DDD, IN THE MARINE ENVIRONMENT OFF SOUTHERN CALIFORNIA, 1949–72

JOHN S. MACGREGOR[1]

ABSTRACT

This paper is about the contamination of the ocean and its biota off southern California by the pesticide, DDT. The accumulation of DDT and the changes in proportions of DDT and its metabolites in the ocean are described for the years 1949 to 1972 especially as they are reflected in the myctophid fish, *Stenobrachius leucopsarus*. This time period was characterized by continuous dumping of DDT wastes into the ocean by a large manufacturer of DDT and the cessation of this dumping in 1970. Aspects and implications of the pesticide pollution problem in the marine environment are discussed.

In January and May 1970, the Fishery–Oceanography Center, La Jolla, Calif., collected samples of fish off southern California and Baja California as their part in a survey of chlorinated hydrocarbon (CHC) pesticides in marine fishes by the U.S. fish and Wildlife Service Bureau of Commercial Fisheries (now the National Marine Fisheries Service). Each sample consisted of the livers of several specimens of a single species from one locality. The samples were sent to the Environmental Protection Agency Laboratory at Gulf Breeze, Fla., for analysis.

The results (Duke and Wilson, 1971) showed that off southern Baja California 9 samples (170 fish) contained an average of 0.14 parts per million (ppm) wet weight of DDT and its metabolites; in Sebastian Vizcaino Bay (central Baja California) 3 samples (29 fish) averaged 1.2 ppm; along the southern California coast south of Oceanside and at two offshore banks 15 samples (179 fish) averaged 13 ppm; in Santa Monica Bay 8 samples (65 fish) averaged 370 ppm. Two samples (26 fish) of Pacific hake, *Merluccius productus*, taken by a Russian trawler off northern California and Oregon averaged 2.7 ppm, and fish sampled farther to the north by the Seattle Laboratory contained less than 1 ppm or no detectable DDT residues in the livers. The highest levels of DDT and its metabolites were found in the Los Angeles area with DDT levels declining greatly in samples taken to the north, south, and offshore from Los Angeles.

Previous pesticide residue surveys of marine birds and fish (Keith and Hunt, 1966; Risebrough et al., 1967; Risebrough et al., 1968) had been confined primarily to central California and did not reveal the extent of DDT pollution in the ocean off Los Angeles. Risebrough et al. (1967) reported one sample of northern anchovy, *Engraulis mordax*, taken off Los Angeles that contained 12.7 ppm DDT and its metabolites compared with additional samples of anchovies and three other species of fish taken north of Los Angeles to San Francisco that ranged in DDT residue content between 0.2 and 2.8 ppm.

In the spring of 1969, Keith, Woods, and Hunt (1970) investigated the breeding pelican, *Pelecanus occidentalis*, colony on Anacapa Island, about 35 nautical miles west of Santa Monica Bay, and found extensive reproductive failure caused by thin-shelled eggs which broke under the brooding pelicans. They found that the contents of a composite sample of many broken eggs contained 1,818 ppm DDT residues (lipid basis) while nine intact eggs averaged 1,215 ppm. They also sampled pelican eggs from three breeding colonies in the Gulf of California and found DDT residues averaging 58, 61, and 105 ppm. Jehl (1970) sampled pelican eggs from Los Coronados Islands, about 95 nautical miles south of Anacapa. These contained 810 ppm DDT residues. At San Martin Island 250 nautical miles south of Anacapa, egg residues were 192 ppm.

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More recent data (Southern California Coastal Water Research Project, 1971)[2] for the *p,p'*DDE content of the mussel, *Mytilus californianus*, show that two samples taken on the Palos Verdes Peninsula, near Los Angeles, contained 61 and 151 ppm of *p,p'*DDE while samples taken at a greater distance from Los Angeles declined greatly to between 0.3 and 3 ppm at San Diego, Point Conception, and on the farther outlying islands.

Burnett (1971) determined DDT residues in samples of the sand crab, *Emerita analoga*, from 19 locations along the coast between northern Baja California and San Francisco. Only in those crabs from the Los Angeles area did he find values greater than 1 ppm (up to 7.2 ppm). The DDT values fell off rapidly north and south of Los Angeles and averaged about 0.1 ppm at most of these locations.

These results of the above studies demonstrate that geographical proximity to Los Angeles was accompanied by greatly elevated levels of DDT and its metabolites in marine organisms.

High DDT residues in marine life in the ocean off Los Angeles had an adverse effect on the fishing industry. In June 1970, canned jack mackerel, *Trachurus symmetricus*, shipped from Los Angeles was condemned by the U.S. Food and Drug Administration in New York for high DDT content (13 ppm). The FDA had set a maximum tolerance of 5 ppm on fish products. In the following year jack mackerel was withheld from distribution by the packers, and jack mackerel and Pacific bonito, *Sarda chiliensis*, were condemned by the FDA in the Los Angeles area. In December 1970, the FDA seized about 8,000 lb of white croaker, also called kingfish, *Genyonemus lineatus*, that had been caught near Los Angeles. These contained 19 ppm DDT residues.

While the fishing industry was unable to pinpoint any particular area of heavy DDT contamination of pelagic fish off southern California, it seemed to be fairly well defined for the more sedentary bottom dwelling species. Although the total DDT in the flesh of the Santa Monica Bay fish samples taken in May 1970 ranged from 12 to 57 ppm, about 30 nautical miles away at Farnsworth Bank on the west side of Santa Catalina Island, DDT in the flesh of a sample of sculpin, *Scorpaena guttata*, and in flesh samples of four species of rockfishes, *Sebastes* spp., had a range of only 0.23 to 0.49 ppm; and, a sample of white croakers taken off Oceanside, 40 nautical miles south of Los Angeles, contained only 0.61 ppm of DDT residues in the flesh.

The pelagic fish were not good indicators of the source of pesticide contamination because they are much more migratory than the bottom dwelling species, and the area in which they are caught is not necessarily the area in which they were contaminated. Even though this would also mean that their exposure to heavy contamination would be of shorter duration than for bottom fishes living in these areas, they still built up high concentrations of DDT in the flesh because pelagic fish tend to store fat throughout the body rather than in the liver as do bottom dwelling, more sedentary species. The DDT residues are stored in the fats, and the distribution of the total body load of DDT residues in the fish is roughly related to the distribution of fat.

Although we have no flesh sample analyses from pelagic fish to illustrate this point, concentrations of DDT were found to be two to six times higher in the livers of samples of four different species of bottom dwelling fish taken in 1970 along the coast between San Diego and Oceanside than they were in the livers of a sample of jack mackerel from the same area, and seven to 19 times higher than in the livers of a sample of Pacific sardine, *Sardinops sagax*, taken in San Diego Bay at about the same time. And even among bottom fish taken from the same area at the same time, those that have more oil in the flesh seem to carry relatively more of the total DDT load in the flesh. For five species of bottom dwelling fishes taken from Santa Monica Bay in 1970, there is an inverse relation between the ratio of DDT in the liver to DDT in the flesh and the percent of oil in the flesh as given in Table 1.

Because of the prevalence of winds from the Pacific, and the concentration of agriculture in the inland valleys, we considered it unlikely that the heavy DDT contamination in the ocean off Los Angeles was caused by airborne pesticide residues. Surface runoff was also an unlikely source. Southern California's arid climate, the damming of rivers, the large population and importation of water have resulted in a condition in which the annual discharge by sewers into the ocean is at least twice the average annual surface runoff of

[2]Southern California Coastal Water Research Project, 1971. Comments on the policy for water quality control proposed by the State Water Resources Control Board. Presented at the State Water Resources Control Board public hearing, San Diego, Calif., 2 Dec. 1971, 27 p.

TABLE 1.—Relation between ratio of DDT in liver to DDT in flesh and percent of oil in flesh of five species of bottom dwelling fishes from Santa Monica Bay in 1970.

Species	Number of fish	Total DDT Liver (ppm)	Total DDT Flesh (ppm)	Ratio of DDT Liver:flesh	Percent oil in flesh
Bocaccio, *Sebastes paucispinis*	9	590	12	49:1	1.4
Starry rockfish, *S. constellatus*	5	1,030	57	18:1	1.8
Vermilion rockfish, *S. miniatus*	10	163	16	10:1	2.2
Dover sole, *Microstomus pacificus*	13	63	13	5:1	3.6
Sablefish, *Anoplopoma fimbria*	10	103	23	4:1	6.0

water. The "rivers" of southern California are its sewers, and the two largest of these, in the 400 million gallons (1.51 million m^3) per day class, are the outlets of the Hyperion treatment plant that serves the city of Los Angeles and those of the White Point treatment plant that serves Los Angeles County.

The Hyperion plant empties into the head of an underwater canyon in the northern half of Santa Monica Bay, and the White Point plant empties into the ocean off Palos Verdes Peninsula. Fish samples that showed very high DDT residues came from southern Santa Monica Bay about midway between the two sewer outfalls.

The County Sanitation Districts of Los Angeles County (CSDLAC) began a monitoring program to test for CHC pesticides in its sewerage system in December 1969 (Carry and Redner, 1970). They found that very high concentrations of DDT were present in the sewer system. In March 1970, they began to sample the sewer trunk lines in order to pinpoint the sources of DDT input into the sewer system.

They soon discovered that the source of most of the DDT pollution was the Montrose Chemical Corporation, a major manufacturer of DDT, located in the city of Torrance. Los Angeles Times staff writer, John Dreyfus, reported (7 October 1970), after interviewing a Montrose official, that at that time, Montrose was the only manufacturer of DDT left in the United States, and that it accounted for two-thirds of the world's sales of DDT.

The CSDLAC found that water samples taken from the sewers immediately upstream from Montrose contained 34 parts per billion (ppb) of DDT and its metabolites (DDD and DDE) in a flow of 25.3 million gallons (95.8 thousand m^3) per day or 7.2 lb (3.27 kg) of total DDT per day, while samples taken immediately downstream contained 2,950 ppb in a flow of 26.6 million gallons (100.7 m^3) per day or 654 lb (297 kg) of total DDT per day (Carry and Redner, 1970).

In April 1970, Montrose began hauling most of its processing wastes to a storage area, which caused a considerable drop in CHC entering the CSDLAC disposal plant. However, in May 180 lb (81.6 kg) per day CHC, of which 150 lb (68.0 kg) was DDT and its metabolites, were still found to be entering the White Point plant. The primary source of this was found to be the sewer trunk line serving Montrose Chemical Corporation. Because the composition of the total DDT sampled, 14% DDT, 48% DDD, and 38% DDE, was different from the Montrose effluent previously sampled, 74% DDT, 5% DDD, and 21% DDE, CSDLAC personnel concluded that the primary source of pollution was from old deposits in the sewer lines.

Between 11 December 1970, and 1 July 1971, 567,000 lb (257,000 kg) of deposits, of which 7,700 lb (3,500 kg) were total DDT, were removed from the interceptor system that served Montrose (Redner and Payne, 1971). The cleaning of this section of the sewer lines also stirred up old deposits which were washed down into the sewerage disposal plant, resulting in an increase in total DDT entering the plant. By October 1971, the total CHC entering the disposal plant had decreased to 60 lb (27 kg) a day of which 28 lb (13 kg) was total DDT and the remaining 32 lb (14 kg) polychlorinated biphenyls (PCB).

Since March 1971, an average of 22,000 gallons (83.3 m^3) a day of alkaline waste from the Montrose plant has been trucked to the Sanitation District's landfill on Palos Verdes Peninsula, and another 700 gallons (25.9 m^3) of acid waste has been trucked to a quarry. The alkaline waste was found to contain about 3,000 ppm of total DDT (Redner and Payne, 1971) or about 550 lb (250 kg)

per day. The acid waste was not tested, but if the concentration of DDT was similar to that in the alkaline waste, it would amount to an additional 175 lb (79 kg) of DDT residues per day.

The average inflow of DDT into the White Point sewerage plant during December 1969 through March 1970 was estimated at 652 lb (296 kg) per day. The amount measured in the sewers at the Montrose plant was 647 (293 kg) per day. The amount trucked out as alkaline waste only was estimated at 550 (250 kg) per day. Considering the difficulties in sampling such large volumes of material and the fact that the samples were taken in different localities at different times, there is remarkable agreement among them.

It is difficult to determine just how much DDT finally was pumped into the ocean after treatment at the sewerage plant. Some of it was undoubtedly removed in grit, grease skimming operations, and in dried sludge.

At the Hyperion treatment plant (city of Los Angeles), the digested sludge is pumped into the ocean, although some of it, at least in the past, has been used for fertilizer. The DDT input into the Hyperion plant was estimated to be on the order of 0.6 lb (0.27 kg) a day (tests by Hyperion personnel cited in Los Angeles Times, 7 October 1970) so, insofar as the DDT input into the ocean is concerned, it has had little impact. The White Point treatment plant has never discharged its sludge into the ocean (Terry Hindrichs, Southern California Coastal Water Research Project, pers. commun.) except during a short period of heavy rains in 1955. Until 1959, digested sludge was spread on nearby fields to air dry. Since 1959 a centrifuge has been used to partially dry sludge. The resulting cakes have been used for fertilizer or landfill.

CSDLAC personnel were unable to get reliable estimates of the DDT content of their effluent into the ocean until December 1970 (Carry and Redner, 1970), long after Montrose stopped dumping most of their wastes. Nine samples that they took from the effluent into the ocean in December showed that the average total CHC entering the ocean was 130 lb (59 kg) a day. The influent into the sewerage disposal plant in December had a load of 153 lb (69 kg) per day. The influent samples were taken after the grit chambers so any CHC removed in grit would not have been included. If we assume that sludge removal accounted for a 15% loss of CHC in December 1969 through March 1970, between influent (average 652 lb or 296 kg per day) and effluent into the ocean, then, the ocean discharge would have been about 552 lb (250 kg) per day of CHC for these months. This is about 100 short tons (91 metric tons) per year or about 10 times the amount of pesticides estimated to be carried into the Gulf of Mexico each year by the Mississippi River (Butler, 1969).

Montrose received a permit to dump its wastes into the CSDLAC sewer system in 1953, but it had been dumping for a few years before that according to company personnel. The continuous dumping of large quantities of DDT wastes into the ocean at a single point over a period of about 20 yr presented an unparalleled opportunity to study the effects of DDT on the ocean environment. Unfortunately the one-time opportunity to take advantage of the situation was not fully realized until some time after the dumping had stopped, and no large-scale coordinated investigation was undertaken to exploit this ecological windfall.

An investigation of pesticide pollution of the marine environment was initiated at the Fishery Oceanography Center (FOC), La Jolla, in 1970. Personnel at FOC have collected samples of bottom muds, fishes, and other biological samples primarily from the ocean off Los Angeles in order to study the effects of heavy DDT pollution in the marine environment.

Collections of marine organisms taken for other purposes, some dating back to 1949, were available for study. Most of the present paper is based on DDT levels found in specimens from one of these collections of a myctophid fish, *Stenobrachius leucopsarus*, found in the ocean off southern California in an attempt to trace the historical buildup of DDT and its metabolites in the marine environment as reflected in this species.

MATERIALS

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has taken plankton samples over an extensive area off California and Baja California since 1949. These samples were obtained over a predetermined pattern of stations in order to determine the species present, their numbers, and their distribution. The most intensive sampling took place during the 1950's; during the 1960's the number of CalCOFI cruises was reduced considerably.

All fish and fish eggs are routinely sorted out of the collections for identification. About 600

specimens of the myctophid fish, *S. leucopsarus*, that had been sorted from the plankton collections, were selected for this study to give best areal and temporal coverage.

Initially a few plankton samples, which were available in much greater quantity, were tested for pesticides. However, the plankton species composition varied in time and with locality, and it was felt that the samples might not be comparable. The plankton samples also appeared to contain both Aroclor 1242[3] and Aroclor 1254 (polychlorinated biphenyls (PCB) manufactured by Monsanto Corporation) while the myctophids generally contained only Aroclor 1254 in quantity. Plankton samples can include man-produced debris that contains relatively large amounts of CHC or other organic chemicals which interfere with analysis, while individual myctophids are relatively free of such material. Myctophids do not undergo any more horizontal movement than other plankton organisms, and, if they use their motility at all, at least in the coastal waters, it is probably to maintain position over the deeper basins. In addition, they tend to contain more pesticide than the invertebrate constituents of the plankton with which they are taken, and they are convenient material to work with.

The myctophids tested for pesticide residues ranged in standard length (SL) from 14 to 77 mm. They are apparently short-lived fish. Fish of the year can be followed through their first year and into their second by length-frequency distributions (Figure 1). Most of the myctophids tested appeared to be comparable in DDT content to other fish taken at the same time and place, but the amounts in smaller fish were erratic. Some

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

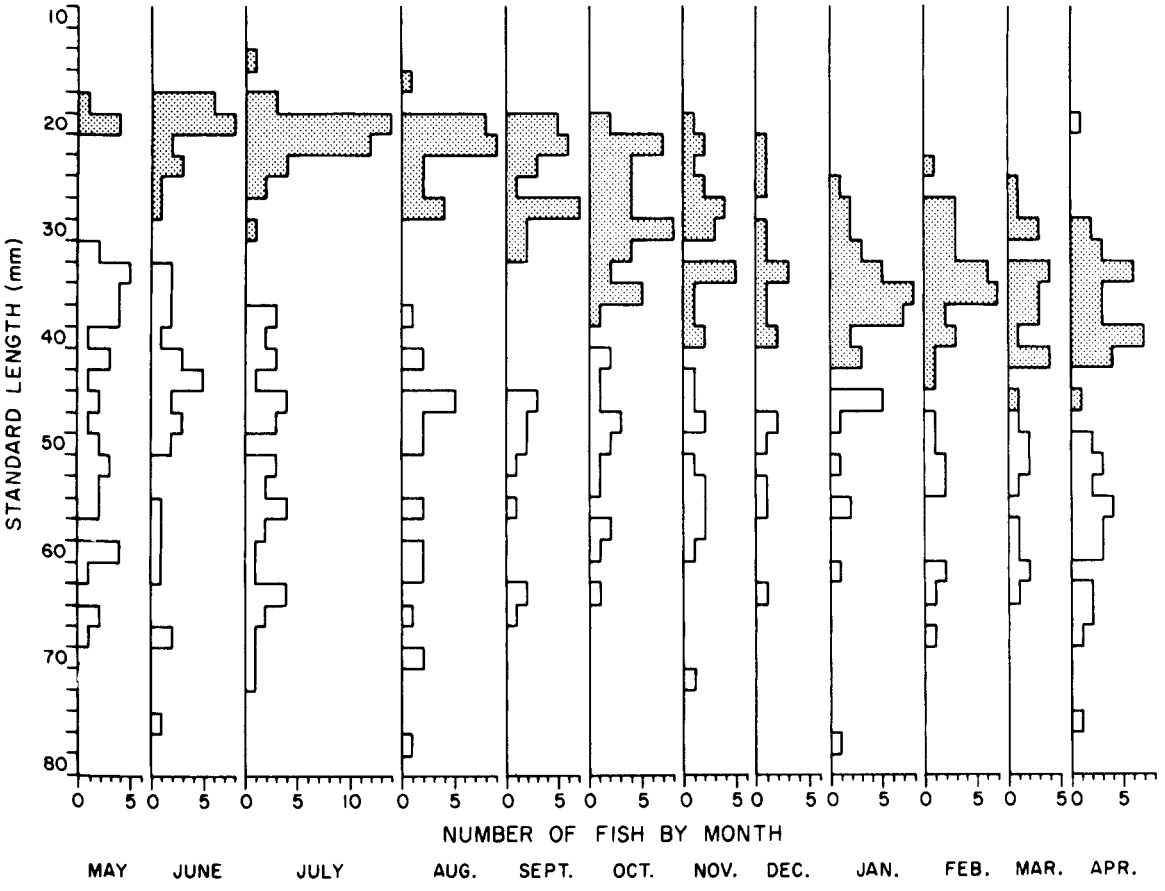


FIGURE 1.—Length-frequency distribution of *Stenobrachius leucopsarus* by month. Shaded area is entering year class.

were comparable to larger fish, while others contained less DDT than might be expected in larger fish taken at the same time and in the same locality.

This variation in pesticide content appeared to be related to the "fat" content (hexane extractable portion of the fish) of the specimens. The fat content of the fishes (Figure 2) increased very rapidly and with considerable variation to 30 mm length, 6.5% fat of the dry weight of the fish in an 18-mm specimen to 42.5% in a 29-mm specimen) where it began to level off. In mature fish the fat is about 49% of dry weight and 16% of wet weight. There is no apparent seasonal fat cycle. For comparison of DDT in time and space, only myctophids 30 mm or longer were used.

METHODS

The myctophids used in this study were preserved in Formalin which had no apparent effect on the pesticides to be analyzed. The specimens were measured and weighed and placed in tared disposable pipets that had been plugged with glass wool at the small end, or for larger fish in similarly prepared glass tubing of appropriate size. The fish were dried in an oven at 65°C to constant weight and reweighed to obtain dry weight. Each fish was macerated in the tube and extracted into a 15-ml graduated centrifuge tube with 10 ml of hexane. The remains of the fish in the pipet were dried and reweighed to obtain the weight of material extracted.

The extract in the centrifuge tube was mixed to uniformity, and an aliquot equal to 20 mg or less of fat removed. This was reduced in volume if necessary and passed through an activated alumina column as described by McClure (1972). The cleaned up sample was again reduced in volume if necessary and injected into a model 402 Hewlett Packard gas chromatograph (GLC) with a Ni^{63} electron capture detector. The 6-foot glass column contained 1.5% OV-17/1.95%QF-1, on 100/120 mesh Supelcoport.

DDT gets its name from its former chemical designation, *p,p'*-dichlorodiphenyltrichloroethane. The current chemical designations for DDT and its metabolic products mentioned in this paper are:

p,p'-DDT	1,1-dichloro-2,2-bis(*p*-chlorophenyl)ethane
p,p'-DDD (TDE)	1,1-dichloro-2,2-bis(*p*-chlorophenyl)ethane
p,p'-DDE	1,1-dichloro-2,2-bis(*p*-chlorophenyl)ethylene
p,p,'-DDMU	1-chloro-2,2-bis(*p*-chlorophenyl)ethylene
Kelthane (Dicofol)	1,1-bis(*p*-chlorophenyl)-2,2,2-trichloroethanol

For the ortho-para isomers of DDT, DDD, DDE, and DDMU substitute 2(*o*-chlorophenyl)-2-(*p*-chlorophenyl) for 2,2-bis(*p*-chlorophenyl). In this paper total DDT includes *p,p'*DDT, *o,p'*DDT, *p,p'*DDD, *o,p'*DDD, and *p,p'*DDE. While *o,p'*DDE and *p,p'*DDMU are present, although not as major constituents of the fish samples, both have the same short retention times on the column used and are interfered with by a number of other unknowns as tends to be true of anything having a shorter retention time than *p,p'*DDE in these samples; therefore they were omitted because of the difficulty in identification and quantification. Kelthane was also omitted because it breaks down on this column (Morgan, 1967) to a material that has a low response and an even shorter retention time than DDMU.

For the purposes of this paper we assume that DDT is metabolized (O'Brien, 1967; Morgan, 1967; Menzie, 1969) as follows:

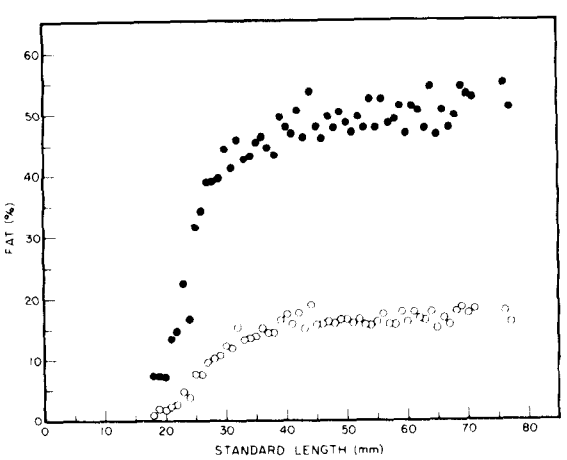
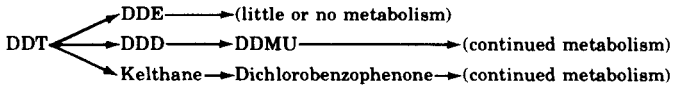


FIGURE 2.—Increase in percent fat with increase in length for *Stenobrachius leucopsarus*. Dark circles equal fat as a percent of dry weight; open circles, as a percent of wet weight. Fat equals hexane extractable substances. Pesticide values for fish less than 30 mm standard length (SL) were not used because of the greater variation in these values than in larger fish in which fat content was more stabilized.



Since we have no measurements of Kelthane, the scope of this paper includes only the measurement of the metabolism of DDT to DDE and DDD. As mentioned earlier, the effluent from the Montrose plant was already partly metabolized (Carry and Redner, 1970). In seven samples taken between 14 August and 24 November 1970, the total DDT portion of the effluent contained 74% (range 62–84) of DDT, 5% (3–7) of DDD, and 21% (9–35) of DDE. During this period the effluent contained 2 lb or less of DDT per day. The proportions of DDT, DDD, and DDE at the time when dumping was 650 lb (295 kg) per day were 73:2:25.

At the beginning of this investigation some pesticides were separated on other columns to confirm the identification of DDT and its metabolites. Additional confirmation was obtained by dehydrochlorinating samples with alcoholic KOH which converts DDT and DDD to their respective ethylene derivatives, DDE and DDMU, but does not change the PCB, Aroclor 1254.

Because there are so many possible sources of variance to the estimates of pesticide content, we cannot obtain a precise measure of this error. Based on the least accurate measurements made in the course of analysis, the standard error of the amount of pesticide in a sample should be about plus or minus 10%. The error may be increased by shortcomings in methodology and by the presence of other peaks that interfere with those to be quantified. At low pesticide values the error increases, and it may be more like plus or minus 100% at values on the order of 10 ppb. However, the absolute error is only a few parts per billion also and makes little difference when values that differ by orders of magnitude are being compared.

In the myctophid samples, Aroclor 1254 seemed to be the only substance that contributed peaks on the chromatogram of any significance which could interfere with quantification of the DDT series. Six Aroclor 1254 peaks span the retention time range of *p,p'*DDE, *o,p'*DDD, *o,p'*DDT, *p,p'*DDD, and *p,p'*DDT (Figure 3). In all the marine samples examined, *o,p'*DDT and *o,p'*DDD are present in either very small quantities or not detectable at all unless the samples contain very large quantities of *p,p'*DDT or *p,p'*DDD. In the myctophid samples, Aroclor 1254 seems to maintain its integrity very well. There is no apparent selective breakdown of its components, and the pattern of peaks from myctophid samples containing this PCB and very little pesticide closely resemble the Aroclor 1254 standard (Figures 3 and 4).

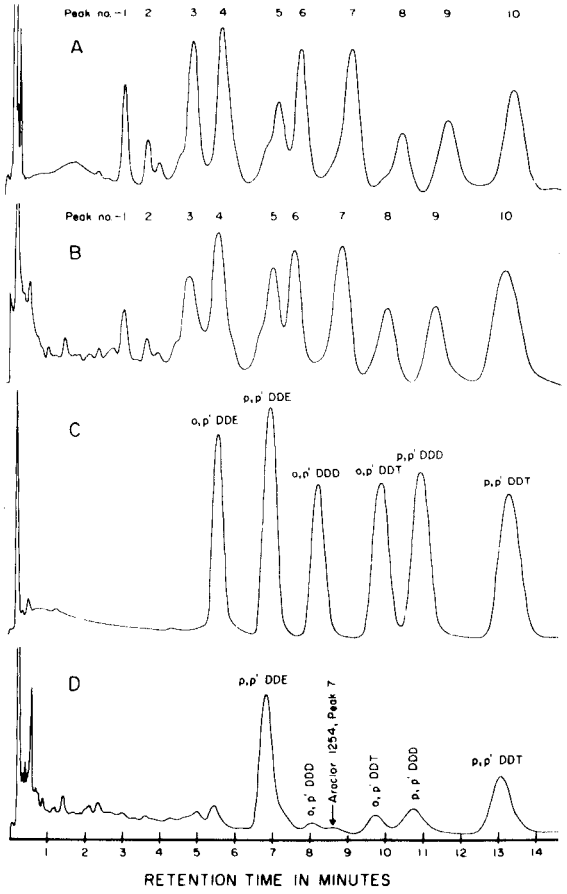


FIGURE 3.—A. Aroclor 1254 standard; column: 1.5% OV-17/1.95% QF-1, 100/120 mesh Supelcoport. B. Sample of two *Stenobrachius leucopsarus* each 20 mm standard length (SL) taken in July 1951, at CalCOFI station 70.100. About 0.54 ppm Aroclor 1254 with peak no. 5 increased slightly by 0.2 ppm DDE and peak no. 10 by 0.3 ppm DDT. Less highly chlorinated Aroclor peaks no. 1, 2, and 3 may be breaking down in the environment; more highly chlorinated peaks (no. 4 through 10) tend to maintain their integrity of pattern. Same column as A. C. Standard of six DDT analogs. Same column as A. D. Sample of a 33-mm *S. leucopsarus* taken in November 1955 at CalCOFI station 83.40. This sample contains 2.3 ppm total DDT. Because of the high DDT content of this sample, it was not concentrated as much as sample B. It probably contains at least half as much Aroclor 1254 as sample B. Same column as sample A.

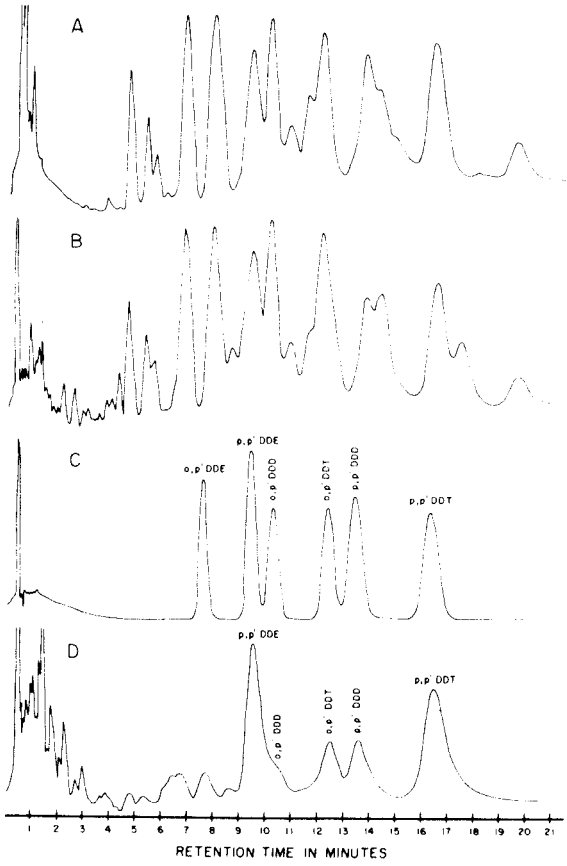


FIGURE 4.—A. Aroclor 1254 standard; column: 4% SE-30/6% QF-1, 100/120 mesh Supelcoport. B. Sample of a 28-mm *S. leucopsarus* taken in November 1955 at CalCOFI station 83.55. Aroclor 1254, 4.2 ppm; pesticides not measured. Same column as A. C. Standard of six DDT analogs. Same column as A. D. Sample of one 37-mm *S. leucopsarus* taken in March 1954 at CalCOFI station 85.45. 1.0 ppm total DDT. Same column as A.

It is apparent (Figure 3) that the seventh of the Aroclor peaks is not interfered with by the DDT series. The two ortho-para prime peaks bracketing it are generally small or absent. Therefore, it may be used to correct the DDT series for PCB interference and to quantify the Aroclor 1254.

An estimate of peak area, peak height times width at one-half peak height, was used in quantification. Increasing chart speed makes it possible to measure the width more accurately. Peak area rather than peak height is a more accurate measurement of the combined effects of two CHC when their retention times are about the same. Because GLC operating conditions may change gradually during a sample run, one pesticide standard was injected for every two samples so that each sample would have an adjacent standard for quantification.

To correct the areas of the combined peaks of the DDT series and Aroclor 1254 to the area representing pesticide only, we let X equal the area of each peak at the respective retention time of each of the DDT series and Y equal the area of Aroclor peak no. 7. Then for our operating conditions and Aroclor standard, the areas allotted to the components were:

Combined peaks	Area of Aroclor	Area of DDT series
*p,p'*DDE + Aroclor no. 5	$0.24Y$	$X - 0.24Y$
*p,p'*DDD	0	X
*o,p'*DDT + Aroclor no. 8	$0.54Y$	$X - 0.54Y$
*p,p'*DDD + Aroclor no.9	$0.73Y$	$X - 0.73Y$
*p,p'*DDT + Aroclor no. 10	$0.95Y$	$X - 0.95Y$

An estimate of Aroclor 1254 was obtained by multiplying the area of the no. 7 Aroclor peak by 12.3 and quantifying against the area of the *p,p'*DDE standard, or multiplying by 9.6 and quantifying against the area of the *p,p'*DDT standard. The subtractive corrections for the DDT series were confirmed in part for a few samples by calculating values both before and after dehydrochlorination with alcoholic KOH.

In a few samples taken far from the sewer outfall and in the earlier years, Aroclor 1254 was high enough to mask out the DDT residues except for slight increases in some peak areas (Figure 3). In such cases the pesticides were present in such small quantities that it made no appreciable difference in the overall results what small values were assigned to them. The illustrated example is an extreme case of masking.

In most of the samples the DDT residues dominated the PCB peaks and over the range of the six pesticide standards (Figure 3), only peaks no. 6 and 7 of Aroclor 1254 were evident. If DDT residues were high, peak no. 6 was evident as a widening of the base of the *p,p'*DDE peak (Figure 3).

RESULTS AND DISCUSSION

The pattern of CalCOFI stations from which the samples were obtained extends across the north flowing coastal countercurrent out into the south flowing California Current cutting across the counterclockwise eddy or eddies that develop between the two currents. At a depth of 200 m the

California Current is usually farther offshore than at the surface (Wyllie, 1966). In April and May this current moves inshore eliminating the countercurrent at the surface and sometimes at 200 m. When the California Current is offshore, the surface countercurrent develops; when it moves onshore, the surface countercurrent is absent although the southern California eddy usually persists.

The currents, and consequently the distribution of the sewer discharge, are influenced locally by such factors as the configuration of the coast, the presence of islands, the topography of the ocean floor, and the short range effects of winds and tides.

The total DDT data for the myctophids were divided into four time periods, and the average DDT value determined for all specimens taken at each station, or combined stations if they were very close together, for each time period (Figures 5-8). The total DDT content of the fish tended to be high near the sewer outlet and decreased away from the outlet. Total DDT values increased with the passage of time.

Total DDT for the purpose of this discussion consists of DDT, DDE, and DDD. Although total DDT content in the myctophids increased with time, this did not hold true for each of the three constituents. DDT increased for a few years until metabolism and dispersion equalled input and then leveled off. DDD acted in a similar manner but at a lower level. Most of the increase in total DDT after the first few years was caused by the increase in the persistent metabolite, DDE. The

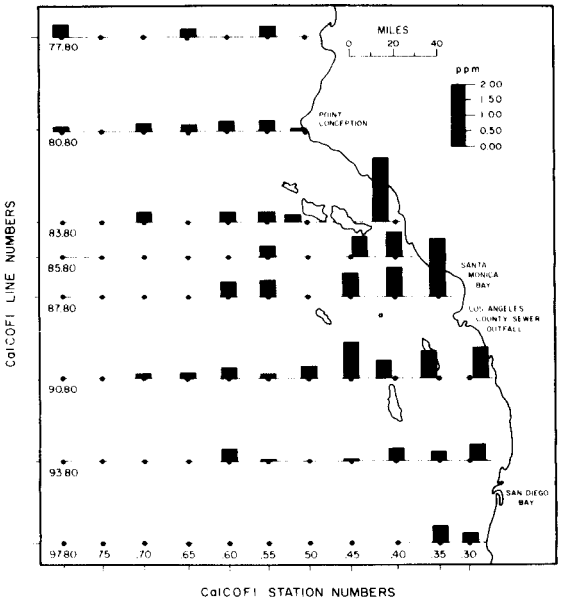


FIGURE 6.—Average total DDT at CalCOFI stations off southern California for the 4 yr 1953–56.

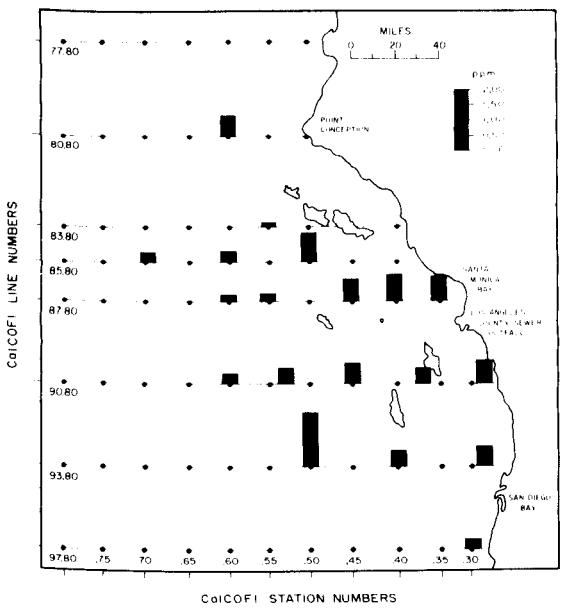


FIGURE 5.—Average total DDT at CalCOFI stations off southern California for the 3 yr 1950–52.

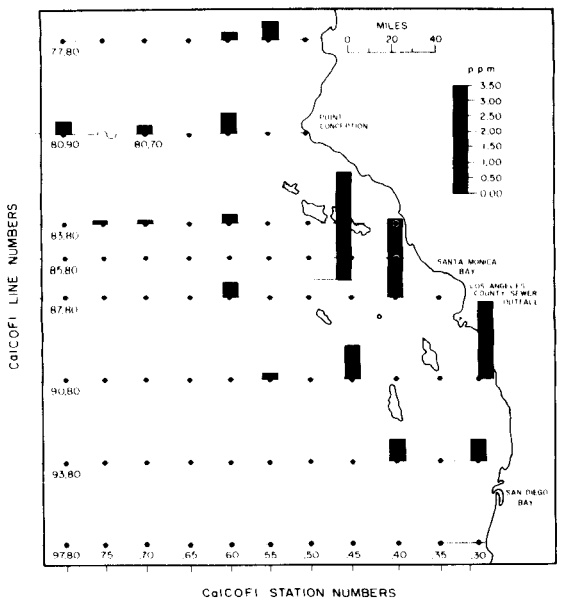


FIGURE 7.—Average total DDT at CalCOFI stations off southern California for the 4 yr 1957–60.

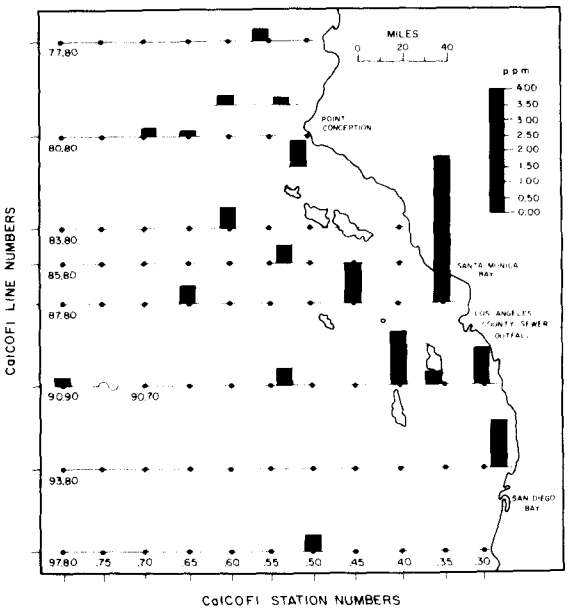


FIGURE 8.—Average total DDT at CalCOFI stations off southern California for the 6 yr 1961–66.

increase in *p,p'*DDE relative to *p,p'*DDT for the years 1950-51 through 1965-66 in the myctophids was:

Year	*Ratio of DDE to DDT*
1950–51	0.33:1.00
1952–53	0.36:1.00
1954–55	0.69:1.00
1956–57	1.06:1.00
1959–60	1.14:1.00
1961–62	2.02:1.00
1963–64	2.39:1.00
1965–66	3.96:1.00
(1970)	(4.74:1.00)
(1972)	(8.80:1.00)

These data show a 12-fold increase in the amount of DDE relative to DDT from 1950–51 to 1965–66. The ratio for the fish taken in 1970, 65–70 nautical miles southeast of the sewer outlet (in La Jolla Canyon) indicates a continuing increase in the ratios, although there were only two fish in the sample. The 1972 sample, consisting of only five myctophids, was taken west of Santa Catalina Island and about 25–30 nautical miles south southwest of the sewer outfall about 2 yr after the dumping of DDT into the sewer system had stopped. The high ratio may reflect in part continued metabolism of DDT without replenishment.

Because there are no data on the amount of DDT discharged into the ocean through the White Point sewer outfall each year, I have assumed that it was constant and discharged continuously throughout the year. Under these circumstances the amount of DDE (and DDD) entering the marine environment should gradually have increased in the earlier years until the input of DDT equalled the amount of DDT metabolized, when the input of DDE (and DDD) would also be constant. This is indicated by the initial slower increase in ratios of DDE to DDT.

If we assume that the same amount of pesticide is released into an environment each year and that it is released continuously throughout the year we may empirically represent the accumulation of the pesticide in the environment by the formula

$$Y = K(1 - S^X)$$

in which Y equals the amount of pesticide accumulated at the end of X years; K equals the maximum amount of pesticide that could be accumulated by the organism under the prevailing conditions; and S equals the "survival" rate of the pesticide for 1 yr.

In some of the years from 1949 to 1966, CalCOFI cruises were limited, and fewer samples were taken. Also the fish were not uniformly sampled with respect to distance from the sewer outfall in each of the years. But, by averaging the *p,p'*DDE content of all fish taken in each year and grouping years by twos, a rough indication of the increase in *p,p'*DDE was obtained to compare with theoretical values of the formula, $Y = K(1 - S^X)$ (Figure 9).

The almost linear increase in *p,p'*DDE indicates that its metabolism is very low. In fact, metabolism in this case would include *p,p'*DDE lost by removal from the area under study, and, therefore, the data indicate that very little was lost from this area during the years in which dumping occurred.

Because of the apparent lack of metabolism of *p,p'*DDE, this metabolite of *p,p'*DDT should give the best picture of areal and temporal buildup of a CHC in the ocean as a result of the sewer discharge.

Data on *p,p'*DDE content of the myctophids, year of capture (with 1949 equal to year 1), and distance in nautical miles from the sewer outlet to the place of capture were fitted to the formula:

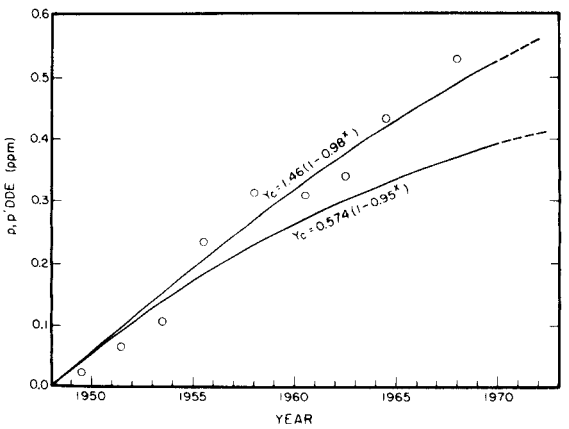


FIGURE 9.—Increase in *p,p'*DDE in the ocean off southern California, 1949–70. The points are averages of all stations combined in 2-yr groupings. Because the same patterns of stations were not run each year, myctophids were not obtained from the same stations or the same number of stations each year. Also pesticide concentrations were more dependent on distance from the point source of contamination than on year. This makes the coarse grouping of data necessary when increase in DDE with time only is considered. The two theoretical lines are computed to the formula $Y_c = K(1-S^X)$, in which Y_c = computed value of *p,p'*DDE, K = value at which metabolism, excretion, and dispersal of DDE equals input, S = survival of DDE for 1 yr, and X = year with 1949 considered as year no. 1. The data indicate that *p,p'*DDE is very stable. For the 98% survival curve, which more closely fits the data, 90% of the equilibrium value would not be attained for 114 yr.

$$\log Y = \log a + b \log X + c \log X'$$

in which Y = calculated value of DDE in parts per billion, X = distance from sewer outfall in nautical miles, and X' = year. The data were grouped for greater ease of computation and to minimize individual variations which tend to distort the actual values transformed from log–log calculated values if not minimized by averaging.

The values determined for the above equation are:

log a	3.054
b (distance)	−1.062 (SE 0.057)
c (year)	1.423 (SE 0.122)

The correlation coefficients are:

multiple	0.978
partial (b)	−0.829
partial (c)	0.522

all of which are significant at P of less than 0.001.

The computed lines did not fit the data for 1949, 1950, and 1951 very well. These years were left out of the calculations because the input of DDE was rising relatively rapidly at this time and did not begin to stabilize until about 1953. Also in these earlier years, the influence of the sewer discharge of pesticide extended out to only about 100 nautical miles from the outfall. In the following years the influence of the sewer discharge increased rapidly to between 300 and 400 nautical miles from the outfall before becoming indistinguishable from the ocean background. Although there are no extensive data for any one station throughout the period under study, we can now calculate values for a theoretical station 20 nautical miles from the sewer outfall from the DDE-time–distance formula and in conjunction with the observed changes in ratios among the various DDT analogs, obtain a description of the metabolism of DDT in the marine environment as reflected in the myctophid fish, *S. leucopsarus*.

Because *o,p'*DDE was not quantified, we used only *p,p'*DDE, *p,p'*DDT, and *p,p'*DDD in the ratios. In more than 300 myctophids 30 mm or longer in standard length in which the above three constituents and *o,p'*DDT and *o,p'*DDD were measurable, *o,p'*DDT and *o,p'*DDD averaged 22.3% of *p,p'*DDT and *p,p'*DDD. In samples of commercial DDT that were tested *o,p'*DDT averaged about 25% of *p,p'*DDT.

From the calculated values of DDE and ratios of DDE to DDT, we can calculate that at our theoretical 20 mile station DDT accumulates in the fish up to 1.077 ppm when input equals metabolism. From this we may calculate that:

$$Y_t = 1.077(1 - 0.708^X)$$

in which Y_t equals calculated *p,p'*DDT and X equals the year with 1949 equal to year 1. From the values obtained (Table 1, Figure 10) we may recalculate values for DDE. These values remain essentially the same as those calculated from the DDE–time–distance formula for the later years but make allowances for lower input from DDT for the earlier years if we use the formula:

$$2.046Y_e = 0.368X - 1.077 + 1.077(0.708^X)$$
$$\text{or} \quad Y_e = 0.180X - 0.526 + 0.526(0.708^X)$$

in which Y_e = calculated *p,p'*DDE and X equals the year and in which we assume that there is no further metabolism of DDE.

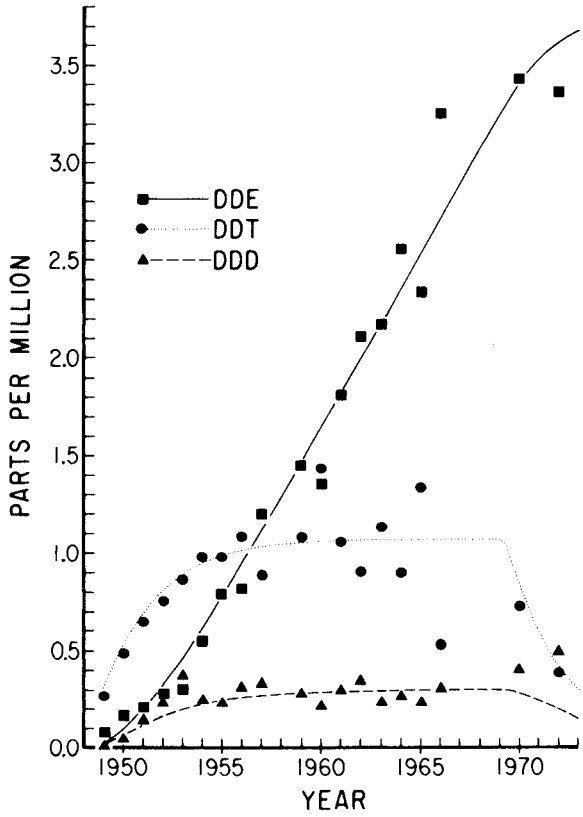


FIGURE 10.—Trends of *p,p'*DDE (squares), *p,p'*DDT (circles), and *p,p'*DDD (triangles) in the ocean off southern California, 1949–72, at a theoretical station 20 nautical miles from the point source of pesticide contamination. Computed lines show persistant DDE increasing until dumping of DDT wastes ceased in 1970. Both DDT and DDD increase for several years and then level off when metabolism, excretion, and dispersion equal input. Points are based on calculated total value of the three analogs distributed among them on the basis of the observed ratios of the three analogs to each other for each year. The 1972 ratios were affected by sewer cleaning operations that caused large quantities of DDD to enter the ocean.

From the calculated values of DDT and the DDD:DDT ratios we may estimate values for DDD. From these it appears that DDD accumulates in the fish up to 0.303 ppm where input equals metabolism. From this we may calculate that $Y_d = 0.303(1 - 0.525^X)$. However, this formula is based on a constant input equivalent to 0.189 ppm. The actual input from metabolism of DDT was only 0.028 ppm the first year and increased to 0.181 by the 10th year, and 0.188 by the 20th year. By adjusting for these increasing inputs we obtain accumulative values for DDD, for DDMU, and other metabolites of DDD (Table 2, Figure 10).

The percent distribution of total DDT among *p,p'*DDT, *p,p'*DDE, and *p,p'*DDD did not appear to change in myctophids with distance from the sewer outfall. Therefore the percent distribution which is based on large numbers of fish in most years can be used to prorate the total *p,p'*DDT obtained from the curves to obtain "observed" values of *p,p'*DDT, *p,p'*DDE, and *p,p'*DDD (Table 1, Figure 10). Both the curves and their observed values are based on observed percent changes in the composition of total DDT transformed to ppm values of the three constituents at a theoretical station 20 nautical miles from the sewer outfall.

It should be emphasized that the above description of metabolism is only an indication of what is taking place in the ocean. It neither describes the metabolism of DDT in the myctophid fish nor the metabolism in the marine environment, but rather reflects selective storage of DDT and its environmental metabolites in one species of fish.

Three factors determine the amount of CHC found in myctophid fishes: 1) The CHC present in the fish's environment during its brief life span; 2) the selective absorption of CHC through the gills and the ingestion of selected food particles; 3) and the selective storage, metabolism and excretion of CHC. Factors 2 and 3, above, should remain constant for each generation of fish. Therefore, the changes in composition of total DDT probably reflect changes occurring in the environment. However, the percent composition found in the myctophids may not represent the percent composition in the environment because of the selective nature of intake and excretion.

Some of the DDT was changed to DDE and DDD before entering the ocean. Sixteen samples of sewer discharge from the Montrose Chemical Corporation taken between 14 August 1970, and 12 May 1971, averaged 74% DDT, 20% DDE, and 6% DDD (Redner and Payne, 1971). Although these samples represented discharges averaging less than 0.5 lb (0.23 kg) a day, samples taken earlier in 1970 when dumping was estimated at 640 lb (290 kg) per day also had ratios of 73:25:2. These percent ratios are very much like the 74:23:2 distribution in the myctophids in 1949 and the 70:23:7 distribution in 1950.

Although some DDT was converted to DDD and DDE before it left Montrose, most of the metabolism took place after it was discharged from the plant. This is indicated by the percent distribution of DDT, DDE, and DDD in the myctophids in 1970, 16:75:9, by the bottom fish taken

TABLE 2.—Calculated values of *p,p'*DDT, *p,p'*DDE and *p,p'*DDD and their observed percent distribution in the myctophid fish *Stenobrachius leucopsarus*, at a distance of 20 nautical miles from the point source of pollution in the ocean off southern California for the years 1949 through 1973.

Year	Annual input (ppm)	Accumulated input (ppm)	Calculated accumulated *p,p'*DDT (ppm)	Metabolites of *p,p'*DDT		Metabolites of *p,p'*DDD (DDMU and others excreted or not measured) (ppm)	Accumulated total DDT (ppm)	Observed percent			Concentration based on observed percent		
				Accumulated *p,p'*DDE (ppm)	Accumulated *p,p'*DDD (ppm)			*p,p'*DDT (%)	*p,p'*DDE (%)	*p,p'*DDD (%)	*p,p'*DDT (ppm)	*p,p'*DDE (ppm)	*p,p'*DDD (ppm)
1949 (1)	0.37	0.37	0.31	0.03	0.02	0.01	0.36	74.4	23.3	2.3	0.27	0.08	0.01
1950 (2)	.37	.74	.54	.10	.07	.03	.70	70.0	23.3	6.7	.49	.16	.05
1951 (3)	.37	1.10	.69	.20	.12	.09	1.01	64.0	21.1	14.9	.65	.21	.15
1952 (4)	.37	1.47	.81	.33	.16	.18	1.29	58.5	21.9	19.6	.76	.28	.25
1953 (5)	.37	1.84	.88	.47	.20	.29	1.55	55.9	19.7	24.4	.87	.31	.38
1954 (6)	.37	2.21	.94	.62	.22	.42	1.79	54.8	31.1	14.1	.98	.56	.25
1955 (7)	.37	2.58	.98	.78	.24	.57	2.01	48.9	39.5	11.6	.98	.79	.23
1956 (8)	.37	2.94	1.01	.95	.26	.73	2.22	48.7	37.0	14.3	1.08	.82	.32
1957 (9)	.37	3.31	1.03	1.12	.27	.89	2.42	36.5	49.7	13.8	.88	1.20	.33
1958 (10)	.37	3.68	1.04	1.29	.28	1.07	2.61	No data					
1959 (11)	.37	4.05	1.05	1.47	.29	1.24	2.80	38.4	51.4	10.2	1.08	1.44	.29
1960 (12)	.37	4.42	1.06	1.64	.29	1.42	2.99	47.9	45.1	7.2	1.43	1.35	.22
1961 (13)	.37	4.78	1.06	1.82	.29	1.61	3.18	33.4	57.0	9.6	1.06	1.81	.31
1962 (14)	.37	5.15	1.07	2.00	.30	1.79	3.36	26.9	62.8	10.3	.90	2.11	.35
1963 (15)	.37	5.52	1.07	2.18	.30	1.97	3.55	32.0	61.3	6.7	1.13	2.17	.24
1964 (16)	.37	5.89	1.07	2.36	.30	2.16	3.73	24.0	68.7	7.3	.89	2.56	.27
1965 (17)	.37	6.26	1.07	2.54	.30	2.35	3.91	34.1	59.8	6.1	1.33	2.34	.24
1966 (18)	.37	6.62	1.08	2.72	.30	2.53	4.09	12.9	79.5	7.6	.53	3.25	.31
1967 (19)	.37	6.99	1.08	2.89	.30	2.72	4.27	No data					
1968 (20)	.37	7.36	1.08	3.07	.30	2.91	4.45	No data					
1969 (21)	.37	7.73	1.08	3.25	.30	3.10	4.63	No data					
1970 (22)	.11	7.84	.85	3.41	.29	3.28	4.56	15.9	75.3	8.8	.72	3.43	.40
1971 (23)	.00	7.84	.60	3.54	.25	3.45	4.39	No data					
1972 (24)	.00	7.84	.43	3.62	.20	3.59	4.25	9.0	79.2	11.8	.38	3.37	.50
1973 (25)	.00	7.84	.30	3.68	.15	3.70	4.14	No data					

in Santa Monica Bay in 1970, 8:87:6, and by a bottom sediment sample taken near the sewer outfall in 1971, 6:82:12. Samples of sewer water taken in 1970 that derived their DDT content from sewer sediments had ratios of 14:38:48 (Redner and Payne, 1971).

A few specimens of another myctophid, *Triphoturus mexicanus*, also showed a change in CHC ratios with time. Twenty-one specimens taken between 1950 and 1959 contained an average of 69% DDT, 9% DDD, and 22% DDE, while 12 specimens taken between 1961 and 1970 contained 23% DDT, 15% DDD, and 62% DDE. These fish were taken between Los Angeles and southern Baja California (lat 26°20′N). This species has a more southern distribution than *Stenobrachius leucopsarus*, and therefore the population was less influenced by the sewer discharge.

One might expect that DDE would be more abundant in samples taken farther from the sewer outfall, indicating older deposits, but this is not the case. The proportions are very similar in all samples, even those taken outside of the influence of the sewer. For the fish samples taken in 1969-70 for the survey, the percentages are given in Table 3.

Each sample contained several fish of the same species, and only the livers were tested. Where the pesticide levels were very high, the proportions were remarkably similar among samples. For the eight Santa Monica Bay samples, the DDE ranged from 85.2 to 87.7%, DDD from 5.1 to 6.6%, and DDT from 5.7 to 9.1%.

TABLE 3.—Distribution of *p,p′*DDE, *p,p′*DDD, and *p,p′*DDT in fish samples by area taken, 1969–70.

Location	Number of samples	Percent as DDE	DDD	DDT
Southern Baja California	8	80.6	8.9	10.5
Sebastian Vizcaino Bay	3	74.2	8.8	17.0
Cortez Bank	4	86.5	4.7	8.8
Southern California coast	6	86.0	5.1	8.9
Farnsworth Bank	6	86.9	5.6	7.5
Santa Monica Bay	8	86.6	5.8	7.6

The high proportions of DDE relative to DDT and DDD seem to be typical of fishes, porpoises, and crustaceans in the ocean off southern California (Tables 4 and 5). In six adult pelicans taken on Anacapa Island in 1969 (Keith et al., 1970), DDE made up 99% of the total DDT found in the fat, and 93% in eggs taken at the same time. Lamont, Bagley, and Reichel (1970) tested 10 pelican eggs from the same place and year and found that DDE constituted 96% of the total.

Stout (1968) gives data for 17 samples representing seven species of marine fishes taken off Washington and Oregon. In these, DDE averaged

TABLE 4.—Percent distribution of total DDT and ratio of DDD to DDT in rockfishes and sablefish from Santa Monica Bay. Major dumping of DDT wastes into sewer system stopped in April 1970. Samples of May 1970 and August 1971 are averages of five separate samples each for fat, liver, and flesh. In each of these 15 samples the ratio of DDE to DDT was greater than one.

Species	Part tested	Total DDT (ppm)	Percent distribution DDE	DDD	DDT	Ratio DDD:DDT
May 1970:						
Sebastes paucispinis	Liver	519.0	86.3	5.6	8.1	0.69:1.00
S. paucispinis	Flesh	11.6	80.6	8.8	10.6	.82
S. miniatus	Liver	162.0	87.0	5.6	7.4	.75
S. miniatus	Flesh	16.0	92.3	trace	7.7	.0?
S. constellatus	Liver	1,026.0	87.7	5.5	6.8	.80
S. constellatus	Flesh	57.2	88.2	5.5	6.3	.86
S. constellatus	Fat	2,588.0	85.0	7.0	8.0	.87
Anoplopoma fimbria	Liver	103.0	87.3	5.8	6.9	.85
A. fimbria	Flesh	23.4	81.2	10.1	8.7	1.15
August 1971:						
S. paucispinis and *S. mystinus*	Liver	156.0	84.0	10.3	5.7	1.78
A. fimbria	Liver	38.0	84.2	12.9	3.9	4.45
January 1972:						
S. paucispinis	Liver	17.0	78.5	15.5	6.0	2.58
S. paucispinis	Flesh	.20	81.4	12.7	5.9	2.15
S. paucispinis	Fat	115.0	78.8	16.1	5.1	3.15
August 1971:						
Bottom sample	Mud		82.0	72.0	6.0	2.00

TABLE 5.—Distribution of *p,p'*DDE, *p,p'*DDD and *p,p'*DDT in various animals from southern California marine waters. Porpoises found dead on beach north of San Diego, various dates May 1970. Fishes and crustaceans taken in net haul in San Pedro Channel 4 August 1971.

Species	Organ tested	Standard length (mm)	Wet weight (g)	Total DDT (ppm)	Percent as DDE	DDD	DDT
Porpoises:							
Lagenorhynchus obliquidens	flesh			84.	92.0	2.3	5.7
Delphinus sp.	flesh			208.	86.5	5.8	7.7
Delphinus sp	flesh			31.	85.0	7.2	7.8
Delphinus sp.	liver			44.	90.7	4.8	4.5
Delphinus sp.	liver			300.	92.0	4.0	4.0
Delphinus sp.	head oil			196.	89.8	2.6	7.6
Delphinus sp.	blubber			497.	88.5	3.4	8.1
Fishes:							
Leuroglossus stilbius	whole	84	5.20	.49	75.9	11.6	12.4
Melanostigma pammelas, eelpout	whole	89	2.40	5.63	87.9	2.7	9.4
Argyropelecus sp., hatchetfish	whole	30	.50	.09	49.5	7.6	42.9
Cyclothone acclinidens	whole	48	.36	2.01	80.7	4.7	14.6
Cyclothone acclinidens	whole	43	.37	.64	76.1	6.9	17.0
Cyclothone acclinidens	whole	47	.39	2.46	83.2	5.9	10.9
Cyclothone acclinidens	whole	38	.18	3.56	89.5	4.5	6.0
Cyclothone acclinidens	whole	34	.15	1.55	84.9	8.5	6.6
Crustaceans:							
Gnathophausia gigas, pelagic mysid	whole		.42	.55	76.7	7.2	16.1
Sergestes sp.	whole		.64	4.38	85.1	6.1	8.8
Sergestes sp.	whole		.38	4.59	82.9	6.1	11.0
Nematoscelis sp., euphausiid	whole		.019	.35	90.3	4.3	5.4
Nematoscelis sp., euphausiid	whole		.043	.26	90.2	3.0	4.9

52% (26–81), DDD 20%, and DDT 28% of total DDT.

Keith and Hunt (1966) list DDT content for samples of mammals, birds, and freshwater fishes taken throughout California. The proportion of DDE tends to be high in categories that include birds of prey and fish eating birds, but varies considerably in their other samples. In their warm-water fish samples and the fish eating birds, white pelican, western grebe, and common egret, DDD is unusually high. This may be because of the former use of DDD as a spray on some California lakes (Murphy and Chandler, 1948; Brydon, 1955; Hunt and Bischoff, 1960).

Following the cessation of DDT dumping into the ocean off Los Angeles in 1970, a change occurred in the DDD:DDT ratios found in fish samples. The five *S. leucopsarus* taken in April 1972 contained 79% DDE, 12% DDD, and 9% DDT. Each of the five specimens contained more DDD than DDT. In the period 1949–70, only 8 out of more than 500 *S. leucopsarus* tested contained more DDD than DDT. The five myctophids taken in April 1972 ranged from 40 to 50 mm SL, indicating that most or all of their growth had taken place since dumping stopped in 1970.

The shift in DDD:DDT ratios also appeared in some other species. The ratios in rockfishes and sablefish, *Anoplopoma fimbria*, taken in Santa Monica Bay in May 1970, indicated that DDT was more abundant than DDD while 15 and 20 mo later the reverse was true (Table 4, Figure 11). The pelagic crustaceans and fish taken in the midwater trawl in August 1971 (Table 5) did not show the increased DDD to DDT ratio as did the bottom fish taken at that time, or the five *S. leucopsarus* taken in April 1972. A mud sample taken in August 1971 (Table 4, Figure 12) about 3 nautical miles from the White Point sewer outfall contained about twice as much DDD as DDT.

The work of Burnett (1971) on DDT residues in the sand crab along coastal California showed that the high ratios of DDD to DDT were a local condition. Twelve samples taken in November 1970 and February 1971 from eight stations on either side of the White Point sewer outfall between 33°22′N and 34°28′N contained more DDD than DDT in all but two samples. The 11 stations north and south of this area all contained less DDD than DDT. The four samples taken closest to the outfall averaged more than three times as much DDD as DDT.

This shift in DDD:DDT ratios was undoubtedly caused by the deposits in the sewer system. CSDLAC cleaning operations started in December 1970, and ended in July 1971. Although large quantities of these deposits were removed directly from the sewers, additional large quantities were moved through the system to the White

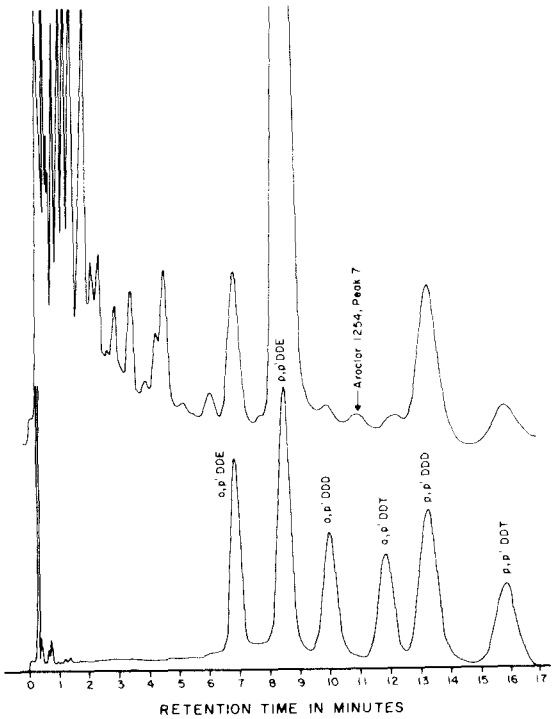


FIGURE 11.—Chromatogram of DDT analog standard and of a fat sample from *Sebastes paucispinis* taken in Santa Monica Bay 7 January 1972. *p,p'*DDE (98 ppm) is off scale. Following cessation of dumping of DDT wastes and flushing out of sewer lines in 1970, *p,p'*DDD (15 ppm) has exceeded *p,p'*DDT (6.1 ppm) in most fish specimens tested. Prior to cessation of dumping and flushing of sewer lines, DDT was almost always present in greater quantities than DDD.

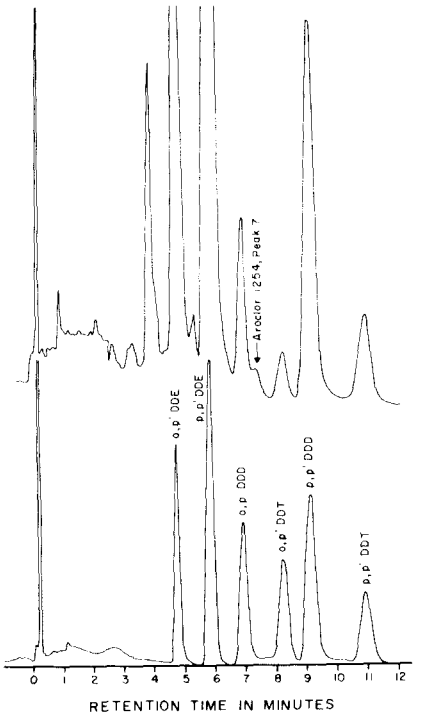


FIGURE 12.—Chromatogram of DDT analog standard and sample of mud from the ocean floor in the Los Angeles area taken in August 1971, 16 mo after most dumping of DDT wastes stopped. DDD greatly exceeds DDT. This may have resulted from the sewer cleaning operations, or it may have been the condition existing before and merely reflect what the biota can excrete more easily. In the *Sebastes* chromatogram (Figure 11), the *o,p'*DDE peak is within the limits of the right proportions to *p,p'*DDE for it to be considered *o,p'*DDE. In the mud sample it is much too high and may be DDMU (a metabolite of DDD) which has the same retention time on this column as *o,p'*DDE.

Point plant and out into the ocean. Sewer water from these deposits contained 48% DDD as opposed to 2–6% in the original Montrose discharges, and although the total amount of DDT and its metabolites was much less than before April 1970, the total amount of DDD entering the ocean appeared to be several times greater than it had been before the dumping stopped in April. This would account for the increase in DDD in the myctophids taken in 1972 rather than the expected decrease indicated by the calculated line (Figure 10, Table 1). A mud sample taken from the ocean floor a few miles from the sewer outfall in July 1971, just after the sewer cleaning operations ceased contained 6%DDT, 82%DDE, and 12%DDD (Figure 12). This compares favorably with the myctophids taken in April 1972, 9:79:12, and the *S. paucispinis* fat samples (Figure 11) taken in January 1972, 5:79:16, and indicates that the fish reflect the values of these analogs in the environment fairly well.

The most noticeable difference between the pesticide metabolites in the fish (Figure 11) and the mud (Figure 12) were the two prominent peaks preceding *p,p'*DDE. The peak at the locus of *o,p'*DDE also may contain DDMU, a metabolite of DDD. The other peak could be a metabolite of Kelthane. However, several dozen additional mud samples tested subsequently did not contain these peaks except for expected amounts of *o,p'*DDE. The mud sample (Figure 12) was run while we were experimenting with methods of determining pesticide content of the mud samples. The subsequent samples were run after we had settled on a different method that gave maximum recovery of DDT, DDD, and DDE without special regard to other CHC. These subsequent mud samples yielded chromatograms almost identical with those of fish and other biological samples from the same general area.

There was also a large decrease between May 1970 and January 1972, in total pesticides in the fish taken in Santa Monica Bay (Table 4). The *S. paucispinis* taken in 1972 were smaller than those taken in 1970 which may account in part for the lower values. The five specimens taken in January 1972, averaged 312 mm total length. Phillips (1964) gives the total length of this species at age 2 as 267 mm and at age 3 as 343 mm. Thus, most of the growth of these specimens had taken place since dumping stopped.

On land where soil has been subjected to DDT spraying for long periods of time, the situation is very different. In New York State vineyard soils (Kuhr, Davis and Taschenberg, 1972) the residues consisted of 73% DDT and 27% DDE after 24 yr of spraying with DDT. In Oregon (Kiigemagi and Terriere, 1972) samples of soil from one orchard contained 80% DDT, 17% DDE, and 3% DDD after 25 yr of spraying, while soil samples from another orchard in a different area contained 78% DDT, 14% DDE, and 8% DDD after 24 yr. Forests in New Brunswick, Canada (Yule, 1973) were sprayed heavily from 1956 to 1967 in which year spraying with DDT ceased. Many samples taken of soils in this area in 1968 contained 92% DDT and 8% DDE. Three years later a second sampling of the soils in the same locality contained 90% DDT and 10% DDE. DDD was present only in trace amounts in both sampling years.

As a general rule soil samples from land areas that have been sprayed with DDT tend to contain a much higher proportion of DDT than DDE or DDD even after many years. This is not necessarily true of the fauna that inhabit the land unless their contamination is the result of recent spraying. Keith and Hunt (1966) give examples of a number of species of mammals and birds in which the proportions of the three analogs vary greatly.

Within some species of birds, which are more wide ranging than mammals, there seems to be remarkable uniformity in the proportions of the three analogs. Martin and Nickerson (1972) tested 125 10-bird samples of starlings from throughout the (48) United States. These samples averaged 91% DDE, 3% DDD, and 6% DDT. Although the total residues ranged from 0.05 to 15 ppm, in only two samples did the amount of DDD exceed DDT, and in only one did the amount of DDT exceed DDE.

The proportions of the three analogs of DDT in the starlings is very similar to the proportions found in the fish taken in Santa Monica Bay in 1970 (Table 4), in the porpoises found dead on the beach in 1970, and the small fishes and invertebrates taken off Los Angeles in the mid-water trawl in 1971 (Table 5). And, in fact, except in cases of recent contamination by DDT, most fauna have tended to approach these proportions in recent years. This is in spite of the fact that soil samples from areas of land that have long histories of spraying with DDT almost without exception contain very high proportions of DDT. From this it would appear that the selective storage, metabolism, and excretion of DDT is somewhat similar for all animals.

When investigators first became aware of the pesticide problem, methods of measuring residues were considerably less refined than they are at present, and few samples were run. Very little work has been done on preserved specimens from these earlier years. But, in view of the similarity in proportions of DDE and DDT in so many different species in recent years, it seems probable that the increase in DDE and the change in ratios of DDE and DDT in *S. leucopsarus* are descriptive of the general change in these analogs that has taken place in the earth's environment.

There was no pattern discernible in the distribution of Aroclor 1254. In 472 myctophid samples taken between 1949 and 1966, the median values of Aroclor 1254 fluctuated around 0.17 ppm and showed no trend with time. Sixty-eight percent of the samples contained less than 0.25 ppm. The only indication of an areal relationship was that while the three stations closest to the White Point sewer outfall, and the city of Los Angeles (CalCOFI stations 87.35, 90.28, and 90.30) constituted only 8% of the total samples, they accounted for 34% (12 out of 35) of the myctophids containing more than 1ppm of Aroclor 1254. However, there were some samples taken 175–200 nautical miles offshore that contained more than 1 ppm, and there were others taken near shore in the Los Angeles area that contained none or traces only. These higher values could result from the myctophids ingesting nondigestible particles of man-made substances either while feeding or accidentally while in the cod end of the plankton net.

In the larger fish taken in the Los Angeles area, the high values of the DDT residues tend to mask the presence of Aroclor 1254. What might be recorded as a trace amount could actually be a rather significant amount in view of the dilute

solutions of sample used in such cases in order to keep the DDT residue recordings on scale.

SUMMARY

1. Between 1949 and 1970, total DDT increased in the ocean off southern California. The major source of this insecticide apparently was wastes discharged into the Los Angeles County sewer system by a major manufacturer of DDT.

2. As measured in the myctophid fish, *Stenobrachius leucopsarus*, *p,p'*DDT and *p,p'*DDD increased for several years until metabolism, excretion, and dispersion equalled input, at which point the content of these CHC stabilized in the fish.

3. The more persistent, less easily metabolized *p,p'*DDE continued to increase in *S. leucopsarus* throughout the time period under study. The amount of *p,p'*DDE decreased with distance from the sewer outfall.

4. During the earlier years the abundance of the other analogs in decreasing order was *p,p'*DDT, *p,p'*DDE, and *p,p'*DDD. During the later period through 1970, the more persistent *p,p'*DDE became more abundant than *p,p'*DDT. Following cessation of dumping, in 1970, *p,p'*DDD became more abundant than *p,p'*DDT in the myctophids and most of the other fish species tested.

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I am especially indebted to E. H. Ahlstrom for sacrificing part of his collection of the myctophid fish, *S. leucopsarus*, for the present study. Shirley Imsand donated the five myctophids taken in 1972 on the University of Southern California MV *Velero IV*. Carol Talkington assisted in some of the analyses. I am indebted also to R. Lasker for his invaluable criticism and guidance in the preparation of the paper and to V. McClure and W. Rommel for technical advice and assistance. This work was supported in part by NOAA, Office of Sea Grant, under grant #UCSD 2-35208 with the Institute of Marine Resources, University of California.

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QUANTITATIVE NATURAL HISTORY OF *PLEUROBRACHIA BACHEI* IN LA JOLLA BIGHT

JED HIROTA[1]

ABSTRACT

An assessment of the quantitative natural history of *Pleurobrachia bachei* A. Agassiz was made by estimating growth rates, metabolic rates, distribution, abundance, occurrence of prey, predators and parasites, population parameters, and net production. These were then integrated to give an indication of the ecological significance of this animal in the plankton.

Rates of somatic growth and digestion of prey were observed in laboratory experiments and applied to field data. A comparison of growth curves of *P. bachei* at 20° and 15°C showed development rates from hatching to the same diameter which were 10–15 days faster at 20°C. In addition, a much higher mortality of the ctenophores was observed at 20°C. Maximum growth rate coefficients on a daily basis were 0.21–0.47 and were for 2.5– to 6.5–mm ctenophores (0.1–2 mg bodily organic weight). Studies on the rates of digestion of six frequently ingested prey species by various sizes of *P. bachei* showed marked differences between species. Although *Labidocera* was the largest prey offered, it was digested the fastest per unit weight.

The horizontal, offshore distribution of *P. bachei* postlarvae often showed maxima within 5 km from the shore and decreased about tenfold by 10 km. Patterns of water movement in La Jolla Bight were described as a prerequisite to the distributional studies. The near–surface current velocities showed counterclockwise rotational motion over the submarine canyon complex of La Jolla Bay; otherwise the water generally moved onshore and towards the north at speeds of about 5 km/day. The high abundances of the animal nearshore are believed to be caused in part by these water movements. The ctenophores occurred in the upper 50–60 m, living mostly in the upper 15 m in the day and at about 30 m at night. The range of average abundances of postlarvae was from 1,000/m^2 and 1,000 mg organic matter/m^2 in August to being nearly absent in December.

Hyperoche mediterranea, a parasitic amphipod, and *Beroë* sp., a potential predator, showed patterns in seasonal abundance similar to that of *P. bachei* postlarvae, except that *H. mediterranea* was absent in winter and spring. The higher frequency of occurrence of endoparasites with larger sized hosts and few multiple infections suggests that the parasites are adapted to prevent overexploitation of hosts. The stomach contents of postlarvae showed a pattern of larger prey in larger ctenophores, and within some prey species increasing frequency of occurrence in larger ctenophores was observed, e.g., *Acartia tonsa*. The diel and seasonal variations in stomach contents were also considered. Prey selection by *P. bachei* may be determined by the following attributes of prey: density, size, avoidance and escapement behavior, strength and protective spination.

Size–specific instantaneous mortality rates, the mean schedule of live births, and somatic growth rates were used to estimate population parameters and compute rates of net production. The highest rate of population growth was 0.02 on a per day basis, which would enable a population doubling in about 35 days. The first 50–100 eggs laid by young postlarvae are most important to replace the population. The mean and range of annual net production by postlarval *P. bachei* are 5.24 and 2.32–7.65 g organic matter per square meter; mean values for eggs and larvae are 0.08 and 0.10 g/m^2, respectively. The mean annual net production of all stages is 5.4 g/m^2, with 95% confidence limits for the mean being 4.4–6.5 g/m^2.

The ecological significance and functional role of *P. bachei* are as: 1) a seasonally dominant carnivorous zooplankter which preys selectively on small crustaceans and may regulate their abundances; 2) a vehicle which provides shelter and nutrition for parasites and; 3) an organism which transfers a substantial amount of organic matter and potential energy in the food web of La Jolla Bight.

Ecological studies may be grouped into four categories, depending on the level of complexity being considered: 1) single individuals, 2) single species populations, 3) communities, and 4) ecosystems. The long–term objective in ecology is the description of ecosystems. More specifically, two important objectives in studies of ecosystems are: the elucidation of complex interactions between species in a food web and the understanding and prediction of the dynamic processes that occur

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in this web. To obtain this information, one approach is the investigation of basic trophic relationships among the various developmental stages of different species in the food web (e.g. for herring, Hardy, 1924) and the quantitative measurement of matter or energy transferred along these paths (e.g., for a lake, Lindeman, 1942). From the four categories of complexity I chose to study *Pleurobrachia bachei* A. Agassiz at the single species population level. I have attempted to integrate three basic aspects of the population ecology of *Pleurobrachia* into a study of its quantitative natural history: 1) the structure of its food web, 2) the population parameters and attributes which most affect the population growth rate, and 3) the trophic–dynamic aspect of the quantitative transfer of organic matter. In previous work (Hirota, 1972) the culture and metabolism of *P. bachei* have been described.

Studies on the trophic–dynamics of marine planktonic food webs have concentrated on the measurement of primary production and the factors which influence its level. Mullin (1969) suggested that similar production studies of total zooplankton or of single species are few, because no simple, direct methods exist for the measurement of secondary production in situ. He stated that two basic approaches exist for these studies: the laboratory "carbon balance" study and the population dynamics approach. A somewhat more direct measurement could be made as a modification of the approach used in lakes by Haney (1971). In situ population feeding rates (measured using food particles labeled with isotopes) multiplied by the population gross growth efficiency is the rate of net production. This method has the advantages of being more direct and made in nature, but it is impractical for complex marine plankton communities with their numerous and relatively large, mobile species. It also requires detailed knowledge of factors which affect gross growth efficiency.

Most marine planktonic species are not amenable to culture in the laboratory for entire life cycles, and results of laboratory experiments may fail to represent accurately activity in nature. Present field sampling techniques and variability in plankton studies are often such that it is neither possible to obtain sequential samples from the same target population nor calculate the rates of biological activity. In spite of these difficulties and such severe limitations (Hall, 1964), more and better data are needed in different ecosystems from their functionally distinct component species before a clear understanding of the structure and dynamics of food webs is obtained and generalizations of predictive nature concerning the systems can be made.

Studies on the population dynamics and production of marine zooplankton (reviews by Mann, 1969 and Mullin, 1969) almost exclusively pertain to "herbivorous" calanoid copepods. At present little information exists on the production rates of carnivorous marine zooplankters (McLaren, 1969; Petipa, Pavlova, and Mironov, 1970; Sameoto, 1971), and the study of *Sergestes lucens* (Omori, 1969) is one with the supportive catch data of a commercial fishery. The lack of data for higher trophic levels is in part the result of an inability to culture and maintain delicate or large, mobile forms. Nearly all laboratory data on the long–term metabolism and life cycles of zooplankton species come from successful rearing of one or more generations of facultative herbivorous copepods (see Hirota, 1972 for references). Hamilton and Preslan (1970) and Gold (1971) have cultured ciliate protozoans.

The genus *Pleurobrachia* (Tentaculata, Cydippida) includes about 12 species (see Ralph and Kaberry, 1950 for the most recent summary of the species), some of which may be synonymous. The current taxonomic status of the synonymies in this genus is uncertain, because there are few sets of general characteristics which have been set up as important for the separation of species. In particular, some possibly distinct species have been grouped with the boreal species *P. pileus* O. Müller of the North Atlantic. One of these, *P. bachei,* is the boreal form which inhabits the Pacific coast of North America from Puget Sound to San Diego. This species is believed synonymous with *P. pileus,* based on the works of Moser (1909) and Mayer (1912). However, I agree with Torrey (1904), Bigelow (1912), and Esterly (1914) that *P. bachei* is a distinct and separate species. This distinction is supported by work in progress on the differences between these two forms in both meristic and metric characters (Hirota and Greve, unpubl. data).

Studies of spatial distribution, vertical migration, seasonal variations in numerical abundance, and natural history in the planktonic ctenophores have provided some data on natural populations, but information on population dynamics and rates of production are especially needed. Patterns of the geographic distribution of

Pleurobrachia species and other ctenophores have been described (Moser, 1909; Mayer, 1912), but no attempt was made to relate abundance quantitatively to geographic location. Only a few workers have studied vertical distribution of ctenophores (Esterly, 1914; Russell, 1927; Alvariño, 1967; Rowe, 1971) and only the study of *P. pileus* in Kaneohe Bay, Oahu (Rowe, 1971) could show that diel vertical migration occurs. *Pleurobrachia pileus* in Kaneohe Bay follow the "normal" pattern for zooplankton with the ctenophores living at depth during the day and moving up near the surface at night. However, the vertical displacement of the migrants was only on the order of 10 m because the bay is very shallow. More is known about quantitative seasonal changes in numerical abundance of *P. pileus* (Wear, 1965; Fraser, 1970; Greve, 1971) and *P. bachei* (Esterly, 1914; Parsons, LeBrasseur, and Barraclough, 1970). There are also numerous qualitative reports of ctenophore swarms in coastal waters (Chopra, 1960; Rajagopal, 1963; Fraser, 1970). Fraser (1962, 1970) reviewed the role of ctenophores and salps in marine food webs and their natural history. Greve (1970, 1972) provided laboratory studies of the effects of temperature, salinity, and food on growth of *P. pileus* and a field study (Greve, 1971) of variations in abundance of *P. pileus* and two of their predators, *Beroë gracilis* and *B. cucumis*. These studies did not relate seasonal variations in abundance to rates of population recruitment, growth, mortality, net production, or advection.

In order to describe the quantitative natural history of *P. bachei* as outlined above, it was necessary to sample natural populations and to carry out laboratory experiments. The field work was needed for data on the food web and for demographic purposes, and the laboratory data were used to calculate metabolic rates which could not be measured from field samples. Metabolic rates measured or calculated from individuals reared from eggs to adults in the laboratory were applied to field populations. Preliminary field studies were then made of the variations in abundance of *P. bachei* as a function of distance from shore. The vertical distribution was determined by sampling with opening-closing bongo nets (McGowan and Brown, 1966[2]) while tracking parachute drogues in those locations where ctenophores were most abundant. From the data on water movement and the horizontal and vertical distributions of *P. bachei*, sampling stations and sample depths (the maximum depth to which a net sample is taken) were allocated for a study of spatial and seasonal variations in numerical abundance, standing stocks and net production. Size or stage-specific instantaneous mortality rates were calculated from the observed size-frequency distribution in field samples and development rates calculated from laboratory growth data. Standing stocks per unit area of sea surface were calculated as the summation of the organic weight (ash-free dry weight) of all individuals in a sample multiplied by the ratio of maximum sample depth to the volume of water filtered. The organic weights were estimated from regression equations of bodily weight on bodily diameter. Rates of net production per 24-h day were calculated from the estimated standing stocks of each stage and the stage-specific instantaneous rates of mortality and growth on a daily basis. For a given set of stage-specific instantaneous mortality rates, and using the mean schedule of live births derived from laboratory data, the following population parameters were calculated: T, r, d, b, C_x, which are the generation time, instantaneous rate of natural increase, death and birth rates, and stable age distribution, respectively. More than 12,000 specimens of *P. bachei* were counted and measured during the seasonal study, of which 1,352 postlarvae in 10 size classes contained partially digested food organisms and 1,007 postlarvae contained internal parasites of the hyperiid amphipod, *Hyperoche mediterranea*. Attempts were made to quantify changes in the absolute numbers and the proportions of various prey categories with changes in bodily size of *P. bachei*. A study of the seasonal variation in numbers of parasites, percent hosts parasitized, and the frequency distribution of numbers of parasites per host and percent hosts parasitized at different host sizes is also presented.

GROWTH IN CULTURE AND METABOLIC RATES

Methods

Techniques for the laboratory culture of *P. bachei* at 15°C have been described previously

[2]McGowan, J. A., and D. M. Brown. 1966. A new opening-closing paired zooplankton net. Scripps Inst. Oceanogr. Ref. 66-23. (Unpubl. Manuscr.)

(Hirota, 1972); culturing has also been done at 20°C to examine the effect of temperature on growth rates. The rates at which different prey species were digested were measured in the laboratory in order to make corrections for predation by *P. bachei* on the most abundant crustaceans during field sampling with nets (Judkins and Fleminger, 1972, discuss feeding by *Sergestes* in nets).

Six ctenophores were cultured from eggs at 20°C and about 20 μg C/liter as prey for the adult ctenophores in order to evaluate the effect of temperature on growth rate (the surface temperature in summer is about 20°C). The basic techniques were the same as described previously (Hirota, 1972, Table 1), except that adult *Paracalanus parvus* replaced *Artemia* nauplii as food for 2– to 3–mm ctenophores. In this manner, it was possible to raise ctenophores without "artificial" foods of any kind and instead raise them on prey species which they utilize in nature. In addition, antibiotics (streptomycin sulfate and penicillin G each at concentrations of 50 mg/liter) were added after 4 wk of culturing at 20°C when several specimens appeared very weak or moribund. When changes in bodily diameter indicated that the last two specimens might also die, the experimental temperature was changed back to 15°C to determine whether or not recovery might occur and whether the mortality effect was due to lethal temperature.

In order to determine whether or not a prey species found in the gut of *Pleurobrachia* sampled with nets was eaten prior to or during capture, a number of observations were made of the rate at which five prey species were ingested and digested after initial entanglement with the tentacles. The time elapsed to achieve one of four scores was recorded during observations with a dissecting microscope through the transparent bodily wall of the ctenophore. These scores are: (4) the prey enters the mouth and is in the distal half of the stomach; (3) the prey is moved into the proximal half of the stomach but no digestion of the prey is indicated; (2) the prey is being digested and assimilated, as indicated by less than 10% of the bodily tissues clearing and the occurrence of prey tissues in the aboral, transverse, and pharyngeal canals; (1) the prey is almost fully digested and assimilated, as indicated by transparent skeletal remains (crustacean exoskeletons are not digested) and the presence of digested tissues throughout the canal network. The elapsed time to achieve a given score was then compared to the maximum time period a prey organism was at risk in the net sample with the ctenophores. This time period is the elapsed time from the start of the tow until preservative was added to the sample jar. Those prey found in the ctenophore stomachs whose score required more time than the maximum period at risk are presumed to have been eaten in nature prior to capture by the net.

Results and Discussion

The growth curve of bodily diameter up to 6 mm at 20°C indicates similar patterns as is the case for 15°C (Hirota, 1972, Figure 1), except that the development rates to the same bodily diameter are 10–15 days faster at 20°C (Figure 1). The other important differences are: 1) very much higher mortality rates at 20°C than at 15°C, 2) 60% mortality despite the addition of antibiotics on day 29, and 3) the recovery and prolonged growth and survival of two specimens after the temperature was lowered to 15°C from 20°C when growth had ceased at 20°C. Note that there is a lag of over a week before the apparent effect of lowered temperature is indicated by a response in bodily diameter. The significance of the effect of temperature on growth rate will be discussed below in relation to the stratification of water temperature in nature, the diel vertical distribution of the ctenophores, and the effect of these distributions on seasonality in the standing stocks and net production of the ctenophores.

Using the data for growth in bodily diameter at 15°C (Hirota, 1972, Figure 1), it is possible to calculate rates of growth in bodily organic weight from regressions of organic weight on bodily diameter (Figure 2). A curve for the mean growth in organic weight and the ranges for weight at a given age and age at a given weight are shown in Figure 3. The mean growth rates are highest from 0.1 to 2 mg (2.5 and 6.5 mm diameter, respectively); the exponential growth rate coefficients on a daily basis are 0.21–0.47. Below 0.1 mg and over 2 mg the exponential growth rates are slower, the values being 0.12–0.17 and 0.04–0.17, respectively. The range for weight at a given age is about tenfold and for age at a given weight about 15 days.

The rates of digestion of five prey species are shown in Table 1. These data show that undigested prey present in ctenophore stomachs (scores 4 and 3) can be ingested during a 0.3– to

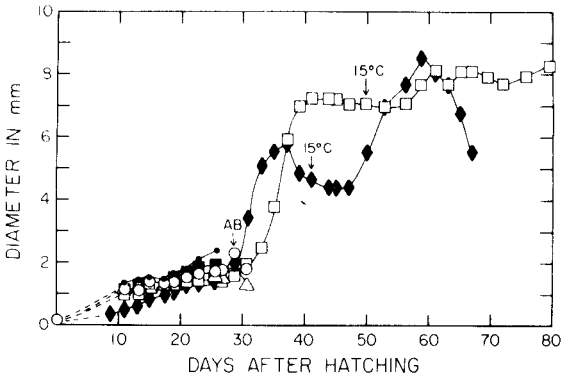

FIGURE 1.—Growth in bodily diameter of *Pleurobrachia bachei* at 20°C, expressed as a function of age in days. Each symbol represents measurements of a different individual. The point indicated by AB refers to the starting date with antibiotic additions and the points indicated by 15°C refer to change of the experimental temperature from a constant 20°C to a constant 15°C. All ctenophores died after the last observation shown for each individual, except that one which was still alive after 80 days.

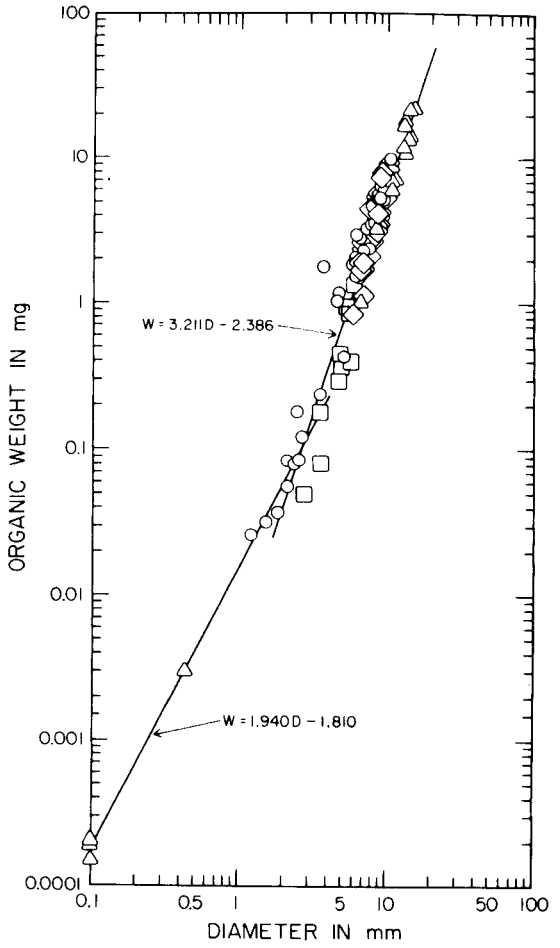

FIGURE 2.—The relationship between bodily organic weight and bodily diameter of *P. bachei* on a double logarithmic scale. The open circles represent data on field-collected ctenophores from La Jolla, Calif.; the triangles represent data on laboratory cultured ctenophores; and the diamonds and squares represent data on ctenophores grown in the deep tank facility at Scripps Institution during experiments 1 and 2, respectively. The lowest four values are calculated from determinations of organic carbon. In the equations the upper line is for ctenophores larger than 3 mm and the lower line for those smaller than 3 mm. In both equations $W = \log_{10}$ (bodily organic weight in milligrams) and $D = \log_{10}$ (bodily diameter in millimeters).

5-min period at risk while both the predator and prey are being sampled by nets. Partial or fully digested states (scores 2 and 1), however, required more than 9 and 15 min, respectively. Prey of scores 2 and 1 in ctenophore stomachs are, therefore, very likely to have been ingested by ctenophores prior to capture by nets in samples of short duration (i.e., less than 5 min). Only prey of these scores were used in the study of stomach analyses presented below, unless the prey were too small to be retained by the 0.363-mm meshes of the net and, therefore, were not at risk to predation during the sampling. Examples of these smaller prey species not at risk are nauplii of *Acartia* and all stages of *Euterpina acutifrons*, a copepod of 0.7 mm length.

Measurements of the organic weight of six species of "important" planktonic marine crustaceans in La Jolla Bight are given in Table 2. The first four species are copepods and the remainder are cladocerans. Note that for adults, *Labidocera* is tenfold larger than *Acartia* and *Evadne* and about twentyfold larger than *Paracalanus*, *Corycaeus*, and *Penilia*.

A trend exists in the data for scores 2 and 1 when the respective medians for the elapsed time to achieve these scores are expressed per unit bodily organic weight for each prey species (Table 1). *Labidocera trispinosa* is the most easily digested prey per unit bodily mass although it is the largest. *Acartia* is digested slightly faster than *Paracalanus* and each of these faster than either *Corycaeus* or *Penilia*. Part of the cause for the delay in digestion of *Corycaeus* and *Penilia* relative to the above-mentioned calanoid copepods is the protective spination. In addition to stout furcal spines, caudal rami, and very sharp projecting corners of the last thoracic joint, *Corycaeus* has a large, smooth cephalothorax which encloses much of the bodily tissues and may retard penetration of digestive enzymes. The spi-

nation causes great difficulty for the movement of this prey into the proximal half of the gut where digestion occurs. For example, the median time for score 3 of *Acartia* is significantly shorter than the corresponding median of *Corycaeus* as determined by a U-test ($P<0.05$). Similarly, the rigid bifurcate rostrum, caudal spines, and denticulate carapace of *Penilia* are often hooked into the gut wall of the ctenophore and delay passage of the prey to the site of digestion. Contrary to this delay in the passage of *Corycaeus* and *Penilia*, the relatively smooth-bodied calanoids are translocated quite easily by peristalsis of the gut. More detailed studies might indicate differences in the integument to penetration by the digestive enzymes or perhaps differences in the specificity of the enzymes for protein or lipid components of the substrate.

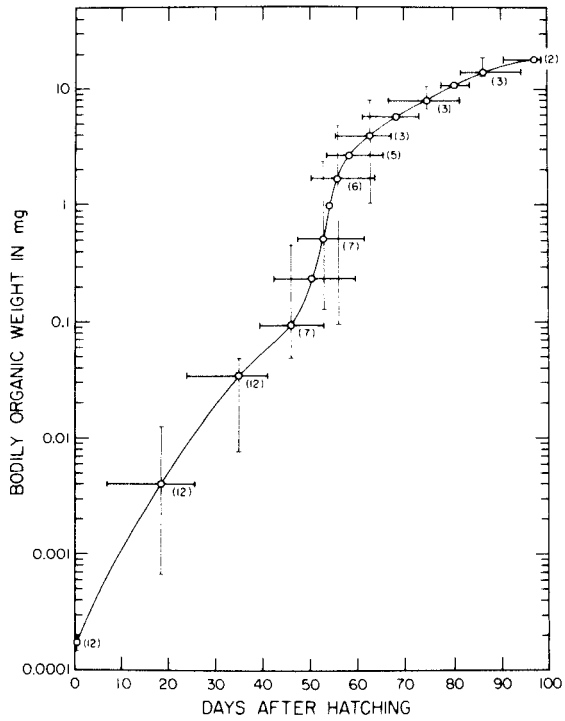

FIGURE 3.—Growth in bodily organic weight of *Pleurobrachia bachei* at 15°C during the second laboratory generation, expressed as a function of age in days. The values for bodily organic weight at different ages were calculated from the observed growth in diameter and a regression of organic weight on diameter. The horizontal and vertical bars indicate the ranges for age at weight and weight at age, and the numbers in parentheses are the number of specimens observed in the data.

FIELD ECOLOGY OF *P. BACHEI*

Study Area and Previous Plankton Work

The study location is La Jolla Bight (long. 117°20′W, lat. 33°N), including the coastal waters (hereafter coastal waters refers to that area bounded by the shoreline and a line parallel to it out to a distance of about 8 km) south to Point Loma and north to Oceanside (Figure 4). The major physiographic features of the area are: 1) Point La Jolla, which extends about 2 km west of the shoreline at Scripps Institution and forms the southern boundary of La Jolla Bight; 2) two submarine canyons (La Jolla and Scripps Canyons) in La Jolla Bight which bring water over 100 m deep within 2 km of shore; 3) numerous kelp beds located both north and south of Point La Jolla generally in 10- to 20-m depth and extending out to 1 km from shore. The area is not strongly influenced by precipitation and runoff, so that seasonal and annual variations in salinity are within 32–34 ‰ (Fager, 1968). The range of sea-surface temperature is 14–21°C annually and approximates the temperature difference between the surface and 50 m in July (Mullin and Brooks, 1967). The tides are of a mixed semidiurnal type with a diurnal inequality and total daily range that change twice each month. Within a given month the maximum daily tidal range is about 2 m and the minimum about 1 m. Wind velocities are highly variable; storms with wind speeds greater than about 7 m/s generally come from the southwest to the northwest quadrant. Santa Ana winds blow occasionally from the northeast in fall, and diel variations in wind velocities predominate in the east-west directions.

Previous plankton work in the study area include the extensive phytoplankton work of Allen (1928, 1941), the California Cooperative Oceanic Fisheries Investigations programs, and the plankton study off La Jolla by the Food Chain Research Group (Strickland, 1970). In general these previous studies provide basic information on species lists and levels of abundance and variability of phytoplankton, microzooplankton, and macrozooplankton. In these coastal waters, however, very little information is available on the patterns of water circulation, variations in abundance of organisms in relation to variations in the physical parameters (e.g., tidal motion, wind velocities etc.), or the organization and interaction of the species which inhabit this coastal region.

TABLE 1.—Rate of digestion experiments at 20°C for individual adults of five prey species and various sizes of *Pleurobrachia bachei*. Medians and ranges are given for the diameters of the ctenophores used in the trials and for the elapsed time in minutes from the prey entanglement with the tentacles until each score of digestion is achieved. The values in parentheses are the medians for the elapsed time to achieve scores 2 and 1 divided by the bodily organic weight of each respective prey. Refer to the Methods for details.

	Diameter (mm)	Prey	Trials	Score of digestion 4	3	2	1
Md	10.9	*Labidocera*	5	1.00	2.67	20	46
W	7.6-12.4	*trispinosa*		0.42-2.84	1.58-8.50	14.5-35	37->60
						(0.23)	(0.53)
Md	6.4	*Acartia*	12	0.50	1.83	15	25
W	2.0-11.7	*tonsa*		0.25-1.50	0.92-3.00	10-29	18-45
						(2.08)	(3.47)
Md	7.2	*Paracalanus*	9	1.00	2.29	12	21
W	2.0-11.7	*parvus*		0.25-2.00	1.00-6.00	9-27	15-37
						(3.16)	(5.53)
Md	7.5	*Corycaeus*	7	0.33	3.0	16	30
W	4.0-10.3	*anglicus*		0.04-1.50	1.0-6.0	9->35	18-37
						(5.3)	(10.0)
Md	8.0	*Penilia*	4	1.83	4.8	>40	—
W	5.4-12.0	*avirostris*		0.42-2.84	0.83->9	21->50	—
						(10.1)	—

TABLE 2.—The mean and range of organic weight of six prey species of *Pleurobrachia bachei*. F, M, A, CV, and J refer to females, males, adults, fifth copepodids and juveniles, respectively.

Prey category		Mean (μg)	Range (μg)	Number of observations
Labidocera trispinosa	F	88	85-94	3
	M	86	83-89	2
	CV	29	—	1
Acartia tonsa	A	7.2	6.2-7.9	8
Paracalanus parvus	A	3.8	3.7-3.8	2
Corycaeus anglicus	F	2.2	—	1
	M	3.4	3.0-3.5	3
Penilia avirostris	A	3.6	3.3-4.0	3
	J	1.2	1.1-1.2	2
Evadne tergestina	A	7.4	6.8-8.2	3

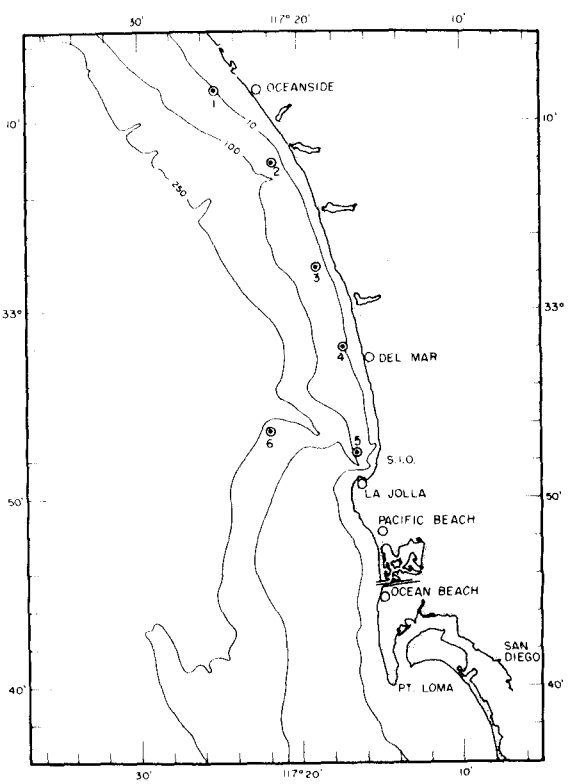

FIGURE 4.—The study area: La Jolla Bight and adjacent waters. Sampling stations 1-5 and 6 are located 1.6 and 10 km offshore, respectively. The juncture of Scripps Canyon with La Jolla Canyon is near station 5. The depth contours are in fathoms.

Methods

The three main physical parameters considered in the course of the field studies are current velocity, water temperature, and tidal stage. Current velocities in La Jolla Bight were measured on five occasions between November 1969 and June 1970 by tracking surface floats attached to parachute and "vane" drogues (vane drogues were made of

parachute silk attached to a wooden frame, creating three intersecting planes normal to each other; each plane covers about 9 m^2) set at depths in or near the thermocline (about 15–m depth). During the field studies surface temperatures were measured by bucket thermometer to the nearest 0.1°C, and the vertical distribution of temperature was measured by mechanical bathythermograph (BT) or salinity–temperature–depth recorder (STD). Tidal heights for the time of particular events are taken from tide calendars for predicted tides by the U.S. Coast and Geodetic Survey for La Jolla.

For studies of the offshore and seasonal distributions of *P. bachei* two types of nets were used. The net to collect postlarval ctenophores (i.e., ctenophores larger than 0.5 mm in diameter) is a ring net of 0.5 m diameter and 0.363–mm mesh apertures. This net was used for oblique sampling. The second net is a 0.17–m diameter ring net of 0.035–mm mesh apertures equipped with a 20–cm metal collar that attaches the net onto the wire. This net was towed vertically, and it was used for sampling the eggs and larvae of *Pleurobrachia* and the smaller zooplankters which were available as prey but not sampled quantitatively by the 0.363–mesh net. Both nets were equipped with a calibrated TSK (Tsurumi-Seiki Kosakusho) flowmeter[3] to measure volumes of water filtered.

Two studies of the vertical distribution of *P. bachei* were made, the first during 3–6 November 1969 and the second during 22 May–1 June 1970. In both cases, 0.7–m diameter paired, opening–closing bongo nets with mesh apertures of 0.053 and 0.153 mm were used. In each vertical profile of abundance, four to six depth intervals were sampled at 10– to 20–m intervals for shallow depths and at greater intervals below 50 m. Thus, a set of four to six pairs of samples comprised each vertical profile. The volumes of water filtered were between 5 and 50 m^3, as determined from calibrations of numerical settings on the net release gear against the calculated cubic meters of water filtered using a TSK flowmeter.

In all cases net samples were preserved with 10 ml of 40% formaldehyde solution, buffered with calcium carbonate, in about 750 ml of seawater. This solution is about 0.5% formaldehyde. Preliminary experiments with preservation of *Pleurobrachia* showed this to be the best concentration and type of preservative. Relatively small changes occur in length frequencies of *P. bachei* after 27 mo in this preservative (Table 3).

A preliminary survey of the horizontal, offshore distribution (the distribution of numerical abundance of *Pleurobrachia* in samples taken at increasing distances from the shore) was made on 28 August 1969. Samples were taken at 10 stations with closely spaced intervals out to 11 km from shore off Scripps Institution. Results of this study showed that the ctenophores occurred in highest abundances within 3 km of shore.

Samples were taken in the following manner during the two field studies of the vertical and offshore distributions of *P. bachei* mentioned above. In both studies of vertical distributions, about 10 sets of four to six pairs of samples were taken alongside or between parachute and vane drogues. Each sample set permitted the description of abundances at various depth intervals for one time of the day. In the study of November 1969 the offshore distribution sampling consisted of six transects of stations perpendicular to shore. The transects were about 3–8 km apart, beginning off Del Mar and ending off Point Loma. Each transect consisted of three or more stations located between 1 and 13 km from shore. In the second study the offshore distribution sampling consisted of two transects of seven and nine stations out to 50 km from shore. In all offshore distribution studies replicate samples were taken at each station except in five cases where time prohibited it or second samples were lost.

TABLE 3.—Changes in size-frequency distribution of *Pleurobrachia* with duration in 2% Formalin-seawater preservative. Samples A and B were analyzed 16 and 12 days after sampling, respectively, and a second time after 27 months as indicated in columns A′ and B′. The variable indicated is the number of occurrences of each size class. One specimen in sample A was lost.

Mean diameter (mm)	A	A′	B	B′
¼	0	0	1	0
1	10	10	64	69
2	28	24	28	28
3	23	23	17	15
4	12	11	3	1
5	5	4	1	2
6	11	14	4	3
7	5	6	1	3
8	6	8	2	0
9	2	1	1	1
10	2	2	2	2
11	0	4	0	0
12	5	1	0	0
13	2	2	0	0

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

From 8 March to 1 May 1970 sampling for the seasonal variations in the coastal plankton was done at stations located between Del Mar and Scripps Institution 1–3 km from shore. Results of the study of current velocities during 22 May to 1 June 1970 indicated that the plankton were advected northward on the order of tens of kilometers per week. Therefore from 18 June 1970 to 2 June 1971 the sampling stations for seasonal variations in the coastal plankton were changed to those six stations in Figure 4. Five stations are located 1.6 km from shore about 8 km apart between Oceanside and Scripps Institution, and the sixth station is located about 8 km beyond the station off Scripps. Replicate samples were taken at stations 1–5 with each of the two kinds of ring nets described above. Samples with only the 0.363–mm mesh net were taken at station 6. Analysis of the 0.363–mm mesh net samples, as described below, was carried out on samples at all stations from 8 March through 29 August 1970 (this period includes the seasonal maximum in abundance). From 29 August 1970 to 2 June 1971 mainly samples from stations 1, 3, 5, and 6 were analyzed once it became apparent that the variations between the five stations parallel to shore could be about as well accounted for by variations at stations 1, 3, and 5.

Samples were taken on two occasions for special studies related to the diel variation in predation by *Pleurobrachia,* their stomach contents in net tows of short duration and their selectivity of prey species with which they co–occur. During a field study from 23 to 27 July 1971, five sets of triplicate samples were taken with the 0.5–m net of 0.363–mm mesh in the upper 50 m off Del Mar. Three of these sets were taken at midnight and two sets at midday. All samples were sorted and counted as described below. The ctenophores were measured and the stomach contents identified to determine whether diel variations exist in: 1) the proportion of ctenophores which contain prey and 2) the numbers and kinds of prey which occur in stomachs during the day and at night. This study is important because all other information about the stomach contents of *P.* bachei during the seasonal study were derived entirely from samples taken between 0900 and 1600 h. On 25 August 1970 a pair of samples was taken at the surface with the 0.363–mm mesh net on station 5 at 1500 h. The tows were for 60 s duration and the maximum period which prey were at risk is 95 s. Samples were sorted and counted and the stomach contents of ctenophores identified for: 1) comparison of these prey species to other data from field samples of longer sample durations and periods at risk, and 2) calculations of the electivity indices of prey on a numerical and organic weight basis. Counts were made of all zooplankters in 2.5% subsamples of each net tow, and the proportions of prey in stomachs and in the net samples were used to calculate electivity indices (Ivlev, 1961).

Whole samples of each of two replicates per station taken with the 0.363–mm mesh net were sorted at 6–12× magnification under a dissecting microscope, and all postlarval ctenophores were counted and measured in polar diameter with an ocular micrometer. These procedures apply to all field samples taken for the offshore distribution, seasonal distribution, and special sets of samples taken for the analysis of diel variations in feeding and prey selectivities. For the sets of samples taken during the seasonal study, postlarvae of one or the other replicate sample selected at random were dissected and the contents of stomachs identified and given one of four scores described above. All specimens were examined if there were less than about 100/sample, but during a few periods of high abundances subsamples of about 50 specimens were taken. For each of 30 sampling dates between 8 March 1970 and 2 June 1971, data on stomach contents of about 100 specimens were obtained, except on those dates with very few specimens captured in all samples lumped together. For these same ctenophores which were measured and dissected, counts were also made of the numbers of larval and early juvenile stages of the facultative endoparastic amphipod, *H. mediterranea.* Also enumerated in these samples of the seasonal study were the numbers of adult and late juvenile *H. mediterranea,* which were not attached to ctenophores, and the numbers of *Beroë* sp.

Each replicate sample of the eggs and larvae of *P. bachei* taken at station 5 with the 0.035 mm mesh net was concentrated to 400 ml by settling overnight, siphoning off the excess water and transferring it to a graduated cylinder. Each of two subsamples of 20 ml was removed by Stempel pipet, examined under 12–25× magnification and the numbers of eggs and larvae counted. Numbers per square meter of sea surface were calculated as ten times the total numbers in both subsamples times the ratio of the sample depth in meters to the volume of water filtered in cubic meters.

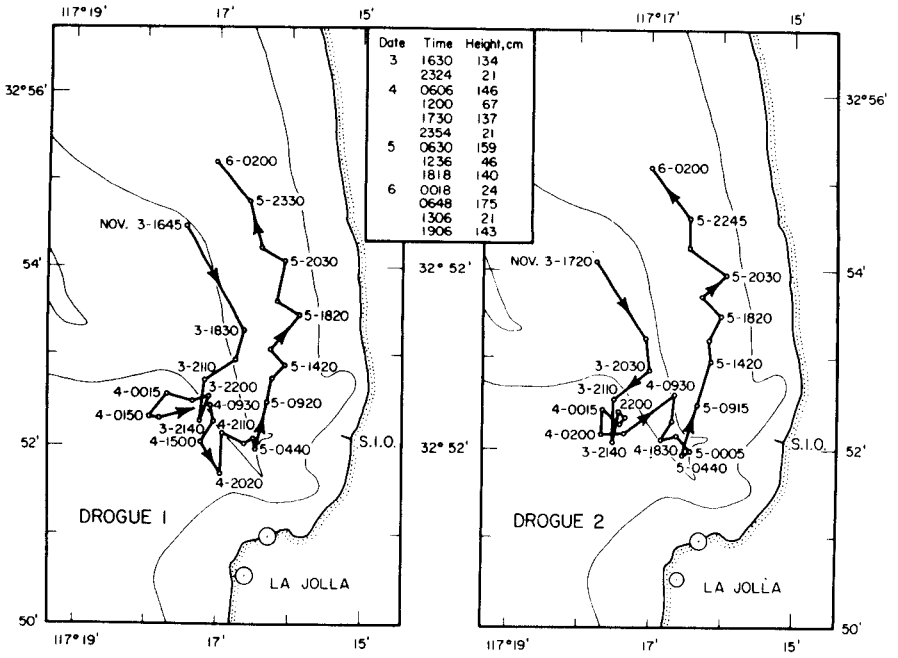

FIGURE 5.—Trajectories of two drogues during the field study of 3-6 November 1969. Observed positions of the drogues are indicated by the open circles, and the date and time of the triangulation are indicated by the one–four digit sequence of numbers near the circles. The date and predicted times (Pacific standard time) and heights of tides in centimeters are given in the inset.

Estimates of the standing stocks of food available to *P. bachei* were obtained from counts of prey taxa in subsamples of the 0.035–mm mesh net samples at station 3, the centrally located station (Figure 4). These pairs of replicate samples were treated in a manner similar to the counts of ctenophore eggs and larvae, except that counts of all zooplankters were made in a 5–ml subsample of a 500–ml sample. Over 100 specimens were counted in each subsample. The counts of numbers were converted to mass of organic carbon using the data from six species (Table 2) which frequently occur in these waters, data in the literature, and approximations by proportions of body volumes relative to the known mass of species for which data exist.

Counts of ctenophores in samples for vertical distribution studies were made as follows. First, all large ctenophores which could be seen by the unaided eye were removed with pipets from one of the pair of bongo net samples selected at random. When no further specimens could be found by eye, subsamples of 5–12.5% of the whole sample were taken by Stempel pipet or Folsom splitter and examined under 12–25× magnification for all sizes of ctenophores, including larvae and eggs. The diameters were measured as described above. Numbers per cubic meter were calculated by appropriate corrections for subsample fraction and volume of water filtered.

Results

Physical Parameters and Distribution of *Pleurobrachia*

Patterns in the currents of La Jolla Bight appear to be affected by: 1) the configuration of the coastline (especially in the Point La Jolla–La Jolla Cove complex, 2) the bottom topography and bathymetry in the La Jolla Canyon–Scripps Canyon complex, and 3) the surface tides. During the first field study in November 1969 a pair of drogues drifted toward Point La Jolla, paralleling the axis of La Jolla Canyon during an ebb tide (Figure 5). Both changed directions several times over La Jolla Canyon and made a complete counterclockwise rotation before moving northward nearly parallel to shore. Note that the rotational motion and major changes in direction occur over

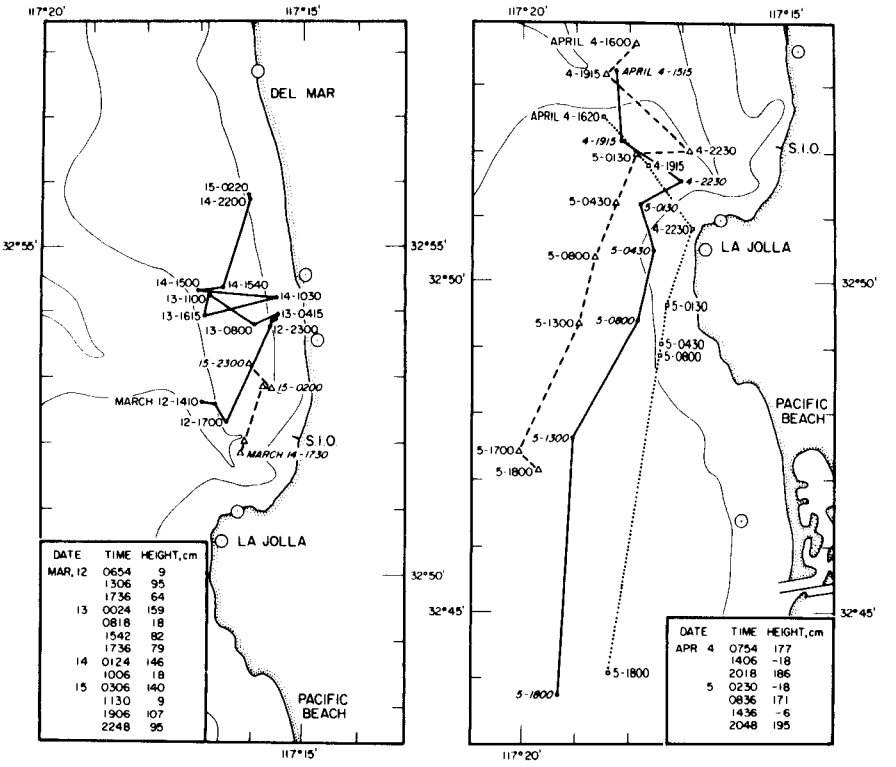

FIGURE 6.—Trajectories of drogues during studies on 12–15 March and 4–5 April 1970. Observed positions of the drogues are indicated by open circles, triangles and squares, and the date and time of the triangulation are indicated by the one–four or two–four digit sequence of numbers near the symbols. The respective dates and predicted times (Pacific standard time) and heights of tides in centimeters are given in each inset.

or near La Jolla Canyon. The surface tides associated with the commencement of the rotational motion were slack ebb tides, and completion of the loops during rotation occurred during flood tides. From 1800 h 3 November until 2300 h 4 November wind speeds were less than 3 m/s with variable direction. From 0240 h 5 November until 0600 h 6 November the winds increased to a steady 3–5 m/s from the south southeast to south southwest. The northward drift of the drogues after 0400 h 5 November may have been a response to changes in the wind velocity. Some changes in direction occurred on the northward drift of the drogues once they were beyond the submarine canyon complex, but these were relatively slight. While the drogues were over shallow water, the mean drifts were slightly onshore during flood tides and slightly offshore during ebbs. The net eastward drift was about 0.3 km and the westward drift about 1 km relative to a line true north at 0400 h 5 November.

During two other drogue studies on 12–15 March and 4–5 April 1970 drogues were tracked for 1 to 2 days. The study of March 1970 provided the best information associating the surface tides with changes in direction (Figure 6). A drogue set in the axis of La Jolla Canyon drifted slowly toward the southeast along the canyon axis until flood tides changed its direction to northeasterly. On the following slack flood tide the drogue slowed and then moved offshore toward the west on the next ebb and smaller flood. The onshore–offshore motions occurred during the following flood–slack–ebb sequences but are not as well associated with the surface tide as in the first cycle. During this drogue study the weather was foggy, especially in the early morning hours, and the winds were less than 3 m/s during the day from the northwest. At night and in the early morning hours offshore winds were about 2–4 m/s. Note that the east–west horizontal translation during a tidal cycle is on the order of 1-2 km. This effect will

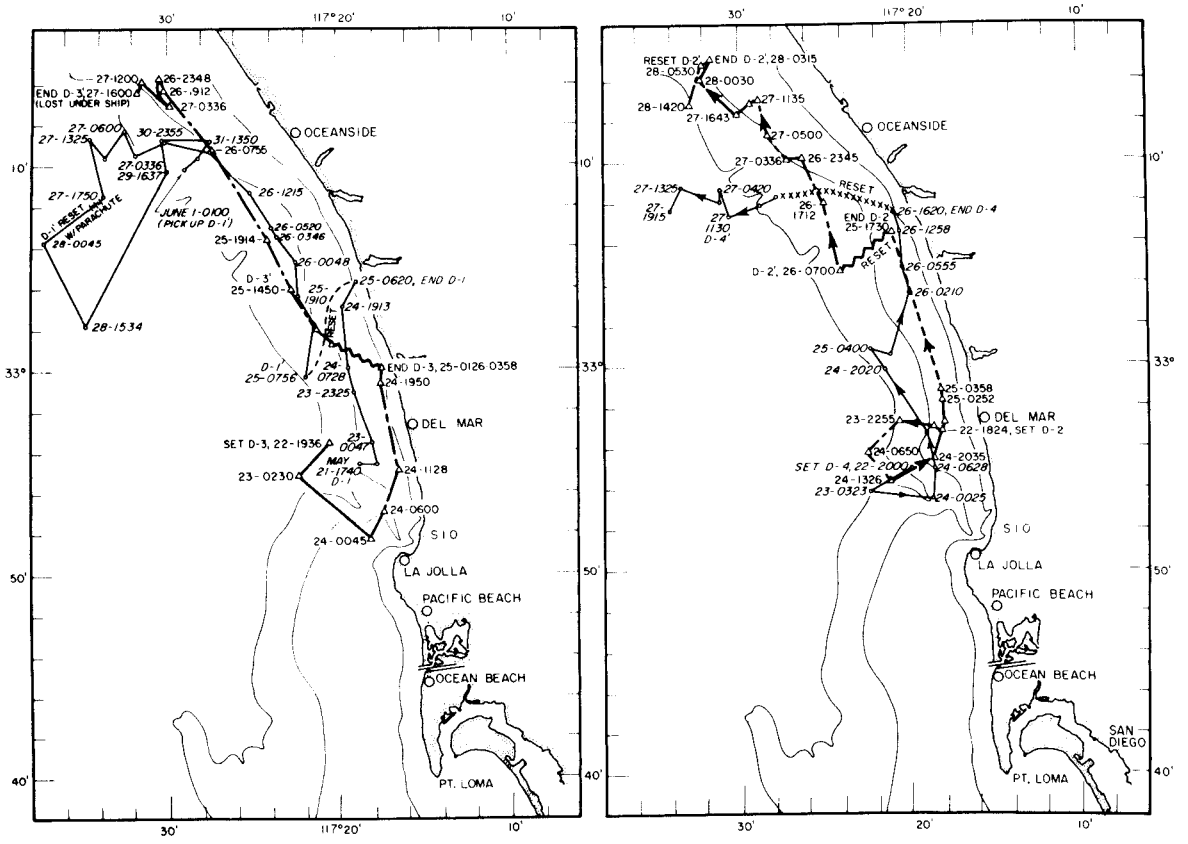

FIGURE 7.—Trajectories of four drogues during the study of 22 May to 1 June 1970. Observed positions of the drogues are indicated by circles and triangles for each pair of drogues, and the date and time of the triangulation are indicated by the one–four or two–four digit sequence of numbers near the symbols. Reset drogues indicated by primes refer to other drogues placed into the water after ones placed earlier either ran aground or broke down. Refer to the text for further details.

be considered below as one of the physical variables which may affect the offshore distribution of *Pleurobrachia* and present a bias in the sampling program for estimates of ctenophore abundance in the coastal waters. In the study during April 1970 three drogues set in a line about 1 km apart in a north–south direction moved southeast toward Point La Jolla on flood tide and changed direction on ebb tide, moving west or southwest (Figure 6). After moving beyond Point La Jolla all drogues continued toward the south. Note that after 0800 h the two drogues closest to the shore apparently became detached from their surface floats in kelp beds, because only the floats were recovered at the end of the study, 1800 h 5 April. No dramatic changes in direction occurred with changes in the surface tide for the drogues off Pacific Beach. Wind data were not recorded for this study, but the weather reports for 4–5 April indicated easterly winds at 6 m/s in the morning becoming westerly at 4–7 m/s in the afternoon.

The current velocities measured with drogues in La Jolla Bight for periods up to a week confirmed the presence of a counterclockwise gyre over or nearby the La Jolla Canyon complex (Figure 7). The four drogues moved northward, generally paralleling the shore and finally ran aground or broke down near Encinitas and Carlsbad, seasonal sampling stations 3 and 2, respectively. Drogues which ran aground or lost the subsurface parachute or vane were reset nearby the other drogues. Drogues no. 2 and 3 were reset about 5 km from shore, and they continued to move northward parallel to shore until they were lost. Drogues no. 1 and 4, however, tended to move offshore. Drogue no. 1 made a large counterclockwise loop about 16 km long and returned to cross its original path about 5 days later. Mean

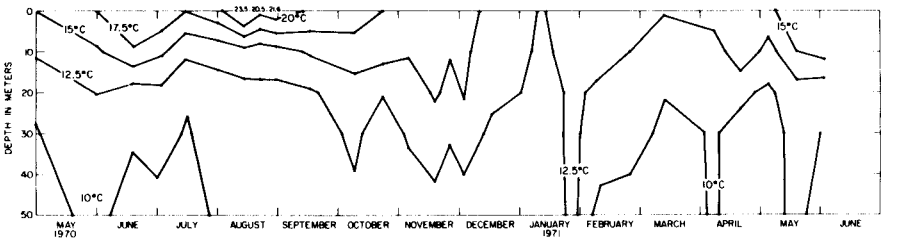

FIGURE 8.—Distribution of water temperature during the seasonal study at stations located 1.6 km from shore.

wind velocities during the study were: southwesterly at 3 m/s from 23 to 26 May, northwesterly at 5 m/s from 27 to 28 May, and northwesterly at 3 m/s from 29 May to 1 June. The range on any given day was 0–7 m/s. No clear pattern of the effect of wind velocity on drogue trajectory was observed.

From these studies the limited data for "near-surface waters" indicated predominantly northerly flow near the coast with some counterclockwise rotational motion in La Jolla Cove and off Oceanside. Some data also showed small scale onshore-offshore motion associated with the surface tidal cycle. South of Point La Jolla the currents on one occasion indicated southerly flow and little east–west motion associated with tidal cycles. The larger scale rotational motion off Oceanside was not associated with a promontory and a submarine canyon complex and remains to be explained by other means.

The water temperature in the upper 50 m for the period from May 1970 to June 1971 was measured by BT casts at stations 1–5. Since the stations were located in water of different depths, only the upper 20 m values were represented by averages for all stations. Data at 30 m were from stations 2, 3, and 5; data at 50 m were only from station 5. Thermal stratification began in May and June and reached maximal development in August and early September (Figure 8). The 12.5°C isotherm rose to the surface in January, and at this time the smallest gradients were found. Note that the annual temperature range at the sea surface was almost identical to the range of temperature in mid-August between the surface and 20 m.

The vertical distribution of *P. bachei* on 3–6 November 1969 (Figure 9) showed three main features: 1) very low abundances below 50 m for those profiles which sampled that deep, 2) the pattern of vertical distribution indicates that *P. bachei*

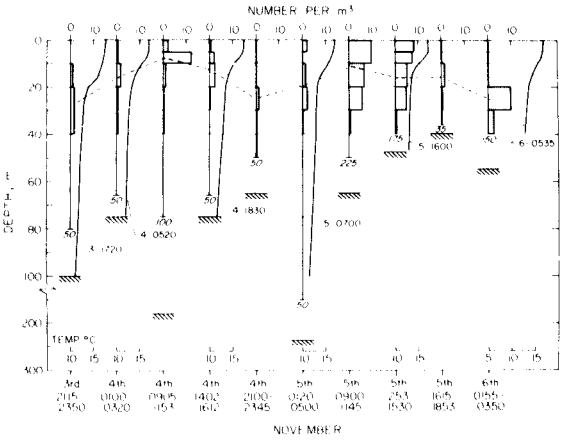

FIGURE 9.—The vertical distributions of *Pleurobrachia bachei* and temperature during the study of 3–6 November 1969. The scale of numerical abundance is given at the top, and the scale of temperature and the time interval required to sample each profile are given at the bottom of the figure. Note that the depth is given with a change of scale below 100 m. The hatched lines below each profile indicate the sea bottom and the numbers at the last sample depth give the approximate numbers of ctenophores per square meter of sea surface. The dashed line between successive profiles connects the centers of gravity of the distributions.

occurred nearer the surface during the day and deeper at night, and 3) the extent of the "vertical migration" as measured by diel vertical displacement of the center of gravity of the population was less than 20 m. The modal class of ctenophore sizes at all depths was 8 mm with a range from 4 to 12 mm. Neither larvae nor eggs were found in these bongo net samples. Vertical separation of different size classes of ctenophores was slight, the 20– to 40–m depth interval consisting of a modal size class at 9 mm and the 0– to 5–m interval consisting of a modal size class at 6 mm. Note that the relatively small vertical movements of *P. bachei* enabled these animals to spend part of the day in or above the thermocline near 17°C and part of the

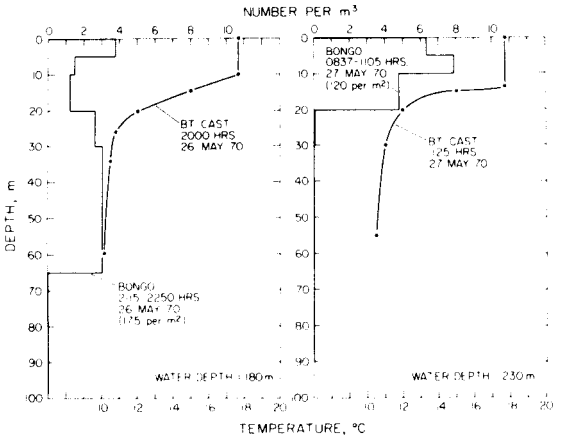

FIGURE 10.—The vertical distributions of *Pleurobrachia* and temperature during the study of 22 May to 1 June 1970. Profiles are during the evening of 26 May and the following morning. The times of sampling, the depth of the water, and the numbers of ctenophores per square meter of sea surface are also indicated.

night at about 13°C. In addition, individuals may have been displaced from each other horizontally during the migration by currents moving at different velocities at different depths (Hardy, 1935). A physical process of this nature superimposed on the biological activity of diel vertical migration may help account for the observed variations in numbers of ctenophores per square meter. Profiles taken from 0900 to 1530 h 5 November and from 0155 to 0350 h 6 November indicated abundances threefold or fourfold higher than at other times. It is apparent that following a target population with drogues will have limited success over increasingly longer time periods, even for cases in which vertical migration is restricted to shallow depths.

The vertical distribution of *Pleurobrachia* on the evening of 26 May 1970 and the following morning (Figure 10) showed patterns similar to those observed in November 1969, but with more clearly defined vertical migration from about 40 m at night to about 10 m the next morning. Note that very low abundances occurred below 65 m day or night. The size frequency distribution of ctenophores in these samples was more rectangular than in the previous November, with a range of 1–12 mm and the 5–9 mm sizes being most frequent. Again no larvae or eggs were found in these bongo samples, and it is suspected that these smaller, more delicate stages may have been broken during sampling or they did not occur in sufficient abundance to be counted in small subsamples.

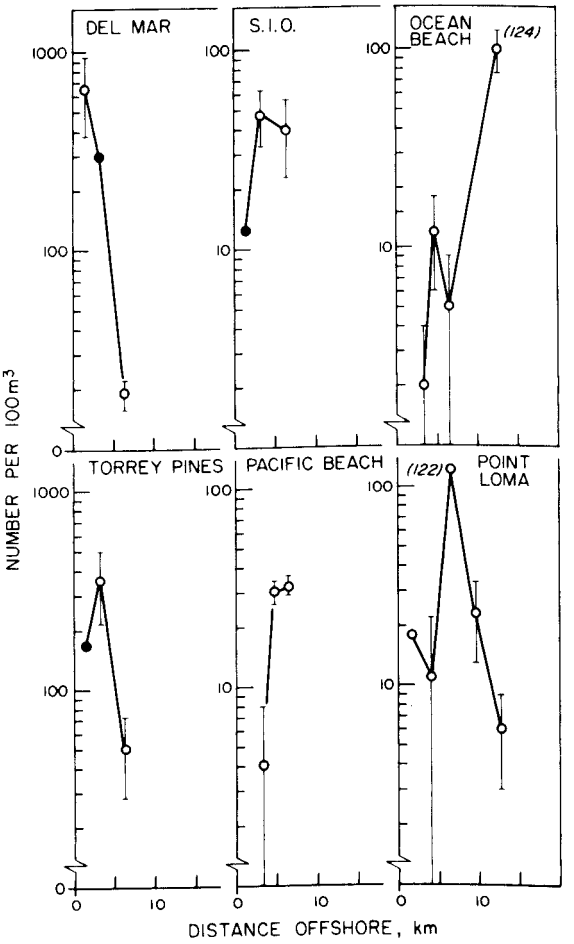

FIGURE 11.—The horizontal, offshore distribution of *Pleurobrachia* postlarvae on 6 November 1969 at stations along six transects perpendicular to shore. Note the tenfold greater abundance off Del Mar and Torrey Pines and the break of scale in order to account for absence data. The vertical bar represents the range of values for the replicate samples, and dots indicate that the range is less than the size of the dot; the open symbols off Point Loma without any vertical bar are single observations.

Thermal stratification was more pronounced than in November 1969, and these ctenophores experience a 7°C average temperature differential during the course of diel migration.

The horizontal, offshore distribution of postlarval *P. bachei*, as deduced from three field studies, indicated higher abundances at the shoreward stations and lower abundances offshore (Figures 11 and 12). Note that: 1) data are presented on semilogarithmic plots to the same linear scale of distance offshore, 2) there is a tenfold lower abundance scale shift for stations located south of Scripps Institution in Figure 11, and 3) breaks occur in the scale of abundance to account for

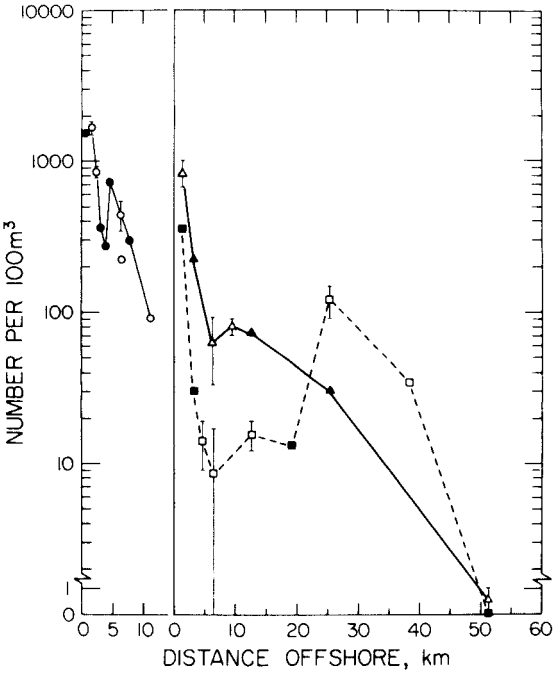

FIGURE 12.—The horizontal, offshore distribution of *Pleurobrachia* postlarvae on 28 August 1969 (circles) and 29-30 May 1970 (triangles and squares). The profile indicated by the triangles is off Scripps Institution and that indicated by squares is off Encinitas, about 20 km to the north. Note that both distributions are plotted to the same scale of distance as in Figure 11 and that the scale of abundance is broken in order to account for absence data. The vertical bar represents the range of values for the replicate samples, and solid symbols indicate that the range is less than the size of the symbol; open symbols without any vertical bar are single observations.

samples with absences. Shifts were found in the offshore locations of the highest ctenophore abundances at different positions along the coast (Figure 11). All sampling over the six lines of stations was completed between 0700 and 2300 h, 6 November. At the northernmost station at Del Mar, highest values were closest to shore and decreased over tenfold by 6.4 km. Off Torrey Pines, Scripps Institution, Pacific Beach, and Point Loma the observed maxima were located between 3.2 and 6.4 km. The exceptional case was the maximum abundance observed beyond 10 km off Ocean Beach. The surface tides associated with these six lines of stations were slack flood tide at Del Mar and Ocean Beach, slack ebb at Scripps Institution, flood at Pacific Beach and ebb at Torrey Pines and Point Loma (refer to the inset of Figure 5 for the times and heights of tides). The nearshore maximal abundance at Del Mar may represent the slack flood tide onshore movement of water and ctenophores, while the ebb and slack ebb tides at Torrey Pines and Scripps Institution, respectively may have caused offshore movements of surface water and ctenophores such that the maximal abundances occurred at 3.2 km. After sampling the outer stations off Scripps Institution, a strong southerly wind about 10 m/s generated short period swells 1–2 m high. Increased wind stress and turbulence may have altered the current pattern south of Point La Jolla and added considerable variation to the expected pattern of the distribution. The presence of high abundances of salps in the net tows at stations off Ocean Beach and Point Loma, which were not present north of Scripps Institution, indicated that the water to the south was different in faunal composition than the normal coastal assemblage. On 28 August 1969 and 29–30 May 1970, the offshore distributions indicated a tenfold decrease in abundance in the first 10 km from shore (Figure 12). The maximal abundances between 1 and 2 km were associated with slack flood or flood tides nearing slack flood. The secondary peak at 5 km on 28 August occurred during sampling on midebb tide, and it may

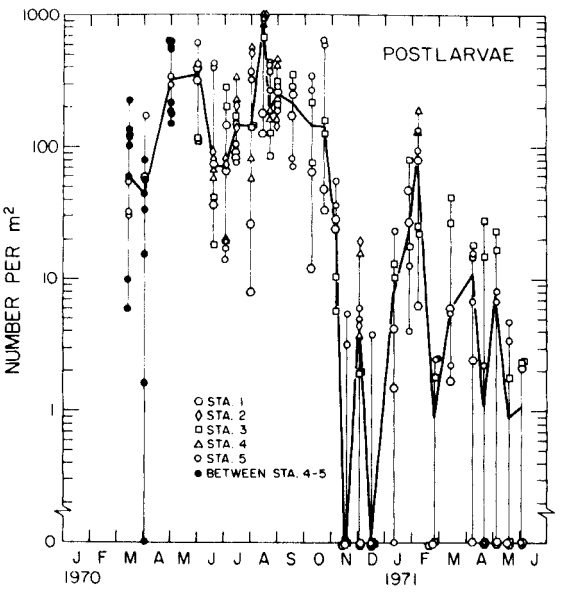

FIGURE 13.—Seasonal variation in abundance of *Pleurobrachia* postlarvae from 8 March 1970 to 2 June 1971 at stations located 1.6 km from shore. The solid line connects the medians of each sample date. Note the break of scale to account for absence data. Each type of symbol represents a different station, except for those sample dates prior to May 1970. Refer to the text for details of the field sampling.

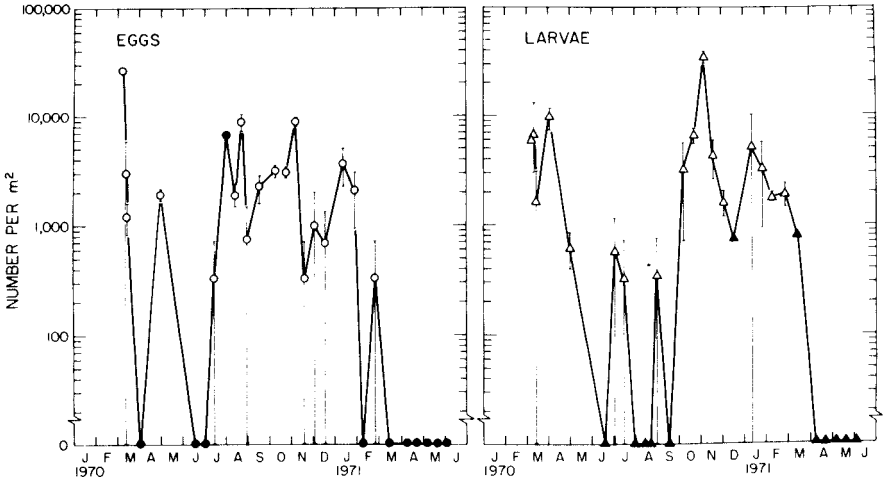

FIGURE 14.—Seasonal variation in abundance of *Pleurobrachia* eggs and larvae from 8 March 1970 to 2 June 1971 at station 5 located 1.6 km offshore at Scripps Institution. The solid line connects the mean of the replicate samples for each sampling date. The vertical bar represents the range of values for the replicate samples, and solid symbols indicate that the range is less than the size of the symbol; open symbols without any vertical bar are single observations.

represent the offshore movement of the high ctenophore abundance while field sampling was taking place. Note the secondary peak in abundance which was 25 km from shore. Deviations from an exponential decay function are perhaps the result of coastal water eddies (Figure 7), which move offshore with their surface-living species and give rise to offshore aggregations in moderate abundance. An important question to resolve is whether or not the expatriated or advected aggregations are able to survive, grow, and reproduce as well in offshore areas as they do in the coastal waters.

Seasonal variations in abundance of *P. bachei* postlarvae, larvae, and eggs on semilogarithmic plot indicated different patterns between these stages in life history (Figures 13 and 14). Recall that egg and larval abundances are based on samples from station 5 only, whereas those of postlarvae are based on the replicate tows of three to five stations. Note the wide range for the median in abundance of postlarvae (Figure 13), which usually was on the order of one-fifth to five times the overall median. In several instances the values from different stations were closer to each other than they were to their respective replicate sample at the same station. This indicates that spatial heterogeneity within a station on the scale of 100 m was often as large as the spatial plus temporal heterogeneity between stations on the scale of 8 km apart in distance and 1 h apart in time to 32 km apart in distance and 5 h apart in time. The 95% confidence limits for the mean of replicate samples at one station is the mean multiplied and divided by 2.15 (determined by two-way analysis of variance estimate of the mean square error using 90 pairs of replicate samples at five stations from 18 June 1970 to 2 June 1971). The 95% confidence limits for the mean of all stations at one sampling date is the mean multiplied and divided by 6.23 (also determined by the two-way ANOVA referred to above). The ratio of the 95% confidence limits for the mean of all stations at one sampling date to that for the mean of replicate samples at one station is 8.4 (the ratio is equal to $6.23^2/2.15^2$). This latter residual variability is comprised of time-dependent physical variations plus spatial variation and is 1.8 times larger than replicate sample error ($1.8 = 8.4/2.15^2$). The seasonal pattern of postlarvae showed high abundances in May to October 1970, low values in November–January and moderate densities in February–June 1971. Note that median abundances in March–June 1970 were one or two orders of magnitude higher than the same interval in 1971. The seasonal distribution of larval abundance was 180° out of phase with that of postlarvae for most of 1970 (Figure 14). In 1970 larval numbers were low during the summer maximum of postlarvae and highest in November when post-

larvae were in very low abundance. The abundance of eggs was generally the same as that for larvae, except for the absence of eggs in April 1970 and the high abundances of eggs relative to larvae in August–September. There were about 1,000–10,000 eggs/m² in August–September, which are presumed to be spawned by the high abundance of postlarvae. The hatching time of eggs is about 24 h at 15°C, so that the low densities of larvae during this time were the result of large seasonal changes in hatching success, increased mortality rates of larvae, or both, assuming that the observed abundances were not determined mainly by physical processes. The data on seasonal variation in length frequency distributions of postlarvae considered below will provide some information to support the interpretation of increased larval mortality. From the abundance of eggs, larvae, and postlarvae at station 5 it was calculated that on 13 March, 1 May, 31 July, 21 August, 5 November, and 27 January the eggs and larvae made up 89–99% of the numbers of individuals per square meter. On 13 August the eggs and larvae constituted 69% of the total population. The sample dates in which the eggs and larvae made up a very low percentage of the population are those in June 1970 and April–June 1971.

During the seasonal study 18 pairs of replicate samples were taken between 31 July 1970 and 2 June 1971 at both stations 5 and 6, 1.6 and 10 km off Scripps Institution, respectively. The mean abundance of postlarvae per cubic meter was calculated at each respective station on each sampling date, and a U–test was performed on these means to determine whether or not medians of mean abundance over time were significantly different at stations 5 and 6. The null hypothesis is no significant difference, with a one–tailed alternate hypothesis that the median of station 5 is greater than that of station 6. Results indicate significantly greater median abundance at station 5 than at 6 ($P<0.025$). The median difference is a factor of 4.2 and the mean difference is a factor of 4.8. This result supports the three offshore distribution studies which indicated decreasing abundance with increasing distance from shore. However, the observed decrease in abundance in the first 10 km from shore was about tenfold for the offshore distribution studies and about half this for the seasonal study. The discrepancy of a factor of two is probably real and may be caused by sampling bias in relation to stage of the tide and to seasonal changes in the patterns of currents. The

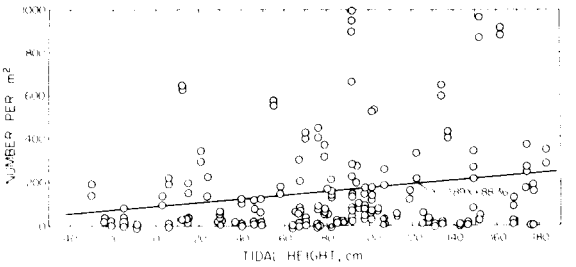

FIGURE 15.—The relationship between abundance of postlarval *Pleurobrachia bachei* and the tidal height. The abundances are in number per square meter of sea surface (Y), and the heights are in centimeters (X) for samples at all stations located 1.6 km from shore. The data are for all stages of the tide.

more accurate measure of variations in abundance with distance offshore should be found in the seasonal comparisons, but more carefully planned sampling could now be carried out to better sort out variations due to small scale tidal motions, larger scale "true" spatial variations offshore, and the effect of other types of motion and the wind on patterns of abundance.

When all of the 180 samples for the seasonal study (15 samples on five sampling dates are excluded from the analysis as five or fewer ctenophores occurred in all samples lumped per date) are plotted against predicted tidal height in centimeters for all tidal stages (Figure 15), the resulting least squares regression is $Y = 0.89X + 88.36$. Y is the number of ctenophores per square meter and X is the tidal height in centimeters. The slope of the line is significantly different from zero in a two-tailed t–test ($P<0.01$). It is surprising to find a significant positive regression coefficient. The strength of the test is in the many degrees of freedom and the removal of 15 samples which might otherwise tend to pull the line down toward a zero slope because of frequent absence data at any tidal height. This result is unexpected because the tidal currents are probably not the same at different locations along the coast. Variations exist in depth, bottom topography, exposure to wind, strike of the beach, etc. The pattern of circulation will also be differentially affected by spatial and temporal variations in the wind field. The results suggest that over an annual average, abundance at any one time and place of sampling could be affected by as much as a factor of four due to tidal variations alone at locations 1.6 km from shore. This average range due to tidal effects is about the same magnitude as the annual average difference between mean abundances of stations 5

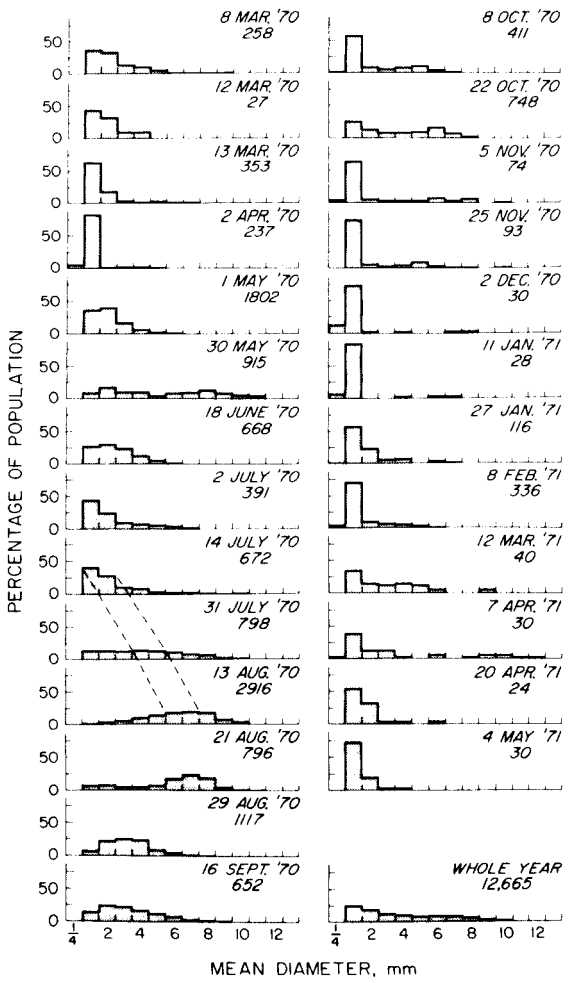

FIGURE 16.—Seasonal variations in the size frequency distributions of *Pleurobrachia bachei* captured by the 0.363-mm mesh 0.5-m net, expressed as the percentage in each size class of total numbers of all sizes on each sampling date. Each histogram is based on all sample data from each respective sampling date. The date and number of individuals measured are given with each histogram.

and 6, whose difference should be less influenced by tidal currents and represents the order of true spatial variation within the first 10 km from shore.

The size-frequency distributions of postlarvae for the 8 March 1970–2 June 1971 period indicate that most of the year the 1- to 2-mm size classes made up the highest proportion of all postlarvae (Figure 16). The lower abundance of the 0.25-mm class relative to the 1-mm class is the result of sampling gear mesh selectivity caused by the inability of the 0.363-mm mesh to retain larvae quantitatively. At sporadic intervals the size-frequency distributions show drastic changes, and these are attributed to immigration of individuals in advected water. Between 14 July and 21 August 1971 note the decline in proportion of 1 and 2 mm sizes and a shift in modal class from 1 to 7 mm. During this same period the occurrences of eggs and larvae showed that while up to 9,000 eggs/m² were present in the water, seven of eight samples for larvae indicated none present (Figure 14). Assuming that these changes in size-frequency distribution over the 4-wk period are the result of biological activity rather than sampling error and advective change, it is con-

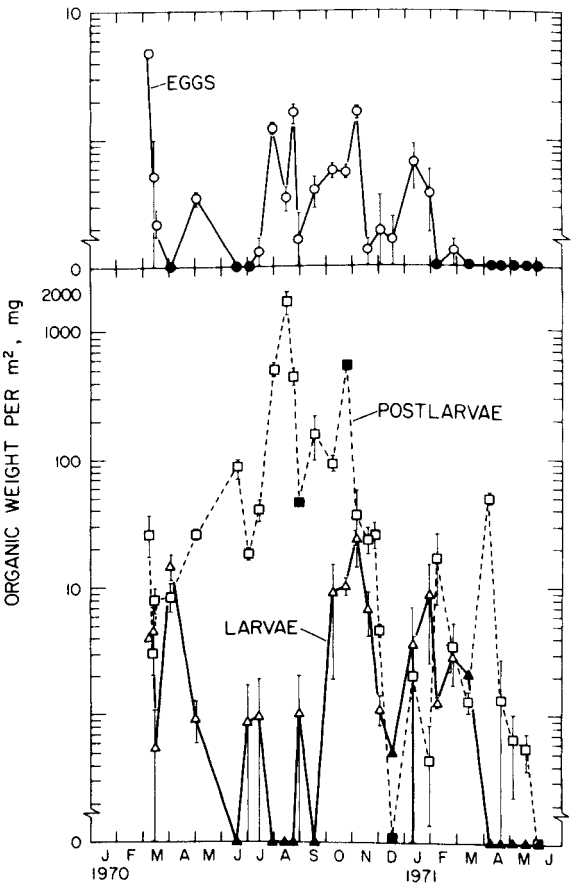

FIGURE 17.—Seasonal variations in standing stocks of postlarvae, larvae, and eggs at station 5. Each type of line connects the respective mean values for the replicate samples at each sampling date. The vertical bar represents the range of values for the replicate samples, and solid symbols indicate that the range is less than the size of the symbol; the open symbols without any vertical bar are single observations.

cluded that the ctenophore population was releasing eggs into the water but that the larvae were eaten or died from other causes as fast as they were hatching from eggs. A feedback control mechanism which can account for the presumed high mortality of larvae, high abundance of eggs, and rapid growth of postlarvae is discussed below.

The calculated development rate from 1.5 to 6.5 mm in 30 days from field sample data is about 10 days slower than the growth rates in laboratory cultures at both 15° and 20°C.

Patterns in the seasonal distribution of standing stocks of postlarvae, larvae, and eggs at station 5 (Figure 17) are similar to the respective seasonal variations in numerical abundance. Postlarval values in 1970 increased from March to a seasonal maximum of 1,500 mg organic matter/m² in August, then decreased to a minimum in December. The range over the year for standing stock of postlarvae was about four orders of magnitude. Note that the mean standing stock of larvae was high relative to that of postlarvae in April and November 1970 and the following winter months. Except for a few instances in August and September, the mean standing stock of larvae was about twofold to tenfold greater than that for eggs. The crops for postlarvae were about equal to those of the larvae, except from May to October when they were much greater.

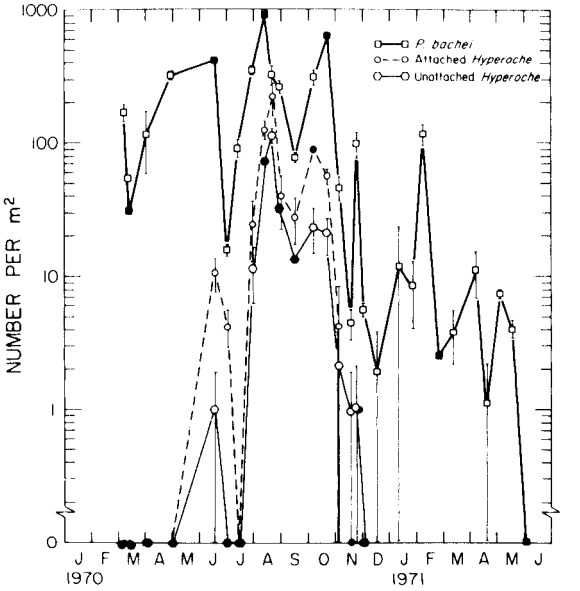

FIGURE 18.—Seasonal variations in numerical abundance of postlarval *Pleurobrachia bachei* and attached (endoparasitic) and unattached (free-living) *Hyperoche mediterranea* at station 5. Values are expressed as number per square meter of sea surface in logarithmic scale, and the lines connect respective means at each sampling date. The vertical bar represents the range of values for the replicate samples, and solid symbols indicate that the range is less than the size of the symbol. *Hyperoche* was absent after December 1970.

Seasonal Variations in Parasites, Predators, and Prey

Coincident with seasonal variations in the abundance and size frequency distribution of postlarval *P. bachei* are variations in abundance of the hyperiid amphipod, *H. mediterranea* (Figure 18). The data shown are from station 5 off Scripps Institution, but patterns in the seasonal distribution 16 and 32 km to the north (stations 3 and 1, respectively) are essentially the same. Plots of abundance per square meter on a semilogarithmic scale are for postlarval ctenophores, attached endoparasitic larvae and early juveniles of *H. mediterranea*, and unattached free-living late juvenile and adult *H. mediterranea*. The appearance of *Hyperoche* in the plankton is associated with *P. bachei* when the abundance of hosts exceeded about 100 ctenophores/m², which was May–June to November 1970. Prior to June 1970 and after January 1971 *H. mediterranea* was sparse enough to be absent in 6 to 10 samples of 15–20 m³ each. Maximal abundance of *Hyperoche* occurred about a week after the ctenophore maximum, and may represent an "overshoot" phenomenon in a density-dependent, parasite-host system. Note that the larger amphipods occurred in highest abundance when most postlarval ctenophores were at 6–8 mm sizes. Little concerning the dynamic aspect of this parasite-host interaction can be deduced from the data because of uncertainties in immigration and emigration over time. In August and September 1969–72 the occurrence of *Hyperoche* in and on *P. bachei* has been noted during plankton sampling. The co-occurrence and relative abundance of these two species is predictable and should follow the same pattern from year to year, with temporal shifts in the maxima and minima, depending on the type of "meterological year" and the sequence of events that occur in the plankton during the increase and decline of the ctenophore summer–fall maximum. The important problems to resolve are where the amphipods occur in the winter–spring months, and whether the observed seasonal pattern of co-occurrence is determined

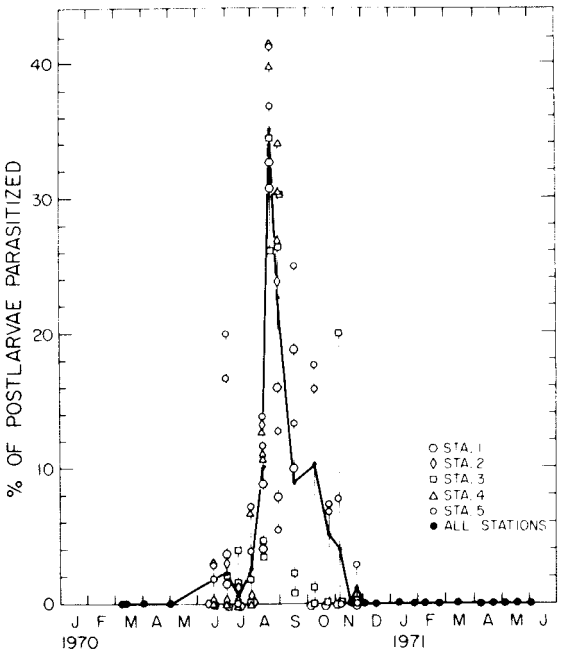

FIGURE 19.—Seasonal variation in the percentage of postlarval *Pleurobrachia bachei* parasitized by *Hyperoche mediterranea* at five stations located 1.6 km from shore. The line connects the mean value at each sampling date, and the various types of open symbols represent different stations.

by a periodic convergence of water types containing *Hyperoche* and *Pleurobrachia*.

Data from all stations during the seasonal study were plotted as the percentage of postlarval *Pleurobrachia* containing one or more *Hyperoche*. The mean percentage over time shows that August was the month of highest percentage hosts parasitized (Figure 19); at this time over one in three postlarvae were infected. The rate of increase of percentage infection appears to be faster than the decrease, although the range of 3 mo time around the maximum was the same for both. The very large variability on some sample dates was more a result of differences in percentages between stations than an artifact of sample size, since several hundred ctenophores were examined per sample date.

The frequency distributions of the percentages of total occurrences and of total numbers of parasites for single and multiple infection and for different sizes of hosts show two interesting results (Table 4). First, there is a central tendency in the percentages of total occurrences of parasites, and in the total number of parasites, with 6–8 mm sizes being the most frequently infected. This result is caused by the seasonal distribution of parasites in relation to the seasonal distribution of length frequency of postlarval *Pleurobrachia* (see Figures 16 and 18). Note that the 6–8 mm sizes with highest frequency of infection are at the size range for beginning reproduction as adults indicated by results from laboratory cultures. Also notice that only about 1% of all postlarvae in the 1- to 2-mm size classes were parasitized. These are the sizes of ctenophores which reproduce at an early age with small numbers of eggs. Secondly, the distribution of percentages of total occurrences and total numbers of parasites for single infection and multiple infection show a decreasing occurrence of multiple infection, such that over 90% of the occurrences and numbers of parasites are as one, two, or three parasites per host.

Seasonal variations in abundance of *Beroë* sp., a known predator of other ctenophores, show a pattern very similar to that of *P. bachei* (Figure 20). The data plotted are numbers per 2 m² (the sum of numbers per square meter of each replicate sample) at station 5. The distributions show seasonal maximum values in July–October with secondary high abundances in winter months. This pattern of seasonal co-occurrence is similar

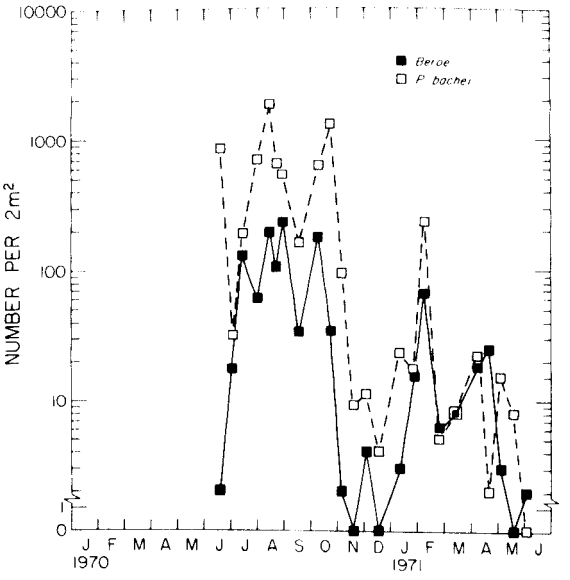

FIGURE 20.—Seasonal variation in the numerical abundance of postlarval *Pleurobrachia bachei* and postlarval *Beroë* sp. at station 5. Values are expressed for simplicity as the numbers per 2 m² (the sum of numbers per square meter in the replicate samples). The range for the mean of replicate samples has been indicated previously (e.g., Figures 13 and 18).

TABLE 4.—The frequency distribution of the number of parasites per host for 14 size classes of postlarval *Pleurobrachia bachei*, the percentage of total occurrences (A) and of total numbers (B) of parasites for each size class, and the percentages of total occurrences (C) and of total numbers (D) of parasites for single and multiple infections. The blank spaces indicate absences.

Mean diameter (mm)	Number of parasites per host									
	1	2	3	4	5	6	7	8	A	B
1		1							0.10	0.14
2	9	2							1.09	0.92
3	42	10	7	1					5.96	6.19
4	100	30	8	1					13.80	13.37
5	82	35	9	3	1				12.91	13.94
6	147	29	11	7	2	1		1	19.66	20.63
7	145	31	10	3			1		18.87	18.21
8	119	36	7	4					16.48	16.22
9	58	14	1	1					7.35	6.61
10	20	6	1						2.68	2.49
11	4	3							0.70	0.71
12	1			1					0.20	0.36
13	1								0.10	0.07
>13		1							0.10	0.14
C	72.29	19.66	5.36	2.09	0.30	0.10	0.10	0.10		
D	51.78	28.16	11.52	5.97	1.07	0.43	0.50	0.57		

to that of *P. bachei* and *H. mediterranea*, except that *Beroë* persists through the year rather than being absent for the winter and spring months. The patterns in the seasonal distribution of *Beroë* and *P. bachei* at station 3 were much the same as at station 5, except that the abundance of *Beroë* was fourfold lower at station 3, and the secondary high abundances of *Beroë* in the winter and spring months at station 5 was not as well defined at station 3.

The partially digested stomach contents of *P. bachei* captured at the surface in tows of short duration (60 s duration, 95 s maximum period at risk to feeding in the net) showed that the same species groups occur as in tows of fivefold longer duration. These species are : 1) copepods—*L. trispinosa, A. tonsa, P. parvus, C. anglicus, E. acutifrons,* and 2) cladocerans—*Evadne nordmanni, E. spinifera, E. tergestina,* and *P. avirostris*. The results provide evidence to support the contention (see results of stomach contents below) that the prey in stomach contents of *P. bachei* captured in tows of short duration are those which were ingested and digested in nature prior to capture by the net. The same species would probably occur in stomachs of *P. bachei* if the ctenophores were pipetted from the sea surface and preserved immediately. Seven species of zooplankton, which were retained quantitatively in the 0.363-mm mesh net as adults, were considered in calculations of electivity indices. In the Ivlev electivity index, $E = (r - p)/(r + p)$, r and p being the proportions of a food item in the stomach and in the environment respectively. *Paracalanus parvus, C. anglicus,* and *E. acutifrons*, which occurred frequently in the stomachs but passed through the net, were not included in the calculations. The results on the basis of numbers show moderate positive selection for *Acartia, Labidocera,* and *E. tergestina;* high positive selection for *E. nordmanni* and *E. spinifera;* and moderate and strongly negative selection for *Penilia* and *Sagitta* (Table 5). The indices on the basis of organic weight show the same trends, but the values for both copepods and *Evadne* are increased somewhat, and that for *Penilia* decreased, due to differences in bodily weights. *Penilia* has a negative electivity and was a slowly digested prey species (Table 1), whereas *Labidocera* and *Acartia* have positive electivity indices and were more rapidly digested. Prey selection by *Pleurobrachia* is more complex than dependence on prey digestibility alone. Data on the stomach contents of *P. bachei* during the seasonal study and observations in the laboratory of avoidance behavior and prey protective mechanisms will be discussed below in the context of prey selection.

In the study of diel variation in feeding, differences in the percentage of ctenophores with

TABLE 5.—Electivity indices for seven species of zooplankton which are retained by the 0.363-mm mesh net as adults. The range for the mean is calculated from the replicate samples from the proportion of the numbers and the proportion of the calculated organic weight present in the sample and in the stomach of the ctenophores. Refer to the text for further details.

Prey Species	On a numbers basis		On an organic weight basis	
	$\bar{E}$	range E	$\bar{E}$	range E
Acartia tonsa	0.191	0.118-0.264	0.464	0.434-0.495
Labidocera trispinosa	0.130	0.099-0.160	0.413	0.408-0.419
Evadne tergestina	0.244	0.183-0.305	0.506	0.430-0.582
E. nordmanni	0.806	0.748-0.864	0.953	0.936-0.970
E. spinifera	0.770	0.748-0.792	0.776	0.659-0.893
Penilia avirostris	−0.345	−0.300 to −0.391	−0.055	−0.143 to +0.033
Sagitta euneritica	−1.000	−1.000 to −1.000	−1.000	−1.000 to −1.000

TABLE 6.—Diel variation in the percentage of ctenophores which have empty stomachs. The numbers in parentheses are the numbers of specimens examined per sample.

Replicate sample	Midnight station			Midday station	
	A	B	C	A	B
1	70 (27)	62 (40)	75 (8)	69 (16)	62 (32)
2	76 (38)	76 (41)	57 (46)	77 (13)	64 (14)
3	71 (55)	90 (10)	62 (26)	71 (24)	67 (18)

empty stomachs at midnight and midday were small, the medians being 71% and 68%, respectively (Table 6). These medians are not significantly different as determined by a two-tailed U-test ($P>>0.20$). It is concluded that no day–night differences exist in the proportion of the postlarval ctenophores feeding, at least at the time of this study.

The prey categories most frequently found during the diel study in both day and night stomach contents were copepods and cladocerans—*A. tonsa*, unidentified copepods, *P. parvus*, copepod nauplii, *Clausocalanus* spp., *E. tergestina*, *C. anglicus*, *Oithona* spp., *E. acutifrons*, *Oncaea* spp., and unidentified material. In these samples *A. tonsa* was over 50% of all prey by numbers. The species which were present in stomachs of *P. bachei* captured at night include the same groups captured during the day, the larger and deeper-living copepods, euphausiids and other crustaceans being absent in the stomachs. If redundancy in the presence of prey species day and night (a qualitative aspect) occurs at other times of the year, then the prey species of *Pleurobrachia* could be adequately described by stomach analyses of ctenophores captured during the daytime. However, in quantitative aspect diel variations of percentages of each species may vary. For two of the species most frequently present, *A. tonsa* and *P. parvus*, the results are different. As determined by a two-tailed U-test, there is no significant difference in median percentage *Acartia* of the total number of prey for day vs. night samples ($P>0.20$); however, the same test for *Paracalanus* indicates significant day–night differences ($P<0.05$), there being more frequent occurrences at night than during the day. Further investigation of prey selection by *Pleurobrachia* in relation to time–space distributions of prey and predators is important for understanding the ecology of *P. bachei* but beyond the scope of the present study.

The stomach contents (on the basis of numbers and mass of organic carbon) of postlarval *Pleurobrachia* in 10 size classes over the period 8 March 1970 to 2 June 1971 indicated some patterns in the frequency distribution of prey categories (Table 7). The patterns or trends exist as four types: (I) decreasing frequency with increasing ctenophore size, (II) increasing frequency with increasing ctenophore size, (III) little change in frequency with increasing ctenophore size, and (IV) non-systematic change and low frequency of occurrence for all ctenophore sizes. Examples of each pattern type are: (I) *E. acutifrons*, copepod eggs, *E. spinifera;* (II) *A. tonsa*, *L. trispinosa;* (III) *Oithona* spp., *C. anglicus*, *P. parvus*, copepod nauplii; (IV) *Rhincalanus nasutus*, euphausiid calyptopis, brachyuran zoea, *Sagitta euneritica*.

These results are subject to several sources of bias, three of which are: 1) the occurrence of the stomach contents of ctenophore prey in the stomachs of ctenophores, 2) the numbers of observations per ctenophore size category and the number of total occurrences per prey category, and 3) seasonal variations in the length-frequency distributions of ctenophores and their co-occurrences with prey. The diatom and dinoflagellate prey categories may be biased toward higher frequencies of occurrence if some of these types of organisms which occur in the stomachs of herbivores are released into the gut of a ctenophore during digestion. Fortunately, these

TABLE 7.—Stomach contents over the period 8 March 1970 to 2 June 1971 for 10 size classes of postlarval *Pleurobrachia bachei*. Data are the percentage by numbers (upper value) and by carbon mass (lower value) of each prey category in the stomachs for each size class of ctenophore calculated separately. The first 10 prey categories are given in ascending order of body mass; thereafter the order is by taxonomic group (e.g., copepods, cladocerans, crustaceans, chaetognaths, etc.). The numbers indicated in parentheses below each size class are the number of ctenophore stomachs examined per size class. Total numbers and total carbon refer to values of all prey in each ctenophore size class. Carbon mass is not calculated for protozoans.

		Size class, mean diameter (mm)									
Prey category		1 (189)	2 (211)	3 (235)	4 (190)	5 (158)	6 (150)	7 (105)	8 (68)	9 (24)	>10 (22)
Euterpina acutifrons	%N	20.85	18.33	15.36	15.58	7.41	5.54	4.05	4.00	0	7.06
	%C	9.15	5.56	2.98	3.05	0.80	0.71	0.40	0.23		1.00
Oithona spp.		6.81	3.33	5.03	3.43	4.04	0.98	0.40	4.67	5.17	2.35
		2.18	0.47	0.24	0.14	0.27	0.06	0.01	0.12	0.58	0.17
Oncaea spp.		0.85	2.33	0	1.25	0	0.33	1.21	1.33	0	0
		0.50	0.91	0	0.13	0	0.06	0.15	0.06		
Corycaeus anglicus		4.26	9.33	9.50	8.41	9.76	4.56	5.26	7.33	3.45	14.12
		2.58	9.76	5.25	4.44	3.45	1.80	1.60	0.77	1.43	4.46
Paracalanus parvus		1.70	3.00	4.47	3.43	6.40	3.91	4.86	6.00	5.17	7.06
		2.40	2.22	2.01	1.23	2.11	1.16	1.24	0.67	1.07	2.17
Acartia tonsa		10.64	21.67	25.14	29.91	36.03	47.23	55.87	49.33	60.34	47.06
		39.59	48.04	36.94	39.21	33.66	43.17	37.49	16.80	53.78	37.62
Calanus helgolandicus		0	0	0.28	1.25	1.01	0.65	0.81	0.67	0	1.18
				3.18	7.83	10.14	2.85	4.61	3.26		6.97
Labidocera trispinosa		0	0	2.51	2.49	3.37	2.93	4.45	5.33	1.72	2.35
				29.33	28.44	30.60	37.24	37.50	21.96	10.52	25.08
Metridia pacifica		0	0	0	0	0	0	0	1.33	0	1.18
									4.89		13.94
Rhincalanus nasutus		0	0.33	0	0	0.34	0	0	0	1.72	0
			0.05			4.78				23.90	
Clausocalanus spp.		0	0	0.56	0.62	0.67	0.33	0	0.67	0	0
				0.37	0.27	0.36	0.17		0.06		
Ctenocalanus vanus		0	0	0	0	0	0.33	0	0.67	0	0
							0.09		0.06		
Tortanus discaudatus		0	0	0	0.31	0.34	0	0	0	0	0
					0.45	0.17					
Copepod eggs		14.47	10.67	8.38	4.36	2.69	1.30	0.81	2.00	3.45	0
		6.12	3.20	1.66	0.70	0.33	0.07	0.05	0.09	0.49	
Copepod nauplii		11.91	6.67	3.35	4.05	9.43	4.89	5.67	4.67	3.45	0
		0.78	0.25	0.08	0.08	0.13	0.07	0.06	0.02	0.05	
Unidentified copepods		4.26	4.00	2.79	3.12	2.02	2.28	1.21	1.33	3.45	0
		5.60	3.03	1.27	1.26	0.57	0.64	0.25	0.13	0.96	
Evadne nordmanni		5.96	7.00	6.70	5.61	1.01	4.89	5.26	1.33	8.62	8.24
		16.47	11.12	6.42	4.77	0.60	2.90	2.24	0.27	5.02	4.10
Evadne spinifera		2.13	1.00	0.56	0.31	0.67	0.33	0	0	0	0
		5.88	1.59	0.54	0.26	0.40	0.19				
Evadne tergestina		0.85	1.33	1.96	2.80	1.68	6.84	4.45	0.67	0	1.18
		2.35	2.12	1.87	2.39	1.00	4.06	1.90	0.14		0.58
Evadne spp.		0	2.67	3.91	3.43	0	0	0	0	0	0
			4.24	3.75	2.92						
Penilia avirostris		0.42	0.67	2.51	2.18	3.03	2.93	0.40	1.33	1.72	4.71
		0.56	0.50	1.15	0.88	0.86	0.83	0.08	0.13	0.48	1.11
Podon polyphemoides		0	0.67	0.28	1.25	1.35	0.33	0	0	0	0
			1.06	0.27	1.06	0.80	0.19				
Euphausiid calyptopis		0	0	0.28	0	0	0.33	0	0	1.72	0
				0.46			0.33			1.72	
Cirriped nauplii		0	0	0	0	0.34	0	0	0	0	0
						0.02					
Mysids		0	0	0	0	0	0	0.40	0	0	0
								12.34			
Brachyuran zoea		0	0	0	0	0.34	0.65	0	1.33	0	1.18
						0.96	1.84		1.30		2.79

(Continued)

TABLE 7.—Continued

Prey category	Size class, mean diameter (mm) 1 (189)	2 (211)	3 (235)	4 (190)	5 (158)	6 (150)	7 (105)	8 (68)	9 (24)	>10 (22)
Unidentified crustaceans	3.83 2.52	1.67 0.63	1.12 0.25	1.56 0.32	1.35 0.19	0.98 0.14	0.40 0.04	2.00 0.10	0	0
Sagitta euneritica	0	0.33 2.14	0	0	0.34 6.10	0	0.40 0.01	0.67 48.88	0	0
Oikopleura spp.	0.42 2.02	0	1.12 1.83	0	1.01 1.03	1.30 1.32	0	0	0	0
Echinopluteus, doliolids	0	0	0	0	0	0	0	0	0	2.36
Fish eggs	0	0.67 2.77	0	0	0.34 0.53	0	0	0	0	0
Sarcodina	0	0	0	0.31	0.34	0.65	0	0	0	0
Noctiluca scintillans	0	0	0	0	0	0	0.40	0	0	0
Dinoflagellates	0.85	0	1.12	0.31	0.67	1.95	0.81	0	0	0
Diatoms	0	0	0	0.62	0	0	1.62	0	0	0
Unidentified material	9.79 1.29	4.33 0.33	3.07 0.14	3.43 0.14	4.04 0.11	3.58 0.10	1.21 0.02	3.33 0.03	0	0
Total numbers	235	300	358	321	297	307	247	150	58	85
Total carbon, μg	178.47	396.48	784.76	791.93	1045.87	1087.39	1215.87	1534.41	209.17	358.80

taxa made up less than 2% of any one category by numbers and less on a mass basis because of their small size. The number of observations per ctenophore size category are similar for classes 1–6, but thereafter they decrease sevenfold. There are few observations in the last two size classes, because these sizes are relatively infrequent and occur in high numbers only during July–August. Some of the larger copepods (e.g., *Calanus, Metridia,* and *Rhincalanus)* occur relatively infrequently in stomachs, perhaps because of their relative rarity and spatial separation from the ctenophores. Other infrequent groups such as fish eggs, cirriped nauplii, euphausiids, etc., may not be spatially separated but are perhaps rare, not selected as prey or are unavailable because of temporal separation during different seasons. Whatever the reasons for the infrequent occurrence of these groups in the stomachs of *Pleurobrachia,* the data for these prey are much less reliable and many more observations are required to establish patterns of occurrence with size of the ctenophore predator. The potential effect of seasonal variations in size–frequency distribution of ctenophores and co–occurrence of prey on patterns of stomach contents is suggested when the annual data are examined separately by seasons. The results indicate that some prey are very seasonal in occurrence, while many are present throughout the year. The seasonal data are given (Table 8) for only those categories which showed strong seasonal variations. The first two prey were most frequent in summer–fall, *E. tergestina* in summer–winter, the next four in fall and the last one in winter–spring. Note the differences in occurrence of three species of *Evadne* regarding seasonal separation and predation by different sizes of *Pleurobrachia.*

When all stomach content data are grouped to include all sizes of postlarval *Pleurobrachia* and prey categories are ordered by rank of occurrence, the results show that *A. tonsa* and *E. acutifrons* account for nearly one–half of all prey items (Table 9). Thereafter, the percentage contribution from each category decreases to less than 1% by the sixteenth category, at which point the cumulative percentage is 94.2%. On a mass basis *Calanus, Labidocera,* and *Sagitta* join *Acartia* as the main large prey items. While these larger items may afford good growth to a few individuals, most of the ctenophore population is being nourished by *A. tonsa, E. acutifrons* and several other species of copepods and cladocerans.

Variations in the standing stock of food avail-

TABLE 8.—Seasonal variations in the stomach contents of ctenophores for eight prey categories. All values are expressed as the number of occurrences per 1,000 stomachs. The seasons spring (SP), summer (SU), fall (F) and winter (W) are groups of three months starting with February 1970 and ending in January 1971; the following spring 1971 is also included. The dashed lines indicate absence of data.

Prey category		Size class, mean diameter (mm)									
		1	2	3	4	5	6	7	8	9	>10
Paracalanus parvus	SP	0	100	154	0	200	0	0	—	0	—
	SU	46	50	52	44	146	67	91	91	91	300
	F	0	22	85	55	79	98	125	26	111	0
	W	33	0	0	182	400	0	125	429	—	500
	SP	0	0	0	83	0	0	0	3,000	333	250
Labidocera trispinosa	SP	0	0	0	0	0	0	500	—	0	—
	SU	0	0	21	0	49	0	45	318	91	100
	F	0	0	66	77	79	88	125	26	0	250
	W	0	0	0	91	0	0	0	0	—	0
	SP	0	0	0	0	125	0	0	0	0	0
Evadne tergestina	SP	0	0	0	0	0	0	0	—	0	—
	SU	0	0	21	44	0	100	0	0	0	0
	F	42	0	47	55	56	167	139	26	0	250
	W	0	364	0	91	0	91	125	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Calanus helgolandicus	SP	0	0	0	0	0	0	0	—	0	—
	SU	0	0	0	0	0	33	0	0	0	100
	F	0	0	9	44	34	10	28	26	0	0
	W	0	0	0	0	0	0	0	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Evadne spinifera	SP	0	0	0	0	0	0	0	—	0	—
	SU	0	8	0	0	0	0	0	0	0	0
	F	21	43	18	11	22	10	0	0	0	0
	W	33	0	0	0	0	0	0	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Penilia avirostris	SP	0	0	0	0	0	0	0	—	0	—
	SU	0	8	0	0	49	100	0	45	0	300
	F	21	22	85	77	79	59	14	26	111	250
	W	0	0	0	0	0	0	0	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Podon polyphemoides	SP	0	0	0	0	0	0	0	—	0	—
	SU	0	8	0	0	0	0	0	0	0	0
	F	0	22	9	44	45	10	0	0	0	0
	W	0	0	0	0	0	0	0	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Evadne nordmanni	SP	0	0	0	0	0	0	0	—	0	—
	SU	0	58	72	59	0	0	0	0	0	0
	F	62	22	19	0	0	29	14	0	0	0
	W	30	1,000	1,333	909	0	364	1,500	286	—	0
	SP	111	143	538	333	375	1,600	0	0	1,667	1,750

able to *Pleurobrachia* from 18 June 1970 to 2 June 1971 showed a twentyfold range, with high values in May to early November and low values from mid-November to mid-March (Table 10). The food concentrations were about 10–30 mg C/m^3 during the summer–fall maxima in numbers and standing stocks of *Pleurobrachia* postlarvae. The decrease in abundance of *Pleurobrachia* during November and December (see Figure 13) was associated with a fivefold decrease in the standing stock of prey. The winter increase of *P. bachei* occurred while food concentration doubled from the minimum in December. The higher food concentrations in May and June do not seem to cause increases in ctenophore abundance.

DISCUSSION

The vertical distribution of *P. bachei* in La Jolla Bight is related to the diel light–dark cycles, but in reverse to the pattern for most migrating zooplankton; the pattern is the result of one or more causes of differing selective advantage to the temporal persistence of this species. Four potential

TABLE 9.—Rank order in frequency of occurrence by numbers of all developmental stages per prey category in all sizes of *Pleurobrachia* postlarvae and the corresponding estimates of total carbon mass per prey category.

Prey category	Frequency	Percent	μg C	Percent
Acartia tonsa	815	34.56	2,644.23	34.78
Euterpina acutifrons	270	11.45	114.04	1.50
Corycaeus anglicus	180	7.63	225.73	2.97
Copepod nauplii	139	5.89	6.95	0.09
Copepod eggs[1]	129 (1,649)	5.47	49.47	0.65
Evadne nordmanni	122	5.17	256.20	3.37
Paracalanus parvus	101	4.28	108.80	1.43
Unidentified	89	3.77	8.90	0.12
Oithona spp.	83	3.52	15.99	0.21
Unidentified copepods	62	2.63	62.00	0.82
Evadne tergestina	61	2.59	128.10	1.68
Labidocera trispinosa	58	2.46	2,085.54	27.43
Penilia avirostris	45	1.91	45.00	0.59
Unidentified crustaceans	34	1.44	17.00	0.22
Evadne spp.	33	1.40	69.30	0.91
Oncaea spp.	19	0.81	8.86	0.12
Dinoflagellates	17	0.72	—	—
Calanus helgolandicus	14	0.59	355.00	4.67
Evadne spinifera	14	0.59	29.40	0.39
Podon polyphemoides	12	0.51	25.20	0.33
Oikopleura spp.	12	0.51	43.20	0.57
Clausocalanus spp.	8	0.34	11.74	0.15
Brachyuran zoea	6	0.25	60.00	0.79
Diatoms	6	0.25	—	—
Sagitta euneritica	4	0.17	822.4	10.82
Sarcodina	4	0.17	—	—
Metridia pacifica	3	0.13	125.0	1.64
Rhincalanus nasutus	3	0.13	100.2	1.32
Euphausiid calyptopis	3	0.13	10.80	0.14
Fish eggs	3	0.13	16.50	0.22
Ctenocalanus vanus	2	0.08	2.00	0.03
Tortanus discaudatus	2	0.08	5.40	0.07
Cirriped nauplii	1	0.04	0.2	0.003
Mysids	1	0.04	150.0	1.97
Echinopluteus	1	0.04	—	—
Doliolids	1	0.04	—	—
Noctiluca scintillans	1	0.04	—	—
Total	2,358		7,603.15	

[1]The frequency value refers to the number of groups of copepod eggs and the value in parenthesis below it refers to the total number of eggs.

advantages of migration to *P. bachei* are the ability to: 1) seek locations and depths with favorable food types and concentrations, 2) seek locations and depths with few predators and parasites, 3) avoid lethal or near-lethal surface temperature after the downward migration at night and increase the rate of development by living in warmer water during the day, and 4) maintain the pattern of high abundance close to shore and decrease the chance of drifting offshore. No data have been collected on quantitative changes in the abundance of prey and predators with *P. bachei* during vertical migration; such information would enable qualitative evaluation of the effect of these changes on the pattern of vertical distributions. Limited data from the study of diel changes in the species composition of prey in stomachs of ctenophores indicated no major changes between day and night, although

TABLE 10.—Seasonal variations in the calculated standing stocks of prey for *Pleurobrachia* at station 3.

Sample date	Mean (mg C/m³)	Range (mg C/m³)
18 June 1970	10.9	10.8–11.0
14 July	10.7	10.4–11.1
13 August	15.5	6.0–25.0
29 August	17.8	16.4–19.1
22 September	27.8	20.2–35.4
5 November	15.7	13.4–17.9
18 November	5.8	3.4– 8.1
16 December	2.7	2.6– 2.8
11 January 1971	6.8	3.7– 9.9
8 February	6.0	2.2– 9.7
12 March	5.2	5.1– 5.3
4 May	58.4	52.2–64.6
2 June	9.3	9.3– 9.4

Paracalanus occurred more frequently in stomachs of ctenophores captured at night. Another major study would be required to quantify changes in the temporal and spatial co-occurrence of *Pleurobrachia* with their prey and predators. The data on vertical and seasonal distribution of *P. bachei* and the thermal stratification of water; the failure of laboratory cultures at 20°C; and growth experiments in the deep tank facility at 14.5° and 19.5°C are interpreted to indicate that vertical migration for this ctenophore is beneficial for survival and would optimize the rates of development and increase of bodily mass. A constant temperature of 20°C was detrimental to survival and growth of bodily weight (Figure 1), relative to conditions at 15°C. It is suspected that in August when the ctenophore abundance is highest and the maximum thermal stratification occurs, vertical migration from the surface to 20-m depth increases the chance of survival by lowering the ambient temperature at night by nearly 10°C. In addition, the detrimental effect of high temperature on somatic growth may be decreased and the ctenophores develop at some rate intermediate to the rate at 12° and 22°C. Growth experiments using the deep tank facility in which stratification of temperature is made to simulate conditions in nature might support some of these speculations. Alternatively, laboratory growth experiments could be made in which temperature is varied with a semidiurnal period. Another complication in these experiments, if they are to simulate conditions in the field, is the co-occurrence of the parasite *Hyperoche* and its possible temperature-dependent effect on the growth and survival of *P. bachei*.

A consequence of diel vertical migration in the

coastal waters off southern California is the potential effect on the horizontal, offshore distribution of a species. Stevenson (1958)[4] summarized some wind data for the Newport Beach to Los Angeles Harbor area, which show that in the sea breeze–land breeze diel variation of wind velocity there is a stronger sea breeze component from the west–northwest quadrant during the afternoons and a more variable and weak wind in the mornings. Robert Arthur has suggested that a possible result of the diel variation in wind velocity and the observed pattern of vertical migration in *P. bachei* may in part account for the maintenance of high ctenophore abundances close to shore. By living in the wind–mixed layer during the day with a westerly–northwesterly sea breeze, ctenophores are moved shoreward. At night through the early morning hours the weaker land breeze moves the surface waters offshore, but by living deeper at night the net offshore movement of ctenophores should be relatively smaller than the shoreward displacement. The frequent stranding or grounding of drogues nearshore suggests a net onshore movement of water. One mechanism of horizontal, seaward transport is the rip currents, but these are probably important only a few hundreds of meters seaward of the surf zone and are dependent on the size of sea swells. It is not known how important stranding is as a source of mortality to *Pleurobrachia*, but in summer months *Pelagia* (Scyphozoa) are frequently stranded on La Jolla beaches and are broken apart in the surf zone. Other macrozooplankton, such as salps and *Velella*, periodically occur on the beach and in waters near the shore. It is not clear what cues or mechanisms the ctenophores use to maintain their distribution to within 1 km of shore without most being washed into the surf and killed. A number of net tows taken near the end of Scripps Institution pier and just seaward of the surf zone indicate absence of *P. bachei*.

The estimates of abundance of *P. bachei* at fixed stations located alongshore 2–3 km from the shoreline are subject to variability in time and space from several causes. At a single station the abundance will be affected by: 1) spatial heterogeneity and patchiness on the scale of 100–m horizontal distance and 20– to 50–m depth over the course sampled during a tow, 2) the stage of the tides and the tidal current velocity (see Figure 15), and 3) the water temperature stratification and near–surface drift due to the wind. The magnitude of replicate sample error is one–half to twice the mean, and the variability in abundance due to the presumed horizontal motion generated by the tides and wind for the annual average is about the same as replicate sample error.

For estimates of abundance on a given sampling date at stations 1.6 km from the shore at different locations along the coast, "true spatial" variability exists in addition to replicate sampling error and aliasing due to physical effects of tides and the wind. It is difficult to sort out quantitatively the separate error components due to physical effects and true spatial effects alone, because the time period for the physical effects to bias sampling (about 6 h) is about the same as that required to move through space and sample different stations. Variability around the mean of all stations at one sampling date includes variations due to replicate sampling error, variations due to physical effects, and variations due to true spatial differences. The relative magnitudes of these components of variation estimated from the 95% confidence limits of the two–way analysis of variance and the regression of abundance on tidal height are: 1) the 95% confidence limits about the mean of all stations at a given time of sampling is the mean multiplied and divided by 6.23, 2) the 95% confidence limits about the mean of replicate samples is the mean multiplied and divided by 2.15, 3) the range of the expected abundance from the regression equation over the observed values of tidal heights is fourfold, or a range of about one–half to twice the overall annual mean, and 4) the residual true spatial variation calculated by difference is the mean multiplied and divided by 1.45 (i.e., $6.23^2 = 2.15^2 \times 2^2 \times 1.45^2$). In terms of the relative contribution of these three components to the total variability, the values are 2.2:1.9:1 for replicate sampling error, physical effects, and true spatial variation, respectively. The relative contribution of replicate sampling error vs. physical plus true spatial variations to the total variability of all stations on one sampling date is 1:1.8. These results from a sampling program not designed specifically to separate each effect suggest that physical effects on sampling bias and the replicate sample error are important relative to real spatial differences of abundance between stations equidistant from shore. A synoptic sampling program with two or

[4]Stevenson, R. E. 1958. An investigation of nearshore ocean currents at Newport Beach, California. Unpubl. Rep. to Orange Cty. Sanit. Dist., 108 p.

more ships would better enable separation of the total variability into variations from time-dependent physical effects, true spatial differences, and replicate sample error. It is indeed discouraging that confidence limits for the mean of replicate samples could not be reduced below about one-half to twice the mean, even with a *t* value based on 90 degrees of freedom. Zooplanktologists may continue to be plagued with the inability to reduce field sampling variability much below this level, given reasonable time and manpower limitations and no significant changes in sampling methodology. Because of their large size and lack of rapid escapement, postlarval *P. bachei* are as easy to sample accurately as any zooplankter is likely to be.

Seasonal changes in abundance of *P. bachei* postlarvae observed in La Jolla Bight during my study (Figure 13) agree with the earlier work of Esterly (1914) off San Diego and work by Parsons et al. (1970) in the Strait of Georgia, British Columbia (the values reported in the Strait of Georgia work are numbers of *Pleurobrachia* plus *Philidium* per cubic meter). These two studies showed that seasonal maxima occurred in July or August; high densities were from June to September and lower values and absences were observed from October to March. Esterly (1914) noted that *P. bachei* were more abundant at temperatures above 18°C than below; they were especially abundant at about 19°C in August. He also noted that although *P. pileus* and *P. bachei* are similar in morphology, their distributional pattern and temperature optima are widely different. In the Atlantic *P. pileus* was abundant at lower temperatures during the year (<15°C); in the Pacific the reverse seemed to be the case.

Seasonal studies of *P. pileus* in Wellington Harbor, New Zealand (Wear, 1965) and the North Sea region (Russell, 1933; Fraser, 1970; Greve, 1971) show that it differs from *P. bachei* in the season of maximal abundance. In Wellington Harbor *P. pileus* was dominant in the winter plankton, and it was the most variable planktonic species. *P. pileus* was absent in February-March, rare (1-10/20-min tow) in April-May, and December-January, common (20-100/tow) in June and September-November and abundant (500-1,000/tow) in July-August (note that this is the winter in New Zealand). Critical temperature for the occurrence of *P. pileus* was between 15° and 16°C. When the temperature fell below this level, *P. pileus* occurred in great abundance; in early summer at temperatures above 16°C they were rare or absent. In the North Sea off Plymouth, *P. pileus* occurred in a bimodal seasonal distribution with early summer (May-June) and fall (October) maxima (Russell, 1933). In the North Sea near Helgoland *P. pileus* occurred with a May-June maximum at 10-15°C and a less distinct fall peak (Greve, 1971). Long-term mean seasonal distributions in the Scottish North Sea showed a clear November maximum with a less distinct secondary mode in June (Fraser, 1970); however, the month of the seasonal maximum can be as early as July-August in "abnormal" years compared to the expected fall maximum of normal years. Highest numerical abundance of postlarval *P. pileus* in the North Sea was on the order of 10-20/m^3 (Fraser, 1970; Greve, 1971). This is about the same as the maximum of 40/m^3 I found for *P. bachei* postlarvae, but through most of the year the population of *P. bachei* was dominated by numbers of larvae and eggs. Contrary to the annual or biannual spawning patterns of *P. pileus* in the North Atlantic (Fraser, 1970), *P. bachei* produced eggs throughout the year except for spring and some summer months.

Important differences exist between *P. pileus* and *P. bachei* in addition to the pattern of seasonal distributions and the surface temperature at the season of maximum abundance. Patterns in the seasonal co-occurrence of *Beroë* with *Pleurobrachia* and the parasitism of each *Pleurobrachia* species are different for *P. pileus* and *P. bachei*. In the North Sea, *P. pileus* occurred in patterns of seasonal abundance which were 180° out of phase with the abundance of *Beroë* (Russell, 1933; Greve, 1971). In La Jolla Bight abundances of *P. bachei* and *Beroë* sp. generally increased and decreased in phase without time lags. The seasonal patterns for the co-occurrence of *Beroë* with *P. pileus* and *P. bachei* suggest that *Beroë* and other predators may overexploit *P. pileus* temporarily to decrease the population abundance seasonally, whereas *Beroë* and *P. bachei* appear to co-occur in a less intense predator-prey association. In the North Sea, *P. pileus* were parasitized by nematodes (Greve, 1971) and cercaria of *Opechona*, a trematode (Fraser, 1970). In La Jolla Bight, *P. bachei* were parasitized by *H. mediterranea*. Farther to the north *Hyperoche mediterranea* is replaced by *H. medusarum* (Bowman, 1953), and *P. bachei* is parasitized by this species in waters off northern

California (Brusca, 1970).

Off southern California, the strongest equatorward surface flow occurs during spring and summer, and south of Point Conception the semipermanent cyclonic eddy produces a northward inshore circulation (Wyley, 1966). Beneath the California Current, the undercurrent is a subthermocline poleward flow of water of relatively high temperature and salinity; for example in August 1966 the undercurrent at lat. 31°N, long. 177°W was close to the continental slope, being about 20 km wide and 300 m thick (Wooster and Jones, 1970). This undercurrent below 200 m surfaces well inshore of the main stream in late fall and early winter when northerly winds are weak or absent (Reid et al., 1958).

The seasonal distributions of *P. bachei* in La Jolla Bight showed some features which are consistent with seasonal changes in the vertical movement of the California undercurrent (also called the Davidson Current). Postlarvae decreased by over two orders of magnitude from the end of October through December, and reappeared at moderate abundance in late January and February. For larvae and eggs, the timing and magnitude of the winter decrease were about the same, but the frequency of absences was less than for postlarvae (see Figures 13 and 14). Another variable associated with the presumed winter shoaling of the undercurrent is the fivefold decrease in prey standing stock from early November to the middle of December (Table 10). A subsurface current which rises to the surface in winter is expected to contain relatively low crops of animals and plants, and poleward advection of water from the south should cause decreases in abundance of *Pleurobrachia*.

Studies of stomach contents of *P. pileus* in the Scottish North Sea (Fraser, 1970) and in Kaneohe Bay, Oahu (Rowe, 1971) indicate that this ctenophore is predominantly a crustacean feeder, especially of copepods, cladocerans, and cirriped nauplii. In the Scottish North Sea, *P. pileus* fed about 80% of the time on *Acartia, Calanus, Evadne,* invertebrate eggs, *Temora longicornis, Oithona,* unidentified copepods, cirriped larvae, *Spiratella,* and *Podon*. In Kaneohe Bay 75% of the prey were nauplii of barnacles and copepods and the appendicularian *Oikopleura longicauda* (Rowe, 1971). The evidence indicated that *Pleurobrachia* very rarely fed on fish eggs and larvae. The North Sea study included seasonal and annual data, the differences between which Fraser attributed to differences in the composition of the plankton rather than prey selectivity by *Pleurobrachia*.

The gut contents of *P. bachei* in La Jolla Bight generally agree with the results for *P. pileus* in that they fed: 1) predominantly on crustaceans, especially copepods; 2) very rarely on fish eggs and larvae; and 3) on a broad spectrum of organisms some of which appear seasonally for only limited periods. The major difference between the results from the three study areas is that in Kaneohe Bay *Pleurobrachia* fed on relatively few prey categories, the number being about one-fifth that in my study and the North Sea study. The three most frequent foods on a numerical basis were: 1) barnacle and copepod nauplii, *Oikopleura* and other copepods in Kaneohe Bay; 2) *Acartia, Calanus,* and *Evadne* in the Scottish North Sea, and 3) *Acartia, Euterpina,* and *Corycaeus* in La Jolla Bight. Both studies of *P. pileus* gut contents considered the postlarvae as a homeogeneous group. I have treated the postlarvae of *P. bachei* as being made up of 10 separate size classes to show that some changes do occur in prey frequency during ontogeny (Table 7). All studies of ctenophore gut contents have been inadequate to describe quantitatively the developmental stages of prey species eaten by different life history stages of ctenophores, including the larvae. Great difficulties and amounts of work would be required for such a study (each copepod species has 13 developmental stages counting the eggs). Many important biological interactions probably occur during different developmental stages during ontogeny, yet we know very little about them.

Feeding rate experiments with 9- to 10-mm diameter *P. bachei* (Bishop, 1968) have shown differences between mean ingestion rates of copepodids of *Epilabidocera amphitrites* and *Pseudocalanus minutus; P. bachei* also fed at a faster rate on copepodids and adults of *P. minutus* than on their nauplii. These results showed that rates of feeding depend on prey size and other differences between the same stages of different prey species and between different developmental stages of one species. The study of feeding behavior of *P. pileus* indicated that this ctenophore regulates its feeding rate by changing the average size of the tentacles in response to different concentrations of *Artemia* nauplii (Rowe, 1971).

During laboratory culturing and rate of digestion of prey experiments, differences were observed in: 1) the avoidance and escape behavior of

prey, 2) the protective spination of various species, 3) the strength and sensory acuity of larger zooplankters, and 4) the active search patterns of "setting out" tentacles by the ctenophore. Each of these four factors in addition to other variables, which are determined by the relative abundance and movement of species in nature, have some bearing on the selection of prey by *Pleurobrachia*. The first consideration is time–space co–occurence of prey with the ctenophore. Since the ctenophores are neritic and mostly live close to shore in the upper 50–60 m, they will occur with surface–living holoplanktonic and meroplanktonic species, only coexisting with deeper-living, migratory species at night. Secondly, the ctenophores will most frequently encounter the most abundant organisms in numbers per unit volume. Size and swimming activity of the prey are also important to determine the chance of encounter with the tentacles. Bodily length determines the likelihood of retention of a given organism by the tentacle net, and swimming activity determines how often the prey will encounter a given ctenophore if swimming in a random manner. Rowe (1971) has shown, using *Artemia* nauplii, that the instantaneous feeding rate of *P. pileus* follows the form for effusion of an ideal gas; this requires the assumption that prey move about randomly. However, I have seen *P. bachei* make at least three different types of settings of its tentacles in apparent attempts to alter the pattern of search for prey: 1) a double helix set like two interwoven corkscrews perpendicular to a level surface with the body at the uppermost end, 2) a pair of spirals parallel to a level surface with the ctenophore body at the outer end of the spiral, and 3) linear and curved sets which are placed at different angles with respect to the vertical and with the ctenophore body either heading up or down. The types of tentacle settings may be adaptive responses to the nonrandom swimming patterns of different zooplankton species, some of which move more in a horizonal or a vertical plane. It is at this point that animal behavior becomes very important. Species which co–occur with *Pleurobrachia* and are relatively abundant (up to several hundred per cubic meter) are not necessarily eaten by this ctenophore, because these potential prey probably use their sensory acuity and locomotive power to avoid danger. One outstanding example is *S. euneritica*, a species which is very fast and difficult to catch compared to most zooplankton; it had a highly negative electivity index (Table 9). Assuming that a prey organism has just made contact with the ctenophore tentacles, three possible outcomes have been observed in the laboratory for different species: 1) the prey is too strong and breaks away from the tentacle hold; 2) the prey provides a strong escape response, becomes further entangled and is eaten; and 3) the prey provides little or no escape response, remains nearly motionless and "plays dead," often being dislodged from the tentacle hold and not eaten. A species which is too powerful for *P. bachei* to capture is *H. mediterranea*. The adults of this amphipod can break away from the entanglement and also have the ability to exploit the ctenophores as a predator. Prey which provide a strong, "calanoid escape response" are almost always further entangled by swirls of the tentacle branches and are eaten. The immediate struggling and pulling away appears to signal the ctenophore of a successful prey capture, much as I would expect that a spider detects the impact and vibrations of the prey struggling on its web. The copepods such as *Acartia, Labidocera, Calanus*, etc., exhibit strong escape responses when stimulated by contact or approaching danger. Two prey species were observed to exhibit the motionless or "play dead" response. These are *C. anglicus* and *P. avirostria*. *Penilia* is also one of the species which has a negative electivity index or is taken less frequently than in proportion to abundance in the water. Once the prey is brought to the mouth of the ctenophore, the next limitations are the configuration of the prey body and appendages plus the protection from external spination. Bodily shapes such as those of *Sagitta* and zoea larvae of Porcellanidae (a family of crabs) create difficulties for their ingestion by *Pleurobrachia*. Large *Sagitta* must be bent in half and ingested at the middle section first (observations are from the laboratory work; gut contents from field sampled ctenophores show that this event is very infrequent). The long anterior and posterior spines of the porcellanid zoeae prevent full ingestion and digestion entirely, although the prey probably do not survive the capture. Many other decapod larvae possess stout spines and very thick exoskeletons (e.g., *Emerita* larvae), which prevent ingestion and would retard digestion as well. Some brachyuran zoeae which have dorsal and lateral spines have been observed to cut open the ctenophore gut wall during ingestion. Recall that brachyuran zoeae only make up 0.25% of the total number of prey in ctenophore guts (Table 7).

DEMOGRAPHY AND NET PRODUCTION

Methods

Computations of stage–specific instantaneous mortality rates (hereafter referred to as mortality rates or mortalities) were made in order to use these values in other calculations to estimate population parameters and rates of net production. Mortalities were calculated using field data on stage frequencies treated as a composite of all samples taken on each sampling date and laboratory data on rates of development, with temperature and food concentrations being similar to average values observed in the field study area. The growth or development rate data are from laboratory cultures at 15°C and 35 μg C/liter food concentration. The mortalities were computed by a computerprogram (Fager, 1973) which solves an equation to fixed level or error by a specified number of iterative calculations.

$$\bar{N}_{x+1}/\bar{N}_x = t_x\,(1 - e^{-Mt_{x+1}})/t_{x+1}\,(e^{Mt_x} - 1). \quad (1)$$

The variables t_x and t_{x+1} are the duration of development in days for stage x and $x+1$, respectively; variables $\bar{N}_x$ and $\bar{N}_{x+1}$ are the numbers of each stage in the composite divided by the respective duration of development. The mortality rate on a per day basis from stage x to stage $x+1$ is M; for an organism with continuous growth, such as a ctenophore, a "stage" is a size category. Positive mortalities can be calculated only when $\bar{N}_x$ exceeds $\bar{N}_{x+1}$. Implicit in the calculation are the assumptions that: 1) successive stages of the organisms were born during a period of constant recruitment and 2) successive stages have lived together in spatial proximity, or emigration is balanced by immigration in the water parcel.

The life table calculations were based on the estimated mortalities for different time periods of field sampling and the mean schedule of live births from laboratory cultures at 15°C. The equations used to calculate population parameters and stable age distributions are from Birch (1948).

The rate of net production per day of each developmental stage is a function of the numbers and weights of the animals and their instantaneous rate of tissue growth and of mortality on a per day basis; the rate of net production by a species population of a given age structure is simply the sum of the rates for each stage. These rates are calculated from the equation of Ricker (1958), which relates the rate of net production to the mean daily standing stock and the rates of growth and mortality.

$$NP_i = G_i B_i\,(1 - e^{G_i - M_i})/(M_i - G_i) = G_i \bar{B}_i\,. \quad (2)$$

In this equation G_i and M_i are the mean exponential coefficients or mean instantaneous rates of growth and mortality of the ith stage on a per day basis. The variables B_i and $\bar{B}_i$ are the calculated standing stocks per sample in milligrams organic matter per square meter of the ith stage at the beginning of the day (B_i) and the average over a 24–h period ($\bar{B}_i$). This function equates the rate of net production per day for the ith stage (NP_i has units of milligrams organic matter per square meter over a 24-h period) to the instantaneous rate of tissue growth times the standing stock at the beginning of the day (the beginning of the day is the time a field sample is taken) corrected for differential increases due to tissue growth and differential decreases due to mortality. For further details refer to the work of Ricker (1958) and Mullin and Brooks (1970). Note that the rate of net production per day is actually an average value, because it is calculated using means for growth and mortality rates.

The rates of net production for postlarvae and larvae of *P. bachei* were calculated according to Equation (2) above. No values for mortality rates of eggs were calculated, but the hatching time of eggs at 15°C is about 24 h. In calculation of the net production of eggs per day, it is assumed a steady state in the standing stock of eggs with a hatching time of 24 h. This is equivalent to the assumption that the rate of net production of eggs per day is equal to the standing crop at the time of sampling the eggs.

From calculations of the net production per day of postlarvae for each replicate sample at each station, the mean value and the variance of the mean are calculated according to standard parametric statistics. At a given station, the total amount of organic matter produced over some interval of time, Δt, equals the product of the mean rate per day and the time interval in days. For calculations of the annual net production (ANP), it is assumed that the mean rate per day on a given sampling date at one station applies linearly over an interval of time equal to the sum of one–half

the period between the given sampling date and the previous sampling date plus one-half the period between the given sampling date and the next following sampling date.

The ANP equals the sum of all net production increments over the year.

$$\mathrm{ANP} = \underset{t_n=1}{\overset{t_n=n}{\mathrm{SUM}}} \overline{NP}_{t_n}(t_{n+1} - t_{n-1})/2. \quad (3)$$

In the equation t_n refers to the nth sample date, $\overline{NP}_{t_n}$ refers to the mean rate of net production per day on the nth sample date, and ANP is the mean value of the annual net production for any life history stage being considered. For the first and last sampling dates of the year, the mean rates per day were applied over one-half the following sampling date interval and one-half the previous sampling date interval, respectively. Calculations using Equation (3) were carried out separately for postlarvae, larvae, and eggs at station 5 off Scripps, and the total for all life history stages is the sum of the annual values for the eggs, larvae, and postlarvae at that station. ANP was also calculated at stations 1, 3, and 6 for postlarvae only.

The variance of the mean value of the ANP at a given station was calculated as the product of the variance of the mean rate of net production per day and the square of the time interval over which it was applied, summed for all time intervals during the year. The equation was derived from the variance formula of a dependent variable which equals the product of two independent variables (net production over a time interval, $\triangle t$, equals the product of the mean net production per day and $\triangle t$), by solving for the square of the differential of net production over a time interval $\triangle t$. The covariance term is zero since the daily net production and time interval between sampling dates are independent. The term for the square of the mean daily net production multiplied by the variance of $\triangle t$ is presumed to be small, because sampling during the year was within a few hours at the same time of the day for all sampling dates.

$$\mathrm{Var}(\overline{\mathrm{ANP}}) = \underset{n=1}{\overset{t_n=n}{\mathrm{SUM}}} \mathrm{Var}(\overline{NP}_{t_n})(t_{n+1} - t_{n-1})^2/4. \quad (4)$$

The symbols are as given above in Equation (3), and Var ($\overline{\mathrm{ANP}}$) and Var $(\overline{NP}t_n)$ refer to the variance of mean annual net production and the variance of mean daily net production on sampling date t_n, respectively.

Results

During the field study from 8 March 1970 to 2 June 1971, 100 mortality values were obtained for postlarvae and larvae. On any one sampling date it was not possible to calculate mortality values for all size classes, especially with small sample sizes in older stages. Therefore, the mortalities from all sample dates were grouped into seven time periods and seven size classes (excluding eggs) in order to obtain an estimate of mortality for each class over time. The mortalities were grouped according to the subjective criterion that medians of a group would differ from any other by at least 50%. The mortalities for size classes were set by the comparisons of mean numbers per class between successive classes.

For the time period of 1 May to 18 June 1970 a life table calculation is given in Table 11. The mean hatching success of eggs is 94%. The l_x values are the probability that an individual born will survive to the beginning of each age interval. The instantaneous mortality rates which were used to construct the l_x schedule are as follows: 1) 0.170 for larvae of age 1–19 days, 2) 0.021 for stage 1–2 mm postlarvae of age 19–45 days, 3) 0.150 for stage 3–4 mm postlarvae of age 45–53 days, 4) 1.047 for stage 5 mm postlarvae of age 53–54 days, 5) 0.572 for stage 6 mm postlarvae of age 54–55 days, 6) 0.378 for stage 7–8 mm postlarvae of age 55–63 days, and 7) 0.260 for stage 9–13 mm postlarvae of age greater than 63 days. These mortality rates were applied equally for each age interval over the duration of the respective stages. Note that up to age 53 days (4.5 mm) the first 45 live births give a net reproduction of 1.0405 (60% of the total), enough to replace the population. The next 53 live births add 23% of the total net reproduction. The enormous potential reproductive capacity at age 61–63 days and older is not fully realized because of the miniscule numbers which survive to this age. These results show the great importance of early reproduction in size classes 1–2 mm toward the net reproduction.

The population parameters and stable age distributions in May–June and three other time periods, each with its own schedule of survival and the mean schedule of births, are shown in Table 12. For the 1 May to 18 June period, the observed

TABLE 11.—The life table for *Pleurobrachia bachei* during 1 May–18 June 1970 based on laboratory growth and reproduction data at 15°C and calculated mean rates of mortality for this period. The symbols dx, l_x, b_x and x represent the age interval in days, survival to the beginning of the age interval, the numbers of live births during the age interval, and the pivotal age, respectively.

dx	l_x	b_x	$l_x b_x$	$l_x b_x x$
0-1	1.0000			
1-3	.9400			
3-5	.6691			
5-7	.4762			
7-9	.3390			
9-11	.2413			
11-13	.1717			
13-15	.1222			
15-17	.0870			
17-19	.0619			
19-21	.0441			
21-23	.0423			
23-25	.0405	1	0.0405	0.9720
25-27	.0388	0		
27-29	.0372	0		
29-31	.0357	1	.0357	1.0710
31-33	.0342	0		
33-35	.0328	0		
35-37	.0315	0		
37-39	.0302	0		
39-41	.0290	0		
41-43	.0277	6	.1662	6.9804
43-45	.0266	15	.3990	17.5560
45-47	.0256	3	.0768	3.5328
47-49	.0189	13	.2457	11.7936
49-51	.0140	4	.0560	2.8000
51-53	.0103	2	.0206	1.0712
53-55	.0077	53	.4081	22.0374
55-57	.00152	102	.1550	8.6800
57-59	.00071	8	.0057	.3306
59-61	.000336	53	.0178	1.0680
61-63	.000158	353	.0558	3.4596
63-65	.000074	325	.0240	1.5360
65-67	.000044	302	.0133	.8778
67-69	.000026	204	.0053	.3604
69-71	.000015	557	.0084	.5880
71-73	.000009	298	.0027	.1944
73-75	.000006	960	.0058	.4292
75-77	.000003	1026	.0031	.2356
77-79	.000002	1319	.0026	.2028
		R_0 =	1.7481	85.7768

mean age distribution in field samples was 66.7% eggs, 20.0% larvae, 8.7% 1- to 2-mm postlarvae, and 4.7% all other stages. The field age distribution is unlike the stable age distribution in that the proportions of eggs and larvae are reversed and the proportion of late stages is sevenfold higher than in the stable age distribution. The population growth rates (r) in other time periods predict decreases of population abundance from 8 March to 2 April ($r = -0.105$) and increases in 14 July to 21 August ($r = 0.020$) and in October ($r = 0.0115$). Eggs and larger ctenophores were again more frequent, and larvae less frequent in the field during July–August than calculated for the stable age distribution.

For postlarvae the mean rate of net production per day for all stations located 1.6 km from the shore (Table 13) followed the seasonal variation in the standing stocks. The maximum rate of net production on 13 August, 212 mg organic matter m^{-2} day^{-1}, was about 20% of the standing crop. About two-thirds of ANP occurred during August. The variance of the mean ANP is quite large, but since the confidence limits for the mean are determined by standard deviations, the 95% confidence interval for the mean ANP is 4,200–6,280 mg organic matter m^{-2} yr^{-1}.

Mean ANP of postlarvae at stations 1, 3, and 5 (1.6 km from shore) and at station 6 (10 km from shore) are given in Table 14. Note that "annual" net production at the stations 1, 3, and 5 are for 0.956 yr and at station 6 for 0.84 yr; these values were not corrected to a full year by proportion, because statistical tests based on variances would not be valid. Tests for differences of variances (F-ratio) and means (t-tests) between stations 1, 3, and 5 were made. The variance of station 3 was significantly different from that of stations 1 and 5 ($P<0.01$), but the variances of stations 1 and 5 were not different from each other ($P>0.05$).

The difference between means of all pairs of contrasts for stations 1, 3, and 5 are significant ($P<<0.01$). The net production at station 6 located 10 km from shore off Scripps Institution was about

TABLE 12.—Summary of population parameters for *P. bachei* during four time periods in 1970. The symbols R_0, r, T, B, b, d and C_x refer to net reproduction, instantaneous rate of population growth, generation time, finite birth rate, instantaneous birth rate, instantaneous death rate and stable age distribution respectively. The percentages of eggs (E), larvae (L), 1-2 mm, and ≥ 3 mm stages are given in that order for the stable age distribution.

Time period	R_0	r	T	B	b	d	C_x
8 Mar.-2 Apr.	0.0058	-0.105	49.0	0.2485	0.2617	0.3667	—
1 May-18 June	1.7481	0.0115	48.6	0.2348	0.2328	0.2213	23.3 *E* 69.0 *L* 7.0 1-2 mm 0.7 ≥ 3 mm
14 July-21 Aug.	2.9271	0.020	53.7	0.248	0.248	0.228	24.6 *E* 69.3 *L* 5.6 1-2 mm 0.5 ≥ 3 mm
8-22 Oct.	1.7565	0.0115	49.0	0.2348	0.2328	0.2213	Same as 1 May–18 June

TABLE 13.—Seasonal variation of the mean rate of net production per day ($\overline{NP}t_n$ is in mg organic matter m^{-2} day^{-1}) for postlarval *Pleurobrachia bachei* at stations located 1.6 km from shore in La Jolla Bight. The mean annual net production is given as the sum of the mean rate per day multiplied by the appropriate time interval, $\triangle t$; the variance of the mean annual net production is also given. Note that the sum is for 0.956 yr.

Sampling date	Number of samples	$\overline{NP}t_n$	$\overline{NP}t_n(\triangle t)$	Var $(\overline{NP}t_n)\triangle t^2$
18 June 1970	10	5.188	36.316	270.5065
2 July	10	5.356	69.628	216.5228
14 July	10	9.080	131.660	639.0759
31 July	10	38.396	575.940	35,286.5025
13 Aug.	10	212.287	2,229.014	102,152.1706
21 Aug.	8	70.454	563.632	11,169.1520
29 Aug.	10	22.712	295.256	2,370.3264
16 Sept.	6	21.416	428.320	2,824.7200
8 Oct.	6	10.843	195.174	7,217.9748
22 Oct.	6	41.882	586.348	91,135.2960
5 Nov.	6	1.775	23.962	141.4260
18 Nov.	6	0.350	4.725	7.4322
2 Dec.	10	0.114	1.596	0.7291
16 Dec.	10	0.0003	0.006	0.0003
11 Jan. 1971	6	0.321	6.741	14.4207
27 Jan.	6	0.962	13.468	87.1612
8 Feb.	8	1.745	25.302	102.6440
25 Feb.	6	0.240	3.840	4.9306
12 Mar.	6	1.148	24.108	221.5584
7 Apr.	6	1.018	20.360	48.4800
20 Apr.	6	0.202	2.727	2.8978
4 May	6	0.061	0.854	0.1764
18 May	6	0.044	0.638	0.1051
2 June	6	0.002	0.015	0.0004
SUM			5,239.63	253,914.2097

sevenfold lower than that at station 5 (1.6 km off Scripps Institution) and fivefold lower than the mean for all stations located 1.6 km from shore. For these comparisons, the production at station 6 was extrapolated to 0.956 yr. The net production of larvae and eggs at station 5 contributed only about 3% of the sum of net production of eggs, larvae, and postlarvae at that station.

For stations 1, 3, and 5 the annual mean ratio of the net production per day of postlarvae to their mean daily standing stock ($\bar{B}_i$ of Equation (2)) are 0.197, 0.196, and 0.211, respectively. The mean ratios are based on 32, 43, and 54 observations for stations 1, 3, and 5, respectively. There are no significant differences between the variances (F-ratio tests) of all paired contrasts of stations ($P>0.05$). There are no significant differences between all paired contrasts of station means ($P>0.50$). The overall annual mean ratio at these three stations is 0.202, with 95% confidence limits for the mean being 0.187–0.217. Thus, the ratio of production to biomass on the day of maximal production was no greater than the annual mean.

In order to estimate the food chain efficiency (defined for any trophic level L as the steady state ratio of yield to predators at level $L+1$ to the net production of trophic level $L-1$) of the transformation of materials or energy by trophic levels, the two parameters stated above must be known: 1) the net production of potential food at level $L-1$ and 2) the yield to predators from the level L, which in steady state is the total net production of level L minus losses to decomposers. This concept can be extended to include more than three trophic levels, e.g., the square root of the ratio of ingestion by secondary carnivores to net primary production might be termed the equal transfer efficiency of herbivores and primary carnivores.

In practice it is very difficult to accurately "measure" the secondary production of the entire herbivore trophic level in the sea, and such data are not available in my study area. Further, the estimates of net production by *P. bachei* could not be partitioned into the fractional losses to decomposers and as yield to predators. Therefore, two simplifying assumptions were made in calculating the transfer efficiency for the macrozooplankton of La Jolla Bight: 1) all of the net production by *P. bachei* resulted in yield to predators and none to decomposers and 2) the efficiency was constant and equal from the primary producer level through the first-order carnivore level of *P. bachei*. Given these limiting assumptions, the efficiency calculated is referred to as the "equal transfer efficiency." Thus, if net production data were not available for trophic levels between primary producers and the trophic level of in-

TABLE 14.—Summary of "annual" net production (ANP) values (in mg organic matter m^{-2} $time^{-1}$) of *Pleurobrachia bachei*, at four stations in La Jolla Bight. The value at station 6 is for 0.84 yr; all other values are for 0.956 yr. The standard deviation of ANP for each respective value is also given. Values are for postlarvae unless otherwise specified. The mean production for larvae and eggs at stations 1-5 were calculated assuming that the same fraction of production would be as larvae and eggs at all stations as at station 5.

Station	Number of sample dates	ANP	SD
1	24	2.320	104
3	24	4.320	377
5	25	7.650	125
		144 Larvae	18
		111 Eggs	6
6	17	950	85
Mean of station 1-5	24	5.240	504
Mean of station 1-5 plus eggs and larvae	24	5.240	
		99 Larvae	
		76 Eggs	
		5.415	504

terest, a general equation to calculate equal transfer efficiency for n transfers is

$$ETE = (NPL/NPP)^{1/n} \quad (5)$$

In the equation ETE is the equal transfer efficiency, NPL is the net production of trophic level L (which is equal to ingestion by level $L+1$), NPP is the net primary production, and n is the number of transfers from primary producers (the zeroth trophic level) through trophic level L. This equation was derived from the works of Schaefer (1965) and Ryther (1969). The equal transfer efficiency calculated in this manner for $n>2$ says nothing about the efficiency of a given trophic level, but only the equal efficiency of all trophic levels from primary producers through trophic level L.

The equal transfer efficiency from primary producers through *P. bachei* was calculated using estimates of annual net primary production in the coastal waters of southern California, ANP of *P. bachei*, and the weighted mean number of transfers from primary producers through *P. bachei*. The mean number of transfers was calculated from the percentage contribution from each of 21 prey categories to the total numbers of prey (these 21 categories are 98% of the total numbers of prey in the stomachs of *P. bachei* over a year) and best guesses as to the number of transfers from primary producers to each of the 21 prey species. The mean and range of ANP by all stages of *P. bachei* extrapolated to 365 days (5,700 and 8,300–2,500 mg organic matter) were converted from units of organic matter into organic carbon by taking 50% of the organic matter as organic carbon. The mean and range of annual net primary production (400 and 600–200 g C m^{-2} yr^{-1}) were estimated from the mean and range of the rates per day in southern California coastal waters (Eppley, Reid, and Strickland, 1970; W. Thomas, pers. commun.) and multiplication by 365. The expectation of the number of transfers from primary producers through *P. bachei* is 2.3 with an upper limit of the estimate equal to 2.5. These fractions occur because species of animals often do not fall into a single trophic level, and this is in fact the case with *P. bachei*; some of its prey organisms are herbivorous and some are themselves carnivorous. The equal transfer efficiency was calculated and presented in a matrix for the means and ranges of the three variables stated above (Table 15). Note that the range of equal efficiency is found on the diagonal from the lower left to the upper right of the table. The overall central value is an equal efficiency of 11%. This efficiency of transfer involves phytoplankton, herbivores, and those primary carnivores on which *P. bachei* feeds, *P. bachei*, and the predators and parasites of *P. bachei*. This efficiency equals the nth root of the ratio of ingestion by predators of *P. bachei* to net primary production.

TABLE 15.—Calculations of the equal transfer efficiency in percent for different numbers of transfers from primary producers through *Pleurobrachia*, given the observed range and mean of annual net production of *P. bachei* and the estimated range and mean of annual net primary production in g C m^{-2} yr^{-1}. In each group of three values, the first is for the highest value of ctenophore net production (4.1 g C m^{-2} yr^{-1}), the second is for the mean (2.8 g C m^{-2} yr^{-1}) and the third is for the lowest value (1.2 g C m^{-2} yr^{-1}).

Net primary production	Number of transfers		
	2.0	2.25	2.5
200	14.3	17.8	21.1
	11.8	15.0	18.1
	7.7	10.3	12.9
400	10.1	13.0	16.0
	8.4	11.0	13.7
	5.5	7.6	9.8
600	8.3	10.9	13.6
	6.8	9.2	11.7
	4.5	6.3	8.3

DISCUSSION

Life table parameters of *P. bachei* show adaptive value in the interdependence of the schedule of births and the rates of development and mortality on population growth. Early reproduction makes a very important contribution to net reproduction and population growth rate, but only in relation to the rates of development and mortality. The larvae have relatively high rates of mortality and lower rates of growth compared to other stages. The 1- to 2-mm postlarvae have the lowest rate of mortality and grow slowly, but they are able to reproduce at an early age and thereby contribute an important fraction of net reproduction. The 3- to 7-mm stages have very rapid tissue growth (instantaneous rates of 0.21–0.47) but do not contribute many young to the population. Instead, these larger stages are important to net production of organic matter because of their rapid growth and high abundance in summer. The stages larger than 8 mm are able to produce enormous numbers of young, but few survive to

this size in nature. Regulation of population growth rate would be very sensitive to changes in mortality rates during production of the first 50–100 young and again during the production of the several hundred young by later stages.

The seasonal occurrence of *H. mediterranea* and the frequency distribution of single and multiple infections and of the percentage of cases for different stages of hosts show two kinds of patterns that are related to life history episodes: 1) the parasites do not often attack the 1– to 2–mm stage postlarvae which are important to net reproduction as discussed above and 2) the parasites occur mainly as one or two individuals per host and most frequently in 6– to 8–mm postlarvae. The early stages of parasites infect the larger hosts more frequently than the smaller hosts because of seasonal availability and perhaps also because of the ability of the larger hosts to better accommodate the extra metabolic burden. The "strategy" of the parasites appears to be infection of larger hosts with few young to provide sufficient food and shelter during their development, but not overexploit each host with too many parasites. The larger stages of hosts are buffered against local extinction by adult parasites, because suitable hosts become more difficult to locate the faster they die. The total ctenophore population has some protection from overexploitation of postlarvae by parasites and other predators in the presence of relatively large numbers of eggs and larvae and the ability of young postlarvae to reproduce soon after development to 1–mm size.

The calculated population growth rates of *P. bachei* indicate that the minimum time for a population doubling is about 35 days (0.693/0.02). This suggests that rapid increases of *Pleurobrachia* observed on a time scale less than a month are probably due to gross advective change if reference of a "bloom" is made to total abundance of all stages. However, the growth in bodily size of *Pleurobrachia* from 2 mm to 6–7 mm diameter may occur in about 2 wk, and this may account for the visual impression of a bloom. Regarding individual and potential population growth rates the salp *Thalia democratica* as another macrozooplankter, is much faster than *P. bachei* (Heron, 1972a, b).

The statistical treatment of variances for mean net production per day describes precision of the estimates, which probably is not the same as inaccuracy in the estimates. For example, it is questionable whether growth rates in the laboratory under constant temperature, food concentration, and food type are accurate estimates of the rates in nature. Variation during a day in ambient conditions appear to be at least as important or more important than the average condition (e.g., temperature). The rates of tissue growth and mortality both depend on the duration of development within a stage, and they are not fully independent variables although they are treated as such in Equation (2). Another error ignored in the statistical treatment is the variance of the standing stock calculated for each replicate sample. I assumed in the calculation of the net production per day for each replicate sample at one station that the variance for the best estimate of the crop is negligible compared to the deviations between the best estimates from the regression equations for each sample. The net production per day for each replicate sample is based on the mean rates of growth and mortality and the best single estimate of the standing crop.

The variance for the mean value of the ANP depends on the variance of the mean net production per day and the square of the time interval over which the rate is linearly applied (Equation (4)). Assuming that the data on net production per day would have a Poisson distribution (variance equals the mean), reasonably small 95% confidence limits for the annual net production (ANP$\pm$ANP/10) are obtained with replicate samples if each of ten sampling dates is spaced evenly during the year. The limits are relatively insensitive to whether the seasonal distribution of production is rectangular and continuous, rectangular and discontinuous, or triangular and discontinuous. The important considerations to minimize the confidence limits for the mean annual production are: 1) the number of observations per sampling date, 2) the number of sampling dates, and 3) the time interval between sampling dates in relation to the seasonal maximum abundance and rate of production. The number of observations per sampling date is determined by the number of replicate samples and the number of stations. More stations and replicate samples improve the accuracy in estimating the mean and should decrease the variance of the overall mean for a given sampling date. The number of sampling dates minus one is the number of degrees of freedom for the t–statistic which is multiplied by the standard deviation of the mean to give one tail of the confidence limit. The time interval between sampling dates will affect the variance for the net

production over a given period as the square of the interval; therefore, sampling should be carried out on a regular basis without long intervals between dates unless previous information is available on the seasonal distribution of production and the relationship between means and variances.

Three parameters can influence the magnitude of net production by *P. bachei* in addition to errors in the estimation of abundance: 1) water temperature, 2) food supply, and 3) parasitism. In the first two cases, it would appear that for the observed range of temperature and food supply in the study area temperature is more important than food supply. A 10°C range of surface temperature over the year or the temperature change experienced during a postulated 20-m vertical migration in August (see Figure 8) should affect the rate of growth in length and weight and survival. Data are not sufficiently good for quantitative statements about the effect of vertical migration during August on rates of tissue growth, net production, and population growth. The case for the effect of food supply on rates of net production is somewhat better than for temperature. Rates of growth in the laboratory at 15°C are essentially the same for ctenophores cultured on *Acartia* at 35 μg C/liter and 500 μg C/liter. The rates of growth in length and weight at 14.5°C and 1-2 μg C/liter of mixed natural food organisms indicated that the postlarvae grow about as well as at tenfold higher food concentrations. From field samples in which the calculated food concentration was about 10 μg C/liter growth rates in the laboratory and from the field size frequency distributions agree within ±20% of the mean rate. It appears therefore that *P. bachei* postlarvae are very efficient at the extraction of prey from the water at very low concentrations. The estimates of gross growth efficiency showed that over one-half of the food ingested was incorporated into somatic tissues. Perhaps the "passive" feeding mode of these carnivores allows them to have a very low threshold for the commencement of feeding activity, especially since the area of the tentacles is very large in relation to the bodily size of the ctenophore, and relatively low metabolic expenditure is generated while waiting for prey to contact the tentacles.

The estimates of ANP by *P. bachei* are also inaccurate, because no corrections were made for effects of parasitism by *Hyperoche* on rates of tissue growth and duration of development. Since the occurrence of parasitism and high rates of production both were in August (two-thirds of the ANP was in August), correction may not be trivial. It is not possible to make a quantitative estimate of the error based on any data, but the following sources of error must be considered: 1) the standing stock, B_i, was overestimated by the amount of ctenophore tissue in the volume that the parasites occupy; 2) the instantaneous rate of tissue growth, G_i, was overestimated by the difference between the instantaneous growth rates of nonparasitized and parasitized ctenophores; 3) the instantaneous rate of mortality, M_i, was overestimated by the difference between the durations of development of nonparasitized and parasitized ctenophores (see Equations 1 and 4) the total loss of ctenophore tissue (due to mortality of all types and to ingestion of tissue by parasites that does not result in mortality) in one time increment was underestimated by that fractional amount of tissue removed from the mean standing crop during the time increment by parasitism. Overestimation of the standing stock of ctenophores due to presence of parasites is believed to be negligible, especially since only one or two parasites were present in 92% of all cases (Table 4). For given values of standing stock and rates of growth and mortality (e.g., B_i = 100 mg/m^2, G_i = 0.2, and M_i = 0.5), the effect of additional tissue loss due to parasitism on the rate of net production is relatively small (ca. 10%) for instantaneous rates of parasitism up to 50% of the rate of mortality. The mean net production per time interval was overestimated. The actual extent of the overestimate can not be evaluated without more information on the effect of parasitism on ctenophore growth.

The ratio of net production per day to mean standing crop during the day for all postlarvae is the biomass-weighted mean instantaneous rate of tissue growth (Allen, 1971), assuming that growth and mortality rates are exponential. The similarity of mean values between stations 1, 3, and 5 is due partly to the bias of having used only the growth rates at 15°C throughout the year, but the range between stages of the mean exponential growth rate is at least tenfold. Some of the consistency in ratios of production to mean standing stock is due to similarity in the length frequency distributions between stations and relative contribution of different stages to the total crop. The overall annual mean production to standing stock value of 0.202 indicates that net production per day is 20% of the mean daily standing stock. This value is within the range of values summarized by Mullin (1969), but is quite high considering the

relatively large size of postlarvae (e.g., over 10 mg organic weight).

The 11% overall mean in the equal transfer efficiency is surprisingly close to the values of ecological efficiency measured in the laboratory (Silliman, 1968; Slobodkin, 1968); food chain efficiency is the same as ecological efficiency if all food available to a consumer level is ingested (the range for ecological efficiency is generally accepted to be 5–20%). The stability and convergence characteristics of these efficiencies must be set by two boundary conditions: 1) the minimum net production and food required to just replace the component species within a trophic level and 2) the age-structure weighted maximum gross growth efficiency of the component species within a trophic level. The upper limit is set by the physiological maximum gross growth efficiency of each developmental stage weighted over all stages and species in proportion to their relative abundance. In this regard the adults of *P. bachei* are very efficient (60%) at converting food ingested into somatic tissues, and this is probably near the upper limit of gross growth efficiency. Low ecological efficiency is found in species populations dominated by older, slowly growing individuals with low growth efficiency and low rates of mortality (Mann, 1965). In nature it would seem unlikely that food chain efficiency through several successive trophic levels could vary widely. For example, a low efficiency through producers to herbivores means that less net herbivore production would be available to first-order carnivores, all else being equal. Under these circumstances the efficiency through herbivores to first-order carnivores should also be low, because the carnivores must search a larger volume or area to feed and this decreases growth efficiency. Conversely, a high efficiency through producers to herbivores should perpetuate a high efficiency through herbivores to carnivores, unless the age or size distributions of herbivores which yields high net production from producers is not conducive to maximize the efficiency through herbivores to first-order carnivores (i.e., the herbivores are predominantly younger stages which are not available to those stages of carnivores which possess the highest growth efficiency).

There is some evidence from lakes and from theoretical considerations of growth patterns that food chain efficiency is at least in some cases determined by growth efficiency of component species in a food chain and their metabolic flexibility in response to size and abundance of prey (Kerr and Martin, 1970; Kerr, 1971). In complex marine systems considerable effort must be expended before the predator–prey interactions are described and the metabolic rates and efficiencies are measured. Meanwhile, an explanation based on sound theoretical grounds is needed to show why the food chain and ecological efficiencies tend to converge on 10% and have a relatively small range from about 5 to 20%.

SIGNIFICANCE OF *P. BACHEI* IN THE PLANKTON

The coastal waters of southern California represent an ecotone which includes the boundary of land and sea. It is influenced strongly by physical processes and the biota in the water from several sources. The relatively shallow depths within the first 2–3 km from shore emphasize the interdependence and coupling of the benthic and planktonic communities. The benthic community depends on the planktonic community for some of its food supply and for removal of the least fit individuals of those meroplanktonic larvae released by benthic animals. The plankton community receives some of its food in the form of meroplanktonic larvae, and the benthic community returns the materials removed from the water in the form of regenerated nutrients, detritus, and decomposing tissues. It is not surprising, therefore, that *Euterpina* and *Oithona* are the prey of young stages of newly settled juvenile garibaldi, *Hypsypops rubicunda* (Clarke, 1970) and also of *P. bachei*.

The pattern of high standing stocks of different trophic levels and intense biological activity within the first 5–10 km from shore is probably associated with the high regeneration rates of nutrients and high productivity in shallow water (Anderson and Banse, 1961) and life history adaptations of coastal water species to exploit highly productive zones. The short generation times of microcopepods, parthenogenesis in cladocerans and spined eggs of *Acartia* are some adaptations to enable rapid exploitation of favorable conditions in the plankton. The coastal waters may be compared to a chemostat. The rates of dilution by physical forces vary in time and space, but the specific growth rates of the organisms plus their refugial seed stocks and immigrants enable them to persist over time. The quasi-continuous change

in the physical–chemical habitat of the coastal waters prevents the formation of a stable, time–independent assemblage of organisms, although the system appears to be basically composed of the same recurrent species in seasonally varying proportions. Occasionally expatriates from oceanic, southern waters, and northern waters appear (e.g., *Candacia*, *Eucalanus attenuatus*, *Tortanus discaudatus*, *Velella*, etc.). The transients are joined by some organisms which appear seasonally in this area during spawning migrations (e.g., gray whale, squid, grunion).

The regulation of population size in *Pleurobrachia* is postulated to be through density–dependent feedback meahanisms proposed by Greve (1972), in which the prey of larger ctenophores (e.g., adult stages of copepods) are detrimental to survival of the small ctenophore larvae. Balance in the abundance of predators and prey is conferred by selection of larger copepods by the larger ctenophores (Bishop, 1968), but with dependence of ctenophore larvae on copepod nauplii for food supply and low abundance of adult copepods for their survival. A high density of copepod nauplii and low density of copepod adults would favor occurrence of ctenophore larvae and early postlarvae. As both prey and predators grow the roles of predator and prey become reversed to some extent. The large ctenophores may nearly deplete the water of large copepods to satiate their metabolic demands, but this condition is unstable, because the larger ctenophores will become food limited. The population size will not increase greatly because few adult copepods are available to produce eggs, and the nauplii which are hatched from eggs are needed for food of larval ctenophores. If the abundance of postlarvae should increase and some threshold is exceeded, the ctenophore population also becomes vulnerable to density–dependent predation by *Beroë* and other predators and infection by parasites.

All organisms in nature consume food, recycle materials through excretion (and exuviation), and are themselves consumed. In this regard the functional role or ecological significance of a species population is closely related to its relative abundance and rates of turnover. *Pleurobrachia bachei* is a dominant carnivorous zooplankter during summer and fall in the coastal waters off San Diego. Its functional role can be divided into three parts: 1) a predator which regulates the abundance of small crustaceans (copepods and cladocerans) and removes least fit individuals, 2) a vehicle which provides shelter and nutrition for parasites such as *Hyperoche*, and 3) an organism which transfers and transforms material and potential energy in the planktonic food web. As a predator, the role of selective removal of prey is an important factor for both the evolution of size, shape, behavior, etc. in the coastal water species and for regulating the abundance and species composition of prey. *Pleurobrachia bachei* is not unique as a planktonic form in providing shelter and nutrition for co–occuring species; salps are exploited in a similar manner by copepods, except that details of the life histories differ (Heron, 1969). As a seasonally dominant carnivore, *P. bachei* is also undoubtedly an important species which transfers organic matter and potential energy to higher trophic levels in the food web of La Jolla Bight.

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SOME ASPECTS OF THE ECOLOGY OF STOMIATOID FISHES IN THE PACIFIC OCEAN NEAR HAWAII

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ABSTRACT

Forty-seven species of eight families of stomiatoid fishes were collected in the upper 1,000 m near Hawaii. Most species appear to undertake diurnal vertical migrations; only two definitely did not. Many of the abundant species showed changes in size composition within both day and night depth ranges, the smaller fish occurring shallower. All sizes of several other species appeared to occur throughout their depth ranges. Seasonal changes in the size composition of several species indicated that they spawn principally in the summer. Several species appear to avoid the Isaacs-Kidd trawl better during the day than at night. Some species appeared to avoid the Isaacs-Kidd more than a larger trawl, but many were sampled as well or better by the former. Absence or rarity of mature individuals of several species indicated that the larger fish avoided both trawls.

Relationships between vertical distribution and morphology of some species are proposed, and potential interactions between species are considered relative to the degree of similarity of depth ranges or size-depth patterns.

Stomiatoids are a dominant and diverse group of mesopelagic fishes. Most previous work on the group has been of a systematic or zoogeographic nature, and only recently have the systematics of some families come into order. With the exception of a few works such as Kawaguchi and Marumo (1967) and Krueger and Bond (1972), ecologically pertinent information such as depth ranges, migration habits, etc., has been appended to other studies and is usually based on so few specimens or inappropriate sampling programs that it is of dubious value. Consequently, even for the frequently collected species, little is known of their ecology—especially in comparison to knowledge of the myctophids, another important group of mesopelagic fishes.

This paper considers data on 47 species of stomiatoids collected by a mid-water trawling survey in the central North Pacific near the Hawaiian Islands. (Specimens of the Sternoptychidae and the gonostomatid genus *Cyclothone* are being investigated by other workers, and the systematics of three genera of the Melanostomiatidae are so confused at present that these genera cannot be considered in detail here.) For many species, sufficient numbers were collected to present reliable estimates of depth ranges, migrations, and seasonal changes in size composition. The habits of this diverse group are compared with those of other mesopelagic fishes.

METHODS

All specimens considered here were collected near the island of Oahu, Hawaii (lat. 22°20-30′N, long. 158°20-30′W). Details of the sampling program are given in Clarke (1973), and will be only summarized here. Four series of samples were collected with a 10 foot Isaacs-Kidd mid-water trawl (IK). These were taken at approximately quarterly intervals (September 1970, December 1970, March 1971, and June 1971) and attempted to cover the upper 1,000 m of the water column both day and night for each season. Useful information was also derived from a series of samples collected with a 6-foot IK in the upper 400 m at night and between 400 and 1,000 m during the day in June 1970, from a series of samples with a 10-foot IK in the upper 190 m at night during periods of new and full moon in September-October 1971, and from preliminary samples taken in September-November 1969. Also included are data from a series of tows made by the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service (NMFS), NOAA in conjunction with the March 1971 IK series; these sampled the

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upper 200 m at night with a modified Cobb pelagic trawl (CT) described by Higgins (1970). I have also examined specimens of some species taken near Hawaii by R. E. Young with a modified Tucker trawl equipped with an opening-closing device.

The IK and CT were fished without opening-closing devices. Winch and ship speed were adjusted to minimize forward motion of the trawl during descent and ascent. Time-depth recorders were attached to the trawls. A few oblique tows were made, but mostly the trawls were towed for 2-3 h at the same depth. Actually, the trawls often sank or rose gradually during the "horizontal" part of the tow, but the range fished was small relative to spacing of different tows. A single, most frequently fished depth was assigned to each tow. The IK was towed at about 1.75 m/s and the CT at about 1.5 m/s. All "night" samples were taken between 2000 and 0500 h, "day" samples between 0800 and 1700 h.

Specimens were identified principally from data given by Grey (1964), Morrow (1964a, b, c), Morrow and Gibbs (1964), Gibbs (1964), Barnett and Gibbs (1968), Goodyear and Gibbs (1969), and Novikova (1967).[2] Standard length of all specimens was measured to the nearest millimeter. With a few exceptions, gonads of only larger specimens were examined to determine size at maturity and any seasonal changes in gonad development in mature females. Size at maturity was taken as that of the smallest female which carried obviously ripened ova. For each species considered, the total number of specimens examined and the length range in millimeters are given in parentheses after the species name.

The lower limits of depth ranges of the species are, of course, open to some question since the trawls were fished without opening–closing devices. The reliability of estimated depth ranges for the more abundant species (50-100 specimens) is probably fairly high. Catches from tows within the depth range were obviously greater than those of deeper tows which passed through the depth range. The latter were comparable with catches of short oblique tows taken during the program and were considered to be contaminants, i.e., caught during ascent or descent, unless data from the opening-closing Tucker trawl indicated otherwise. Any catches below the "normal" depth range that were unexpectedly high or different in size composition, etc., are discussed under the species headings.

Many species considered here were, however, so rarely taken that there is considerable doubt about estimates of depth ranges and vertical migration. The chances of being taken in a tow within the actual range were not much greater than those of being taken during descent or ascent of a deeper tow. Catches with the opening-closing Tucker trawl were helpful in only a few cases since the species where greatest doubt exists were rare to begin with and many were not captured at all or as frequently by the Tucker trawl.

For species which were collected in sufficient numbers (ca. 10/tow or more) in more than one tow during a series, changes in size composition with depth were assessed by comparing the size-frequency curves of individual samples from different depths using the Kolmogorov-Smirnov test (Tate and Clelland, 1957). Size composition was considered significantly different if the probability associated with the difference between curves was 0.05 or less. For rarer species, plots of size vs. depth were made using pooled data for all specimens. Trends in size composition with depth were noted, but no statistical significance can be attached to these.

Only one species, *Vinciguerria nimbaria*, was caught consistently in high enough numbers to permit a quantitative consideration of abundance and size composition throughout the water column (cf. treatment of data on the more abundant myctophids in Clarke, 1973). Thus considerations of day-night or seasonal differences in abundance in the remaining species are subject to some doubt. For these, the data from each series were simply pooled without any attempt to weight the catch of each tow for the relative thickness of the depth stratum it represented. Nevertheless, comparisons between seasonal series are merited since the total trawling times and depth coverages for each of the series were reasonably similar. In comparing data from different seasons, I have assumed that changes were not a result of horizontal advection or migration.

RESULTS

Gonostomatidae

Diplophos taenia (169; 35-153 mm)

The day depth range of *D. taenia* was 450-610 m and the night range 15-100 m. The smaller fish

[2]Specimens of all species considered here will be deposited at the U.S. National Museum.

tended to occur shallower during both periods. During the day those over 70 mm long were mostly below 525 m and those over 120 mm were below 575 m. At night none over 90 mm were caught shallower than 50 m and none over 120 mm were above 75 m.

Smaller *D. taenia* (< 70 mm) were more frequently taken in June, July and September, and larger fish appeared most abundant in March. This suggests that spawning is seasonal, but the season cannot be estimated since the age of 35–to 70-mm individuals is not known. Size at maturity was about 140 mm. It was not possible to determine the spawning season from gonad state of females since very few mature females were taken. The data from the March 1971 series indicated that individuals 100-140 mm long avoided the IK better than the CT, but that neither trawl sampled larger individuals adequately.

Vinciguerria nimbaria (2,927; 8-49 mm)

For most series, the data indicated that *V. nimbaria* occurred at 400-560 m during the day and migrated to 20-125 m at night. In December 1970, two night tows in the day depth range caught substantial numbers of *V. nimbaria*—more than expected on the basis of short oblique tows and other night tows below 150 m. The size composition of these catches was within the range of that of the shallow night catches and close to those of day catches at similar depths. The number of mature fish in the deep night catches was low, but there was no obvious difference in sex ratio or gonad state between these and those of other tows. Thus it appears that a fraction, roughly 60%, of the population did not migrate in December.

The larvae of *Vinciguerria* are restricted to the surface layers and do not apparently undertake substantial migrations until metamorphosis (Ahlstrom and Counts, 1958). Those collected during this study (8-14 mm) were taken mostly at 15-50 m at night. (No day tows were taken above 250 m.)

Consistent and frequently significant differences in size-frequency curves indicated that smaller *V. nimbaria* occurred shallower in the water column both day and night (Figure 1). Few fish over 25 mm were captured shallower than 75 m at night and few less than 20 mm were captured below this depth. In the day, the small fish occurred mostly above 500 m and the large individuals were taken almost exclusively below 500 m.

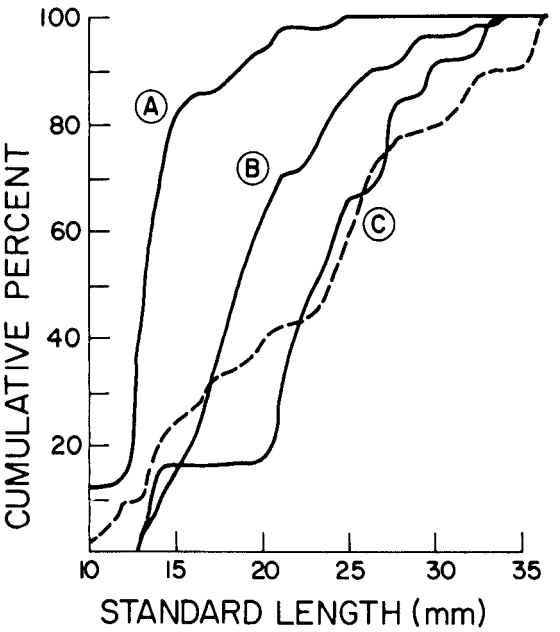

FIGURE 1.—Cumulative size-frequency curves for *Vinciguerria nimbaria* taken at 60 m (A, 35 individuals), 80 m (B, 96), 100 m (C dashed line, 44), and 125 m (C, solid line, 12) at night in September 1971. All pairs were significantly different ($P<0.05$) from each other except 100 m vs. 125 m.

The full-new moon series of night tows in the upper layers during September-October 1971, indicated substantial differences in depth distribution related to phase of the moon (Figure 2A), but the picture was complicated by the presence of many more larvae and recently transformed juveniles during the October (full moon) series. Calculated (see Clarke, 1973) total numbers in the

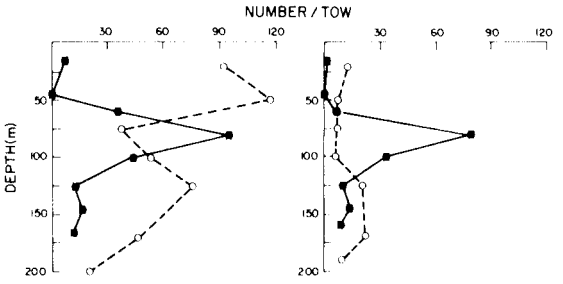

FIGURE 2.—Catches of *Vinciguerria nimbaria* per tow (1½ h each) at several depths at night at new moon (solid circles and lines) and full moon (open circles, dashed lines) during September-October 1971. Left: total catches including larvae and recently transformed juveniles. Right: catches of fish larger than 15 mm.

water column for each series were similar, but the calculated size compositions indicated that during full moon 90% of the population were larvae or recently transformed juveniles as opposed to only 50% in the new moon series. Since the tows were taken during the season of highest recruitment to the trawlable population (see below), the difference possibly was due to recruitment during the intervening 2 wk.

When only the individuals over 15 mm were considered (Figure 2B), it appeared that most of the larger fish occurred about 50-75 m deeper at full moon. The calculated total number for the new moon series was about twice that for the full moon series, and the calculated size-frequency curves were similar. In addition to moving deeper, *V. nimbaria* also appeared to avoid the net better during full moon.

Vinciguerria nimbaria was by far the most abundant of the fishes considered here. Among all the species which occurred in the upper layers at night, *V. nimbaria* ranked eighth after seven species of myctophids, but because of its small size, contributed little to the total estimated biomass (Clarke, 1973). Calculated total numbers in September and December were about twice those for March and June (about 30-35/10^3m^2 vs. 15-18/10^3m^2). The calculated biomass was about 7-8 g/10^3m^2 at all seasons.

Vinciguerria nimbaria appears to spawn principally in the summer and fall and reach maturity (27 mm) within 1 yr. The calculated size compositions indicated that about 75% of the population in June were less than 15 mm, while in March, 75% of the fish were over 20 mm and about 40% were mature. The September and December series had substantial percentages of small fish, but about 50% were 15-25 mm. Among the mature females examined, the proportion bearing ripened ova was higher in June and September (15/16 and 7/9, respectively) than in December and March (5/10 and 4/11).

Vinciguerria poweriae (365; 9-35 mm)

Only 35 *V. poweriae* were caught during the day by IK tows. These were mostly 25- to 30-mm fish caught around 500 m. A daytime CT tow at 300 m caught seven individuals (15-29 mm), suggesting that this species occurs rather shallow in the water column during the day and avoids the net due to higher light intensities. At night, *V. poweriae* occurred at 100-200 m. Few larger than 20 mm were caught above 150 m and practically none under 15 mm were taken below 150 m.

Seasonal changes in size composition indicated that *V. poweriae* spawns in the spring and summer. All caught in March were over 15 mm and over 50% were larger than the size at maturity (27 mm). Ten of 11 mature females from the March series carried ripe ova. In June, few of any size were caught, but these included both juveniles (< 15 mm) and mature fish. Three of the four mature females caught in June were ripe. In July and September, the bulk of the fish were 9-20 mm and very few mature. The few caught in December were all over 15 mm. Of the five mature females taken in September and December, only one was ripe.

Ichthyococcus ovatus (45; 12-55 mm)

All but nine *I. ovatus* were taken during the day between 400 and 500 m. The night catches consisted of two small fish (15 mm) taken near the day depth, two larger ones taken at 350 m, and five others (26-35 mm) taken at 150 m and 260 m. Since it seems unlikely that this species occurs as shallow as 150-260 m during the day, at least some fraction of the population apparently moves into the upper layers at night. *I. ovatus* matures at about 35 mm.

Gonostoma atlanticum (680; 10-66 mm)

Gonostoma atlanticum was taken principally at 490-560 m during the day and at 150-300 m at night. In several cases, the size-frequency curves from samples at different depths within the same series differed significantly and indicated that the smaller fish occurred at shallower depths. In December, at night all fish from 170 m were less than 30 mm, most from 190 to 200 m were 30-45 mm, and most from 250 to 300 m were 40-60 mm. Catches from day tows in both March and September indicated that few fish less than 50 mm occurred deeper than 500-525 m.

Gonostoma atlanticum apparently spawns over most of the year. Between 90 and 100% of the mature females (over 50 mm) in each series carried well-developed ova, and there were no evident seasonal changes in size composition of the catch.

Gonostoma ebelingi (306; 12-158 mm)

Gonostoma ebelingi occurred at 520-700 m during the day and at 125-300 m at night. The size composition of the catches changed with depth for both day and night series. The largest taken shallower than 150 m at night was 45 mm, and most fish taken below 200 m exceeded 60 mm. During the day, few fish over 100 mm were caught above 600 m, and none less than 75 mm were caught deeper.

Female *G. ebelingi* matured at about 120 mm, but males, as far as could be told without histological studies, appeared to mature at about 100 mm. There was, however, no evidence to suggest that this species is a protandrous hermaphrodite as observed in *G. gracile* by Kawaguchi and Marumo (1967). There were no obvious seasonal differences in the percentages of ripe females among mature females, but differences in size composition of the catches of different series suggested some seasonality in spawning.

All *G. ebelingi* caught in December were over 70 mm. In March, all fish were either less than 50 mm or over 70 mm. In June, 40% of the catch was 20-60 mm and the rest about evenly distributed between 61 and 150 mm. In September, the catch was again bimodal with all fish either smaller than 70 mm or over 100 mm. Recently transformed juveniles were taken only in March and September and were most abundant in March. More data would, of course, be helpful, but it seems that *G. ebelingi* spawns principally in early spring and early fall.

Gonostoma elongatum (1,346; 10-218 mm)

In all series but December 1970, *G. elongatum* occurred at 560-725 m during the day and moved to 60-265 m at night. In December, no individuals over 115 mm long were caught in the upper layers at night, but larger fish were taken in two night tows within the day depth range (of 22 fish, 9 were 117-200 mm, Figure 3). These deep night catches were not large relative to those expected from contamination, and consequently may have resulted from encountering patches in the shallow layers. However, the difference in size suggests that the large individuals did not migrate.

Size-frequency curves from night samples at different depths during the same series were frequently significantly different and consistently indicated that small fish occurred shallower (Figure 3). Those caught above 100-125 m were less than 35-40 mm, most caught between 175 and 200 m were 60-80 mm, and larger fish were taken mostly in tows below 200 m. It was not clear whether a similar pattern existed at depth during the day.

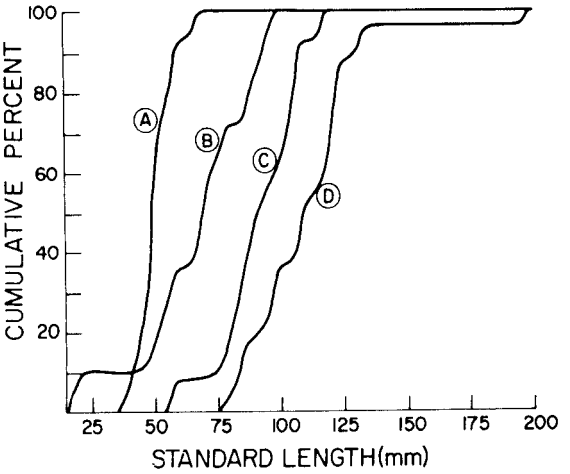

FIGURE 3.—Cumulative size-frequency curves for *Gonostoma elongatum* taken at 170 m (A, 25 individuals), 190-200 m (B, two tows, 11), 265 m (C, 13), and 750 m (D, two tows, 22) at night during December 1970. The curves were all significantly different ($P<0.05$) from each other.

There was considerable sexual difference in size at maturity. Males appeared to reach maturity at about 120 mm; the largest male was 161 mm. The smallest mature female was 193 mm. Some small, clearly immature females (120-140 mm) were found, but unfortunately, no fish between 161 and 193 mm was collected. Although histological studies of specimens of all sizes are obviously necessary, the above data suggest that some *G. elongatum* mature directly as females, while others are protandrous hermaphrodites. Kawaguchi and Marumo (1967) have shown that a congener, *G. gracile* is a protandrous hermaphrodite. Butler (1964) has shown that in some species of pandalid shrimps, a group within which protandrous hermaphroditism frequently occurs, the degree of hermaphroditism varies throughout the species' ranges. Butler suggests that this is a result of varying ecological factors. Varying degrees of protandry may similarly occur among the *Gonostoma* spp.

Too few mature females were collected to assess any seasonal trends in gonad ripeness, but the pooled size composition data for each series indi-

cated that the principal spawning season was in the spring or early summer. A few small (10-30 mm) *G. elongatum* were taken in March and June, but these were far more abundant in July and September. In December, substantial numbers of 35– to 50–mm fish were taken, but none were less than 30 mm. Too few large individuals were taken to indicate any further trends, but it seems probable that *G. elongatum* requires several years to reach maturity. Krueger and Bond (1972) have suggested a 3-yr life cycle for this species in the subtropical Atlantic.

Danaphos oculatus (229; 19-41 mm)

Danaphos oculatus does not appear to migrate vertically. The night depth range was 430-600 m and the day range 480-650 m. The day-night difference is an artifact due to depth spacing of the samples. There were no trends in size composition with depth. *Danaphos oculatus* matures at about 30 mm. There were no seasonal trends in size composition or reproductive condition.

Valenciennellus tripunctulatus (600; 10-32 mm)

During the day, *V. tripunctulatus* was taken principally between 400 and 550 m. The size-frequency curves for tows at 500 and 525 m taken in September 1970 were significantly different; 70% in the shallower tow were 20-25 mm, and 75% in the deeper were over 25 mm. The day depth range and evidence of changes in size composition with depth agree with results reported by Krueger (1972) for *V. tripunctulatus* in the central North Atlantic.

Krueger's data show that *V. tripunctulatus* remains at the same depths during the night, but near Hawaii this species undertakes a limited, but definite upward migration. The night depth range was 200-330 m. The catches per effort within this range were roughly equivalent to those during the day at 400-500 m. Catches below 330 m at night were lower and probably due to contamination. All sizes were taken within the night depth range. Changes in size composition with depth were evident, but numbers sufficient to make statistical comparisons were taken at more than one depth only in December 1970. In that case, the curve from the 200–m depth sample differed significantly from those from samples at 270 and 320 m. About 90% of the fish in the shallower sample were 10-16 mm and over 90% in the deeper were over 20 mm. Thus the upward extension of the depth range at night was not due solely to shallow catches of postlarvae or juveniles as Krueger (1972) has suggested may be the case for Badcock's (1970) earlier observation of limited diurnal vertical migration by *V. tripunctulatus in the eastern Atlantic.*

Valenciennellus tripunctulatus matures at about 25 mm. Large proportions of the mature females (90-100%) carried well-developed ova at all seasons. There were no obvious seasonal trends in size composition.

Other Gonostomatidae

Two *Woodsia nonsuchae* (39 and 106 mm) were taken at 530 and 620 m at night, respectively. A damaged specimen (22 mm) that was probably *W. nonsuchae* was taken in a day tow to 875 m.

Margrethia obtusirostra (18; 8-44 mm) was taken mostly at night between 180 and 200 m. The two day catches were in tows at 350 and 540 m. The two largest specimens, 44 mm, were mature females and the next largest, 34 mm, was a female with ova beginning to develop.

Chauliodontidae

Chauliodus sloani (147; 21-250 mm)

Chauliodus sloani appeared to migrate from a day depth range of 450-825 m to 45-225 m at night. No individual over 65 mm was taken above 100 m at night nor above 500 m during the day. All fish over 120 mm were taken below 175 m at night or below 600 m during the day.

The pooled data from each series showed significant differences in size composition (Figure 4A) which indicated that *C. sloani* spawns principally in the spring or early summer and reaches lengths of 70-100 mm by the following March. Individuals less than 40 mm were present only in June, July, and September and were most abundant in the June and July series. These were likely represented by the large numbers of 40– to 70–mm fish present in September and December and 70– to 100–mm fish which dominated the March samples. Too few large fish were collected to assess any further trends in size composition. *Chauliodus sloani* almost certainly takes several years to reach maturity. Only the two largest specimens (females, 225 and 250 mm) were mature. The next largest was only 185 mm.

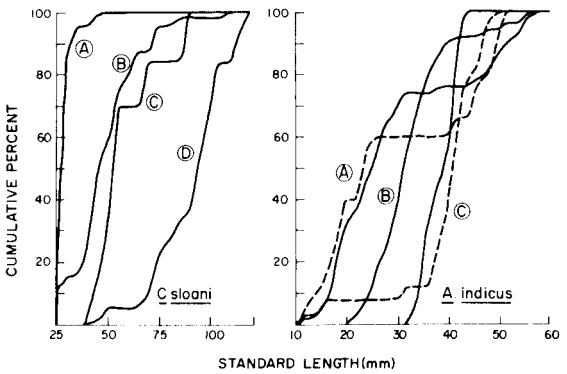

FIGURE 4.—Left: Cumulative size-frequency curves for the pooled catches of *Chauliodus sloani* (exclusive of individuals over 120 mm) in June 1971 (A, 21 individuals), September 1970 (B, 42), December 1970 (C, 13), and March 1971 (D, 19). The curve for the catch in July 1970 (not shown) did not differ significantly from and was almost identical with that for June 1971. All other curves differed significantly from each other ($P<0.05$). Right: Cumulative size-frequency curves for the pooled catches of *Astronesthes indicus* (exclusive of individuals over 60 mm) in September 1970 (A, dashed line, 20 individuals), December 1970 (A, solid line, 41), March 1971 (B, 128), June 1971 (C, solid line, 18), and July 1970 (C, dashed line, 27). All pairs except June-July and September-December differed significantly ($P<0.05$).

Stomiatidae

Four *Stomias danae* (55-75 mm) were taken at night. Two were from tows at 100 m and two from a tow at 250 m that extended well past dawn. A larger (154 mm), damaged *Stomias* sp. was taken in a night tow at 225 m.

Three specimens (99-290 mm) of the genus *Macrostomias* were taken, but depth information on the samples was questionable for all three. Fedorov and Melchikova (1971) described a new species of *Macrostomias*, *M. pacificus*, which they distinguish from *M. longibarbatus* mostly on the basis of anal fin ray and photophore counts. Two of the specimens I collected had 14 anal rays, and one had 15. Complete photophore counts were possible on only one specimen with 14 anal rays: PV = 81, OV = 82, VAV and VAL = 64. The other specimen with 14 anal rays had PV = 82, OV = 80. The estimated PV + VAV for the remaining specimen was 148. Thus the photophore counts definitely indicate *M. longibarbatus*, while the anal ray counts fall between those given for the two forms by Fedorov and Melchikova (1971). I suspect that additional specimens will indicate there is only one valid species, *M. longibarbatus*.

Astronesthidae

Astronesthes cyaneus (45; 16-66 mm)

Astronesthes cyaneus is used here pending further study of the systematics of this species group in the Pacific. The specimens were closest to *A. cyaneus* as defined by Goodyear and Gibbs (1969), but all had rudimentary barbels. Also, the luminous tissue on the operculum of the few larger specimens was not exactly as described by Goodyear and Gibbs.

Only eight specimens were caught during the day, six of these between 600 and 700 m. Three-fourths of the night catches were at 80-100 m; the few collected deeper were scattered throughout the water column and were probably contaminants. None of the specimens were near maturity; only eight were over 25 mm. Larger fish undoubtedly avoid the trawl and may occur deeper than the small individuals. It appears that even the small ones avoid the trawl during the day.

Astronesthes indicus (307; 11-117 mm)

Astronesthes indicus was taken principally at 500-800 m during the day and at 30-200 m at night except in the December 1970 series. In that series, no *A. indicus* were taken in the upper layers at night, but 21 were taken in three night tows at 625-750 m, within the day depth range. The numbers collected in these tows were larger than expected if they had been due to contamination and were comparable to catches of day tows at this time. At night, no individual over 50 mm was taken shallower than 125 m, but smaller individuals were taken with roughly equal frequency throughout the night depth range. The small fish also appeared to occur throughout the day depth range, but large fish were taken mostly in tows near the deep end.

The size composition of the catch varied considerably with season and suggested that spawning occurred principally in the summer and fall and that about 2 yr were required to reach 50-60 mm. A few small individuals (< 20 mm) were taken in July 1970, many in September and December, and none in March or June of 1971 (Figure 4B). The small individuals of the September and December samples appear to be represented by a 21- to 35-mm group in March and a 34- to 45-mm group in June. A similar sized group, 37-49 mm,

was present in the July 1970 samples and appeared to be represented by a 42–to 51–mm group in September and a 46– to 57–mm group in December. The CT series in March collected 99 specimens, 56 of which were 24-36 mm or roughly equivalent to the majority of the IK specimens. Of the remaining CT specimens, 26 were 50-76 mm-perhaps representative of the 46– to 57–mm group in the December IK series.

The catch per effort and size composition of IK catches were roughly equal for day and night indicating no differential avoidance. However, 22 of the 35 specimens over 60 mm were taken by the CT. The largest taken by the CT was 89 mm and only four larger individuals were taken by scattered IK tows. Thus it appears that individuals over 60 mm regularly avoid the IK and that larger ones avoid both trawls. The largest individual (117 mm) was a female that appeared to be nearing maturity. Judged from the above data, it is likely that this species takes at least 3 or 4 yr to mature.

Astronesthes splendidus (82; 22-110 mm)

About 75% of the *A. splendidus* collected were taken at 25-130 m at night. There was no obvious trend in size composition with depth. Only 16 specimens were taken during the day, all but 2 of these between 600 and 800 m. Nearly transformed larvae with photophores (< 25 mm) and small juveniles were present only in June, July, and September suggesting summer or early spring spawning. These young may have been represented by 40– to 60—mm fish which made up 85% of the March catch, but so few fish were caught in December that the connection between the two size groups is tenuous. Only 15 of the 82 specimens were over 60 mm and none were mature. The size composition of IK and CT catches in March was similar. Thus both trawls were avoided by most larger juveniles and consistently by adults.

Astronesthes sp. (near *similis*) (37; 21-133 mm)

The specimens of this species of *Astronesthes* agreed with the description of *A. similis* by Gibbs (1964) except for the barbel tip. Instead of being unornamented, the barbel tip of the Hawaiian specimens had a dark terminal filament about as long as the bulb and often a pale tip at the end of the filament. The lateral filaments on the bulb were much shorter than the bulb itself. The systematic status of this form is presently under study by other workers (Gibbs, pers. commun.).

Twenty-four of the specimens were taken at 50-200 m at night and eight were taken at 500-640 m during the day. Only four of the specimens exceeded 60 mm indicating that the large, mature fish consistently avoided both trawls.

Astronesthes spp.

Three other species of *Astronesthes* were taken. *A. gemmifer* (6; 91-138 mm) was taken once at night at 245 m, four times at 580-690 m during the day, and once by a day tow to 1,150 m. *Astronesthes lucifer* (10; 26-49 mm) was taken five times at night at 25-195 m, and by day at 250, 550 (3), and 640 m. *Astronesthes luetkeni* (6; 26-74 mm) was taken in only three tows for which depth information was valid: 125 and 200 m at night and 600 m during the day.

Heterophotus ophistoma (28; 32-245 mm)

Of 17 *H. ophistoma* taken at night, 15 were taken between 50 and 200 m. The other two were nearly transformed larvae taken in a closing net tow at about 630 m. Ten of the 11 day specimens were taken at 625-775 m; one was taken at 1,000 m. Eighteen were larvae or recently transformed juveniles (32-64 mm), and all but two of these were taken in July or September. The two largest specimens, 235 and 245 mm, were males and appeared to be mature or nearly so.

Neonesthes microcephalus (2; 135-147 mm)

One *N. microcephalus* was taken at 640 m at night and the other in oblique tow to 1,600 m.

Melanostomiatidae

Eustomias bibulbosus (20; 80-145 mm)

Fourteen *E. bibulbosus* were taken at 75-300 m at night; however, only two large (131 and 145 mm) individuals were taken below 125 m. During the day, six were taken between 600 and 960 m. Sixteen of the specimens were small (80-102 mm), and none of the large ones were mature.

Eustomias bifilis (128; 41-170 mm)

All but 5 of the 92 night catches of *E. bifilis* (40 by IK, 51 by CT) were at 15-200 m. The day depth range appeared to be 635-800 m; only 5 of the 29 day catches were at greater depths. There was no obvious trend in size composition with depth. Size at maturity was about 140 mm.

Eustomias gibbsi (28; 55-131 mm)

All but three *E. gibbsi* were taken at night. The night depth range was about 50-200 m, and the three day catches were at 680-800 m. There was no obvious trend in size composition with depth among the night catches. None of the specimens were mature.

Eustomias spp.

Of the remaining specimens of *Eustomias*, about 130 were too badly damaged to be identified with certainty. The great majority of these had pectoral ray and photophore counts within the range of the three species considered above (most were probably *E. bifilis*). Some 150 other specimens include about 20 different forms, most of which cannot be reliably identified due to present uncertainties in the systematics of the genus. These along with other specimens from the Central Pacific will be considered in a later, more systematically oriented report.

Thysanactis dentex (340; 39-177 mm)

Thysanactis dentex, the most frequently collected melanostomiatid, occurred principally at 75-200 m at night. A few individuals were taken as shallow as 40 m, and there were scattered night catches throughout the water column. The principal day depth range was 600-800 m with a few caught between 400 and 600 m or scattered deeper than 800 m. Within both ranges, the larger fish tended to occur deeper and the smaller shallower. At night few over 100 mm occurred above 150 m, and catches of those smaller than 80 mm below 125 m were low and probably due to contamination. During the day those over 100 mm were caught mostly below 700 m and those less than 100 mm mostly between 600 and 700 m. Size at maturity was about 160 mm.

Bathophilus spp.

Seven species of *Bathophilus* were taken. Although data are incomplete for most, it seems that all occur at about 500-700 m during the day and migrate to the upper 250 m at night. *Bathophilus kingi* (23; 24-95 mm) was taken most frequently. At night, 18 specimens were taken between 50 and 225 m. Three specimens were taken at 590-725 m during the day and one each at 1,000 and 1,100 m. *Bathophilus brevis* (3; 12-43 mm) was taken only at night between 200 and 225 m. *Bathophilus digitatus* (9; 23-91 mm) was taken seven times at night at 125-175 m and twice during the day at 520 and 550 m. *Bathophilus longipinnis* (10; 25-97 mm) was taken seven times at night scattered throughout the water column (100-1,175 m) and three times between 520 and 590 m during the day. *Bathophilus pawneei* (7; 30-90 mm) was taken at night between 40 and 195 m and once at 690 m during the day. *Bathophilus* cf. *altipinnis* ? (3; 26-59 mm; pectoral rays 26-28, pelvic rays 15-18) was taken at 170 and 265 m at night and at 640 m during the day. A single *B. schizochirus* (76 mm) was taken at 265 m at night.

Other Melanostomiatidae

Pachystomias microdon (33 mm) was taken once in a day tow at 660 m. Two small (55-56 mm) *Flagellostomias boureei* were taken at 500 m (day) and 750 m (night). Five juvenile *Echiostoma barbatum* (29-89 mm) were taken, four at 30-185 m at night and one in an oblique day tow to 800 m. Four species of *Photonectes* which were collected could be identified with reasonable certainty. *Photonectes achirus* (9; 43-146 mm) was taken at 125-225 m at night and at 400, 550, 620, and 1,400 m during the day. A single *Photonectes caerulescens* (127 mm), which is likely to be proven indistinct from *Photonectes achirus*, was taken in a day tow at 800 m. *Photonectes albipennis* (8; 22-87 mm) was taken once at 620 m during the day and between 60 and 165 m at night. *Photonectes fimbria* (34 mm) was taken once at 620 m during the day. The above specimens of *Photonectes* fit the descriptions given in Morrow and Gibbs (1964) reasonably well. In addition, two specimens (208 and 255 mm), taken at 650 m at night and 490 m during the day, were close to, but not identical with, *Photonectes margarita*.

Leptostomias spp. (15; 68-134 mm) were taken predominantly at night between 100 and 250 m;

four were taken during the day at 500-625 m. *Melanostomias* spp. (23; 48-238) were mostly taken at 50-250 m at night or 520-800 m during the day. Due to either damage to the barbels (mostly *Leptostomias)* or lack of data on the variability of characters used to separate nominal species in these genera, definite identifications cannot be given.

Idiacanthidae

Idiacanthus fasciola (341; 13-375 mm)

Larval *I. fasciola* (13-50 mm) were taken mostly at night in the upper 200 m; deeper catches both day and night were scattered and probably contaminants. Males (30-50 mm) were taken principally between 550 and 800 m during the day. Fourteen of the 20 night captures were also in the day depth range, but 6 were taken at 200-300 m.

At night, females (47-375 mm) were taken principally between 30 and 300 m. All taken below 200 m were over 145 mm, but larger ones did occur shallower. In the December 1970 series seven females were taken, but only one was taken at night in the upper 300 m, the remainder were taken within the day depth range. During the day, females were taken mostly between 600 and 800 m, but one was caught at 250 m and several at 400-600 m. Too few were taken to make detailed comparisons of day and night catch per effort, but the data indicated no gross differences in abundance or size frequency.

Female *I. fasciola* mature at about 250 mm, but too few large individuals were taken to assess any seasonal trends in gonad ripeness. There were no clear seasonal trends in size composition of the catches. Larvae and males were taken most frequently in December. Few were taken in March, with catches for June, July, and September intermediate. In July, September, and December, 84-91% of the females were shorter than 150 mm, while the percentages for March (59%) and June (30%) indicated relatively fewer smaller females. There were, however, no definite size groups which could be traced from season to season.

Malacosteidae

Photostomias guernei (159; 24-158 mm)

Photostomias guernei was taken principally at 15-300 m at night and at 350-800 m during the day. A few specimens were taken in deep night tows with the opening-closing trawl indicating that the entire population does not regularly migrate. Small fish were caught throughout these ranges, but only two fish over 100 mm were caught above 185 m at night and none over 80 mm were taken above 750 m during the day.

Mature female *P. guernei* showed a rather curious size distribution. Of 41 females examined (46-158 mm), 11 bore ripened ova. Nine were 64-85 mm and two were considerably larger—147 and 158 mm. Of the specimens with undeveloped ova, seven were less than 63 mm, and the remainder 93-149 mm. Some of the large individuals could possibly have spawned already, but the individuals between 93 and 125 mm were clearly immature. The bimodal size distribution suggests that two populations were present in the samples, but there was considerable overlap or agreement in photophore and fin ray counts of both large and small females. Also there was no indication that one type of female had a different depth distribution or seasonal pattern than the other.

Photostomias guernei probably spawns over most of the year. Individuals under 40 mm were most frequently taken in June, but were present in all series. There was no obvious seasonal trend in size composition of the larger fish.

Aristostomias spp.

Aristostomias lunifer (12; 30-151 mm) was taken only between 120 and 260 m at night. The largest specimen, a 151 mm female, was mature or nearly so. *Aristostomias grimaldii* (5; 33-117 mm) was taken at 100 and 500 m at night and at 690 and 750 m during the day. The largest specimen, a male, appeared immature. *Aristostomias polydactylus* (10; 33-140 mm) was taken at 100, 175, 320, and 590 m at night and at 625, 850, 875, and 1,100 m during the day. The largest individual was an immature female. Two specimens similar to *A. tittmanni* (68 and 75 mm) were taken at 15 and 250 m at night.

Malacosteus niger (133; 26-186 mm)

Malacosteus niger occurred between 520 and 900 m during the day and 500-850 m at night; the day-night differences were due to sample spacing. Most were taken between 600 and 700 m. The

depth-size plot indicated a trend for greater size with increasing depth, but since 106 of the 133 specimens were 75-125 mm any trends for smaller or larger fish are of dubious significance. The only mature females collected were the four largest specimens (172-186 mm). There was no seasonal trend in size composition of the the catches.

DISCUSSION

In spite of the fact that the stomiatoids in the study area were quite diverse and that there have been no really comprehensive studies based on extensive sampling programs in the Pacific, only a few species are either undescribed or of uncertain status (with the exception of the *Eustomias* spp.). To paraphrase Gibbs (1960), it is indeed a relief that most specimens fit descriptions based primarily on Atlantic material.

Eight species were previously unrecorded in the Pacific: *Astronesthes gemmifer*, *Neonesthes microcephalus*, *Aristostomias grimaldii*, *A. lunifer*, *A. polydactylus*, *Eustomias bibulbosus*, *Photonectes achirus*, and *Bathophilus altipinnis*. Three of the more commonly collected species were previously known only from a few specimens. *Gonostoma ebelingi* (Grey, 1960) and *Eustomias bifilis* (Gibbs, 1960) were described on the basis of two and one specimens, respectively, and no other specimens have been reported since. *Thysanactis dentex*, which was taken regularly by the present study and by King and Iversen (1962), is listed by Morrow and Gibbs (1964) as known from only five captures in the North Atlantic. Further studies of material from other tropical areas will be necessary to determine if these species are for some reason present in high numbers only in the Central Pacific.

Inadequate information from other areas of the Pacific does not permit detailed consideration of zoogeographic patterns of these species. Negative records of several studies and reports cannot necessarily be considered conclusive. It is likely that the majority of the species recorded here occur throughout the warm water masses. However, preliminary examination of samples from the central equatorial Pacific indicates that at least *Vinciguerria nimbaria* and *Gonostoma ebelingi* do not occur continuously across the equatorial region and also confirm Gibbs' (1969) statement that *Stomias danae* is replaced by *S. affinis* in equatorial waters. Two species, *Vinciguerria lucetia* and *Idiacanthus antrostomus*, which appear to occur in eastern and equatorial waters, were not taken during this study. *Vinciguerria lucetia* has been recorded near Hawaii (King and Iversen, 1962; Ahlstrom and Counts, 1958) and *Idiacanthus antrostomus* may also be expected to occur here occasionally, but their absence from the material collected during the study indicates that some warmwater species do not normally occur in the central water mass.

It is clear from the absence or extreme rarity of mature fish, that neither of the trawls used were adequately sampling the larger sizes of many species—particularly the *Astronesthes* spp. Although differences in day-night catches have not been rigorously demonstrated, it also appears that many large species and individuals avoid the IK better during the day than at night.

For most species, the numbers caught by the paired series of IK and CT tows in March 1971, were not sufficient for detailed analyses, but rough comparison of the catches and size ranges (Table 1) indicates some differential avoidance. The total volume sampled by the CT tows was about 10 times that of the IK tows in the same depth range. In 10 species, the ratio of CT/IK catches was considerably lower than 10 (1.3-6.0) suggesting that the IK's greater towing speed was more of an advantage than the greater size of the CT. In these cases, the CT/IK ratio was little affected by considering only the fish larger than the smallest caught by the CT; i.e., the passage of smaller fish through the coarser CT meshes did not seem to be an important factor.

Three species, *Diplophos taenia*, *Gonostoma*

TABLE 1.—Total numbers and size ranges of 15 species of fish taken in nine tows with the IK and eight tows with the CT in the upper 200 m at night during February-March 1971. The tows with each net were roughly equally distributed between 25 and 200 m. The total volume sampled by the CT tows was about 10× that of the IK tows.

Species	Total catch		Size range (mm)	
	IK	CT	IK	CT
Diplophos taenia	5	62	66-83	61-153
Vinciguerria poweriae	29	122	16-34	15-33
Gonostoma atlanticum	10	40	15-45	20-64
Gonostoma ebelingi	11	100	12-37	16-162
Gonostoma elongatum	97	236	10-139	30-165
Chauliodus sloani	4	13	81-162	68-123
Astronesthes cyaneus	4	13	18-19	17-44
Astronesthes indicus	18	83	21-89	24-89
Astronesthes splendidus	10	13	29-58	30-65
Eustomias bibulbosus	0	10	—	81-141
Eustomias bifilis	2	49	93-115	52-158
Eustomias gibbsi	1	10	77	70-131
Thysanactis dentex	17	102	58-173	44-165
Idiacanthus fasciola	17	81	58-297	54-301
Photostomias guernei	9	26	30-113	40-133

ebelingi, and *Eustomias gibbsi*, were taken in roughly the predicted ratios, and the other two species of *Eustomias* treated here were clearly sampled better by the CT. Size ranges, of course, were greatly influenced by just one large individual, but in general the CT caught considerably larger individuals of the five species which it appeared to sample relatively better in terms of numbers. Although not shown by the figures in Table 1, large *Astronesthes indicus* were also apparently sampled better by the CT (see above).

Of the 47 species considered here, only *Danaphos oculatus* and *Malacosteus niger* clearly did not migrate to shallower levels at night. All the other abundant species migrated to the upper layers at night and, in spite of the fact that no opening-closing device was used, even the data on many of the rarer species are consistent with migrations of several hundred meters. It is, of course, possible that, as in the case of *Photostomias guernei*, a small percentage of some species may not migrate at any given time. Diurnal vertical migration has been shown to occur in a few of the species considered here (e.g., Badcock, 1970; Krueger and Bond, 1972), but due to limited data it had been only "suspected" for many others. Possibly because of the deeper mixed layer and thermocline and greater transparency of the water, migrations in the tropics are greater in extent and thus more easily detected than elsewhere.

As with several species of myctophids (Clarke, 1973), there was evidence that some of the stomiatoids did not regularly migrate during the winter. For *Vinciguerria nimbaria, Gonostoma elongatum, Astronesthes indicus,* and *Idiacanthus fasciola,* night catches within the day depth range during December 1970 were higher than expected if due to contamination and indicated that a fraction of the population remained at depth. Too few of the latter two species were taken to permit consideration of any differences between the migrating and nonmigrating fractions. The evidence for nonmigration was weak for *G. elongatum* but suggested that the large fish did not migrate. There were no obvious differences in the two fractions of the population of *V. nimbaria.* Thus as with the myctophids, there is no explanation for the apparent change in behavior.

Many of the species showed trends for increased size with depth both day and night. Similar trends were noted for many species of myctophids (Clarke, 1973), and qualitative reports (e.g., Badcock, 1970) indicate that this trend is shown by a variety of mesopelagic species. The trend was clearest for the abundant vertically-migrating gonostomatids, *Diplophos taenia, Vinciguerria* spp., *Gonostoma* spp., and *Valenciennellus tripunctulatus,* but was also evident for *Chauliodus sloani, Astronesthes indicus* and *Thysanactis dentex.*

The size-depth patterns at night of 10 species are shown in Figure 5 by straight lines connecting the coordinates for the smallest size, upper limit of depth range with those for the largest size, lower limit of depth range (extremes of size and depth have been ignored). These are only rough approximations of the size-depth patterns; in reality the patterns are rather complex polygons. The straight lines serve mainly as a basis for considering the possible interactions of the various species.

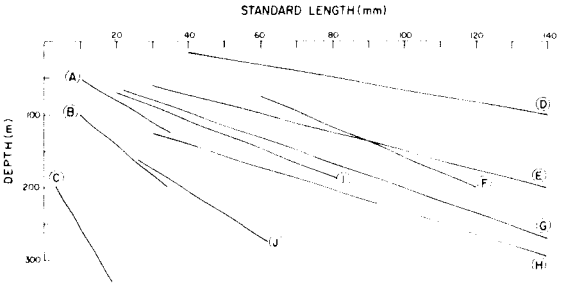

FIGURE 5.—Depth-size profiles (see text) for 10 species in the upper 300 m at night: *Vinciguerria nimbaria* (A), *Vi. poweriae* (B), *Valenciennellus tripunctulatus* (C), *Diplophos taenia* (D), *Chauliodus sloani* (E), *Thysanactis dentex* (F), *Gonostoma elongatum* (G), *G. ebelingi* (H), *Astronesthes indicus* (I), and *G. atlanticum* (J).

Two very similar species, *Vinciguerria nimbaria* and *V. poweriae*, showed distinctly different size-depth patterns. As with many similar species of myctophids, individuals of similar sizes were well separated in the water column. Where the depth ranges overlapped, at 100-125 m, the larger *V. nimbaria* co-occurred with the smaller *V. poweriae*. *Vinciguerria nimbaria* generally co-occurred with similar-sized or slightly larger individuals of several abundant species of myctophids in the upper 100 m, while *V. poweriae* co-occurred with the deeper living myctophids (Clarke, 1973).

Although their size-depth patterns were slightly different, similar-sized individuals of *Gonostoma elongatum* and *G. ebelingi*, two very similar species, co-occurred over much of their depth ranges. *G. atlanticum*, in addition to being rather different from its congeners in size range, color, and several morphological aspects, also had

a quite different size-depth pattern and tended to co-occur with much larger individuals of its congeners. The former two species co-occurred throughout much of their depth range with similar-sized individuals of three species of the myctophid genus *Lampanyctus*. Thus in the 100-250 m layer at night similar species of at least two genera of two families co-occur. This is in contrast to the upper 100 m where only rather different or distantly related species co-occur.

Other gonostomatids exhibited nighttime patterns quite different from any of the other species considered. *Danaphos oculatus* remained at the day depth and showed no trend in size composition with depth. *Valenciennellus tripunctulatus* occurred much deeper than similar-sized individuals of any other species. *Diplophos taenia* occurred much shallower, with respect to size, than any of the species thus far investigated. It is possible that some of the shallow-living myctophids, e.g., *Myctophum* spp., which were not adequately sampled by the trawl also have patterns similar to that of *D. taenia*.

The larger stomiatoids with fanglike teeth, dorsal or mental "lures," or various adaptions for swallowing large items, are generally thought to be predators on small nekton. Near Hawaii, the dominant "predatory" species exhibited a variety of patterns at night. *Astronesthes indicus, Chauliodus sloani,* and *Thysanactis dentex* showed trends for increased size with depth. In the upper 100 m, these species co-occurred with roughly similar-sized or slightly smaller individuals of the more abundant myctophids and *Vinciguerria nimbaria*. Although there are, scattered throughout the literature, several records of larger stomiatoids ingesting rather large prey, it seems unlikely that these three species are important predators on the abundant fishes in the upper 100 m or that the latter are important items in the former's diet. All sizes of *Idiacanthus fasciola, Eustomias bifilis,* and *Astronesthes splendidus* appeared to occur throughout their night depth ranges. Thus it would seem that, if indeed any of the larger stomiatoids are important predators on the small fishes in the upper 100 m, species such as these are more likely candidates.

Malacosteus niger did not migrate, and its depth range was somewhat deeper than the day ranges of most of the vertically migrating species considered here. *Malacosteus niger* has very poorly developed serial, ventral–lateral photophores in comparison with most other stomiatoids. The only nonmigrating species of myctophid, *Taaningichthys bathyphilus,* occurs in the same depth range and has greatly reduced serial photophores in comparison with the other myctophid species. If, as Clarke (1963) has suggested, ventral-lateral photophores are a counter-shading device, their absence or reduction in these deep-living, nonmigrating species is likely related to lower light levels and more nearly spherical radiance distribution at such depths even during the day in comparison to the regime which most of the migrating species experience day or night.

Three of the species which occurred together at 400-600 m during the day, *Danaphos oculatus, Valenciennellus tripunctulatus,* and *Ichthyococcus ovatus,* all have dorsally directed eyes and markedly ventrally directed serial photophores. These characteristics are shared by the sternoptychids of the genus *Argyropelecus* which also occur in the same depth range (S. S. Amesbury, pers. commun.). The argentinoid, *Opisthoproctus soleatus,* which shares the same day depth range, also has dorsally directed eyes and a ventrally directed luminescent apparatus. At night, none of these species appear to undertake extensive migrations. *Danaphos oculatus* remains at the same depths, *V. tripunctulatus* undertakes a limited upward migration, and *I. ovatus* either migrates or disperses upward. The *Argyropelecus* spp. either move upward slightly or remain at the same depths (S. S. Amesbury, pers. commun.). *Opisthoproctus soleatus* was for some reason nearly absent from the night samples; out of the 114 specimens only 4 were taken at night.

Several investigators (see review by McAllister, 1967) have suggested that the dorsally directed eyes are an adaptation for better detection of prey or predators above the fish and that the ventrally directed light organs serve to disrupt the silhouette of the fish to predators below. These adaptive values would be realized only under a situation where light levels were low but still sufficient for vision and where the radiance distribution was dominated by the downwelling component. Such conditions probably obtain only during the day for the above species. This would suggest that they feed primarily during the day and that they are exposed to heavier predation then also. At least the former seems likely. These species probably feed on zooplankton, and preliminary analyses of zooplankton in the study area indicates that these species encounter higher concentrations during the day owing to vertical

migrations of the zooplankton. The situation is just the opposite for most of the other fishes which share the same day depth range and have neither upwardly directed eyes nor as pronounced a ventral orientation of their light organs. The latter fishes undertake more extensive vertical migrations at night and encounter higher concentrations of zooplankton and probably predators then rather than during the day.

The species which showed seasonal trends in size composition or gonad ripeness all appeared to spawn primarily in the spring and summer or summer and fall. These were *Vinciguerria* spp., *Chauliodus sloani*, *Astronesthes indicus*, and probably *A. spendidus* and *Heterophotus ophistoma*. Their seasons of peak reproduction were thus similar to those of the abundant myctophids (Clarke, 1973). The data on *Gonostoma elongatum* and *Idiacanthus fasciola* suggested rather inconclusively that these species spawn primarily in the summer and winter, respectively. Several fairly abundant species, *Gonostoma atlanticum*, *Danaphos oculatus*, *Valenciennellus tripunctulatus*, *Eustomias bifilis*, *Thysanactis dentex*, *Photostomias guernei*, and *Malacosteus niger*, showed no indication of seasonality in reproduction. Possibly the larvae of those species which exhibit no seasonality either hatch at a larger size or live at greater depths than those of the seasonal species and thus the former's spawning is not timed to any seasonal fluctuations in food concentration or size distribution in the upper layers.

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REARING OF PLAICE (*PLEURONECTES PLATESSA*) LARVAE TO METAMORPHOSIS USING AN ARTIFICIAL DIET

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ABSTRACT

Newly hatched larval plaice were grown to metamorphosis using an artificial diet. The overall survival rate to metamorphosis was of the order of 20%. This compares with a survival rate of 38% in control larvae fed *Artemia* in a similar tank system.

The preparation of the artificial diet is described. The main protein component was freeze-dried cod muscle and the diet contained 70.7% crude protein, 9.7% lipid, 7.9% ash, and 5% digestible carbohydrate.

This food in particle sizes ranging from 180 to 355 μ was introduced automatically into the inflowing water of a cylindrical tank containing 200 yolk sac larvae. Water temperature was 10±2°C. After about 13–14 days a relatively high larval mortality occurred, leaving approximately 70 established feeding larvae. Unfed larvae in an identical control tank did not survive beyond this time.

Once feeding had been established larval mortalities were occasional and sporadic. Thirty-five days after commencement of the experiment some larvae began to metamorphose, and 56 days from the start some 35 metamorphosed fish were transferred to a separate tank. These fish have since continued to feed and grow on the same diet.

The rearing of marine flatfish from egg to metamorphosis and subsequently to more adult stages was achieved under laboratory or hatchery conditions using live food (*Artemia salina*) about 10 yr ago ((Shelbourne, 1964). The experimental animal was plaice, *Pleuronectes platessa*. Since then other flatfish (lemon sole, *Microstomus kitt;* Dover sole, *Solea solea*; and turbot, *Scophthalmus maximus*) have been similarly reared to metamorphosis, using either the same food organism for sole or a combination of organisms such as rotifers followed by *Artemia* for turbot.

While such methods have been applied successfully on a pilot scale the ability to rear these fish on an artificial diet may confer certain advantages such as: (1) the ability to change the composition of the food and so ultimately arrive at a composite ration approaching the optimal requirement of the larva; (2) continuity of a food supply of standard quality (the large scale production of live food other than *Artemia* involves cultivation of several organisms, e.g. rotifers, and food for rotifers. Thus the whole cultivation program must be carefully synchronized and there must be certainty that production of food will keep pace with the increasing demands of the growing larval fish. Moreover, *Artemia* themselves may vary in nutritional quality and may contain variable amounts of pesticide residues (Bookhout and Costlow, 1970)); (3) elimination of the need to wean metamorphosed larvae from a natural to an artificial food. There can be little doubt that the availability of compounded foods has contributed greatly to the growth of fish farming procedures for freshwater fish such as trout, salmon, and channel catfish in several countries. All these species of fish have large eggs which give rise to large fry so that, compared with the early rearing of marine fish larvae, few technical problems arise.

The present paper describes a partially successful attempt to rear plaice from egg to metamorphosis using artificial food under small scale laboratory conditions.

EXPERIMENTAL

The apparatus used is shown in Figure 1 and Figure 2. The larval rearing tank was cylindrical and measured 26 cm in diameter with a depth of 23 cm. It was contained in an outer vessel which was normally full of seawater. The bottom of the tank was formed from a circular piece of rigid polyvinyl chloride pipe (Durapipe[2]) which fitted closely

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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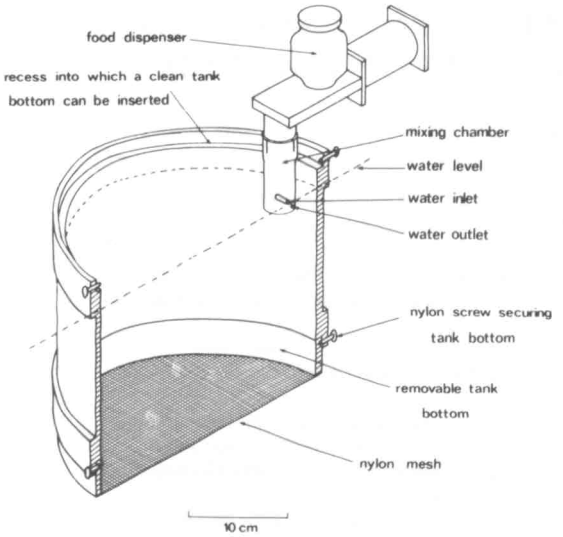

FIGURE 1.—Vertical section through the larvae rearing tank. In use the tank is suspended within a larger plastic vessel.

FIGURE 2.—Photograph of one of the larvae rearing units in use.

round the cylindrical tank and was firmly clipped onto it by a bayonet attachment. This circular piece of Durapipe was covered with 0.75 mm aperture nylon mesh to retain larvae and possibly permit uneaten food to escape. In the event the food tended to swell after being in the water for some time and only a portion of it passed through the screen at the bottom of the tank. To facilitate tank cleaning and hygiene, therefore, an exactly similar cover could be fitted over the top of the cylindrical tank and the tank slowly and carefully inverted in the outer vessel so that the bottom cover was now at the top and could readily be removed together with adhering uneaten food. This cleaning arrangement is not ideal, but by permitting the removal of much of the uneaten food from the bottom of the tank, it allowed positive control over tank hygiene and water quality. These factors have been a major obstacle to cultivation of larval fish on artificial diets in earlier experiments. As the larvae grew larger it became more and more possible to siphon uneaten food from the bottom of the tank without endangering or losing larvae.

Food was dispensed into the tank with the inflowing water by means of an automatic feeder of the type described by Adron (1972). This feeder was held on a clamp stand adjacent to the tank and could readily be removed when the tank was being cleaned by inversion. Approximately 15 mg dry food was introduced into the water via a mixing chamber at 10 min intervals, the flow rate of water being about 150 ml/min. The experiment was carried out at a temperature of 10° ± 2°C with a light intensity at the water surface of 250 lux provided by fluorescent light.

The composition of the food used is shown in Table 1. Freeze-dried cod muscle and shrimp meal were prepared as in Cowey, Pope, Adron, and Blair (1972). Freeze-dried whole hen's egg was prepared by drying homogenized hen's egg in a bulk centrifugal freeze drier. The gelatin (pre-

TABLE 1.–Composition of diet used for rearing larval plaice.

Component	g/100 g dry diet
Freeze dried cod muscle	53.4
Freeze dried whole hen's egg	10.0
Shrimp meal	10.0
Cod liver oil	4.0
Encapsulated vitamin mixture	3.3
[1]Vitamin mixture	2.8
[1]Mineral mixture	1.0
Glucose	5.0
α-tocopherol	0.4
Sunset yellow F.C F.	0.1
Furanace	0.8 mg
Gelatin	10.0
[2]Water	150 ml

[1]Cowey et al. 1972
[2]Removed finally by freeze drying

pared from swine skin 300 bloom) and α-tocopherol (500 mg α-tocopherol per g) were obtained from the Sigma Chemical Co., Ltd. Sunset yellow was a gift from Imperial Chemical Industries; it was included in the diet to simulate the color of *Artemia* nauplii. Furanace, a broad spectrum antibiotic developed specifically for fish (Shimizu and Takase, 1967) was obtained from Dainippon Pharmaceutical Co., Ltd. Half of the vitamin supplement was encapsulated in hydrogenated coconut oil to prevent the leaching out of the vitamins into the seawater. Lest this procedure rendered vitamins unavailable to the larvae, the other half of the supplement was added without further treatment. To encapsulate the vitamin mixture 28 g were homogenized in 100 ml of di-ethyl ether in which 5 g of hydrogenated coconut oil MP 32-34°C (Loders and Nucoline Ltd., London) had been dissolved. The homogenate was dried in a Bucchi Rotary evaporator.

Freeze-dried cod muscle, freeze-dried whole egg, and shrimp meal were finely ground together in a hammer mill. To these ground components were added the vitamin mixture, mineral mixture, and glucose. The cod liver oil and α-tocopherol were mixed together and then thoroughly mixed with the dry components, mixing being carried out in a Hobart food mixer. The furanace and sunset yellow were dissolved in ⅔ of the allotted water and mixed with the dry components. The gelatin was dissolved in the remaining water at 50°C before being mixed with the other dietary components. While still warm the moist diet was pressed into slabs 5 mm thick and cooled to room temperature. The slabs of diet were then dried in a bulk freeze-drier, ground with a pestle and mortar and graded with sieves, to give sizes of 250 μ-355 μ and 180 μ-250 μ. For the first 2 days of feeding the larvae were given only diet of 180 μ-250 μ; for the next 8 days increasing quantities of the 250 μ-355 μ size were mixed with the 180 μ-250 μ size until only the 250 μ-355 μ size was offered. By analysis the diet contained protein (N × 6.25) 70.7%, lipid 9.7%, and ash 7.9%.

Two hundred newly hatched larvae were put into each of three tanks on 2 April 1973. These larvae were obtained from eggs kindly supplied by White Fish Authority, Hunterston; the eggs had been artificially fertilized on 12 March. Food was introduced into one of the tanks on 5 April; *Artemia* nauplii were added to the second tank, while the third tank was kept as an unfed control mainly because unfiltered seawater was being used, and it may have contained enough natural food to maintain a number of the larvae.

For the first few days of the experiment relatively few mortalities occurred in any of the tanks but then 10–12 days after hatching, a rapid mortality occurred in the unfed control, together with relatively high mortalities in the tanks fed artificial and natural (*Artemia* nauplii) diets. By 15 April no larvae remained alive in the unfed control tank, while the numbers surviving in the two tanks receiving food were about 70 in the tank receiving the compounded artificial diet and about 100 in the tank receiving *Artemia* nauplii. It seems possible that this high mortality corresponds with the complete utilization of the yolk and that the fish surviving in the tanks receiving food correspond to Shelbourne's "established feeders."

After about 15 April mortality rates fell to a low level in both the remaining tanks; some of the deaths in the tank receiving the artificial food were a direct consequence of tank-cleaning operations. Fish began to metamorphose in both these tanks as early as 6 May and by 28 May some 35 metamorphosed plaice from the tank receiving the artificial compounded diet were transferred to a conventional tank in our recirculated system where they continued to eat the same powdered diet. This represents a 17.5% survival of metamorphosed fish from hatched larvae. Of the larvae which were reared on *Artemia* some 76 survived to metamorphosis (last day of May), representing 38% of the original newly-hatched larvae. No abnormalities of pigmentation were discernible in the larvae, possibly because of the relatively uncrowded conditions in which they were reared.

The survival rates with the artificial food were much lower than with larvae fed *Artemia*; this may be due to the greater acceptability of the live moving diet as compared to the inert artificial food; the higher number of "established feeders" obtained when feeding *Artemia* perhaps supports this view. Both our survival rates are considerably lower than those achieved by Shelbourne (1963) using *Artemia*, his most successful regime giving about 67% survival to metamorphosis (including mortalities between fertilization and hatching). However, with a temperature regime somewhat similar to that used by us (his water bath 4) Shelbourne obtained survival rates not greatly different from our "*Artemia*" tank, i.e. 55% survival (when egg incubation was carried out in the pres-

ence of antibiotics) and 30% survival (eggs irrigated with seawater free of antibiotics during incubation).

Despite the lower larval survival rate when fed artificial food it is felt that this rate is sufficiently high to demonstrate the technical feasibility of using non-living food for rearing marine fish larvae. Moreover, eggs are produced in enormous numbers by marine fish and are extremely cheap so that a 20% survival rate to metamorphosis is an acceptable level. If such a survival rate can be achieved with the more exacting larvae of highly esteemed species (Dover sole, turbot) it would give a considerable impetus to the cultivation of these fish.

DISCUSSION

Reviewing marine fish larval rearing, May (1970) named the provision of a suitable food (i.e. "one which the larvae will consume and grow on and which can be supplied in sufficiently large quantities") as the prime obstacle. Several attempts have been made over the years to rear marine fish larvae on non-living, composite foods but none of these have yet been successful (Fishelson, 1963; Blaxter, 1962; Ivanchenko and Ivanchenko, 1969). In practice we have had no great difficulty in getting plaice larvae or at least a relatively high proportion of them to ingest the food and develop on it. The main obstacle has been one of tank hygiene and it remains the overriding problem. This too is recognized by May (1970) who comments on the use of non-living food: "uneaten food accumulates on the bottom of the rearing container and decays rapidly, fouling the water". Although the present set-up does permit control of the quantity of uneaten food in the water, any improvements in tank design which release uneaten food completely while retaining the larvae are desirable. Various modifications of tank design to this end are under consideration. The problem is particularly acute in the early stages as the food particles tend to swell in the water and fail to pass the screen at the bottom of tank. As larvae increase in size, and a screen of larger mesh size can be substituted at the bottom of the tank, the problem becomes less acute.

Some bacteriological control of water may be attained by sterilizing the incoming water by means of ultraviolet light and such a device should be incorporated into future experiments.

Microencapsulation of the food may offer a further means of improving tank hygiene. The microcapsules currently available seem to sink very rapidly through a water column. This militates against their chances of being consumed by larval fish in a rearing tank. The development of neutrally buoyant microcapsules, however, could lead to rapid strides in the controlled cultivation of larval marine fish.

The use of an antibiotic in the diet calls for some comment. The relatively free use in animal feeds of those antibiotics which are commonly employed in human medicine has obvious social dangers. Attention has yet again been focused on these dangers by Williams-Smith (1973). It must, therefore, be emphasized that furanace was used in very low concentrations and that it has been developed specifically for use in fish. Thus any resistant strains which could result from its use should still be sensitive to antibiotics currently in use in clinical medicine.

The diet used was designed empirically with the objects of providing a relatively large intake of high quality protein, marine oil, and a luxus of B vitamins all allied to reasonable water stability. The diet is by no means ideal and there is clearly scope for improvement in this ration in many ways. However, it does provide a basic experimental formula from which more nearly optimal diets may evolve.

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THE INVASION OF *SAURIDA UNDOSQUAMIS* (RICHARDSON) INTO THE LEVANT BASIN – AN EXAMPLE OF BIOLOGICAL EFFECT OF INTEROCEANIC CANALS

M. BEN-YAMI[1] AND T. GLASER[2]

ABSTRACT

The Red Sea lizardfish, *Saurida undosquamis* (Richardson), invaded the Levant Basin and established a population of considerable commercial importance. Its expansion came at the expense of other commercial fishes on which it preys and with which it competes. The explosion of the Red Sea lizardfish population in the Levant Basin was made possible by a combination of changes in the environmental conditions (abiotic and biotic), one of these being the retreat of, or the recession in, the native hake population. The dynamic coexistence between the lizardfish and the hake, its main competitor, is affected by fluctuations in the abiotic conditions to which the hake seems to be more sensitive than the lizardfish.

A faunistic, zoogeographical approach to the marine animal migration through the Suez Canal is common to most investigators of the canal's influence. Animal species native to one sea and found in the other after the opening of the canal serve as main indicators of its biological influence and of its effectivity as a link to the migrant species and as a barrier to others (Ben-Tuvia, 1966, in press; Kimor, 1970[3]; Por, 1971; Steinitz, H., 1968; Steinitz, W., 1929; Thorson, 1971). Many authors listed and described migrant species (Barash and Danin, 1971[4]; Ben-Tuvia, 1953; Collette, 1970; Gilat, 1964; Gohar, 1954; Gordin, 1966[5]; Holthuis and Gottlieb, 1958; Kosswig, 1951; Steinitz, H., 1967; Tortonese, 1953).

Some authors have discussed the Red Sea-Mediterranean animal migrations in relation to ecological conditions in the canal and in the adjacent sea areas (Gilat, 1966[6], 1969[7]; Oren, 1969, 1970; Por, 1969[8], 1971[9]), suggesting that the mechanism of the penetration of some species through the canal and their expansion in the Mediterranean is associated with environmental conditions (salinity, currents, nature of substrate, etc.).

In this paper we discuss the ecology of the migration and expansion in the new habitat of an important commercial fish. We examine its dynamic coexistence with its native competitor in view of the changing environmental conditions.

The Relative Importance of Species

It is a well-known fact that, while some of the migrant species have established themselves in the new environment, creating populations with a significant impact on the ecosystem, other species may just survive under the new and, perhaps, hostile conditions.

The relative importance of a species in terms of biomass and its role and weight in the food chain is often neglected when two species are listed as "common" or "abundant." One of them may be an important commercial fish with a biomass of an order of tens of thousands of tons or more, and the

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[3]Kimor, B. 1970. The Suez Canal as a link and a barrier in the migration of planktonic organisms. Submitted to the Ocean World-Joint Oceanographic Assembly, Tokyo, 13-25 Sept. 1970, 20 p.

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other is, say, a frequently met small, commercially unimportant, *Apogon*. However, such discrimination should be made: the first fish is a wholesale consumer and also a supplier of important food for other species; the other, although frequently collected, occurs in small numbers, and whatever its importance may be in its immediate biotope, its effect on the whole ecosystem is of little consequence. Therefore, in studying the impact of one sea on the other, number of migrant species should not be overemphasized and more attention should be paid to species of ecological importance.

Commercial Fish Populations as Indicators of the Biological Effect

The most important aspect of interrelations between two seas, especially where a new canal is planned, are the ecological effects which influence the human ecological conditions and economy. To obtain a meaningful picture of the biological effect of the Suez Canal on both seas, emphasis should be put on changes which have considerably affected the large or the commercial populations of either. Obviously, almost any fish species which occurs in great numbers and biomass becomes sooner or later commercially important, either as a marketable product or as a food to commercial piscivores.

Changes in the quantity and composition of important commercial fishes are contained in most fisheries statistics. Of course, this can only be shown where fish landings are reasonably well recorded and where the data obtained may be evaluated to eliminate technological and socioeconomical factors.

Commercially Important Red Sea Migrants and Their Mediterranean Competitors

A number of immigrant Red Sea species have become commercially important in the Levant Basin and/or provide food for both Red Sea immigrants and native fish populations. Sufficient data are available to discuss the expansion of the Red Sea lizardfish, *Saurida undosquamis* (Richardson), and the dynamics of its coexistence with its main native competitor *Merluccius merluccius* (Linnaeus), the hake.

Unfortunately, other species which could serve perhaps as better examples, the yellow-striped goatfish, *Upeneus moluccensis* Bleeker, and its Mediterranean counterpart the red mullet, *Mullus barbatus* Linnaeus, or the barracudas, *Sphyraena chrysotaenia* Klunzinger (a Red Sea migrant), *S. sphyraena* (Linnaeus), and *S. viridensis* Cuvier (both Atlantic species), cannot be used for this purpose as the catch statistics do not discriminate between the species of the same family or genus.

From the information available on the Mullidae (*Upeneus* and *Mullus*), the following can be summarized: Red mullets (Mullidae) represent one of the most important components of the Israeli trawl catches. Their share in the total trawl landings varied between 1956 and 1970 from 29 to 46%, (Sarid, 1951-71). The bulk of the red mullets consists of two species: the red mullet and the yellow-striped goatfish. The latter species is a Red Sea migrant. According to Wirszubski (1953) in the late 40's the share of the yellow-striped goatfish in the Mullidae catch was 10 to 15%. Four years later, Oren (1957) estimated on the basis of Gilat's unpublished data that *Upeneus* formed over 83% of the total number of red mullets caught in trawls during the first half of 1956.

These are two closely related fish species, very similar in their appearance and behavior and apparently competing for the same food (E. Gilat, pers. comm.). Although the red mullet evidently prefers cooler and, thus, in periods, deeper waters than the yellow-striped goatfish (Ben-Yami, 1955; Ben-Tuvia, in press), they mostly occupy overlapping territories. One of them–the invader–succeeded in becoming a majority during 1955 (Ben-Yami, 1955; Oren, 1957). Since 1956, fluctuations continue to occur in the *Mullus* to *Upeneus* ratio. Ben-Tuvia (in press) estimates the average share of the latter fish in the catches of red mullets to be approximately 30%.

What are the reasons for such fluctuations? What are the factors which determine whether a fish which has crossed the canal will establish itself as a sizeable population?

Is it possible that after some years of blooming a migrant population will recede into its previous state, and why? Will an expanding migrant population contribute to the total fish biomass in the new area, or come at the expense of the other fishes?

SOURCES AND RELIABILITY OF DATA

Fishery Statistics

All fisheries data presented in the graphs and

tables are based on statistics collected by the Department of Fisheries (Sarid, 1951-71). These are in general reliable, and the proportion of the hake and the lizardfish in the total trawl catch is well represented. The figures, however, may be biased in some aspects, and the following must be borne in mind:

1. The catch per unit effort for all fish and for each of the two species separately is expressed in kilograms per day at sea of a trawler. The Israeli trawlers operating in the Mediterranean during 1950-70 were powered by 110-to 240-horsepower engines. The average power per trawler varied with time, due to transfer of some to the Red Sea, loss of others, and acquisition of new vessels and engines. It increased steadily in the 50's, decreased in the early 60's, and started increasing again during the recent years (Table 1). Therefore, when examining the data in Figure 5A and B, it should be remembered that the unit of effort varied from year to year.

2. The total fishing effort and the total catches fluctuated partly because of the changing socioeconomical and geopolitical conditions, which determined the extent of the fishing grounds on which the Israeli trawlers could operate in the Mediterranean, and its effect on the size of the active trawling fleet.

3. The character and extent of the trawling grounds available to and/or preferred by the fishermen partly affect the data: In deepwater operations the hake is one of the main fish caught (Ben-Yami, 1971; Zismann, 1971), while the lizardfish is almost absent. In shallow water, trawling depends on the accessibility of the southern trawling grounds, which fluctuated with the Egypto-Israeli relations. On these grounds good summer catches could be obtained in shallow waters, conditions preferred by some skippers to deepwater trawling.

From 1953 to 1960, some of the Israeli trawlers operated during the summer months in the northeastern area of the Mediterranean, between Cyprus and Turkey, mostly in the Bay of Tarsus. Their catches were included indiscriminately in the general statistical data. In these catches, the lizardfish greatly outweighed the hake. Therefore, the catch composition data for these years may be slightly biased in favor of the lizardfish and to the disadvantage of the hake as compared with the other years, but by no means to a degree which might change the general picture.

Sea Temperature

In order to study effects of changes in the environmental factors on the catches of the hake and the lizardfish, the temperatures recorded from the sea between Ashdod and Tel Aviv, an area

TABLE 1.—Changes in the fishing effort, catch and catch-per-effort, 1950-1970, in the Israel Mediterranean trawling fishery.[1]

Year	Number of trawlers	Horsepower Total	Horsepower Average per trawler	Number of days at sea	Catch total of the selected boats (tons)	Catch/100 hp per day (kg)
1950	7	840	120	976	312	265
1951	19	2,420	127	3,102	1,031	211
1952	14	2,070	146	2,152	667	221
1953	14	2,070	146	2,728	997	250
1954	17	2,350	139	3,047	1,160	273
1955	22	3,120	142	3,523	1,494	298
1956	16	2,530	158	2,616	1,162	281
1957	16	2,520	158	3,185	1,335	225
1958	20	3,020	151	4,350	1,575	239
1959	23	3,330	145	5,208	1,878	235
1960	17	2,580	152	3,386	1,077	208
1961	15	2,130	142	2,957	874	295
1962	14	1,990	142	2,694	766	284
1963	13	1,760	135	2,505	647	191
1964	10	1,390	139	1,765	530	215
1965	13	1,800	138	2,443	676	200
1966	13	1,840	141	2,579	561	155
1967	14	2,010	143	2,933	720	195
1968	14	2,070	147	2,985	925	210
1969	14	2,140	153	2,967	979	224
1970	14	2,290	163	3,013	886	180

[1]The data do not include research and training vessels, and vessels which fished less than 100 days per year (E. Grofit, private communication).

situated in the center of the trawl grounds, were examined.

The water temperatures at, or closely below, the 75-m depth (Figure 1), and a number of sea surface temperatures were collected during monthly cruises of Israeli research vessels (Oren and Hornung, 1972, and pers. comm.). During the 21 yr, many monthly cruises were not carried out, hence the numerous gaps (Figure 2).

Additional surface temperature data for the period from 1958 to 1970 are monthly averages of daily monitored temperatures at Ashdod. These were supplied by the Coast Study Division of the Israel Port Authority (pers. comm.).

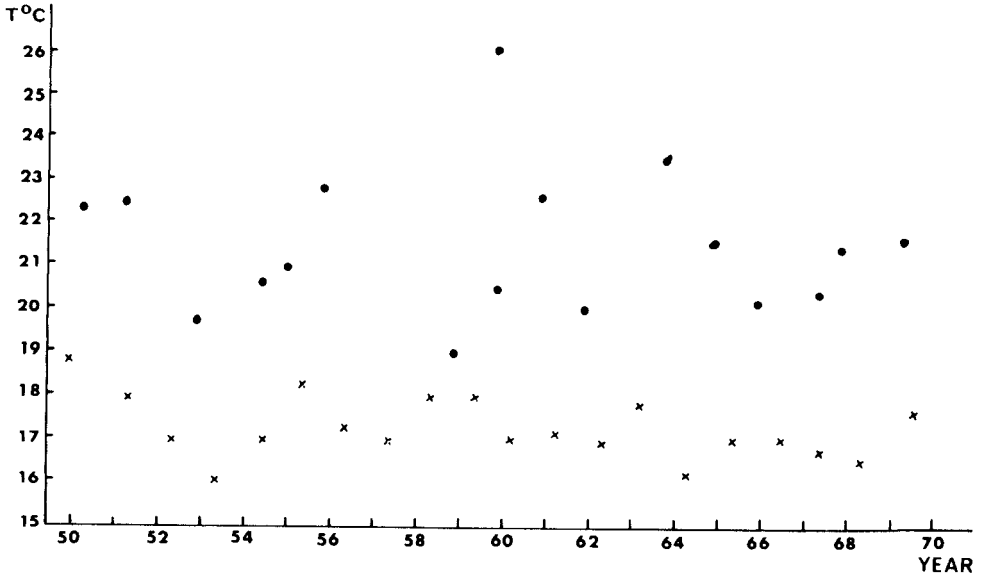

FIGURE 1.—Sea temperatures at depths of 75 m or below, collected during monthly cruises in or near the Tel Aviv-Ashdod area between 1950 and 1970 (Oren and Hornung, pers. comm.). Dots – yearly maxima; cross – yearly minima. In this graph each year begins in January.

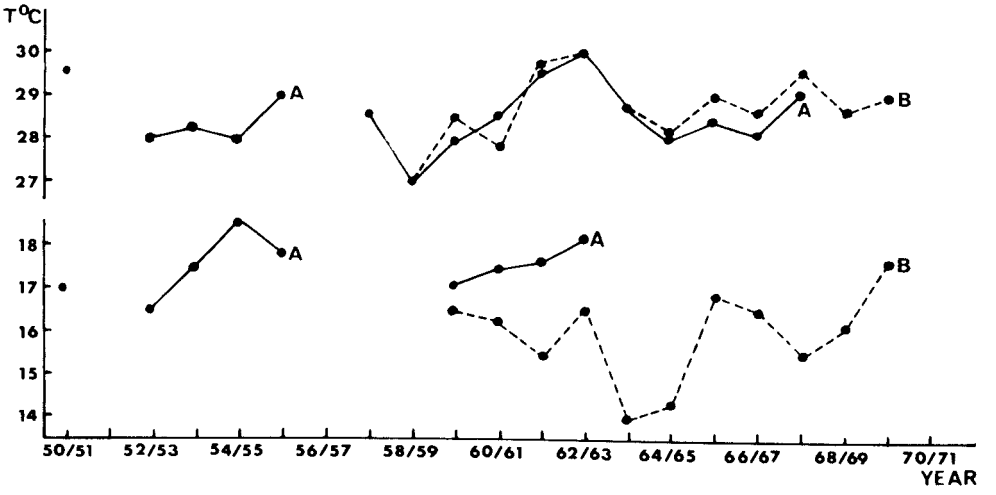

FIGURE 2.—Sea surface temperature. Top – summer maxima; bottom– winter minima. A - Data collected during monthly cruises in the area of Tel Aviv-Ashdod (Oren and Hornung, pers. comm.); B – (dashed line)—monthly means of daily collected data at Ashdod, inshore (Coastal Survey Unit, pers. comm.). Each year starts 1 September.

Meteorology

Air temperature (monthly averages) and precipitation data for 1950-70 were published by the Israel Meteorological Service. These data are complete and uninterrupted for the whole period. Only those data which were collected at stations between Tel Aviv and Ashdod (Anonymous, 1950-71) were chosen (Figures 3, 4).

Presentation

In attempting to find the relationship between climatic phenomena and fish catches, it is simpler to follow a calendar based on seasons with the year beginning in the fall, at the beginning of the rainy season in this area. Thus, for the purpose of this study, the environmental and most of the fisheries data are given according to years which start on 1 September and end on 31 August, i.e., 1 September 1950–31 August 1951 forms the year 1950/51.

In some instances, extreme values rather than annual averages may be influential factors affecting crops or populations. One year may be a rainy year, but most of the rains may not have been timely, etc. For this purpose, some data are presented selectively to emphasize the more critical points. Thus, e.g., the average of the three coldest months, whatever these months may be in each

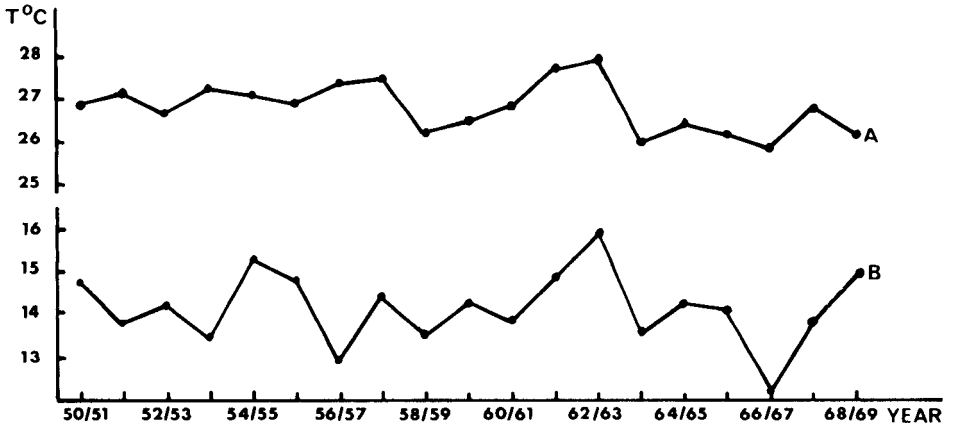

FIGURE 3.—Air temperatures, 1950/51-1968/69 (Anonymous, 1950-70). A – Summer maxima, mean of the warmest month; B – average of three coldest months. Each year starts 1 September.

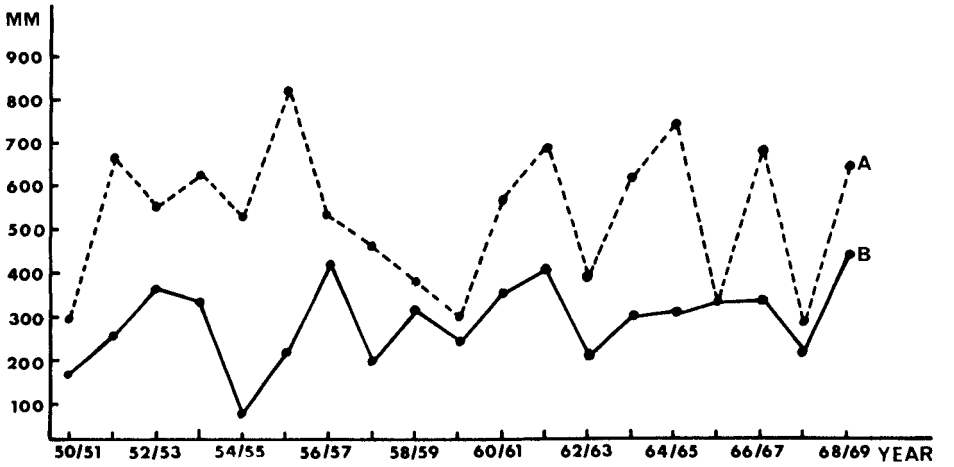

FIGURE 4.—Precipitation, 1950/51-1968/69 (Anonymous, 1950-70). A – September-January; B – January-April. Each year starts 1 September.

year, rather than the annual averages are used. Neither the data presented in this paper nor other available pertinent data have been statistically processed. Therefore we have limited ourselves to seek only most general patterns based on the most obvious dramatic changes and to point out apparent or likely correlations.

THE RED SEA LIZARDFISH

The Invasion

Prior to 1954, two species of lizardfish (Synodontidae) occurred rather infrequently in the catches of the Israeli Mediterranean trawlers: *Synodus saurus* (Linnaeus), a tropical Atlantic and Mediterranean species (Fowler, 1936), and the Red Sea lizardfish, an Indo–Pacific species. The latter was first reported from the Mediterranean as *Saurida grandisquamis* (Gunther) by Ben-Tuvia (1953, in press), who found it for the first time in December 1952. At that time, neither species was of commercial value, and *S. undosquamis* was much rarer than *Synodus saurus* (Ben-Tuvia, 1953, in press; Oren, 1957).

Ben-Tuvia (in press) observed that as early as August 1953 the lizardfish was fairly common in trawl catches taken in the Gaza–El Arish area, with 10 to 20 specimens caught usually in each haul.

In the winter of 1954-55, together with other changes in the composition of trawl catches, the proportion of the Red Sea lizardfish increased to such an extent that the fishermen attempted to market them as a food fish (Ben-Yami, 1955). Consequently, in 1955 lizardfish appeared for the first time in the statistics of landings (Sarid, 1956).

In the summer of 1955, unusual numbers of fingerlings were found in the cod ends of trawl nets. The bulk of them consisted of two Red Sea species, the yellow-striped goatfish and the lizardfish (Ben-Yami, 1955).

In 1955-56, the lizardfish became one of the main commercial fishes in Israel; its proportion in the total landings of Israel's marine fishery reached 11% (Sarid, 1956), and in the trawl fishery landings approximated 20% (Figure 5). Catch data collected during 1955 and 1956 (Oren, 1957) indicate that the Red Sea lizardfish made its first significant appearance in the trawl catches in the fishing grounds off the Gaza Strip and North Sinai. By the end of summer and autumn of 1955 it had expanded all over Israel's fishing grounds.

During the period 1952-60, most Israeli trawlers fished in the summer months in the northeastern part of the Mediterranean (Gulf of Tarsus and neighboring waters). The Red Sea lizardfish, however, was not found in those waters in 1952 by Gottlieb and Ben-Tuvia (1953), who produced a detailed list of 52 fish species caught in a trawl catch. By summer 1956, it was common in the trawl catches in the Bay of Tarsus (Ben-Tuvia, pers. comm.), and since then it has become well established and is one of the most important commercial fish in that area.

The quantity of lizardfish caught by the trawlers continued to increase until 1959 when almost 400 tons (20% of the total trawl catch) were landed (Sarid, 1960). This was followed by a 4-yr recession. In 1963, the catches dropped to an approximately 120-ton low, and since then, they apparently stabilized near this level with "normal" annual fluctuations.

Food and Habitat of the Red Sea Lizardfish

The lizardfish is a demersal piscivore. Its food in the Levant Basin was studied by Bograd–Zismann (1965) and by Chervinsky (1959). Bograd–Zismann examined some 1,500 stomachs, of which 859 contained food. Of these, 77.3% contained fish; the rest contained invertebrates, mostly crustaceans, and digested matter. Chervinsky examined some 500 stomachs, of which 131 contained identifiable food. Large invertebrates were found in only 16 stomachs; the rest contained fish. Both authors indicate that the most frequent prey of the Red Sea lizardfish are clupeoid fish–according to Chervinsky (1959) anchovy, and according to Bograd–Zismann (pers. comm.) mostly anchovy, but also some sardines.

The second important group in the food of the lizardfish are fish of the family Mullidae (Bograd–Zismann, 1965; Chervinsky, 1959). Other important groups in the lizardfish food are Gobiidae, Centracanthidae (listed as Maenidae by Bograd-Zismann, 1965, and by Chervinsky, 1959), and *Leiognathus klunzingeri* (Steindachner) (Bograd-Zismann, 1965; Chervinsky, 1959; Ben-Tuvia, 1966).

No direct information is available on the diurnal-nocturnal feeding activity of the lizardfish in the Levant Basin. Nonetheless, the high proportion of anchovy in the food of the

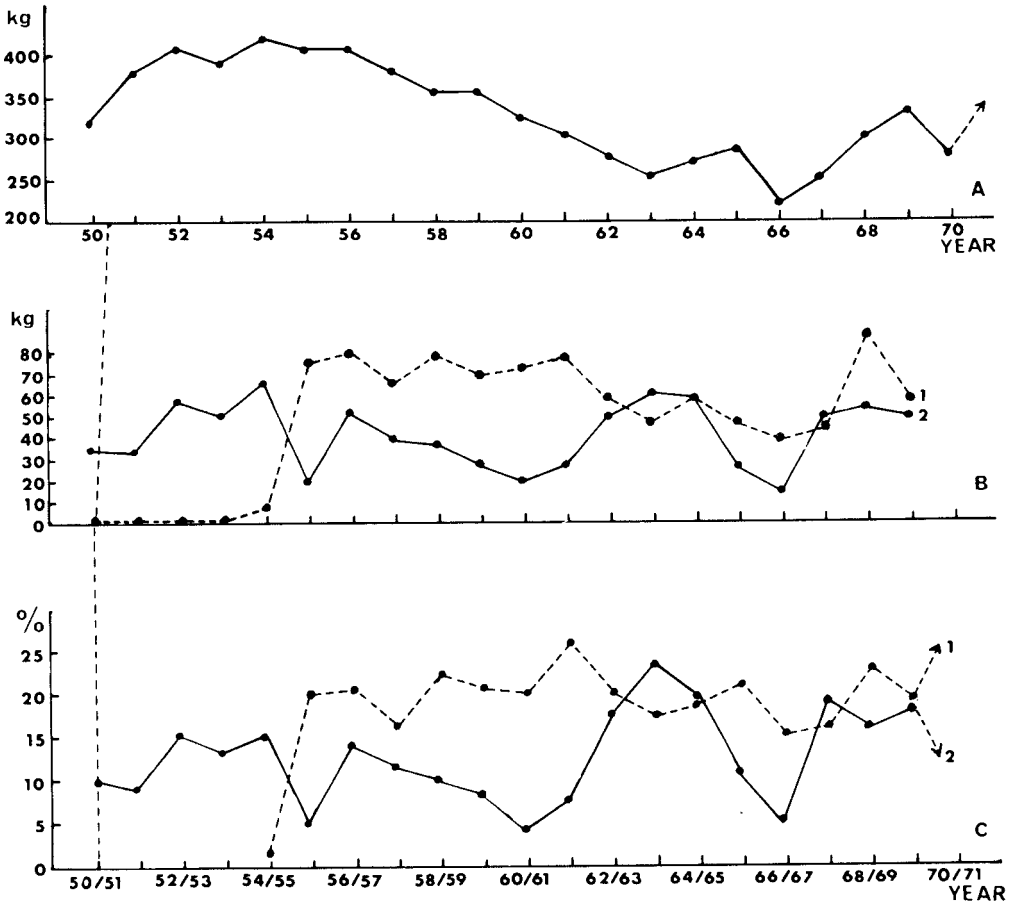

FIGURE 5.—Changes in the hake—Red Sea lizardfish relationship in catches and the catch-per-unit-effort (cpu) in the Israel trawl fishery in the Mediterranean, 1950-70 (Sarid, 1951-71). A - cpu—all fish, each year starts 1 January; B - cpu—(1) lizardfish, (2) hake; C - proportion in catch, percent: (1) lizardfish, (2) hake. B and C—each year starts 1 September.

lizardfish may indicate that either the lizardfish is a demersal feeder, feeding on clupeoids only when it approaches the bottom of the sea during the hours of light, or that it ascends during the night to the upper water layers where it could feed on these pelagic fish. We favor the first hypothesis, for the lizardfish almost never occurs in the night catches of purse seines in light fishing. This hypothesis is corroborated by observations of Hiatt and Strasburg (1960) of two lizardfishes, *Saurida gracilis* and *Synodus variegatus*, of the Marshall Islands. The lizardfish lie motionless, on or partly buried in the sand, and are virtually impossible to detect. Only when small fish come within a distance of a few feet, the lizardfish seize them in a rapid dart. They were rarely observed to ascend for more than 3 to 4 feet while attacking their prey.

Hayashi, Yamaguchi, and Hanaoka (1960) and Tōriyama (1958) reported on the basis of stomach examinations that *S. undosquamis* in Japanese waters feeds during most hours of day and night. According to Tōriyama, however, feeding activity is most intensive during the early morning hours.

According to Chervinsky (1959), the lizardfish is cannibalistic. Bograd-Zismann (1961-62) observed that the occurrence of lizardfish in stomachs may rather be a result of panicky indiscriminate attacking in the trawl cod end.

The Red Sea lizardfish in the Levant Basin prefers rather shallow waters. It is caught in the cooler seasons at depths generally not exceeding 45 fm

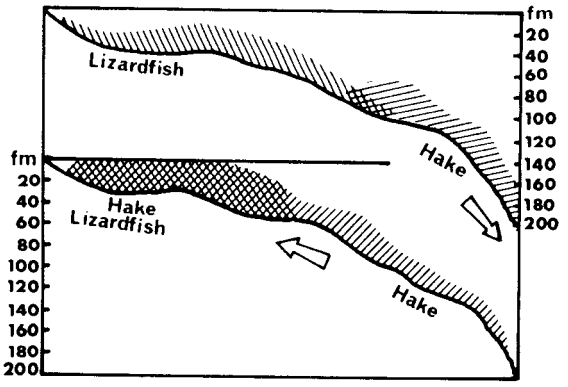

FIGURE 6.—The overlapping habitats of the Red Sea lizardfish and the hake over the Israel continental shelf. Top – summer; bottom – winter. Depth in fathoms.

(fathoms), but mostly at less than 35 fm (Figure 6). During the warm season the lizardfish may spread over deeper trawling grounds. Occasionally it occurs in catches made at 80 to 100 fm. In general, however, the lizardfish is of no commercial significance over the deepwater trawling grounds (Ben-Yami, 1971; Zismann, 1971).

Spawning

There is very little biological information on the Red Sea lizardfish in this area. Bograd-Zismann (see footnote 10) and Chervinsky (1959) found that ripe, nearly ripe, and partly spent females occur in catches almost all year long, though the former author indicated that the greater proportion of nearly ripe females occurs in the early summer. It has to be borne in mind that a fish may spawn over a prolonged season, while the survival of its fry may be confined to a much shorter period controlled by favorable, seasonal conditions.

The area of spawning can only be speculated as being offshore and in deep water. This is based on the following information: Neither larvae nor juveniles of *Saurida* were taken during an extensive survey of fish larvae made using neuston nets (Ben-Yami et al., 1970) and Isaacs–Kidd midwater trawl off the coast of Israel and Sinai during 1967-69. This survey consisted of 25 cruises covering inshore (Haifa Bay, Bardawil Lagoon), shallow water, and offshore stations. Only once, in December 1968, were *S. undosquamis* fry taken: nine 11-20 mm specimens were caught in deep water in the Isaacs-Kidd trawl, at a station situated 7 miles west of Cape Carmel, over 200 fm depth (Lourie, Herzberg, and Ben-Yami, 1969[11]; Lourie, pers. comm.).

The very fact that *S. undosquamis* larvae and juveniles did not occur either among the thousands of fish larvae and juveniles caught in neuston nets during day and night tows (Lourie et al., see footnote 11; Lourie, pers. comm.) or in samples taken by means of a light trap for small photokinetic organisms (Zismann, 1969) seems to indicate that they do not occur in the surface water layer, neither during the day nor by night. On the other hand, the capture of the young in December, over deep water and apparently deep in the midwater, coincided with the seasonal temperature increase at this level (Oren, 1970) (Figure 1).

Growth

Chervinsky (1959) has measured the length frequency of the lizardfish between June and December 1957, concluding that while the bulk of the lizardfish catch consisted of fish between 16 and 24 cm long, they grew fast; 2 cm per month. No males exceeding 24 cm were found, although females exceed 30 cm.

Bograd-Zismann (see footnote 10) examined the scales of the lizardfish. Two annuli were found on the scales of fish 22 to 30 cm total length (TL). On the scales of fish 19 to 22 cm TL, one annulus was seen, but there are indications that the year's growth is not marked by a clear annulus. Thus, it seems that the age of the lizardfish at recruitment is about 2 yr or may be 3 yr, the bulk of the fish in the catch being at least 2 yr old.

Relation with Relative Species

To complete the ecological picture of the Red Sea lizardfish, its relationship with two of its relatives should be mentioned: one is the Atlantic-Mediterranean lizardfish, *Synodus saurus*, and

[10]Bograd-Zismann, L. 1961-62. Interim report on the study of the food of *Saurida undosquamis* in the Mediterranean Sea. Unpubl. manuscr. In files of the Isr. Sea Fish. Res. Stn., Haifa.

[11]Lourie, A., A. Herzberg, and M. Ben-Yami. 1969. A survey of neustonic fishes off the Mediterranean coast of Israel and Sinai, 1968. *In* Interim Report, Joint Research Project "Biota of the Red Sea and the Eastern Mediterranean," p. 133-150. The Hebrew University of Jerusalem and the Smithsonian Institution, Washington, D.C. [Processed.]

the other is the Indo-Pacific species greater lizardfish, *Saurida tumbil* (Bloch). The first is a quantitatively insignificant and hence noncommercial demersal predator in the Levant Basin. Although a natural competitor to the latter, the native *S. saurus* was superseded by the invader, being now as rare as ever.

Saurida tumbil is one of the main commercial fishes and dominates in the south Red Sea trawl fishery. Another species, *S. undosquamis,* is the "underdog" there, though not as rare as *Synodus saurus* is in the Levant Basin. *Saurida undosquamis* holds ground only in deeper and, evidently, cooler waters, while *S. tumbil* dominates over most of the trawling grounds (Ben–Tuvia, 1966). On the other hand, it is *S. undosquamis,* probably the euryecous of the two, which spread into the northern Red Sea, becoming the only significant lizardfish in the Gulf of Suez and the Levant Basin.

HAKE

Another important commercial fish whose habitat and food in the Levant Basin indicate that it is the main competitor of the lizardfish is the hake, *Merluccius merluccius.* This is an eastern Atlantic species which is also native to these waters (Ben-Tuvia, 1953), and whose biology and habits in the Levant Basin still remain to be studied.

In the Atlantic Ocean the hake is known as a voracious predator, feeding during the day at the bottom and rising at night into higher water layers. It is known as a deepwater species caught at depths down to 400 fm. Off the British Isles, it seems to prefer water temperatures of around 10°C.

Spawning and Growth

Near the British Isles, the hake spawns mostly at or near areas over the 100-fm isobath. Females spawn up to a million eggs each. The eggs are pelagic, floating on the sea surface. Before hatching, which occurs within a fortnight, the eggs descend to midwater, where the larvae hatch and develop. The yolk is absorbed within 3 to 4 wk after which the postlarvae feed on zooplankton. The fry descend to the bottom, where hake 3 to 4 cm long were taken. They reach 10 cm at the year's end and become mature at 20 cm (Marshall, 1965; Travis Jenkins, 1954).

Feeding in Israel Waters

Shmida (1964)[12] investigated 76 stomachs of which 49 contained food. The fish were from catches taken in summer and spring. While the bulk of the food taken in spring consisted of crustaceans (mostly Decapoda, Macrura), the food of hake caught in summer was mostly fish. Shmida concludes that, in general, the food in terms of weight was half crustaceans and half fish. All identifiable fish were anchovy. Unfortunately, Shmida had at his disposal only small individuals, less than 27 cm long. Larger, faster, and stronger hake may have a different diet in which the proportion of fish may be higher. This was indicated by a slight trend of more fish in the stomachs of the larger hake, even within the narrow length range investigated (Shmida, 1964).

Habitat

The hake prefers cool water. This is evident from its occurring over the shallow trawling grounds only during the cooler season of the year. Its proportion in trawl catches can be considerable, even at depths less than 20 fm, if the water is cold enough. With the approach of the warm season, the hake retreats to the deepwater regions where it remains available to trawls at depths over 100 fm throughout the season (Ben-Yami, 1971). Figure 6 illustrates the relative distribution of the lizardfish and the hake over the Israeli continental shelf and their overlapping habitats.

RED SEA MIGRANTS AS PREY OF THE HAKE AND THE LIZARDFISH

As mentioned above, both our predators feed extensively on anchovy. It seems, nevertheless, that the hake competes with the lizardfish also for other fish, some of them Red Sea migrants. Ben-Tuvia (1966) reports that two of them, *Leiognathus klunzingeri* and a Red Sea goatfish, *Upeneus asymmetricus* Lachner (reported previously as *U. tragula* Richardson), are components of the food of both the lizardfish and the hake. *Leiognathus,* a trash fish in trawl catches, has been, undoubtedly, of major importance in the food

[12]Shmida, A. 1964. T'zunat dagim b'Yam Tikohn uv'Yam Suf (Food of fishes in the Mediterranean and the Red Sea). [In Hebrew.] Unpubl. manuscr. In files of the Isr. Sea Fish. Res. Stn., Haifa.

chain of demersal piscivores (Ben-Tuvia, 1966), and has declined (Ben-Tuvia, in press b) since its peak bloom in the 50's. Ben-Tuvia attributes this decline to the spread of the lizardfish, one of its main predators. The *U. asymmetricus*, usually small, does not occur in commercial quantities, and in the catches it is classified with the other red mullets.

Another Red Sea migrant, the yellow-striped goatfish, *Upeneus moluccensis* has not yet been identified from the stomachs of the hake. There are good indications that, ecologically, both the *Upeneus* and the lizardfish are closely related in a prey-predator relationship. They occupy the same habitat, the goatfish being an equally rare visitor at the deepwater trawling grounds (Zismann, in preparation). Both species seem to increase in catches during the same years (Ben-Yami, 1955; Oren, 1957), which may be associated with environmental conditions.

It is, thus, very likely that in areas where they are both found, the hake and the Red Sea lizardfish compete for food.

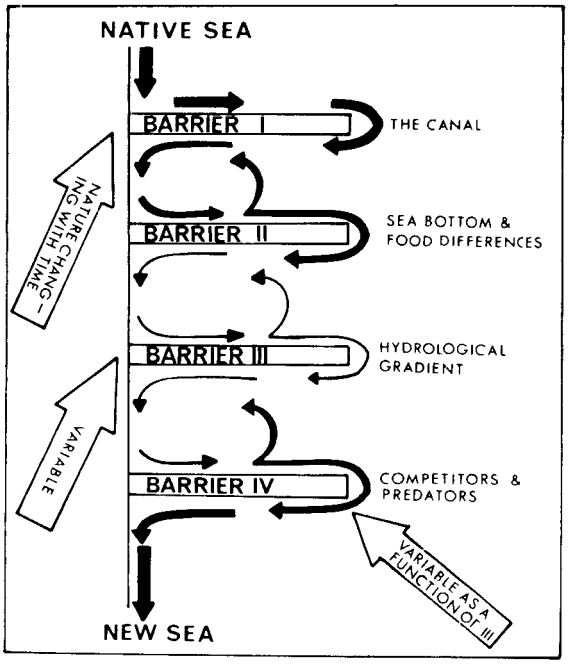

FIGURE 7.—"Barriers" on the path of a migrating species of demersal fish the last three "barriers" may occur in any order and/or overlap.

THE MECHANISM OF AN INVASION

Ecological "Barriers" to Migrating Species

A demersal fish expanding from one sea to another through a man-made canal encounters several barriers which it must overcome before a significant population can be established in the other sea (Figure 7). The "height" of an ecological barrier differs for each separate species. Hypersalinity, e.g., which may be prohibitive to some purely marine species, may not be a barrier or may even possess attractive environmental qualities to euryhaline organisms. The height of an ecological barrier may also change with seasonal, annual, and multiannual fluctuations in the environmental conditions.

The first barrier is the canal itself which may represent a less or more hostile environment for the migrating species. Migration through the Suez Canal must have been very difficult for some and impossible for other species, because of the complex hydrological conditions in the canal (the high salinity of the Bitter Lakes, freshening of the water due to influx of fresh water at some places, and the seasonal Nile floods) (Oren, 1970; H. Steinitz, pers. comm.). The nature of the Suez Canal, as a barrier, has changed, however, with time. Animal migration through the canal may now become easier (Thorson, 1971).

The second barrier, especially for demersal species, is the difference in bottom conditions. The importance in the character of the substrate for the expansion of migrating benthic invertebrates was emphasized by Gilat (see footnote 6) and Por (1971). The type of bottom influences the type and quality of food available. Bodenheimer (1966) emphasized the negative effect which lack of food may have on fecundity. De Vlaming (1971) has shown that starvation affected the gametogenesis and gonadal regression in a goby, *Gillichthys mirabilis*. Undoubtedly, it is not enough for a bottom fish just to cross a canal. To survive and reproduce, it must find in its new habitat either the food to which it is accustomed or a food which can replace the former both quantitatively and qualitatively at all stages of its life cycle. This condition is, generally, controlled by the character of the sea bottom.

A third barrier is the hydrological gradient (if any) between both seas. A species may cross a canal, may even find an apparently suitable habitat, but all its spawn may be killed by extreme winter or summer temperatures. Also, adverse

temperature conditions may affect prespawning, reproductive processes in fish (De Vlaming, 1971), while difference or seasonal changes in salinity may affect survival of a stenohaline species.

Oren (1970) has noticed, e.g., that after the critical 1954/56 years, the minimum seawater winter temperatures over the Israel continental shelf have never returned to their values of 15°C measured prior to this period. He also found that the salinities in the same area increased since the closure of the Aswan Dam in 1964. It seems, thus, that in the long run, the hydrological gradient between the Gulf of Suez, where the temperatures and salinities are higher than in the Levant Basin (Kosswig, 1951; Oren, 1957; Ben-Tuvia, 1966) and the Mediterranean, is on the decrease.

The fourth barrier is the predators and competitors. Darwin (1859) emphasized the role of prey, predators, and competitors on the distribution range of species. Obviously, the abundance and distribution of the native predators and competitors are affected by fluctuations in the hydrological conditions. Therefore, changes in the hydrological conditions may affect establishment of the migrant species both directly and, through their competitors, indirectly.

Human Interference May Facilitate Invasion

An invasion may succeed because of human interference in the environment. Elton (1958) has shown that such interference, especially where associated with depletion of native populations, considerably increases the vulnerability of an area to invasions. We consider commercial fisheries to be an example of an extreme interference.

The Explosion of the Red Sea Lizardfish Population

The lizardfish, *Saurida undosquamis*, is an important component of the Egyptian trawl catches in the Gulf of Suez (Latif, 1971). The early records of lizardfish in the Suez Canal by Gruvel and Chabanaud (1937), as *S. sinaitica*, *S. tumbil*, and *S. gracilis*, may have been *S. undosquamis* (Ben-Tuvia, pers. comm.).

Fifteen years later, and 83 years after the opening of the Suez Canal, the Red Sea lizardfish appeared in the southeastern Mediterranean in sufficient numbers to be described as a "rare" fish (Ben-Tuvia, 1953). But within 2 to 3 yr, it became one of the most important commercial trawl fishes forming 20% of the catch. This recalls the invasion of the sea lamprey, *Petromyzon marinus*, in the Great Lakes in North America (Elton, 1958). Although the Welland Ship Canal was opened as early as 1829, the sea lampreys were observed in Lake Erie 100 yr later. Then, within 10 yr, the lamprey population expanded rapidly and dramatically both in space and in number, causing a collapse of the lake trout fishery in Lake Michigan and Lake Huron.

The population explosion of the Red Sea lizardfish was much faster, for its 1959 all-time record landings occurred only 4 yr after its first appearance in the trawl catch as a fraction of a percent.

Although the subsequent decline in the lizardfish catch may be associated with decrease of the fishing effort (Tables 1 and 2), particularly in the northeast Mediterranean, its relatively stable proportion in the total catch indicates that an ecological balance was reached within the first 2 yr of its appearance in the commercial catch (Figures 5, 8). Subsequent annual fluctuations seem to be normal to natural populations.

TABLE 2.—Israel trawl fishery, 1948-70.

Year	Number of trawlers	(activity %)[1]	Total landings (tons)
1945	25	(56)	508
1946	11	(73)	333
1947	12	(67)	258
1948	12	(46)	111
1949	14	(57)	430
1950	30	(54)	1,092
1951	27	(43)	929
1952	23	(49)	1,000
1953	23	(56)	1,286
1954	22	(75)	1,480
1955	27	(63)	1,518
1956	26	(60)	1,391
1957	27	(69)	1,550
1958	29	(77)	1,740
1959	27	(92)	1,952
1960	25	(69)	1,274
1961	19	(70)	992
1962	18	(75)	830
1963	17	(74)	706
1964	15	(76)	615
1965	18	(70)	761
1966	18	(77)	638
1967	16	(87)	741
1968	16	(80)	926
1969	16	(91)	1,028
1970	19	(82)	930

[1]Activity index (100%):
below 150 hp 210 days at sea per trawler.
over 150 hp 230 days at sea per trawler.

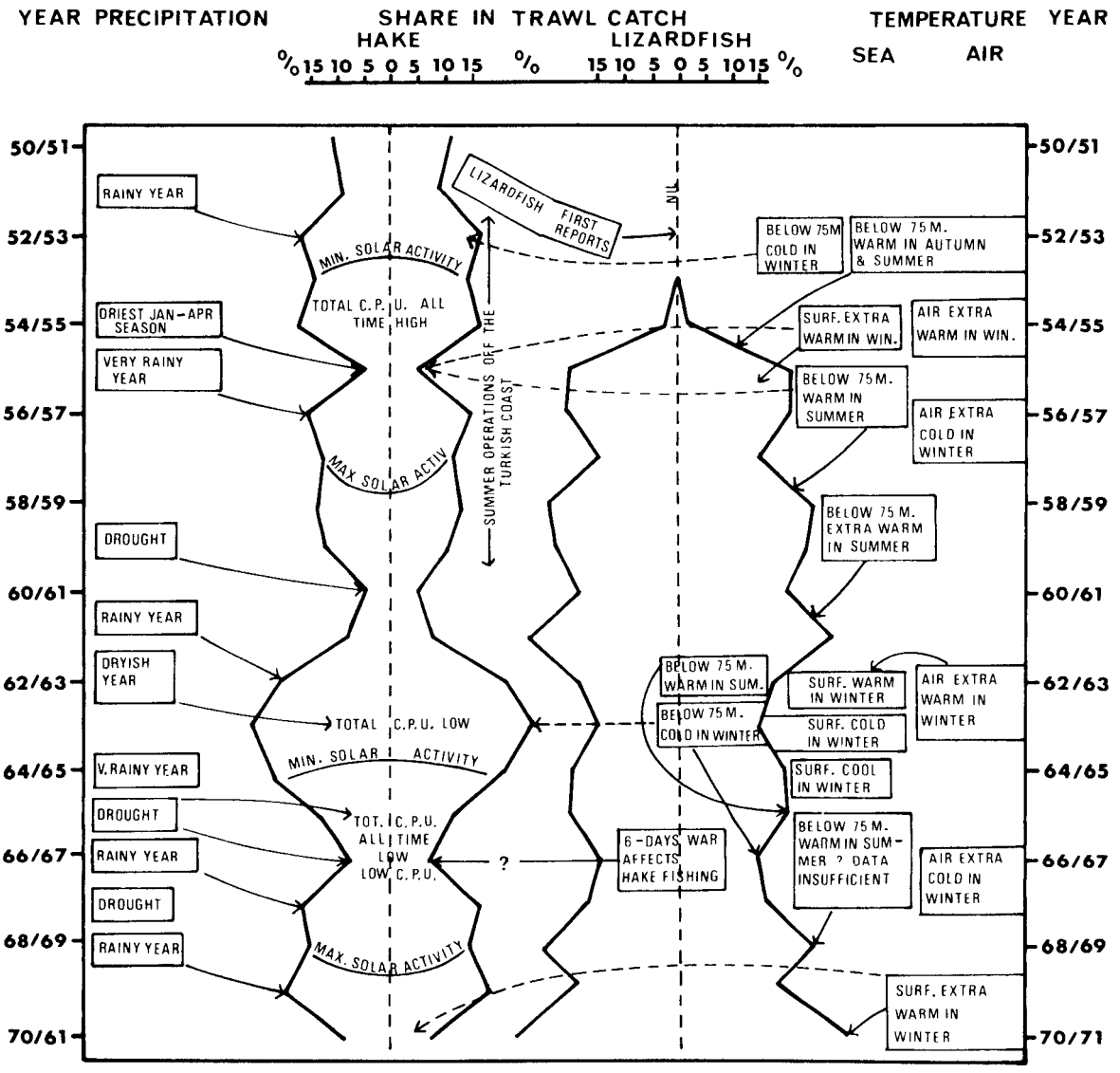

FIGURE 8.—Changes of the proportion of the hake and the Red Sea lizardfish in the Israel trawl landings and their relationship with environmental conditions, 1950-71.

Hence, in the case of the lizardfish, the population-growth logistic curve (Bodenheimer, 1966) would have been extremely steep in its central part with extremely sharp flexes between the first and the central sections and, again, between the central and the third sections of the curve. It can be, therefore, speculated that this invasion and expansion were not only a product of a "normal" population growth but were also aided by additional factors.

The Role of Environmental Factors

The sudden buildup of the Red Sea lizardfish population which occurred between 1954 and 1956 was accomplished by a series of unusual phenomena: 1) unusually high temperatures, both of air and water (Ben-Yami, 1955; Oren, 1957), especially in winter (Figures 1, 2, 3); 2) the extremely dry January-April season of 1955 (Figure 4), as well as a very pronounced absence of winter

gales of anticyclonic depression origin, during the same winter (Ben-Yami, 1955); 3) the hake made a very poor appearance in the 1955/56 Israel trawl catches (Figures 5, 8), decreasing to approximately 40% of its 20 yr average (Figures 5, 8) in the catch and to approximately 42% of its 20 yr average (Figure 5) in its catch per fishing day. Since then, such low catches of the hake only occurred in 1960/61 and in 1966/67. In all three cases, the drop in the hake catches seems to be associated with drought: it followed the January–April drought in 1955, in 1959/60 and 1966/67 it followed a drought in the preceding winter (Figure 8).

Trawl Fishery's Rapid Development

The rapid intensification of the Israel trawl fishery 1949-54 (Table 2) was probably another important factor contributing to the expansion of the Red Sea lizardfish. The landings, which before 1940 were 100 to 500 tons, rose to approximately 1,000 tons/year during 1950–52 and to almost 1,500 tons in 1954, when the first commercial catches of the lizardfish were taken.

Before 1950, the Israeli trawlers did not fish in waters deeper than 50 to 60 fm. Since 1950, deepwater trawling operations have been carried out, and hence there has been considerable exploitation of the hake resources (Ben-Yami, 1971).

DISCUSSION AND CONCLUSIONS

The set of conditions which prevailed just before and during the explosion of the Red Sea lizardfish population and which, apparently, facilitated this explosion included:

1. "Preparation" of the area due to the intensification of the trawling fishery by the factor of 3-4 (Table 2);
2. Water temperature conditions which contributed to good survival of several strong year classes of lizardfish;
3. A combination of climatic (drought) and water temperature conditions which caused the withdrawal of the hake from most of the trawling grounds, leaving ample space for the spread of the lizardfish.

It is possible that the population of the Red Sea lizardfish in the Levant Basin has been and, without these conditions, might have remained "dormant" and suppressed by its competitors and by unfavorable environmental conditions. It may have been still waiting for its opportunity to expand.

The fluctuation in the abiotic conditions, subsequent to the lizardfish explosion years, seems to be correlated with the fluctuations in the catches of both the lizardfish and the hake, though with an "anomaly" in 1961-63 when, in spite of two consecutive warm winters, the proportion of hake increased in comparison to the lizardfish. Here, e.g., the abundant rains of 1961-62, or other factors might have intervened (Figure 8).

The hake is much more sensitive to the fluctuations of physical conditions than the lizardfish, as may be seen from the shape of the respective columns in Figure 8. The declines in the hake catches indicate either recessions in the population or a geographical retreat from the usual fishing grounds, probably into deeper and cooler waters, or a combination of both.

An interesting feature of the fluctuation of the hake proportion in catches is that so far they are in phase with those of the solar activity index (Figure 8), though this correlation may be purely incidental.

The interrelations discussed in this paper are very complex. Different and, perhaps, even variable time lags have to be employed to correlate abiotic, biotic-natural, and man-activated (fisheries) factors. A study for further pursuit along this line will require the application of computer technique. Unquestionably, a good opportunity for studying the influence of environmental conditions on the relationship of competing migrant and native species was lost when data on the *Mullus–Upeneus* and Red Sea Barracuda–Atlantic Barracuda proportion in catches were not collected during the past years. Such studies should be undertaken in the future.

An examination of the available statistical data (Sarid, 1951-71) could not establish any significant influence of the appearance of the Red Sea lizardfish in the total trawl catches on the landings, catch per unit effort, or returns of the trawl fishery. Undoubtedly, the lizardfish is not just an additional inhabitant, and its invasion did not enrich the existing ecosystem in terms of biomass. It occurs in the catches at the expense of other fish, partly its competitors, such as the hake, and partly its prey, such as the yellow-striped goatfish, red mullet, etc.

The proportion of the lizardfish in the trawl catches has never, after its 1954-56 invasion, been less than 13%, although there have been several

cold winters since (Figures 2, 3, 8). This, besides indicating that the Red Sea lizardfish is fairly eurythermic, may also support Kosswig's (1972)[13] suggestion of the role of the modificability of species in new environments. It is quite probable that the Mediterranean stock of the Red Sea lizardfish today is better adapted to the local environmental conditions than it was 20 yr ago.

The Red Sea lizardfish proved vigorous enough to establish itself in a niche in a habitat occupied by other species; it is euryecous enough to withstand fluctuations in environmental conditions; and, barring an ecological disaster, it is here to stay.

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SUMMARY OF SELECTED EARLY RESULTS FROM THE ERTS-1 MENHADEN EXPERIMENT[1]

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ABSTRACT

A 15-mo study was initiated in July 1972 to demonstrate the potential of using satellite-acquired environmental data to provide fisheries information. Imagery from ERTS-1 (Earth Resources Technology Satellite) was used in conjunction with aerial photographically sensed menhaden distribution information, sea-truth oceanographic measurements, and commercial fishing information from a 8,670-km² study area in the north central portion of the Gulf of Mexico. Objectives were to demonstrate relationships between selected oceanographic parameters and menhaden distribution, ERTS-1 imagery and menhaden distribution, and ERTS-1 imagery and oceanographic parameters. ERTS-1, MSS Band 5 imagery density levels correlated with photographically-detected menhaden distribution patterns and could be explained based on sea-truth secchi disc transparency and water-depth measurements. These two parameters, together with surface salinity, Forel-Ule color, and chlorophyll *a*, also were found to correlate significantly with menhaden distribution. Eight empirical models were developed which provided menhaden distribution predictions for the study area based on combinations of secchi disc transparency, water depth, surface salinity, and Forel-Ule color measurements.

A need of managers and users alike of living marine resources is timely synoptic information about the distribution and abundance of the resources. For users, this need is particularly critical in that daily decisions must be made about where to deploy fishing vessels and less frequent decisions about investment strategies for men and equipment. The increasing pressures placed on living marine resources by domestic and foreign fishing fleets interacting with environmental changes demand that resource managers also be kept fully aware of the current status of the stocks to prevent possible catastrophic fluctuations in specific fish populations. Unfortunately, the tools required to satisfy this need economically are lacking, forcing users to base decisions on inituition and often biased personal knowledge and resource managers to formulate recommendations based on historical rather than current information. In response to this need, a number of relatively new technologies are being examined by the National Marine Fisheries Service and, in particular, the technologies associated with aerial and satellite remote sensing, to determine if they can be used to provide pertinent fisheries resource information.

A 15-mo study was initiated in July 1972 to demonstrate the potential of using satellite-acquired information to predict the distribution and abundance of a fishery resource. The study represented a combined Federal Government and private industry effort and stressed acquisition of data to:

1. determine the reliability of satellite and high-altitude aircraft-supported sensors to provide information about selected oceanographic parameters in coastal waters;
2. demonstrate the feasibility of using remotely-sensed oceanographic information to predict the distribution and abundance of a selected species;
3. demonstrate the potential of using satellite-acquired information for improving the harvest and management of a fishery resource and;
4. identify necessary sensor techniques or developments to satisfy selected needs of resource users and managers.

This paper presents a summary of selected results from the experiment. Earlier publications dealing with the experiment have stressed its management (Stevenson, Atwell, and Maughan,

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1972), relationships between selected oceanographic parameters and fish distribution and abundance (Kemmerer and Benigno, 1973), and commercial fishing operations (Maughan, Marmelstein, and Temple, 1973).

EXPERIMENTAL RATIONALE

With existing technology, fish cannot be detected directly with sensors aboard orbiting satellites. It may be feasible, however, to use satellite sensors to measure selected environmental parameters and then to use these parameters to predict, and in some cases even forecast, the distribution and abundance of a fish species. The quality of these predictions or forecasts would depend on how accurately the parameters are measured with the sensors, how precisely the parameters correlate with the distribution of specific fish populations, and how accurately the values were predicted.

The rationale employed in the experiment was to convert data obtained with ERTS-1 or aircraft-supported sensors into oceanographic parameter information, attempt to derive correlations between these parameters and the distribution and abundance of a selected fishery resource, and then determine if the relationships have meaning for commercial fishing operations and resource management. Data obtained with the satellite were supplemented with data obtained with sensors aboard aircraft to provide a broader spectrum of environmental information. In addition, a massive sea-truth sampling effort was undertaken to provide calibration data for remote sensors and backup information for correlation analyses.

STUDY AREA AND FISHERY

The study area was a 8,670-km^2 rectangle situated in the north central portion of the Gulf of Mexico (Figure 1). It included coastal areas of Alabama, Mississippi, and Louisiana and encompassed all of the Mississippi Sound, the southern portion of Mobile Bay, and extended offshore from the Mississippi Sound to approximately the 18-m depth curve. The study area is divided in half lengthwise by five barrier islands which isolate the typically turbid, low-salinity waters of the Mississippi Sound from the relatively much clearer oceanic waters of the offshore portion of

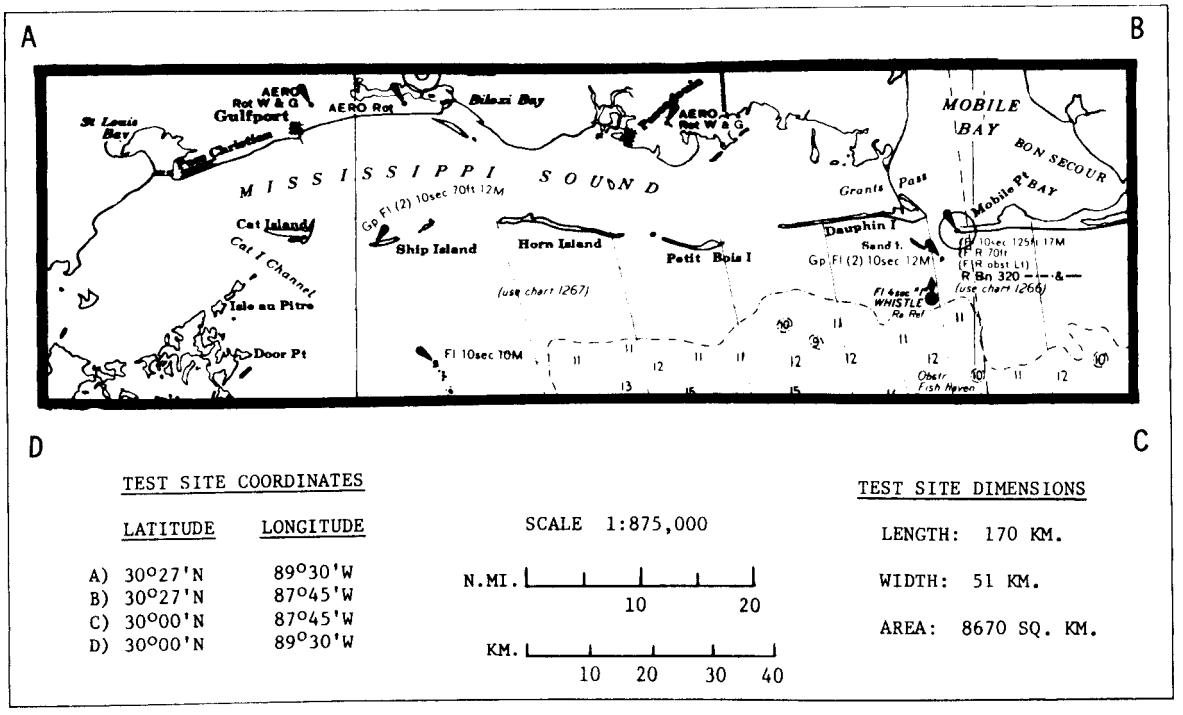


FIGURE 1.—ERTS-1 menhaden experiment study area.

the study area. A comprehensive description of the area is given by Christmas (1973).

The target fish species for the study was the small (mean weight about 85 g), herringlike, surface-schooling Gulf menhaden (*Brevoortia patronus*). These fish occur along the Gulf of Mexico coast and are considered to be an estuarine-dependent species. They are used commercially as a source of fish meal, oil, and condensed soluble proteins. In the Mississippi Sound, menhaden are fished from about mid-April to October by twin purse seine boats assisted by spotter pilots flying light aircraft. The spotter pilots direct the purse boats to the menhaden and then through radios notify the boat captains when to encircle a school with their purse seine. Once a school is captured and concentrated in the net, a larger mother or carrier vessel is brought alongside and the fish are pumped into the hold of the ship.

Menhaden are plankton feeders using a sievelike branchial apparatus to strain plants and animals from the water (Reintjes, 1969). Their characteristic schooling behavior, which seems innate from late larval stage to old age, makes them particularly available to commercial fishing. School size varies from about 25 to in excess of 2,000 m^2 (surface area) and averages about 125 m^2. Although Gulf menhaden have been the subject of many investigations (Christmas and Gunter, 1960; Gunter and Christmas, 1960; Reintjes, Christmas, and Collins, 1960; and Rounsefell, 1954), little is known about their distribution in relation to environmental parameters.

DATA ACQUISITION

Data acquisition events were divided into four operations categories: main day, secondary day, special purpose, and commercial fishing operations. Main day activities occurred at or near the time of selected ERTS-1 overpasses (7 August, 25 August, and 28 September 1972) and included an intensive sea-truth sampling effort-up to 144 stations were occupied. Only a few sea-truth stations were occupied during secondary day missions, which were conducted weekly, weather permitting, to record temporal environmental and fishery changes. Special purpose missions were designed to satisfy limited objectives and as such did not follow set schedules. Oceanographic and fisheries data were obtained from one to three commercial fishing vessels, usually on three days of each week, June through September 1972.

ERTS-1 and Aircraft Environmental Sensors

A number of oceanographic parameter sensors were used during the experiment from NP3A (NASA) and D18 Beechcraft[4] (NASA/ERL) aircraft at altitudes ranging from 610 to 7,620 m. The sensors included a RC 8 camera, RS-14 scanner, PRT-5 radiation thermometer. KA 62 multiband camera, Hasselblad EL-500 cameras, RS-18 thermal IR scanner, multifrequency microwave radiometer, and an Exotech spectroradiometer. The sensors were configured to measure sea-surface temperature, water color as a function of wavelength, surface current patterns, surface salinity, and surface turbidity patterns.

The ERTS-1 satellite, launched on 23 July 1972, operates in a circular sun-synchronous near polar orbit at an altitude of 915 km. It circles the earth every 103 min, completing 14 orbits per day and providing repetitive coverage of specific areas every 18 d. Two consecutive orbits, 24 h apart, are required for complete coverage of the study area.

The only environmental sensor aboard the satellite operating during the study was a multispectral scanner (MSS) which provided images in four discrete portions of the light spectrum (Freden, 1972): Band 4, 0.5–0.6 micron; Band 5, 0.6–0.7 micron; Band 6, 0.7–0.8 micron; and Band 7, 0.8–1.1 microns.

Sea-Truth Oceanographic Parameter Measurements

Sea-truth measurements during main day data acquisition events were taken from 25 research boats. Because two orbits 24 h apart of ERTS-1 were required for complete coverage of the study area, only about half of these measurements coincided with the passage of the satellite. On 7 and 25 August 1972, coincidental measurements occurred for the western portion of the study area, resulting in a 24-h difference for measurements from the eastern portion. A main day occurred on 28 September 1972, which did not correspond to

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

either orbit of ERTS-1. Orbits instead occurred on the 29th (eastern portion) and 30th (western portion) of September 1972, representing 24- and 48-h differences, respectively.

The 25 research boats generally occupied 95 stations in the Mississippi Sound and 46 stations in the offshore portion of the study area. These stations were spaced to provide a sampling density of about one station per 29 km^2 in the Sound and one station per 60 km^2 in the offshore waters. Parameters measured included surface temperature, salinity, chlorophyll *a*, currents, sea state, water color, water depth, and secchi disc transparency. Surface water temperature, salinity, and chlorophyll *a* measurements were obtained from bucket samples. Temperature was determined immediately in the bucket, and polypropylene bottles were used to store samples for chlorophyll *a* and salinity measurements in the laboratory. Color was estimated with a Forel-Ule color comparator (Hutchinson, 1957), and current speed and direction were measured by timed drifts of neutrally buoyant floats.

Fisheries Data

Aerial photography provided most of the fisheries distribution and abundance information augmented periodically with nighttime, low-light-level television sensor missions and commercial fish-spotter pilot reports. Menhaden are particularly susceptible to aerial sensing techniques because of their characteristic surface or near-surface schooling behavior. Discussions on aerial photography and low-light-level television sensing of fish schools have been published by Bullis (1967), Benigno (1970), Drennan (1969), and Roithmayr and Wittman (1972).

Photographic fish sensing missions were flown to provide 95% coverage of the study area at a scale of 1:16,200. The camera used was a Zeiss RMK-1523 mapping camera with a 15.24-cm focal length lens and 22.86-cm film format. The camera was supplied with GAF-1000 blue insensitive (2575) film, selected for its speed and reported ability to penetrate the hydrosphere (Vary, 1969). Photographic missions were divided into morning and afternoon flights corresponding to sun angles of 15 to 50 degrees, with morning flights covering the Mississippi Sound and afternoon flights covering the offshore section of the study area. A Houston-Feerless film viewer, providing magnifications of 3 × to 33 ×, was used to aid in the search of processed film for imaged menhaden schools. Fish school locations were recorded according to latitude and longitude with an accuracy of ±0.4 km. Menhaden schools could be subjectively differentiated from other schooling species in the study area on the basis of size, shape, and color.

Commercial Fishing Data

Fishery and oceanographic parameter measurements were obtained June through September 1972 from one to three commercial fishing vessels. These measurements were taken at the time and location of capture or attempted capture of a menhaden school. Data collected included surface water temperature and salinity, secchi disc transparency, Forel-Ule color, number of fish captured (visual estimate), date, time, and location. Usually, these observations were made the first three days of each fishing week (Monday through Saturday) except during periods when an ERTS-1 overpass or main day occurred, in which case the sampling period was extended over the entire fishing week.

DATA ANALYSIS AND INTERPRETATION

General Analytical Rationale and Data Limitations

Because the overall success of the experiment depended upon finding relationships between menhaden distribution and abundance and oceanographic parameters, the logical point of departure was with these relationships. Thus, impetus initially was given to finding relationships between fish distribution and abundance and selected oceanographic parameters, and then to determine if parameters which had fisheries meaning could be measured remotely with sufficient accuracy for precise correlation analysis. The last step in the analytical rationale was to determine what, if any, uses these relationships might have for commercial fishing and resource management.

The principal data limitation placed on early analyses was a general lack of remotely acquired synoptic oceanographic parameter measurements. The conversion of remotely acquired

oceanographic data into meaningful information has proceeded slowly because of interpretation difficulties. Thus, reported fisheries oceanographiuc–parameter relationship analyses depend primarily upon sea–truth measurements. An essential exception was the photographically acquired menhaden distribution and abundance information.

Oceanographic Parameter–Fish Distribution Relationships

Analysis

The distribution and abundance of menhaden in the study area, principally in the Mississippi Sound, can be placed into a simplified systems context (Figure 2). Factors directly affecting the system, i.e., the distribution and abundance of menhaden, include fish input, fish output (including harvest, death, and emigration), the environment, and the innate behavior of the menhaden not directly or immediately influenced by environmental conditions. Examples of this latter factor include fish age and degree of sexual maturity. This systems concept can be modified slightly and expressed as an algebraic argument as:

$$A_{x,y} = f(E,B,P) \tag{1}$$

where:

A = number of menhaden schools,
x and y = refer to school location coordinates,
E = environmental conditions,
B = innate fish behavior, and
P = instantaneous menhaden school population.

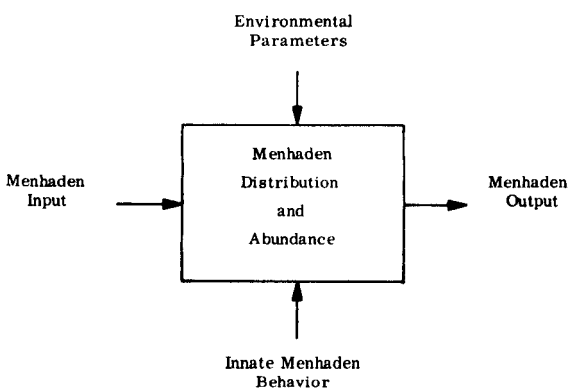


FIGURE 2.—Simplified systems view of the Mississippi Sound menhaden population described only in terms of distribution and abundance.

The problem with the argument is that the dependent variable $A_{x,y}$ is a function of more than just the environment, E, and as such cannot be solved with available information. To simplify the expression, two assumptions were made. First, it was assumed that B was constant (i.e., the innate behavior of the menhaden did not vary significantly) and thus could be ignored in the expression, an assumption which led to the development of a new expression where $A_{x,y}$ became a function of E and P alone. This assumption appeared reasonable because only adult menhaden were considered in the experiment while they were in the Mississippi Sound, a relatively short period of time. The second assumption made was that $A_{x,y}$ could be expressed in relative terms such that:

$$\frac{A_{x,y}}{P} = f(E) \tag{2}$$

This assumption permitted the normalizing of $A_{x,y}$ relative to P and has its roots in many fisheries catch/effort related expressions.

In the subsequent analyses, the number of photographically detected menhaden schools at any given point was used as an estimator of $A_{x,y}$, and the total number of detected menhaden schools was used as an estimator of P. If there was a constant sensor–caused bias in the photography data, the quotient $A_{x,y}/P$ should not be affected seriously, as the bias cancels. However, if the bias was not constant but instead was a variable function of the environment, then the bias would affect the quotient. Whether or not the effect would be significant would depend on the magnitude and variability of the bias.

Because of a concern about the possibility of bias affecting the relationships, a second approach also was used which should have reduced sensor bias. A new dependent variable, D, was defined which reflected only the distribution of menhaden and was related to the environment as:

$$D = f(E) \tag{3}$$

Inherent in this expression is the assumption that P does not affect the distribution of menhaden within the extremes of P characteristic of the

menhaden population during the experiment. Neither photographic nor commercial fishing data indicated a major change in P on main days, which lends credibility to this assumption. As defined, D can have two possible outcomes: yes, menhaden are present and no, menhaden are not present. In the analysis, areas where menhaden were detected were assigned a value of 1 and areas where fish were not detected were assigned a value of 0. Although D is clearly a discontinuous dependent variable, the statistical techniques used in the analyses converted it into a continuous variable ranging from about 0 to 1. The general interpretation applied to predicted values is that as the values approached 1, the chance of finding fish increased proportionately.

Regression techniques were used exclusively to define relationships between the abundance and/or distribution of menhaden and available measurements of oceanographic parameters. Because remotely sensed oceanographic data were not available, environmental conditions where fish were detected had to be interpolated and, in some cases, extrapolated from nearby sea–truth sampling stations. This procedure probably introduced experimental error into the analyses and, as such, may have obscured subtle relationships.

Results

Photographically sensed menhaden distribution and abundance ($A_{x,y}/P$) and distribution (D) information were regressed against available oceanographic parameter measurements (Table 1). These analyses reflect only those data collected on 7 August, 25 August, and 28 September 1972 (i.e., main days) from the Mississippi Sound portion of the study area. Forel–Ule color data were not collected on 7 August 1972; consequently, color analysis was limited to 25 August and 28 September. Clouds and cloud shadow obscured portions of the Sound on 25 August and 28 September; these areas were ignored in the analysis.

In general, the two approaches, i.e., relative abundance and distribution dependent variables, gave similar results. The type of relationship, either positive or negative, was the same in every case. Their precision varied, however, which affected level of significance. Of the two approaches, relationships derived using distribution as the dependent variable probably are the most reliable. Recent work has shown that there may have been a variable bias associated with the photographic sensor system used to obtain the fisheries data (Benigno and Kemmerer, 1973). The bias appeared to relate to school size and atmospheric conditions and apparently affected the number of schools detected more than where they were detected.

Assignment of biological significance to these correlations is difficult in that the parameters may be serving as indices of unmeasured parameters. In other words, there is a question of concomitance. Nevertheless, there does appear to be support for the distribution significant (≥ 90% confidence level) correlations presented in Table 1. Menhaden fishermen frequently are frustrated

TABLE 1.—Correlations between menhaden relative abundance ($A_{x,y}/P$) and distribution (D) estimates and selected oceanographic parameters (E).

Parameter	Degrees of freedom	Correlation coefficient (r)		Mean conditions where menhaden were detected (±95% confidence limit)
		Relative abundance	Distribution	
Temperature (°C)	195	0.009	0.044	29.75 (0.33)
Salinity (ppt)	195	−0.257***	−0.222***	25.53 (1.85)
Chlorophyll *a* (mg/m³)	195	0.025	0.119*	5.61 (1.95)
Current speed (cm/s)	195	−0.062	0.027	13.61 (5.50)
Sea state (m)	195	−0.064	−0.103	0.25 (0.08)
Forel—Ule color (units)	113	−0.256***	−0.150*	13.69 (1.21)
Water depth (m)	195	−0.216***	−0.404***	1.91 (0.47)
Secchi disc transparency (m)	195	−0.093	−0.146**	1.25 (0.17)

* 90% significance level
** 95% significance level
*** 99% significance level

in attempts to capture schools because the schools often inhabit waters too shallow for efficient boat and net operations (negative correlation associated with depth). Spotter pilots tend to concentrate their fish-searching efforts on turbid waters because of a relatively high frequency of fish encounter in these waters (negative correlation associated with secchi disc transparency). The positive correlation associated with chlorophyll *a* seems reasonable in that menhaden are plankton feeders. Salinity is a questionable concomitant factor although, because these fish are euryhaline organisms and inhabit estuarine waters throughout most of their lives, a preferred association with waters of low salinity seems plausible (negative correlation associated with salinity). Christmas and Gunter (1960) reported that 70% of the catch from 87 sets in the Mississippi Sound came from waters ranging from 5 to 24 ppt salinity, suggesting also a menhaden preference for low salinity waters. No biological significance can be attached directly to Forel–Ule color (negative correlation) yet, although this color may manifest water transparency and chlorophyll content. Correlation coefficients between Forel–Ule color and secchi disc transparency and chlorophyll *a* were −0.404 and 0.369, respectively, significant at the 99% confidence level.

The lack of statistical significance for several of the parameters listed in Table 1 should not necessarily be construed as meaning that no such correlations exist. For example, surface water temperature was relatively constant spatially throughout the study period and therefore its effect, if any, on the distribution and abundance of menhaden may not have been sufficient to gain statistical significance. In the long run, however, temperature may be a very important parameter. One also should be reminded that the correlations were developed from linear expressions for the sake of statistical tractability. The correlations, therefore, may not factually represent real world situations where most responses probably are nonlinear.

The concern over a possible significant sensor bias in the menhaden distribution estimates prompted attempts to substantiate the results through other approaches. The set of commercial fishing data which included measurements of selected oceanographic parameters provided the only avenue through which substantiation could be accomplished. However, these data were noticeably biased in that environmental measurements were obtained only from areas where catches were made or attempted. In addition, the boats did not fish randomly throughout the study area; rather, they fished according to fish availability, distance from home port (minimized to reduce operating expense), day of the week (tendency to fish farther from home port as the fishing week progressed), and water depth (usually about 2 m for efficient boat operation). Nevertheless, if caution is used in the analysis, the data can be used to substantiate some of the results gained through photographic sensing of the menhaden stocks.

In the classical statistical situation, one generally attempts to differentiate between two presumably different populations, e.g., with and without menhaden. As noted previously, the principal problem with the commercial fishing data is that data were not obtained from areas without fish. However, if the assumption is made that all other environmental measurements collected throughout the study period (main and secondary day events) were taken at random in terms of temporal and spatial coverage, then it is logical to assume that these latter measurements included areas with and without menhaden. The commercial fishing data can then be handled as a "with fish" subset of the total data population, i.e., with and without fish.

The difficulty in this approach is that differences are difficult to demonstrate with a high level of statistical significance because the subset (with fish) is not discrete from the total population (with and without fish). The hypotheses which can be tested are that the means ($\bar{x}$) and standard deviations (s) of the subset and total population are different, resulting in the following four general conditions and accompanying conclusions:

1. Means and standard deviation are not significantly different; conclusion: fish distribution is not related to the parameter tested.
2. Means are significantly different but standard deviations are not; conclusion: fish distribution is related to the parameter tested.
3. Means are not significantly different but standard deviations are; conclusion: fish distribution is related to the parameter tested.
4. Means and standard deviations are both significantly different; conclusion: fish distribution is related to the parameter tested.

A note of caution should accompany the conclusions, however. They are valid only for the data collected under the conditions of the experiment, and therefore extrapolation to other areas or to the same area under different experimental conditions might not be valid.

The commercial fishing data demonstrated a Condition 4, i.e., means and standard deviations different with respect to water depth, salinity, Forel–Ule color, and secchi disc transparency (Table 2). Temperature and sea state were not tested, and data were not available for chlorophyll *a* and currents. The subset of fishing data included measurements from 237 "fish sets" and the total population of oceanographic conditions included measurements from 29 June, 30 June, 6 July, 7 August, 25 August, and 28 September 1972. For each parameter, a negative correlation is indicated as the mean parameter values for the fishing subsets were significantly less than the mean values for the total parameter populations. The lack of high significance levels for mean salinity and Forel–Ule color value differences was not particularly surprising in that the subset approach tends to preclude such significance. In any case, the relationships shown in Table 2 substantiate those shown in Table 1.

A second approach was used to substantiate still further the correlations formed between fish distribution and salinity, Forel–Ule color, secchi disc transparency, and water depth. Mean parameter values for conditions where menhaden were photographically detected (Table 1) were compared with similar values from the fishing subset (Table 2). None of these values were significantly different at levels down to 80% (*t*-test).

In summary, water depth, secchi disc visibility depth, surface salinity, and Forel–Ule color were found to correlate negatively with the distribution of menhaden. Chlorophyll *a* correlated positively with fish distribution, although independent data were not available with which to corroborate this relationship as in the case of the other four parameters.

ERTS– Imagery and Fish Distribution Relationships

Analysis

The only complete docket of quality ERTS–1 MSS imagery coincidental with main day acquisition events was from 7 August 1972. Band 5 imagery from 25 August 1972 was of poor quality and no imagery was available for 28 September 1972.

The four MSS bands from 7 August 1972 were examined to determine if their density levels related to fish distribution. Bands 6 and 7 did not contain any readily apparent useful density detail. Band 4, for reasons which are still unclear, seemed to contain too much density detail. Density levels in Band 5, however, appeared to relate to menhaden distribution.

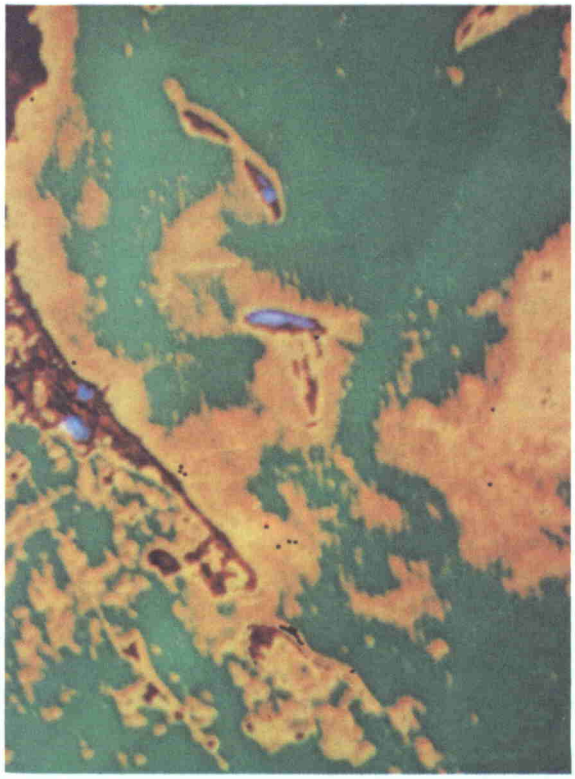
Results

Figure 3a shows a portion of the ERTS–1 Band 5 imagery covering the western portion of the Mississippi Sound and adjacent offshore waters as displayed on a I^2S DIGICOL video screen. Superimposed on the image are locations of 23 photographically detected menhaden schools. Water imagery densities were divided into two density ranges and color-enhanced (Figure 3b). All menhaden schools were found to lie in the less dense range, enhanced as orange. This density range was further reduced by slicing it to the narrowest range possible with the instrument. All of the fish schools can be found to either lie in or immediately adjacent to this range, enhanced as

TABLE 2.—Comparison of total parameter populations (with and without fish) and fish parameter population subsets (with fish).

	Total population			Fishing subset population			Level of significant difference (%)[1]	
Parameter	n	$\bar{x}$	s	n	$\bar{x}$	s	$\bar{x}$	s
Water depth (m)	354	3.41	1.27	237	2.19	1.17	99	90
Secchi disc transparency (m)	348	1.45	0.71	237	1.10	0.32	99	99
Salinity (ppt)	357	26.30	4.15	237	25.85	2.95	80	99
Forel–Ule color (units)	166	14.16	3.04	237	13.78	2.44	80	99

[1]*t*-tests for differences between means for populations with unequal variances and *F*-tests for differences between standard deviations (Ostle, 1963).



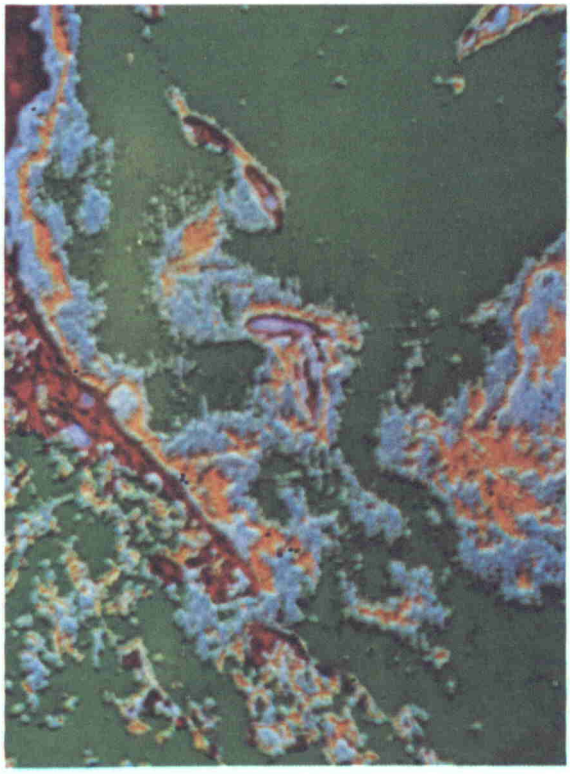


FIGURE 3.—ERTS-1, Band 5, 7 August imagery of the western portion of the study area (fish school locations are shown as small black dots). St. Louis Bay is in the upper left portion of the imagery, Cat Island is mid-center, and the western tip of Horn Island protrudes into the upper right portion.

a (upper left). I²S DIGICOL television screen image.

b (upper right). Image water densities divided into two ranges and color enhanced.

c (lower left). Enhancement of a narrow density range within the range containing the fish school locations. Note how the fish schools either fall adjacent to or within this narrow range.

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orange (Figure 3c). The 10 tightly grouped school location indicators in the middle–left portion of the image overlie a small orange enhanced area making the latter difficult to see.

Unfortunately, the lack of additional data to test the persistence of the relationship between menhaden distribution and MSS Band 5 imagery density levels precludes any but the most tentative of conclusions. However, the data are sufficient to warrent an observation that the imagery does appear to contain information relating to the distribution of menhaden schools.

ERTS–1 Imagery and Oceanographic Parameter Relationships

Analysis

An analysis was performed on the MSS Band 5 imagery for 7 August 1972 to determine if image densities could be explained based on oceanographic parameter measurements. An isodensity tracing was made of that portion of the imagery covering the study area to provide quantitative relative density data. The tracing was not particularly satisfactory because of instrument limitations which caused more than one density range to be represented by the same color trace, but accurate enough to demonstrate relationships.

Results

Water depth, secchi depth visibility, and the interaction between the two parameters (formed by their product, Mott, 1967) were regressed against relative image densities. Simple correlations *(r)* between these parameters and image density were 0.56, 0.73, and 0.69, respectively, significant at the 99% confidence level. A slight improvement in precision ($r = 0.77$) was realized when the parameters were combined through multiple regression (Table 3) into the following equation:

$$\text{Image Density} = 0.5776 + 0.0222B + 0.0762T - 0.0051BT \quad (4)$$

where:

B = water depth in meters,

T = secchi disc transparency in meters,

BT = interaction formed as the product of B and T

Of the parameters, secchi disc transparency was the most important one in the equation as indicated by the relative magnitude of the coefficients and the simple correlation coefficients. The most meaningful facet of this analysis is that the two parameters correlating significantly with image density levels also correlated significantly with menhaden distribution (Tables 2 and 3). Thus, it appears that the apparent correlation between menhaden distribution and Band 5 density levels (Figure 3) is more than a chance occurrence and can be explained based upon secchi disc transparency and water depth measurements.

TABLE 3.—Analysis of variance for the relationship between ERTS–1 image density and two oceanographic parameters.

Source of variation	Degrees of freedom	Mean square	F-value
Total	47	0.0051	
Regression (secchi disc transparency, water depth, and interaction)	3	0.0469	21.040***
Error	44	0.0022	

PREDICTION MODELS FOR RESOURCE MANAGEMENT AND UTILIZATION

A potential management and utilization benefit from this experiment is identification of an approach through which remotely sensed environmental data could be used to provide distribution information about menhaden stocks in the study area. This information could be used to reduce search time for commercial concentrations of menhaden by fishermen and as a means to develop efficient survey designs by resource managers. Ideally, distribution information should be valid for the entire Gulf Coast menhaden fishery; however, this ideal case cannot be supported with results from this experiment but can be realized only through future experiments specifically designed to test demonstrated relationships in other areas.

Model Development

Demonstrated menhaden distribution–oceanographic parameter relationships (Table 1) were placed into a context potentially useful to commercial fishermen and resource managers. Multiple regression analysis was used to develop eight empirical models to predict menhaden distribution (D) in the study area based on

four oceanographic parameters: water depth, secchi disc transparency, Forel–Ule color, and salinity (Table 4). The models contain selected 2–factor interactions formed as products between parameters and treated as additional independent variables. Interaction selection was based on whether or not an interaction significantly increased the precision of the estimate ($\hat{D}$). The models were constructed from data collected on main days (i.e., 7 August, 25 August, and 28 September 1972) and are presented separately and in combination and with and without the inclusion of color as an independent variable.

Model Testing and Interpretation

The models were tested by playing them with oceanographic data collected during commercial fishing operations and main day sea–truth station data stratified to include only those stations where menhaden were not detected photographically (Figure 4). Ideally, model products for fishing data should have grouped close to 1, and products for the "without fish" sea–truth stations should have grouped close to 0; obviously, this type of grouping is not demonstrated in Figure 4, indicating a general lack of accuracy and precision in the models. Product populations, however, are significantly

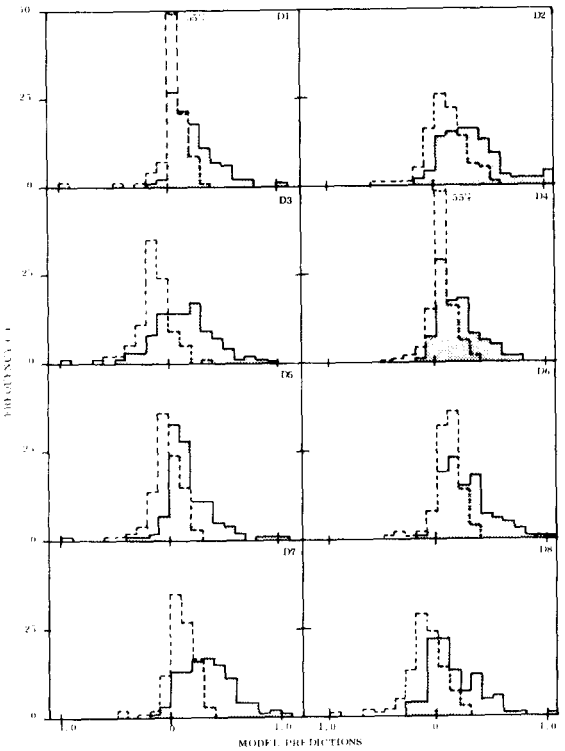

FIGURE 4.—Histogram plots of "with fish" (shaded) and "without fish" (unshaded) model products.

TABLE 4.—Empirical regression models which predict menhaden distribution (D) in the ERTS–1 study area.

B = water depth (m) S = salinity (ppt)
T = Secchi disc transparency (m) C = Forel–Ule color (units)
BT, BS, ST, CT, and CS = interactions formed as the products of the respective parameters.

Model	Inclusive dates (1972)	n	Regression model	Standard error of $\hat{D}$	Model correlation coefficient	Significance level (%)
D1	7 Aug.	82	$\hat{D} = 1.9959 - 0.0664S + 0.7453T - 0.6820B - 0.0233ST - 0.0144BT + 0.0230BS$	0.2492	0.596	99
D2	25 Aug.	42	$\hat{D} = 5.1537 - 0.1740S - 0.9195T - 0.0371C - 0.4350B + 0.0502ST - 0.1243BT + 0.0195BS$	0.3793	0.630	99
D3	28 Sept.	73	$\hat{D} = 2.3473 - 0.0934C - 0.8117B - 0.0358ST - 0.0007CS + 0.0528CT + 0.0516BT + 0.0235BS$	0.2443	0.409	90
D4	7 and 25 Aug.	124	$\hat{D} = 2.4691 - 0.0855S + 0.3948T - 0.6477B - 0.0054ST - 0.0441BT + 0.0223BS$	0.3009	0.584	99
D5	7 Aug. and 28 Sept.	155	$\hat{D} = 1.8559 - 0.0577S + 0.5604T - 0.6954B - 0.0191ST - 0.0079BT + 0.0232BS$	0.2489	0.480	99
D6	25 Aug. and 28 Sept.	115	$\hat{D} = 2.9396 - 0.1024S + 0.1522T - 0.7486B - 0.0026ST - 0.0547BT + 0.0268BS$	0.3118	0.488	99
D7	25 Aug. and 28 Sept.	115	$\hat{D} = 3.6035 - 0.0987S - 0.1249T - 0.0416C - 0.6717B + 0.0087ST - 0.0441BT + 0.0234BS$	0.3090	0.508	99
D8	7 and 25 Aug. and 28 Sept.	197	$\hat{D} = 2.3759 - 0.0797S + 0.3928T - 0.7051B - 0.0086ST - 0.0326BT + 0.0242BS$	0.28560.515	99	

different for each model even though the distributions overlap without a wide margin of difference between means (Table 5).

A number of factors probably contributed to the failure of the models to group fishing data closer to 1. It should be pointed out first, however, that no seasonally caused variation in products was noted, suggesting that the nonparametric grouping was caused by factors prevalent throughout the June through September commercial fishing sampling period. One of these factors may have been the effect of commercial fishing operations on the distribution of fish as evidenced by visual observations made during the photographic surveys of the study area. Menhaden schools frequently were observed being chased by purse boats through waters of varying visual qualities (i.e., turbidity). In addition, oceanographic parameter measurements generally were taken from the mother vessel rather than the purse boats, which often was several kilometers distant from the actual site of fish capture. Another of these factors is that there is no biological reason to suspect menhaden distribution to be wholly a deterministic function of environmental conditions; rather, there most likely is a probability associated with how and where fish are distributed in response to these conditions. Also, there were errors associated with all of the parameter measurements used to develop and test the models as well as a distinct possibility that other parameters having a direct influence on menhaden distribution might not have been measured (e.g., zooplankton biomass, presence or absence of predators, oxygen tensions, etc.). And finally, there is the linear additive nature of the models which at best probably only approximates the real world situation.

Selection of a best model was difficult in that they all provide similar products. On the basis of sample size, number of parameters (minimum), and difference between means (Table 5), Model D8 would have to be given selection priority, however.

A number of interpretations and presentation methods can be applied to model products as long as they recognize the imprecision of the models. An example of one method applied to Model D8, for 7 August 1972 sea-truth data, is presented in Figure 5. The categorization of model products was done by dividing the values shown in Figure 4 for Model D8 into three ranges based upon a direct comparison of fishing and nonfishing histograms:

high potential	$= > 0.2$
moderate potential	$= -1.0$ to 0.2
low potential	$= < -1.0$

The interpretation applied to high, moderate, and low potential areas is related to relative probability. In high potential areas, the probability of fish capture is higher than in moderate or low potential areas and higher in moderate than in low potential areas. Incomplete commercial fishing reports from 7 August 1972 indicate that most, if not all, fishing occurred in the high potential areas.

An additional analysis was performed on the commercial fishing data to determine if relationships could be demonstrated between catch size and the four oceanographic parameters which made up the models. Catch size ranged from 5 to 225 and averaged about 38 thousand fish. Catch

TABLE 5.—Tests of empirical models played with oceanographic data taken near sites of commercial fish capture (with fish) and during main day events, the latter stratified to include only those areas where fish were not detected photographically (without fish).

Model	With fish			Without fish			Significance level for difference between means (%)[2]
	n	$\bar{D}$	C.V.(%)[1]	n	$\bar{D}$	C.V.(%)[1]	
D1	225	0.202	86	165	0.071	147	99
D2	225	0.371	78	94	0.100	187	99
D3	225	0.146	184	94	−0.115	132	99
D4	225	0.305	67	165	0.139	80	99
D5	225	0.175	106	165	−0.017	755	99
D6	225	0.288	79	165	0.089	165	99
D7	225	0.338	70	94	0.093	151	99
D8	225	0.145	163	165	0.111	160	99

[1]Coefficient of variation.
[2]t-test for populations with unequal variances (Ostle, 1963).

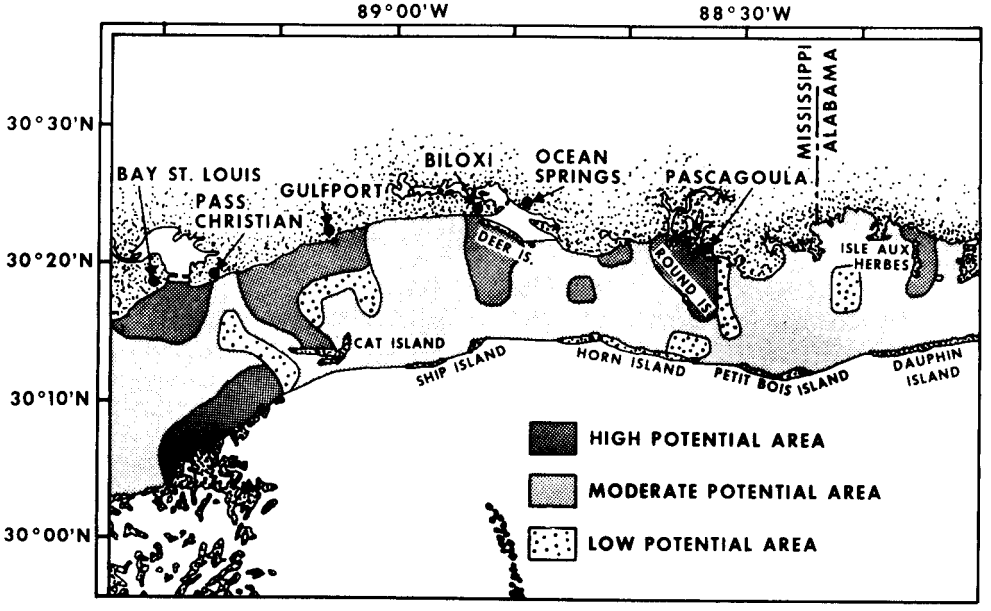

FIGURE 5.—Model D8 predictions for menhaden distribution in the Mississippi Sound on 7 August 1972, between 0900–1500 h (CDT) (based on 95 sea-truth measurements).

size was divided into three categories: 0–50, 50–100, and more than 100 thousand fish, and an analysis of variance applied to the categories to test for differences between mean parameter conditions. No significant differences were found between catch size and salinity, Forel–Ule color, and depth parameters at significance levels down to 50%. However, a significant difference at 95% was found between the first and third catch size category for averaged secchi disc transparency values ($\overline{T}_{0\text{-}50K}$ = 1.09 m and $\overline{T}_{>100K}$ = 1.32 m). This significance probably does not have biological meaning, however. It probably reflects changes in the ability of fishermen to selectively detect and capture fish schools with respect to water clarity.

SUMMARY AND CONCLUSIONS

The feasibility of using satellite-supported environmental sensors to predict fish distribution was demonstrated. ERTS–1, MSS Band 5 imagery was shown to contain density levels which correlated with menhaden distribution. These density levels were further shown to correlate significantly with sea-truth measurements of secchi disc transparency and water depth, two parameters which also correlated significantly with menhaden distribution. Additionally, surface salinity, Forel–Ule color, and chlorophyll *a* were found to correlate significantly with menhaden distribution. Independent tests of four oceanographic parameter–menhaden distribution relationships with oceanographic information taken at or near sites of commercial menhaden captures corroborated these relationships. The correlation between chlorophyll *a* and menhaden distribution could not be substantiated because of insufficient data.

Eight empirical regression models which predict menhaden distribution in the study area were constructed from combinations of four oceanographic parameters: water depth, secchi disc transparency, surface salinity, and Forel–Ule color. Although the models did not provide particularly precise predictions about menhaden distributions, their predictions nevertheless were statistically significant. The importance of the models is that they demonstrate a potential means or direction through which remotely sensed oceanographic information can be used to provide menhaden distribution information on a real-time basis. This information could be used by the commercial industry to reduce spotter-pilot search time by identifying likely areas for concentrations of menhaden and by resource managers as an aid in planning assessment surveys.

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ROLE OF LARVAL STAGES IN SYSTEMATIC INVESTIGATIONS OF MARINE TELEOSTS: THE MYCTOPHIDAE, A CASE STUDY[1]

H. GEOFFREY MOSER AND ELBERT H. AHLSTROM[2]

ABSTRACT

The lanternfish family Myctophidae is the most speciose and widespread family of mid-water fishes in the world ocean. As presently recognized it contains about 30 genera and 300 nominal species. Their larvae are highly prominent in the plankton and make up about 50% of all larvae taken in open-ocean plankton tows.

Our studies of myctophid larvae, on a worldwide basis, have demonstrated that characters of the larval stages of lanternfishes are of great utility in systematic analysis. The genera and species can be recognized on the basis of eye and body shape, the shape and length of the gut, and pigment pattern and by the sequence of photophore development. In this paper the larvae of 55 species representing 24 genera are illustrated and used to demonstrate the usefulness of larvae in understanding the relationships of species within genera.

Characters of the larvae provide insight into generic affinities of lanternfish, allowing us to construct an evolutionary scheme of tribes and subfamilies that differs in some aspects from those proposed on the basis of adult characters. The concept of using larval characters in combination with adult characters to delineate phylogenetic lines in myctophids is discussed, as is our view of evolutionary strategy in the family.

A major facet of comprehensive systematic investigations is the search for functionally unrelated characters. Whether the independence of these characters is actual or merely apparent, they constitute useful elements in the analysis of systematic relationships. Ample evidence of this is the higher classification of teleosts (Greenwood et al., 1966) generated by the synthesis of a diverse array of classical taxonomic characters. The recent surge of serological and biochemical studies on fish has placed a fresh group of characters in the hands of systematic ichthyologists (De Ligny, 1969). Likewise, recent advances in fish cytogenetics (e.g., Ohno, 1970; Benirschke and Hsu, 1971; Ebeling, Atkin, and Setzer, 1971) are providing another group of taxonomic characters. It is likely that behavioral science will be still another source of taxonomic characters, as exemplified by the growing body of information on the acoustic behavior of fishes (Fish and Mowbray, 1970).

One group of well known taxonomic characters, those of the embryonic and larval stages, has received scant attention from all but a few systematic ichthyologists. Characters of the larvae have played a large role in the taxonomy of anguilliform fishes (Castle, 1969) partly because of the conspicuousness of eel leptocephali and partly because of the unavailability of adults of many of the families. Bertelsen's (1951) treatment of the ceratioid fishes is a superb example of the value of utilizing larval stages in a systematic revision of a large group of teleosts. Apart from these two groups, it is the larvae of myctophiform fishes which have received the most attention from taxonomists. Ege (1953, 1957) relied heavily on larval stages in his extensive works on the Paralepididae. Johnson (1971) employed larval characters in defining species and genera of Scopelarchidae. Bertelsen, Marshall, and Krefft (pers. commun.) have used larval stages extensively in their revision of the Scopelosauridae. Our studies on the family Myctophidae itself (Moser and Ahlstrom, 1970, 1972) indicated that larval characters can aid significantly in differentiating taxa and defining evolutionary lineages within this family.

The lanternfish family Myctophidae is the most speciose and widespread family of mid-water fishes in the world ocean. As presently recognized it contains about 30 genera and 300 nominal species. Their larvae are highly prominent in the plankton and make up about 50% of all larvae taken in open-ocean plankton tows.

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Our studies of the larvae of this family have included material from all oceans. We have been able to identify larvae from all recognized genera except *Hintonia* and *Dorsadena*. Larval evidence supports giving generic status to *Metelectrona* and *Parvilux*. Including these, we have developmental series for 29 myctophid genera and for many genera we have series for all known species. This has afforded a more comprehensive view of the range and variability of larval characters, and we are increasingly impressed with the functional independence of the larval and adult characters. It is apparent that the world of the larvae and the world of the adults are two quite separate evolutionary theaters. Our studies of larval lanternfishes have disclosed a full range of characters, from generalized to specialized and from conservative to labile, equal in scope to those of the adults. These characters fall into several categories. An important group is the shape of various structures such as the eye, head, trunk, guts, and fins, especially the pectoral fins. Another group is the sequence of appearance and the position of fins, photophores, and bony elements. Another is the size of the larvae when fins and other features appear and the size of the larvae when they transform into juveniles. Pigmentation provides an important group of characters based on the position, number, and shape of melanophores. Finally, there are the highly specialized larval characters such as voluminous fin folds, elongated and modified fin rays, chin barbels, preopercular spines, etc. It is our purpose here to point out some of these characters and demonstrate how they can be of advantage in defining taxa and establishing phylogenetic lineages.

THE SUBFAMILY MYCTOPHINAE

The most trenchant character of larval myctophids is eye shape. Our studies show that lanternfish larvae fall naturally into two groups on the basis of eye shape—those with narrow elliptical eyes and those with round or nearly round eyes (Moser and Ahlstrom, 1970). The species composition of these two groups agrees closely with that of the two subfamilies, Myctophinae and Lampanyctinae, established by Paxton (1972) on the basis of osteological and photophore characters of adults. Larvae of the Myctophinae have elliptical eyes; some species have ventral prolongations of choroid tissue and some have the eyes on stalks. Paxton recognized 11 genera in the subfamily Myctophinae and distributed them into two tribes, the Myctophini and the Gonichthyini. Larvae of the species in each of these genera generally conform to a particular morph based on form, pigment, and developmental pattern and, although these morphs are remarkably diverse, we can find no character or set of characters that would divide the genera into tribes. Within each genus of the subfamily, however, the larval characters are indispensible in delineating groups of related species or subgenera. This is best illustrated by examining the important genera of the Myctophinae.

Protomyctophum larvae have a slender shape (Figure 1). For all species except *P. anderssoni*, the gut is short during most of the larval period and characteristically there is a marked interspace between the anus and the origin of the anal fin (Figure 1A-D). The gut elongates dramatically in late larvae, to fill the interspace. Gut development is completely dissimilar in *P. anderssoni*, where the gut is long at all larval sizes, in fact longer than in most other lanternfish larvae (Figure 1E). Series of ventral tail melanophores are formed in some species of both recognized subgenera (*Heirops* and *Protomyctophum* sensu stricto), for example in *P. Protomyctophum normani* (Figure 1A) and *P. Heirops thompsoni* (Moser and Ahlstrom, 1970). Larvae of the subgenera can be separated, however, on the basis of eye shape, the eyes of *Heirops* (Figure 1C, D) being characteristically narrower than those of *Protomyctophum* sensu stricto (Figure 1A, B). Choroid tissue is absent from the ventral surface of the eye in all species of the genus except *P. anderssoni*, which has a well-developed "teardrop" (Figure 1E). Larvae of *P. anderssoni* are so markedly different from those of all other species of *Protomyctophum*, which otherwise form a rather cohesive group, that this species should be placed in a separate subgenus or perhaps even in a distinct genus. This suggestion is supported by the unique placement of certain photophores and by the structure of the supracaudal luminous tissue in adults of this species.

Larvae of the genus *Electrona* are a less homogeneous group but are united by a commonality of body shape and especially gut shape (Figure 2). A marked interspace is present between the end of the gut and the origin of the anal fin. This space is closed only at the termination of the

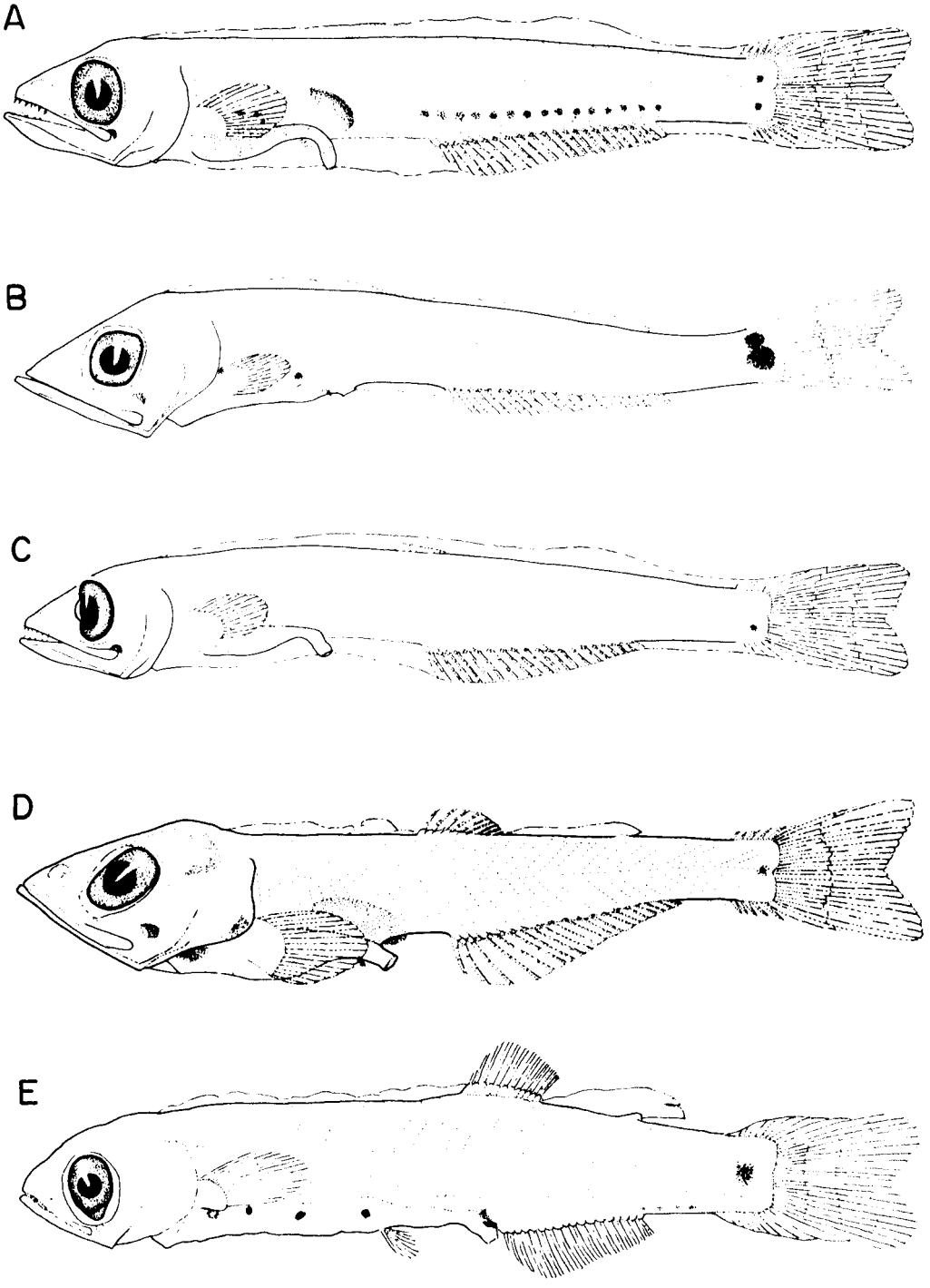

FIGURE 1.—Larvae of *Protomyctophum*. A. *P. Protomyctophum normani*, 15.2 mm; B. *P. Protomyctophum tenisoni*, 14.5 mm; C. *P. Hierops subparallelum*, 15.2 mm; D. *P. Hierops chilensis*, 11.0 mm; E. *P. anderssoni*, 15.7 mm.

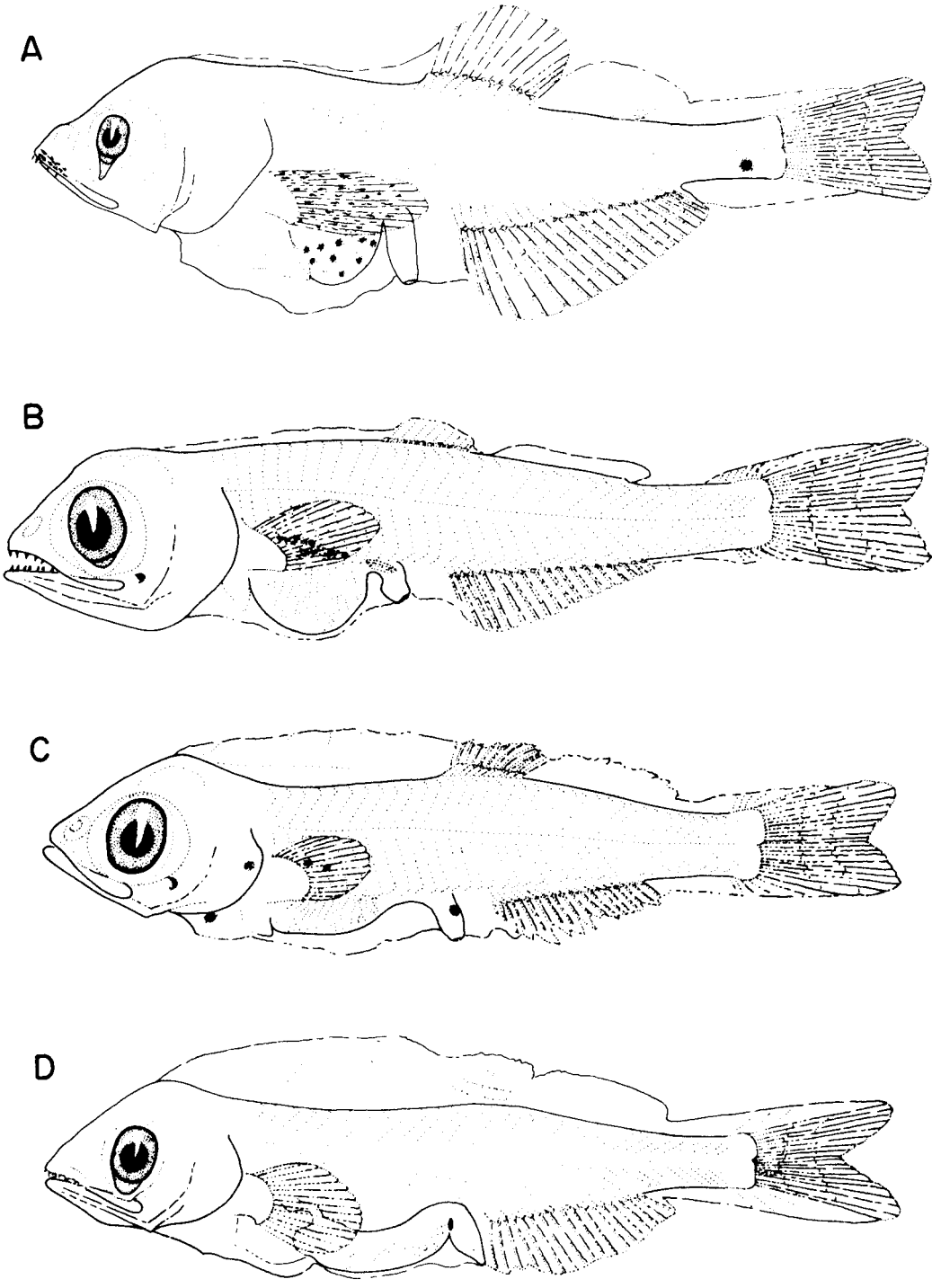

FIGURE 2.—Larvae of *Electrona* and *Metelectrona*. A. *E. antarctica*, 12.7 mm; B. *E. carlsbergi*, 11.1 mm; C. *E. subaspera*, 10.5 mm; D. *M. ahlstromi*, 10.3 mm.

larval period. None of the species forms photophores during the larval period other than the Br_2 pair.

The characters that most clearly separate the three developmental lines in *Electrona* are eye shape and the amount of choroid tissue developed under the eye. *Electrona antarctica* has an elongate choroid mass uniquely divided into two narrow eyes (Figure 2A). Also, *E. antarctica* larvae attain a large size (20 mm), are the deepest-bodied of all *Electrona* larvae, and have the heaviest pigmentation. The two species in the second developmental line transform at a small size (ca. 10 mm in *E. rissoi* and 12-13 mm in *E. carlsbergi*), have a small choroid mass under a moderately narrow eye, and develop scant pigment (Figure 2B). In the third line, consisting of *E. subaspera* and *E. paucirastra,* the eye is the least narrow, has no choroid tissue, and the larvae attain a large size (20 mm) (Figure 2C).

The larva of the species described as *Metelectrona ahlstromi* (Wisner, 1963) is illustrated in Figure 2D. It is more laterally compressed than any species of *Electrona* and has no interspace between the anus and origin of the anal fin. In some features it resembles the larvae of *Hygophum*; it has a late-forming dorsal fin and the gut is shaped very similarly to that in *H. taaningi* and *H. macrochir.* Its pigment is unique and the eye is distinct, with the ventral edge of the scleral envelope characteristically squared off. Also, in late-stage larvae, in addition to the Br_2, a second pair of photophores (PO_5) develops, a feature found in neither *Hygophum* nor *Electrona*. Paxton (1972) synonymized *Metelectrona* with *Electrona* and suggested that *M. ahlstromi* and *E. ventralis* are synonyms, however, the uniqueness of the larva strongly suggests the resurrection of *Metelectrona* as a valid genus.

The genus *Benthosema* is the least cohesive of any genus in the subfamily Myctophinae, from the viewpoint of larval structure (Figure 3). We can find only four types of larvae in the world ocean, although Nafpaktitis (1973) recognizes five species on adult characters. We cannot distinguish larvae of *B. pterota* and *B. panamense* although Nafpaktitis has listed a number of convincing characters that distinguish the adults of the two species. We find two highly divergent species pairs. One is composed of *B. glaciale* and *B. suborbitale* with a narrow eye subtended by a lunate choroid mass and with a pronounced interspace between the anus and the anal fin origin, reminiscent of *Protomyctophum* and *Electrona* (Figure 3A-C). In the other pair, consisting of *B. panamense-pterota* and *B. fibulatum,* the eye is wider, is subtended by a mere sliver of choroid tissue and the gut, of moderate length, lacks a postanal interspace (Figure 3D, E).

The one feature held in common by the four species is the development of some photophores in addition to the Br_2 during the larval period. The only other myctophine genera that develop photophores in addition to the ubiquitous Br_2 during the larval period are *Diogenichthys, Myctophum,* and *Metelectrona.* This feature is much more prevalent among genera of the Lampanyctinae and is helpful in defining groups of related genera there (Moser and Ahlstrom, 1972).

In *B. panamense-pterota* and *B. fibulatum* the Dn pair is formed soon after the Br_2 at about 5.0-6.0 mm. The PO_5 pair is the third to appear in

TABLE 1.—Sequence of photophore formation in larvae of three species of *Benthosema*.

Species	Size larva (mm)	Photophores	No. of photophore pairs	Smallest juvenile (mm)
B. fibulatum	ca. 4.0	Br_2	1	13.2
	5.4	Br_2 Dn	2	
	6.0	Br_2 Dn PO_5	3	
	6.4	Br_2 Dn PO_5 PO_1	4	
	7.3	Br_2 Dn PO_5 PO_1 AOa_1	5	
	7.7-8.7	Br_2 Dn PO_5 PO_1 AOa_1 PO_2	6	
	ca. 10.0	Br_2 Dn PO_5 PO_1 AOa_1 PO_2 Op_2 VLO	8	
B. pterota (panamense)	4.0	Br_2	1	11.8
	5.0	Br_2 Dn	2	
	6.0	Br_2 Dn PO_5	3	
	ca. 7.0	Br_2 Dn PO_5 PVO_1	4	
	7.1	Br_2 Dn PO_5 PVO_1 Op_2	5	
	7.5	Br_2 Dn PO_5 PVO_1 Op_2 VO_1 PVO_2	7	
	8.0	Br_2 Dn PO_5 PVO_1 Op_2 VO_1 PVO_2 PO_1 AOa_1	9	
B. suborbitale	4.1	Br_2	1	10.7
	8.3-9.2	Br_2 PO_1 PO_2	3	
	9.4	Br_2 PO_1 PO_2 Br_1 Br_3 Op_2	6	
	11.5	Br_2 PO_1 PO_2 Br_1 Br_3 Op_2 PO_3 PO_4 PO_5 AOa_1 AOa_2	11	

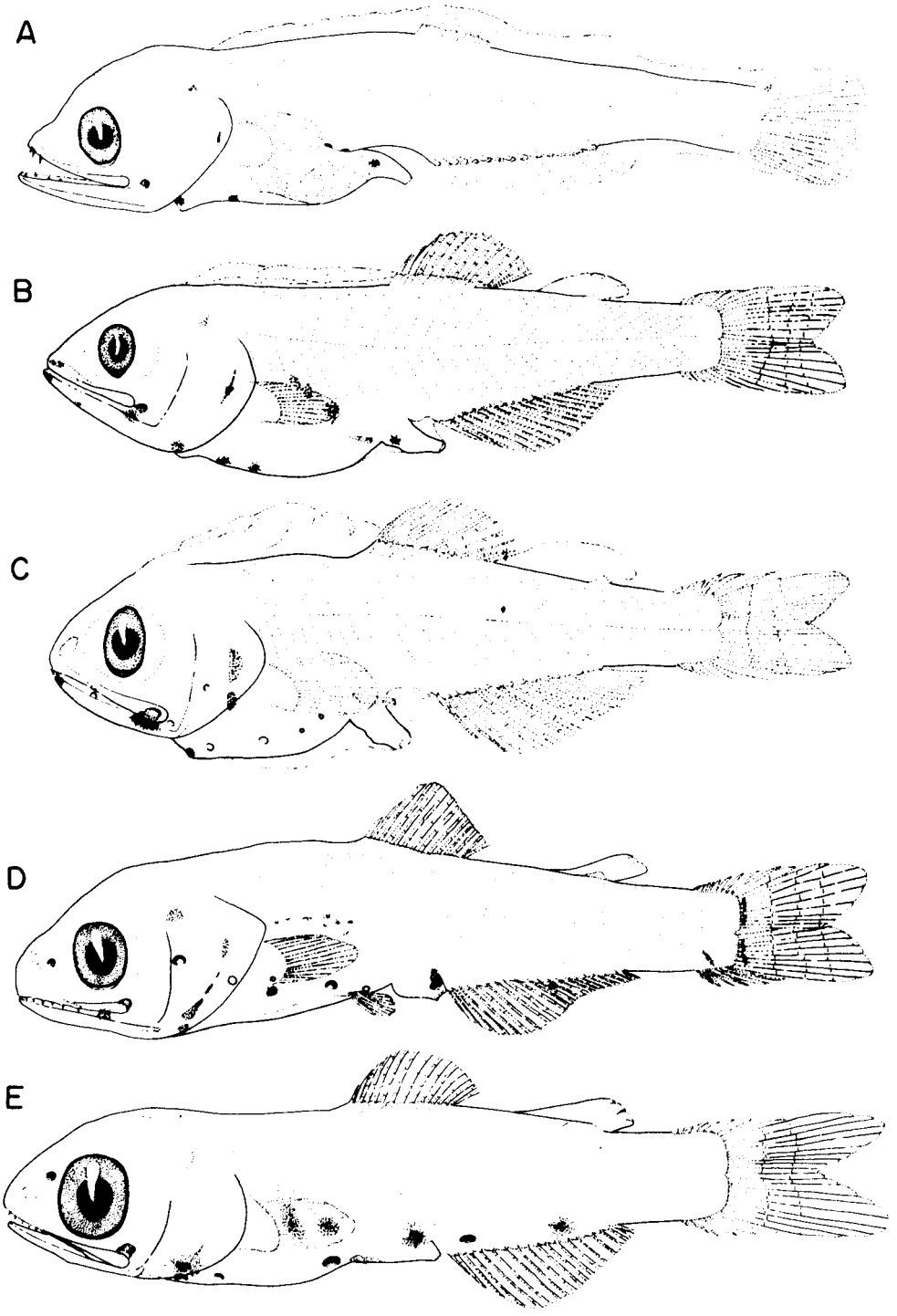

FIGURE 3.—Larvae of *Benthosema*. A. *B. glaciale*, 7.2 mm; B. *B. glaciale*, 10.5 mm; C. *B. suborbitale*, 9.2 mm; D. *B. pterota*, 8.5 mm; E. *B. fibulatum*, 8.7 mm.

larvae about 6.0 mm long. Thereafter the pattern diverges as shown in Table 1, but both species gradually add about a dozen pairs during the larval period. Specimens of *B. pterota* from the Persian Gulf off India, formed photophores at somewhat larger sizes than larvae of *B. panamense*, but in the same sequence. Transformation occurs at a small size, 10-12 mm in *B. panamense-pterota* and 11-13 mm in *B. fibulatum*.

Photophores appear relatively late in larvae of *B. suborbitale* and *B. glaciale*, however, the Br_1, Br_2, Op_2, and PO series appear in late larvae of both species (Table 1). Transformation occurs at about 9-11 mm in both species. The larvae of *B. panamense-pterota* and *B. fibulatum* are close to the larvae of *Diogenichthys* in several characters including body shape, gut shape, and early appearance of photophores.

As in *Benthosema*, the larval characters of *Hygophum* suggest some divergence within the genus, although all species have a highly characteristic series of isthmal melanophores, form the dorsal fin late in the larval period, and develop no photophores other than the Br_2, as larvae (Figure 4). The genus contains three divergent types of larvae. The most unusual of these are the extremely elongate larvae of *H. reinhardti* and *H. atratum*, which have very narrow eyes that are underlain by prominent choroid tissue and are borne on short stalks (Figure 4A). The amount of pigmentation along the gut and tail and on the myosepta and fin fold increases throughout the larval period.

A second larval type is represented by the largest number of species, *H. proximum*, *H. hygomi*, and *H. brunni*, all illustrated (Figure 4B-D), as well as *H. benoiti*, *H. hanseni*, and an undescribed form in our collection. These larvae are only moderately slender and have unstalked eyes of moderate width, subtended by prominent choroid tissue. Melanophores are located chiefly on the head and gut, however some species have pigment on the myosepta and fin fold. The trend in this group of species is for the early larval stages to have the heaviest pigment and for melanophores to be lost as development proceeds.

A third type of larva is exhibited by *H. macrochir*, *H. taaningi*, and an undescribed form in our collection (Figure 4E, F). These are relatively deep-bodied, have large, relatively wide eyes with little or no choroid tissue, and lack tail pigment. Also, the gut has a highly distinctive form; the anterior half has a very small diameter and opens dorsally into a prominent enlarged posterior section. In *H. macrochir* this enlarged section is covered with large melanophores. Larvae of this group occur only in the Atlantic.

The genus *Hygophum* affords an excellent example of the taxonomic utility of larval stages. The juveniles and adults of some species are notoriously difficult to identify. In contrast, the larvae of these species are highly distinct and can be readily identified. We have 11 such distinct larval types, whereas only 9 species are currently known for the adults. Search for adults of the two remaining larval types has led to the discovery of two undescribed species. In addition, characters of the adults of this genus reveal little about the relationships of the member species (Becker, 1965). A study of the larvae, however, shows that there are three highly distinct subgeneric groups, each containing from two to six closely related species. Such an independent view of the complete species complement of a genus is an invaluable tool in the formal revision of that genus.

Larvae of the species of *Symbolophorus* are perhaps the most cohesive of all myctophine genera (Figure 5A). In all species known to us the pectoral fin is large and is supported by an elongate aliform base. Also, the pelvic fins are large and develop earlier than in any other lanternfish genus. The narrow eyes have choroid tissue and are borne on short stalks. The amount of pigmentation decreases towards the end of the larval period. Most species attain a large size—up to 24 mm. The species differ principally in the size at which various larval structures appear.

The closely related genus, *Myctophum*, has a diversity of larval form unmatched in the family (Figures 5, 6, 7). Before taking up the bulk of the species in this genus we must first examine the most aberrant of all lanternfish larvae, that of *M. aurolaternatum* (Figure 5B). In this remarkable larva the eyes are borne on long stalks and the free trailing section of the gut is almost as long as the fish itself. The dorsal fin forms at the margin of the fin fold. These characters are so bizarre that it would seem preposterous to identify it as a lanternfish larva, much less that of *M. aurolaternatum*. Nonetheless, Å. Vedel Tåning first suggested the true identity of this larva (E. Bertelsen, pers. commun.) which we can now confirm since recently receiving the critical transforming specimens through the courtesy of Warren Freihofer (California Academy of Science). The uniqueness of this larva would certainly suggest

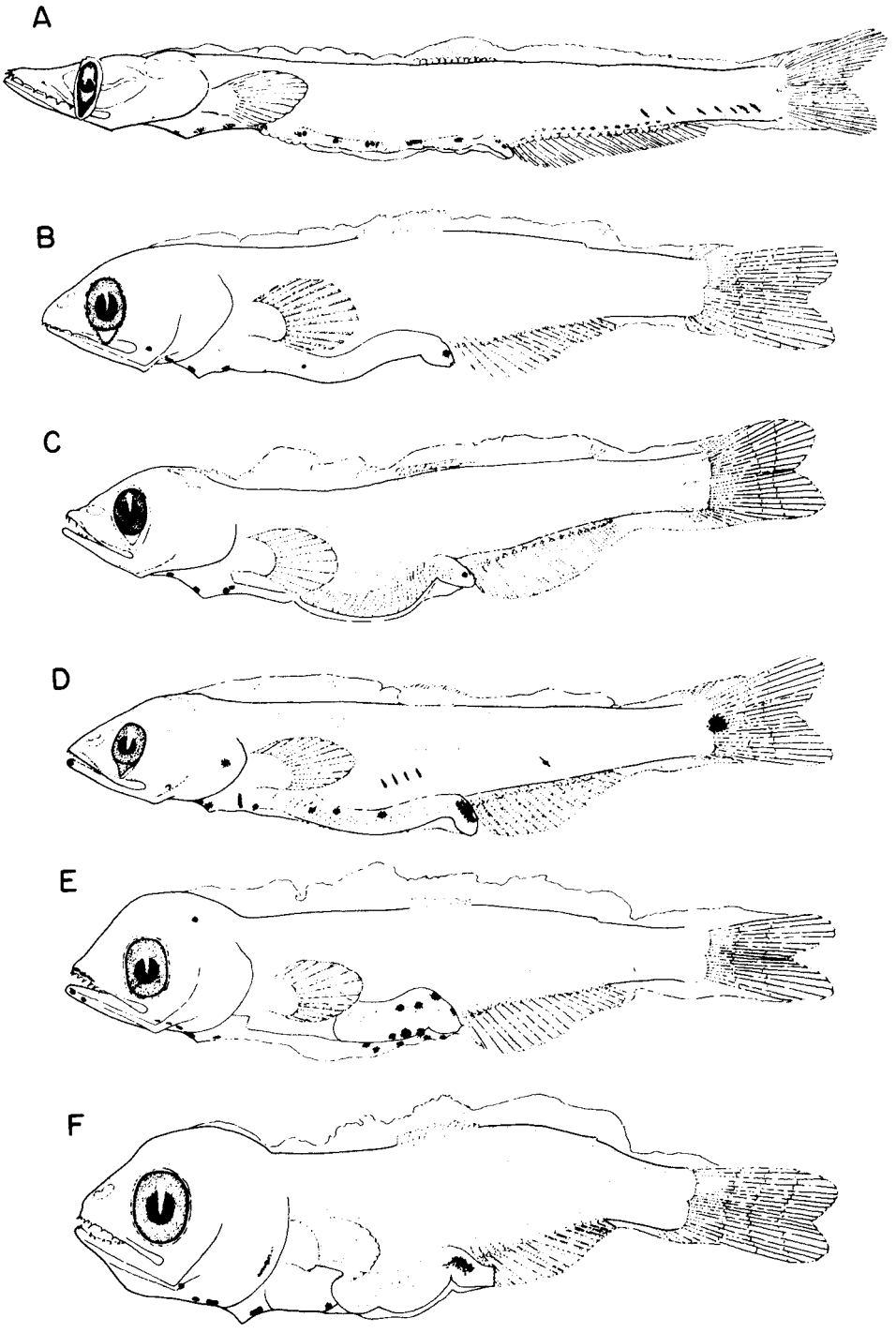

FIGURE 4.—Larvae of *Hygophum*. A. *H. reinhardti*, 12.8 mm; B. *H. proximum*, 8.9 mm; C. *H. hygomi*, 8.1 mm; D. *H. brunni*, 9.7 mm; E. *H. macrochir*, 7.3 mm; F. *H. taaningi*, 6.8 mm.

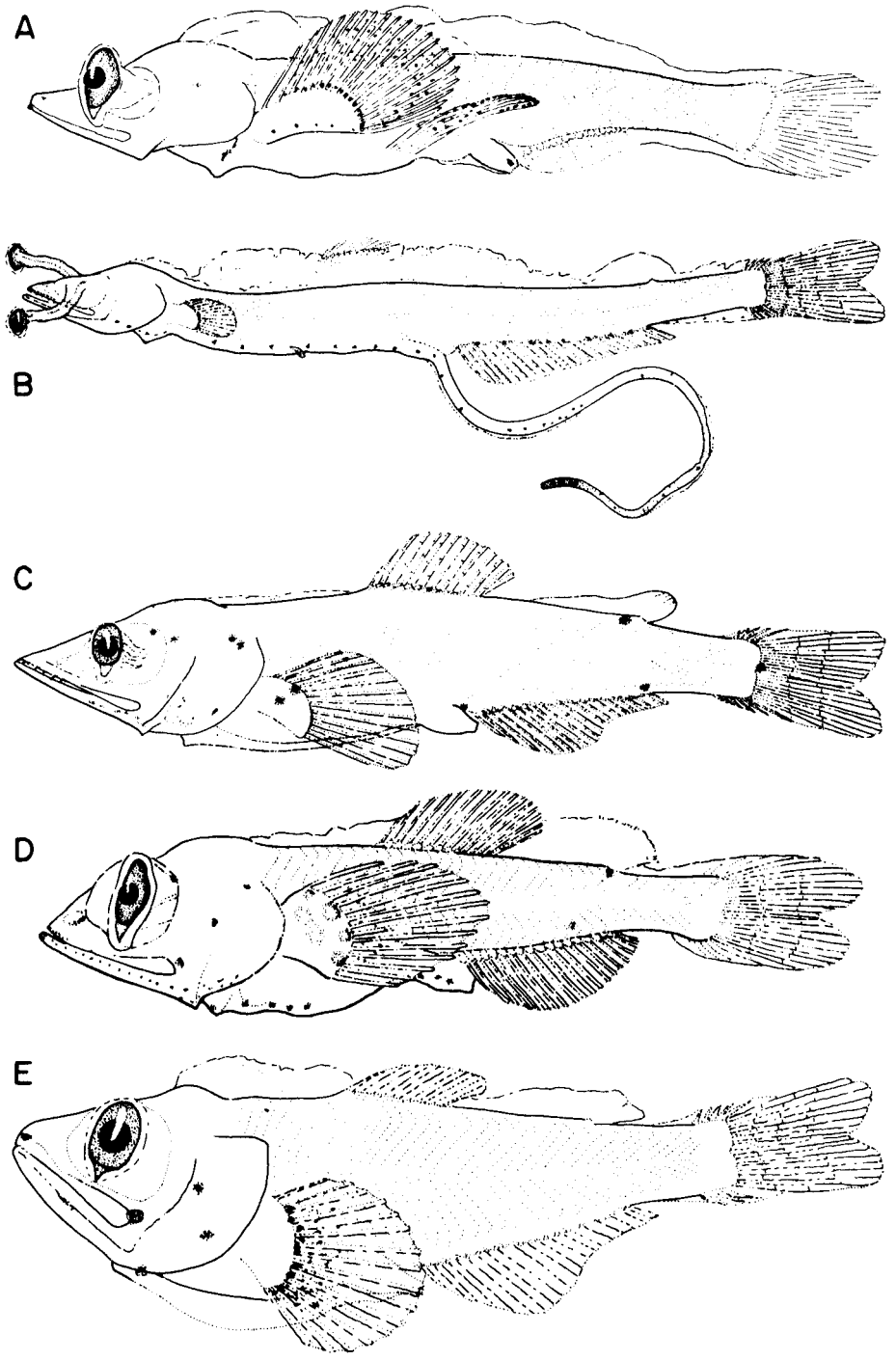

FIGURE 5.—Larvae of *Symbolophorus* and *Myctophum*. A. *S. californiense*, 9.6 mm; B. *M. aurolaternatum*, 26.0 mm; C. *M. punctatum*, 13.6 mm; D. *M. nitidulum*, 8.2 mm; E. *M. phengodes*, 9.8 mm.

the creation of a distinct genus for *M. aurolaternatum* and it is highly probable that corroborative characters will appear after careful reexamination of the adults.

With the removal of *M. aurolaternatum*, the remaining larvae of *Myctophum* form a diverse, yet recognizable, group. All have large broad pectoral fins supported on a highly characteristic fan-shaped base. The species may be divided into two groups, those which form only the Br_2 photophores and those which develop additional photophores during the larval period. In the first group the elongate larva of *M. punctatum* (Figure 5C) has stalked eyes and a slightly aliform pectoral fin base, reminiscent of *Symbolophorus* larvae, and may be the closest relative of that genus among the species of *Myctophum*. A closely related species, *M. nitidulum*, is also stalk-eyed, but is deeper-bodied, more heavily pigmented, and has a more fan-shaped pectoral fin base (Figure 5D). It is obvious from our studies that *M. nitidulum* is one member of a complex, that includes *M. affine* (not illustrated) and several other species. The lightly pigmented larva of *M. phengodes* has only a suggestion of stalked eyes but is similar in body shape to *M. nitidulum* (Figure 5E). The larval characters substantiate Paxton's (1972) decision to abolish the genus *Ctenoscopelus*, established for this species by Fraser-Brunner (1949).

The other major group of *Myctophum* is characterized by the appearance of the Dn photophore anterior to the eye, usually early in the larval period. These species fall into three rather distinct species groups on the basis of body and eye shape. The first is a group of four rotund broad-headed species, which have large unstalked eyes subtended by a short mass of choroid tissue. Of these, the larvae of *M. asperum* are the most heavily pigmented, particularly on the body (Figure 6A). Pigment is confined to the head in *M. obtusirostre*, is heavy under the posterior part of the gut in *Myctophum* sp. (possibly *brachygnathum*) and is developed on the jaws, branchistegal membrane and lower part of the pectoral fin base in *Myctophum* sp. (possibly *fissunovi*) as seen in Figure 6B-D. The latter three species form the PLO photophores on the pectoral fin base soon after the appearance of the Dn organs (Table 2).

Nafpaktitis (1973) has listed a number of characters for distinguishing adult *M. obtusirostre* from *M. brachygnathum*. He showed that *M. pristilepis* is a synonym of *M. brachygnathum*. The status of *M. imperceptum* Bekker and Borodulina has yet to be determined.

A second larval type is represented by *M. selenops* (Figure 7A) and a closely related species restricted to the Indian Ocean and Persian Gulf for which we can find no adult (Figure 7B). In these rotund species, the head is relatively longer and narrower than in the previous group and the slightly stalked eyes are narrower and bear more elongate choroid tissue. The two species differ in that the eyes of the unnamed larva are more definitely stalked than in *M. selenops*. Also the pigment pattern is markedly different, as is the size at which photophores appear. We have carefully examined larvae of *M. selenops* from the Atlantic, Indian, and Pacific Oceans, find them to be identical in all three oceans, and seriously question Wisner's (1971) allocation of the Hawaiian population as a distinct species, based on slight differences in relative eye size and SAO photophore orientation.

The third type of larvae that develop the Dn photophores is represented by *M. spinosum* (Figure 7C) and *M. lychnobium* (Figure 7D). These are elongate fusiform larvae with moderately narrow unstalked eyes, underlain by a pronounced choroid mass. *M. spinosum* is the more slender of the two and is extremely heavily pigmented, especially in older larvae. Pigmentation in *M. lychnobium* is confined to that in the illustrated

TABLE 2.—Sequence of photophore formation in species of *Myctophum* that form two or more pairs during the larval stage.

Species	Size range (mm)	Size at first formation (mm)				Size at transformation (mm)
		Br_2	Dn	PLO	PO_1	
M. asperum	ca. 3.0-9.8	4.2	4.6	9.8	—	Early transf. 11.4
M. obtusirostre	ca. 3.0-8.9	3.8	4.0	ca. 7.1	8.9	Late transf. 12.5
M. sp. (possibly *fissunovi*)	ca. 3.0-7.1	4.1	4.1	7.1	—	—
M. sp. (possibly *brachygnathum*)	6.0-11.4	6.0	6.0	ca. 9.0	ca. 9.0	Late transf. 13.8
M. lychnobium	3.5-12.1	ca. 6.0	6.3	12.1	—	Late transf. 14.2
M. spinosum	3.5-13.7	ca. 5.5	7.2	13.7	—	Late transf. 14.5
M. selenops	3.5-7.5	5.1	5.1	6.2	7.5	Late transf. 11.4
M. sp.	4.0-9.1	ca. 7.0	9.1	—	—	—

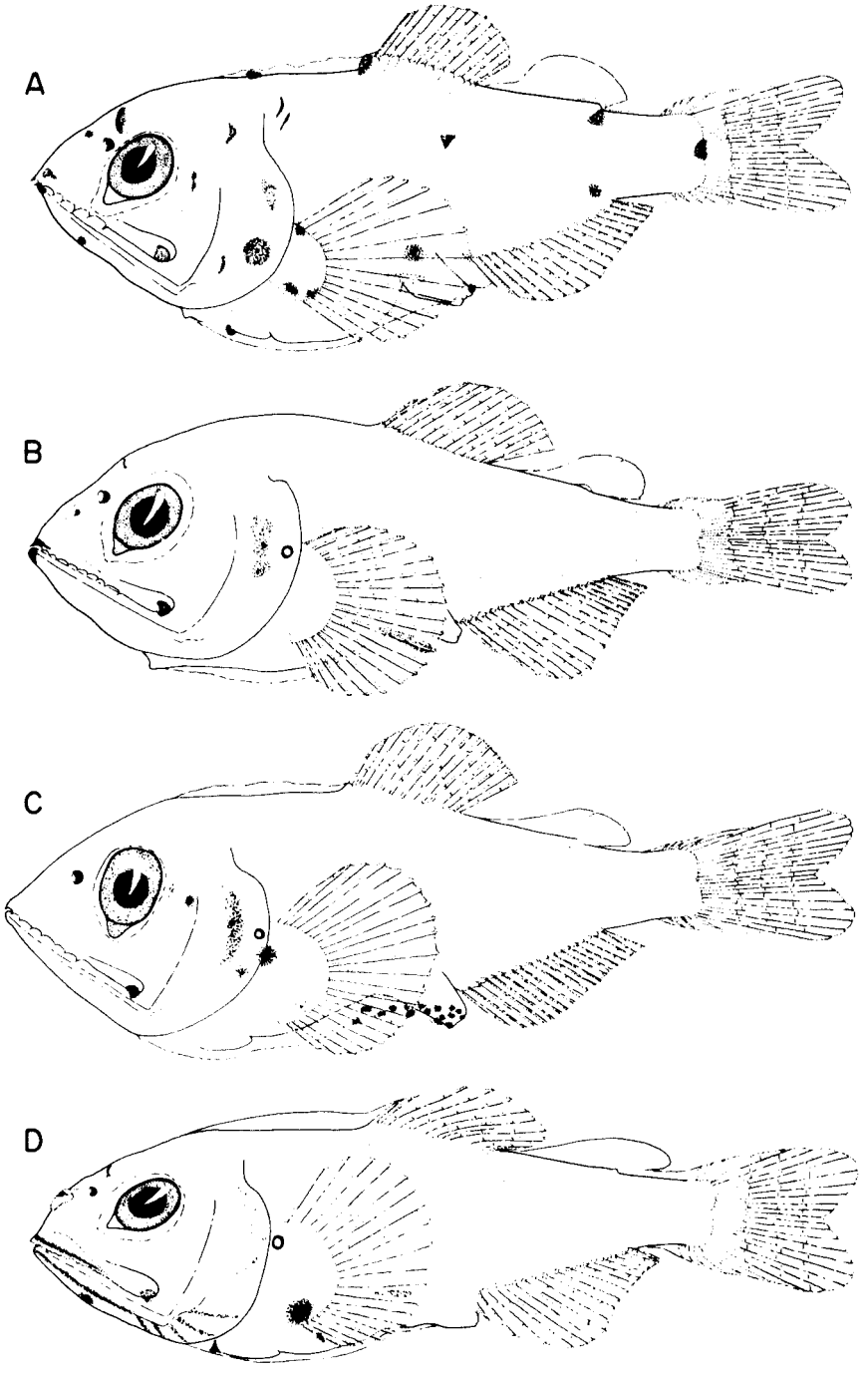

FIGURE 6.—Larvae of *Myctophum*. A. *M. asperum*, 6.8 mm; B. *M. obtusirostre*, 7.6 mm; C. *M.* sp. (possibly *brachygnathum*), 7.5 mm; D. *M.* sp. (possibly *fissunovi*), 7.4 mm.

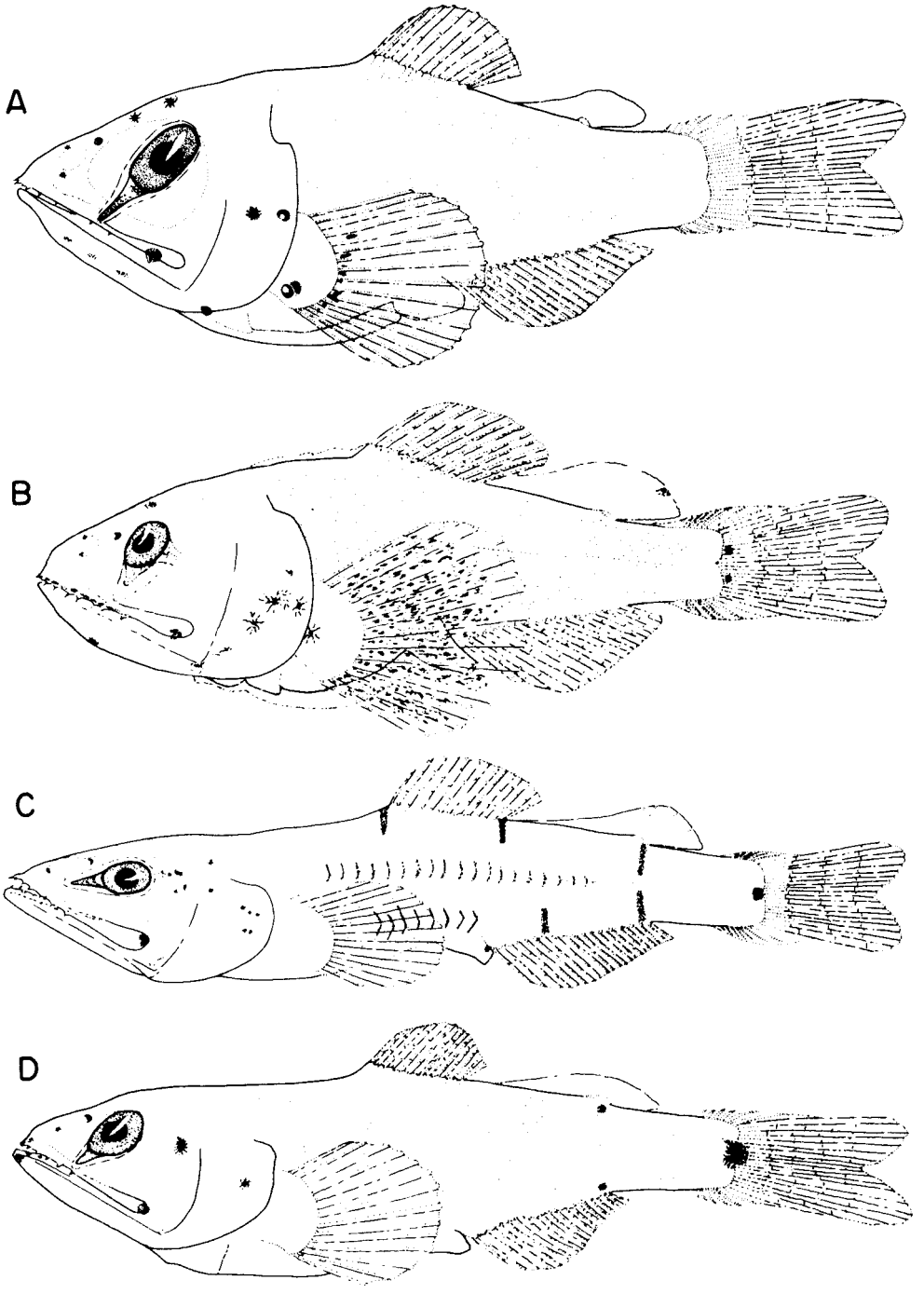

FIGURE 7.—Larvae of *Myctophum*. A. *M. selenops*, 7.8 mm; B. *M.* sp., 9.1 mm; C. *M. spinosum*, 9.0 mm; D. *M. lychnobium*, 9.5 mm.

specimen. Only larvae of *M. lychnobium* have been taken in the eastern Pacific, whereas both species have been taken in the central and western Pacific and in the Indian Ocean. Taxonomists dealing with adult characters only, have placed *M. lychnobium* in synonymy with *M. spinosum* but the distinctiveness of the larvae suggests that the adult characters should be reexamined.

The larvae of *M. spinosum* and *M. lychnobium*, although clearly developing the Dn pair of photophores, resemble the larvae of *M. punctatum* in body shape and pigmentation, a species which does not develop the Dn as larvae. Actually, there are some common characters of pigmentation and eye structure which appear in all of the groups of *Myctophum* species described above. What we appear to be dealing with is a mosaic of larval characters in a highly complex genus. The taxonomy of *Myctophum* presently is confused; our work on the larvae should help define the number of species in the genus and, perhaps, adult characters will emerge that can be combined with larval characters to define the phyletic lines within the genus.

Larvae of the four genera known collectively as the slendertailed myctophids are shown in Figure 8. Quite obviously there are two highly divergent generic pairs. *Loweina* and *Tarletonbeania* are characterized by large oval eyes, posterior placement of median fins to accommodate the immense fin fold, and elongated lower pectoral rays bearing spatulate processes. *Gonichthys* and *Centrobranchus* are characterized by a deep but markedly compressed head and body and small narrow eyes with extremely elongate choroid tissue. As stated earlier, the larval characters suggest strongly that the two generic pairs are not closely related and should not be grouped into a tribe. The *Gonichthys-Centrobranchus* pair is similar in eye shape and gut shape to some species of *Myctophum*, however no species of *Myctophum* even approaches this pair in body shape. The characters of the other pair are so divergent as to give no clue of their affinities within the subfamily Myctophinae.

THE SUBFAMILY LAMPANYCTINAE

The subfamily Lampanyctinae is considerably larger than the Myctophinae; it contains about 19 genera and 200-250 species compared with 12 genera and about 75 species in the Myctophinae. Paxton (1972) divided the genera into four tribes on the basis of a combination of osteological features and characters of the photophores. In a previous paper (Moser and Ahlstrom, 1972) we discussed Paxton's placement of genera in these tribes and indicated that the larval characters suggested a somewhat different distribution of genera among the four tribes. For the purposes of this discussion the tribes referred to here are those suggested by the larval characters.

In general, the larvae of the Lampanyctinae are much less diverse in larval characters and specializations than are the larvae of the Myctophinae, although exceptions to this may be found in two of the lampanyctine tribes, the Diaphini and the Lampanyctini.

The tribe Diaphini is made up of two genera —*Diaphus* contains about 50 species and *Lobianchia* has 3 species. Both genera develop photophores, in addition to the Br_2, during the larval period; in fact more are developed in *Diaphus* than in any other lanternfish genus.

There are two basic larval types in *Diaphus* (Figure 9A, B). One has a slender body, small head, and a series of persistent melanophores on the ventral midline of the tail. The other type has a deeper body, bulbous head, and a single persistent ventral tail melanophore, or none. It is exceptional for larvae of either type to develop pigment on the head and it never occurs between the eyes, as is common in *Lampanyctus*. Both types do form embedded melanophores at the base of the caudal fin rays.

The slender type is restricted to the species that develop a suborbital photophore as adults (*Diaphus* sensu stricto of Fraser-Brunner, 1949) and is represented in Figure 9A by *D. theta*. The stubby type is represented by *D. pacificus* (Figure 9B). The specimens illustrated for the two species are rather early larval stages which have not yet formed their larval photophores, other than the Br_2. The first additional pair to form in both types is the PO_5 and then the PO_1 (Table 3). The large genus *Diaphus*, except for the Atlantic species ably reviewed by Nafpaktitis (1968), is in a state of taxonomic confusion. Various workers (Fraser-Brunner, 1949; Bolin, 1959) have attempted to split the genus into smaller, more cohesive groups; the larval evidence would suggest that at least two divergent groups are present.

The larvae of the three species of *Lobianchia* are

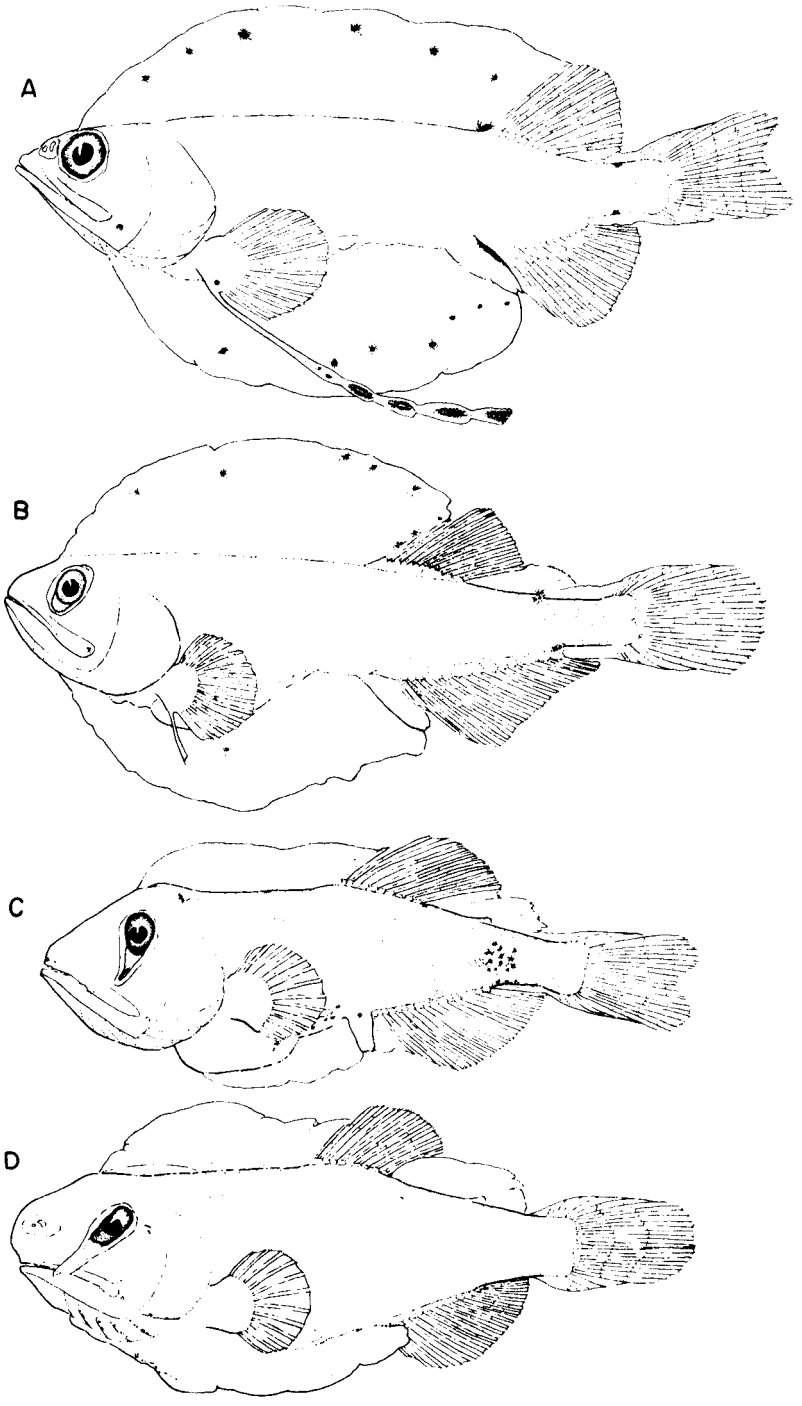

FIGURE 8.—Larvae of Gonichthyini. A. *Loweina rara*, 17.6 mm; B. *Tarletonbeania crenularis*, 18.9 mm; C. *Gonichthys tenuiculus*, 7.7 mm; D. *Centrobranchus choerocephalus*, 7.3 mm.

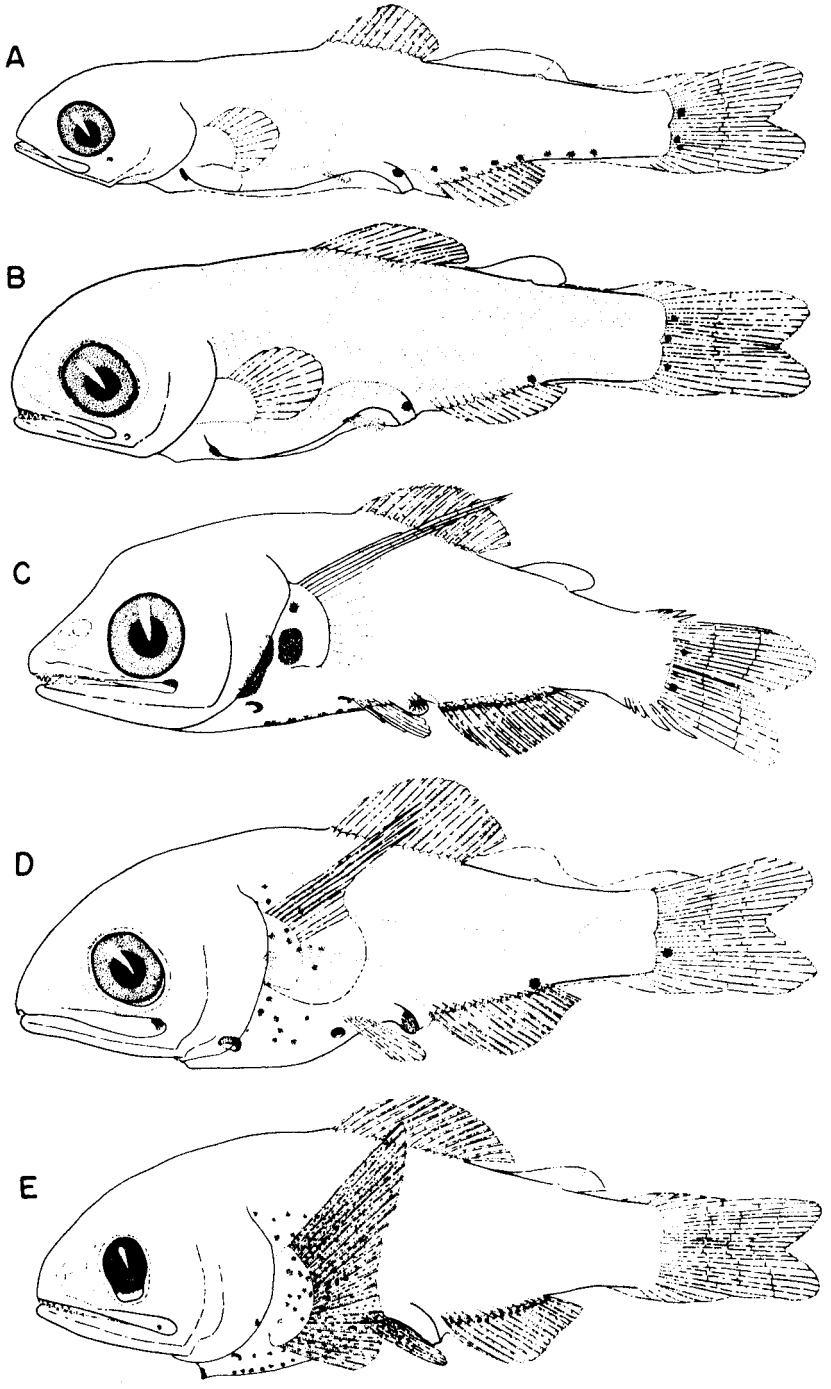

FIGURE 9.—Larvae of *Diaphus* and *Lobianchia*. A. *D. theta*, 6.9 mm; B. *D. pacificus*, 5.2 mm; C. *L. urolampus*, 7.2 mm; D. *L. gemellari*, 6.7 mm; E. *L. dofleini*, 8.2 mm.

TABLE 3.—Sequence of photophore formation in larvae of two species of *Diaphus*.

Species	Size larva (mm)	Photophores	No. of photophore pairs	Smallest juvenile (mm)
D. theta	6.2	Br_2 PO_5	2	ca. 12.0
	7.6	Br_2 PO_5 PO_1	3	
	8.2	Br_2 PO_5 PO_1 VO_1	4	
	8.6	Br_2 PO_5 PO_1 VO_1 PO_2 Op_2	6	
	9.0	Br_2 PO_5 PO_1 VO_1 VO_1 PO_2 Op_2 PO_3 PO_4 VO_5	9	
	9.2	Br_2 PO_5 PO_1 VO_1 PO_2 Op_2 PO_3 PO_4 VO_5 VLO	10	
D. pacificus	5.7	Br_2 PO_5 PO_1	3	9.8
	6.2	Br_2 PO_5 PO_1 PO_2 PVO_1	5	
	6.5	Br_2 PO_5 PO_1 PO_2 PVO_1 PO_3	6	
	7.5	Br_2 PO_5 PO_1 PO_2 PVO_1 PO_3 VO_1	7	

deep-bodied, have large broad heads, and are easily identified by their unique wing-shaped pectoral fins (Figure 9C-E). The larvae of all three species are heavily pigmented and develop the Br_2, PO_1, and PO_5 photophores sequentially. In *L. urolampus* (Figure 9C) and *L. gemellari* (Figure 9D) the eyes are large and nearly round and the lower pectoral rays are delayed in developing. In *L. dofleini* the lower pectoral rays develop along with the produced upper rays and the eye is completely different (Figure 9E). With its narrow elliptical shape and unique squarish mass of choroid tissue, it is the single obvious exception to the rule of narrow eyes in the subfamily Myctophinae and rounded eyes in the Lampanyctinae. All other larval characters identify this species as a *Lobianchia*, and we conclude that the narrowing of the eye in this species occurred independently as a secondary adaptation.

In our view the tribe Lampanyctini contains the genera *Lampanyctus*, *Triphoturus*, *Stenobrachius*, and *Parvilux*. As recently as Fraser-Brunner's (1949) review of the family Myctophidae, *Lampanyctus* was still a catchall genus with a number of disparate subgenera. Since then the subgenera *Stenobrachius*, *Triphoturus*, and *Lepidophanes* have been removed from *Lampanyctus* and afforded generic status. *Lepidophanes* has been further split into the genera *Lepidophanes* and *Bolinichthys*. All of the separated genera have distinctive larval morphs. With their removal, the species of *Lampanyctus* form a more coherent assemblage of 40-50 species, and despite the diversity of larval specializations encountered in the genus, there is a central morph and pattern of larval development.

Lampanyctus larvae are deep-bodied and bigheaded. In older larvae characteristic pigment can develop at a variety of locations such as the tip of the lower jaw, between the eyes, the back of the head, the side of the head, the adipose fin, the pectoral fin, internally in the region of the cleithra, and along the myosepta. The pigment patterns are of prime importance in identifying the larvae to species.

There are several rather distinct larval types in *Lampanyctus*. One of these consists of a group of species whose adults are characterized by having the pectoral fins much reduced or even absent, and has been separated recently as a distinct genus *Paralampanyctus* by Kotthaus (1972) with *P. niger* as type. Previously, Günther (1887) had proposed the generic name *Nannobrachium* for this species and this has priority over *Paralampanyctus* (John Paxton, pers. commun.). There is a remarkable trend of jaw specialization in the larvae of this group (Figure 10). The larva of *L. ritteri* has jaws of moderate length and the other species shown have progressively longer jaws with more prominent teeth, particularly anteriorly. This trend culminates in the larva of *Lampanyctus* sp. (possibly *achirus*) which somewhat resembles a larval billfish. This species will lack the pectoral fin in juveniles and adults, even though it is well developed in the larvae. The pectoral fins are also large in *L. regalis* and *L. niger* larvae, but will be small and weakly developed in adults. This disparity is even more apparent in another eastern Pacific species, which lacks pectoral fins as an adult, but whose larvae have the largest pectoral fins with the highest number of rays that we have encountered among *Lampanyctus* larvae. Other less spectacular specializations appear in the other subgroups of *Lampanyctus*, but it appears that the larval characters will be helpful in defining the species composition of the several subgenera.

Representatives of other genera of Lampanyctini, *Triphoturus*, *Stenobrachius*, and *Parvilux* are illustrated in Figure 11A-C. Small larvae of *Triphoturus* and *Stenobrachius* have a row of melanophores along the ventral margin of the tail

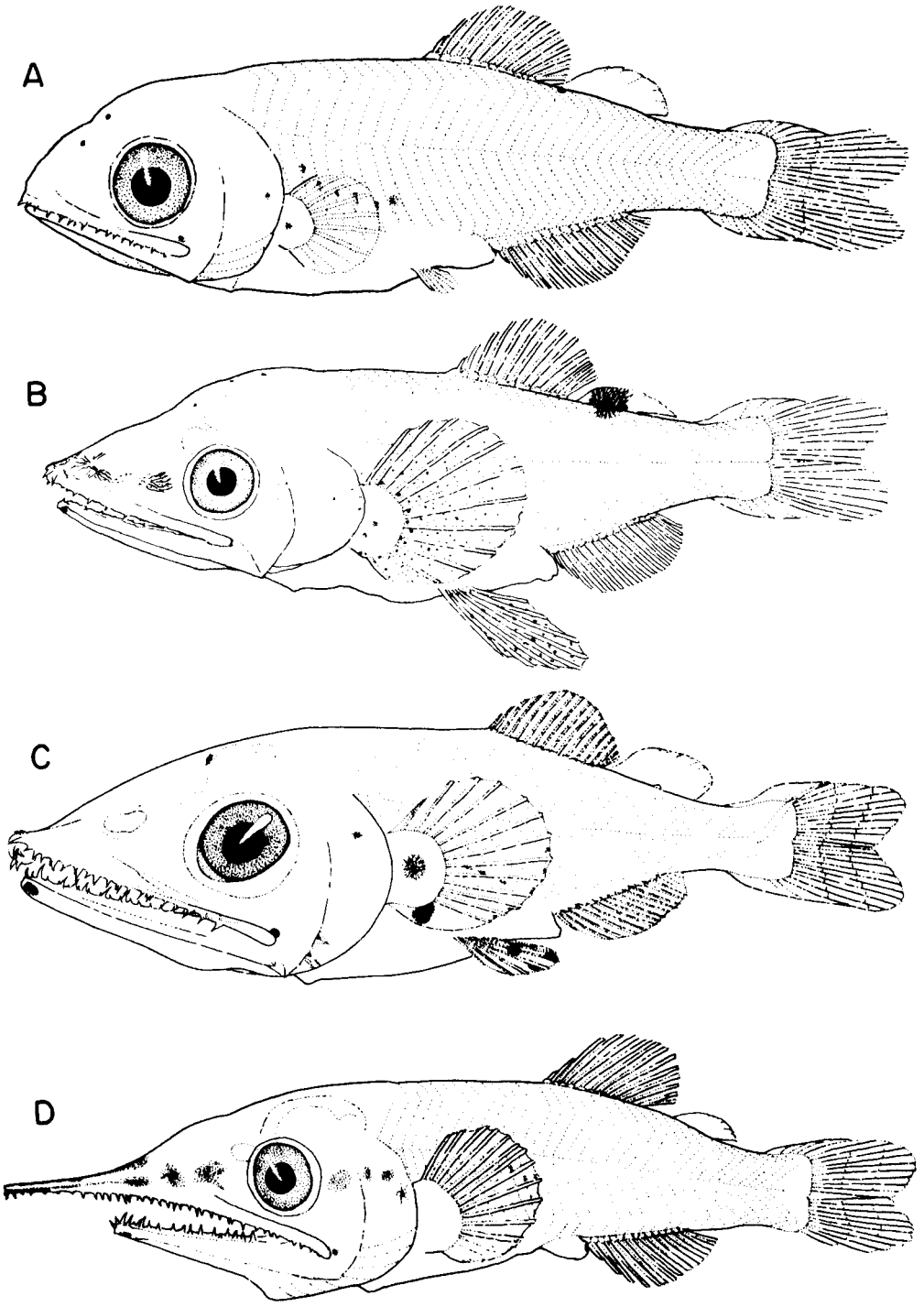

FIGURE 10.—Larvae of *Lampanyctus*. A. *L. ritteri*, 10.1 mm; B. *L. regalis*, 9.1 mm; C. *L. niger*, 8.7 mm; D. *L.* sp. (possibly *achirus*), 13.4 mm.

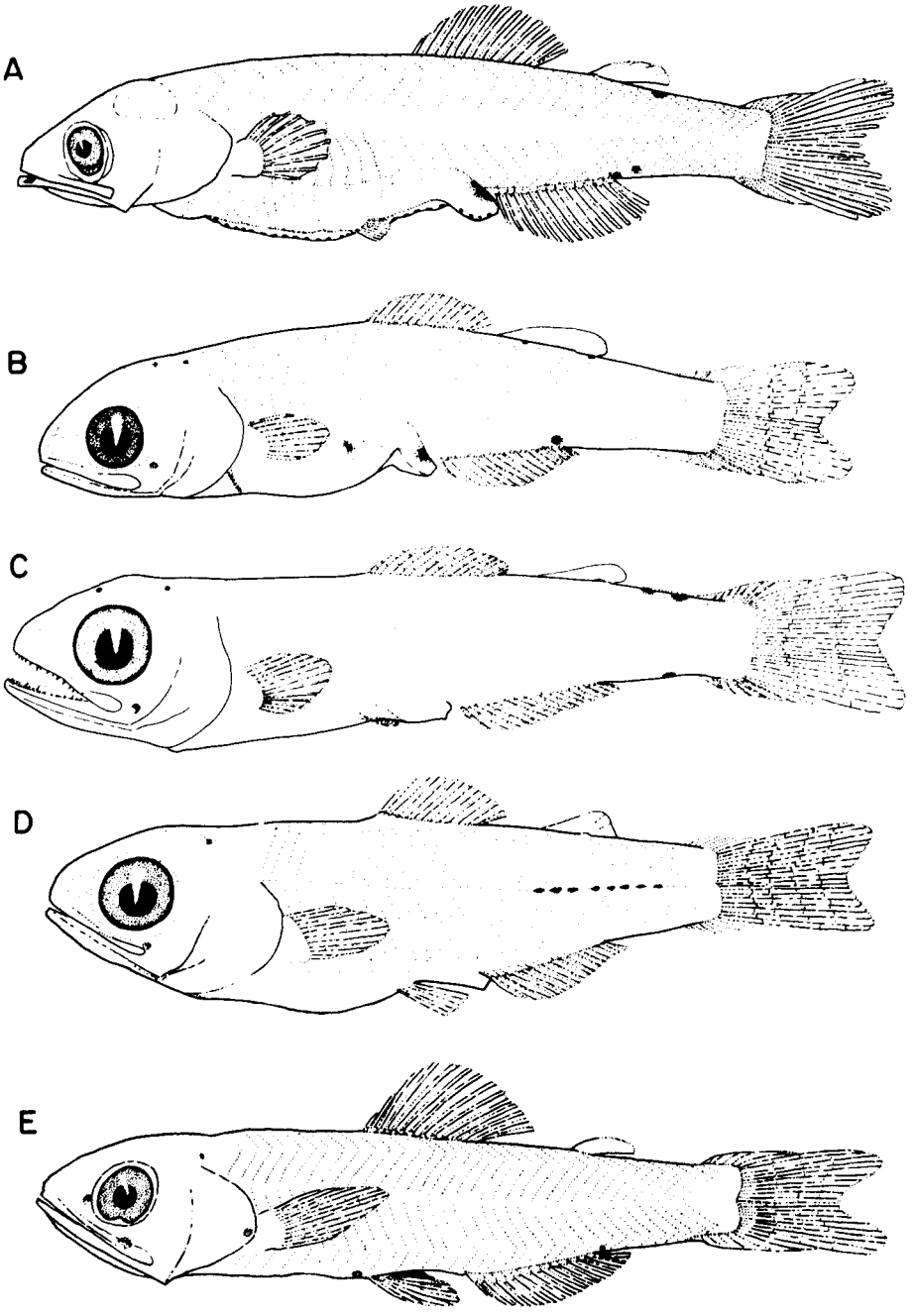

FIGURE 11.—Larvae of Lampanyctini and Gymnoscopelini. A. *Triphoturus mexicanus*, 10.5 mm; B. *Stenobrachius leucopsarus*, 10.4 mm; C. *Parvilux ingens*, 14.4 mm; D. *Bolinichthys supralateralis*, 9.4 mm; E. *Ceratoscopelus townsendi*, 16.6 mm.

but these coalesce into one or two spots in mid-stage larvae. *Triphoturus* larvae are characterized further by their distinctive head shape and by the series of melanophores along the ventral midline below the gut. *Stenobrachius* larvae add considerable pigment late in the larval period, particularly along the dorsum and on the myosepta of the trunk. The larvae of *Parvilux* are distinct in shape and pigmentation. Paxton (1972) placed this genus in *Lampanyctus* based on osteological characters. In certain photophore arrangements, however, particularly in the posterior placement of the VLO and the nonangulate arrangement of the SAO, the genus appears to us to be more closely related to *Stenobrachius* than to *Lampanyctus*. These characters in addition to the distinctness of the larvae would suggest that the validity of *Parvilux* should be reconsidered.

The tribe Gymnoscopelini judged from larval and/or adult characters contains a dozen genera (*Notoscopelus*, *Lampichthys*, *Scopelopsis*, *Ceratoscopelus*, *Lepidophanes*, *Bolinichthys*, *Lampadena*, *Taaningichthys*, *Dorsadena*, *Lampanyctodes*, *Gymnoscopelus*, and *Hintonia*). The larvae of these genera are united by a group of common characters, including a distinctive, usually slender, body outline, a series of melanophores on the dorsal and ventral midlines of the tail (in most genera), and the development of a group of photophores during the larval period, most notably the PO_5, PLO, and Vn. The larvae of this tribe were treated extensively in a previous paper with representative larvae illustrated for 10 of the 12 genera (Moser and Ahlstrom, 1972). Additional species of *Bolinichthys* (*B. supralateralis*, Figure 11D), *Ceratoscopelus* (*C. townsendi*, Figure 11E), *Lampadena* (*L. luminosa*, Figure 12B), *Lepidophanes* (*L. gaussi*, Figure 12C) are illustrated herein. Illustrations of *Notoscopelus resplendens* (Figure 12A) and *Scopelopsis multipunctatus* (Figure 12D) are included for comparative purposes. It need only be mentioned here that the clusters of closely related genera within this tribe are readily apparent from examining the larval characters, especially the sequence of photophore development, and these groupings agree closely with those established on the basis of adult characters.

The species *Notolychnus valdiviae* has so many unique adult characters that Paxton (1972) assigned it to the monotypic tribe *Notolychnini*. Likewise the larva has a number of unusual characters (Figure 12E). The shape of the eye is variable from specimen to specimen; it can be narrow and elliptical or nearly round, but most typically would be classified as irregular in shape. The shape of the head, body, and gut is unusual and distinctive. The larval characters are of little help in elucidating the affinities of this species within the Myctophidae and, when added to the list of unique adult characters, only magnify the problem. It would seem to make just as much sense to establish a separate subfamily for *Notolychnus* as to place it in a monotypic tribe in the subfamily Lampanyctinae.

The larvae illustrated in this paper comprise 55 species representing 24 genera. Illustrations are included for larvae of 11 of the 12 genera in the subfamily Myctophinae; not included are illustrations of *Diogenichthys* (see Moser and Ahlstrom, 1970 for *D. laternatus* and *D. atlanticus*). In the subfamily Lampanyctinae larvae are illustrated for 13 of the 19 genera. The omitted genera (*Lampichthys*, *Lampanyctodes*, *Gymnoscopelus*, and *Tanningichthys*), all from the tribe Gymnoscopelini, are illustrated in Moser and Ahlstrom (1972). Larvae of *Hintonia* and *Dorsadena* have not yet been identified.

SOME EVOLUTIONARY CONSIDERATIONS

With this brief review of lanternfish larvae completed, let us now turn to an interesting problem of myctophid evolution to which study of the larvae may contribute importantly—the evolution of photophore pattern. With a single exception, all adult myctophids have two conspicuous rows of photophores that extend the length of the body on each side of the ventral midline. The photophores are grouped and positioned in a definite and often diagnostic pattern. Also, lanternfishes have a specific pattern of photophores on the sides of the body, below the lateral line, and on the ventral aspect of the head. The exception is *Taaningichthys paurolychnus*, which appears to lack body photophores entirely. In addition to these photophores, some lanternfish genera have photophores positioned in a pattern above the lateral line and some have small "secondary" photophores distributed more generally over regions of the body and head. Another type of luminous structure present on most myctophids are discrete glands located at the caudal peduncle. Typically, these are sexually dimorphic in character and, doubtless, play some part in courtship

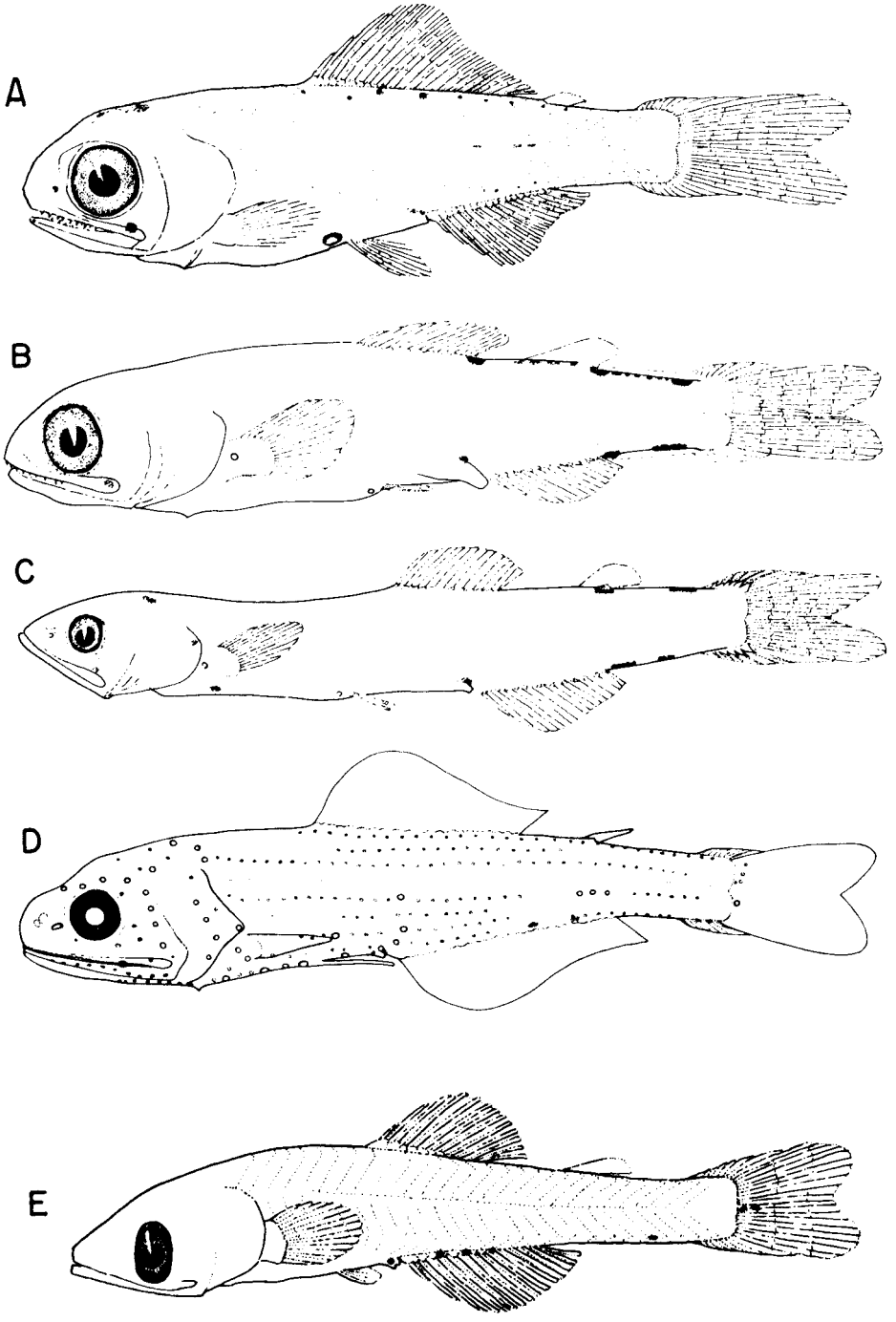

FIGURE 12.—Larvae of Gymnoscopelini and Notolychnini. A. *Notoscopelus resplendens*, 11.2 mm; B. *Lampadena luminosa*, 12.8 mm; C. *Lepidophanes gaussi*, 13.5 mm; D. *Scopelopsis multipunctatus*, 17.5 mm; E. *Notolychnus valdiviae*, 9.2 mm.

behavior. Finally, some myctophids have small patches of soft whitish, apparently luminous, tissue located at various regions of the body.

The most popular speculation as to the possible function of the patterns of photophores and luminous scales is that they function in species recognition (see McAllister, 1967). An explanation for the universality of the two ventral rows was postulated by Clarke (1963). His suggestion that these downward directed rows emit a continuous light of ambient wavelength, which conceals the fish from deeper-living predators by countershading, has much appeal.

We have long been interested in the mechanism by which such patterns of photophores could have evolved and believe we have gained some insight into this mechanism through our studies of the larval stages. Our proposal, as expressed in an earlier paper (Moser and Ahlstrom, 1972), is that ancestral myctophids had a generalized arrangement of unspecialized photophores, one at the posterior margin of each scale pocket, and a group of similar photophores on the head. We further proposed that the specific photophore patterns of contemporary myctophids evolved through progressive enlargement and specialization of certain photophores of the generalized pattern and concurrent diminution or loss of the unspecialized photophores. This idea came to us upon discovering the remarkable transforming specimens of *Scopelopsis multipunctatus*, the adults of which have a small photophore at each scale pocket and a group of photophores on the head. In the adults, the "primary" organs can be distinguished only by their modified lens-bearing scales, but in the transforming specimens (Figure 11D) the primary photophores stand out clearly as enlarged members of the meristic series of light organs. It struck us that a similar arrangement of photophores might have existed in the adults of an ancestral species, and led to the development of our ideas on the evolution of photophore pattern. Our theory was further strengthened by neurological findings and by what we feel are inherent weaknesses in Bolin's (1939) and Fraser-Brunner's (1949) theory that photophore patterns evolved by the upward migration of organs from ventral rows of photophores.

Viewed from the standpoint of our theory the subfamily Myctophinae would be considered highly specialized, since it is here that diminution of secondary photophores has reached its highest degree; they are totally lacking in the subfamily. The individual "primary" photophores are typically highly developed and concentrated ventrally on the body. The ventral location of photophores in Myctophinae is probably related to their habitat. That is, they are generally shallow-living active fishes that have well-developed gas bladders and it is plausible that concentration of photophores ventrally on the body evolved as an adaptation for countershading and protection from deeper-living predators. This view of the Myctophinae is completely contrary to those previously held for this subfamily. On the basis of the "upward migration" theory of photophore evolution, myctophines were thought to be primitive unspecialized forms. Formerly, we too subscribed to this view, and contrasting the then supposed primitive features such as low photophore position and short jaws of the adults with the highly specialized and diverse features of the larvae, we proposed that the evolutionary pace had differed in the larval and adult stages of the subfamily. Our altered opinion would view both larvae and adults of the Myctophinae as highly advanced and would interpret the low photophores, prominent gas bladders, short jaws, and often narrow caudal peduncles as specialized adaptations of active surface-dwelling fishes.

Our view of the Lampanyctinae must also be revamped. Formerly we considered the diverse and often dorsally oriented pattern of photophores and accessary luminous tissue to be highly specialized features. Possibly, the luminous scalelike patches and luminous glands are specialized adaptations, but we feel that the presence of small secondary photophores and the dorsal positioning of primary photophores in many of the genera, indicate a retention of the ancestral condition. The Lampanyctinae are generally deeper-living than the Myctophinae and many genera are lethargic fishes that rest vertically in the water column (Barham, 1970). In deeper-living fishes with such a behavior pattern there would be little evolutionary advantage in having ventrally concentrated photophores, and the fat-invested swim bladders and long jaws typical of many genera could have evolved in relation to habitat and activity pattern. It is interesting that the most obvious exception in the subfamily, the Diaphini, are active, often surface-dwelling fishes with relatively short jaws and ventrally concentrated photophores. It is obvious from the present paper that the larvae of Lampanyctinae exhibit much less diversity than the Myctophinae, but we

no longer view the adult myctophines as being more "primitive" than the adult lampanyctines. We feel that the adults of both subfamilies are equally specialized and that these specializations are basically related to their particular habitat.

In summary, thorough study of the larvae of a teleost family such as the Myctophidae can be most helpful in species validation, in analyzing affinities at all taxon levels, and in assessing phylogenetic lineages. Also, the above discussion would indicate that larval studies can provide interesting insights into the major directions of evolution within a family of fish.

ACKNOWLEDGMENTS

George Mattson executed 15 of the illustrations (Figures 1E, 4A, 5A and D, 8A-D, 10A, B, and D, 11A and E, and 12A and E) and we thank him for his efforts. The remaining illustrations were made by one of us (H. G. Moser). Larval specimens came from a variety of sources and we are especially indebted to the following persons for their generous provision of material: E. Bertelsen and J. Nielsen, Zoological Museum, Copenhagen; N. B. Marshall and A. Wheeler, British Museum; W. Nellen, Institute für meereskunde, Kiel, Germany; R. McGinnis and B. Nafpaktitis, University of Southern California (USC); R. J. Lavenberg, Los Angeles County Museum; R. Rosenblatt and R. Wisner, Scripps Institution of Oceanography (SIO); T. Clarke and J. Miller, University of Hawaii; W. Freihofer, California Academy of Sciences. We would like to thank B. Nafpaktitis and R. McGinnis, USC; R. Wisner, SIO; J. Paxton, Australian Museum, Sydney; and G. Krefft, Fisheries Institute, Hamburg, Germany, for sharing their vast knowledge of lanternfishes with us in numerous discussions. Discussions with N. B. Marshall, British Museum; B. Robison, Stanford University; and A. Kendall, Middle Atlantic Coastal Fisheries Center, National Marine Fisheries Service (NMFS); Sandy Hook, have been helpful in stimulating some of the ideas put forth herein. We appreciate the able technical assistance of Elaine Sandknop, Elizabeth Stevens, and Patricia Lowery, Southwest Fisheries Center La Jolla Laboratory, NMFS. Kenneth Raymond kindly lettered the illustrations.

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EARLY DEVELOPMENT OF FIVE CARANGID FISHES OF THE GULF OF MEXICO AND THE SOUTH ATLANTIC COAST OF THE UNITED STATES

VIRGINIA L. APRIETO[1]

ABSTRACT

Larvae of round scad, *Decapterus punctatus;* rainbow runner, *Elagatis bipinnulata;* banded rudderfish, *Seriola zonata;* lookdown, *Selene vomer;* and leatherjacket, *Oligoplites saurus*, collected in the Gulf of Mexico and off the south Atlantic coast of the United States are described and illustrated. Larvae 2 to 3 mm long show general family characteristics but generic and specific characters are differentiated in later stages. Morphological features including supraoccipital crest, thickness of the first interhemal spine, and body indices; meristic characters; mode of development and modification of the dorsal and pelvic fins; and patterns of pigmentation are useful in distinguishing the family, genera, and species. Information on distribution and spawning is included.

The family Carangidae consists of about 200 species of fishes which vary widely in form and are distributed in tropical and subtropical waters. Various attempts by authors to divide the family into subfamilies proved unsatisfactory in view of the numerous, weak characters used for this purpose and the presence of many transition genera which did not permit delineation of groups which may have been proposed as subfamilies (Ginsburg, 1952).

Twenty-eight species of carangids have been found along the Atlantic and Gulf coasts of the United States (Table 1). The larvae of some of these species occurred frequently in plankton and nekton collected in the Gulf of Mexico and off the south Atlantic coast of the United States during the multiship cruises in October to November 1970 and May to October 1971 during continuing surveys of marine biological communities conducted by the National Marine Fisheries Service (Southeast Fisheries Center) and cooperating agencies. The larval development of five species is described and illustrated in the present work.

Only a few studies dealing with early life history stages of North Atlantic carangids have been carried out by American workers. Hildebrand and Cable (1930) described larvae and early juveniles of *Decapterus punctatus* and *Seriola dumerili*. Fields (1962) described postlarvae of these species of *Trachinotus: T. carolinus, T. falcatus,* and *T. glaucus;* McKenney, Alexander, and Voss (1958) described a rather complete larval series of *Caranx crysos;* Berry (1959) described late-stage larvae and juveniles of five species of *Caranx*, including: *C. crysos, C. bartholomaei, C. ruber, C. hippos,* and *C. latus*. None of the above series included eggs or yolk-sac larvae and the majority lacked early-stage larvae as well.

Over a third of the carangids that occur off the eastern United States are wide-ranging species, and early life history series had been described from other areas for the following: *Selar crumenophthalmus* by Delsman (1926) and Devanesan and Chidambaram (1941), *Naucrates ductor* by Sanzo (1931), *Caranx dentex* by Schnakenbeck (1931), *Seriola dumerili* by Sanzo (1933), *Trachinotus glaucus* by de Gaetani (1940), *Caranx hippos* by Chacko (1950) and Subrahmanyam (1964), *Chloroscombrus chrysurus* and *Alectis crinitus* by Aboussouan (1968), and *Elagatis bipinnulata* by Okiyama (1970). Hence, early life history series—some complete, some fragmentary—were known for 16 of 28 species of carangids that occur along the Atlantic and Gulf coasts of the United States.

A proper understanding of the early life history of fishes, particularly those of species important to man, can never be overemphasized. The presence of larvae is indicative of recent spawning, and

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TABLE 1.—Meristic characters of adult carangids of the Gulf and Atlantic coasts of the United States.

Species	Dorsal fin	Anal fin	Pectoral fin	Gill rakers	Vertebrae	Source
Alectis crinitus	(VII)0; I,18-19	(II)0; I, 15-16	18-20	5- 6+14-16	–	Ginsburg, 1952
Alectis crinitus	–	–	–	–	24	Starks, 1911
Caranx bartholomaei	VIII; I, 25-28	II; I, 21-24	I, 19-21	6- 9+18-21	–	Berry, 1959
Caranx bartholomaei	–	–	–	–	24	Miller and Jorgensen, 1973
Caranx crysos	VIII; I, 22-25	II; I, 19-21	I, 19-23	10-14+23-28	–	Berry, 1959
Caranx crysos	–	–	–	–	25	Miller and Jorgensen, 1973
Caranx crysos	VIII; I, 23-25	–	–		–	McKenney et al., 1958
Caranx crysos	–	–	–	–	25	Starks, 1911
Caranx hippos	VIII; I, 19-21	II; I, 16-17	I, 19-20	6- 9+22-27	–	Berry, 1959
Caranx hippos	–	–	–	–	24	Lane, 1965
Caranx latus	VIII; I, 19-22	II; I, 16-18	I, 18-20	6- 7+16-18	–	Berry, 1959
Caranx latus	20-21	16-18	18-20	16+17	24	Lane, 1965
Caranx lugubris	VIII; I, 22	II; I, 19	I, 19	6+20	–	Berry, 1959
Caranx lugubris	–	–	–	–	24	Lane, 1965
Caranx lugubris	VIII; I, 22	II; I, 18	–	–	–	Fowler, 1936
Caranx ruber	VIII; I, 26-30	II; I, 23-26	I, 18-21	10-14+31-35	–	Berry, 1959
Caranx ruber	–	–	–	–	24	Miller and Jorgensen, 1973
Caranx dentex	VIII; I, 25-26	II; I, 21-23	I, 19-20	11-13+26-28	–	Berry, 1959
Chloroscombrus chrysurus	VIII; I, 26-28	II; I, 25-27	19-20	9-11+31-35	–	Ginsburg, 1952
Chloroscombrus chrysurus	–	–	–	–	24	Miller and Jorgensen, 1973
Chloroscombrus chrysurus	VII-VIII; I, 24-26	II; I, 25-26	–	9-10+32-35	–	Fowler, 1936
Chloroscombrus chrysurus	–	–	–	–	24	Starks, 1911
Decapterus macarellus	VIII; I, 31-37	II; I, 27-31	I, 21-23	9-13+32-39	24	Berry, 1968
Decapterus punctatus	VIII; I, 29-34	II; I, 25-30	I, 18-20	11-16+32-44	25	Berry, 1968
Decapterus punctatus	VIII; I, 28-32	II; I, 25-27	19-21	12-15+34-40	–	Ginsburg, 1952
Decapterus punctatus	VIII; I, 27-31	II; I, 24-27	–	12-15+35-40	–	Fowler, 1936
Decapterus tabl	VIII; I, 29-34	II; I, 24-27	I, 20-22	10-12+30-33	24	Berry, 1968
Elagatis bipinnulata	VI-I, 25-26	0-II; I, 16-17	20-21	10-11+25-26	–	Ginsburg, 1952
Elagatis bipinnulata	V-VI; I, 25-30	II, 18-22	I, 18-21	9-12+25-29	24	Berry, 1969
Hemicaranx amblyrhynchus	VII-VIII; I, 27-29	II; I, 23-25	19-22	8-10+19-23	–	Ginsburg, 1952
Hemicaranx amblyrhynchus	–	–	–	–	26	Miller and Jorgensen, 1973
Naucrates ductor	III-IV; I-II, 26-28	O-II; II, 15-16	–	6+18-19	–	Fowler, 1936
Naucrates ductor	–	–	–	–	25	Starks, 1911
Oligoplites saurus	V-VI; I, 19-21	II; I, 18-21	15-17	6- 9+13-15	–	Ginsburg, 1952
Oligoplites saurus	–	–	–	–	26	Miller and Jorgensen, 1973
Selar crumenophthalmus	VIII; I, 24-26	II; I, 21-23	20-22	9-11+27-30	–	Ginsburg, 1952
Selar crumenophthalmus	–	–	–	–	24	Miller and Jorgensen, 1973
Selar crumenophthalmus	VIII; I, 26	II; I, 22	–	10-12+28-31	–	Fowler, 1936
Selar crumenophthalmus	–	–	–	–	24	Starks, 1911
Selene vomer	VIII; I, 21-23	O-II; I, 18-20	20-21	6- 8+23-27	–	Ginsburg, 1952
Selene vomer	–	–	–	–	24	Miller and Jorgensen, 1973
Selene vomer	VII-VIII; I, 21-23	II; I, 18-19	–	7- 8+24-28	–	Fowler, 1936
Seriola dumerili	VII; I, 30-35	II; I, 19-22	19-22	2- 3+11-13	–	Ginsburg, 1952
Seriola dumerili	–	–	–	–	24	Miller and Jorgensen, 1973
Seriola dumerili	VII; I, 29-35	–	–	11-24	–	Mather, 1958
Seriola fasciata	VIII; I, 30-32	II; I, 19-20	19-20	7- 8+18-20	–	Ginsburg, 1952
Seriola fasciata	VII-VIII; I, 29-32	II; I, 18-21	–	6+15	–	Fowler, 1936
Seriola fasciata	VIII; I, 28-32	–	–	22-26	–	Mather, 1958
Seriola rivoliana	VII-VIII; I, 28-32	I-II; I, 19-22	19-20	7- 8+16-18	–	Ginsburg, 1952
Seriola rivoliana	–	–	–	–	24	Miller and Jorgensen, 1973
Seriola rivoliana	VII; I, 29	II; I, 21	–	–	–	Fowler, 1936
Seriola rivoliana	VII; I, 27-33	–	–	18-28	–	Mather, 1958
Seriola zonata	VII-VIII; I, 33-40	I-II; I, 19-21	16-21	2- 3+11-13	–	Ginsburg, 1952
Seriola zonata	VIII; I, 38-40	–	–	12-13	–	Mather, 1958
Seriola zonata	–	–	–	–	24	Starks, 1911
Trachinotus carolinus	V-VI; I, 23-27	II; I, 20-23	17-19	- + 7-11	–	Ginsburg, 1952
Trachinotus carolinus	V-VI; I, 22-27	II; I, 20-23	I, 16-18	4- 7+ 6-13	–	Fields, 1962
Trachinotus carolinus	–	–	–	–	24	Starks, 1911
Trachinotus falcatus	VI; I, 18-20	II; I, 17-18	18-20	- + 9-13	–	Ginsburg, 1952
Trachinotus falcatus	–	–	–	–	24	Miller and Jorgensen, 1973
Trachinotus falcatus	VI; I, 17-21	II; I, 16-19	I, 17-19	3- 8+12-14	–	Fields, 1962
Trachinotus glaucus	VI; I, 19-20	II; I, 16-18	16-19	- +8-12	–	Ginsburg, 1952
Trachinotus glaucus	VI; I, 19-20	II; I, 16-18	I, 15-19	3- 8+9-14	–	Fields, 1962
Trachurus lathami	VIII; I, 28-33	II; I, 26-30	21-22	12-14+34-39	–	Ginsburg, 1952
Trachurus lathami	VIII; I, 30	II; I, 28	–	15+36	24	Merriman, 1943
Uraspis heidi	VIII; I, 29	0-I, 21	23	6+14	–	Ginsburg, 1952
Vomer setapinnis	VIII; I, 20-23	0-II; I, 17-19	17-19	5- 8+25-29	–	Ginsburg, 1952
Vomer setapinnis	VIII; I, 21-22	II; I, 18-20	–	6- 8+26-30	–	Fowler, 1936
Vomer setapinnis	–	–	–	–	24	Starks, 1911

data derived from the study of larvae provide useful tools in gaining insight into the abundance and fluctuation of the size of spawning populations (Farris, 1961). Patterns of larval development and larval structures, when sufficient groups are studied, are potential keys to possible relations which often are not adequately illustrated in adult morphology and osteology. The present paper aims to contribute to the understanding of the early life stages of members of the family Carangidae.

MATERIALS, METHODS, AND TERMINOLOGY

Larvae, juveniles, and adults were largely in the collections of the Miami Laboratory, Southeast Fisheries Center. The larvae and juveniles were collected with 1-m bongo plankton (Posgay, Marak, and Hennemuth, 1968) and nekton nets on board research vessels during oceanographic and biological surveys and during the routine sampling for larval fish in the Gulf Stream off Miami. Descriptions of vessels, cruise tracks, and sampling methods are available at the Miami Laboratory, Southeast Fisheries Center. Some specimens were contributed from a private collection and from the fish museum of the Center. One species was raised in the marine fish larvae rearing system of the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

The larval development of the carangids in this work is based on 551 larval and early juvenile specimens of *Decapterus punctatus*, 94 of *Elagatis bipinnulata*, 86 of *Selene vomer*, 64 of *Seriola zonata*, and 31 of *Oligoplites saurus*. Meristic characters and sequence of ossification data were taken from stained and cleared specimens. The complete sequence of ossification was not observed, however, in *Selene vomer* and *Oligoplites saurus* on account of the lack of transforming specimens and poorly preserved materials, respectively.

The embryological and anatomical terms and measurements used in this study follow largely those of Lagler, Bardach, and Miller (1962), Mansueti and Hardy (1967), and Moser and Ahlstrom (1970). Terms for ossification are those of Starks (1911), Suzuki (1962), and Weitzman (1962). Chromatophore terminology is from Fujii (1969). However, for clarity, certain terms are defined as they relate to larvae of carangids.

Growth stages beyond the yolk-sac stage are defined according to Moser and Ahlstrom (1970), and the terms prolarva and postlarva of Hubbs (1943) are not used. The larval period lasts from hatching to the attainment of juvenile characters. The transformation or metamorphosis of the larvae into juveniles is called the transitional period and the individuals undergoing this process are called transforming, metamorphic, or transitional specimens. The fish is a juvenile when it has the essential features of the adult, particularly the complete fin ray counts. The juvenile period terminates with the attainment of sexual maturity when the fish is considered an adult.

The dynamic approach of Moser and Ahlstrom (1970) is adapted in the description of larval fish. Here, a complete or fairly complete series of growth stages from the smallest differentiated larvae to the juvenile is assembled, and the development of each character is traced sequentially. The method used for determining apparent relative abundance is based on Ahlstrom (1948).

The youngest specimens collected in the plankton were past the yolk-sac stage. While eggs were present in the collections, identification is uncertain in view of the conspicuous absence of the intervening yolk-sac stages. Perhaps, the yolk sac ruptured or collapsed at capture due to mechanical stress.

All specimens used in this study are deposited in the larval fish laboratory of the Miami Laboratory, Southeast Fisheries Center of the National Marine Fisheries Service.

DESCRIPTIONS

Rainbow runner, *Elagatis bipinnulata* (Quoy and Gaimard)

Figure 1

Literature

Larval stages of this species from the Indo-Pacific oceans were illustrated and described by Okiyama (1970) who also traced their development. Berry (1969) illustrated an 18.5-mm juvenile from the Straits of Florida. Schnakenbeck (1931) illustrated an 11.5-mm larva from the Lesser Antilles under the name of *Caranx helvolus*.

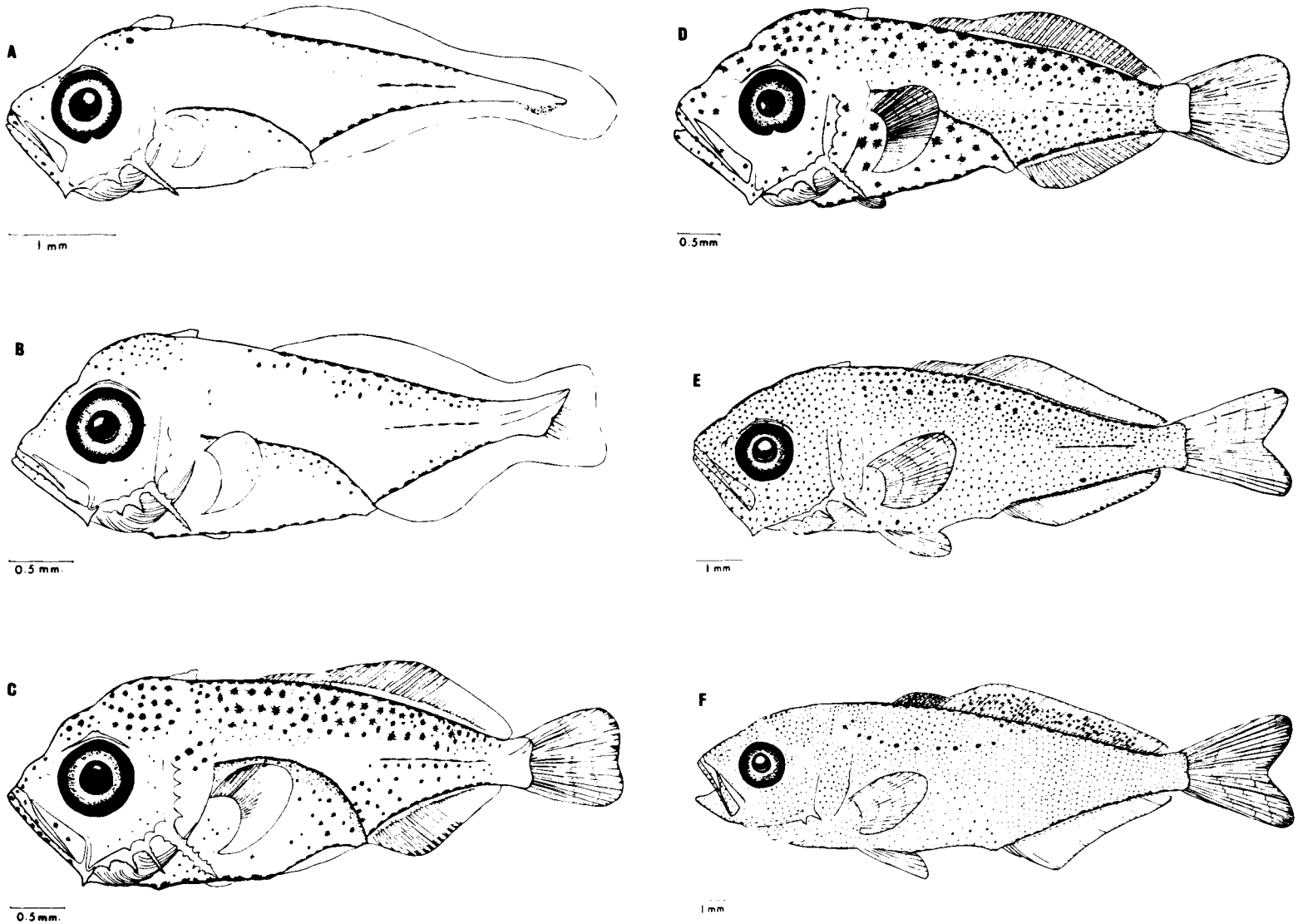


FIGURE 1.—*Elagatis bipinnulata*. **A.** 3.8 mm SL; **B.** 4.6 mm SL; **C.** 5.5 mm SL; **D.** 6.3 mm SL; **E.** 10.0 mm SL; **F.** 15.0 mm SL.

Distinguishing Features

Larvae of *Elagatis bipinnulata* are distinct from those of other carangids in having only two spines in the anal fin. Following transformation, the terminal dorsal and anal soft fin rays become gradually separated from these fins. These larvae are remarkably similar to those of *Seriola* species in size, structure, and pigmentation. Unlike the larvae of *Seriola,* however, they have a supraoccipital crest, serrations on the preopercular spines, and all the dorsal spines are about equal in length. The first interhemal spine is only slightly swollen and is not pressed nor fused with the hemal spine of the first caudal vertebra (Starks, 1911). The larvae transform at 10 to 14 mm.
the other interhemal and hemal spines. In many carangids the first interhemal spine is much enlarged and pressed against or fused with the hemal spine of the first caudal vertebra (Starks, 1911). The larvae transform at 10 to 14 mm.

Morphology

Larvae of *E. bipinnulata* are deep-bodied. Body depth at the base of the pectoral fin is 32% of the standard length at 3.8 mm; it attains a maximum of 40% at initial notochord flexion and is never less than 33% during the entire period of larval development (Table 2).

The head is large and deep. Relative length of the head increases throughout the larval and transition periods. Head length is 31.6% at 3.8 mm, increases to 35 to 49% at notochord flexion,

TABLE 2.—Measurements (mm) of larvae and juveniles of *Elagatis bipinnulata*.

(Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-to-anus distance	Head length	Head depth	Body depth at base of pectoral fin	Orbit Snout length	Orbit diameter	Snout to fin origin		
							Predorsal	Prepelvic	Preanal
3.8	1.9	1.2	1.2	1.2	0.32	0.30	–	–	–
3.9	1.96	1.25	1.25	1.2	.32	.30	–	–	–
4.6	2.9	1.6	1.7	1.5	.48	.55	2.0	2.0	2.0
5.0	3.5	2.0	2.0	2.1	.58	.50	2.7	2.0	4.0
5.2	3.5	2.1	2.2	2.1	.59	.60	2.7	2.2	3.6
5.9	3.5	2.2	2.3	2.2	.50	.65	2.8	2.4	3.6
6.1	3.9	2.1	2.2	2.3	.52	.65	3.0	2.5	4.4
6.2	3.9	2.3	2.4	2.2	.55	.65	3.0	2.5	4.1
7.0	4.4	2.5	2.6	2.4	.60	.70	.35	2.8	4.5
8.5	5.1	2.8	3.0	2.8	.75	.77	4.0	3.2	5.2
8.7	5.3	3.0	3.2	3.1	.75	.77	4.1	3.4	5.5
9.5	6.0	3.2	3.3	3.2	.80	1.0	4.1	3.5	6.1
9.7	6.0	3.2	3.3	3.3	.85	1.0	4.5	3.6	6.2
[1]10.0	6.1	3.8	3.5	3.4	.90	1.2	4.6	3.6	6.2
[1]11.0	7.2	3.8	3.8	3.8	1.0	1.0	5.2	4.0	7.4
[1]11.2	7.2	4.2	4.0	3.5	1.1	1.2	5.5	4.3	7.4
[1]11.5	7.2	4.3	3.8	3.8	1.2	1.2	6.0	4.3	7.5
[1]11.8	7.3	4.0	3.6	3.6	1.1	1.2	6.0	4.3	7.5
[1]12.0	7.4	4.0	3.8	3.8	1.2	1.3	6.0	4.5	7.4
[1]12.5	7.5	4.2	3.8	3.8	1.1	1.4	5.9	4.8	7.8
[1]13.0	7.5	4.0	4.0	3.9	1.2	1.3	6.0	5.0	8.0
[1]13.2	7.8	4.0	4.0	3.9	1.0	1.4	5.8	4.8	8.0
[1]13.3	8.1	4.5	4.1	4.2	1.2	1.3	6.1	5.0	8.6
[1]14.0	8.5	5.3	4.9	4.5	1.5	1.3	6.3	5.5	9.0
[2]14.1	8.5	5.0	4.9	4.5	1.5	1.4	6.1	5.4	9.0
[2]14.5	9.5	5.0	4.8	4.6	1.7	1.3	6.0	5.2	9.8
[2]14.8	9.0	4.8	4.6	4.5	1.7	1.4	6.5	5.4	9.8
[2]15.2	9.5	5.3	4.7	4.3	1.6	1.5	6.5	5.3	9.9
[2]15.5	9.0	5.4	4.7	4.6	1.6	1.3	6.6	5.2	9.7
[2]16.2	10.0	5.6	4.9	4.8	1.7	1.6	7.0	6.0	11.0
[2]16.8	10.2	5.7	5.0	4.7	1.8	1.5	8.0	7.0	10.6
[2]17.0	10.0	5.6	5.0	4.9	1.9	1.3	7.0	6.0	10.5
[2]18.0	10.0	6.0	5.0	5.0	1.9	1.5	7.5	6.0	11.0
[2]18.4	10.5	6.0	5.0	5.6	1.8	1.5	8.1	5.9	11.0

[1]Transforming.
[2]Juveniles.

and averages 35% during the late larval and early juvenile stages. The head is as deep as long at 3.8 mm and is deeper than long for most of the larval period. Head depth reaches a maximum of 110% of the head length at 5 mm and averages 101% in the late larvae. The dorsal profile of the snout is slightly concave at 3.8 mm; at notochord flexion, it becomes indented at the anterior and posterior margins of the slightly swollen forebrain. These indentations disappear in older larvae and at transformation, the dorsal profile becomes convex.

The eyes are round and large. Relative eye diameter ranges from 26.3 to 31.3% of the head length. A low orbital crest is formed above the eyes in early larvae but regresses at metamorphosis.

A supraoccipital crest is present throughout the larval stages. At 15 mm, the crest is much reduced and is no longer visible externally but may be observed in cleared and stained specimens.

There are two series of preopercular spines: one along the margin and another on the lateral surface. Spines on the lower margin are bigger and more serrated than those on the lateral surface. All preopercle spines gradually diminish in size and are completely overgrown by the expanding preopercle bones following metamorphosis.

The gut is long and coiled in a single, rounded loop in larvae up to a length of 12 mm; at 18 mm, a second loop is added. Hypaxial muscles enclose the gut at 5 mm and completely cover the abdominal cavity except at the opening of the gut at 8 mm.

The number of myomeres is constant—10 preanal plus 14 postanal—throughout the larval and early juvenile periods.

The first scales formed are those found along the lateral line near the caudal peduncle. Lateral line scales ossify in a posteroanterior direction at 15 mm. Regular body scales are not ossified until the juveniles are at least 20 mm long.

Pigmentation

Larvae are among the most intensely pigmented of carangids. In the early larvae (3.8-4.6 mm), the most conspicuous pattern of pigmentation includes melanophores along the bases of the dorsal and anal fins and along the lateral midline (Figure 1A, B). Small patches of melanophores are present on the head, jaws, snout, and on the upper sides of the body. Internal pigmentation is concentrated on the dorsal wall of the peritoneum. At 5 to 6 mm, melanophores develop profusely all over the body leaving only a small unpigmented area at the caudal peduncle (Figure 1C,D). A row of closely spaced pigment cells along the midventral line below the gut is notable and distinguishes early larvae from similarly pigmented larvae of *Seriola*. Xanthophores (yellow) develop profusely on the head and back in late larvae. At metamorphosis, iridiophores (reflecting), xanthophores, and melanophores cover the whole length of the body except on the jaws and fins, and an irregular row of large melanophores is formed on the upper side of the body (Figure 1E). The melanophores are capable of expansion and contraction and the larvae are pale or dark depending on the state of the pigment cells. Iridiophores and xanthophores fade upon preservation. The only chromatophores apparent in preserved specimens are the melanophores.

Fin Development

Rudiments of all fins except the ventral fins are present in the smallest larva (3.8 mm) and are situated in about the position they occupy at older stages. The fins ossify in the following sequence: 1) caudal, 2) first dorsal and anal, 3) second dorsal and pectoral, 4) ventral. All fins are essentially complete at metamorphosis (Table 3).

In the pectoral fins the dorsalmost rays are the first to ossify at 5 mm, and the rest of the rays are added ventrally. The full complement of 18 to 21 rays is present at 8 mm.

The pelvic fins ossify at 6 mm, and the full complement of 5 rays is present at 8 mm. The pelvic fin rays grow fast, and at transformation they are about as long as the pectoral fins.

Ossification of the dorsal and anal fin rays proceed in an anteroposterior direction in an orderly manner. The anteriormost rays are the first to ossify at 5 mm, and ossification continues posteriad. The last two fin rays are gradually separated beginning at metamorphosis in a manner described by Berry (1969). The full complement of 7 spines and 25 to 30 soft rays is present at 10 mm. The dorsal spines are of almost uniform height in the larvae. In early juveniles (17 mm), their height is about half that of the soft rays. The first and second dorsal fins are continuous throughout the larval and transition stages. The full complement of 2 spines and 19 to 20 soft rays in the anal fin is completed at 10 mm.

Caudal fin formation has begun in the smallest larva (3.8 mm). This is indicated by the presence of a thickening near the tip of the notochord. When

TABLE 3.—Meristic characters of cleared and stained larvae and juveniles of *Elagatis bipinnulata*.

Standard length	Dorsal fin	Anal fin	Left pectoral fin	Left pelvic fin	Primary caudal fin rays		Secondary caudal fin rays		Gill rakers, left first gill arch	Left preopercular margin spines
					Dorsal	Ventral	Dorsal	Ventral		
3.8	–	–	–	–	–	–	–	–	–	7
4.6	–	–	–	–	2	2	–	–	0+5	7
5.4	V; 18	I, 10	5		7	8	–	–	0+11	8
6.0	V; 24	I, 16	13	I, 2	8	8	2	4	2+13	8
7.0	VI; I, 25	I, 18	17	I, 4	9	8	4	5	4+15	7
8.0	VI; I, 24	I, 19	18	I, 5	9	8	8	9	5+18	6
9.0	VI; I, 26	I, 20	19	I, 5	9	8	9	9	5+18	8
10.4	VI; I, 27	II, 20	19	I, 5	9	8	9	9	6+22	7
11.5	VI; I, 26	II, 19	20	I, 5	9	8	10	9	7+21	5
12.0	VI; I, 27	II, 20	19	I, 5	9	8	10	10	7+21	5
13.1	VI; I, 28	II, 19	20	I, 5	9	8	10	9	7+21	4
14.7	VI; I, 28	II, 19	20	I, 5	9	8	10	10	8+21	2
15.2	VI; I, 27	II, 19	20	I, 5	9	8	11	10	8+23	2
16.0	VI; I, 27	II, 19	20	I, 5	9	8	11	10	8+22	2
17.1	VI; I, 27	II, 19	20	I, 5	9	8	10	11	8+23	1
18.0	VI; I, 26	II, 19	20	I, 5	9	8	11	11	8+22	1
19.0	VI; I, 27	II, 19	19	I, 5	9	8	11	10	8+24	1
19.5	VI; I, 27	II, 19	20	I, 5	9	8	11	11	8+24	1
20.0	VI; I, 27	II, 19	19	I, 5	9	8	10	10	9+25	1
23.3	VI; I, 27	II, 19	21	I, 5	9	8	11	10	8+27	1

the larvae are 4 to 5 mm long, the thickening differentiates into hypural elements, the notochord starts flexion, and the median caudal rays ossify. The hypural elements ossify at 6 mm, the full complement of 9 dorsal and 8 ventral principal rays is present at 7 mm, and notochord flexion is completed at 8 mm. The secondary rays ossify at 6 mm beginning with the posteriormost rays. The full complement of 10 to 11 dorsal and of 10 to 11 ventral secondary rays is formed at 12 mm.

The last 3 vertebrae, the hypural elements, and 5 dorsal structures including the neural spine of the antepenultimate vertebra, 3 median epurals, and a specialized neural process support the caudal fin. The supporting structures articulate with the principal and secondary caudal rays. They are generally similar to those occuring in *Trachurus symmetricus* (Ahlstrom and Ball, 1954).

Distribution and Spawning

Elagatis bipinnulata has a circumtropical distribution (Briggs, 1960). It has been previously reported from Texas, Florida, and Long Island (Ginsburg, 1952) and is also known from the West Indies (Jordan and Evermann, 1896), Japan (Okada, 1966), Hawaii (Gosline and Brock, 1960), Africa (Fowler, 1936), Philippines (Herre, 1953), and the Great Barrier Reef (Marshall, 1965). The larvae were reported by Okiyama (1970) to be the most abundant form of epipelagic larval carangid in the tropical as well as in the subtropical Indo-Pacific ocean where spawning occurs throughout the year with a peak in March.

In the present study, larvae and early juveniles less than 20 mm have been taken in every month except in May and December. While the specimens are too few to give conclusive information, it appears that spawning may occur throughout the year. The larvae were taken mainly in offshore waters in the eastern Gulf of Mexico, in the Santaren Channel, the Straits of Florida, and the Carolina Bight off New Brunswick, Ga. (Figure 2). They occurred in 2.6% of the net stations and constituted 2.3% of the young carangids collected.

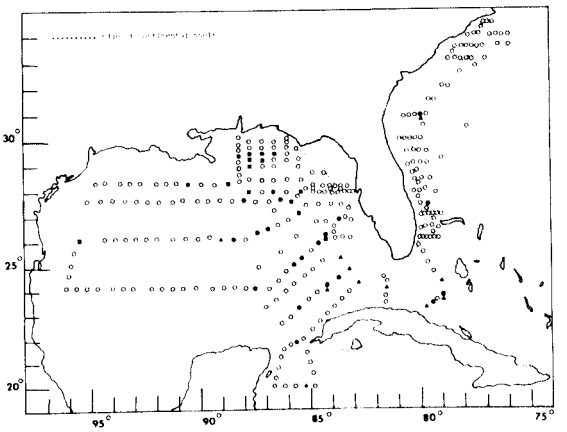


FIGURE 2.—Locations of collections of larval carangids during two cruises of the *Oregon II* from July to August and from October to November 1970 and a cruise of the *Tursiops* in August 1971. Records of occurrences of *Elagatis bipinnulata* are shown as solid circles, those of *Seriola zonata* as solid triangles, and those of *Selene vomer* as solid squares. Open circles represent other stations occupied.

During its larval life, *Elagatis bipinnulata* is planktonic. Some larvae and juveniles become associated with the pelagic sargassum community (Dooley, 1972) and are carried along the Florida Current and Gulf Stream.

Banded rudderfish, *Seriola zonata* (Mitchill)

Figure 3

Literature

Larvae of *Seriola zonata* have not been previously described. Early juveniles of the banded stage were described by Nichols (1946), Ginsburg (1952), and Mather (1958). Lutken (1880) illustrated an unbanded 20-mm juvenile.

As noted earlier, larvae of *Seriola dumerili* were described by Hildebrand and Cable (1930) and Sanzo (1933). Japanese workers have described life history series of three species of *Seriola*. The most detailed study of development from eggs to juveniles was made on *Seriola quinqueradiata* [Uchida, Dotu et al. (1958), Uchida in Uchida, Imai et al. (1958), Mitani (1960), and Mito (1961)]. Larvae and juveniles of two other Japanese species, *S. aureovittata* and *S. purpurascens* were covered by Uchida in Uchida, Imai et al. (1958).

Distinguishing Features

Seriola larvae resemble most those of *Elagatis bipinnulata* in size, body structure, and pigmentation. Unlike *E. bipinnulata*, however, there is no supraoccipital crest; the spines of the dorsal fin are of unequal length, the anterior and posterior ones being shorter; and the preopercular spines have smooth sides until the transition period when the longest spine develops 1 to 2 denticles. The larvae transform at about 13 mm. They are deep-bodied and robust. The head is massive and slightly depressed, and the eyes protrude slightly from the orbit at the dorsal side.

Early larvae of *Seriola zonata* (3-7 mm) are differentiated from those of other species of *Seriola* by the presence of 5 to 6 large melanophores on the middorsal line at the base of the dorsal fin (Figure 3 B). These large melanophores which are apposed to the myomeres stand out among the more numerous and smaller pigment spots on the back and sides. In older larvae these melanophores become embedded in the muscles and covered by superficial melanophores. When the full complement of dorsal fin rays is formed at about 8 mm, larvae of *S. zonata* are distinct in having 35 to 40 soft rays in the second dorsal fin, the highest second dorsal fin ray count of all species of *Seriola*. All dorsal fin rays are sharply visible even in unstained specimens.

The first interhemal spine of the first ventral pterygiophore is only slightly enlarged and does not press against the first hemal spine.

Morphology

Maximum body depth at 3.6 mm is 30% of the standard length. It increases to 37% at initial notochord flexion and does not change significantly during larval and transition periods. In early juveniles, the body depth is never less than 30% of the standard length (Table 4).

Head length is 33% of standard length in the smallest larva (3.6 mm) and attains a maximum of 43% at 7.0 mm. Thereafter, head length decreases gradually, with an average of 35% in early juveniles 18.0 mm in length. Depth of head is 91% of the head length at 3.6 mm and attains a maximum of 122% at 5 mm. Thereafter, head depth decreases slightly and is never less than 89% of the head depth throughout the larval and juvenile periods. The dorsal profile of the snout is slightly concave at 3.6 mm but becomes straight at about 5 mm and then convex in the older larvae and juveniles.

The eyes are round and large, and the orbit diameter increases in relation to head length. Relative orbit diameter ranges from 28 to 36% of the head length in larvae and transforming specimens and gradually increases in early juveniles. A low orbital crest with a weak spine is present in the early larvae and is resorbed at metamorphosis.

Marginal and lateral surface preopercular spines are present. The marginal angle spine which is the longest develops 1 or 2 denticles on its dorsal side in transforming larvae and early juveniles. All preopercular spines gradually diminish in size and become overgrown by the expanding preopercle.

Scales along the posterior end of the lateral line in front of the caudal peduncle are formed at 20 mm. Subsequently, the scales along the anterior portion of the lateral line ossify, followed by those on the head and sides of the body.

The slender gut is coiled in a single loop in larvae up to 10 mm long. The number of loops

TABLE 4.—Measurements (mm) of larvae and juveniles of *Seriola zonata*.

(Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-to-anus distance	Head length	Head depth	Body depth at base of pectoral fin	Snout length	Orbit diameter	Snout to fin origin		
							Predorsal	Prepelvic	Preanal
3.6	2.1	1.2	1.1	1.1	0.35	0.36	–	–	–
3.7	2.3	1.25	1.15	1.2	.36	.36	–	–	–
4.7	3.0	1.6	1.5	1.5	.42	.42	–	–	–
5.5	3.5	1.8	2.1	2.0	.50	.60	2.5	2.1	3.6
5.6	3.5	1.8	2.2	2.0	.52	.62	2.5	2.1	3.7
6.2	4.0	2.0	2.3	2.0	.65	.70	2.9	2.2	4.0
6.4	3.9	2.3	2.3	2.1	.65	.70	2.9	2.5	4.0
6.5	4.0	2.5	2.5	2.3	.65	.72	3.0	2.5	4.2
6.8	4.5	2.8	2.6	2.4	.67	.72	3.4	2.8	4.6
7.0	4.6	3.0	2.8	2.5	.70	.75	3.4	2.9	4.8
7.1	4.7	3.0	3.0	2.6	.72	.75	3.5	2.8	5.0
7.5	4.8	3.0	3.0	2.5	.80	.85	3.8	3.0	5.0
8.0	5.2	3.0	2.8	2.5	.85	.90	3.8	3.0	5.3
8.2	5.2	3.1	3.1	2.8	.90	1.0	3.9	3.2	5.3
8.4	5.4	3.2	3.5	3.2	1.0	1.1	4.0	3.5	5.5
9.1	5.8	3.5	3.5	3.2	1.0	1.2	4.1	3.9	5.9
9.5	6.2	3.5	3.6	3.2	1.0	1.2	4.3	3.9	6.4
9.8	6.2	4.0	3.8	3.5	1.2	1.3	4.3	4.1	6.4
[1]10.0	6.5	4.0	3.8	3.5	1.1	1.3	4.3	4.1	6.6
[1]10.3	6.6	4.0	3.8	3.5	1.1	1.3	4.5	4.1	6.8
[1]10.8	7.4	4.2	4.0	3.6	1.3	1.5	5.2	4.4	7.6
[1]11.9	8.4	4.7	4.8	4.5	1.5	1.6	5.8	5.5	8.6
[1]12.0	8.5	4.9	4.8	4.5	1.6	1.6	6.0	5.6	8.6
[1]12.1	8.5	5.0	4.6	4.5	1.6	1.6	5.9	5.6	8.6
[1]12.5	8.6	5.0	4.8	4.5	1.6	1.6	6.0	5.2	8.7
[1]13.1	8.8	5.0	4.8	4.5	1.4	1.8	6.1	5.3	8.3
[2]13.5	9.2	5.0	4.8	4.6	1.5	1.9	6.1	5.6	9.5
[2]13.6	9.2	5.0	4.6	4.5	1.4	2.0	6.2	5.5	10.0
[2]15.0	9.8	5.5	5.0	5.0	1.4	2.0	6.0	5.5	10.2
[2]15.1	10.0	5.6	5.0	5.0	1.5	2.0	6.3	5.5	10.5
[2]15.2	10.0	5.7	5.1	5.2	1.5	2.0	6.4	5.6	10.6
[2]16.2	10.5	5.8	5.2	5.4	1.6	2.1	7.5	5.8	11.0
[2]17.5	10.5	6.0	5.5	6.0	1.5	2.2	7.5	6.0	11.0
[2]18.1	11.0	6.5	5.8	6.2	1.7	2.3	7.5	7.0	11.0

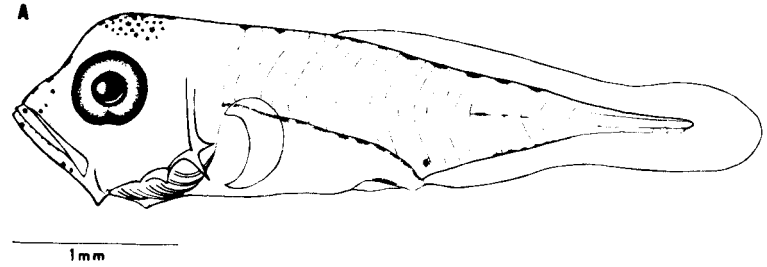
[1]Transforming.
[2]Juveniles.

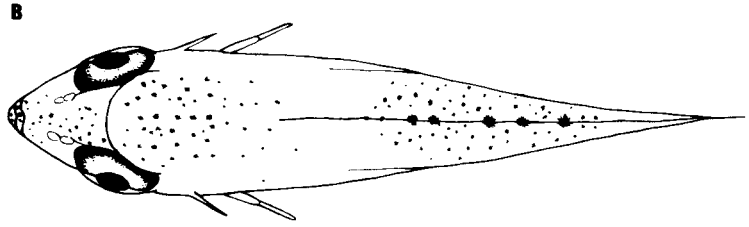
increases with growth and at 15 mm four loops are present. Snout-to-anus distance increases in relation to standard length. It is 58.3% at 3.6 mm and gradually increases to 70% at transformation. Hypaxial musculature develops at 6 mm and completely surrounds the abdominal cavity except at the gut opening at 10 mm.

There are 24 myomeres—10 preanal plus 14 postanal—throughout the larval and juvenile stages.

Pigmentation

Larval pigmentation consists of conspicuous melanophores along the bases of the dorsal and anal fins, on the lateral midline, and in the peritoneum lining the middorsal wall of the abdominal cavity. In a freshly preserved 9-mm larva there are dense concentrations of xanthophores on the head, preopercle, and on the back and upper sides of the body while iridiophores are profuse on the sides of the body below the lateral midline. In older larvae, the melanophores are apparently actively expanding and contracting as most larvae have either contracted melanophores and are pale looking, or are dark when the melanophores are expanded. Other larvae have alternating patches of expanded and contracted melanophores forming false bands (Figure 3F-H). In early juveniles (17 mm), the body definitely becomes banded. A bold color pattern develops including a distinct nuchal bar and 6 solid bands which extend to the dorsal and anal fins (Figure 3I). In a young juvenile 23 mm long, the lobes of the unpigmented caudal fin have a brown spot developing at the tips. Alcohol-preserved metamorphic larvae and early juveniles have chocolate-brown bands over a silvery background. With the exception of


A
1mm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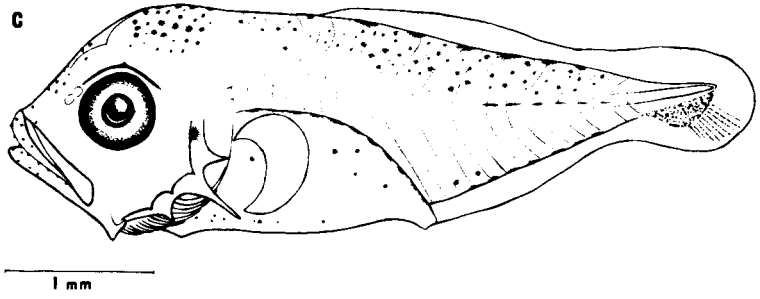
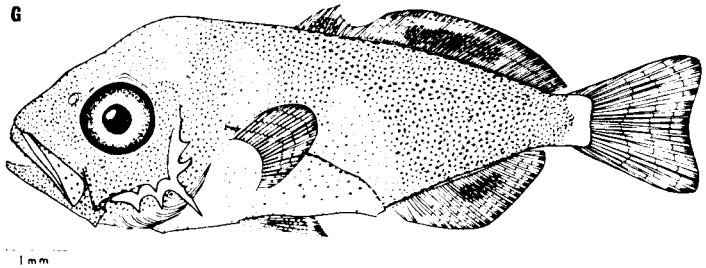

C
1 mm


G
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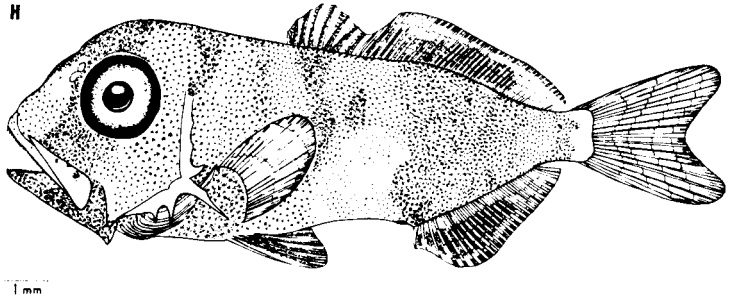
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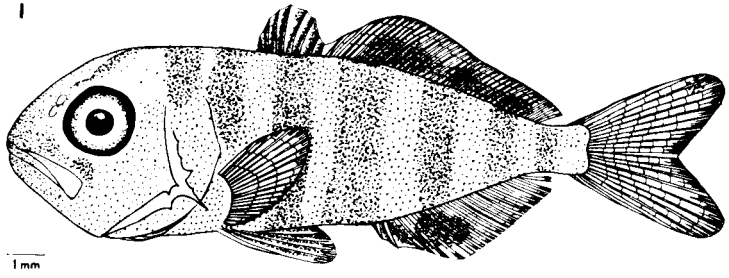

I
1 mm

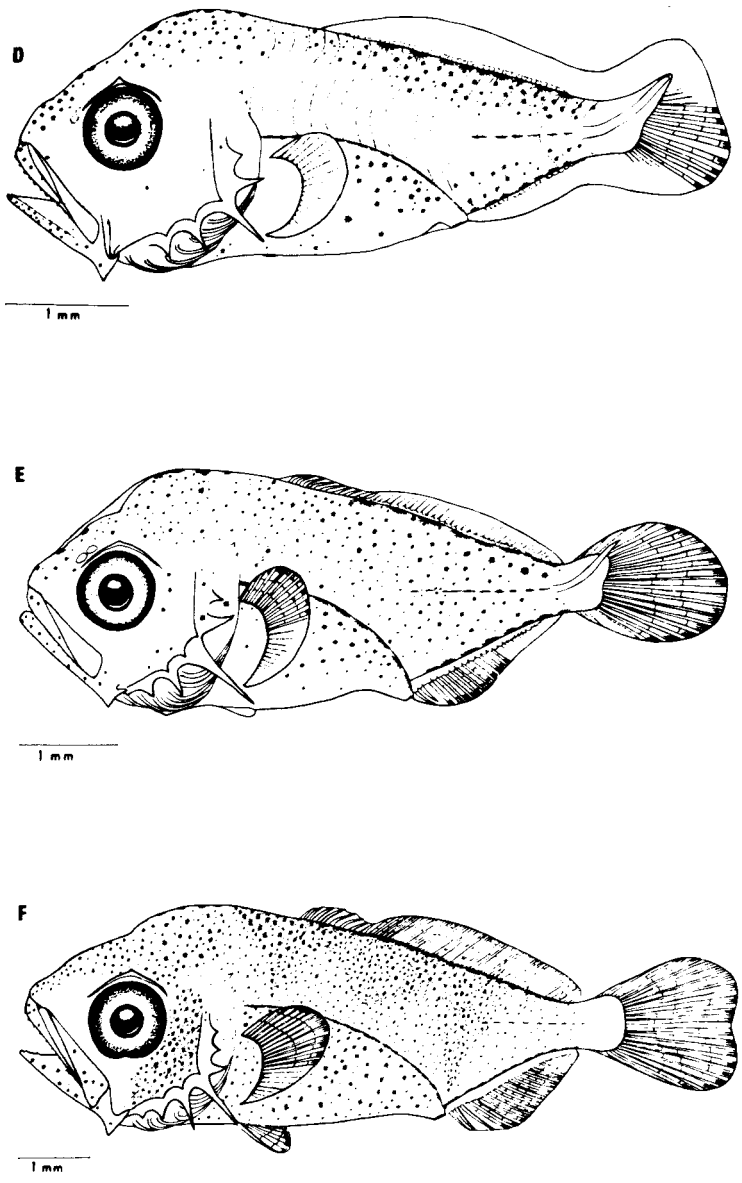


FIGURE 3.—*Seriola zonata*. **A.** 3.6 mm SL; **B.** 4.8 mm SL (dorsal view); **C.** 4.8 mm SL (lateral view); **D.** 5.5 mm SL; **E.** 6.5 mm SL; **F.** 8.7 mm SL; **G.** 10.6 mm SL; **H.** 13.5 mm SL; **I.** 18.0 mm SL.

melanophores, all other chromatophores fade on preservation in formaldehyde solution.

Fin Development

The dorsal, anal, caudal, and pectoral finfolds are present in the youngest larva (3.6 mm). Differentiation of the fin rays occurs in the following sequence: 1) caudal, 2) first dorsal and anal, 3) second dorsal and pectoral, 4) ventral. All fins are essentially formed at 9 mm (Table 5).

The pectoral fin rays ossify at 6 mm beginning with the most dorsal rays, and the rest ossify ventrally. The full complement of 19 to 20 rays is formed at 10 mm.

The pelvic fin rays differentiate at 7 mm, and the full complement of 5 rays is present at 9 mm.

The dorsal and anal fin rays ossify anteroposteriorly. At 8 to 9 mm the full number of 8 spines in the first dorsal fin and 1 spine and 35 to 40 soft rays in the second dorsal is completed. The first dorsal fin becomes arch-shaped as the spines increase in height and remains continuous with the second dorsal fin until in early juveniles (15-17 mm) a deep notch demarcates the 2 fins. The anal fin rays begin to ossify at 5 mm, and the full complement of 3 spines and 19 to 22 soft rays is completed at 10 mm.

The caudal fin begins to develop at 4 to 5 mm in a manner similar to that occurring in *Elagatis bipinnulata*. The full complement of 9 dorsal and 8 ventral principal rays is present at 7 to 8 mm, while the full complement of 10 to 11 dorsal and of 9 to 10 ventral secondary rays is completed at 9 mm.

Distribution and Spawning

Juveniles of *Seriola zonata* (12-23 mm) have been reported to be regular summer visitors in Cape Cod waters which appear to be their most northernly record (Mather, 1952). Adults have been recorded from various points of the Atlantic coast and in the Gulf of Mexico (Ginsburg, 1952).

Larvae and early juveniles up to 26 mm were taken in all months except in February, April, September, and December. They were caught with a 1-m plankton net in the Gulf Stream off Miami, with dip nets at the pier of the Southeast Fisheries Center in Biscayne Bay, and with neuston nets in the Gulf of Mexico, Yucatan Channel, Straits of Florida, and south Atlantic coast. The larvae occurred in 1.4% of the net stations and constituted 1.8% of the larval carangids in the collection. The occurrence of the larvae is too erratic to indicate whether or not the spawning period is continuous over 12 mo or broken into two parts, winter-spring and fall. Spawning occurred mainly in offshore waters in the eastern Gulf of Mexico, Yucatan Channel, Santaren Channel, along the edge of the continental shelf in the Straits of Florida, and in the Carolina Bight off New Brunswick, Ga. (Figure 2). The planktonic larvae are presumably carried along the Florida Current and Gulf Stream and reach their northern limits as juveniles.

Round scad, *Decapterus punctatus* (Agassiz)
Figure 4

Literature

The early growth of this species were described

TABLE 5.—Meristic characters of cleared and stained larvae and juveniles of *Seriola zonata*.

Standard length	Dorsal fin	Anal fin	Left pectoral fin	Left pelvic fin	Primary caudal fin rays		Secondary caudal fin rays		Gill rakers, left first gill arch	Left preopercular margin spines
					Dorsal	Ventral	Dorsal	Ventral		
3.6	-	-	-	-	-	-	-	-	-	4
4.4	-	-	-	-	4	5	-	-	-	4
5.5	IV	II; 5	-	-	8	7	-	-	0+6	5
6.5	VI; 22	II; 11	8	-	9	8	-	-	0+8	6
7.5	VII; 30	II; 16	10	I, 3	9	8	1	2	0+11	7
8.4	VIII; I, 34	II; 19	13	I, 4	9	8	3	3	3+13	7
9.5	VIII; I, 36	II; 20	17	I, 5	9	8	5	5	4+15	7
10.3	VIII; I, 38	II; I, 20	18	I, 5	9	8	7	8	5+15	7
11.2	VIII; I, 39	II; I, 21	20	I, 5	9	8	8	8	5+15	7
12.0	VIII; I, 36	II; I, 22	20	I, 5	9	8	9	8	5+15	5
13.0	VIII; I, 37	II; I, 20	20	I, 5	9	8	9	9	5+16	3
14.2	VIII; I, 36	II; I, 19	20	I, 5	9	8	10	9	6+16	4
15.2	VIII; I, 38	II; I, 20	19	I, 5	9	8	11	10	6+16	4
16.0	VIII; I, 40	II; I, 21	20	I, 5	9	8	11	10	6+17	4
17.0	VIII; I, 38	II; I, 20	20	I, 5	9	8	11	10	8+18	3

by Hildebrand and Cable (1930) who also studied the abundance and distribution of the young up to 50 mm taken from the coastal and offshore waters of Beaufort, N.C. In addition, life history series were described for two species of *Decapterus* from the Indo-Pacific region: *D. russelli* by Vijayaraghavan (1958) and *D. maruadsi* by Shojima (1962). The latter series is quite similar to that of *D. punctatus*.

Distinguishing Features

Larvae of *D. punctatus* are decidedly deep-bodied although the adults are the most slender of all carangids. The head has a supraoccipital and an orbital crest and preopercular spines. During metamorphosis, the ultimate rays of the dorsal and anal fins become separated and modified into finlets. The first interhemal spine is slightly swollen. Together with the hemal spine of the first caudal vertebra to which it is closely apposed it forms a strong brace at the posterior border of the abdominal cavity. There are 25 vertebrae—10 trunk plus 15 caudal. *D. punctatus* is one of the few carangids with a vertebral count of 25, the usual number being 24; this is a useful character for separating the larvae from other species of *Decapterus*. Berry (1968) used the scales, scutes, and lateral line spots in the identification of the older juveniles from 90 mm long. These characters are not yet formed in the larvae.

Morphology

Body depth decreases relative to standard length and is 30.6 to 35.4% during the entire larval period (Table 6). In transforming larvae and early juveniles, body depth decreased to 28%. The head is long and deep; relative head length increases throughout the larval and juvenile stages. It is 27% in the smallest larvae (3.0 mm) and attains a maximum of 35% in the larval period. In transforming larvae and early juveniles, it is never less than 31% of the standard length. The head is deeper than long in the early larval stages up to notochord flexion and ranges from 108.3 to 113%. Thereafter, head depth decreases gradually with an average of 90% but is never less than 80% of the head length in the early juveniles. A supraoccipital crest is present during the larval period but is resorbed at metamorphosis. The snout is slightly concave in the youngest larvae (3.0 mm), but becomes straight at initial notochord flexion. In older and transforming larvae, the snout develops a convex profile.

The eyes are large and round, and the orbit diameter increases relative to head length. Eye index ranges from 30 to 46.1% during the larval and transition periods and is highest at notochord flexion. A low orbital crest bearing a weak spine is present above the eyes in larvae 3 to 7 mm long. In older larvae, the crest is gradually resorbed and is no longer visible at 10 mm.

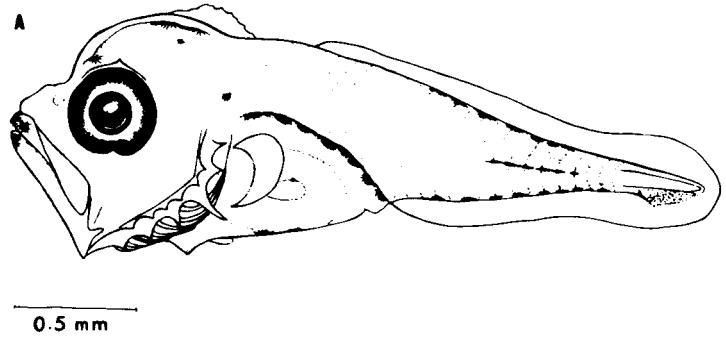
Marginal and lateral surface spines are present on the preopercle. They increase in size and number during the larval period but are gradually resorbed at metamorphosis. At 17 mm, the lateral surface spines are gone and the margin spines are reduced to fine crenulations on the preopercular margin.

The slender gut is coiled in a single loop in the early larvae. A second loop is formed at transformation and a third is added in the early juveniles. Snout-to-anus distance increases relative to standard length; it is 52.3 to 59.5% of the standard length during the entire larval and transition periods and does not change noticeably during the early juvenile stages. Hypaxial muscles begin to develop around the gut in 5-mm larvae, and at 7 mm, the abdominal cavity is completely enclosed except at the anal opening of the gut.

The first scales to ossify are those at the posterior region of the lateral line in juveniles 17 mm long. Ossification of the lateral line scales proceeds anteriad and the full complement of scales and scutes is present at 20 mm when the body scales are formed.

Pigmentation

Chromatophores are slow to develop in the larvae and remain sparse until the early juvenile stages. There are a few melanophores on the back of the head, on the jaws, and infrequently on the snout and cheeks. As in other carangid larvae, there is a row of melanophores on each side of the bases of the dorsal and anal fins, along the lateral line at the caudal region, and on the dorsal wall of the peritoneum. Compared to those of *Seriola zonata* and *Elagatis bipinnulata*, the larvae of *Decapterus punctatus* are pale. Melanophores are not profusely developed until metamorphosis, and they are mostly located above the midline. In the early juveniles, iridiophores spread all over the body but are most dense below the lateral line, giving the fish a metallic sheen.


A
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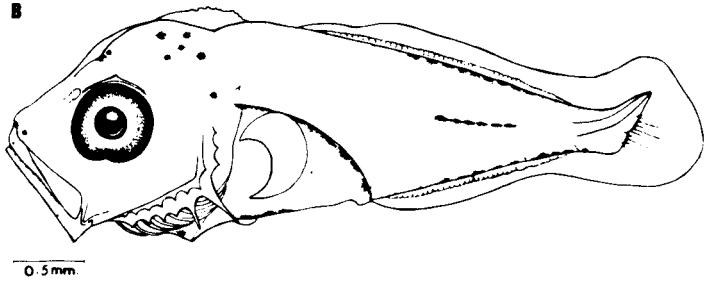
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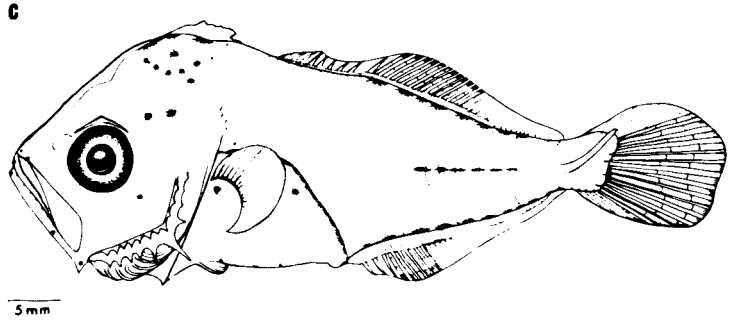
C
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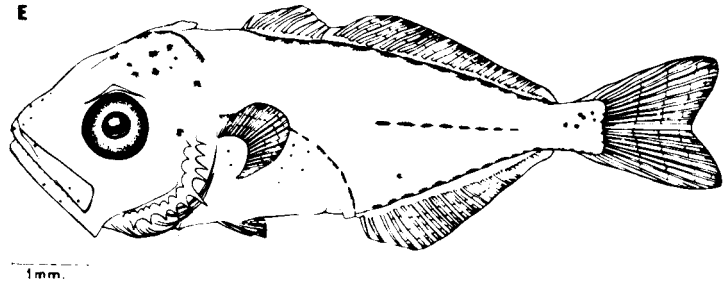
E
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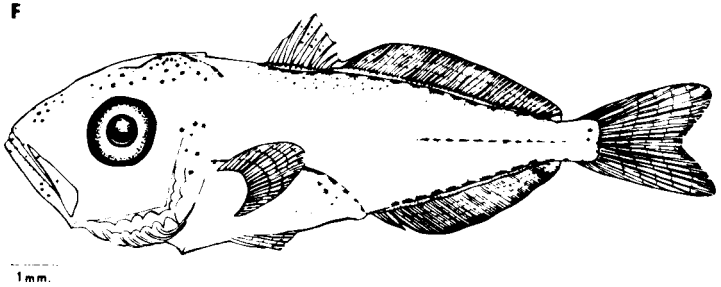
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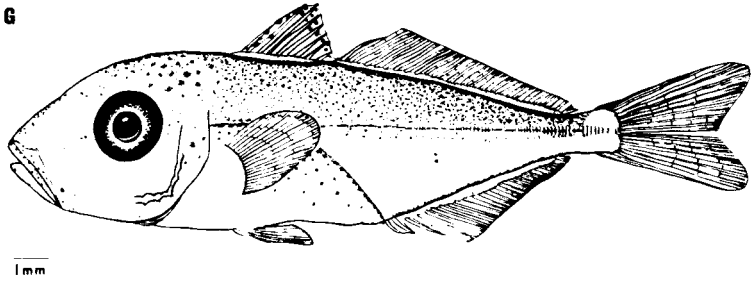
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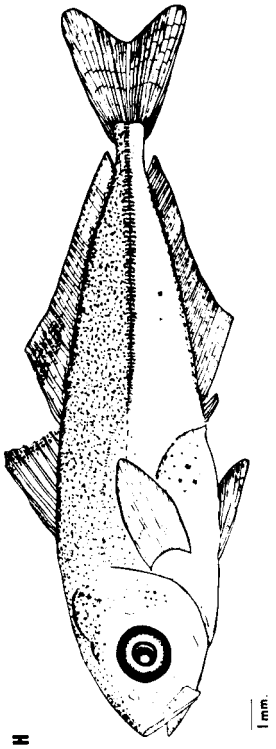


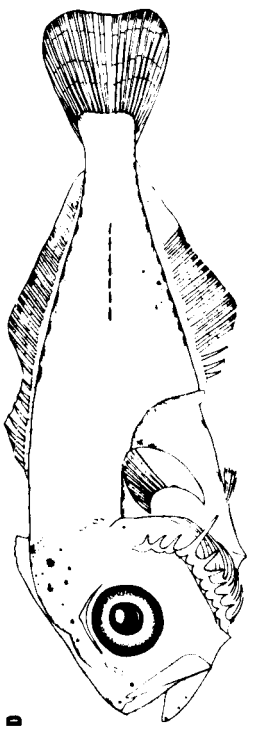


FIGURE 4.—*Decapterus punctatus*. **A.** 3.1 mm SL; **B.** 4.2 mm SL; **C.** 5.5 mm SL; **D.** 6.5 mm SL; **E.** 8.0 mm SL; **F.** 12.0 mm SL; **G.** 17.5 mm SL; **H.** 23.0 mm SL.

Fin Development

The dorsal, anal, caudal, and pectoral finfolds are distinct in the smallest larvae (3.0 mm), but the fin rays begin to ossify at 4 to 5 mm in the following sequence: 1) caudal; 2) dorsal, anal, and pectoral; 3) ventral (Table 7).

The pectoral fin rays are differentiated at 5 mm, and the full complement of 19 to 21 rays is present at 11 mm.

The pelvic fin buds are present at 4 to 5 mm, but the fin rays ossify at 6 mm, and the full complement of 1 spine and 5 soft rays is formed at 7 mm.

As in *E. bipinnulata* and *S. zonata*, ossification of the dorsal and anal fin rays proceed anteroposteriorly. The full complement of 8 spines in the first dorsal fin and of 1 spine and 31 to 34 soft rays in the second dorsal fin is present at 10 mm. At this stage also, the ultimate fin rays gradually separate from the dorsal and anal fins and each modifies into a much branched finlet. The anal fin rays start to ossify at 5 mm, and the full complement of 3 spines and 27 to 31 rays is completed at 9 mm.

The pattern of caudal fin formation is generally similar to that of *E. bipinnulata*. Caudal fin structures initially develop at 4 mm, and all 17 principal rays are present at 6 mm. The full complement of 9 dorsal and 9 ventral secondary rays is formed at 13 mm. Unlike *E. bipinnulata*, only two median epurals are normally developed as the center epural is markedly reduced.

Distribution and Spawning

Adults of *D. punctatus* have been reported from both sides of the Atlantic from Nova Scotia to Brazil (Jordan and Evermann, 1896) and West Africa (Fowler, 1936). The first record of the larvae was reported by Hildebrand and Cable (1930) in Beaufort, N. C. They noted that spawning occurred throughout the summer or from May to November with a peak from July to September. Larvae and juveniles 2 to 50 mm long were present in inshore as well as offshore waters, possibly extending beyond the Gulf Stream, from the surface to the bottom up to a depth of 20 fathoms. In the present study, larvae and juveniles of *D. punctatus* were taken in all the months during the routine fish larvae sampling in the Gulf Stream off Miami and in numerous net stations in the Gulf of Mexico and the south Atlantic coast. Spawning occurs in pelagic inshore as well

TABLE 6.—Measurements (mm) of larvae and juveniles of *Decapterus punctatus*.
(Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-to-anus distance	Head length	Head depth	Body depth at base of pectoral fin	Snout length	Orbit diameter	Snout to fin origin		
							Predorsal	Prepelvic	Preanal
3.0	1.7	0.8	0.9	1.0	0.26	0.32	-	-	-
3.1	1.8	.8	1.0	1.1	.30	.37	-	-	-
3.5	2.0	1.0	1.1	1.2	.37	.42	-	-	-
3.7	2.0	1.1	1.2	1.2	.40	.47	-	-	-
4.0	2.2	1.2	1.3	1.2	.45	.52	-	-	-
4.2	2.5	1.3	1.5	1.3	.47	.60	-	-	-
4.8	2.6	1.5	1.6	1.6	.50	.65	-	-	-
5.2	3.0	1.6	1.8	1.8	.55	.70	-	-	-
5.5	3.2	1.8	2.0	1.9	.57	.75	-	-	-
6.4	3.7	2.2	2.1	2.0	.62	.82	2.8	2.2	3.8
6.5	3.8	2.2	2.1	2.0	.62	.82	2.9	2.1	3.8
6.7	3.9	2.2	2.2	2.1	.65	.80	2.8	2.0	3.7
7.1	4.0	2.2	2.4	2.2	.67	.85	3.1	2.4	4.2
7.5	4.1	2.5	2.5	2.4	.72	.90	3.2	2.3	4.2
7.8	4.2	2.5	2.5	2.5	.75	.92	3.2	2.6	4.5
8.0	4.2	2.7	2.6	2.6	.75	.95	3.2	2.6	4.3
8.3	4.5	2.8	2.6	2.6	.75	1.0	3.5	2.7	4.7
8.6	4.5	3.0	2.6	2.7	.80	1.0	3.2	2.6	4.6
9.8	5.5	3.2	3.0	3.0	.85	1.2	3.9	3.0	5.6
10.0	5.8	3.5	3.0	3.0	1.0	1.1	4.5	4.0	6.2
10.2	5.8	3.5	3.2	3.4	1.1	1.2	4.5	4.3	6.6
10.5	6.2	3.5	3.2	3.2	1.1	1.25	4.6	4.0	6.3
11.0	6.1	3.5	3.5	3.4	1.1	1.2	4.5	4.3	6.6
11.2	6.2	3.5	3.5	3.5	1.2	1.2	4.6	4.0	6.4
11.4	6.4	3.7	3.7	3.6	1.2	1.2	4.6	4.5	6.6
[1]12.0	6.9	4.0	3.8	3.7	1.2	1.3	4.8	4.5	6.8
[1]12.3	6.8	4.0	3.8	3.7	1.2	1.3	4.8	4.5	6.8
[1]12.5	7.0	4.2	4.0	3.8	1.2	1.3	5.0	4.8	7.2
[1]13.0	7.2	4.2	4.0	4.1	1.3	1.3	5.2	4.9	7.5
[1]13.2	7.4	4.2	4.0	4.1	1.2	1.4	5.4	4.7	7.6
[1]13.5	7.5	4.3	4.1	4.2	1.3	1.5	5.2	5.0	7.8
[1]14.0	8.0	4.4	4.5	4.3	1.3	1.6	5.8	5.8	8.5
[2]14.4	7.8	4.5	4.1	4.3	1.3	1.6	5.6	5.4	8.3
[2]14.9	8.0	4.8	4.2	4.3	1.4	1.6	5.9	6.0	8.6
[2]15.2	8.2	5.0	4.2	4.4	1.5	1.6	5.8	5.6	8.2
[2]15.5	8.6	5.2	4.1	4.5	1.6	1.6	5.9	5.5	8.3
[2]16.0	8.7	5.3	4.5	4.6	1.5	1.7	6.5	5.8	9.0
[2]16.2	8.8	5.6	4.6	4.6	1.6	1.7	6.4	5.9	9.0
[2]16.5	8.8	5.7	4.7	4.7	1.7	1.8	6.3	5.9	9.0
[2]17.0	9.5	5.7	5.0	4.8	1.8	1.9	7.0	6.0	9.8
[2]17.5	9.2	5.7	4.6	4.9	1.9	1.9	6.4	5.8	9.3
[2]18.0	9.5	6.0	5.0	5.2	1.9	2.0	7.0	6.3	10.0
[2]18.5	9.6	6.0	5.2	5.3	1.8	2.0	7.0	6.5	10.0
[2]19.2	10.0	6.1	5.4	5.5	2.0	2.0	7.0	6.8	11.3
[2]19.5	10.0	6.1	5.4	5.7	1.9	2.0	7.3	6.6	11.5

[1]Transforming.
[2]Juveniles.

as offshore waters and along the edge of the continental shelf (Figures 5, 6). In the Gulf of Mexico, the larvae appear to have their center of abundance in the eastern area. They have the highest frequency of occurrence and are the most abundant among the larval carangids considered

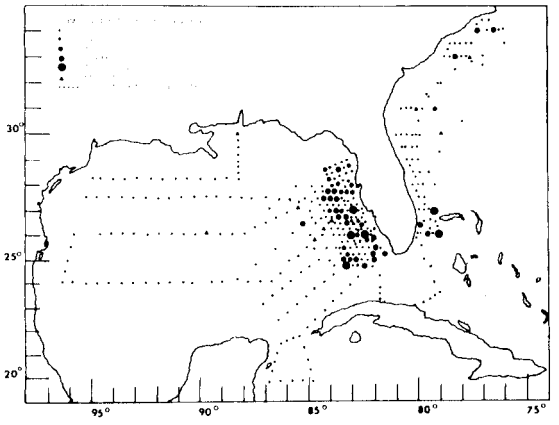


FIGURE 5.—Distribution and apparent relative abundance of the larvae of *Decapterus punctatus* in the Gulf of Mexico and the South Atlantic coast of the United States: a composite record of occurrences at stations occupied in October to November 1970 by the *Joie de Vivre* and in August, October, and November 1971 by the *Dan Braman* and *Oregon II*. Open circles indicate other stations occupied.

TABLE 7.—Meristic characters of cleared and stained larvae and juveniles of *Decapterus punctatus*.

Standard length	Dorsal fin	Anal fin	Left pectoral fin	Left pelvic fin	Primary caudal fin rays		Secondary caudal fin rays		Gill rakers, left first gill arch	Left preopercular margin spines
					Dorsal	Ventral	Dorsal	Ventral		
3.1	—	—	—	—	—	—	—	—	—	5
3.5	—	—	—	—	—	—	—	—	—	6
4.2	—	—	—	—	4	3	—	—	0+ 6	8
5.3	V; 6	II; 6	3	—	6	—	—	—	0+12	10
6.6	VI; I, 19	II; I, 16	10	I, 5	9	8	3	2	0+14	11
7.6	VII; I, 20	II; I, 18	14	I, 3	9	8	4	4	0+16	12
8.2	VIII; I, 25	II; I, 19	17	I, 5	9	8	5	6	0+17	12
9.0	VIII; I, 30	II; I, 21	18	I, 5	9	8	7	8	0+17	11
10.4	VIII; I, 31	II; I, 24	17	I, 5	9	8	8	8	3+17	11
11.5	VIII; I, 23	II; I, 26	19	I, 5	9	8	8	8	3+21	11
12.5	VIII; I, 34	II; I, 31	19	I, 5	9	8	9	9	6+24	10
13.5	VIII; I, 32	II; I, 28	20	I, 5	9	8	9	9	6+25	10
14.4	VIII; I, 32	II; I, 27	20	I, 5	9	8	9	9	6+26	9
15.1	VIII; I, 33	II; I, 29	20	I, 5	9	8	9	9	6+25	10
16.5	VIII; I, 32	II; I, 27	19	I, 5	9	8	9	9	6+25	7
17.0	VIII; I, 31	II; I, 27	20	I, 5	9	8	9	9	6+27	5
19.0	VIII; I, 34	II; I, 27	20	I, 5	9	8	9	9	6+28	3
23.0	VIII; I, 32	II; I, 28	21	I, 5	9	8	9	9	8+28	2
28.2	VIII; I, 31	II; I, 28	20	I, 5	9	8	9	9	9+28	0

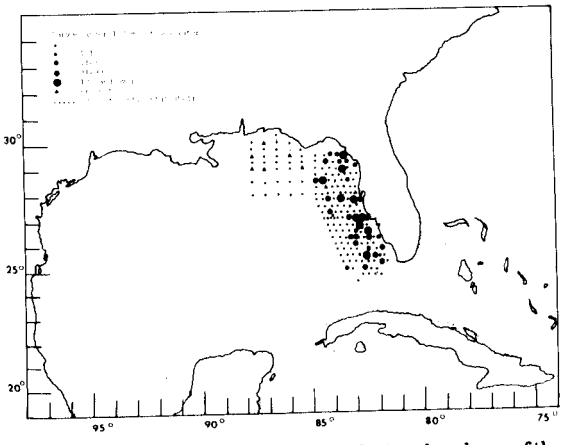


FIGURE 6.—Distribution and apparent relative abundance of the larvae of *Decapterus punctatus* in the Gulf of Mexico: a composite record of occurrences at stations occupied from May to August 1972 by the *Tursiops*, *Dan Braman*, and *Gerda*.

here. They occurred in 18.5% of the net stations and constituted 44.7% of the larval carangids collected.

Lookdown, *Selene vomer* (Linnaeus)

Figure 7

Literature

Larvae of *S. vomer* are previously undescribed. Fowler (1936) illustrated a 15-mm juvenile and Lutken (1880) a 28-mm juvenile.

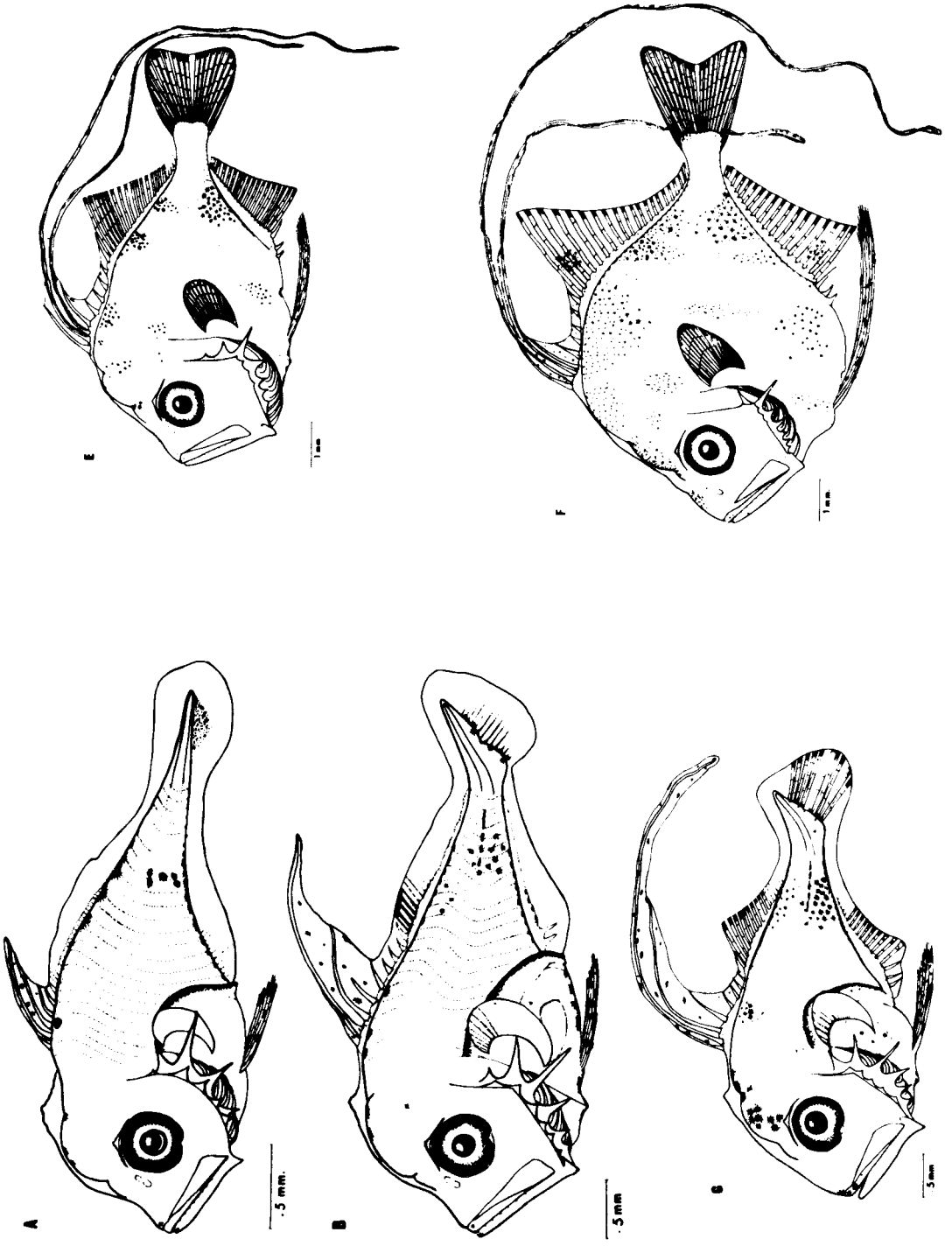
Distinguishing Features

Larvae of *S. vomer* have extremely deep and trenchant bodies. The advanced development of the dorsal and ventral fins is perhaps the most notable feature of their development; it is the earliest observed among carangid larvae. The second and third dorsal spines develop into long filaments often twice the length of the body. The ventral fins are elongated, often extending to the anal fin. The larvae probably attain a maximum length of 12 mm before transformation. The biggest larva in the series in 9 mm long (Figure 7F) and the next size, 13.5 mm, (Figure 7G) is a transforming larva hatched from a planktonic egg and reared in an aquarium. The smallest juvenile is 23.9 mm long and has attained most adult features.

As in most larval carangids, there is a bony crest in the supraoccipital bones, two rows of preopercular spines, and a supraorbital crest. The distance from the snout to the occipitals is long and slopes into an abrupt angle. The first interhemal spine is much enlarged and pressed against an equally enlarged hemal spine.

Morphology

The larvae are among the most deep bodied of all larval carangids. Relative body depth increases during the larval and early juvenile periods (Table 8). It is 32% at 2.5 mm and increases steadily, attaining a maximum of 96% at 23.9 mm. Thereafter, body depth gradually declines but is never less than 74% of the body length in the juveniles. Simultaneous with the deepening of the body is the enlargement of the first interhemal and hemal spine of the first caudal vertebra. The


E
1 mm
F
1 mm
A
.5 mm
B
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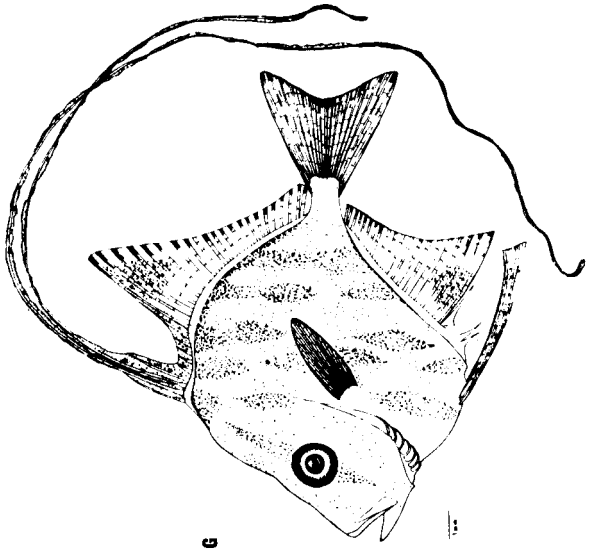
C
.5 mm



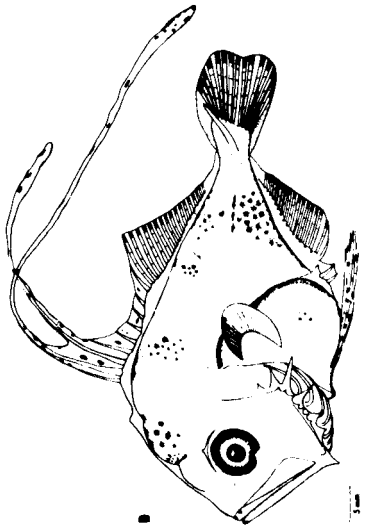


FIGURE 7.—*Selene vomer*. A. 3.2 mm SL; B. 3.9 mm SL; C. 4.5 mm SL; D. 5.8 mm SL; E. 7.7 mm SL; F. 9.0 mm SL; G. 13.5 mm SL.

two spines fuse at the posterior wall of the abdominal cavity which becomes elongated vertically. Consequently, the long and slender gut forms vertical loops following the shape of the abdominal cavity. The gut opening is pushed anteriorly and lies adjacent to the base of the pelvic fins. Snout-to-anus distance decreases relative to standard length. It is 56% at 2.5 mm and declines to 40% at the end of the larval period. During the early juvenile stages, snout-to-anus distance had an average of 38%.

The length and width of the head increases relative to standard length. Head length is 31.0% in the smallest larva (2.5 mm) and does not increase substantially until the juvenile period when it attains a maximum of 41.9% at 23.9 mm. To obtain the true depth of the head and not the body depth at the head region, the measurement is taken from the posterior margin of the preopercle from the dorsal margin of the head to the articulation of the mandible and maxillary. Head depth is 100% of the head length at 2.5 to 3.2 mm. Thereafter, head depth exceeds head length. During the larval period, the head is deepest at 4.6 mm when it is 140% of the head length. This is, however, exceeded by the progressive deepening of the head during the transition and juvenile stages with a maximum of 182% and an average of 158%. The dorsal profile of the snout is slightly concave in the early larval period (2.5-3.8 mm) but becomes straight in older and transforming larvae. The nasal, frontal, and supraoccipital bones become markedly elongated and slope steeply, giving the head an almost vertical anterior profile.

The eyes are round and large. Relative orbit diameter increases during the larval and juvenile development; it is 32% at 2.5 mm and attains a maximum of 37% at notochord flexion with an average of 31% during the larval and transition periods. In the juveniles, orbit diameter decreases to a range of 20 to 27%.

The orbital and supraoccipital crests are well marked in early larval stages up to 5 mm. The crests are gradually resorbed and are vaguely visible at metamorphosis. Preopercular marginal spines consist of 4 to 7 long and strong spines while the lateral surface spines are smaller and limited to the lower surface. All preopercular spines are resorbed at transformation. Scales are absent.

Pigmentation

The common larval pattern of pigmentation in

TABLE 8.—Measurements (mm) of larvae and juveniles of *Selene vomer*.

(Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-to-anus distance	Head length	Head depth	Body depth at base of pectoral fin	Snout length	Orbit diameter	Snout to fin origin		
							Predorsal	Prepelvic	Preanal
2.5	1.4	0.78	0.78	0.80	0.25	0.25	1.0	0.7	—
3.2	1.7	1.0	1.0	1.0	.37	.32	1.1	1.2	1.7
3.5	1.8	1.1	1.2	1.3	.37	.35	1.2	1.0	1.8
3.8	1.8	1.2	1.4	1.5	.42	.42	1.2	1.35	2.0
4.0	2.0	1.2	1.5	1.5	.47	.37	1.3	1.2	2.0
4.3	2.2	1.5	1.9	1.9	.52	.50	1.5	1.6	1.9
4.4	2.1	1.5	2.0	2.1	.55	.50	1.4	1.6	1.8
4.5	2.2	1.5	2.0	2.0	.52	.45	1.4	1.5	2.0
4.6	1.8	1.5	2.1	2.1	.55	.42	1.6	1.6	2.1
4.8	2.6	1.7	2.0	2.1	.55	.45	1.8	1.7	2.8
5.0	2.7	1.7	2.2	2.2	.52	.47	1.8	1.9	3.0
5.3	3.0	1.7	2.1	2.3	.55	.45	1.7	2.0	3.0
5.5	2.7	2.0	2.5	2.9	.62	.60	1.8	1.8	3.1
6.1	2.8	2.0	3.0	3.2	.87	.62	2.0	2.0	3.0
7.5	3.6	2.6	3.5	3.9	.90	.85	2.4	2.5	4.0
8.2	4.5	3.0	3.8	4.8	1.2	.87	2.9	3.0	4.6
[1]9.0	3.6	3.1	5.2	5.8	1.3	1.0	2.9	2.8	5.0
[1]13.5	6.7	5.2	9.5	6.2	2.2	1.7	5.5	5.5	6.2
[2]23.9	8.7	10.0	14.0	23.0	3.1	2.5	7.0	8.0	11.0
[2]27.5	11.5	10.0	15.0	24.5	3.5	2.6	11.0	8.0	14.0
[2]30.0	12.0	11.0	17.0	27.0	5.0	3.0	14.0	12.0	14.0
[2]34.0	12.0	13.5	22.0	31.0	6.5	3.0	14.0	13.0	14.0
[2]38.0	14.0	14.5	20.0	31.0	5.0	3.2	15.5	11.5	16.0
[2]42.5	14.0	17.0	28.0	35.0	5.5	3.9	17.0	15.0	14.0
[2]47.0	16.0	20.0	30.0	35.0	8.0	4.2	16.0	18.0	17.0

[1]Transforming
[2]Juveniles

carangids, including melanophores along the bases of the dorsal and anal fins and along the lateral-midline, is present in *S. vomer*. In the early larvae (2.5-5.0 mm), a few melanophores develop on the tips of the jaws, head, sides of the body, pelvic fin, dorsal fin, and base of the caudal fin. The earliest patch of melanophores is formed on the lower side of the body anterior to the caudal peduncle. In older larvae, the melanophores gradually proliferate all over the body and form discrete patches which develop into broad spots at transformation and in the juvenile stages. The heaviest concentrations of pigment cells comprise those lining the dorsal wall of the peritoneum. Reglarly spaced melanophores similar to those in *Elagatis bipinnulata* (Figure 1B-D) are present along the midventral line in the trunk region.

Fin Development

The sequence of fin formation and ossification is as follows: 1) pelvic; 2) first dorsal; 3) second dorsal, caudal, and anal; and 4) pectoral (Table 9).

The pectoral finbud is formed at 2.5 mm but the rays are not differentiated until the larvae are 5 to 6 mm. The full complement of 18 to 21 is formed at 9 mm.

The pelvic fins are fully formed in the smallest larva (2.5 mm). They steadily increase in length and at metamorphosis extend beyond the origin of the anal fin.

The first 3 dorsal spines are ossified at 2.5 mm. The second and third spines progressively increase in length throughout the larval period, forming extremely long filaments. At metamorphosis, they are about twice the length of the body. The full complement of 8 spines in the first dorsal fin and of 1 spine and 20 to 22 soft rays in the second dorsal fin is present at 9 mm.

Rudiments of the anal fin are discernible at 3.2 mm and the rays ossify at 4 to 5 mm. The full complement of 3 spines and 16 to 18 soft rays is present at 6 mm.

The development and structure of the caudal fin and supporting structures are similar to those of *E. bipinnulata*. The full complement of 17 principal and 7 to 9 dorsal, and 7-8 ventral secondary caudal rays is present at 9 mm.

TABLE 9.—Meristic characters of cleared and stained larvae and juveniles of *Selene vomer* (Linnaeus).

Standard length	Dorsal fin	Anal fin	Left pectoral fin	Left pelvic fin	Primary caudal fin rays		Secondary caudal fin rays		Gill rakers, left first gill arch	Left preopercular margin spines
					Dorsal	Ventral	Dorsal	Ventral		
2.5	III	—	—	I, 5	—	—	—	—	—	—
3.2	V	—	—	I, 5	—	—	—	—	—	—
3.4	V	—	—	I, 5	—	—	—	—	—	—
3.5	VI	—	—	I, 5	—	—	—	—	—	—
4.0	V; 3	II	—	I, 5	2	3	—	—	0+11	1
4.4	VIII; I, 10	II; 10	—	I, 5	5	6	—	—	0+11	2
4.9	VIII; I, 15	II; I, 14	—	I, 5	7	7	—	—	0+16	2
5.2	VIII, I, 18	II, I, 16	—	I, 5	7	8	—	—	3+16	2
5.5	VIII; I, 18	II; I, 17	6	I, 5	7	8	—	—	3+18	3
6.1	VIII; I, 19	II; I, 17	10	I, 5	8	8	—	—	4+19	2
6.3	VIII; I, 20	II; I, 16	13	I, 5	8	8	3	4	5+20	2
7.6	VIII; I, 21	II; I, 17	17	I, 5	9	8	5	4	6+20	2
8.6	VIII; I, 20	II; I, 17	17	I, 5	9	8	6	6	6+20	2
9.0	VIII; I, 20	II; I, 18	18	I, 5	9	8	7	8	6+22	1
13.5	VIII; I, 21	II; I, 18	18	I, 5	9	8	8	7	6+23	—
23.9	VIII; I, 21	II; I, 18	20	I, 5	9	8	9	8	6+25	—

Distribution and Spawning

Adults of *Selene vomer* have been recorded on both coasts of the United States, from Cape Cod to Brazil and from Lower California to Peru (Jordan and Evermann, 1896). They have also been reported from the Gulf of Mexico (Ginsburg, 1952), the Bahamas (Böhlke and Chaplin, 1968), and West Africa (Fowler, 1936).

Larval and early juveniles of *S. vomer* were taken in all months except in June, October, and December. The monthly occurrence and distribution of the larvae is a composite of the records of specimens which include those taken from the coastal waters of the eastern tropical Pacific from Baja California to Costa Rica, the Gulf of Mexico, and the tropical Atlantic off Brazil and Liberia (Aprieto, 1973). In the Gulf of Mexico, larvae were abundant mainly in the northeastern offshore waters in August which suggests a short spawning period in that area (Figure 2). The larvae occurred in 2.2% of the net stations and constituted 2.6% of the larval carangids collected in the Gulf of Mexico and the south Atlantic coast.

Leatherjacket, *Oligoplites saurus* (Bloch and Schneider)

Figure 8

Literature

Larvae of this species have not been described previously.

Distinguishing Features

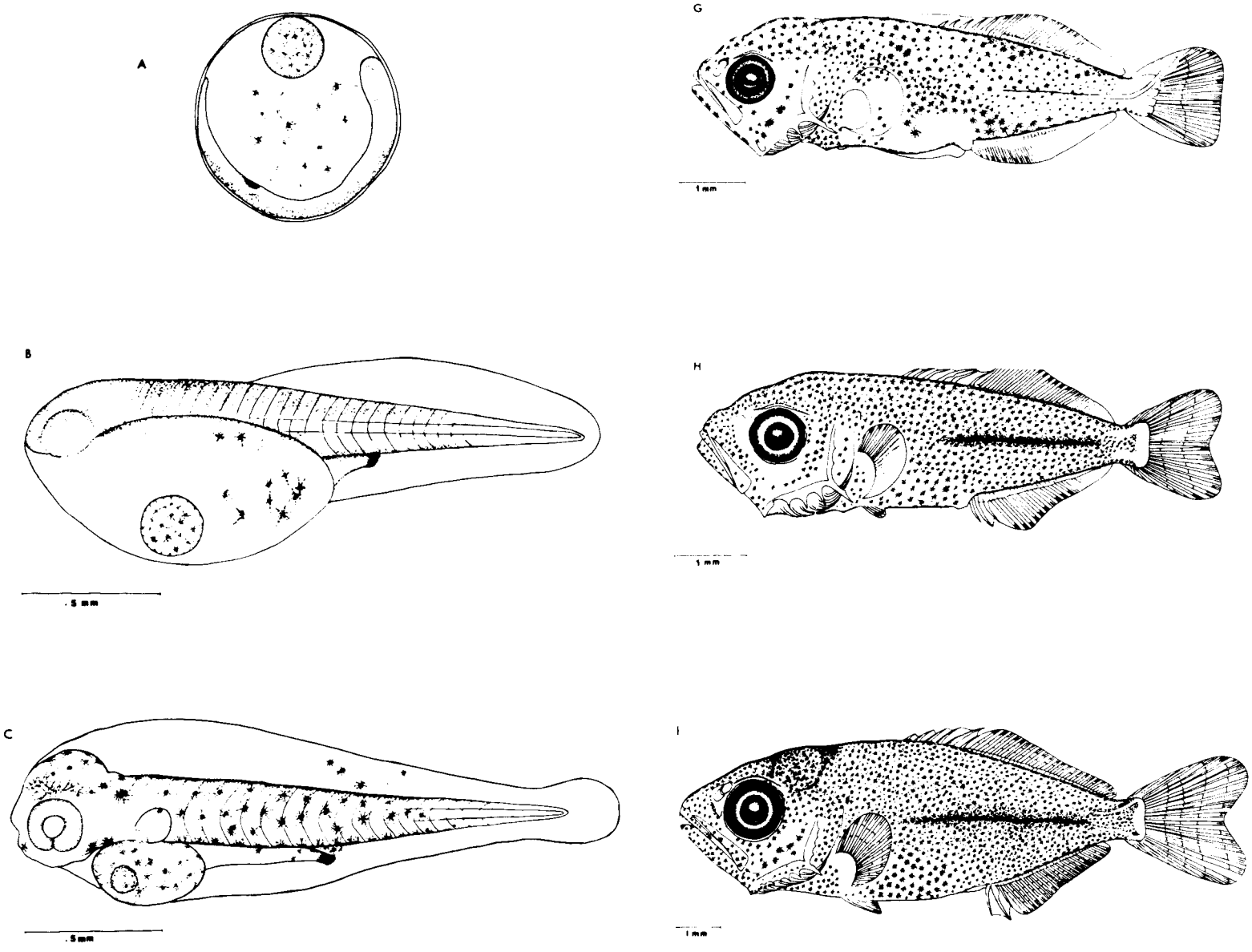
Larvae of *O. saurus* resemble those of *Elagatis bipinnulata* and *Seriola zonata*. Further, as in *E. bipinnulata*, the first interhemal spine is thickened and, as in *S. zonata*, the supraoccipital crest is lacking. Larvae of *O. saurus* are distinct from those of the two species mentioned in having an orbital crest with fine serrations, 1 to 3 denticles which appear early in the larval period on the dorsal side of the longest preopercular spine, and 26 vertebrae—the highest vertebral count among carangids. The number of dorsal spines and pectoral fin rays formed is fewer than in most carangids, 5 to 6 and 15 to 17 respectively. Larval pigmentation is moderately profuse and, as in most carangid larvae, conspicuous melanophores are present along the bases of the dorsal and anal fins, on the lateral midline, and on the dorsal wall of the abdominal cavity. The larvae transform at 7 to 10 mm.

The Embryo

Two preserved eggs of *O. saurus* are 0.87 and 0.88 mm in diameter. They have ventral, single oil globules, 0.33 and 0.34 mm in diameter. The oil globule consists of minute oil droplets and is enclosed in a rather tough, pigmented capsule. The pigmented yolk is bright yellow and unsegmented. The perivitelline space is narrow and the egg case smooth. The embryos are well developed and have stellate melanophores along the back and upper sides of the body. A large melanophore is present at the posteroventral midline (Figure 8A).

Morphology

The larvae are 1.87 and 1.97 mm at hatching.


A
B
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I
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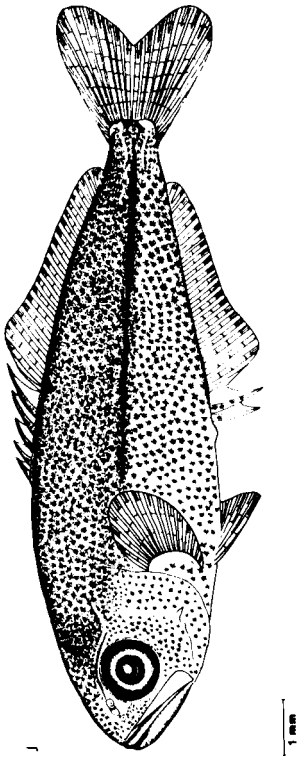

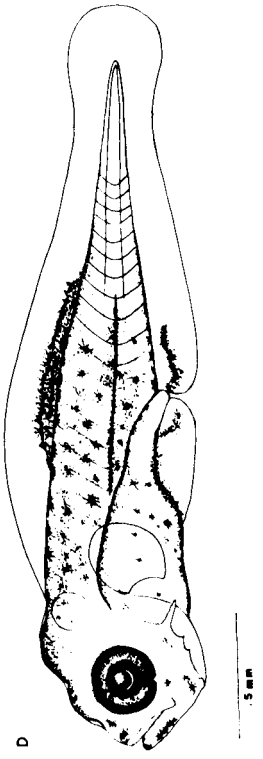

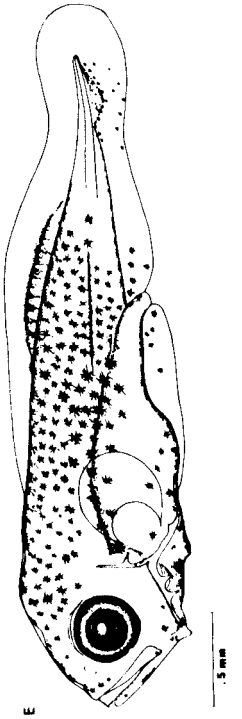

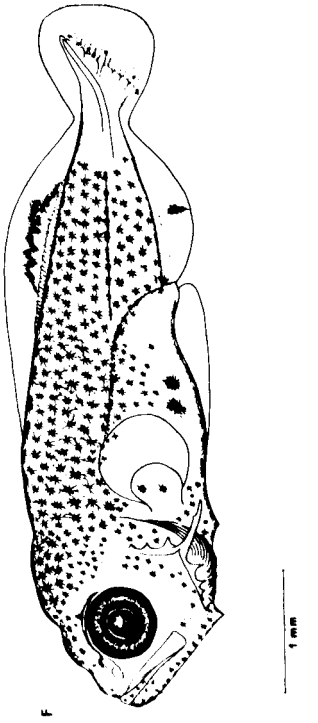

FIGURE 8.—*Oligoplites saurus*. **A.** Embryo; **B.** 1.8 mm SL; **C.** 2.2 mm SL; **D.** 3.0 mm SL; **E.** 4.1 mm SL; **F.** 5.2 mm SL; **G.** 5.9 mm SL; **H.** 7.2 mm SL; **I.** 10.0 mm SL; **J.** 18.0 mm SL.

The body is slender but appears robust at the anterior end in view of the distended yolk sac (Figure 8B). The head is well marked and the eye buds are discernible. The dorsal finfold originates behind the nape and is continuous with the anal finfold at the tail region. At the first day of hatching, the yolk sac is reduced to a spherule, the eyes are formed but unpigmented, and the dorsal and anal finfolds completely surround the larva except at the mouth. More and bigger melanophores are formed along the sides and back, and a large ventral melanophore is located at the opening of the gut (Figure 8C).

Early larvae of *O. saurus* are slender compared to other larval carangids. Body depth increases relative to standard length and ranges from 20 to 26.9% during the larval period (Table 10). It increases to a maximum of 32% at metamorphosis and thereafter declines to 28 to 29%. The slender gut is straight and forms a single loop at 4 mm. A second loop develops at metamorphosis, and a third is added in the early juvenile period. Snout-to-anus distance ranges from 51 to 61% during the larval period and decreases slightly in subsequent

TABLE 10.—Measurements (mm) of larvae and juveniles of *Oligoplites saurus*.

(Specimens between dashed lines are undergoing notochord flexion; W - wild, L - laboratory reared.)

Specimen number	Standard length	Snout-to-anus distance	Head length	Head depth	Snout length	Orbit diameter	Body depth at base of pectoral fin	Snout to fin origin		
								Predorsal	Prepelvic	Preanal
1(L)	1.87	—	—	—	—	—	—	—	—	—
2(L)	1.95	—	—	—	—	—	—	—	—	—
3(L)	2.17	1.25	0.50	0.45	0.05	0.10	0.45	—	—	—
4(L)	2.25	1.3	.51	.50	.07	.10	.50	—	—	—
5(L)	2.3	1.3	.57	.54	.09	.20	.60	—	—	—
6(L)	2.5	1.4	.60	.59	.09	.25	.60	—	—	—
7(L)	2.5	1.5	.60	.60	.12	.25	.50	—	—	—
8(L)	2.6	1.5	.60	.55	.12	.25	.55	—	—	—
9(L)	2.8	1.6	.67	.65	.12	.30	.60	—	—	—
10(L)	4.1	2.4	1.1	.95	.25	.40	.87	—	—	—
11(W)	4.3	2.2	1.3	1.2	.37	.37	1.0	1.9	—	2.0
12(W)	4.9	2.7	1.4	1.3	.40	.45	1.3	2.1	—	2.8
13(L)	5.2	3.0	1.5	1.4	.40	.52	1.4	2.1	—	3.0
14(L)	5.9	3.5	1.8	1.5	.45	.62	1.4	2.5	—	3.5
15(L)	7.2	4.4	2.6	2.2	.75	.75	2.2	3.6	3.2	4.6
16(W)	8.7	5.1	3.0	2.5	.80	.80	2.4	4.0	3.6	5.4
17(W)	10.4	5.4	3.3	3.0	.75	1.1	3.0	4.7	3.9	5.7
18(L)	10.5	5.8	3.5	2.9	.90	1.0	3.4	4.9	3.7	6.0
19(W)	10.5	5.5	3.5	3.0	1.0	1.0	3.0	4.9	3.7	5.6
20(W)	11.0	5.9	3.6	3.2	1.0	1.0	3.3	5.2	3.8	6.1
21(W)	15.0	6.9	4.4	3.7	1.3	1.3	4.1	6.0	4.8	7.0
22(W)	16.0	8.0	4.5	4.0	1.2	1.3	4.5	6.5	5.0	8.1
23(L)	18.5	9.5	5.3	4.6	1.3	1.9	5.3	8.0	6.0	9.5
24(L)	21.0	10.5	6.0	5.3	1.5	2.1	6.1	8.9	6.0	11.0

stages. Hypaxial muscles enclose the gut at 4 mm, and the abdominal cavity is completely covered at 7.2 mm.

As in most carangid larvae, the head is long and deep. Relative head length ranges from 23 to 36% of standard length during the larval and juvenile periods. Depth of head ranges from 82 to 100% of the head length. The dorsal profile of the snout is convex except for a slight indentation at the anterior margin of the forebrain. The eyes are round and large; eye index ranges from 20 to 44% during the larval and early juvenile periods and is highest in larvae 2 to 3 mm long. Pigmentation develops on the second day of hatching. A finely serrated orbital crest is present in larvae from 4 mm long and is gradually resorbed following metamorphosis. Preopercular spines are present but only the marginal ones are well developed. One to three denticles occur on the dorsal side of the longest marginal spine.

The scales and lateral line are not yet developed in 25-mm juveniles, the oldest of the laboratory-reared specimens.

Pigmentation

Larval pigmentation is well developed and progressively increases during the larval and juvenile stages. Pigment cells are more abundant in laboratory-reared specimens than in the wild ones. A conspicuous U-shaped, unpigmented area at the caudal peduncle persists from 7.2 mm up to the early juveniles 20 mm long (Figure 8H-J). Throughout the larval and juvenile stages xanthophores are present on the sides of the body, but they readily fade on preservation. Melanophores form at the base of the dorsal finfold in the early larvae but disappear when the fin rays are differentiated. The conspicuous anal pigment spot in the embryo and newly hatched larvae disappear at the third day of hatching. In the early juveniles, pigmentation develops on the membrane of the dorsal and anal fin spines.

Fin Development

The dorsal, anal, and caudal finfolds are present at hatching, and the sequence of ossification is as follows: 1) dorsal, anal, and caudal; 2) pectoral and pelvic (Table 11).

The pectoral finfold is formed a day after hatching. As in other larvae described here, the pectoral fin rays begin to ossify dorsally and the rest are added ventrally. The full complement of 15 to 17 rays is completed at 10 mm.

The pelvic fin buds appear 13 days after hatching at 6 mm and the rays soon become differentiated. The full complement of 1 spine and 5 soft rays is present at 10 mm.

TABLE 11.—Meristic characters of cleared and stained larvae and juveniles of *Oligoplites saurus*.

Standard length	Dorsal fin	Anal fin	Left pectoral fin	Left pelvic fin	Primary caudal fin rays		Secondary caudal fin rays		Gill rakers, left first gill arch	Left preopercular margin spines
					Dorsal	Ventral	Dorsal	Ventral		
4.1	—	—	—	—	—	—	—	—	—	4
4.3	—	—	—	—	—	—	—	—	—	4
4.9	—	—	—	—	—	—	—	—	—	4
5.9	III; 8	II; 7	—	—	3	3	—	—	0+4	6
7.2	V; 18	II; I, 16	7	2	9	8	1	2	0+10	8
8.7	V; I, 17	II; I, 17	10	I, 5	9	8	—	—	0+9	9
10.4	IV; I, 20	II; I, 19	13	I, 5	9	8	9	9	3+12	12
11.0	V; I, 20	II; I, 18	14	I, 5	9	8	9	9	3+11	9
12.2	V; I, 21	II; I, 19	14	I, 5	9	8	10	9	3+11	10
13.0	V; I, 19	II; I, 18	14	I, 5	9	8	9	9	3+10	9
15.1	V; I, 20	II; I, 19	14	I, 5	9	8	9	9	5+11	8
15.2	V; I, 21	II; I, 19	15	I, 5	9	8	9	9	5+11	6
16	V; I, 21	II; I, 18	16	I, 5	7	9	9	9	5+11	5
17	V; I, 21	II; I, 20	16	I, 5	9	8	9	10	5+12	6
18.5	V; I, 20	II; I, 20	16	I, 5	9	8	9	8	5+13	4
19	V; I, 20	II; I, 18	15	I, 5	9	8	10	9	5+13	3
21.0	V; I, 21	II; I, 18	16	I, 5	9	8	9	9	5+13	3

The dorsal and anal fin rays differentiate simultaneously in an anteroposterior direction. Unlike previously described species, in which either the middle or anterior spines are longer, the posterior spine of the first dorsal fin is slightly longer than the rest. The full complement of 6 spines and 19 to 21 rays is present at 10 mm. The anal fin rays of 3 spines and 18 to 20 soft rays are also complete at 10 mm.

Caudal fin formation is similar to that of the other species described. The full complement of 9 to 10 dorsal and 8 to 10 ventral principal rays and 18 to 20 secondaries is present at 10 mm.

Distribution and Spawning

Adults of *O. saurus* are known from both coasts of Central America and in the West Indies (Jordan and Evermann, 1896). They also occur along the Atlantic coast of the United States from Massachusetts to Florida and in the Gulf of Mexico (Ginsburg, 1952). The wild larvae and juveniles in the present work were taken from Escambia Bay, Fla., and at Sapelo and St. Simons Islands, Ga., in May and July by means of channel nets and beach seines. The laboratory-reared larvae were hatched from planktonic eggs collected from Biscayne Bay. Larvae and juveniles were not collected in any of the net stations in the Gulf of Mexico and the south Atlantic coast. Distribution of the young in these regions is obscure, and abundance and frequency of occurrence in relation to the other larval carangids could not be established. The wild larvae obtained were too few to derive conclusive information, but apparently spawning occurs in summer. Unlike the other carangids which spawn in offshore pelagic waters, *O. saurus* spawns in inshore and shallow waters. Further investigation is necessary to establish with certainty the spawning period and sites and the distribution of the young.

Laboratory Rearing

Planktonic eggs of *O. saurus* were collected in a 1-m, 505-μ mesh plankton net at the pier of the Rosenstiel School of Marine and Atomospheric Science on 15 July 1972, at 9:00 A.M., EDT. A total of 75 eggs was sorted from the plankton and incubated in a 50-liter glass aquarium. The aquarium water was drawn from Biscayne Bay through the School's seawater system. It was oxygenated and circulated with compressed air added through airstones and lighted continuously by two cool, white, fluorescent bulbs. Temperature ranged from 23.9° to 28°C and salinity from 32 to 36‰ during the experiment. The larvae were fed wild plankton collected from Biscayne Bay as well as nauplii of brine shrimp (*Artemia salina*). A detailed description of the rearing technique employed is given in Houde and Palko (1970).

The eggs began hatching in the afternoon of the day of collection and after 24 h all the eggs were presumed hatched. The larvae averaged 1.92 mm at hatching, were 5.2 mm 8 days after hatching, and about 21 mm at 34 days (Figure 9). Mortality in the first 18 days included 2 eggs and 16 larvae preserved for describing larval development. Six young juveniles averaged 25 mm after 45 days. Thereafter, the juveniles failed to feed and all but one died at 51 days when the rearing experiment was terminated.

Ossification

The sequence of ossification of the skull, axial, and appendicular skeleton is generally similar among the four species in which ossification was observed (Table 12). Without exception, the premaxillaries, preopercular spines, and cleithra ossify in the smallest larvae (2.5-3.8 mm). Next to ossify at 4 to 5 mm are the maxillaries, dentaries, parasphenoid, supraoccipital, articulars, frontals, angulars, and the branchial arches. The entire maxillary arch is ossified before the larvae are 6 mm long. Teeth are formed along the entire margin of the premaxillaries and anterior region of the dentaries in the youngest larvae following the ossification of these elements. It is apparent that the bones related to feeding ossify early, and this is consistent with the need of the larvae for food from external sources following the absorption of the yolk.

Seven branchiostegal rays on each side are present in 3-mm larvae. Ossification begins with the posterior and longer rays and proceeds anteriad. The ceratohyal and epihyal to which the branchiostegal rays are attached ossify simultaneously with the rays. The rest of the hyoid arch including the glassohyal, urohyal, and hypohyal ossify at metamorphosis.

Aside from the quadrate and hyomandibular which ossify during the larval period, the rest of the palatine arch is not calcified until metamorphosis.

The branchial arches initially ossify in larvae 4 to 5 mm long and all arches are calcified at 6 mm. The first branchial arch is the first to ossify starting from the center of the ceratobranchial towards both ends. The epibranchial is the next to ossify beginning from near the angle of the arch outward. Ossification of the other arches follows in a similar sequence.

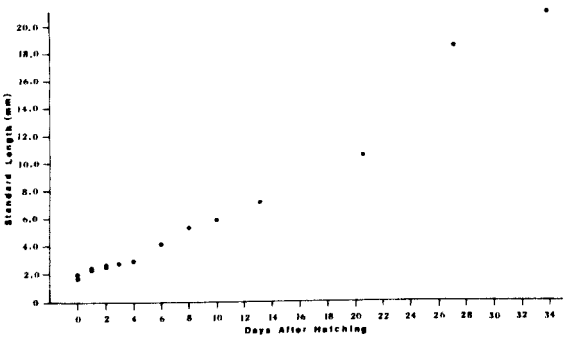

FIGURE 9.—Growth of *Oligoplites saurus* larvae reared in the laboratory at an average temperature of 26.0°C.

The gill rakers calcify following the ossification of the elements to which they are attached. The number of gill rakers increase as growth progresses but gill rakers are slow to ossify, and the full complement usually is not completed until the transition and early juvenile stages. The adult count in *Seriola zonata* is fewer than is formed in the juveniles due to the reduction of the terminal gill rakers into tubercles in the ceratobranchial. Patches of fine teeth are formed on the superior pharyngeals of the third and fourth gill arches while the fifth and shortest gill arch has teeth patches for most of its length. Pharyngeal teeth ossify in larvae 6 to 8 mm long.

In the cranium, the parasphenoid, frontals, and supraoccipitals ossify in the youngest larvae (2.5-3.8 mm). Except for the parietals which ossify in the midlarval period, the rest of the cranium is not ossified until the late larval and transition periods.

The cleithra, postcleithra, and posttemporals are ossified in the early and midlarval stages, but the rest of the pectoral girdle calcifies in late and transforming larvae. From 2 to 4 posttemporal spines protrude from the myotomes during the early larval period. These are small and hardly visible in most species except in stained specimens. These spines are soon overgrown by the developing muscles.

The pelvic girdle calcifies following the ossification of the pelvic fins.

Ossification occurs at 5 to 8 mm in the vertebral column and proceeds in an anteroposterior direction. The neural and hemal spines ossify ahead of the centra of their respective vertebrae. The centra ossify at their anterior margins and ossification proceeds posteriorly. This pattern of ossification in the vertebrae was noted in *Trachurus symmetricus* (Ahlstrom and Ball, 1954).

Ribs similarly ossify in an anteroposterior direction. The pleural ribs are the first to ossify followed by the epipleural ribs. All trunk vertebrae have ossified pleural and epipleural ribs in juveniles 15 to 17 mm long except on the first and second in which pleural ribs are lacking.

Teeth are initially uniserial but become multiserial as tooth formation progresses. Following

TABLE 12.—Sequence of ossification of the skull, branchial arches and girdles in four species of carangids. Numbers indicate length (mm) of smallest specimen in which ossification of each element was observed; dashes indicate undetermined size.

Bone	*Elagatis bipinnulata*	*Seriola zonata*	*Decapterus punctatus*	*Selene vomer*
Cranium:				
Vomer	6.0	6.5	7.6	9.0
Mesethmoid	8.4	8.5	9.0	9.0
Ectethmoid	9.4	8.5	9.0	9.0
Parasphenoid	3.8	3.5	4.2	4.0
Frontal	4.6	4.7	4.2	4.0
Supraoccipital	4.6	4.7	4.2	4.0
Exoccipital	6.0	6.5	7.6	6.3
Basioccipital	6.0	6.5	7.6	9.0
Parietal	7.0	5.5	5.2	6.3
Pterotic	10.4	9.5	9.0	8.6
Prootic	8.4	8.5	9.0	8.6
Epiotic	10.4	9.5	9.0	8.6
Sphenotic	9.5	8.5	9.0	8.6
Opisthotic	11.5	10.3	9.0	9.0
Basisphenoid	11.5	11.2	9.0	9.0
Orbital bones:				
Preorbital	8.4	11.2	10.0	—
1st suborbital	17.1	17.0	15.0	—
2nd suborbital	15.2	16.0	15.0	—
3rd suborbital	12.0	13.0	14.0	—
4th suborbital	13.0	14.0	16.0	—
5th suborbital	13.0	15.0	16.0	—
Opercular apparatus:				
Opercle	5.4	5.5	10.0	9.0
Interopercle	7.0	5.5	12.0	9.0
Preopercle	3.8	3.6	3.5	2.5
Subopercle	7.0	5.5	14.0	9.0
Hyoid apparatus:				
Hypohyal	13.1	11.0	10.0	7.6
Ceratohyal	5.4	5.5	5.3	4.9
Epihyal	6.0	6.5	5.5	5.2
Glossohyal	8.0	7.5	9.0	7.6
Urohyal	8.0	10.0	11.0	7.6
Interhyal	17.0	15.0	22.0	13.5
Maxillary arch:				
Premaxillary	3.8	3.6	3.1	2.5
Maxillary	3.8	3.6	4.2	4.0
Supramaxillary	—	—	—	13.5
Maxillary arch:				
Dentary	4.6	3.6	4.2	4.0
Articular	4.6	4.7	5.2	4.0
Angular	4.6	4.7	5.2	5.2
Palatine arch:				
Hyomandibular	6.0	7.5	7.6	8.6
Metapterygoid	12.0	10.4	12.5	8.6
Mesopterygoid	12.0	10.4	12.5	9.0
Pterygoid	12.0	11.5	13.5	9.0
Quadrate	4.6	4.7	5.3	4.0
Symplectic	—	—	—	—
Palatine	10.4	9.4	12.5	13.5
Branchial arches:				
1st Branchial arch	4.6	4.8	4.2	4.9
2nd Branchial arch	5.4	5.5	5.3	5.2
3rd Branchial arch	6.0	5.5	5.3	5.5
4th Branchial arch	7.0	5.5	5.3	6.1
5th Branchial arch	7.0	5.5	5.3	6.1
Gill rakers:				
1st Branchial arch	4.6	4.8	4.2	4.9
2nd Branchial arch	5.4	5.5	5.3	5.2
3rd Branchial arch	6.0	5.5	5.3	5.5
4th Branchial arch	7.0	5.5	5.3	6.1
Pharyngeal teeth:				
3rd Branchial arch	8.0	6.5	6.6	8.0
4th Branchial arch	8.0	6.5	6.6	8.0
5th Branchial arch	8.0	6.5	6.6	8.0
Pectoral girdle:				
Cleithrum	3.8	3.6	3.1	2.5
Postcleithrum	5.4	4.8	5.2	6.1
Hypercoracoid	7.2	8.4	11.0	9.0
Hypocoracoid	7.2	8.4	11.0	9.0
Posttemporal	5.4	4.8	4.2	4.9
Supracleithrum	10.4	13.0	—	—
Pelvic girdle:				
Post pelvic process	8.0	10.0	8.0	5.0
Pelvic keels	8.0	10.0	8.0	5.0

metamorphosis 2 to 3 irregular rows of sharp teeth are present.

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SOME EFFECTS OF DREDGING ON POPULATIONS OF MACROBENTHIC ORGANISMS

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ABSTRACT

Populations of epi- and infauna were studied from 10 mo before to 11 mo after a navigation channel was dredged through a small, shallow lagoon. A new sampler which penetrated 20-30 cm into the substratum was used.

Current velocities and sedimentation patterns were changed due to an altered distribution of tidal currents, although flushing time was not appreciably altered.

Values of certain particulate and dissolved nutrients changed after dredging, but no correlation was observed between animal populations and fluctuations in nutrients.

Significant reductions in standing crop figures and species and specimen numbers occurred in both the bay and the dredged channel. *Mercenaria mercenaria* populations were reduced, but there was no evidence of mass mortality. Recovery of biomass in the channel was affected by sediment composition, but seasonal and sediment type variations were not significant in the bay as a whole.

Goose Creek had a high predredging epi- and infaunal standing crop estimated at 36.83 g/m^2, but the number of organisms/m^2 was relatively low, indicating a preponderance of large forms.

Productivity of Goose Creek was calculated at 89.87 g/m^2/yr before dredging and 31.18 g/m^2/yr after dredging. Productivity figures for the mixed peripheral marsh were calculated and the annual loss due to replacement of 10.87 ha of marsh by spoil areas was estimated at 49,487 kg. Altered land usage patterns tended to fix this loss on a permanent basis.

The unusually profound effects of dredging reported for Goose Creek are attributed to its small size and shallowness.

In 1965, Suffolk County, N. Y., obtained the services of a consortium of universities to study the characteristics of a small embayment before and after a channel 22.8 m wide × 2.1 m deep × 1,037 m long was dredged from the narrow inlet through most of the bay. The investigations reported in this paper are confined to the population dynamics and ecology of the macrobenthic organisms. Reference will be made to the other areas of investigation only as they affect the macrobenthos.

The following phenomena will be considered in relation to their effects on epi- and infaunal population dynamics:

1. Changes in the hydrodynamics of Goose Creek as the result of the introduction of the newly dredged channel.
2. Changes in the morphology of the sediment effected by the dredging process.
3. Changes in physical and chemical characteristics of the water associated with the dredging process.
4. Changes in populations of macrobenthic organisms which occurred during 1966 and 1967.

The Study Area

Goose Creek is a small, shallow lagoon located on the north fork of Long Island in the town of Southold, N. Y. (lat. 41°03′00″N, long. 72°25′23″ W). Its dimensions are 1,464 m east-west by 533 m north-south, a total area of about 0.32 km^2. A channel approximately 30.5 m wide at the eastern end opens into Southold Bay, thence into Shelter Island Sound, an arm of Little Peconic Bay (see Figure 1).

The mean high water depth before dredging was 1.7 m, but much of the bay was extremely shallow and at low water it was impossible to navigate even a small boat in the western half of the bay. Mean tidal range was 68.5 cm, and the mean depth at mean low water was 1.0 m.

The prevailing wind is from the southwest in

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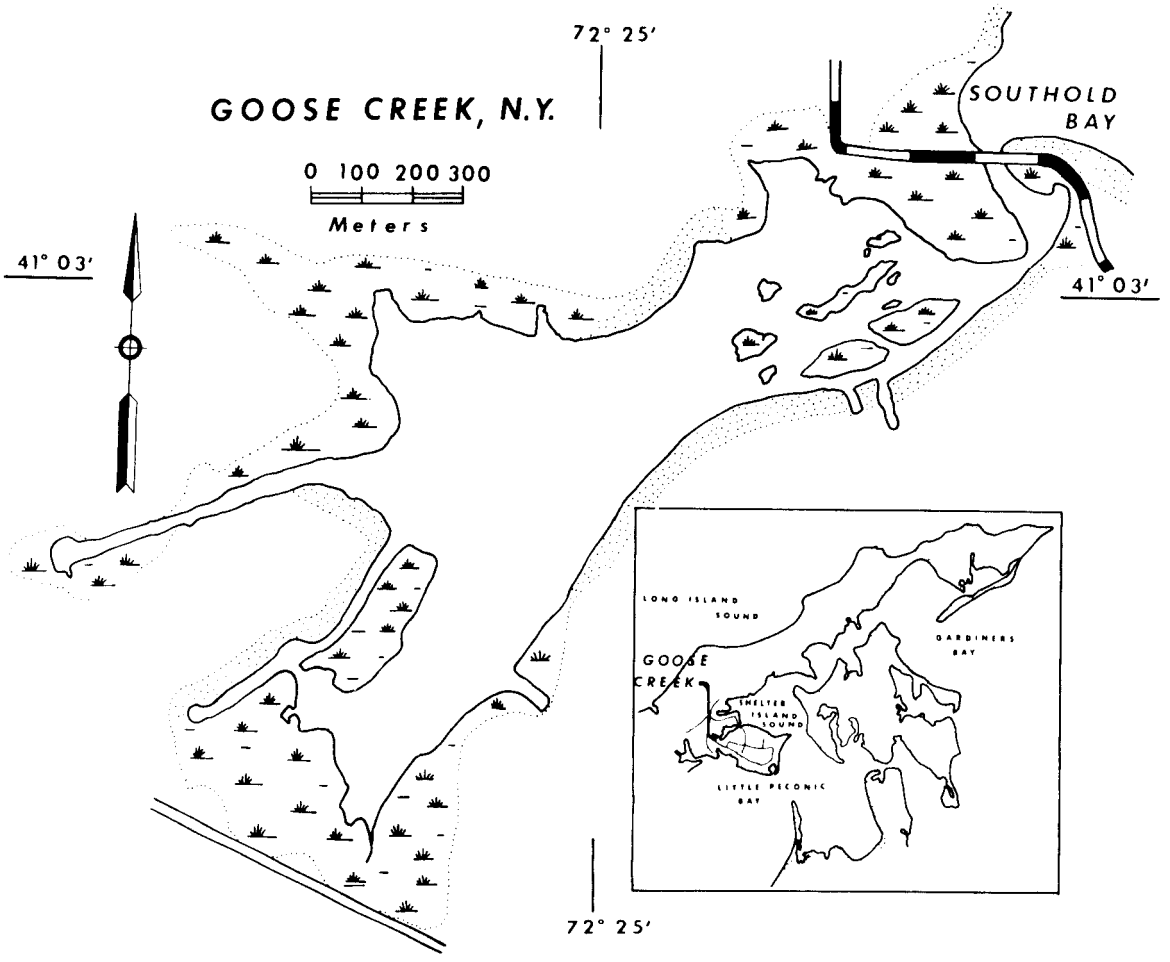

FIGURE 1.—Location map of Goose Creek, N.Y.

the summer months and from the northwest in winter.

There are four "minor" and five "major" islands in Goose Creek, the largest of which is 115.6 m by 42.4 m. They sustain a heavy growth of *Spartina alterniflora* with dense colonies of *Modiolus demissus* and *Uca pugnax*.

The entrance of Goose Creek was dredged from a mean low water depth of 0.8 m to a minimum of 2.1 m below mean low water. In cross section the channel was changed from a gentle depression to a steep-sided U. As a consequence of dredging the channel, the main water flow was shifted from one channel to another and current velocities dropped approximately one-half, except in the western half of the bay where previously negligible velocities increased.

The substratum of the bay consists of coarse gravel and sand in the main channel before it trifurcates into channels A, B, and C, which are characterized by sand grading into fine sand and mud in areas with reduced current velocity. The bottom sediments in the western half of the bay consist of thick silt over gray clay mixed with shell and sand.

The surrounding upland consists of *Spartina* marsh edged by stands of *Phragmites communis*. Before dredging, the south shore was almost completely developed, with small summer homes along the shores. The north and west shores were undergoing partial development with year-round homes. Five years after the dredging (1972), the area was almost completely developed, much of the marsh having been replaced by areas filled for homesites.

In 1966-1967 salinities ranged from a mean low of 26.79 ‰ to a mean high of 28.34 ‰. The pH ranged from 7 to 8. The dissolved oxygen levels varied seasonally and from station to station from a low of 4.50 ml O_2/liter to a high of 9.95 ml O_2/liter. Readings were always at saturation. The mean temperature range was between −1.0°C and 26.18°C over the 2 years; the bay is too shallow to exhibit a pronounced thermocline. Portions of the surface were frozen solid during parts of the months of February and March, 1966, and January, February, and March, 1967.

The tidal currents were relatively rapid in the eastern section of the bay, reaching a velocity of 56.7 cm/sec at station 1, at the confluence of the three channels, but they rapidly lost velocity until negligible readings were recorded in most of the western half of the bay.

Yearly rainfall (1967) amounted to 126.09 cm. Pollution by effluents from cesspools along the southern periphery of the bay consisted of fecal material, other organic material, and detergents as indicated by coliform bacteria and phosphate levels.

Previous Dredging of Goose Creek

Goose Creek was chosen for this investigation because of its unspoiled nature. This is a relative term, however, and on Long Island, with its high population density, it is unlikely that any bay or inlet has escaped some form of dredging operation.

There have been a number of private drag-line dredgings in Goose Creek reported by local residents. The earliest incident described was a dredging operation along channel A in 1930; a 1904 map of the region reveals, however, that the general contours of the bay remained unchanged.

The first officially recorded dredging in the environs of Goose Creek performed by Suffolk County occurred in November, 1959. A channel approximately 500 m long and 30 m wide was dredged from the bridge east by southeast into Southold Bay as an aid to small boat navigation. The depth of the channel was increased from approximately 0.5 m to 3 m mean depth below mean low water, and 35,653 m^3 of spoil were placed along the southeast shore of the inlet, covering 20,920 m^2 of *Spartina* marsh.

Another area, smaller in size, received some spoil from this dredging. It was contiguous with what was to become spoil area C.

The second dredging operation began on 27 June 1967 and ended on 2 August 1967. The effects of that operation are the subject of this investigation.

A channel 23 m wide by 825 m long was dredged from the bridge at the inlet to the bay in an easterly direction along Channel B. A total of 57,383 m^3 of spoil was removed and placed on spoil areas A, B, and C. Spoil area A covered approximately 6,000 m^2 of *Spartina* and *Phragmites* marsh adjacent to a previously used spoil area of approximately 26,000 m^2 covered to a maximum height of 3 m above mean low water. Spoil areas B and C in the southwest corner of Goose Creek covered 44,640 m^2 and 23,250 m^2 of *Spartina* marsh respectively.

A third dredging took place from 22 December 1967 to 12 April 1968. A 15.25–m wide channel was dredged to extend the previously constructed channel across the bay to the cut opening into the eastern shore. A small extension to an existing channel was also dredged through the center of Thyone Cove. The combined dimensions of these extensions were 427 m × 15.25 m and 8,508 m^3 of substratum were removed and placed on spoil area B.

During the spring and summer of 1970, drag-line operations in the northwest corner of Goose Creek obliterated 13,950 m^2 of *Spartina* marsh along a frontage of 152 m as site preparation for a housing development. This was part of the largest portion of the original peripheral marsh which remained after the dredging operations of 1967-1968. The only remaining marsh in Goose Creek at the time of this writing was an area approximately 16,000 m^2 bordering the north-western edge of the bay (see Figure 2).

Estimates of the areas of marsh covered by dredge spoil along the periphery of Goose Creek can be seen on Table 1.

An estimate of the remaining marsh in Goose Creek comes to 43,826 m^2 (islands) plus 23,715 m^2 (peripheral) or a total of 67,541 m^2. This is 31.4% of the total acreage covered by marsh in 1959. Excluding the islands, only 10.7% of the 1959 peripheral marsh remains. Examination of a map of the Goose Creek area drawn in 1904 reveals that the entire periphery of the bay was surrounded by extensive marshes. Probably less than

FIGURE 2.—Aerial photograph of Goose Creek, May 1972. Note straight edge of northwest shoreline (light area) caused by 1970 private dredge and landfill operation. Upper embayment is Jockey Creek. Note dredged channels in both bays and virtually complete eradication of marsh around Jockey Creek.

1% of the original Goose Creek marsh is still present.

METHODS AND MATERIALS

In order to determine what changes occurred in the macrobenthic population in Goose Creek, 23 stations were established in the bay, exclusive of the area to be dredged for the deepened channel. Fifteen additional stations were located at 30 m intervals in the path of the proposed channel.

The present study was initiated 1 yr before the scheduled dredging operation. Since a complete characterization of Goose Creek was necessary before the onset of dredging, it was deemed necessary to use a sampling procedure which could cover the whole of Goose Creek once every month. As the western half of the bay is uniform in bottom composition, being composed of deep, gray-black silt over muddy gray sand, there is little need to sample it as extensively as the eastern half of the bay, which is characterized by frequent changes in sediment type caused by variegated current flow patterns and topographic variability. Faunistic distribution was found to be dependent on the nature of the sediment, whose characteristics were, in turn, dependent on the erosion and deposition rates of the overlying tidal currents. Consequently, it was decided to divide the bay into zones of high, medium, and low current velocities, sampling each region by

TABLE 1.—Dimensions of known dredging operations in Goose Creek.

Dredged area	Spoil area	Area covered	Amount of spoil
Navigation channel in Southold Bay to bridge.	Edge of Southold Bay on either side of inlet to Goose Creek.	20,920m²	35,653m³
June-August 1967 dredging of channel through Goose Creek.	Spoil areas A, B, and C.	73,842m²	57,383m³
Dec. 1967-April 1968 dredging of spur channel to western shore, plus navigational channel through Thyone Cove.	Spoil area B.	Included above.	8,508m³
Spring-summer, 1970 private drag-line operation in NW corner of Goose Creek.	Northwest edge	ca. 13,950m²	Unknown
Totals		108,712m²	101,544m³

means of transects across the zone. In addition, a number of intertidal stations were set up, and a "characterization" survey was embarked on which sampled the intertidal area 2 m from shore and the sublittoral 6 m from shore every 30 m around the periphery of the bay. Using data from the preliminary surveys, sampling stations were established as representative of major substratum categories in Goose Creek. The advantages of placing greater sampling emphasis on certain areas rather than randomly sampling or using established as representative of major substratum (1967), Stickney and Stringer (1957), and Lee (1944).

Figure 3 indicates the positions of the stations in Goose Creek.

Each station was sampled with a "suction-corer" (Kaplan, Welker, and Kraus, In press-a) once a month for 9 mo preceding dredging and 11 mo after dredging terminated. A small shallow-draft vessel was propelled to the stations by an outboard motor. Locations were fixed by triangulation.

Once the vessel was located over a station, "spuds" consisting of 7.62 cm OD galvanized pipes were lowered fore and aft to keep the barge from swinging with current or wind. The sampler consisted of a chamber 36 cm in diameter by 30 cm high from which extended a hydraulic hose leading to a 3 hp pump on the deck of the barge. The corer was then lowered through a hole in the center of the deck until it reached the bottom. The pump was started and the water was withdrawn from the coring chamber. The evacuated chamber had negative pressure relative to the water column above it; this pushed it into the bottom. In practice depth of penetration varied, but a sample was not considered adequate unless the chamber had penetrated to a minimum depth of 20 cm. After maximum penetration the chamber was inverted by means of a winch and the sample was hauled to the deck where it was emptied onto a 60 cm × 90 cm sieve of 1.4 mm mesh size and washed. The screenings were placed in gallon bottles and formaldehyde was added to a concentration of 10%.

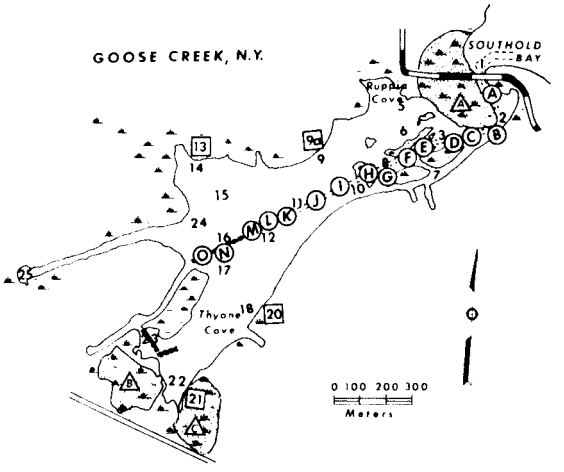

FIGURE 3.—Location of stations, Goose Creek. Letters in circles represent channel stations; letters in squares represent intertidal stations; letters in triangles represent spoil areas. Shaded extension of channel represents 1968 dredging.

Holme (1953) and Reish (1959) established that 1.5 mm and 1.4 mm mesh sieves recovered 90% of the biomass from their samples, respectively. In view of the importance of large forms in the Goose Creek species composition, it is likely that the 10% potential error described by Reish and Holme is a conservative estimate. Since the purpose of this investigation required an accurate estimate of total standing crop, with special emphasis on such commercially important species as *Mercenaria* and *Mya*, no attempt was made to separate the "large" and "small" forms by using an arbitrary cut-off point, as the 0.2 g of Sanders (1956). Thirty-eight stations and the once-a-month sampling schedule produced over 400 separate samples; this large *N* helped compensate for statistical inaccuracies introduced by the presence of large forms.

After a minimum of 1 yr of storage the specimens were identified, weighed (blotted wet weight), and dried at 40°C until uniform dry weight was obtained. Pelecypods were shelled, but crustaceans did not have their carapaces removed, since many were too small for this procedure to be performed with precision. Instead the major weight factor of the shells, the carbonates, was substantially removed by the acidic action of the unbuffered formaldehyde. The use of an acidic medium to remove carbonates was employed by Sanders (1956), Holme (1953), and others.

The data were expressed as number of organisms/wet weight/dry weight (biomass) per m^2 of substratum, including all animals recovered, according to the recommendation of Lee (1944).

RESULTS

Hydrography of Goose Creek

The hydrographic data recorded below were obtained from the reports of Hair (1968), Fazio (1969), and Black (pers. comm.). Salinity was measured by a portable Beckman salinometer (Model RS 5-3),[4] dissolved oxygen and temperature readings were taken with a portable oxygen meter (Electronic Instruments Ltd. Model 15 A) and pH was determined with a portable Orion Instruments Specific Ion Meter (Model 401). Light penetration was measured by a Secchi disc.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Water Temperature

Average daily temperatures ranged from 25.5°C to 0.5°C in the bay in 1967-68. The lowest individual reading was −1.5°C on 11 January 1968 and the highest 29.0°C on 7 July 1967. In January, February, and March, the bay was often covered by ice.

Salinity

Maximum salinity values occurred in mid-July to mid-October with a 1966-1968 high of 30.12‰. Low salinities occurred from mid-January to mid-April, with the 1966-68 low of 18.38‰ recorded on 28 March 1968.

Mean 1966-67 salinity in the bay proper (excluding the relatively less saline cut extending from the west shore) was 28.37‰.

pH

Average daily pH in Goose Creek ranged from 7.1 to 8.3 (excluding the somewhat more variable western cut) in 1967 and 7.7-8.2 in 1966. The highest individual value in 1967 was 8.6, occurring during a phytoplankton bloom in Thyone Cove, on 27 July 1967. The highest individual value for 1966 was 9.0 during a dinoflagellate bloom.

Light Penetration

Secchi disc readings were taken at weekly intervals throughout the duration of the study. In the bay itself the photic zone usually reached to the bottom, since the total water column was never more than 3.5 m. Virtually the entire bay could be considered euphotic except during the month in which the dredging took place, July 1967, when the minimum light penetration as recorded by the Secchi disc was 0.4 m (Fazio, 1969). It appears, then, that light penetration values were not substantially affected by the introduction of suspended materials into the water as the result of dredging. This is not surprising in view of the shallow nature and relatively rapid flushing time of the region of the bay most severely affected by the dredging, the eastern half. On the other hand, deposition of a canopy of flocculent material on the leaves of the *Ruppia* and the thalli of the *Enteromorpha* was observed during and after the dredging process.

This factor almost certainly reduced available light to the plants despite the relative clarity of the water.

Current Velocity

Readings of current velocities were taken on 9 June 1967, before dredging, and on 19 July 1968, after the new channel was completed. Attempts were made to match the tide height and wind direction and velocity on both occasions so as to minimize variables related to natural fluctuations of water level and current velocity. During both readings the wind was from the southwest and differences in wind velocity between the two days were not greater than 10 mph. The wind velocity was slightly higher during the post-dredging series (7 mph vs 15 mph) as was the tidal range (70 cm vs 73 cm). These factors would tend to increase the velocity of the flood tide rather than decrease it. Since current velocities decreased, this effect cannot be attributed to the influences of wind and/or tide.

The bridge readings were made with an Ekman current meter at 20 min intervals, 0.5 m beneath the surface and 0.5 m above the bottom of the channel. The meter was allowed to run for 120 sec and the readings were converted into centimeters per second according to the standard formula.

The readings in the channels were taken with Price meters on hand-held rods. The meters were set at 0.5 m above the bottom. Maximum depth of water at any station was approximately 1.2 m so that lamination or stratification according to current velocity was minimized. Maximum intervals between readings at the same station were less than 30 min.

The data consisted of the number of revolutions of the wheel during a 70 sec interval converted into centimeters per second from a nomograph calibrated to each meter. One replication of each measurement was taken as a check on the accuracy of the meters.

Table 2 and Figure 4b compare current velocities before and after dredging. Figure 4a indicates the current velocity sampling stations.

Maximum current velocity before dredging was through channel A. After dredging, the most westerly portion of channel A still has the maximum current velocity, but approximately 100 m east of the point of trifurcation at stations 4 and

TABLE 2.—A comparison of current velocities at flood tide in Goose Creek, before and after dredging.

Station	Before (cm/sec)	After (cm/sec)	Difference (cm/sec)
1	56.7	25.8	−30.9
7	41.4	13.1	−28.3
6	40.2	7.2	−33.0
2	55.2	25.2	30.0
[1]3	43.9	2.6	−41.3
4	23.2	13.1	−10.1
5	17.2	18.0	+ 0.8
1D	28.8	NA	NA
2D	38.4	5.5	−32.9
3D	12.1	2.7	− 9.4
4D	Neg (0)	5.5	+ 5.5
5D	Neg (0)	4.8	+ 4.8
Bridge	92.0	47.2	[2]−44.8
Bridge	83.8	39.6	[3]−44.2

[1]Station 3 was a sand bar with a thin, rapid flow. The water was never more than 30 cm deep over this bar. It was removed by the dredging operation and replaced by a 2.1 m deep channel.
[2]Maximum surface velocity.
[3]Maximum bottom velocity.

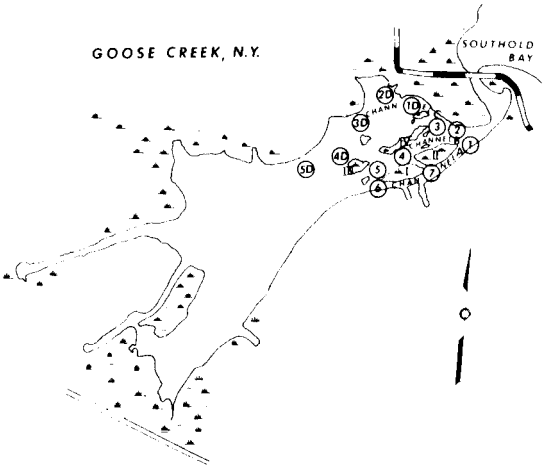

FIGURE 4 a.—Map of current velocity sampling stations.

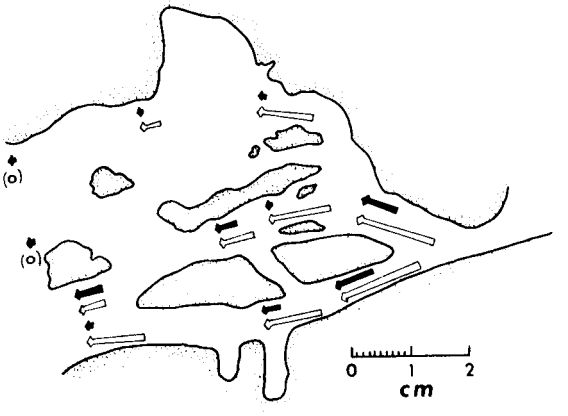

FIGURE 4 b.—Map of current velocity differences before (open arrows) and after (solid arrows) dredging. Each millimeter represents 4 cm/sec current velocity.

7, the current velocities in channels A and B were matched at 13.1 cm/sec. Thereafter, the postdredging velocity in channel B was greater than in channel A, i.e., 18.0 cm/sec at station 5 and 7.2 cm/sec at station 6. Thus, maximum flow was changed from channel A to channel B as a result of the dredging.

Channel B was converted from a shallow, wide passage with maximum surface area in contact with the current (hence maximum friction and impedance of water flow) to a deep channel, whose depths at mean low water before and after dredging were 0.4 m and 2.1 m at the entrance.

The substratum of channel A was gravel and sand at the most westerly end, changing to sand for most of the length of the channel as it passed islands I and II, after which it gradually became muddy sand. Near Thyone Cove only the shoreline and 3 m of littoral remained muddy sand; below this level the substratum was gray sand covered by 2 cm of silt.

As indicated earlier, channel B had a lower velocity before dredging than channel A. The transitional area was compressed in channel B; the area of sand at the westerly end merged rapidly into muddy sand, then silt, a short distance past the easterly end of island I.

Channel C, both pre- and postdredging, was characterized by an initial high velocity (55.17 cm/sec at station 2 and 38.40 cm/sec at station 2D), but this rapidly dissipated over the sand flats and eddies north of islands III and IV.

Maximum surface and bottom velocity was halved after dredging at the inlet to the bay. This, of course, would have a most profound influence on transport of materials, since it represented a section of water approximately 22 m wide by 2.8 m deep. Since the original mean depth of the channel was approximately 1 m, the cross section of the dredged channel was approximately three times greater than the original channel, increasing its volume commensurately.

Isaac (1965) stated that current velocities of 0.6 to 1.3 ft/sec (18.29 to 39.62 cm/sec) are sufficient to resuspend bottom deposits with 1.0 mm particle diameter. According to changes in current velocity at Goose Creek, the deposition of such particles would have taken place at the following stations after dredging, although not before dredging: station 7 (41.4 to 13.1 cm/sec), station 6 (40.2 to 7.2 cm/sec), station 3 (43.9 to 2.6 cm/sec), station 4 (23.2 to 13.1 cm/sec) and station 2D (38.4 to 5.5 cm/sec).

Mass Movement of Water

Hair (1968) calculated the volume of water moving in and out of Goose Creek during each phase of the tidal cycle. Assuming the average depth to be 1.3 m at high tide with a tidal range of 0.8 m and an area of $2.59 \times 10^5 m^2$, he calculated the volume of the bay at high tide to be $3.88 \times 10^5 m^3$. At low tide the corresponding calculation was $1.44 \times 10^5 m^3$. The volume lost at each falling tide would then represent approximately 60% of the volume at high tide. Fazio (1969) recalculated the tidal exchange on the basis of the increased volume of the bay caused by the construction of the dredged channel. His volumes were $7 \times 10^5 m^3$ at high tide and $3.1 \times 10^5 m^3$ at low tide. This represents a loss of 66% at each ebb and is considered by Fazio as a corroboration of Hair's calculations.

Of importance in any consideration of the benthos in Goose Creek is the fact that during the 6 h of ebb tide roughly 60% to 66% of the total volume of water in Goose Creek (approximately $2 \times 10^5 m^3$ before dredging and $4 \times 10^5 m^3$ after dredging) flowed out of the bay. All of this water passed through channels A, B, and C which, at a maximum value of 23 m wide and 3.0 m deep for channel B and 30 m × 1.5 m for the combined channels A and C, represents a total cross-sectional volume of 114 m^3 for the passage of ca. $3.9 \times 10^5 m^3$ of water. The relatively small volume of channels A, B, and C and the 244 m channel formed by their confluence and flowing eastward into Southold Bay accounts for the rapid current velocity in the eastern half of Goose Creek.

On 21 May 1966, an attempt was made to determine the proportion of water exchanged in various parts of the bay. Rhodamine B was released into the easternmost portion of Goose Creek (near the bridge) on an incoming tide, so that the average dilution was approximately 27 ppm after 2 h over the entire surface area of the bay. Six weeks later the readings on the fluorometer revealed values of the order of 1.7 ppm in most of the eastern half of the bay while Thyone Cove and the western shore of Goose Creek had readings as high as 9.6 ppm and lows rarely below 6.3 ppm.

Figure 5 demonstrates that the exchange of water, as revealed by residues of Rhodamine B, was greater in the eastern half of the bay, with areas of Thyone Cove and the west shore having

maximum values for the dye and, therefore, a comparatively low exchange rate.

Dissolved Nutrients

Fazio (1969) and Hair (1968) studied the distribution of certain nutrients in Goose Creek before and after the dredging operation. The results of their investigations are summarized in Table 3 and fluctuations in pre- and post-dredging concentrations of chlorophyll *a*, silicate, dissolved organic phosphate, and nitrite are depicted in Figure 6.

Fazio reported that there were significant changes in the values of particulate phosphorus, silicates, and chlorophyll *a* as a result of the dredging. He demonstrates high correlations between particulate phosphorus and chlorophyll *a* ($r = 0.83$), but is unwilling to suggest a direct relationship between this nutrient and phytoplankton productivity.

Instead, he explains the congruent increases in particulate phosphates and chlorophyll *a* as either a suspension of living benthic organisms introduced into the water by the disturbance of the sediment, or resuspension of detrital material and/or land runoff. Analysis of the water near a leaking spoil area revealed great amounts of particulate phosphorus and chlorophyll *a* were being added to the water column.

The distribution of silicates was shown to be related to the dredging process since highest readings were associated with stations in the vicinity of the dredge pipe and spoil areas; these high readings shifted down the bay following the movements of the dredge. There was, however, a low positive correlation between silicates and chlorophyll. Coupling high concentrations of chlorophyll *a* with extreme turbidity and very low light penetration in the vicinity of the dredge, Fazio (1969) concludes that the chlorophyll is not necessarily an indicator of the presence of phytoplankton, since the opacity of the sediment-laden water would prevent photosynthesis and limit phytoplankton production. Instead, he suggests that plant detritus in the spoil runoff is the main source of the high chlorophyll *a* readings and that phytoplankton populations might be very low.

Examination of Figure 6 reveals a second high in chlorophyll *a* readings in December 1967-January 1968. This corresponds with a second dredging which occurred from 22 December 1967 to 12 April 1968 in the western quarter of the bay. The picture is very much like that of the first dredging. A similar peak chlorophyll *a* reading occurred at the onset of dredging followed by a sustained high yield throughout the late winter and early spring. Mean chlorophyll *a* readings for the months of December 1967 to June 1968 are consistently two to five times those of the comparable 1966-1967 period. Resolution of the problem of whether the chlorophyll readings represent an increase in phytoplankton or are artifacts resulting from runoff will be decided when Cassin publishes his analysis of the phytoplankton cycle 1967-1968.

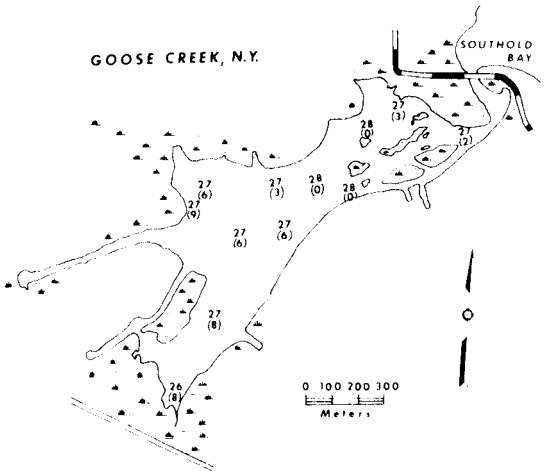

FIGURE 5.—Rhodamine B residues in ppm on day of administration and after 6 weeks. Figures in parentheses represent the later readings. (Drawn from data from Black, pers. comm.)

TABLE 3.—The fluctuations in certain dissolved and particulate nutrients in Goose Creek, 1966-1968.

Nutrients	Mean concentration 1966 (Hair)	Mean concentration 1967 (Fazio)
Dissolved inorganic phosphorus	0.81 μg at. P/liter	0.86 μg at. P/liter
Nitrates	2.8 μg at. NO_3-N/liter	3.5 μg at. NO_3-N/liter
Silicates	July-Aug. values between 8 and 16 μg at. Si/liter	July-Aug. dredging period values between 30 and 35 μg at. Si/liter. Variable from station to station according to proximity to dredge.
Particulate phosphorus	Mean of 8 readings 6/16-7/18, 1966 4.94 μg at. P/liter	Mean of 8 readings 7/5-8/7, 1967 18.30 μg at. P/liter

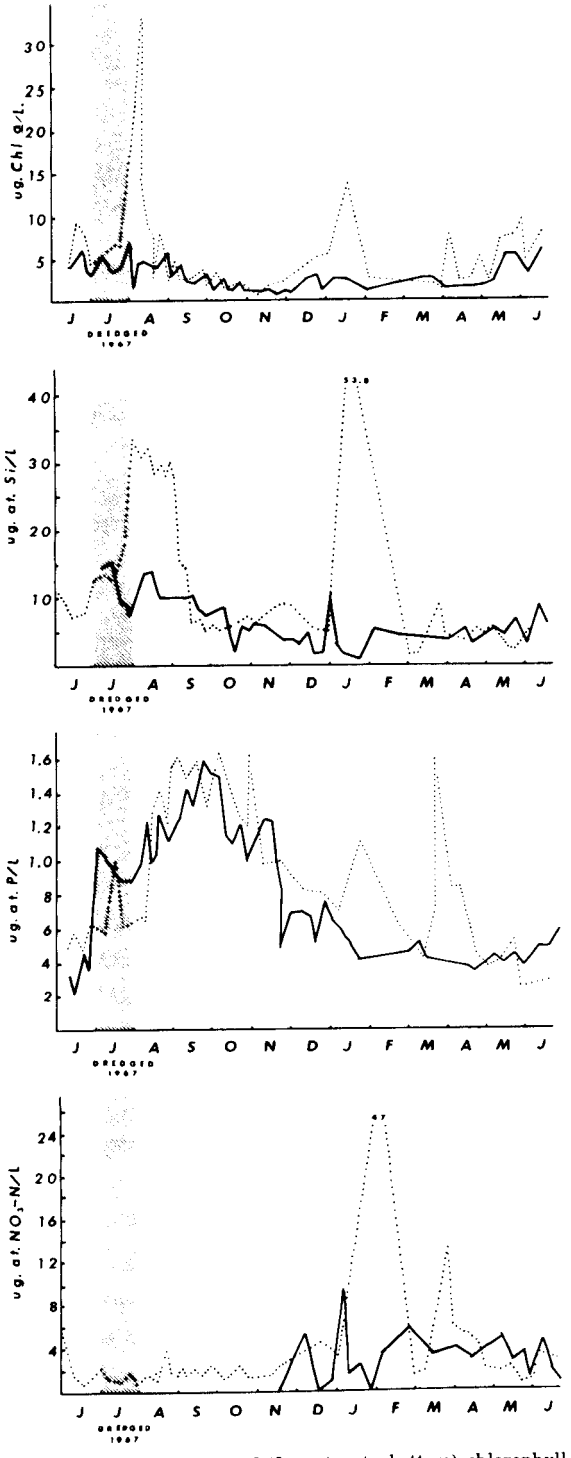

FIGURE 6.—Fluctuations of (from top to bottom) chlorophyll *a*, silicates, dissolved inorganic phosphates, and nitrites in Goose Creek, 1966-1968. (Redrawn from Hair, 1968; Fazio 1969.) Solid line represents 1966-1967 data; dotted line represents 1967-1968 data.

In general, the results of the Goose Creek nutrient studies are similar to those carried on in Chesapeake Bay by Flemer (1970) and Biggs (1968). Particulate phosphates, silicates, and chlorophyll *a* increased significantly. Concentrations of nitrates, nitrites, and dissolved organic and inorganic phosphates were not appreciably different before and after dredging.

Copeland and Dickens (1969) report that in Maryland, Texas, and South Carolina there was an initial diminution of phytoplankton productivity due to shading and a later enhancement due to resuspension of nutrients from dredge spoil. Flemer (1970) indicates that he found no demonstrable effect of the deposition of fine sediments from dredging on the production of phytoplankton in Chesapeake Bay.

There is no evidence that the release of nutrients from dredging produces an effect similar to that described by Raymont (1947, 1949) where the addition of fertilizer to small, enclosed embayments raised the level of benthic productivity up to 300% by stimulating production of phytoplankton.

Mechanical Analysis of the Sediment

Sanders (1956) points out the great variability in establishing criteria for the differentiation of particles constituting the sediment. He expressed the composition of the sediment in terms of the proportion of the particular component which was either most predominant or most relevant to the point he was making (e.g., *Mulinia lateralis* is either absent or present in low numbers when the proportion of silt-clay in the sample is greater than 40%). In the present study the samples were sieved and the lighter fractions analyzed by pipetting. Phi values were calculated and eight fractions recorded, one for sand (up to a maximum phi coefficient of 4.0), six for the various fractions of silt (phi = 4.5-8.0) and one for clay (phi = 9.0 and beyond). Data are recorded in percent sand, silt, and clay to conform with common practice.

Three sets of sediment samples were obtained during the course of the study. A preliminary survey was performed in September 1966, using a 1 m Phleger corer at each of the permanent sampling stations. Figure 7 delineates the sediment facies distribution compiled during this survey. Also found on this map are the stations

for the second survey (triangles) taken just before the dredging in June 1967, and the post-dredging survey (circles) in July 1968, 1 yr after dredging.

Table 4 reveals that 1 yr after dredging, sediments in those stations in the path of the dredge (3, 10b, 11, and 11a) contained less sand after dredging in the previously sandy, high current velocity stations (3, 10b) and more sand in the previously silty, low current velocity stations (11, 11a).

Station 10a, in channel A, experienced a reduction in its sand proportion and an increase in silt. This conforms to the hypothesis that the lowered current velocity in channel A, resulting from a shift in the main volume of water transport to channel B, would favor the settling of lighter particles in the post-dredging period. Similarly, station 5 in channel C increased in its silt and clay components.

Stations 16 and 17 were located in the west-central portion of the bay, south of the channel. Both stations maintained a constant proportion of sand. Station 17 exhibited a marked increase in silt and a decrease in the clay facies.

Stations 14 and 24 exhibited an increase in sand and a decrease in silt and clay. Since these stations were near the western shore in an area of negligible current flow, it is difficult to envision pronounced sediment transport brought about by normal tidal flow, even with the slightly enhanced exchange rate brought about by the deepening of channel B. It is possible that spring tides and strong easterly winds could have acted synergistically with the deepened channel to bring about this effect.

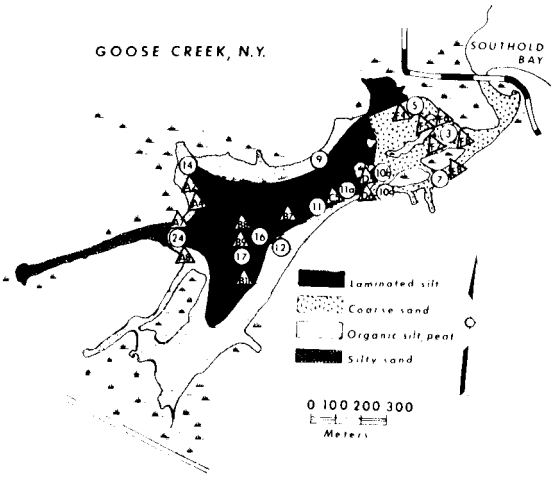

FIGURE 7.—Sediment facies and station locations, Goose Creek. Triangles represent pre-dredging stations, circles represent post-dredging stations.

The foregoing data must be viewed in conjunction with data on current velocities, wind-driven currents, etc., as further presumptive evidence of what appear to be permanent changes in the sediment transport patterns of Goose Creek brought about by current velocity modifications in the tidal channels.

The Effects of Wind-Driven Currents on Sediment Deposition

The importance of wind-driven water currents on the deposition of sediment in shallow-water estuarine situations has been emphasized by

TABLE 4.—Comparison of pre- and post-dredging sediment composition at selected stations, Goose Creek.

Pre-dredging				Post-dredging				
Station	%Sand	%Silt	%Clay	Station	%Sand	%Silt	%Clay	Comparison
F6	97	3% silt, clay						
F7	97	3% silt, clay		3	78	14	8	Less sand
F8	97	3% silt, clay						
F4	97	3% silt, clay						
F5	65	18	17	5	30	41	29	Less sand
E8	97	3% silt, clay		7	70	20	10	Less sand
D5	97	3% silt, clay		10b	91	8	1	Less sand
D6	97	3% silt, clay		10a	72	24	4	Less sand
C5	40	26	34	11a	75	17	8	More sand
B7	44	26	30	11	74	13	13	More sand
B8	48	28	24					
B9	49	18	33	16	49	29	22	No change
B11	34	34	32	17	35	64	1	More silt
A2	24	24	52					
A4	21	39	40	14	80	17	3	More sand
A7	37	44	19					
A8	55	12	33	24	62	28	10	More sand

TABLE 5.—Wind velocity recordings at or above 15 mph on days when there were two or more such recordings, 1967.[1]

Wind direction	Number of 3-hourly recordings
NE (10°-80°)	76
E (90°)	2
SE (100°-170°)	23
S (180°)	2
SW (190°-260°)	77
W (270°)	10
NW (280°-350°)	224
N (360°)	29

[1]Source: Local Climatological Data, 1967, John F. Kennedy Airport. U.S. Dep. Commer., Environ. Sci. Serv. Adm.-Environ. Data Serv. U.S. Gov. Print. Off., Wash., D.C.

Biggs (1968), Häntzschel (1939), Hellier and Kornicker (1962), and others.

In a shallow, almost completely enclosed embayment like Goose Creek, with a relatively broad exposure to prevailing winds, the effect of wind on the distribution of fine sediments becomes accentuated. Biggs (1968:481) states that "strong and persistent winds may cause high suspended sediment loads . . ."

The wind velocity data for Kennedy airport on Long Island were tabulated, and those days with two or more recordings of winds at 15 mph or above were compared. As can be seen from Table 5, the prevailing winds 15 mph and above come from the northwest on Long Island. Individual recordings from the northwest were more than ten times as common as those coming from the opposite direction, and at least three times more common than winds coming from any other quarter.

All other factors being equal, one would expect that the difference in mean wind velocity favoring the northwesterly prevailing winds would result in a net deposition of sediment in the southeastern region of the bay. Examination of Figure 1 reveals that this is the region where the channel opens to Southold Bay, the area of maximum tidal current velocity. This complex interaction of factors would probably result in an unusually high suspended sediment load in the incoming and outgoing tidal currents and the deposition of light particles carried by incoming tides in the southwestern margins of the bay.

This hypothesis is given substance by three sets of data: Hair (1968) and Fazio (1969) demonstrate that the transport of nutrients in Goose Creek was strongly influenced by wind-induced currents both before and after dredging. By drawing isopleths of NO_3 concentrations and relating them to wind direction and velocity, they were able to show that nitrate concentrations were responsive to both factors, with progressive diminutions of concentration across the bay in the direction of the wind source (see Figures 8 and 9).

Minimum wind velocity required to induce clear-cut distribution of particulate constituents was 5 mph according to Fazio. He also showed that a wind increase from 13 to 20 mph caused a resuspension of bottom material affecting concentrations of particulate phosphorus, chlorophyll a, dissolved inorganic phosphate, and nitrate.

Nuzzi (1969) shows a correlation between bacterial count and wind velocity in Goose Creek. He suggests that a critical wind velocity is

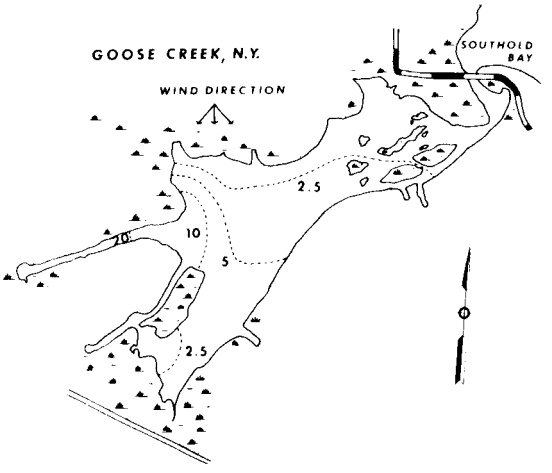

FIGURE 8.—Isopleths of NO_3 concentration in μg at. NO_3-N/liter, wind coming from the northern quarter. (Redrawn from Hair, 1968).

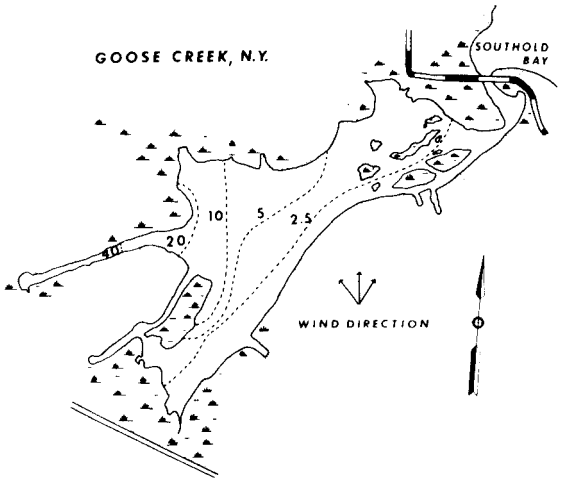

FIGURE 9.—Isopleths of NO_3 concentration in μg at. NO_3-N/liter, wind coming from the southern quarter. (Redrawn from Hair, 1968).

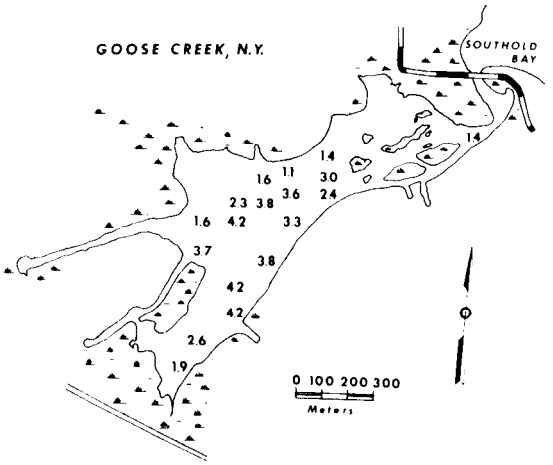

FIGURE 10.—Depths of sediment below mean low water in meters. Data taken from Suffolk County map dated 4/5/67.

necessary to overcome the inertia of the sediment particles as well as associated bacteria.

Further substantiation of the hypothesis that sediment distribution in Goose Creek was affected by wind-driven currents can be obtained from an examination of Figure 10. Depth of the sediment increases in a north-south direction, irrespective of the probable contour of the basin.

Table 6 tabulates the number of 3-hourly records of winds at or above 15 mph for 1967.

Suspension of fine sediments during dredging occurred during the months of least occurrence of high winds (July-August). The absence of strong winds would tend to minimize the distribution of suspended sediment but it also prevents the removal of the canopy of flocculent material observed covering the *Enteromorpha* and *Ruppia* stipes and leaves during and after dredging.

Flemer et al. (1968) suggest that late fall is the season which would be most desirable for dredging, since benthic animal populations are lowest then. On the other hand, the months of November and December are characterized by frequent windy days and any disturbance of the sediment would be accentuated by wind-driven currents. Saila, Polgar, and Rogers (1968) describe summer surface and bottom current patterns which caused maximum harmful effects of dumped dredged sediment. Such factors as water depth, contour of basin, and wind- and water-driven currents must be studied further to determine the optimal season for dredging.

Mercenaria Survey

Mercenaria mercenaria is exploited commercially in Goose Creek and it supports a substantial sport fishery. Both before and after dredging, from two to four commercial clammers regularly visited the creek. In 1968, less than a year after the dredging, two clammers were interviewed regarding changes in the productivity of clams over the interval of the dredging operation. They reported that there was no substantial difference in the size of their catch which, according to the local conservation officer, was 4-5 bushels of clams per day.

Apparently there was no mass mortality of clams resulting from the release of flocculent and suspended material into the water as a result of dredging.

Four major clam producing areas of the bay were sampled before and after dredging, on 8 July 1967 and 4 July 1968 (dredging was completed on 2 August 1967 (see Figure 11)).

TABLE 6.—Number of days of at least two recordings of winds over 15 mph by months (recordings taken at 3 h intervals), 1967.

Month	Number of days	Month	Number of days
January	7	July	1
February	13	August	1
March	9	September	13
April	17	October	5
May	18	November	13
June	10	December	11

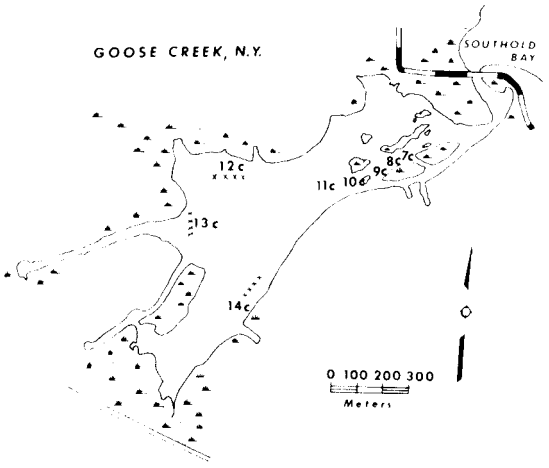

FIGURE 11.—Map of stations, *Mercenaria* study.

A 3.35 m² square frame was placed on the substratum and a skin diver sampled the area by hand, removing all clams. These were sorted as to size in the following categories: up to 1.90 cm; 1.90-3.80 cm; 3.81-5.70 cm; 5.71-8.90 +cm.

The areas sampled were channel B (destined to be the region of the newly dredged channel) and the three major clamming areas used by local residents. Stations 7c to 11c were 30 m apart running east to west down channel B. Stations 12c, 13c, and 14c were located on the north, west, and south shores of the bay respectively.

Each station in channel B comprised two sampling areas, one 1.5 m from shore and the other in midchannel or about 9 m from shore.

Each station in the clam beds used by local residents (stations 12c, 13c, 14c) comprised four sampling areas beginning 6 m from the shoreline at the east end of the bed and progressing westerly at 6-m intervals. The total area sampled was 33.5 m² in the channel and 39.25 m² on the clam beds (total 72.75 m²).

The data obtained on the pre- and post-dredging surveys are compared in Table 7.

Clams in Goose Creek not directly exposed to mechanical disturbance by the dredge (such as clam beds at stations 12c and 13c) were able to survive the dredging process itself, even though they were located within 400 m of the channel (see Table 7). The considerable reduction in the size of the clam populations at stations 12c and 13c suggests that some mortality-inducing factor was at work.

The effects of the mechanical removal of the clams by the dredge are obvious. Whether or not finding a few clams in the post-dredging survey at stations 10c and 11c means that there are signs of recovery in the population remains to be seen.

No evaluation of the long-term effects of changes in the environment has been attempted. These include processes such as the gradual incursion of silt towards the mouth of the bay due to lowered current velocity, factors affecting productivity such as a reduction of the quantity of organic materials introduced into the water as the *Spartina* marshes were covered with spoil, and an increase in pollutants as the population density of humans along the periphery of the bay increased.

Changes in Land Usage Patterns

At the inception of the study (1966) most of the periphery of Goose Creek was composed of *Spartina* and *Phragmites* marshes, except for the south shore and a neck of land on the southeastern corner which were developed with summer homes.

On a map of the area drawn in 1954, 41 homes are recorded bordering the bay. The total number of houses within 300 m of the bay was 114. At the present writing most of the previously undeveloped north shore of the bay is undergoing intensive development of houses used year round.

An aerial photograph taken in 1972 (Figure 2) revealed 223 houses within 300 m of the bay, an increase of 94%. All of the houses along the shore of Goose Creek were built on spoil taken from public or private dredging operations. All homes have cesspools.

Smith (pers. comm.) introduced Rhodamine B into a toilet in one of the homes bordering Goose Creek. In four weeks detectable quantities were found in the bay waters. Nuzzi (1969) speculates that human fecal coliform bacteria (as identified by elevated temperature incubation) were released into Goose Creek from the septic tanks of the surrounding homes. Maximum coliform counts in his 1966-1968 study were 918 MPN (most probable number)/100 ml.

The maximum federal permissible level for waters from which shellfish are taken is a median of 15 readings not exceeding 70 MPN/100 ml, or 10% of 15 readings above 230 MPN/100 ml (Houser, 1965). Individual readings above 230 MPN/100 ml were recorded throughout the period December-March 1967, at one station, and three

TABLE 7.—A comparison of *Mercenaria* populations in four selected areas of Goose Creek before and after dredging.

	Number of clams							
	Before dredging (7/8/67)				After dredging (7/4/68)			
Station	Inshore		Mid-Channel		Inshore		Mid-Channel	
7C	1.9 cm	5	1.9-3.80 cm	9				
	1.9-3.80 cm	8						
		13		9		0		0
8C	1.9 cm	4	3.8-5.7 cm	17				
	1.9-3.8 cm	18						
	3.8-5.7 cm	16						
		38		17		0		0
9C	1.9-3.8 cm	31	1.9-3.8 cm	14				
	3.8-5.7 cm	3						
		34		14		0		0
10C	1.9-3.8 cm	2	to 1.9 cm	2	1.9-3.8 cm	1		
	3.8-5.7 cm	5	3.8-5.7 cm	9				
		7	5.7-8.9 cm	2				
				13		1		0
11C	1.9-3.8 cm	2	0.75-1.50 cm	3	to 1.9 cm	3	to 1.9 cm	1
			1.50-2.25 cm	6				
		2		9		3		1
12C	Station A		Station B		Station A		Station B	
	1.9-3.8 cm	29	to 1.9 cm	12	to 1.9 cm	8	to 1.9 cm	8
			1.9-3.8 cm	11	1.9-3.8 cm	7	1.9-3.8 cm	3
		29		23		15		11
	Station C		Station D		Station C		Station D	
	to 1.9 cm	16	to 1.9 cm	7	to 1.9 cm	5	to 1.9 cm	3
	1.9-3.8 cm	14	1.9-3.8 cm	12	1.9-3.8 cm	1	1.9-3.8 cm	3
	3.8-5.7 cm				3.8-5.7 cm	1		
		30		19		7		6
	Average number of clams per m² = 7.5				**Average number of clams per m² = 2.9**			
13C	Station A		Station B		Station A		Station B	
	5.71-8.9 cm	27	3.8-5.7 cm	18		0		0
			5.7-8.9 cm	10				
		27		28		0		0
	Station C		Station D		Station C		Station D	
	1.9-3.8 cm	22	3.8-5.7 cm	8	1.9-3.8 cm	3		0
	5.7-8.9 cm	9	5.7-8.9 cm	11	3.8-5.7 cm	1		
		31		19		4		0
	Average number of clams per m² = 7.8				**Average number of clams per m² = 0.3**			
14C	Station A		Station B		Station A		Station B	
	5.71-8.9 cm	44	3.8-5.7 cm	17	na.		na.	
			5.7-8.9 cm	20				
		44		37				
	Station C		Station D		Station C		Station D	
	1.9-3.8 cm	24	5.7-8.9 cm	47	na.		na.	
	3.8-5.7 cm	6						
	5.71-8.9 cm	17						
		47		47				
	Average number of clams per m² = 12.1				**Average number of clams per m² = na.**			

times at another, with levels of 542, 918, and 348 MPN/100 ml. These readings appear to exceed the 10% limit mentioned above and may be sufficient grounds for closing the bay to clamming. The densities of presumptive human fecal coliforms found by Nuzzi correlated with increases in human population size, suggesting that the increase in number of homes around the periphery of the bay during the 1968-1972 will further increase the contamination of clams beyond acceptable sanitary standards.

ANALYSIS OF THE EFFECTS OF DREDGING ON MACROBENTHIC ANIMAL POPULATIONS

Dry weights from 263, 0.1 m² samples collected from the bottom of Goose Creek over 22 mo were compared by means of analysis of variance. In addition, chi-square analyses were performed to determine whether or not significant differences existed between pre- and post-dredging populations in number of individuals and species. All

TABLE 8.—Analyses of variance of pre- and post-dredging dry weights and between stations, in the bay and dredged channel.

Source	Sum of squares	Degrees of freedom	Mean squares (variance)	F test	Probability
Stations before and after dredging	158.387	1	158.387	10.623	0.005
Variation between stations	492.212	22	22.373	1.501	Less than 0.05
Interaction of pre- and post-dredging and stations	311.698	22	14.168	0.950	Less than 0.05
STATIONS 2-25 PLUS A-J, M (CHANNEL)					
Stations before and after dredging	491.813	1	491.813	37.211	0.001
Variation between stations	691.024	33	20.940	1.584	Less than 0.05
Interaction of pre- and post-dredging and stations	635.301	33	19.252	1.457	Less than 0.05
STATIONS A-J, M (CHANNEL)					
Stations before and after dredging	341.885	1	341.885	127.426	0.001
Variation between stations	163.579	10	16.358	6.097	0.001
Interaction of pre- and post-dredging and stations	133.872	10	13.387	4.990	0.001

computations were performed on an RCA SPECTRA 70/46 computer.[5]

Two-way analyses of variance were performed on dry weights of the samples drawn from stations 2-25; 2-25 plus channel stations A-J, M; and channel stations A-J, M alone.

Table 8 reveals that pre- and post-dredging biomass varied significantly among stations 2-25, among all stations, and between each channel station. The variances in biomass between stations were not significant in the bay and combination of bay and channel, even though they represented a substantial spectrum of substrata and current velocities. Biomass variances were, however, significant in the channel alone. There was also no significance in the variances of the interaction between stations and dredging, except in the channel.

The macrobenthic biomass in Goose Creek had not returned to its pre-dredged level 11 mo after dredging.

In the channel substratum, which had a virtually linear reduction in particle size and current velocity progressing from east to west, there was significance in both station to station variance and in the interaction between stations and pre- and post-dredging variances. This demonstrates a systematic difference between stations, as well as a significant difference from station to station in the manner in which the animal populations responded to the dredging process.

A second two-way analysis of variance was performed on all three sets of data in an attempt to determine whether or not the variance in biomass was a function of sediment type. The sampling stations were classified according to the sediment map (Figure 7), with verification provided by visual analysis of samples from the suction corer. Table 9 lists the stations according to their sediment classification.

TABLE 9.—Classification of the Goose Creek sampling stations according to sediment type.

Sediment type	Stations
Sand	2, 3, 4, 9, 10 A, B, C, D
Muddy sand	6, 7, 8, 24 E, F, G
Sandy mud	11, 12, 18 H, I, J
Mud-silt	14, 15, 16, 17 22, 23, 25, K
Intertidal	9A, 13, 20, 21

[5]The authors are grateful for the assistance rendered by the Hofstra University academic computing facility, Eugene Ingoglia, Director; John Pizzeriella, Programmer; Claire Gittelman, Statistician.

Table 10 summarizes an analysis of variance of the biomass at the Goose Creek stations according to sediment type. Separate analyses were performed on the data for stations 2-25; 2-25 plus channel stations A-J, M; and channel stations A-J, M alone.

Significance was found in all three analyses only among dry weights before and after dredging. There was no significance in the variances among substratum types, nor among the interactions of substrata and pre- and post-dredging biomass. There was, then, no systematic effect of particular sediment types alone on the rate of recovery of the in- and epifauna, even in the channel.

A four-way analysis of variance was performed to examine the relationship between seasons and variances in biomass at each station, without considering pre- and post-dredging effects. Stations 2-18 were studied. The unrepresented stations are in the less saline western half of Goose Creek which was frozen over during January and February of both years. There were no significant differences in the seasonal variances among stations, indicating that seasonal fluctuations in biomass were not factors which accounted for the differences in biomass, heretofore attributed to the dredging operation. Table 11 summarizes the statistics for the analysis of variance according to seasons.

Another four-way analysis of variance was performed to examine the relationship between seasonal variances and substratum type for stations 2-25. Again, there was no significance in any of the interactions, indicating that variances in biomass are not a function of season, sediment type, or of an interaction between these factors. This analysis is summarized in Table 12.

It was expected that the channel would show substantial effects of the dredging process, since it was from the channel that massive quantities of substratum were removed. The sediment and its inhabitants were physically removed to a depth of 2 m. What is of greater importance is the evidence

TABLE 10.—Analyses of variance of pre- and post-dredging dry weights according to sediment type in the bay and channel.

Source	Sum of squares	Degrees of freedom	Mean squares (variance)	*F* test	Probability
STATIONS 2-25					
Stations before and after dredging	107.634	1	107.634	6.584	0.025
Sediment types	32.746	4	8.187	0.501	Less than 0.05
Interaction of stations and sediment types	62.912	4	15.728	0.962	
STATIONS 2-25 PLUS A-J, M (CHANNEL)					
Stations before and after dredging	206.841	1	206.841	13.899	0.001
Sediment types	42.489	4	10.622	0.714	Less than 0.05
Interaction of stations and sediment types	81.747	4	20.437	1.373	Less than 0.05
STATIONS A-J, M (CHANNEL)					
Stations before and after dredging	160.146	1	160.146	22.043	0.001
Sediment types	17.083	3	5.694	0.784	Less than 0.05
Interaction of stations and sediment types	22.863	3	7.621	1.049	Less than 0.05

TABLE 11.—Four-way analysis of variance of dry weights according to season, stations 2-18.

Source	Sum of squares	Degrees of freedom	Mean squares (variance)	*F* test	Probability
Seasonal variations	10.653	3	3.551	0.250	Less than 0.05
Stations	224.442	16	14.028	0.988	Less than 0.05
Interaction between seasons and stations	566.497	48	11.802	0.831	Less than 0.05

TABLE 12.—Four-way analysis of variance of dry weights according to season and sediment type.

Source	Sum of squares	Degrees of freedom	Mean squares (variance)	*F* test	Probability
Seasons	17.307	3	5.769	0.332	Less than 0.05
Sediments	18.002	4	4.500	0.259	Less than 0.05
Interaction between seasons and sediments	119.121	12	9.927	0.572	Less than 0.05

that the rest of Goose Creek, as represented by stations 2-25, also suffered a reduction in biomass from which recovery was not evident 11 mo after dredging.

Further evidence of the reduction in biomass after dredging can be found in Table 13, which is a comparison of dry weights at stations 2-25 in June 1967 and 1968, 1 mo before and 11 mo after dredging. Only one station of the 13 (station 11) for which comparative data exist had biomass in excess of the 1967 levels. The significance of any individual datum is not great, since the presence of an adult clam or sea cucumber could inordinately affect a particular station. The general trend, however, is clear; 12 out of 13 stations have substantial reductions in biomass. This reduction cannot be attributed to mechanical removal of sediment or specimens, and is attributed to the dredging process itself.

Chi-Square Analysis of Number of Species and Specimens

Chi-square analyses were performed to determine whether or not the number of species and individuals in the post-dredging series differed significantly from the pre-dredging population. Data were further analyzed to determine if substratum and seasonal variations affected species diversity and numbers of individuals. Table 14 represents the chi-square analysis of the number of species before and after dredging for the whole bay (minus the intertidal stations), the bay stations plus the channel stations, and the channel stations alone. In all cases the chi-square was significant, indicating that species number was affected by dredging. Since chi-square analysis is limited by its inability to discriminate between sign (+ or −), Table 15 tabulates the number of species found at stations 2-25 in June 1967, 1 mo before dredging, and in June 1968. A reduction in species number occurred at 75% of the stations after dredging, with three stations or 18.7% exhibiting small increases in species number.

A chi-square analysis was performed on the number of species according to sediment type (e.g., sand, muddy sand, mud-silt). The number of species altered significantly according to substratum after dredging, both in the bay as a whole and in the channel (see Table 16).

TABLE 13.—A comparison of dry weights from stations 2-25, June 1967 and June 1968 (in g).

Station	June 1967	June 1968
2	1.37	0.92
3	1.80	0.31
4	—	—
5	1.92	1.04
6	0.63	—
7	9.44	—
8	4.81	0.15
9	18.25	0.83
9A	0.55	—
10	1.07	0.07
11	0.30	1.64
12	5.86	1.82
13	—	—
14	0.00	—
15	7.68	0.00
16	8.77	0.71
17	2.70	0.41
18	1.41	1.08
20	—	—
21	—	—
22	9.47	0.01
23	—	0.005
24	16.13	—
25	0.00	—

TABLE 14.—Chi-square analyses of the number of species before and after dredging for stations 2-12, 14-19, 22, 23; stations 2-12, 14-19, 22, 23 plus channel stations A-J, M, and stations A-J, M alone.

Stations	Chi-square	Degrees of freedom	Level of significance
2-23	32.763	18	0.025
2-23, plus A-J, M	55.366	26	0.005
A-J, M	21.557	7	0.005

TABLE 15.—Number of species found at stations 2-12, 14-19, 22, 23 on June 1967 and June 1968.

Station	June 1967	June 1968
2	22	5
3	16	5
5	19	17
6	11	3 (4/68)
7	25	—
8	19	13
9	21	13
10	26	5
11	9	5
12	3	6
14	0	4 (4/68)
15	11	0
16	10	3
17	5	1
18	5	7
22	9	3
23	1	1

TABLE 16.—Chi-square analysis of the number of species before and after dredging, as a function of sediment type. Stations 2-25; 2-25 and A-J, M; channel stations A-J, M.

Stations	Chi-square	Degrees of freedom	Level of significance
2-25	8.43	3	0.05
2-25; A-J, M	21.41	3	0.005
A-J, M	38.24	3	0.005

TABLE 17.—Chi-square analyses of number of organisms before and after dredging, stations 2-21, 23; 2-21, 23 plus A-J, M; stations A-J, M only.

Stations	Chi-square	Degrees of freedom	Level of significance
2-25	6,075.22	20	0.005
2-25, A-J, M	6,364.59	29	0.005
A-J, M	152.84	8	0.005

TABLE 18.—Chi-square analysis of the number of organisms before and after dredging as a function of sediment type, stations 2-25; 2-25 plus A-J, M; stations A-J, M.

Stations	Chi-square	Degree of freedom	Level of significance
2-25	2,051.59	3	0.005
2-25, A-J, M	1,679.51	3	0.005
A-J, M	21.57	3	0.005

Similar chi-square analyses were performed using number of individuals at all stations. Here results were even more positive. For example, the pre-dredging number of specimens at station 2 was 6,682; the post-dredging number was 27. Five out of 30 stations, or 16.6%, showed post-dredging increases in population; the others experienced drastic decreases.

Table 17 is a summary of the chi-square analysis of the number of individuals before and after dredging. The difference in specimen numbers was highly significant in both the bay as a whole and in the channel.

Chi-square analyses were made on the number of specimens before and after dredging as a function of sediment type. In both the bay as a whole and the channel the number of specimens was significantly different (0.005) in the post-dredging samples, according to sediment types (Table 18).

In summary, the numbers of species and organisms differed significantly before and after dredging, in the bay as a whole, as well as in the channel. Additional data show that this difference was in the direction of a post-dredging reduction in both species diversity and number of individuals found at each station. A few stations showed apparent recovery by June 1968, 11 mo after dredging. These were invariably low-population stations in the mud-silt region of the bay, where a few influents could appreciably change the population size. Stations 2-11, the sand, muddy sand, sandy mud stations, had drastic reductions in both parameters. Table 19 provides further substantiation for this conclusion.

Standing Crop Estimates

A total of 137 species was taken from the sediment of Goose Creek during the 22 mo of the study. Maximum wet weight at any one station was 2,581.4 g/m^2, with a corresponding dry weight of 355.6 g/m^2. Mean dry weight before dredging (excluding the channel) was 36.8 g/m^2 (49.6 g/m^2 including the channel) while the corresponding weight after dredging was 12.7 g/m^2 (10.1 g/m^2 including the channel), a loss of 63% of dry weight. The loss, including the channel, was 79%. (Pfitzenmeyer, 1970, reported a loss of 64% in his spoil deposition area and 72% in the channel.)

The mean number of species per station (stations 2-24 minus the four intertidal stations) was 5.47 (54.7/m^2) before dredging and 4.02 (40.20/m^2) after dredging, a reduction of 26%.

The maximum number of specimens found at any one station was 3,521, of which 3,470 were the gastropod, *Crepidula fornicata* (station 2, October 1966). The mean number of specimens before dredging for stations 2-24 (minus the intertidal stations) was 120.14 (1201.4/m²), while the after-dredging mean was 25.63 (256.3/m²). This constitutes a 79% reduction in the number of specimens found at the post-dredging stations.[6]

Comparison With Other Areas

Direct comparisons between the standing crop estimates at Goose Creek and other areas is complicated by the diverse methods of obtaining these estimates used by workers in the field. As previously indicated, Holme (1953) and Sanders (1956, 1958) used HCl to remove the carbonates from the carapaces of crustaceans and both removed all specimens greater than 0.2 g dry weight from their samples. For reasons previously mentioned, it is important in this investigation to obtain data on the populations of the larger forms which dominate the communities of the shallow, estuarine study area being investigated. Variation in sieve mesh size between studies is also an important factor accounting for differences in infaunal biomass estimates, but Sanders (1956) attempted to compare numerical results of several investigations by plotting mesh size against the log of the number of animals per square meter. The lowest estimates were those obtained by Holme (1953) from the English Channel (160/m²) and Miyadi (1940, 1941a, 1941b) from Japanese bays (266-1,290/m²). Sanders' mean number of animals for Long Island Sound was 16,443/m², although 63% of his stations had fewer than 8,500 animals/m². The mean number of animals at Goose Creek (1,201.4/m²) is considerably lower than that obtained by Sanders, but it is unlikely that this parameter is the most useful in comparing areas since his *Ampelisca* and *Nepthys incisa-Yoldia limatula* communities contained relatively dense populations of small organisms, while at Goose Creek amphipods and protobranch pelecypods made up a very small proportion of the biomass.

[6]The data for the means of the stations (per 0.1 m² samples) were provided as a more accurate estimate of such quantities as species number, because extrapolations from 0.1 m² to 1.0 m² in the case of small numbers like 5.47 specimens/0.1 m² seem to introduce an inordinate amount of potential error.

TABLE 19.—The number of organisms found at each station before and after dredging, stations 2-25, A-J, M.

Station number	Before dredging	After dredging
2	6,682	27
3	1,499	188
5	466	330
6	266	41
7	566	266
8	342	95
9	153	56
9A	92	80
10	505	239
11	144	49
12	47	117
13	6	5
14	73	92
15	125	100
16	192	121
17	270	79
18	66	241
20	129	809
21	124	21
22	271	38
23	102	1
24	300	325
25	65	4
A	74	35
B	708	43
C	612	208
D	262	33
E	53	23
F	54	11
G	95	26
H	64	5
I	49	1
J	51	7
M	46	0

In a comparison of the dry weights of Long Island Sound with other areas, Sanders gives a figure for the mean total dry weight (including "large animals") of 54.627 g/m². This corresponds to a dry weight of only "small animals" of 15.88 g/m², a figure which is roughly twice as great as the highest mean value for the other areas discussed. Pfitzenmeyer (1970) performed a study closer in purpose to the present investigation than those described by Sanders. His pre-dredging mean dry weight (including large forms) was 0.90 g/m², while the immediate post-dredging mean was 0.67 g/m².

Holme's (1953) mean dry weight was 11.2 g/m², including "large" animals.

The figure obtained by Sanders for total dry weight are in good agreement with those computed for the present study, since the pre-dredging dry weight for Goose Creek was 36.83 g/m², while the Long Island Sound figure was 54.627 g/m². The substantial variance of these data from those of Holme (11.2 g/m²) and Pfitzenmeyer (0.90 g/m²) has been accounted for, in principle, by Sanders in his 1956 paper.

For data reported on the basis of the 0.2 g dry weight cut-off point, it is sufficient, in many cases, to add the factor suggested by Holme when he points out that 64.4% of the dry weight of his samples was excluded by the 0.2 g point, in order to bring the data to comparable levels.

Factors relevant in an explanation of the relatively high standing crop in Goose Creek are:

1. None of the studies referred to sampled to a depth beyond 22 cm, and most examined only the top 6-10 cm of sediment. Deeper-dwelling, large forms were excluded.

2. Virtually all of the investigations previously referred to examined relatively large, slow current velocity, deep bodies of water with relatively unvarying bottom sediments, such as Chesapeake Bay. Often the populations described comprise mud-silt or silt-clay communities, such as the *Ampelisca* community described by Stickney and Stringer (1957). It is well known that this sediment is not highly productive of biomass since most organisms are relegated to the upper few centimeters where gaseous exchange is most rapid (cf. Raymont, 1950; Sanders, 1956; Holme, 1953; Pfitzenmeyer, 1970). In Goose Creek the high current velocity over a substantial portion of the bay and the diversity of sediment types supported sizeable populations of large organisms, such as the 3,470 *C. fornicata* found in one dredge haul at station 2.

3. Phytoplankton production is high. Cassin (1968) studied the phytoplankton cycle in Goose Creek during the year before dredging, and found a mean standing crop of 1.64×10^6 cells/liter. This was lower than that for Long Island Sound (2.38×10^6 cells/liter; Conover, 1952), but considerably higher than those for Block Island Sound and Vineyard Sound. According to Riley (1955), the mean standing crop of phytoplankton in the English Channel is one-quarter that of Long Island Sound; while Flemer (1970) makes a primary production estimate for Upper Chesapeake Bay at one-fifth of that estimated by Riley for Long Island Sound. Phytoplankton population size appears to vary with benthic standing crop in the studies mentioned above.

Population Dynamics and Distribution of Organisms

Most of the dominant and subdominant organisms found in the channel before dredging were present in greatly reduced numbers after dredging (Kaplan, Welker, and Kraus, in press-b). Three species of mollusc increased in numbers after dredging. *Tellina agilis* and *Lyonsia hyalina* increased in sandy sediments while *Mulinia lateralis* became more abundant in the finer substrata. Two polychaetes, *Notomastus latericeus* and *Clymenella torquata*, abundant before dredging, virtually disappeared afterwards. O'Connor (1972) noted an increase in populations of *Mulinia lateralis* and *Tellina agilis* in his study of Moriches Bay. He suggests that *M. lateralis* is a fast-growing, short-lived species that is more successful in silt. If this is so, it may be suited as an indicator organism which would rapidly increase in numbers in areas where dredged channels cause decreased current velocity and, consequently, invasion of sandy areas by softer sediments.

The channel data were not duplicated in the bay as a whole. The most fundamental difference between the two areas was the fact that the substratum and all its infauna were removed in the channel study, while only stations 2 and 3 in the bay study were directly in the path of the dredge. Consequently, the drastic effects of the removal of the habitat were limited, and the reduced population size throughout the bay must be a concomitant of other long-term variables, such as changes in current velocity and anoxia resulting from siltation. Stations 22, 23, and 5 were particularly susceptible to this latter influence, being near spoil areas. Portions of Thyone Cove were inundated when the spoil gate broke during the dredging operation. In addition, station 23 was in the path of the 1968 dredging of an extension of the navigation channel through Thyone Cove.

Most stations, even those in the farthest reaches of the bay, showed reductions in benthic populations; however, no station was farther than 500 m from the dredge at some time during the operation, except for station 25. Figure 12 depicts the changes in population densities of 13 dominant and subdominant benthic organisms before and after dredging. In addition, the abscissa of each histogram represents the sediment type, from the gravel of station 2 to the silt of station 23.

Clymenella torquata, the nearly ubiquitous bamboo worm, was the numerical dominant in the sandy substrata, forming dense colonies. *Notomastus latericeus* shared this habitat, though in reduced numbers. Both species of worm

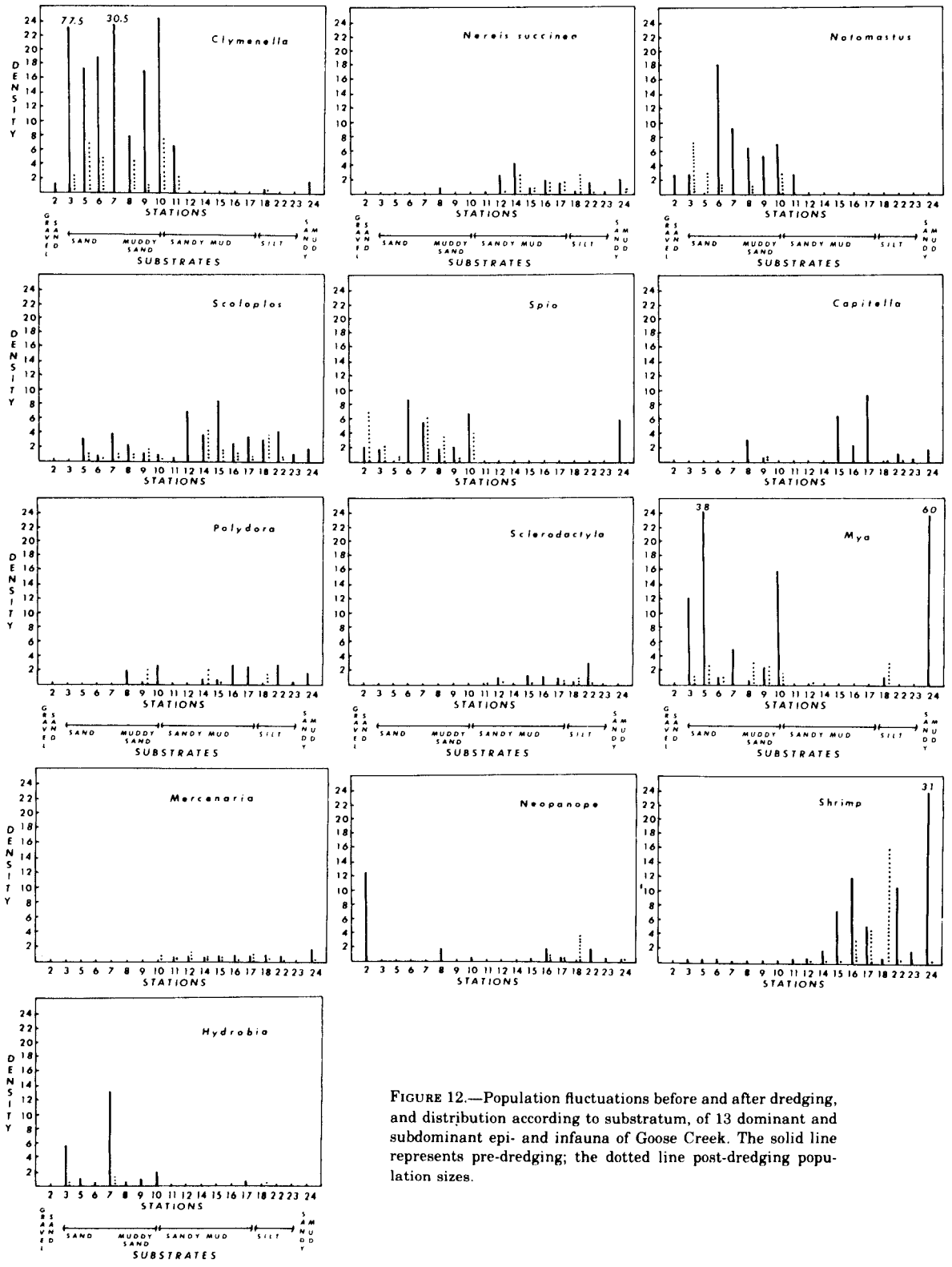

FIGURE 12.—Population fluctuations before and after dredging, and distribution according to substratum, of 13 dominant and subdominant epi- and infauna of Goose Creek. The solid line represents pre-dredging; the dotted line post-dredging population sizes.

showed substantial reductions in density in the post-dredging samples. *Spio setosa*, another inhabitant of sandy substrata, seems to have maintained its population size, with 50% of the stations recording increases in the number of specimens.[7]

Capitella capitata and *Polydora ligni*, inhabitants of sandy mud, also decreased in number. *Nereis areonodacea* was found in muddy sand in small numbers, while *Nereis succinea* was present in densities up to 42/m^2 in the sandy mud and silt stations, which were also frequented by *Mercenaria mercenaria*. Modest reductions in the *Nereis* and *Mercenaria* populations occurred after dredging.

Mya arenaria was found in sand and muddy sand. Certain areas experienced drastic reductions in the densities of these organisms, but since most of the *Mya* recorded were juveniles, population fluctuations independent of dredging may have been an important factor. Factors favorable to larval settling and the growth of juveniles may have been unsuited to their sustenance as adults, resulting in mass mortality of juveniles at critical points in their development.

Of the epifauna, *Neopanope texana sayi* was found in greatest abundance in the high current velocity, stony gravel of station 2. It was also abundant in the muddy sand of station 8 and the silt of stations 16, 18 and 22. It was recovered in five of the samples at station 16 and four at station 18, so it is unlikely that the presence of this crab in the silt regions was accidental. *Neopanope texana sayi* experienced a reduction in population density after dredging.

Crepidula fornicata was found in large numbers (3,470 in one haul) at station 2 before dredging, but since this station was in the channel, it was decimated by the dredge and no recovery was noted in the 11 mo period after dredging. *Crepidula* broods its young; recovery would be expected to be relatively slow in a decimated area as dispersal is not accomplished by free-swimming larvae.

Four species of Caridean shrimp were abundant on the silt substratum of Goose Creek. These were *Hippolyte pleurancanthus, Crangon septimspinosus, Palaemonetes vulgaris*, and *P. pugio*. Their numbers fluctuated seasonally and from station to station, possibly reflecting sampling error inherent in using the cumbersome corers to capture these relatively rapidly moving organisms. There were population decreases at most stations.

The snail, *Hydrobia totteni*, was most common in the sandier sediments, especially at stations 3 and 7 which had substantial current velocities. Its post-dredging density was considerably reduced from pre-dredging levels.

Mulinia lateralis was found to be more abundant in the channel after dredging than before. Too few were encountered in the bay study to corroborate this finding.

The polychaete *Maldanopsis elongata* was found only at station 11 in virtually all samples, reaching a density of 60/m^2. Its population size was maintained after dredging.

The holothurian *Sclerodactyla (=Thyone) briaerius* was common in the silt stations 12-22, reaching a density of 60/m^2 in the deep silt of station 22. The mean numbers at station 22 were 33/m^2 before dredging and 2/m^2 after dredging, reflecting, perhaps, the close proximity of this station to the spoil gate of spoil area C. *Sclerodactyla briaerius* experienced declines at five of the six stations at which it was recorded in substantial numbers.

The tunicate, *Molgula manhattanensis*, was common on the *Enteromorpha* which covered the silt at stations 22, 23, and 24, reaching a concentration of 590/m^2 in December 1966 at station 23 and declining in numbers after dredging at all three stations.

An amphipod community, similar to those described by Stickney and Stringer (1957) and Rhoades and Young (1970), occurred in the silt west of station 12. The most abundant species were identified as *Ampelisca macrocephala* and *A. spinipes*. Maximum abundance recorded for stations 16, 17, and 18 was 310, 490, and 190/m^2, considerably lower than the level of 10,000 m^2 mentioned by Stickney and Stringer for Greenwich Bay. The 1.4 mm sieve size used in this study contrasts with the practice used by Stickney and Stringer of examining the fine sediments completely, using no sieve. However, it seems unlikely that population densities would be comparable, since there was no massive concentration of amphipod tubes in the Goose Creek

[7]The reader should be cautioned in interpreting the fluctuations in population densities on these graphs. Although each column represents six pre-dredging or six post-dredging samples, the distribution of organisms was so patchy that accumulating the data and recording means still does not compensate for possible sampling error as the corer penetrated a worm colony one month and sampled a relatively sterile area 1 m away from it the next. Trends, however, are apparent.

samples. The amphipods found in Goose Creek were limited to the soft sediments, in contrast to Long Island Sound and Buzzards Bay, as reported by Sanders (1956, 1958), making it likely that they are detritus feeders. No pattern was evident between pre- and post-dredging population densities of amphipods.

The *Nepthys incisa-Nucula proxima* community of Sanders was not found in Goose Creek since both species were not abundant enough at any one station to be considered dominant. Instead, a *Nereis succinea-Mercenaria mercenaria-Sclerodactyla briaerius* community was found, with subdominants including *Capitella capitata* and the caridean shrimp previously mentioned as epifaunal subdominants.

Clymenella torquata and *Mya arenaria* can be considered the dominant sandy sediment assemblage, with *Notomastus latericeus* and *Hydrobia totteni* comprising important subdominant populations.

Scoloplos robustus, S. fragilis, and *Neopanope texana sayi* were distributed throughout the sediment types in Goose Creek, apparently without specificity.

There was no evidence that the dredging process eradicated any species. There was, however, evidence of two cyclical fluctuations in population density which occurred naturally and were superimposed on the dredging data. Individual *Aequipecten irradians* were found in only four sampler hauls. Much of the shell in the substratum was contributed to by this species, testifying to its former abundance. In fact, it was commercially harvested from Goose Creek in previous years. Its absence coincided with a cyclical low in its density and had nothing to do with the dredging. Similarly, not one specimen of *Callinectes sapidus* was recorded for the 22 mo of the study, yet in July 1970 large numbers of these crabs were observed in Goose Creek.

Productivity

The mean pre-dredging dry weight for Goose Creek was 36.83 g/m^2 before dredging and 12.78 g/m^2 after dredging, a decrease of 63%. Sanders (1956) suggests that standing crop figures for infauna are a function of productivity by a ratio of 2.1-5.0:1. Taylor and Saloman (1968) used a factor of 4 in their calculations of infaunal productivity in highly productive turtle grass beds.

Sanders' mean ratio for all stations in his Long Island Sound survey was 2.44. He estimated the total productivity of "small infauna" in the sediment of Long Island Sound at 21.49 g/m^2. In computing his estimate he did not consider epifauna and "large" forms. He also makes the assumption that the substratum of Long Island Sound is comprised of 80% fine sediments and 20% coarse. Goose Creek has a distribution closer to 50% of each type of sediment. Correcting for these factors would tend to raise the total value of the estimate, even though the biomass of "short-lived" species is a practically negligible component of the Goose Creek samples, a factor which could lower the figure to 2.1. Because of these considerations, and because of the contiguity of the two study areas, Sanders' figure of 2.44 was adopted for Goose Creek.

Macrobenthic animal production in Goose Creek before dredging is estimated at 89.87 g/m^2/yr, using the factor of 2.44. If Sanders had used his standing crop figure for all epi- and infauna from Long Island Sound (54.627 g/m^2) in a similar calculation, his estimate would be $54.63 \times 2.44 = 133.30$ g/m^2/yr, a figure in essential agreement with the ratios of the standing crop estimates in the two areas.

The after-dredging productivity figure is 31.18 g/m^2/yr for a loss of 58.69 g/m^2/yr. This means that 18,780 kg of animal production were lost from the 0.32 km^2 of bottom in Goose Creek during the post-dredging year. This corresponds to approximately 58,700 kg/km^2/yr reduction in the productivity of the bay, out of a total productivity of 89,870 kg/km^2/yr.

Primary productivity of the extensive *Ruppia* and *Enteromorpha* beds was not estimated.

An Estimate of the Productivity of the Marsh

The islands in Goose Creek are represented on a 1904 map with virtually unaltered boundaries. Their natural isolation makes it unlikely that they have ever been exploited by man. The relative abundance of "bank" or "mud" oysters and extensive colonies of *Modiolus* and *Uca* give further evidence of their pristine state.

The islands evidently have been created by the deposition of materials at the confluence of channels A, B, and C. They are covered with a uniform growth of *Spartina alterniflora*, with

Salsola kali and other plants growing on patches of slightly higher ground. The dominant animal is *Modiolus demissus* which was abundant on all four major islands, averaging 19.58 specimens per m². Colonies of fiddler crabs, predominantly *Uca pugnax*, were found on islands I and II.

The islands are little more than hassocks of *Spartina*. At low tide they project 0.7 m to 1 m above the water surface; at high tide they are virtually inundated. The largest of the islands, island II, was 115.59 m × 42.39 m.

The islands represent the most unspoiled aspect of the Goose Creek marsh. For that reason, they were chosen as the site for estimating the productivity of the *Spartina alterniflora* marsh along the periphery of Goose Creek. The resulting figure will be higher than other productivity estimates because it does not represent the *Spartina patens* and *Phragmites communis* marshes which are both transitory and strongly affected by man in the Goose Creek area.

Island II, the most southeasterly of the islands, was sampled by means of seven stations arranged at 15 m intervals and staggered so that both edges and the center of the islands were sampled at least twice (Figure 13).

A 1.83 m × 1.83 m frame was placed on the area to be sampled so that 3.34 m² were delimited. A team of four collectors was stationed, one collector on each of the sides of the sample area, to prevent motile forms from escaping. All surface-dwelling animals were removed by hand. The area was then spaded to a depth of 20 cm to remove burrowing forms. The total area sampled was 23.4 m².

Table 20 represents the animal biomass of the stations on island II. Animals making up the species mix were: 104 *Uca pugnax*, 6 *Uca pugilator*, 442 *Modiolus demissus*, 28 *Sesarma reticulatum*, 1 *Carcinus maenus*, 3 *Littorina littorea*, and one unidentified Nereid.

The total wet weight of the macrofauna taken from the seven stations is 2,327.01 g, or 90.94 g/m². The corresponding calculation for dry weight is 20.21 g/m². The ratio of dry weight to wet weight is 1:4.9.

The computations for estimating primary productivity of the marsh were taken from Udell et al. (1969) from their study of the Hempstead, Long Island, salt marsh. They calculated a total minimal estimate (harvest method) of annual production of 3.68 tons per acre of tall *Spartina*

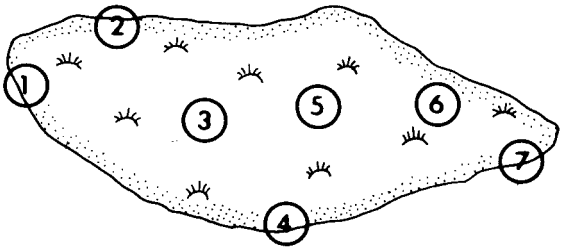

FIGURE 13.—The distribution of stations on island II.

TABLE 20.—Biomass of animals found on island II, Goose Creek.

Station	Animals				
	Wet wt. (g)	Dry wt. (g)	Dry-wet ratio	No. specimens	No. species
1	397.32	78.52	1/5	62	2
2	595.55	108.90	1/5	109	4
3	155.76	28.47	1/6	39	4
4	175.46	34.19	1/5	47	4
5	705.24	156.86	1/5	157	3
6	213.97	41.90	1/4	96	4
7	83.71	16.43	1/5	29	3
Total	2,327.01	475.27			

alterniflora and 2.55 tons per acre of the mixed species comprising the typical Long Island marsh (tall and short *S. alterniflora*, *S. patens*, *Distichlis spicata*, etc.). These weights corresponded to a mean dry weight of 827.2 g/m² for tall *S. alterniflora* and (by extrapolation) 578 g/m² for the mixed species. Animal production taken from our mid-August study is 20.21 g/m², dry weight. Sanders (1956) suggests that standing crop figures for infauna are a function of productivity by a ratio of 2.1-5:1. Since the organisms predominating in our samples are predominantly "long-lived," Sanders' factor of 2.1 was applied. Animal productivity of the marsh comes to 42.4 g/m²/yr, by this calculation. This is roughly 5% of the tall *S. alterniflora* productivity figure or 7% of the overall estimate. The total animal and plant productivity of the tall *S. alterniflora* marsh as represented by island II, is 869.64 g/m²/yr. Thus, if the dredged channel had passed through island II instead of skirting it, its 4,900 m² of marsh or 4,261.2 kg (dry weight) of animal and plant productivity would have been permanently obliterated.

The portion of the Goose Creek marsh inundated as spoil areas has been estimated at 108,712 m². Using Udell's estimate of 2.55 tons/acre (4,553.57 kg/ha), the total primary productivity of the marsh which became the spoil areas would

be 4,553.57 kg/ha × 10.87 ha or 49,497.31 kg/yr.

Animal production of tall *S. alterniflora* marsh has been estimated to be 5-7% of primary productivity. Since mixed marsh is not as productive of animals as tall *S. alterniflora* marsh, a figure of 4% of the *mixed marsh* primary production seems to be a reasonable estimate. Annual animal production on the 10.87 ha of inundated mixed marsh would then be 4% of 49,497.31 kg or 1,979.89 kg.

Virtually the entire spoil areas have been turned into homesites. If they had been left to produce a *Phragmites communis* community, only a relatively small proportion of the original productivity would have been locally available on a trophic level (Johnson, pers. comm.).

Since approximately 45% of the net production of a salt marsh (Teal, 1962) is exported outside the area of its source, the loss of this productivity will have repercussions beyond Goose Creek.

The estimates given herein should be considered conservative, as E. P. Odum (1959) estimated the primary productivity of tall *S. alterniflora* in Georgia salt marshes at a high of 14 tons/acre and Ryther (1959) gives a figure for net organic production of *Spartina* marsh of 9.0 g/m^2/day.

H. T. Odum (1963) indicates that *Thalassia* beds in Redfish Bay, Tex., recovered in the areas not directly in the path of the dredge after one year, but his data indicate that the dredged area and an area 0.25 mile east of the channel had no productivity due to removal of the substratum to bedrock in one case and "beds covered with 30 cm of soft silt" in the other. Virtually all of Goose Creek was within 0.25 mile of the dredge. Studies of large embayments tend to deemphasize dredging effects because of the dissipation of the products of the dredging process and dilution factors. Similarly, regions like Chesapeake and Redfish Bays have relatively extensive bottom areas and circumferences and dredge spoil is either deposited back in the basin where it spreads to form a relatively shallow homogeneous layer often virtually indistinguishable from the bottom (Biggs, 1968, 1970), or covers a relatively small portion of the bay edge.

The effects of dredging appear to be accentuated as the size of the embayment decreases.

DISCUSSION

The Relationship of the Substratum to the Distribution of Organisms

Wilson (1938, 1953), Morgans (1956), Sanders (1958), and Sasaki (1967) related larval or adult infaunal population densities to sediment type. McNulty, Work, and Moore (1962) and Harrison, Lynch, and Altschaeffl (1964) fail to corroborate either degree of sorting or median grain size as definitive factors affecting the distribution of deposit or filter feeders. It appears that animal-sediment relationships are variable depending on such factors as sediment type, life cycles of related fauna, and location.

In the Goose Creek study the analysis of variance between biomass before and after dredging as a function of sediment type revealed no significant interaction between productivity of animal biomass and sediment type in the bay as a whole. In the channel, however, there was a positive correlation between biomass and stations. Since the stations were arranged in linear fashion virtually in descending order of particle size and in the direction of lowered current velocity, these factors appear to have had an influence on productivity.

The recovery rate of the macrobenthic populations varied in different substrata according to a chi-square of the number of species found at the stations representing different sediment types. Similarly, the number of species was significantly different before and after dredging, as a function of sediment type.

It appears, then, that productivity in terms of animal tissue was not independently influenced by substratum in the bay as a whole, but there was a response to the specific conditions in the channel. Recovery of species and specimen numbers appeared to be affected by sediment type in both channel and bay. These data tend to substantiate those of Sasaki (1967).

The Relationship of Current Velocity to the Characteristics of the Sediment and the Distribution of Organisms

In a shallow bay with a narrow mouth like Goose Creek, wind-driven currents probably have a disproportionately large effect on the characteristics of the sediment. Prevailing winds can

cause a net transport of materials towards the lee shore. Wind storms can so pile up water at the mouth of the bay that flood tide current velocities would be considerably above the normal range, causing erosion of the banks of tidal channels and exaggerated depositional patterns, or winds can depress the natural flushing action of the ebb tide, increasing the deposition of light particles. A number of the aforementioned factors have not been considered in the literature in detail, perhaps because most investigations are concerned with relatively large and deep bodies of water. However, Biggs (1968) concludes that most of the suspended material in Upper Chesapeake Bay came from the bottom and had been stirred by wind-waves and currents.

Inman (1949) refers to three basic factors in the transportation and deposition of sediments: degree of bottom roughness, settling velocity, and threshold velocity. He shows that as current velocity drops in a downstream direction, particle size also decreases. The degree of sorting, however, is at a maximum in sediments with a median diameter near the grade of fine sand (0.18 mm). Threshold velocity for grain diameters less than 0.18 mm increases with decreasing grain size. Since the threshold velocity is much greater than the setting velocity for smaller particles, suspended particles entering a bay will, when deposited, have a tendency to remain a part of the substratum rather than move about by surface creep or resuspension. On the basis of these characteristics of fine sands, Sanders (1958) deduces that they must represent a very stable environment. He also emphasizes the role of clay as an efficient binding agent for organic matter, thus influencing the number of deposit feeders present. The simple clay-silt proportion governing the population size of Sanders' deposit feeders is not apparent in the distribution of filter feeders, where more complex factors are at work.

McNulty et al. (1962) related low current velocity to the accumulation of a detritus layer on the sediment surface capable of supporting large populations of detritus feeders.

Rhoads and Young (1970) suggest that biogenic reworking lowers critical erosion velocity and increases the instability of the substratum as manifested by a high resuspension rate and increased turbidity close to the silt-water interface, placing selective pressure on suspension feeders.

In the present investigation, maxima in biomass production occurred in areas of coarse and fine sand in the channel (stations B, C, and H) with current velocities of the order of 56 cm/sec and 17 cm/sec, before dredging.

In the bay as a whole 14 of 113 individual dredge hauls yielded dry weights above 80 g/m^2. Since the distribution of organisms was so patchy, these extraordinarily large standing crop measures are perhaps the best index of the productivity of the various substrata. The highest biomass was recorded for station 2. However, this consisted almost exclusively of *Crepidula fornicata*, an epibenthic gastropod which requires the scouring action of a rapid current to establish a substratum of stones upon which it clings with a broad foot. Stations 7 and 9 had high and medium current velocities (41.5 and 12 cm/sec) and supported extensive colonies of the polychaetes *Clymenella torquata* and *Notomastus latericeus*, as well as large pelecypods (*Mya, Ensis, Mercenaria*) in the case of station 9. Both *C. torquata* and *N. latericeus* are deposit feeders inhabiting sandy sediments.

Stations 16, 17, and 22 were in regions of almost negligible current velocity which were characterized by a substratum of silt over fine gray sand. The major weight contributors at stations 16 and 17 were *Sclerodactyla (Thyone)* and large *Mercenaria*, with the polychaetes, *Capitella capitata, Polydora ligni, Scoloplos robustus*, and *S. fragilis* making important contributions. *Polydora* is almost exclusively an inhabitant of mud, while the other worms are found in sandy mud.

All of the above-mentioned worms are deposit feeders whereas Sanders groups *Mercenaria* and *Sclerodactyla* together as suspension feeders.

Deposit-detritus feeders were important contributors to the biomass in Goose Creek, in both the sandy and muddy habitats. These animals are more or less substratum-specific, as can be seen on their distribution graphs (Figure 12) and in Sanders' data. Changes in current velocity have a profound influence on the nature of the substratum and, consequently, on animal distribution. This is especially true in the regions of the sandier sediments. Stations 2, 7, and 9 had reductions from 50 to 75% of pre-dredging velocities. In the western portion of the bay, wind-driven currents are the predominant means of sediment transport, and, although some changes in the mid-bay region could be expected due to increased current velocities, these would not have a substantial influence on the soft sediment of the western half of the bay.

The most numerous instances of high infaunal standing-crop production were in areas which correspond to the general classification proposed by Sanders (1956), of a relatively high silt-clay composition, although the stations with the highest animal biomass were either somewhat above the 13-25% silt-clay level reported as most highly productive, or toward the lower end of the spectrum. Suspension feeders, with the exception of station 2, were not the dominant forms in the sandy sediments of Goose Creek, except in the littoral. Instead, deposit feeding polychaetes were numerically dominant and often constituted the major weight factor in the biomass. Furthermore, if *Mercenaria* and *Sclerodactyla* are grouped together (Sanders, 1956), the biomass of suspension feeders predominates in high silt-clay regions. An important *Ampelisca* community was not found.

The Effects of Dredging on the Substratum and Its Fauna

Three major categories of environmental disturbance brought about by dredging are:

1. *Immediate effects*, during and directly after the dredging, including suffocation of benthic animals by siltation; flocculation and removal from the water column of planktonic organisms (which affects benthic filter feeders by removing their source of food); and changes in water chemistry, as substances are released from the substratum and dissolved. Large quantities of bottom materials placed in suspension by the dredging process decrease light penetration, change the proportion of wavelengths of light reaching the plants and interfere with the food-getting processes of filter feeders by inundating them with wrong size or nonnutritive particles.

On the other hand, the release of nutrients into the water profoundly affects the composition of the plankton by favoring the growth of some species. This effect could be beneficial or harmful depending on whether or not the plankton bloom is utilized by the filter feeders. If nannoplankton like *Nannochloris* and *Stichococcus*, which have been incriminated in mass mortalities of *Mercenaria*, are the dominant forms in the bloom, selective removal of certain species of filter-feeders could be expected.

2. *Transitory or semipermanent effects* such as the mechanical removal of the benthos from the dredged area and a change in the nature of the substratum by the deposition of spoil. These changes may be temporary, as the dredged area is recolonized or tidal currents reestablish the original substratum composition by scouring away fine particles and reestablishing old channels, or depositing fine sediment over exposed, sandy areas.

Recolonization of areas denuded of organisms has been studied under either artificially induced conditions or as the result of major disturbances such as oil spillage. Reestablishment of the original fauna is estimated to take at least 8 yr in the intertidal zone, as reported by Castenholz (1967) and by North (1967). Clarke and Neushul (1967:47) give some insight into the complexity of the recolonization process when they report: "Apparently a barnacle stage had to be established before the surface of the rock was suitable for the larval stages of *Mytilus* to become established." In their study it took 4 yr for the reestablishment of small *Mytilus californianus* colonies.

In the aforementioned works the environment was not fundamentally changed by the conditions leading to defaunation, namely, storms, oil spillage, or artificial removal of the organisms from the substratum.

If a rock has been manually denuded of organisms, natural succession can begin immediately. In the case of dredging, however, the substratum may remain unstable for a considerable time and final recolonization cannot begin until the climax substratum is reestablished.

3. *Permanent changes* in the ecology brought about by dredging occur if the ambient flow of water and current distribution patterns are disrupted. One of the results of dredging was the reapportionment of maximum water transport into Goose Creek from channel A to channel B. Furthermore, the current velocity in all three channels dropped because of the enlarged capacity of the dredged channel for containing water, since it was approximately three times deeper than the channel it replaced. A different distribution pattern of silt and other fine particles occurred as the result of lowered current velocities which resulted in sediment changes in a substantial portion of the bay.

Spoil deposition on the surrounding marshes has a profound effect on the species composition

and productivity of an estuarine area. Raising the level of the marsh above the inundation zone will replace the highly productive *Spartina* community with the less biologically useful *Phragmites communis*. Much of the food of detritus feeders comes from the disintegrating plant material of the *Spartina* marsh and, in the absence or depletion of this food source, the species mix and/or proportion of detritus to deposit on filter feeders may be permanently changed.

Even the removal of shell from a mud bottom has been suggested as a reason for the exclusion of certain species from a dredged bay. Barnard and Reish (1959) suggest that the amphipod, *Metaceradocus occidentalis* and the polychaete *Scyphoproctus oculatus* were in danger of losing their habitat as the upper shell and rock laden layers of the mud substratum were removed by a dredging operation.

The distribution or removal of materials during dredging in a body of water with even minimal flushing action results in immediate, temporary, and long-term changes in its ecology. The interaction of organisms with this rapidly changing environment is poorly understood. Estuarine organisms are noted for their ability to withstand environmental vicissitudes, yet this adaptability may be overstressed by one or another aspect of the dredging process. For example, Postma (1967:226) refers to the difference in the distribution patterns of dissolved and suspended materials. He points out that dissolved materials have a net transport from regions of high concentration to regions of low concentration, causing a rapid dispersal of the dissolved matter and its consequent removal from the source area: "In the case of suspended matter the reverse often occurs. This material may be trapped and accumulated in the nearshore environment." Thus, a benthic organism in the vicinity of a dredging operation can be subjected to a short-term rapid surge of dissolved nutrients in its environment, with all of the concomitant interactions this represents. Superimposed on this relatively fleeting enrichment of the water would be the longer-term deposition of suspended sediments. The interaction between the two, such as the adsorption of organic compounds on suspended clay particles (e.g. amino acid complexes binding strongly to clays) (Siegel, 1966), the effects of flocculation, etc., is poorly understood. The presence of the dissolved organic compounds liberated by the dredging process also can have beneficial effects on the benthic organisms. Siegel quotes Stephens and Schinske (1961) who found that glucose, glycine, and aspartic acid can serve as energy sources for marine invertebrates. Organic matter may also supply a growth factor such as vitamin B_{12} or may inhibit the growth of bacteria by its antibiotic effect (Saz et al., 1963). It may promote growth by solubilizing trace metals, thus making them available (Johnston, 1964). Udell et al. (1969) analyzed marsh grasses and found a number of vitamins, including vitamin B_{12}. The destruction of peripheral marsh by spoil deposition may eliminate a constant source of vitamins and other nutrients made available by the disintegration of the *Spartina*.

The effects of the dispersion of light rays in the turbid water of a dredged bay is also incompletely understood. It is unlikely that increased turbidity can destroy benthic flora through light deprivation in shallow waters. Clendenning (1958) studied the relationship between photosynthesis and light intensities for *Macrocystis pyrifera* laminae. Compensation (light intensity where photosynthesis balanced respiration) occurred at 15 foot candles using white light. First evidences of saturation occurred at about 400 foot candles and maximum photosynthetic rates occurred at 1,600 foot candles. Since the intensity of daylight delivered to the water surface is about 10,000 foot candles, it is unlikely that the light values would so depreciate in shallow water as to seriously impair photosynthesis. On the other hand, the authors observed a colony of *Ruppia* after dredging and the leaves were covered by a light brown flocculent material which had been deposited from the water. Large areas of *Enteromorpha* and *Aghardiella* showed a similar canopy of fine sediment. It is possible that the deposition of opaque material from the water onto leaves and stipes in areas of negligible current velocity might pose a threat to the plants by inhibiting photosynthetic activity even though the turbidity of the overlying water is not high enough to reduce adequate light penetration.

The estuarine environment is particularly susceptible to particle deposition. Although it shares the factor of close proximity to the source of the particulate matter with open beaches, the beaches have a longshore drift factor which tends to distribute particulate matter. It is well known that beach sands are well sorted. Estuarine areas,

on the other hand, have a circulation cycle which favors deposition. Postma (1967:229) states: "The estuarine circulation therefore acts as a 'sediment trap' in which water flows freely seaward, but particles heavier than the water are retained."

Flemer et al. (1968) list a number of factors associated with the effects of dredging on animal survival and suggest that suspended sediments probably affect many sites in the energy flow sequence of the benthic community.

Several studies have been made on the effects of siltation on the survival of pelecypods.

Loosanoff and Tommers (1948), Davis (1960), Davis and Hidu (1969), and Loosanoff (1962) described harmful effects of heavy sediment loads on eggs, larval development, and adult pelecypods, while Lunz (1938), Wilson (1950), Mackin (1956), and Dunnington (1968) showed that adult oysters do not suffer appreciable physiological damage unless subjected to very heavy siltation or buried.

Pfitzenmeyer (1970) described the effects of dredging and spoil deposition in Upper Chesapeake Bay. The dredging process did not cause major topographical or stratigraphical changes since the spoil was fundamentally identical with the substratum upon which it was deposited and it spread out to form a thin layer over the bottom, undisturbed by strong currents. Species mix and biomass were markedly reduced immediately after dredging, but recovered to original levels after 18 mo.

Of interest in Pfitzenmeyer's study is the superimposition of the natural cycles of certain molluscs on the data related to dredging. The pelecypods *Macoma phenax* and *M. balthica* were in a period of natural decline during the period of the study, while *Rangia cuneata* experienced a short-lived population explosion, reaching a density of 10,000 clams per m^2. One year after the study, the *Rangia* population had disappeared. These rapid and extreme fluctuations in the population densities of organisms profoundly affected biomass calculations because of the relatively large size of the pelecypods, compared with, for example, the three permanent dominants, two of which were an isopod and an amphipod. If the *Rangia* population increase had not compensated for decreases in the *Macoma* populations during the study, it is possible that there might have been significant differences in the results. If the dredging had substantially altered the substratum, e.g., by removing the silt to a depth sufficient to expose the sand underneath, the recovery of the populations might have required a period of substratum stabilization before achievement of normal populations.

Pearce (1970) studied a spoil deposition area of the New York Bight known as the "dead sea." He describes the benthic environment as severely affected by the deposition of large quantities of spoil. He found contamination by heavy metals, pesticides, and petroleum derivatives. The central portion of the spoil area contained no living macrofauna; peripheral areas were frequently barren or impoverished; interstitial waters of spoil sediments had extremely high coliform counts.

In laboratory experiments where the crustaceans *Homarus americanus* and *Cancer irroratus* and the xiphosuran *Limulus polyphemus* were exposed to sludge and spoil sediments, high mortalities, and pathological conditions were described.

Pearce concluded, "... sewage sludge and dredge spoil deposits are incompatible with most normal biological phenomena," (p. 66). He blames this condition on:

1) adults being killed by toxins, anoxia, or inundation by solid wastes;

2) interference with or destruction of eggs and larvae; and,

3) active avoidance by adult and larval organisms.

A number of reasons suggest themselves to explain why the results of Pfitzenmeyer's and Pearce's studies are so diametrically opposed. For one, Pearce's study area was one of constant spoil deposition; Pfitzenmeyer's had only one inundation. Secondly, Pfitzenmeyer records relatively normal concentrations of oxygen while Pearce indicates that oxygen concentrations were frequently 2-3 ppm lower in the water above the spoil.

Finally, there seems to be a very high degree of contamination of the dredged sediments with heavy metals, insecticides, and petroleum fractions in Pearce's study, which is absent in Pfitzenmeyer's.

A number of studies was performed on the effects of dredging on oyster production. Breuer (1962) reported major changes produced by dredging spoil deposition in South Bay, Tex. Water circulation was impaired by reducing the size of the entrance. Water depth decreased, much of the oyster population was silted over and destroyed, and high local turbidity was evident.

Mackin (1961) reviewed the literature on the biological effects of dredging, with special reference to oyster survival. Most of the authors he cited found that oyster mortality was caused by direct inundation with spoil resulting in suffocation. Beyond the area of deposition, oysters and fishes were unaffected.

Mackin found that at low current velocities turbidity is not an important factor in oyster mortality at levels up to 700 ppm. Such levels were higher than those found beyond 250 ft from the outlets of the three types of dredges studied. He also argues that oxygen levels are not appreciably decreased under conditions normally found on oyster beds.

SUMMARY AND CONCLUSIONS

The results of the present study differ from those reported in most other investigations of the effects of dredging in that profound changes are reported in macrobenthic animal populations throughout the bay. Abundant evidence is available concerning long-term depreciation of standing crop in dredged channels (cf. Taylor and Saloman, 1968; Odum, 1963; Murawski, 1969; and O'Connor, 1972), but these reports show limited residual effects beyond the immediate region of the channel and/or spoil areas. This difference in results is attributed to the fact that most previous studies reported on the creation of channels through relatively large bodies of water such as Chesapeake or Boca Ciega Bays. Spoil distribution effects and changes wrought in current velocity and sediment deposition are minimized when the ratio of the dredged area to total bottom area and contained water volume is large. Long flushing time and reduced inlet size of small estuarine bays exaggerates the hydrodynamic effects of channel construction. Wind-induced sediment transport and the effects of spoil deposition on the surrounding peripheral marshes are factors which complicate the evaluation of the effects of dredging, especially in small bays.

In areas of high human population density, combined dredging-landfill operations have become common and their effects have been felt primarily in the small shallow bays which could provide (if dredged) good anchorages for pleasure boats and picturesque settings for homes. Yet these small bays, edged with *Spartina* marshes, are primary trophic energy sources in the economy of the sea. It appears that further long-term investigations of the effects of dredging on these bays is warranted.

A summary of the areas of investigation and conclusions follow:

1. The dredging process caused turbidity throughout the bay. Light penetration was reduced to 0.4 m during dredging, but the particulate matter released was rapidly dissipated. It is unlikely that turbidity affected light penetration enough to interfere with photosynthesis. However, a canopy of flocculent material deposited on the plants as the result of the deposition of suspended bottom material may have interfered with primary productivity in the low current velocity areas of the bay.

2. Water transport patterns were greatly modified as the result of dredging. Current velocity in the eastern half of the bay was reduced approximately 50%, while small increases were noted for the middle portion of the bay, which previously had negligible velocities.

The main mass movement of water shifted from channel A to channel B as the result of deepening the latter channel.

Dye studies revealed that flushing time of the bay as a whole was not appreciably changed.

3. Correlations between sediment particle size and changes in current velocity suggested that the distribution of sediment types in Goose Creek would be permanently changed as the result of modified current velocities.

4. Values of particulate phosphorus, silicates, and chlorophyll *a* increased substantially. Dissolved organic phosphorus and nitrates increased slightly during the post-dredging year.

A number of authors have reported increases in phytoplankton and/or benthic productivity as a result of increased nutrient levels, but no definitive correlation could be observed in the course of this study.

5. It was found that wind-driven currents affected the distribution of nutrients and bacteria in the bay. In view of the predominance of strong northwesterly winds over the year and the shallow, slowly moving water of the western half of Goose Creek, it was suggested that sediment deposition in this region was primarily a function of wind-driven currents. The assertion by Flemer (1968) that late fall is the best season for dredging is disputed on the basis of a high

level of wind-influenced sediment distribution at that season.

6. Standing crop figures for the commercially important clam, *Mercenaria mercenaria*, were reduced in the bay as a whole. Some areas, especially those in the path of the dredge, did not recover one year after dredging.

7. Land usage patterns were drastically altered during the study as well as in the previous 15 yr. Homes within 300 m of the bay increased by 94%.

Rhodamine B placed in a toilet in a house along the periphery of the bay was detected in the bay water, although all houses have septic tanks. Maximum coliform counts exceeded present legal standards in 1968.

8. Significant reductions in standing crop figures occurred in the channel and the bay as a whole. Recovery of biomass in the channel was also affected by sediment composition and an interaction between the sediment and the dredging process itself.

The effect of different sediment types and seasonal variances on the biomass is shown to be not significant, negating two of the most important variables which might confuse the interpretation of the pre-and post-dredging data.

Chi-square analyses were done on number of species and number of individuals in the bay and in the channel. There were significant reductions in both parameters. Recovery of species and specimen numbers appeared to be affected by sediment type.

Drastic reductions in biomass, species number, and population size occurred in the dredged channel as a function of the removal of the substratum and its in- and epifauna. Recovery had not occurred at the termination of this study, 11 mo after dredging.

Of perhaps greater significance are the substantial reductions in all parameters which occured in the bay as a whole, with only a few stations showing recovery to pre-dredging levels. Only one of the stations was more than 500 m from the dredged channel and spoil deposition areas.

9. Goose Creek had a relatively high in- and epifaunal standing crop estimated at 36.83 g/m^2 for the bay as a whole, including large forms. This compares to Sanders' (1956) estimate of 54.627 g/m^2 for Long Island Sound, but is much higher than the standing crop levels obtained for Upper Chesapeake Bay or the English Channel.

The number of organisms per m^2 is lower for Goose Creek than for the other areas reported on, indicating a preponderance of large forms.

10. Phytoplankton production in Goose Creek was lower than that of Long Island Sound, but far higher than that of the English Channel or Upper Chesapeake Bay. There were three maxima in phytoplankton production in Goose Creek in 1966-1967.

11. The removal of the substratum in the channel affected the population dynamics of the infauna. The molluscs *Tellina agilis, Lyonsia hyalina*, and *Mulinia lateralis*, while insignificant components of the standing crop both before and after dredging, increased in numbers in the post-dredging samples.

Two dominant forms, the polychaetes *Clymenella torquata* and *Notomastus latericeus*, virtually disappeared after dredging.

In the bay as a whole there appeared to be no substantial change in the species mix, except for the removal of the dense population of *Crepidula fornicata* (34,000/m^2) by the dredge near the confluence of the three channels. No recovery was noted for this species after 11 mo at that station.

In general, the bay sediments exhibited an overall reduction in epi- and infaunal populations, which did not approach recovery levels 11 mo after dredging.

The *Ampelisca spinipes* and *Nepthys incisa-Nucula proxima* communities described by Stickney and Stringer (1957) and Sanders (1956, 1958) were not found in Goose Creek, being replaced by a *Clymenella torquata-Mya arenaria* community in the sandy sediments, and a *Mercenaria mercenaria-Sclerodactyla briaerius-Nereis succinea* community in the softer substratum.

12. Animal productivity for Goose Creek was calculated at 89.87 g/m^2/yr before dredging and 31.18 g/m^2/yr after dredging. During the post-dredging year, 18,780 kg of animal production was lost from the 0.32 km^2 bottom of Goose Creek.

13. The productivity of island II was considered representative of unspoiled tall *Spartina alterniflora* marsh. Animal productivity was estimated at 42.44 g/m^2/yr, composed almost entirely of *Uca pugnax, Modiolus demissus*, and *Sesarma reticulatum*. This represented 5-7% of the total productivity figures of 869.64 g/m^2/yr. The gross estimate for mixed peripheral marsh came to 4,553.57 kg/ha. Using this figure to calculate the

loss of productivity represented by the spoil areas which had inundated 10.87 ha of marsh, 49,497.31 kg of plant matter were removed from the trophic cycle of Goose Creek in the post-dredging year.

Replacement by houses or *Phragmites* marsh would tend to fix this loss on a permanent basis.

In summary, reductions in the productivity of Goose Creek were induced by the dredging process. Recovery to pre-dredging levels had not occurred 11 mo after dredging. Arguments were proposed which suggested that changes in current velocity and the concomitant modifications in substratum type represented permanent changes which would affect the future productivity of the bay by changing the nature of the habitat.

Spoil disposal and land usage changes brought about an enhanced land value of the disposal areas, stimulating the development of the periphery of the bay, removing or depleting the marsh as an energy source available to the aquatic environment. These changes also were of a permanent nature.

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Appendix Table I.—Faunal list for Goose Creek.

Total number of species = 138.

CNIDARIA—ANTHOZOA
Haloclava producta[1]
Metridium senile
Sagartia modesta[1]
PLATYHELMINTHES—TURBELLARIA
Euplana gracilus[1]
NEMERTINEA
Amphiporus caecus[1]
Carinoma tremaphoros[1]
Cerebratulus lacteus
Zygeupolia rubens[1]
ANNELIDA—POLYCHAETA
Amphitrite affinis[1]
A. cirrata[1]
A. ornata[1]
Arabella iricolor
Arenicola cristata[1]
Capitella capitata
Cirratulus grandis
Clymenella mucosa[1]
C. torquata
Dispio uncinata
Drilonereis longa
Eteone heteropoda[1]
E. lactea[1]
E. longa[1]
Eumida sanguinea
Glycera americana
G. dibranchiata
Glycinde solitaria[1]
Harmothoe imbricata
Lepidametria commensalis[1]
Lumbrineris tenuis
Maldanopsis elongata[1]
Melinna cristata
Nephtys picta
Nereis (Neanthes) arenaceondonta[1]
N. (Hediste) diversicolor[1]
N. (Neanthes) succinea
N. (Neanthes) virens[1]
Notomastus latericeus[1]
Orbinia ornata[1]
Pectinaria gouldii
Phyllodoce arenae[1]
P. groenlandica[1]
Pista cristata[1]
P. palmata
Polydora ligni[1]
Prionspio malmgreni[1]
Sabella microphthalma[1]
Scolecolepides viridis[1]
Scoloplos fragilis
S. robustus
Spio setosa
Sthenelais boa[1]
Tharyx acutus[1]
SIPUNCULOIDEA
Golfingia gouldi
ARTHROPODA—CRUSTACEA
Cirripedia
Balanus amphritrite niveus[1]
B. balanoides
Isopoda
Chiridotea almyra[1]
C. coeca[1]
Cyathura polita (=*C. carinata*)[1]
Amphipoda
Ampelisca macrocephala
A. abdita (=*Ampelisca B.*)
A. spinipes
Gammarus (=*Carinogammarus*) *mucronatus*
Microdeutopus gryllotalpa
Decapoda
Caridea
Crangon septemspinosus
Hippolyte pleuracanthus
Palaemonetes intermedius[1]
P. pugio
P. vulgaris
Thallassinidea
Callianassa atlantica[1]
Upogebia affinis[1]
Brachyura
Neopanope texana sayi
Ovalipes ocellatus
Pinnixa chaetopterana[1]
P. cylindrica[1]
P. sayana
Sesarma reticulatum[1]
Uca pugilator
U. pugnax
Anomura
Pagurus longicarpus
MOLLUSCA
Gastropoda
Acteon punctostriatus
Alexia myosotis[1]
Bittium alternatum
Busycon carica[2]
B. canaliculatum[2]
Columbella lunata[1, 2]
C. translirata[1, 2]
Crepidula fornicata
Crepidula plana[2]
Eupleura caudata
Epitonium multistriatum[2]
Haminoea solitaria
Hydrobia totteni[1]
Littorina littorea
L. obtusata
L. saxatilis
Lunatia heros
Melampus bidentatus[2]
Melanella oleacea[2]
Nassarius obsoletus
N. vibex[2]
N. trivittatus

Odostomia bisuturalis[2]
O. seminuda
Polinices duplicatus
Pyramidella fusca[1 2]
Tornatina canaliculatum[1]
Triphora nigrocincta[1 2]
Urosalpinx cinerea

Pelecypoda
Aequipecten irradians
Aligena elevata[1]
Anadara transversa[2]
Anomia simplex
Clinocardium ciliatum (=*Cardium islandica*)[1 2]
Crassostrea virginica[2]
Cuminga tellenoides[1]
Ensis directus
Gemma gemma
Laevicardium mortoni[1]
Lyonsia hyalina
Macoma balthica[1]
Mercenaria mercenaria
Modiolus demissus
Mulinia lateralis
Mya arenaria
Nucula proxima
Pandora gouldiana
Petricola pholadiformis
Solemya vellum[1]
Spisula solidissima[2]
Tagelus plebeius[1]
Tellina agilis
Yoldia limatula

ECHINODERMATA—HOLOTHUROIDEA
Leptosynapta roseola[1]
Sclerodactyla (=*Thyone*) *briareus*

CHORDATA-UROCHORDATA
ASCIDIACEA
Dendrodoa carnea[1]
Molgula manhattensis
Styela partita[1]

[1]Organisms not heretofore reported in the major faunal lists of Long Island (Sanders, 1956; Hechtel, 1968; Townes, 1938.

[2]Shells only; no living specimens found.

SEASONAL DISTRIBUTION OF SIBLING HAKES, *UROPHYCIS CHUSS* AND *U. TENUIS* (PISCES, GADIDAE) IN NEW ENGLAND[1,2]

JOHN A. MUSICK[3]

ABSTRACT

The seasonal distribution patterns of sibling hakes, *Urophycis chuss* and *U. tenuis*, differ from one another in depth and geographic area and within each species by life history stage.

Urophycis chuss spawns off southern New England in depths of less than 60 fm and probably at temperatures between 5° and 10°C. Two major spawning concentrations occur, one east of Block Island, the other on the southwest part of Georges Bank. Spawning in the Gulf of Maine probably occurs inshore at depths shoaler than 30 fm. After spawning, the adult fish disperse and the larger individuals move offshore into water 60 fm or deeper where the mature fish remain until the following spring. Juvenile *U. chuss* are inquiline within sea scallops, *Placopecten magellanicus*, until they outgrow their hosts or until water temperatures, colder than about 4°C, either kill the hake or force them to seek out warmer temperatures in deeper water. Immature *U. chuss* remain in the vicinity of the scallop beds if water temperatures are compatible until the fish are in their second year of life. During that autumn, the fish migrate inshore to within 30 fm and remain until water temperatures drop to about 4°C, at which time they move to warmer, deeper water along the offshore shelf. The following spring, these fish migrate inshore with the older adult fish during April and by summer are mature and attain the typical seasonal behavior of adults. Immature *U. tenuis* in the Gulf of Maine occur at all depths but tend to remain in shallower water than the adults during the winter. Mature *U. tenuis* migrate inshore in the northern Gulf of Maine in the summer, disperse in the fall, and move into the deepest area of the Gulf in winter. Along the eastern edge of Georges Bank and west of there, both immature and mature *U. tenuis* are fish of the continental slope. Both stages occur over the shelf in small numbers, but at all seasons the highest concentrations are found deeper than 100 fm. The distribution patterns of these two sibling species are not coincidental, as assumed in the past. Rather, they are complementary. *Urophycis chuss* is more abundant in the Mid-Atlantic Bight, whereas *U. tenuis* is more abundant on the Scotian shelf, in the Gulf of St. Lawrence, and on the Grand Banks. They occur together most often in the Gulf of Maine. But even there, *U. chuss* is more abundant in the southwest sector and *U. tenuis* predominates in the northern part and in the Bay of Fundy.

The geographical ranges and seasonal movements of the red hake, *Urophycis chuss* (Walbaum), and of the white hake, *U. tenuis* (Mitchill), have not been defined because previous workers have had difficulty in distinguishing between the two species (Musick, 1973). The purpose of the present paper is to examine the validity of published accounts of the ranges of *U. chuss* and *U. tenuis*; to compare the seasonal distribution of the two species with regard to depth, bottom temperature, and substrate in New England waters; and to determine whether the patterns of seasonal distribution vary among juvenile, immature, and adult stages (these stages are defined below).

Two recent faunal works treat both species together and give the northern limit of distribution of *U. chuss* and *U. tenuis* as Labrador (Leim and Scott, 1966) or the Grand Banks of Newfoundland (Bigelow and Schroeder, 1953). However neither documentation nor voucher specimens are available to establish the presence of *U. chuss* off Labrador or on the Grand Banks (as there are for *U. tenuis*). Kendall (1909) reported *U. tenuis* from Labrador, and the Newfoundland Fisheries Research Commission (1932, 1933, 1934) captured *U. tenuis* along the southwestern edge of the Grand Banks during warmer months of the year. Templeman (1966) reported that all *Urophycis* taken commercially on the Grand Banks have been *U. tenuis* (1966) and that he had never seen a specimen of *U. chuss* from Newfoundland waters (pers. comm.). Jordan and Evermann (1898) and Breder (1948) gave the

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[2] This paper contains parts of a Ph.D. dissertation submitted to Harvard University.
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northern limit of *U. chuss* as the Gulf of St. Lawrence, apparently on the basis of reports of *U. chuss* (under the name of *Phycis americanus* (Block and Schneider)) from the Gulf of St. Lawrence by H. R. Storer (1850), Fortin (1863), Knight (1866), and Gilpin (1867). These authors, however, had followed the nomenclatural usage of D. H. Storer (1839, 1846, 1858) whose descriptions of *Phycis americanus* from Massachusetts obviously referred to *U. tenuis* because of the large size of his specimens (Musick, 1973). Similarly all other reports of *U. chuss* from the Gulf of St. Lawrence are based on nomenclatural errors or were made by workers (Cox, 1905, 1921; Cornish, 1907, 1912; Craigie, 1916, 1927; Vladykov and Tremblay, 1935; Vladykov and McKenzie, 1935; McKenzie, 1959; and Vladykov and McAllister, 1961) who by their own admission or by the species descriptions they published had shown their inability to distinguish between *U. chuss* and *U. tenuis* (Musick, 1969).

Urophycis chuss is absent from or very rare in the Gulf of St. Lawrence. Several thousand specimens of *Urophycis* examined at Souris, Prince Edward Island, in August 1966 were all *U. tenuis* (Musick, 1973). Juvenile and postlarval *Urophycis* captured in the Gulf of St. Lawrence by Fisheries Research Board of Canada personnel from St. Andrews, New Brunswick, and sent to me for identification were all *U. tenuis*. Several hundred *Urophycis* examined on a cruise of the RV *Prince* in the Northumberland Straits and Magdalen shallows in September 1972 were all *U. tenuis* (K. Able, pers. comm.).

The Newfoundland Fishery Research Commission captured one *U. chuss* (a pelagic juvenile) and many *U. tenuis* (benthic adults) on the Scotian shelf between Sable Island and Banquereau Banks (Newfoundland Fisheries Research Commission, 1932). Similarly, trawl collections made from RV *Albatross IV* on the Scotian shelf in March 1969 and 1970 and November 1969 (J. McEachran, pers. comm.) contained few *U. chuss* and many *U. tenuis*. Trawl collections made from RV *Cameron* between Canso, Nova Scotia, and Banquereau Bank in August 1970 and 1971 contained very few *U. chuss* but many *U. tenuis* (C. Wenner and J. McEachran, pers. comms.). To my knowledge the most northeastern locality from which voucher specimens of *U. chuss* are available is lat. 43°39′N, long. 59°26.5′W (Virginia Institute of Marine Science lot No. 01957) collected by otter trawl from RV *Cameron*, 14 July 1971, at a depth of 197 m. Both *U. chuss* and *U. tenuis* have been reported frequently from the Gulf of Maine and the Mid-Atlantic Bight as far south as Cape Hatteras, N.C. (Musick, 1969).

Svetovidov (1955) classified *Phycis borealis* Saemundson 1913, an Icelandic form, as a junior synonym of *U. tenuis*. Icelandic specimens examined during my study confirm Svetovidov's taxonomic judgment and document the range extension of the species to Iceland. Similarly Bullis and Thompson (1965) reported *U. tenuis* from the continental slope of the east coast of Florida. I examined these specimens and confirm their identification as *U. tenuis*.

Fraser-Brunner (1925) reported two small specimens of *U. chuss* from the Irish Atlantic slope but was not certain of their identity: "Two small specimens [25 and 55 mm standard length] apparently referable to this species (*U. chuss*) were taken in the tow net near the surface . . . ." *Urophycis chuss* of this size were considered to be unidentifiable by American workers such as Bigelow and Welsh (1925) who had many opportunities to examine small specimens. It is probable that Fraser-Brunner's postlarvae were a species of *Phycis*, not *Urophycis*.

The known ranges of the two species can now be summarized: *U. chuss* occurs on the continental shelf from southern Nova Scotia to North Carolina and may stray to the Gulf of St. Lawrence. *Urophycis tenuis* occurs on the continental shelf and slope from Iceland, Labrador, and the Grand Banks of Newfoundland to the coast of North Carolina, straying as far south as Florida in deep water.

Sampling Procedures

Data for a study of the seasonal distribution patterns of *U. chuss* and *U. tenuis* were collected during a groundfish survey conducted by the National Marine Fisheries Service at Woods Hole, Mass. The survey consisted of nine seasonal cruises by RV *Albatross IV* from the mouth of the Bay of Fundy to Hudson Canyon. Approximately 1,800 fishing stations were occupied, and cruises were conducted during the summer and fall in 1963, 1964, and 1965 and during the winter in 1964, 1965, and 1966.

The survey area was divided into 42 sampling strata according to depth (Figure 1), and stations were located randomly within strata. A No. 36

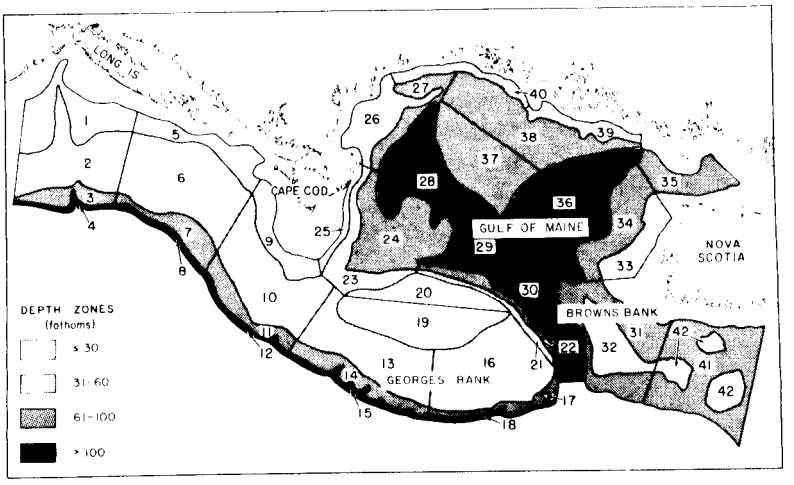

FIGURE 1.—Sampling strata where collections were made during the RV *Albatross IV* groundfish surveys. (After Grosslein, 1969.)

Yankee otter trawl with a cod-end liner (mesh diameter one-half inch stretched) was towed on the bottom for one-half hour at each station. Towing speed was approximately 3.5 knots. The sampling method and design were described in detail by Grosslein (1969). Length of specimens reported in the present paper is total length unless noted otherwise.

Factors Analyzed

Life History Stages

The following summary of the life histories of *U. chuss* and *U. tenuis* is extracted from Musick (1969). *Urophycis chuss* has pelagic eggs and pelagic larvae that descend to the bottom at a length of about 35 to 40 mm. The young then live within the mantle cavity of the sea scallop, *Placopecten magellanicus*. The largest *U. chuss* thus far found inside *Placopecten* have been 130 to 140 mm long. *Urophycis chuss* becomes mature at about 290 mm in length. The otter trawl used in the present study catches no eggs or larvae and very few pelagic juveniles; therefore, the life history of *U. chuss* was divided into three demersal stages defined by length: juvenile, ≤14 cm; immature, 15-28 cm; and mature, ≥29 cm. *Urophycis tenuis* has pelagic eggs and pelagic larvae which migrate to the bottom at a length of about 80 mm (or smaller sizes in shallow harbors and estuaries). *Urophycis tenuis* grows much larger than *U. chuss* and matures at about 500 mm in length. The life history can be divided into only two stages by length in the present study because of the notable lack of young fish in the trawl collections: immature, 9-50 cm; and mature, ≥51 cm. The biology of these species does not change abruptly in all individuals at a certain size. The size range over which major biological changes occur may be quite broad in populations of these *Urophycis*, but most of the individuals in the population within the size ranges cited above are also within the corresponding ontogenetic stage. By classifying individuals into life history stage by size, it is possible to use length-frequency data to determine whether the geographical distribution patterns of species change during ontogeny.

Natural Divisions of the Study Area

The survey region was divided into two natural subareas according to topography and hydrography. The southern New England subarea includes sampling Strata 1 to 19, i.e., the southern parts of Georges Bank, Nantucket Shoals, and the Mid-Atlantic Bight as far south as Hudson Canyon. The Gulf of Maine subarea includes sampling Strata 20 to 40, i.e., the Gulf of Maine including the northern edge of Georges Bank and Browns Bank (Figure 1).

Topography

The southern New England subarea is characterized by a broad, shallow continental shelf

that slopes gently seaward to about the 100-fathom (fm) isobath, the point sometimes designated as the shoreward limit of the continental slope. The slope itself declines much more steeply to the abyssal plain below. The distance between the 100- and 1,000-fm isobaths is 17 miles off New York City, 16 miles off Martha's Vineyard, and no more than 20 miles along the southern edge of Georges Bank. The width of the continental shelf "out to" the 100-fm isobath is 104 miles off New York City and 76 miles off Martha's Vineyard. Most of the southern New England subarea is contained within the 60-fm isobath.

The Gulf of Maine is a basin of irregular relief within the continental shelf, surrounded by a shallow sill formed by Georges Bank on the southeast, Browns Bank on the east, and the Seal Island Banks on the northeast. The sill in turn is pierced by three narrow channels, which have been named according to their locations: the Great South Channel, 40 fm maximum depth; the Eastern Channel, 128 fm maximum depth; and the Northern Channel, 65 fm maximum depth. Most of the Gulf of Maine is deeper than 60 fm, and the central Gulf, occupied by a Y-shaped trough, is deeper than 100 fm. The topography of the Gulf of Maine has been discussed in detail by Bigelow (1927).

Temperature

The following description of seasonal thermal regimes is compiled from Bigelow (1927, 1933) and original data collected during the *Albatross IV* surveys. The southern New England subarea has extreme seasonal temperature changes related to its shallowness. Bottom temperatures reach an annual minimum in late February or early March, and are lowest in the shoal waters close to shore and on Georges Bank and highest at the edge of the continental shelf (Figure 2). Spring warming proceeds most rapidly in the shallowest water. By early summer, thermal stratification occurs and prevents the bottom water from warming at intermediate depths (20 to 60 fm) which remain at 4° to 8°C (cooler than both the shoaler depths inshore and the deeper slope water offshore) (Figure 3).

Bottom temperatures in shallow areas attain the annual maximum by the beginning of fall. However, in intermediate depths the maximum is not reached until the thermocline is broken down, usually during October or November

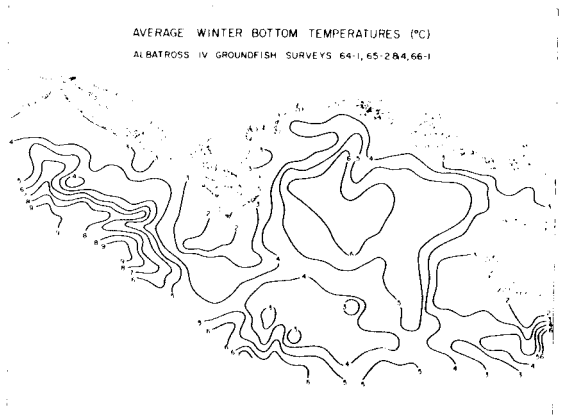

FIGURE 2.—Average winter bottom temperatures compiled from RV *Albatross IV* groundfish surveys 64-1, 65-2, 65-4, and 66-1.

(Figure 4). Winter cooling proceeds more rapidly in shoal water than at intermediate depths. Depths beyond 60 fm under the influence of slope water have relatively little fluctuation in bottom temperatures throughout the year.

In the Gulf of Maine, seasonal thermal changes on the bottom are most pronounced in the shoaler areas. Also, the banks on the Nova Scotian shelf are generally cooler by a few degrees than those to the west, because of the influence of the cold coastal current. Bottom temperatures over most of the Gulf are more stable than those off southern New England, because the deeper Gulf water is made up in part of warm moderating slope water which enters by way of the Eastern Channel.

Procedures of Analysis

Life History Stage by Sampling Strata

An analysis was performed to determine geographical and bathymetric distribution of *U. chuss* and *U. tenuis* by life history stage and season. Taylor (1953), Moyle and Lound (1960), and Roessler (1965) demonstrated that fish are not randomly distributed, but that the sampling distribution of the number of individuals of a species taken per sample in a series of collections is contagious and may be best approximated by the negative binomial distribution. The natural log transformation $Y = \ln(x+1)$, where x represents the number of individuals of a species taken at each station, tends to "normalize" the negative binomial distribution and substantially

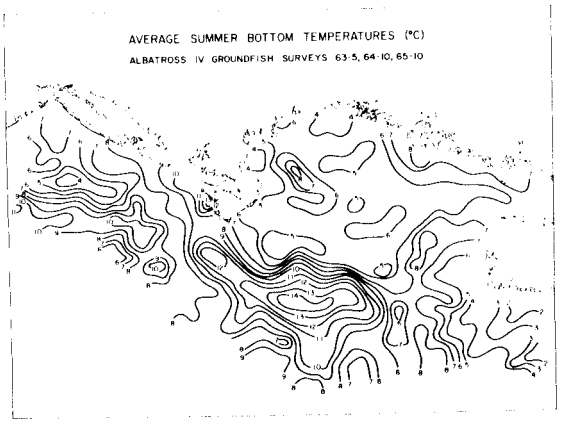

FIGURE 3.—Average summer bottom temperatures compiled from RV *Albatross IV* groundfish surveys 63-5, 64-10, 65-10.

reduces correlation between the mean and the variance (Pereyra, Heyamoto, and Simpson, 1967). An index of numerical abundance of *U. chuss* and *U. tenuis* was computed for each stratum by applying the above logarithmic transformation to each catch and calculating the transformed mean catch per stratum. Catch data from all 3 yr were pooled by season of collection, because *U. tenuis* did not occur frequently enough or in large enough numbers to allow calculation of reliable estimates of mean abundance in some strata on the basis of single cruises. Thus the analysis estimates average seasonal distribution for a 3-yr period probably with little distortion because hydrographic conditions in the principal areas of hake concentration did not differ drastically among the 3 yr.

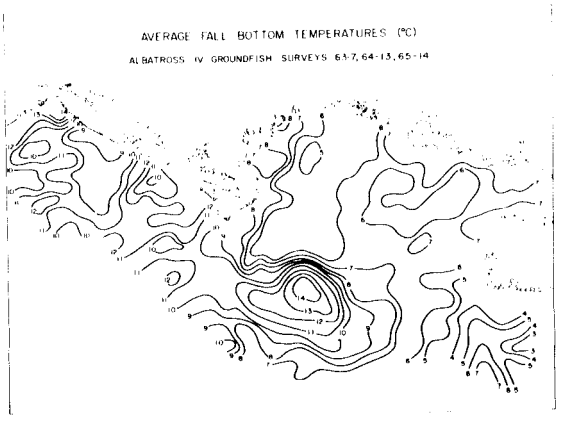

FIGURE 4.—Average fall bottom temperatures compiled from RV *Albatross IV* groundfish surveys 63-7, 64-13, and 65-14.

Analysis of Temperature and Distribution

The mean catch per tow at each 1°C temperature interval was computed by species, life history stage, subarea, and season. A few temperature intervals were not sufficiently sampled to provide reliable estimates of mean abundance.

RESULTS AND DISCUSSION

Seasonal Distribution of *U. chuss*

Juvenile (≤14 cm) *U. chuss* were rarely captured during summer cruises because young-of-the-year were pelagic and unavailable to the trawl, and most yearlings had grown larger than 14 cm and were classified as immature fish (Figure 5). In the fall juvenile *U. chuss* were most abundant off southern New England at depths shoaler than 60 fm (Figure 6). Their distribution coincides with that of the sea scallop, *Placopecten magellanicus*, which serves as a host to the young inquiline *U. chuss* (Musick, 1969). The shoreward distribution of *Placopecten* is limited by temperature off southern New England. Dickie (1958) found the upper lethal range to be 20° to 23.5°C, temperatures which occur normally in the summer in the shallow bays and sounds of southern New England. In the cooler Gulf of Maine, *Placopecten* are most abundant in inshore areas shoaler than 30 fm and occur commonly in shallow bays (Dow and Baird, 1960; Bourne, 1964). Thus in the Gulf of Maine, the

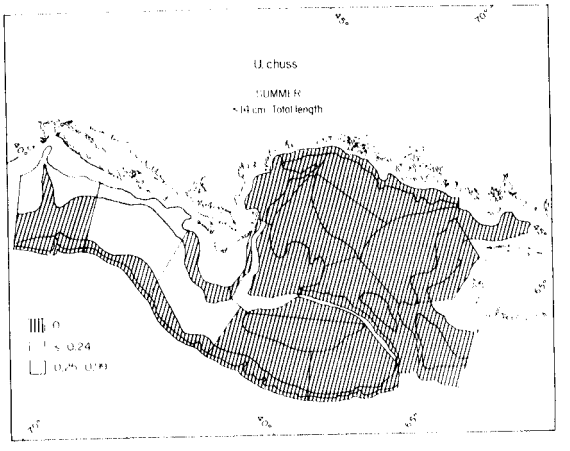

FIGURE 5.—Distribution and abundance of juvenile *Urophycis chuss* during the summer. Abundance in each sampling stratum is indicated on a log scale.

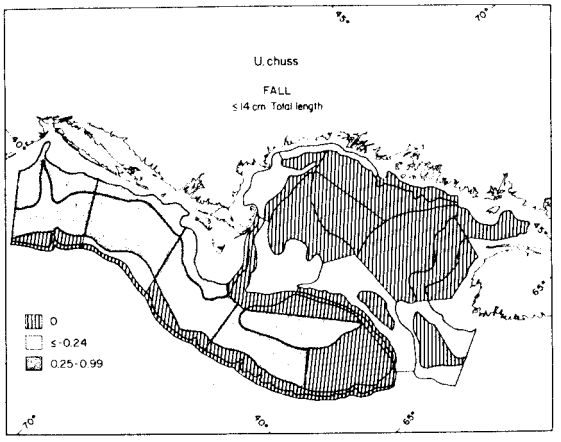

FIGURE 6.—Distribution and abundance of juvenile *Urophycis chuss* during the fall. Abundance in each sampling stratum is indicated on a log scale.

Placopecten habitat (the *U. chuss* nursery) was not sampled because no strata were shallower than 30 fm; consequently estimates of juvenile hake abundance were low.

Juvenile *U. chuss* appear to avoid water colder than 4°C (Figure 7). In winter (Figure 8), abundance of juvenile *U. chuss* increased in the Gulf of Maine probably because the temperature on the inshore *Placopecten* beds had dropped below 4°C, prompting the young *U. chuss* to migrate into deeper water where they became available to our sampling gear. Juvenile *U. chuss* were absent in winter from the shoaler Georges Bank strata where bottom temperatures were below 4°C. The winter temperature histogram for the Gulf of Maine shows juvenile *U. chuss* to be fairly abundant at 3°C (Figure 7). This apparent contradiction to the rest of the data is attributable to a single large trawl catch at 3°C. The winter distribution pattern of juvenile *U. chuss* off southern New England was similar to the fall pattern (Figure 8). Abundance values were lower, probably because of natural mortality and growth of some juveniles beyond 14 cm in length.

During the summer, immature (15 to 28 cm) *U. chuss* were abundant from the southern part of Georges Bank throughout the southern New England area at depths of 60 fm or less. Almost no immature fish were taken at depths of 100 fm or more off southern New England (Figure 9). Fish were most abundant at depths of 30 fm or less between Martha's Vineyard and Long Island (Stratum 5). In the Gulf of Maine, the heaviest

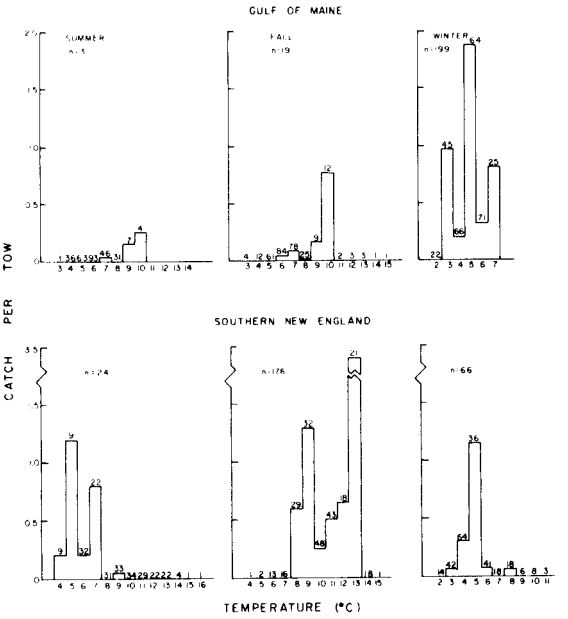

FIGURE 7.—Seasonal catch per tow of juvenile *Urophycis chuss* taken off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = *n*. The number of stations occupied at each temperature is indicated above each respective histogram bar.

concentrations of fish were found in the Great South Channel (Stratum 23). Moderate numbers were taken in the deeper strata to the north of the channel area and in shoal water on Georges Bank.

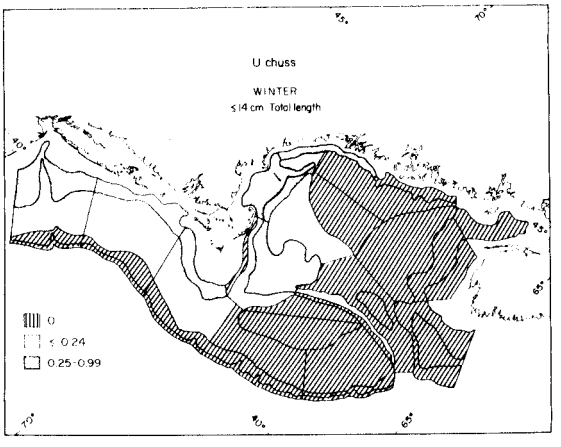

FIGURE 8.—Distribution and abundance of juvenile *Urophycis chuss* during the winter. Abundance in each sampling stratum is indicated on a log scale.

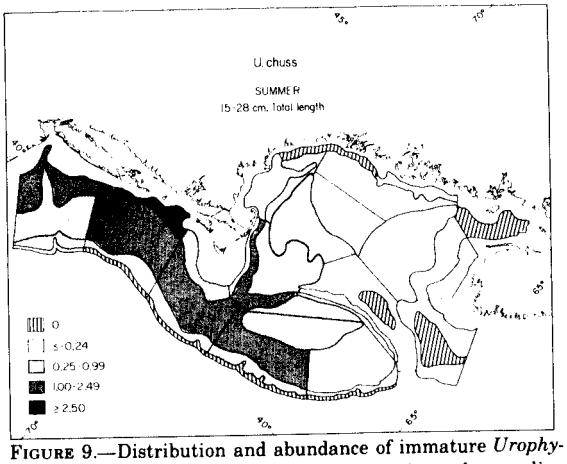

FIGURE 9.—Distribution and abundance of immature *Urophycis chuss* during the summer. Abundance in each sampling stratum is indicated on a log scale.

The fall distribution pattern off southern New England (Figure 10) suggests a movement inshore which is further substantiated by an increase of *U. chuss* in the inshore industrial fisheries landings in October and November (Edwards and Lux, 1958; Edwards, 1958a, 1958b; Edwards and Lawday, 1960). Edwards (pers. comm.) has noted that this fall fishery off southern New England landed mostly small hake. Also reports by Smith (1898) for Woods Hole; Latham (1917) for Orient, Long Island; Breder (1922) for Sandy Hook Bay; and Hildebrand and Schroeder (1928) for the New Jersey coast and New York Bay document an immigration of *U. chuss* in these inshore areas in the fall with an emigration in the winter.

In the Gulf of Maine, immature *U. chuss* were moderately abundant in the fall around the entire perimeter in strata shoaler than 60 fm.

The winter distribution of immature *U. chuss* was essentially limited to those strata deeper than 30 fm off Long Island, 60 fm off Nantucket, and 100 fm along the southern edge of Georges Bank (Figure 11). In the Gulf of Maine immature *U. chuss* were moderately abundant in strata deeper than 60 fm. Concentrations occurred between 60 and 100 fm along the northern edge of Georges Bank and off Massachusetts Bay and Jeffries Ledge (Stratum 27). The only strata shoaler than 60 fm with moderate values of abundance were 26 and 40, located in the southwestern part of the Gulf where temperatures were warmer than to the north and east.

Immature *U. chuss* were taken during three seasons within the entire temperature range with the exception of the highest intervals (15° to 16°C), which were inadequately sampled (Figure 12). Most immature fish were taken between 5° and 13°C. As with the juveniles, immature *U. chuss* were absent from the shallow parts of Georges Bank during the winter and they may avoid water colder than 4°C. Edwards (1965) noted that in the late fall most *U. chuss* had migrated from the inshore industrial fishing grounds when the water temperature dropped to 5°C.

Adult *U. chuss* migrate inshore in the spring of the year. Smith (1898) reported *U. chuss* to be abundant at Woods Hole in May or June but rare

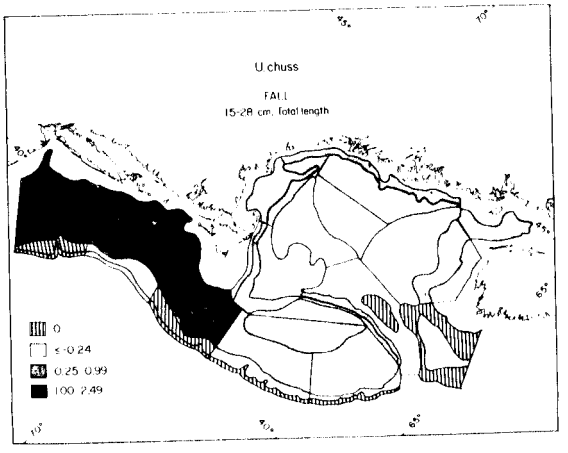

FIGURE 10.—Distribution and abundance of immature *Urophycis chuss* during the fall. Abundance in each sampling stratum is indicated on a log scale.

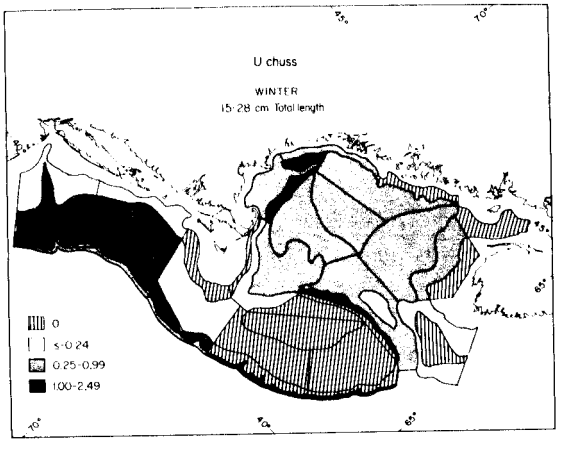

FIGURE 11.—Distribution and abundance of immature *Urophychis chuss* during the winter. Abundance in each sampling stratum is indicated on a log scale.

in the summer. Latham (1917) reported *U. chuss* from Orient, Long Island, in the spring but not summer. Breder (1922) noted *U. chuss* from Sandy Hook Bay in the spring; and Hildebrand and Schroeder (1928) reported that off New Jersey and New York *U. chuss* appeared in April, distended with spawn, that they remained close inshore for a short period, were caught 2 to 6 miles off until late May, and in July were abundant offshore on Cholera Bank. Edwards and Lawday (1960) reported that *U. chuss* were abundant in the industrial fish landings in April and May from the shallow inshore fishing grounds off No Man's Land, Mass., and Point Judith, R.I. The fish dispersed in June and July and were less available to the fishery.

After they migrate inshore in the spring, southern New England *U. chuss* migrate offshore in the summer to spawn. Mature *U. chuss* were heavily concentrated during the summer (Figure 13) in the strata shoaler than 60 fm off Block Island and on the southwest part of Georges Bank.

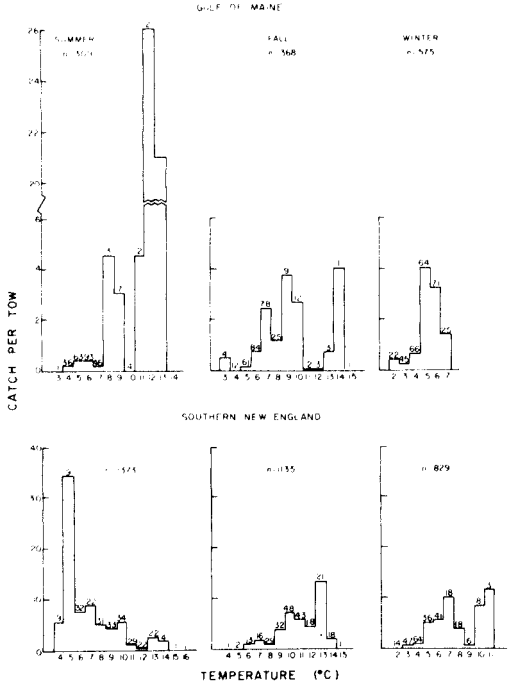

FIGURE 12.—Seasonal catch per tow of immature *Urophycis chuss* taken off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = *n*. The number of stations occupied at each temperature is indicated above each respective histogram bar.

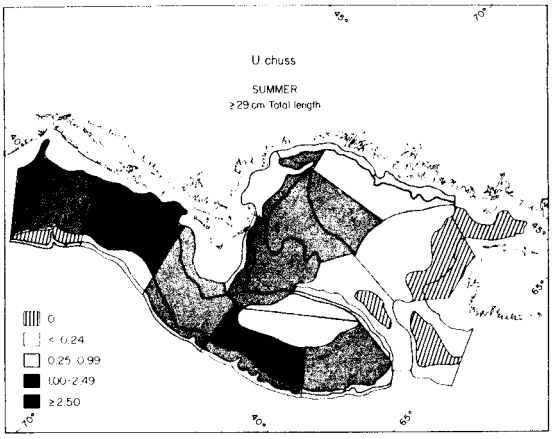

FIGURE 13.—Distribution and abundance of mature *Urophycis chuss* during the summer. Abundance in each sampling stratum is indicated on a log scale.

These concentrations were probably spawning aggregations because ripe fish were taken quite frequently during the survey (Musick, 1969). Also Domanevsky and Nozdvin (1963) reported spawning aggregations of *U. chuss* offshore on Georges Bank in July and August. Although a small number of *U. chuss* remain in the southern New England sounds during the summer (Edwards and Lawday, 1960), these are probably immature fish because spawning does not occur there. Wheatland (1956) found no *U. chuss* eggs or larvae in Long Island Sound, and Merriman and Sclar (1952) took no eggs but captured larvae in Block Island Sound, an area less land-locked and more adjacent to deep water than the previous one.

U. chuss emigration from shallow southern New England waters to offshore spawning grounds is probably correlated with temperature. Figure 14 shows that *U. chuss* were not abundant within adequately sampled temperature intervals higher than 12°C. Riley (1956) noted that temperatures exceeded 12°C over most of Long Island Sound during June and increased until October when temperatures were in excess of 20°C. Edwards, Livingstone, and Hamer (1962) reported that during the summer off southern New England *U. chuss* were most abundant at about 9°C, and Edwards (1965) showed that *U. chuss* migrated offshore when the bottom temperature reached about 10°C in the early summer.

In the Gulf of Maine *U. chuss* became available to the shallow water trawl fishery off Gloucester and Ipswich, Mass., in April or May

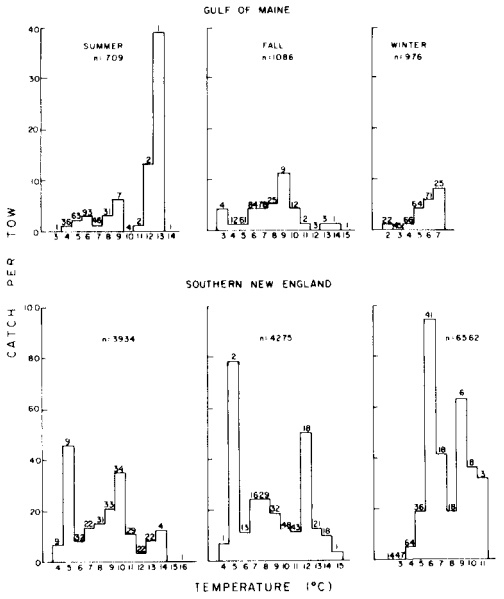

FIGURE 14.—Seasonal catch per tow of mature *Urophycis chuss* off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = *n*. The number of stations occupied at each temperature is indicated above each respective histogram bar.

(Edwards, 1958a; Edwards and Lawday, 1960) and increased in abundance until August. Thus mature *U. chuss* are abundant in the summer at depths less than 30 fm. The *Albatross IV* survey data (Figure 13) which show highest values of abundance in strata 60 fm and deeper are probably not indicative of the true summer distribution of *U. chuss*. Both the industrial fishery and region of greatest abundance in the *Albatross IV* survey are in the southwestern section of the Gulf, but the fishery and survey data were taken at different depths. Additional evidence that *U. chuss* congregate in the summer at depths less than 30 fm comes from Bigelow and Schroeder (1953). They noted that *U. chuss* spawns in the Gulf in the summer and that most eggs and larvae have been collected close to shore. Water temperatures inshore are comparable to those that occur in known offshore spawning areas of *U. chuss* off southern New England (5°-10°C). Similar temperatures also occur in deeper waters of the Gulf, but young *U. chuss* spawned in such areas would have little chance of finding *Placopecten* for shelter after descending because *Placopecten* is restricted to shoal areas of the Gulf (Dow and Baird, 1960). Therefore, there may be selection for inshore spawning in the Gulf of Maine.

During the fall (Figure 15), mature *U. chuss* were dispersed over the entire survey area, but the original data (Musick, 1969) show that most individuals longer than 32 cm had moved into water deeper than 60 fm. The winter distribution pattern of mature *U. chuss* (Figure 16) shows that a very strong offshore movement occurred in water deeper than 60 fm, in the Gulf of Maine, and off southern New England. The fish were most heavily concentrated along the edge of the continental slope from the southwest part of Georges Bank to Hudson Canyon. Edwards et al. (1962) reported *U. chuss* to be most abundant in winter between 100 and 250 fm in their study area south of Nantucket. In addition, Edwards et al. (1962) found that *U. chuss* were "most abundant where the water temperature was between 47°F (8.3°C) and 50°F (10.0°C)," values which are within the range which adult hake were most abundant in the present study (5-12°C).

Juvenile and immature *U. chuss* occurred within a narrower temperature range than the adults. However, the latter were more concentrated within relatively narrow temperature limits. This implies that although adults may tolerate a wider range, they may prefer a narrower range than young fish do or, at least, are more mobile and can undertake longer and faster seasonal migrations, thus remaining within relatively narrower temperature limits throughout the year. Such behavior might allow the fish to maintain an optimal thermal environment for gonadal development, spawning, and feeding during various times of the year.

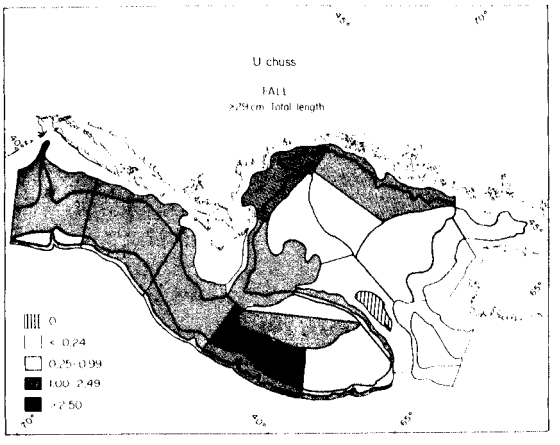

FIGURE 15.—Distribution and abundance of mature *Urophycis chuss* during the fall. Abundance in each sampling stratum is indicated on a log scale.

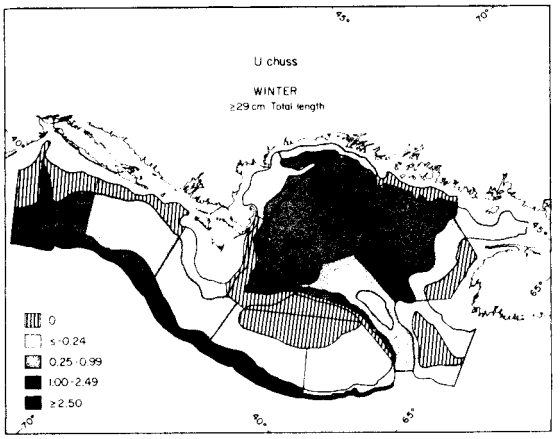

FIGURE 16.—Distribution and abundance of mature *Urophycis chuss* during the winter. Abundance in each sampling stratum is indicated on a log scale.

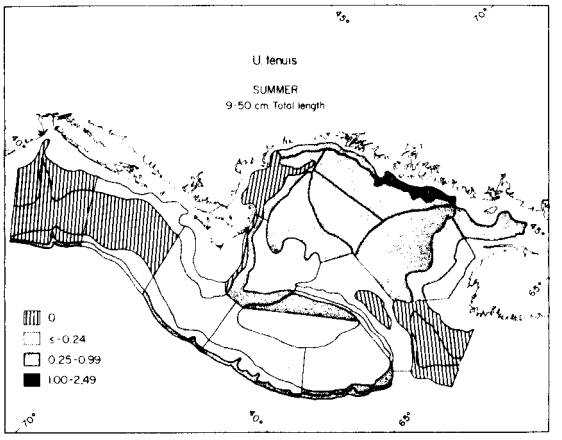

FIGURE 17.—Distribution and abundance of immature *Urophycis tenuis* during the summer. Abundance in each sampling stratum is indicated on a log scale.

Seasonal Distribution of *U. tenuis*

During summer (Figure 17), immature *U. tenuis* were rare or absent over most of the southern New England area. Moderate numbers were taken in the strata deeper than 100 fm off Nantucket and the southern part of Georges Bank and the strata deeper than 60 fm along the eastern part of Georges Bank. In the Gulf of Maine, immature *U. tenuis* were taken in moderate numbers in the Great South Channel (Stratum 23) and in the northern part of the Gulf. The highest abundance value was in Stratum 39 off the northern Maine coast.

In the fall, immature *U. tenuis* were most abundant in the northern and eastern parts of the Gulf (Figure 18), and moderately abundant in the deep central Gulf, the Great South Channel, and on the middle and northern edge of Georges Bank. Immature *U. tenuis* were also abundant in the stratum deeper than 100 fm at the eastern edge of Georges Bank and moderately abundant in strata deeper than 60 fm to the south and west off southern New England. Only one stratum south of Georges Bank less than 60 fm deep (Stratum 2) had moderate numbers of *U. tenuis*. This stratum includes the inshore extension of Hudson Canyon.

In the Gulf of Maine during the winter (Figure 19), immature *U. tenuis* were most abundant in the deeper northern strata (Strata 36 and 38) and along the northern edge of Georges Bank. Immature *U. tenuis* were absent or rare in areas less than 60 fm off southern New England but were fairly abundant in some strata deeper than 100 fm.

Indices of abundance of *U. tenuis* by temperature interval were less reliable than those of *U. chuss* because *U. tenuis* was much less abundant, particularly off southern New England. Single large tows often lowered the precision of mean catch estimates because of the relatively small total number of *U. tenuis* collected. Consequently, for some seasons only temperature ranges can be discussed. In the southern New England area, immature *U. tenuis* were taken from 4° to 14°C in the summer. Only one station was made at 15°C and at 16°C. Although *U. tenuis* was not taken there, the sampling

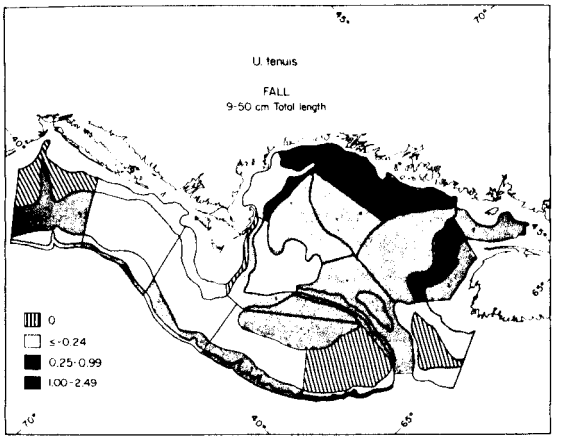

FIGURE 18.—Distribution and abundance of immature *Urophycis tenuis* during the fall. Abundance in each sampling stratum is indicated on a log scale.

intensity does not give a true indication of its presence or absence. During the fall, immature *U. tenuis* occurred over the entire temperature range, 4° to 15°C. In the winter, they were taken from 3° to 10°C. In the Gulf of Maine in the summer, immature *U. tenuis* occurred from 4° to 9°C and the highest mean catch was at 8°C. The fish were absent at 3°C and from 10° to 14°C; however, these temperature intervals were not adequately sampled. In the fall, immature *U. tenuis* occurred from 3° to 11°C and the highest mean abundance was at 9°C. The fish were absent from 12° to 15°C but the sampling intensity at these temperatures was inadequate. In the winter, only a few fish were taken at 2°C and 3°C and mean catches increased from 4° to 7°C. Immature *U. tenuis* were taken over an annual range of 2° to 15°C but were most abundant between 4° and 10°C (Figure 20).

During the summer (Figure 21), mature *U. tenuis* were rare or absent off southern New England except in two strata deeper than 100 fm. They were moderately abundant in the Gulf of Maine and heavily concentrated in Stratum 39 along the northern coast of Maine. In the fall (Figure 22), off southern New England, mature *U. tenuis* were moderately abundant in all strata deeper than 100 fm, in two strata from 60 to 99 fm deep, and in only one stratum from 30 to 59 fm deep. They were rare or absent in all other southern New England strata. Mature *U. tenuis* were moderately abundant in the Gulf of Maine. The highest values of abundance are in Strata 27 and 28, between 60 and 100 fm.

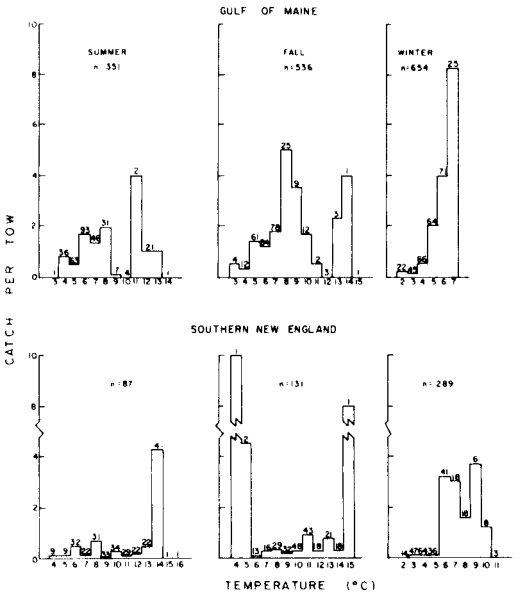

FIGURE 20.—Seasonal catch per tow of immature *Urophycis tenuis* off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = *n*. The number of stations occupied at each temperature is indicated above each respective histogram bar.

During the winter off southern New England (Figure 23), mature *U. tenuis* were rare or absent in all strata shoaler than 100 fm except Stratum 7, which was 60 to 99 fm deep. Mature *U. tenuis* were moderately abundant there and in all strata deeper than 100 fm. In the Gulf of Maine, mature *U. tenuis* were absent from all strata

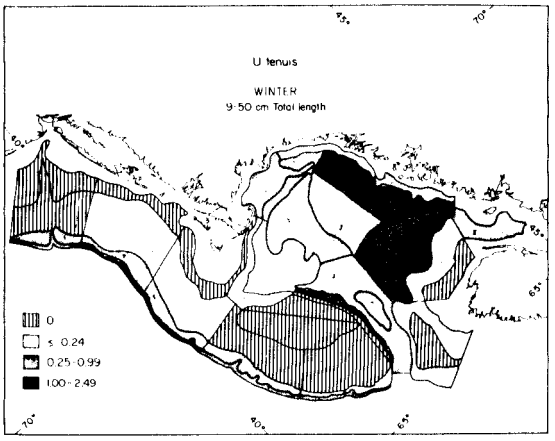

FIGURE 19.—Distribution and abundance of immature *Urophycis tenuis* during the winter. Abundance in each sampling stratum is indicated on a log scale.

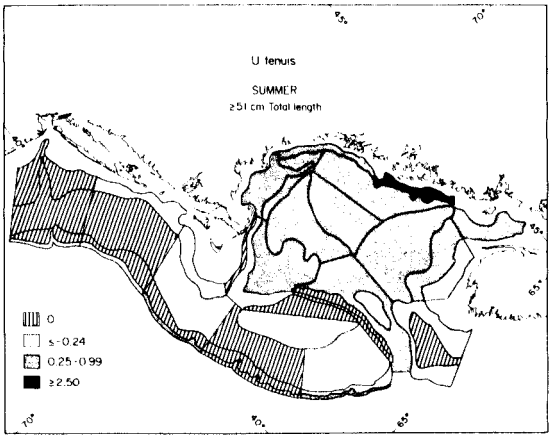

FIGURE 21.—Distribution and abundance of mature *Urophycis tenuis* during the summer. Abundance in each sampling stratum is indicated on a log scale.

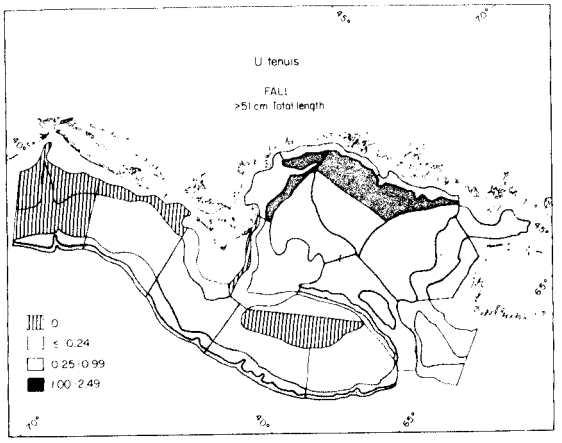

FIGURE 22.—Distribution and abundance of mature *Urophycis tenuis* during the fall. Abundance in each sampling stratum is indicated on a log scale.

shoaler than 60 fm. They were moderately abundant in most deeper strata and most abundant in Strata 28 and 36, which were deeper than 100 fm.

Catches of adult *U. tenuis* off southern New England were very small. Consequently, temperature-abundance estimates (Figure 24) are not reliable. Adult *U. tenuis* occurred from 6° to 12°C in the summer, from 4° to 13°C in the fall, and from 4° to 10°C in the winter. Adult *U. tenuis* were taken in the Gulf of Maine from 4° to 9°C in the summer (Figure 24). The highest mean catch was at 8°C. During the fall, the range of occurrence was 3° to 11°C, the highest mean catch occurring at 9°C, and in the winter the range was 2° to 7°C, the highest mean catch occurring at 7°C.

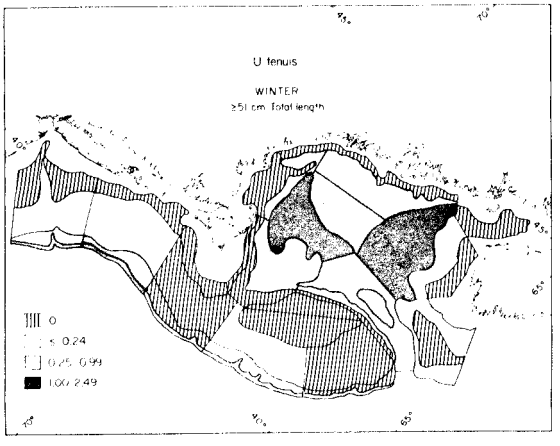

FIGURE 23.—Distribution and abundance of mature *Urophycis tenuis* during the winter. Abundance in each sampling stratum is indicated on a log scale.

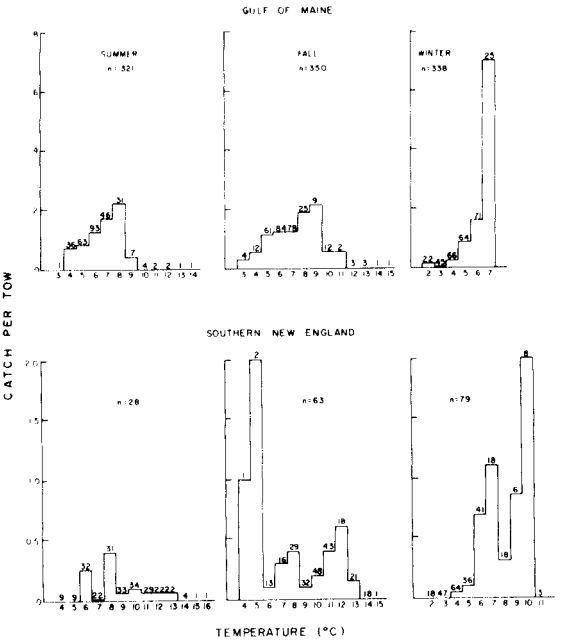

FIGURE 24.—Seasonal catch per tow of mature *Urophycis tenuis* off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = n. The number of stations occupied at each temperature is indicated above each respective histogram bar.

Annually, adult *U. tenuis* were taken from 2° to 13°C but were most abundant between 5° and 9°C. Adult *U. tenuis* appear to occupy a more restricted temperature range than immature *U. tenuis*. Also, adult *U. tenuis* occupy a narrower and lower temperature range than adult *U. chuss*.

U. tenuis may be more abundant off southern New England than the survey data indicate. Edwards et al. (1962) and Schroeder (1955) frequently captured *U. tenuis* along the continental slope off southern New England at greater depths than those sampled during the *Albatross IV* survey and recent research (Musick, unpublished data) indicates that *U. tenuis* is a common member of the continental slope fish fauna of Virginia.

Distribution of *Urophycis chuss* and *U. tenuis* with Substrate

U. chuss and *U. tennuis* are absent or rarely occur on rock, shell, or gravel bottoms. Both "prefer" sand or mud. Few or no *Urophycis* occurred in Strata 24, 32, and 33 during any season.

These strata are dominated by rock or gravel bottoms (Fritz, 1965, Plate B). Storer (1858), Goode (1884), Hildebrand and Schroeder (1928), and Bigelow and Schroeder (1939) noted the association of *U. chuss, U. tenuis*, or both with mud bottoms. Bigelow and Welsh (1925) reported that both species dwelled over soft bottoms (silt, sand, or mud) but that the *U. tenuis* was more strictly a "mud fish" than the *U. chuss*. The *Albatross IV* data appear to agree with the last statement, because the regions where *U. tenuis* occurred most commonly are dominated by muddy or silty substrates—the northeastern Gulf of Maine, the central basins of the Gulf, and along the continental slope on Georges Bank and southwest. However, these areas are also cooler during the summer, and the correlation between *U. tenuis* abundance and mud bottoms (rather than sand) may be an artifact. *Urophycis chuss* were abundant over mud or sand or both depending on season, because the deeper strata were covered with muddy substrates whereas the shallower strata in the southwest Gulf of Maine and off southern New England were covered with sand (Fritz, 1965, Plate B).

ACKNOWLEDGMENTS

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DEVELOPMENT OF EGGS AND LARVAE OF *CARANX MATE* (CARANGIDAE)[1]

JOHN M. MILLER AND BARBARA Y. SUMIDA[2]

ABSTRACT

The development of eggs and larvae of omaka (*Caranx mate*) is described from approximately 2 h after fertilization to day 36 after hatching. The pelagic, spherical eggs (700-740 μ diameter) had a single oil droplet and hatched after about 26 h incubation at 24.5°C. The average growth rate in culture was 0.44 mm/day; feeding began four days after hatching. Fin development and ossification of omaka occurred at smaller sizes, but in the same sequence as jack mackerel (*Trachurus symmetricus*) off California. Of the body proportions measured, body depth was most useful in separating omaka from at least two other species of carangid larvae. The pigment pattern was also of diagnostic value. Reared larvae were indistinguishable from similar-sized field specimens.

Omaka (*Caranx mate*) is one of the most abundant carangids in the Hawaiian Islands. The species is rather widespread throughout the Indo-Pacific, reaching the eastern coast of Africa. In Hawaii, the preferred habitats are estuaries, bays, and harbors with relatively long water residence times. Kuthalingham (1959) described the feeding habits of omaka near Madras, India. The growth rate of captive adult omaka was reported by Watarai (1973).

Omaka have a protracted spawning period in Hawaii; the eggs can be taken with fair regularity from March through September from the surface waters of Kaneohe Bay, Oahu. Little else is known of the spawning habits. However, a biweekly year-round fish-egg survey in Kaneohe Bay indicated three spawning peaks: one in April and May, another in September and October, and a third, smaller, peak in July (Watson and Leis, 1973).[3] During these peaks omaka eggs were by far the most abundant of any, occasionally exceeding concentrations of 10/m^3 in the surface waters of south Kaneohe Bay. Larval densities, on the other hand, were found to be much lower than these egg densities, rarely reaching 0.1/m^3 (Watson and Leis, see footnote 3). As is characteristic of many carangids, young are frequently seen under medusae. Large larvae and juveniles are similarly attracted to floating raffia, and have been collected in this manner. Adult omaka do not appear to make the offshore spawning movements characteristic of many of the resident fish species in Kaneohe Bay.

MATERIALS AND METHODS

Larvae used for description came from two sources: reared specimens and field specimens. Reared larvae of known age were the primary source of material; field specimens were used mainly to verify observations and conclusions based on the former. Over the past 2 yr omaka larvae have been taken in numerous plankton tows. Each time that comparisons were made between similar-sized field and reared specimens, the larvae were indistinguishable.

Larvae were obtained from two cultures (called Series A) begun in February 1971. One of these (A1) supplied larvae through day 5 (Table 1). This culture was terminated on day 6, when high mortality (of unknown cause) was experienced. Although the sizes of these larvae are included in the growth rate curve (Figure 4), they were not used in the description of developmental stages. The second (A2) was maintained for 36 days during which post yolk sac specimens (day 6 and older) were taken for description.

Two other cultures (Series B) were begun in May 1972 to provide eggs and yolk-sac larvae. The first, begun 1 May, was to determine the approximate rate of development and design a

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[3]Watson, W., and J. M. Leis. 1973. Ichthyoplankton in Kaneohe Bay: A one-year study of the fish eggs and larvae. Unpubl. manuscr.

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TABLE 1.—*Caranx mate*—reared larvae, 22 February-31 March 1971.

Date	Age (day)	No. larvae picked	Standard length(mm) mean	Standard length(mm) range
Feb. 22 (eggs collected & hatched)				
SERIES A				
A1				
Feb. 23	1	8	1.36	1.16-1.55
Feb. 24	2	10	2.18	1.47-2.50
Feb. 25	3	10	2.46	2.13-2.58
Feb. 26	4	5	2.59	2.55-2.68
Feb. 27	5	5	2.57	2.35-2.84
A2				
Feb. 28	6	10	3.05	2.94-3.19
Mar. 1	7	10	3.24	2.77-3.39
Mar. 2	8	10	3.46	3.31-3.75
Mar. 4	10	10	3.97	3.50-4.41
Mar. 6	12	10	4.47	3.48-5.33
Mar. 8	14	10	5.17	4.28-5.75
Mar. 10	16	10	6.21	5.83-7.00
Mar. 12	18	10	7.43	5.58-8.42
Mar. 14	20	10	8.27	7.25-8.88
Mar. 16	22	10	9.50	8.13-10.63
Mar. 18	24	10	10.41	8.88-12.00
Mar. 20	26	10	10.89	8.63-11.75
Mar. 22	28	10	11.42	9.38-12.75
Mar. 24	30	10	12.46	10.63-14.95
Mar. 27	33	10	13.83	11.50-17.25
Mar. 30	36	5	16.62	14.28-18.00
Mar. 31 (Terminated—no larvae remaining)				

sampling schedule. The second, begun 5 May, provided most of the specimens used in the description, although certain additional measurements (e.g., size at hatching) were made on specimens from the first culture.

Series A Cultures

One thousand eggs were pipetted from the washed plankton of a surface tow with a 505 μ mesh meter net in south Kaneohe Bay, Oahu, on 22 February 1971. These eggs were placed in a 78-liter fiberglass and glass aquarium which had been filled with triple CUNO[4] filtered (5 μ effective pore size) bay water. The water was previously exposed to long-wave ultraviolet light for 1 min. Penicillin (to a concentration of 50 mg/liter) and Polymixin B (to a concentration of 8 mg/liter) were added before introduction of the eggs. These antibiotics have been shown to substantially reduce bacterial counts in cultures and materially increase hatching success of omaka eggs (Struhsaker, Hashimoto, Girard, Prior, and Cooney, 1973). A *Chlorella* sp. culture was added initially to an approximate cell count of 10×10^4 cells/ml.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Salinity, oxygen, and temperature in the tank were usually measured daily. Salinity remained nearly constant throughout the experiment at 35‰, the value in the bay at the time of collection. Oxygen values ranged from 6.1 to 9.5 mg/liter during the subsequent 36 days. The maximum range of temperature in the tank was 21.5 to 25.9°C, with a 36-day mean of 24.5°C. The bay surface temperature at the time of collection was 24.4°C.

The tank was continuously illuminated by two 40 watt fluorescent "daylight" bulbs. The light intensity at the surface of the water was approximately 6.5×10^3 flux. The tank was aerated with a single airstone, with airflow adjusted to produce a slow single stream of bubbles.

Food was added daily from the third day after hatching. Through day 11 the food was the 75-150 μ fraction of wild zooplankton attracted to a night light suspended in the bay. On day 12 the addition of wild plankton was replaced with additions of *Artemia* nauplii. Wild plankton and *Artemia* were added each time to a concentration in the tank of 5/ml and 1/ml, respectively. No doubt the culture tank supported other (unknown) populations of plankters and microorganisms.

Usually ten larvae were captured by dipping or pipetting at about two-day intervals from hatching (the day after introduction of the eggs) until 36 days after that time (Table 1). No attempt was made to select particular sized larvae.

Series B Cultures

Larvae reared for yolk-sac-stage description were hatched from eggs taken from Kaneohe Bay on 5 May 1972. At the time of collection (midafternoon), eggs were found in both late middle stage and early stage, i.e., from two spawnings. Only the latter (in blastodisc stage) were selected for culture. (The exact time of fertilization is unknown; hence the duration of the early stage was estimated.) Extrapolating from the subsequent rate of development, we estimate the eggs had been fertilized for about 2 h before capture.

Two hundred eggs were placed in each of four 4-liter beakers of unfiltered seawater obtained about two miles offshore from Kaneohe Bay. This "offshore" water contained less plankton

and, in general, was of higher quality than that found in the bay used in the Series A cultures. Salinity was always about 35‰.

Water temperature in the beakers during the experiment ranged from 23.5 to 24.4°C. Bay surface temperature at the time of collection was 25°C. No food or algae was added to these cultures. Erythromycin gluceptate was added to a concentration of 9 mg/liter before introduction of the eggs. The beakers were continuously illuminated with fluorescent lights.

Eggs and larvae were pipetted from these cultures, which were terminated on the sixth day after hatching. Larvae were immobilized in a refrigerator (ca. 10°C) before preservation in 2.5% buffered formaldehyde. This practice resulted in fewer distorted and curled larvae than did placing them directly in preservative.

All measurements and counts were made with a microscope equipped with an ocular micrometer. At the usual magnification (50×) the precision of measurement is ± 0.02 mm. Illustrations are camera lucida drawings, subsequently inked, by B. Sumida. Owing to rapid loss of certain pigments after preservation, a size series of larvae was microphotographed with color film for subsequent reference.

Illustrations of early larvae (day 6 and younger) show pigment patterns observed in live larvae. Pigment patterns retained after preservation are so noted in the text. Pigments stabilized in older larvae so that differences between live and dead larvae became much less pronounced with age. Illustrations of these larger larvae (day 8 and older) were made from preserved specimens.

DEFINITIONS, MERISTICS AND MORPHOMETRICS

Body depth At insertion of pectoral fin. (Prior to pectoral bud formation, taken through shoulder.)

Dorsum Region dorsal to medial horizontal line through body.

Eye diameter Horizontal diameter of orbit.

Head length Tip of snout to posterior margin of operculum.

Larva Larva after yolk absorption completed and prior to metamorphosis when scales and lateral line develop. (All of our specimens were larvae based on this definition.)

Lateral line streak Dashed line of pigment along the lateral midline of body.

Snout to anus length Tip of snout to vertical from anus.

Standard length (SL) Prior to notochord flexion and formation of hypural bones, SL taken from snout to tip of notochord. Thereafter, taken to posterior margin of hypural plate. $\overline{SL}$ = mean standard length. Deviations from means are standard deviations. All length measurements were made on preserved specimens, except where noted.

Ventrum Region ventral to medial horizontal line through body exclusive of abdominal area; generally area inclusive of hypomeres.

Yolk sac larva Larva from hatching to approximately the third day when yolk absorption was nearly complete.

DEVELOPMENT OF THE EGG

Because the development of the omaka egg proceeds rapidly in discrete stages, we have chosen to summarize it as follows:

Early stage

Blastodisc stage to blastopore closure (fertilization to blastopore closure) (Figure 1A).

Egg size:

(diameter) Live: 722 ± 19 μ.

Preserved: 722 ± 19 μ.

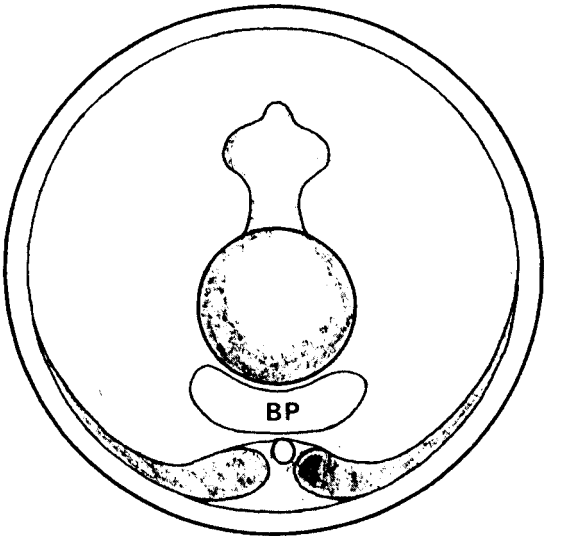

FIGURE 1A.—Ventral view of early stage egg of *Caranx mate*. BP = blastopore.

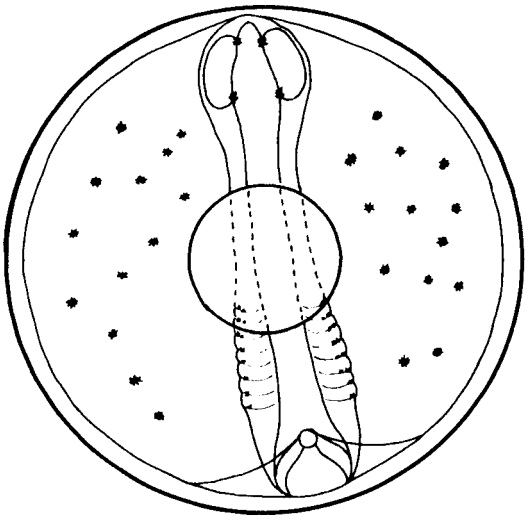

FIGURE 1B.—Early middle stage egg. Ventral view of embryo.

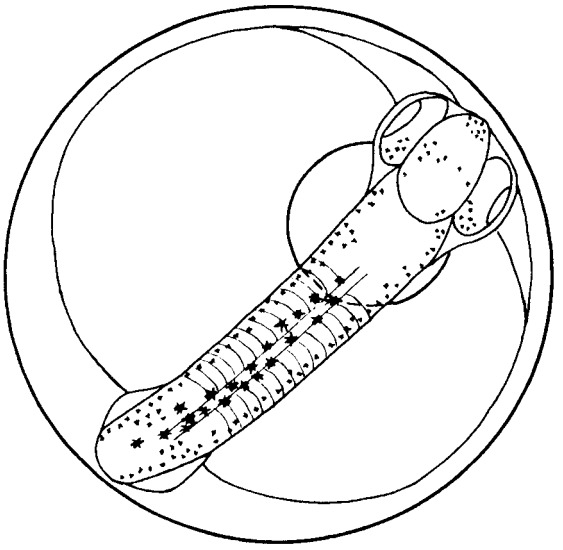

FIGURE 1D.—Dorsal view of advanced middle stage egg. Pigment on oil globule omitted.

The omaka egg is pelagic, clear, and spherical with a single oil droplet at the vegetative pole. At the time of collection the eggs were in the early blastodisc stage.

Oil globule:

Diameter in live egg: 190-200 μ.

Diameter in preserved egg: 176-192 μ.

Positioned at the vegetative pole, the oil globule was almost centered on the polar axis of the developing blastodisc (Figure 1A) and later between the head and tail bud of the early embryo. At the time of blastopore closure, the oil globule was situated slightly off-center and closer to the tail end of the developing embryo. The blastopore closed between the oil globule and the tail end of the embryo.

Perivitelline space:

Size range: 26 ± 4 μ.

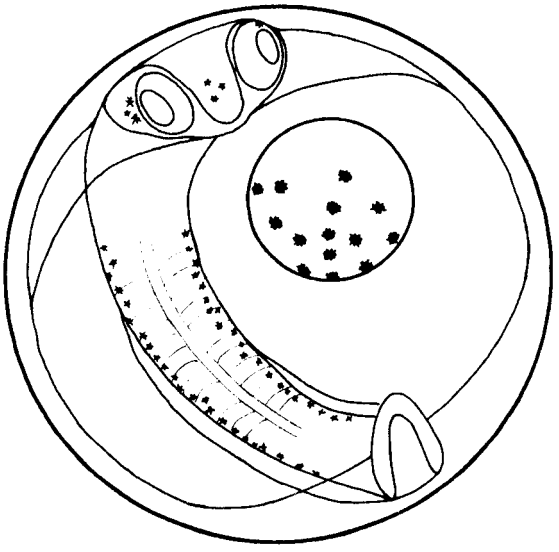

FIGURE 1C.—Ventro-lateral view of advanced middle stage egg, showing oil globule pigmentation.

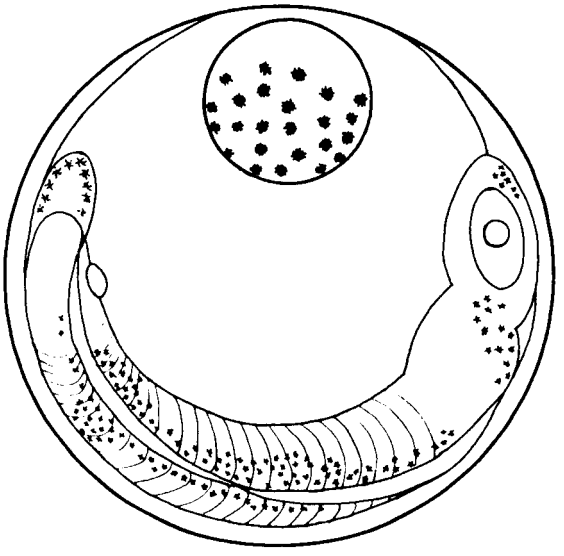

FIGURE 1E.—Lateral view of early late-stage egg.

The perivitelline space was not evident in the early blastoderm stages but developed as the egg advanced.

Yolk:

(diameter) 660± 23 μ.

The segmentation of the yolk was apparent in the form of irregular polygons across the egg diameter in the early stage eggs (not illustrated). This pattern was lost with preservation of the eggs in 2.5% formaldehyde, whereupon the yolk took on a "bubbly" irregular appearance.

Embryo development:

The optic vesicles were evident on the young embryo before blastopore closure of the egg (not illustrated). Initiation of somite development in the anterior end of the embryo was also observed before closure of the blastopore. Kupffer's vesicle was conspicuous at the tip of the rudimentary tail bud.

Pigmentation:

No pigmentation was present in the egg or embryo during this stage.

Duration of early stage:

11-12 h subsequent to capture. Estimated total time—14 h.

Middle stage

Following blastopore closure to separation of the tail bud from the yolk (Figure 1B).

Noteworthy events:

Advanced development of the embryo and pigmentation patterns. Egg size, width of perivitelline space, etc., same as above.

Oil globule:

The oil globule remained nearly centered between the developing head and tail of the embryo. The underside of the oil globule (closest to the embryo) appeared heavily pigmented during the latter part of the middle stage owing to melanophores which had migrated from the surrounding yolk surface (Figure 1C).

Yolk pigmentation:

In the early middle stage, numerous small melanophores were observed overlying the anterior surface of the yolk surrounding the oil globule (Figure 1B). Most of these melanophores migrated during the middle stage and aggregated on the underside of the oil globule.

Embryo pigmentation:

Small, faintly pigmented melanophores first appeared along the lines separating the developing somites and spread laterally covering the dorso-lateral region of the body. A conspicuous patch of pigment was noticeable at the anterior and posterior margins of the optic vesicles, and a small cluster of melanophores in the area of the snout. Later in this stage, larger melanophores appeared in an irregular line along the medial dorsal surface of the body (Figure 1D).

Somite development:

By the end of the middle stage, 21 well-defined myomeres could be counted. Kupffer's vesicle was still evident in the middle stage.

Duration of the middle stage:

11-12 h at 24.5°C.

Late stage

Tail bud completion to hatching of larva (Figure 1E).

Oil globule:

When the advanced embryo had coiled around the yolk, the oil globule shifted in position and became situated closer to the head rather than maintaining a median position under the embryo. Pigmentation became more abundant, extending over the hemisphere of the underside in contrast to the small, dense cluster in the middle stage. Virtually no pigment remained on the surrounding yolk.

Embryo pigmentation:

Dense pigmentation remained on the dorso-lateral surfaces of the body. Melanophores appeared over the top of the head in addition to those on the snout and along the anterior and posterior margins of the eye. A band of small melanophores developed around the body near the tail region. There also appeared a ring of melanophores on the yolk surface posterior to the tip of the tail bud. This was subsequently lost in the final span of the late stage when fin fold formation was completed and tail flexure occurred. Kupffer's vesicle was observed in the early part of the late stage but was subsequently lost.

Somite development:

The adult complement of 24 somites was attained in the late stage embryo.

Duration of late stage:

0.5-1 h at 24.5°C.

YOLK SAC LARVAE

The newly hatched omaka larvae measured 1.32 mm to 1.70 mm $\overline{SL}$ live, with a mean of 1.46 ± 0.12 mm for 47 larvae. Following preservation in 2.5% formaldehyde, a different group of ten larvae ranged from 0.87 mm to 1.03 mm with a mean of 0.98 ± 0.05 mm. The difference between means (0.48 mm) indicates a shrinkage of 33%.

Pigmentation

Live Larvae at Hatching

Newly hatched omaka larvae resembled advanced embryos in pigmentation pattern. Melanophore pigment was heaviest on the dorso-lateral surfaces of the body with melanophores usually forming a loop posterior to the head. Additional small clusters of melanophores were observed on the top of the head and at the anterior and posterior margins of the eye vesicles. A broad band of small melanophores encircled the body about 6 myomeres posterior to the anal papilla. Ventral body pigment was not apparent in the newly hatched larvae but was found in older yolk sac larvae, perhaps due to the migration of some dorso-lateral melanophores and those in the band region (see Orton, 1953). Dendritic melanophores (Figure 2A) lined the posterior margin of the yolk sac. The oil globule displayed heavier pigmentation than in the late egg stage, with melanophores present on both its anterior and posterior surfaces.

Preserved Larvae at Hatching

The remaining pigmentation following preservation in 2.5% formaldehyde for at least 24 h were the melanophores on the head and dorso-lateral region of the body. The band of pigment around the body posterior to the anal papilla was lost except for a few scattered melanophores. The yolk sac and oil globule had contracted and obscured any pigment which may have remained.

Live Larvae One to Three Days Old

The pigmentation pattern of the yolk sac larvae changed markedly during the first few days after hatching. Owing to the rapid change, larvae (preserved) at any time exhibited various stages of pigment development. Therefore the descriptions presented are "average" patterns observed. Had the larvae come from simultaneously fertilized eggs, the differences would probably have been less pronounced. As the pigment pattern stabilized with age, variations among larvae were correspondingly reduced.

There was a loss of lateral pigmentation coinciding with a coalescense of the small dorsal melanophores to form fewer, large melanophores on the dorsal edge of the body, and also with the appearance of pigment on the ventral edge of the hypomeres. These changes were apparent in most of the day-old larvae.

By the end of the second day, the larvae possessed discrete melanophores on the dorsal and ventral edges of the body in a single discontinuous line. The dorsal body melanophores showed branches or "dendrites" which projected up into the fin fold. These were most pronounced in the region of the dorsal fin opposite the divergence of the posterior end of the gut from the body. A network of dendritic melanophores developed about midway along the dorsal and ventral fin folds (Figure 2B). These networks were gradually lost within the next five days of growth.

Also evident on the second day was the cluster of melanophores on the top of the head and over the snout region (present in the advanced embryo). The first indication of eye pigmentation appeared with faintly pigmented melanophores over the iris, but concentrated along its posterior margin.

The caudal region usually possessed a single minute melanophore dorsal and two or three ventral to the end of the notochord (Figure 2A). The dorsal melanophore was lost in the older larvae, but the ventral melanophores persisted and were situated over the early caudal actinotrichia at about the sixth day.

Three-day–old larvae were similar in pigmentation to the two-day–old larvae except in their heavier eye pigmentation and fewer melanophores on the dorsal body edge.

Preserved Larvae One to Three Days Old

Following preservation in 2.5% formaldehyde for 48 h, virtually all pigmentation, except for the dorsal and ventral body, eye, and head melanophores, were lost. In a few specimens,

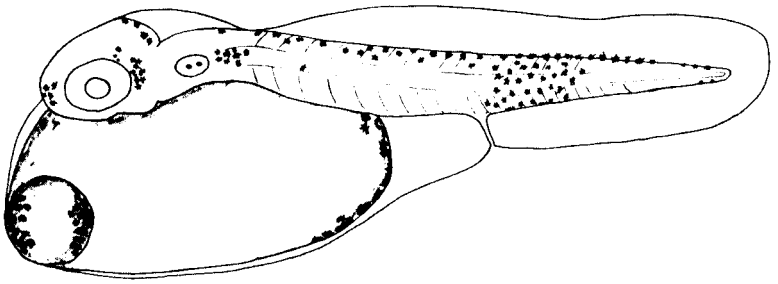

FIGURE 2A.—Yolk sac larva, *Caranx mate*, just after hatching, 1.62 mm SL.

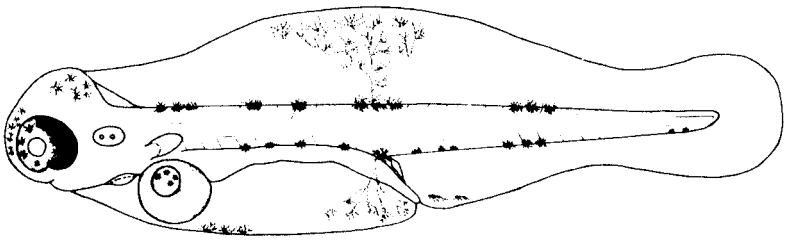

FIGURE 2B.—Three-day old larva, *Caranx mate*, 2.26 mm SL.

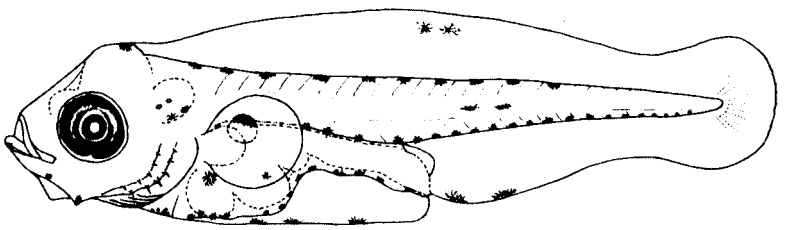

FIGURE 2C.—Six-day old larva, *Caranx mate*, 3.06 mm SL.

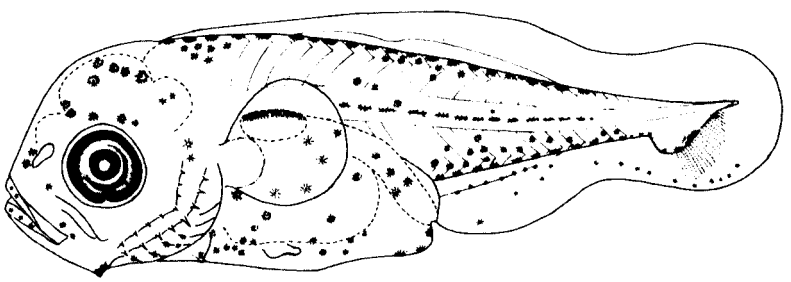

FIGURE 2D.—Twelve-day old larva, *Caranx mate*, 3.96 mm SL.

faint traces of the fin fold and oil globule pigment could be distinguished.

Morphological Development of Yolk Sac Larvae

Omaka larvae hatch in a relatively undifferentiated state, the only conspicuous structures being the large yolk sac, the unpigmented eyes, otic vesicles, and heart. The oil globule, positioned forward of the head at the extreme anterior margin of the yolk sac, is characteristic of carangids (Ahlstrom and Ball, 1954). Ten hours after hatching (1.80 mm $\overline{SL}$), the larvae had developed a narrow, straight gut tube (it became convoluted on the fifth day) terminating at the anal papilla and urinary bladder (Figure 2B). The gradual yolk resorption resulted in the oil globule's shifting its position posteriad while remaining at the anterior margin of the sac. The oil globule lay just ventral to the head at 10 h.

Pectoral buds appeared in the larvae by the end of the second day and the jaw buds by the third day. After three days most of the yolk had been absorbed, and the oil globule had diminished in size to a small, barely noticeable spherical body. The end of the third day was thus selected as the termination of the yolk sac stage of the larvae.

By the fourth day, the eyes were completely pigmented, the mouth was open and the broad, membranous pectoral fins were functional. The small collapsed yolk sac containing the now minute oil globule was still evident ventral to the anterior portion of the abdominal cavity.

LARVAE

Pigmentation

Head Pigmentation

Following yolk absorption (in three-to four-day-old larvae), head pigmentation was present in the following areas: (1) the median dorsal surface of the midbrain (optic lobes) consisting of one or two small melanophores; (2) the floor of the otic vesicle with two or three expanded melanophores which remained visible until obscured by the overgrowth of tissue in older larvae at about day 10 (Figure 2C); (3) along the dorsal margin of the opercle which exhibited a few faintly pigmented melanophores; (4) on the lower jaw with a melanophore situated at the tip of the lower jaw and another at the angular bone, with most of the larvae having a melanophore midway between these two.

As the larvae grew, the density of head pigmentation increased—particularly over the mid- and forebrain region and on the jaws. The number of melanophores increased on the postero-lateral half of the midbrain lobe while a ring of melanophores concurrently outlined the margin of the midbrain capsule. Larvae of approximately 3.5 mm (day 8–not illustrated) exhibited a cluster of expanded melanophores over the midbrain which gradually extended antero-ventrally to the forebrain and snout region. Pigmentation on the surface of the head had intensified in the older larvae, with the cap over the midbrain being especially conspicuous.

By the tenth day (4.0 mm $\overline{SL}$), most larvae possessed a melanophore at the tip of the upper jaw in addition to those on the lower jaw; pigmentation subsequently increased over the premaxillary, maxillary, and dentary region as the larvae advanced. Melanophores located on the jaws were smaller and more punctate than those on the top of the head and along the operculum.

Pigmentation on the membrane overlying the branchiostegal rays and along the gular region developed in eight- to ten-day-old larvae (3.5-4.0 mm $\overline{SL}$) (Figure 2D). The most anterior branchiostegal rays were initially pigmented with pigmentation proceeding distad until the full complement of seven rays was pigmented. Pigmentation of each ray also proceeded distad resulting in larvae of 20 to 22 days (8.3-9.5 mm $\overline{SL}$) possessing as many as two or three melanophores over the basal end of each branchiostegal ray (Figure 3A). This pigmentation was barely discernible in larvae of 26 days (10.9 mm $\overline{SL}$) and eventually lost altogether in larvae of 28 days (11.4 mm $\overline{SL}$). Melanophores along the median gular region similarly increased in density, forming an almost continuous dotted line of contracted melanophores posterior to the isthmus in larvae of 14 days (5.2 mm $\overline{SL}$). Additional melanophores formed along this line but pigmentation in this region gradually disappeared, like the branchiostegal pigmentation, in the advanced larvae.

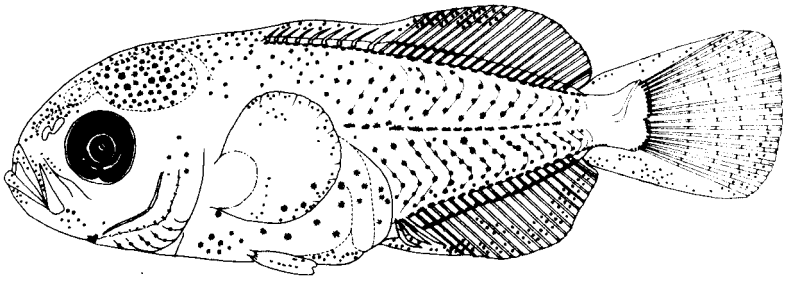

FIGURE 3A.—Eighteen-day old larva, *Caranx mate*, 7.67 mm SL.

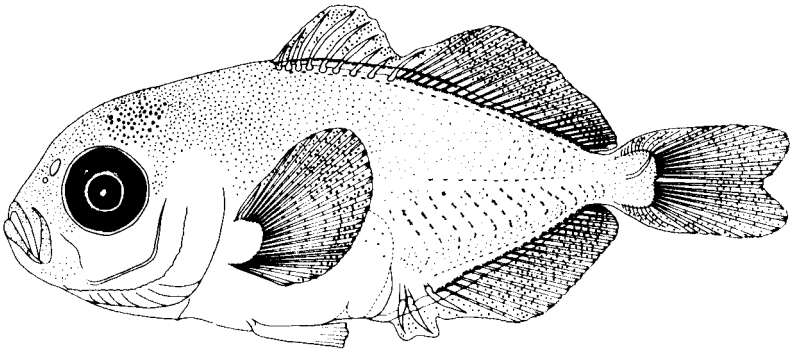

FIGURE 3B.—Thirty-three-day old larva, *Caranx mate*, 12.60 mm SL.

The operculum was never heavily pigmented, although melanophores formed along the region between the preopercular spines of larvae from day 8 to 16 (3.5-6.2 mm $\overline{SL}$), as the spines were being resorbed. In addition there were several melanophores scattered over the upper region of the operculum posterior to the eye.

Body Pigmentation

ABDOMINAL REGION.—The abdominal region of the omaka larvae following yolk absorption as used here refers to the peritoneal cavity with its overlying tissue. At six days (3.0 mm $\overline{SL}$) the one or two faintly pigmented melanophores could be seen immediately ventral to the base of the pectoral fin. These melanophores persisted until the larvae were 14 days old (5.2 mm $\overline{SL}$) (Figure 2C, D). A few melanophores were scattered over the abdominal wall in the early larvae with increasing numbers being formed in older larvae.

The spherical gas bladder was apparent by the sixth day (3.0 mm $\overline{SL}$) with its dorsal cap of embedded pigmentation. The gas bladder was gradually depressed into an elliptical shape by day 10 (4.0 mm $\overline{SL}$) and its pigment largely obscured with the increasing growth of musculature dorsally.

A line of melanophores developed by day 6 (3.0 mm $\overline{SL}$) (Figure 2C) extending along the dorsal wall of the abdominal cavity from the gas bladder to the terminus of the gut where it converged with the ventral line of melanophores along the edge of the hypomeres (see section on ventrum pigmentation). This pigmentation increased in density through day 8 (not illustrated) until it was obscured by the growth of overlying tissue by day 12 (Figure 2D). This pigmentation had a diffused appearance owing to its internal, dorsal position, but consisted of discrete melanophores.

Also evident in six-day–old larvae was peritoneal pigmentation along the ventral edge of the abdominal cavity, including a small precleithral cluster of melanophores, a larger cluster just ventral to the liver (where the pelvic bud subsequently appeared), and a row of melanophores extending from the ventral surface of the stomach to the anus. These pigments gradually diminished

and were obscured or lost in larvae of about 26 days (10.9 mm $\overline{SL}$).

DORSUM.—Dorsum pigmentation of the post yolk sac larvae of four days of age (2.6 mm $\overline{SL}$) consisted of a single line of 9 to 13 large, stellate melanophores extending posteriad from the base of the hindbrain to the 17th to 19th myomere along the dorsal edge of the body (Figure 2C). At ten days (4.0 mm $\overline{SL}$), numerous small melanophores had formed ventro–laterally, interspersed along the prominent line of melanophores of the dorsal edge. The appearance of these lateral melanophores coincided with the appearance of dorsal and anal fin anlagen (which were visible as opaque thickenings in the fin fold).

By day 12 (Figure 2D) (4.5 mm $\overline{SL}$) the dorsal melanophores had become smaller and more numerous, bordering each side of the ventral margin of the dorsal fin anlage. The formerly conspicuous single row of large melanophores on the edge of the dorsum was now lost, having been replaced by these smaller dorsal melanophores in a double row along the base of the fin anlage and continuing in a single row posteriorly.

Larvae of 15 to 16 days of age (5.2-6.2 mm $\overline{SL}$) showed increased lateral spreading of pigmentation. By 18 days (7.4 mm $\overline{SL}$) (Figure 3A), melanophores had formed along the more posterior two-thirds epaxial myoseptal lines, which became more pronounced in 20-day–old larvae (8.3 mm $\overline{SL}$). This epaxial myoseptal pigmentation pattern was gradually obscured by the increasing density of pigmentation over the entire area of the dorsum beginning in 22-day–old larvae (9.5 mm $\overline{SL}$).

The caudal peduncle remained sparsely pigmented both dorsally and ventrally throughout development. (The pigment along the base of the caudal fin is described in the section on fin pigmentation.)

VENTRUM.—The pigmentation changes of the ventrum from the four-day–old larvae followed a similar pattern to that of the dorsum with a few exceptions. The larvae of four to eight days of age exhibited a single line of 12 to 26 small melanophores along the ventral edge of the body from the anus to the 23rd or 24th myomere. These ventral melanophores were smaller and extended more posteriad than those aligned along the dorsal edge of the body until fin formation was well initiated. In addition, two to four minute punctate melanophores appeared on the ventral tip of the notochord (which subsequently migrated ventrally to become situated along the proximal edges of the caudal actinotrichia discussed in the section on fin pigmentation).

With the first appearance of the anal fin anlage in ten-day–old specimens, faint melanophores formed dorsolaterally over the ventrum, followed by the appearance of a double line of melanophores along the base of the anal fin anlage in 12-day–old larvae (4.5 mm $\overline{SL}$) from the previously single line as it occurred along the base of the dorsal anlage. From day 14 to 16 (5.2-6.2 mm $\overline{SL}$), melanophores formed a conspicuous pattern along the hypaxial myoseptal lines, with others scattered in the surrounding region (Figure 3A, B). These latter were most concentrated over the ventral one-third of the hypomeres. The hypaxial myoseptal pigment pattern remained visible in the largest larvae (18.0 mm) in contrast to that on the dorsum and remained as a major distinguishing characteristic.

"LATERAL LINE STREAK".—The "lateral line streak" refers to the dashed line of pigmentation along the lateral midline of the body as described for several other carangid larvae (see Ahlstrom and Ball, 1954; and Kramer, 1960). It appeared in the six-day (Figure 2C) omaka larvae (3.0 mm $\overline{SL}$) with two or three elongate melanophores arising near the vertical of the anterior portion of the hindgut, with as many as 13 melanophores having formed in eight-day–old (3.5 mm $\overline{SL}$) larvae. Indeed, body pigmentation of the larvae at this age was characterized by three lines: along the dorsal and ventral edges of the body, and the lateral line streak.

Although it was largely obscured by the overgrowth of tissue and heavier lateral pigmentation, the streak was still noticeable in the 36-day–old larvae (16.6 mm $\overline{SL}$). It provided a sharp line of demarcation between the heavily pigmented dorsum and the more sparsely pigmented ventrum in the older larvae (Figure 3B).

Fin Pigmentation

CAUDAL.—Prior to notochord flexion, a few small melanophores were present along the distal margin of the early hypural plate (Figure 2D). In addition, a line of minute melanophores had formed along the ventral margin of the caudal

fin fold, but was lost in older larvae (ca. 7.5 mm $\overline{SL}$).

Following flexion of the notochord (ca. 6.0 mm $\overline{SL}$), melanophores were still evident along the posterior margin of the hypural bones and along the dorsal and ventral margins of the fin membrane in the caudal peduncle region, with additional caudal fin pigment developing distally between the rays. The density of melanophores increased in the older larvae, generally forming in one or two rows between the rays.

PECTORAL.—Larvae of ca. 6.0 mm $\overline{SL}$ had minute melanophores scattered along the distal margin of the pectoral fin, but pigmentation remained sparse compared to that of the caudal, dorsal, and anal fins. By 8.5 mm, the pigmentation had increased to rows of three to five melanophores interspersed between the more dorsal rays, with this pigmentation spreading ventrad as the larvae grew.

DORSAL AND ANAL.—Pigmentation of the dorsal fin fold was described earlier. In the early larvae up to ca. 3.0 mm, there were dendritic melanophores lining the edge of the preanal fin fold which were lost in larvae by 4.5 mm.

The pattern of pigment development was similar for both fins, although that on the anal was formed earlier. This was consistent with the apparent earlier formation of the anal fin. By 6.0 mm, larvae displayed the beginning of a row of melanophores along the distal margin of the anal pterygiophores (Figure 3A). Initially each of these melanophores was situated between adjacent pterygiophores in the anterior portion of the fin; more developed posteriad in older larvae. The entire length of the proximal margin of the anal fin had this pigment by 8.0 mm, but the dorsal fin margin showed no evidence of it until ca. 7.0 mm. Approximately three-fourths of the anterior portion of the dorsal fin margin was pigmented at 10.0 mm.

Rows of two to four melanophores were evident along the distal region of the fin membrane between the anteriormost anal fin rays at ca. 6.0 mm. The fin pigmentation process proceeded posteriad, with the melanophore number increasing to as many as 14 in double rows between rays in larvae of ca. 10.5 mm.

Larvae of ca. 8.5 mm showed melanophores forming distally on the fin membrane surrounding the dorsal spines and between the first few dorsal rays. Subsequently, the fin pigment developed posteriad as in the anal fin; and the density of melanophores on the dorsal fin membrane was similar to that of the anal fin by 11.3 mm.

PELVIC (VENTRAL).—Like the pectoral fin, each pelvic fin was sparsely pigmented. Two or three melanophores were observed on the small, rayless fin on larvae of ca. 6.0 mm. By ca. 7.6 mm, two or three rows of a few small, inconspicuous melanophores had formed between the rudimentary fin rays (Figure 3A).

Fin Development

The omaka larvae hatched with no developed fins but a broad, flat fin fold. The subsequent formation of fins (first development of lepidotrichia) followed a sequential pattern much like that described for *Trachurus symmetricus* (Ahlstrom and Ball, 1954), viz. caudal, pectoral, anal and soft dorsal, spiny dorsal, and pelvic (ventral) in that order.

The stage of omaka fin development particularly, appeared to us to be more dependent on size attained than age. Smaller, older larvae were found to have not yet completed certain stages, while some precocious (larger) larvae had. Owing to rapid development of larvae, larger samples at more frequent time intervals would be required to test a hypothesis of size versus age dependence of developmental events.

Caudal

Caudal actinotrichia could be observed in larvae as small as 2.2 mm in the form of faint lines projecting distally from the area around the tip of the notochord. True rays (lepidotrichia) were first evident in larvae ca. 3.4 mm (day 7) and became more prominent in 4.0 mm larvae as ventrally projecting incipient rays from the presumptive hypural plate below the tip of the notochord. These rays were well-defined in larvae of ca. 4.5 mm (day 12), when notochord flexion was initiated. At this time as many as 15 rays of the total 17 principal caudal rays could be observed still projecting obliquely from the developing unossified hypural bones lying ventral to the notochordal tip. Notochord flexion and the formation of the 17 principal caudal rays (nine

above the midline of the hypural plate, eight below) were completed in larvae by 6.0 mm (day 16). (Secondary rays were added anteriad along the dorsal and ventral margins of the caudal peduncle with as many as nine formed on each edge in the largest larvae.)

The rounded caudal fin fold was confluent with the dorsal and anal fin folds in the young larvae, but an indentation of the fin fold occurred in the region of the future caudal peduncle in the older larvae. The caudal fin was separated from the dorsal and anal fin membranes in larvae between 5.3 mm and 6.0 mm (day 14-16). At this stage of development the caudal fin possessed a straight margin, rather than rounded, along its posterior edge and subsequently attained a bilobate shape in larvae of ca. 10.5 mm (day 24).

Pectoral

The pectoral fin developed early during the yolk sac stage (see earlier sections). However, rays did not form until the larvae were ca. 5.4 mm (day 14) when six or more rays could be counted in the upper region of the fin. Addition of rays proceeded ventrally with the rays decreasing in length ventrally to give the pectoral fin an obovate shape in the older larvae compared to the earlier, more rounded, membranous larval fin.

The adult complement of 21 to 22 rays was attained in larvae of 9.3 mm. A short, inconspicuous spine at the extreme dorsal margin of the pectoral was evident upon close examination of our cleared and stained specimens of minimal length 8.4 mm and larger cleared and stained juveniles from our field–collected samples.

Anal

Formation of the anal fin was first evidenced by the appearance of the anal anlage in larvae as small as 3.75 mm. (See section on ventrum pigmentation.) Following the formation of the dorsal and anal anlagen, it appeared that the separation of the fin fold into dorsal, anal, and caudal sections coincided with the development of incipient rays and first few spines of the dorsal and anal fins in larvae from 5.4 mm to 5.5 mm (day 14).

One anal spine formed concurrently with six or more incipient rays in larvae of 5.4 mm or larger; the two remaining spines developed anteriad to the first formed spine in larvae between 7.0 and 9.0 mm which had at least 15 rays formed posteriorly.

Generally by 9.0 mm, the two most anterior anal spines had separated from the third which remained associated with the soft rays. However, a well-defined separation of the fin membrane did not occur until the larvae were 16.0-17.0 mm in length. The adult complement of II-I, 17-19 for the anal fin was completed in larvae by 9.0 mm, although three smaller specimens (8.13, 8.63 and 8.88 mm $\overline{SL}$) had complete anal fins.

An inconspicuous flap of tissue could be observed developing over the bases of the spines and first few rays of the anal fin in most of the larvae by 11 mm. The flap was not completely formed along the basal margin of the anal fin in our largest larva (18 mm) but had covered only about three-fourths of the length of the fin base. This was the precursor to the flap of tissue which overlies the entire length of the dorsal and anal fin bases in adult omaka.

Dorsal

The dorsal anlage appeared at approximately the same size as the anal anlage. Development of the soft dorsal occurred prior to formation of the spiny dorsal. There was no clear difference in the rate of development of the soft dorsal fin and anal fin in contrast to the jack mackerel (Ahlstrom and Ball, 1954).

Distal pterygiophores of the soft rays were evident in larvae of 5.0 to 5.4 mm, with incipient rays becoming differentiated in 5.55 mm (and larger) larvae. Subsequent fin development was rapid. Four to six spines had developed with as many as 16 rays in larvae of 5.8-6.0 mm. Spines were added anteriad and rays posteriad. Most of the larvae of 7.3 to 8.0 mm length had attained a dorsal fin complement of IX-20 to IX-22. In larvae larger than 9.0 mm, the ninth spine had separated from the preceding eight to separate the two dorsal fins. The fourth dorsal spine remained the longest in the larger larvae, with the others progressively decreasing in length. Larvae from 9.0 to 18.0 mm possessed the adult fin complement of VIII-I, 20-23.

By 9.25 mm, only cleared and stained specimens showed a small, embedded, forwardly projecting spine arising from the pterygiophore of the first external spine. We did not count this spine

separately in the fin complement, although some investigators have apparently done so in presenting spiny dorsal meristics for *C. mate* as I+VIII+I (e.g., Smith, 1965; Munro, 1967). The spine is apparent only upon dissection of juveniles and adults of the omaka.

A narrow flap of tissue had begun to form over the basal edge margin of the anterior three to four dorsal spines in larvae of 10 mm. It appeared slightly earlier than that for the anal fin. Like the flap over the anal fin base, the dorsal flap had only developed along three–fourths of the length of the dorsal fin base in our largest reared larva (18 mm).

Pelvic (Ventral)

The inconspicuous pelvic fin bud appeared in larvae of 4.4 to 5.7 mm, except for two specimens of 3.64 and 3.96 mm which had already formed the fin buds. These appeared as small protuberances just ventral to the liver and gradually differentiated into a larval fin in 6.0 mm larvae. Two or three rays had formed in larvae by 6.2 mm, and the adult complement of I, 5 was completed in larvae of 7.7 mm.

OSSIFICATION

Eighteen larvae, one of each age group sampled and representative of the size range in the sample, were cleared and stained with alizarin following the technique described by Hollister (1934). (Three 7-day–old larvae were cleared and stained to further define the sequence of tooth formation on the upper jaw.) The specimens were cleared and stained primarily to confirm the meristics taken and developmental descriptions presented earlier on unstained material.

In order to determine the limits of precision for our statements derived from these cleared and stained larvae about size of first structural development, length differences among our relatively few specimens were measured. They ranged from 0.1 to 0.2 mm for 2.9-3.5-mm specimens, 0.5 mm for specimens 3.5-4.6 mm, and about 1 mm for larger specimens.

Ahlstrom and Ball (1954) present a thorough discussion of the ossification sequence for the carangid, *T. symmetricus* (jack mackerel). Our cleared and stained specimens showed exactly the same sequence, but ossification (defined as taking up alizarin) of each bone began in smaller omaka larvae than jack mackerel (Ahlstrom and Ball, 1954). Likewise, most of these bones had completed ossification at a smaller size in omaka.

The cleithrum, upper and lower jaw bones, and preopercular spines were already ossified in our 2.94 mm larva. Minute teeth (ca. 4 on the upper jaw) had begun staining in the larva of 3.35 mm with numerous small teeth filling in the single row in larger larvae. Teeth on the lower jaw first appeared in the 9.25 mm larve. Five branchiostegal rays were stained in the larva of 3.50 mm, with all seven branchiostegal rays on each side of the base of the operculum being stained in the 4.58 mm larva. Gill arches were ossified or stained in the 4.09 mm specimen, and gill rakers began staining in the 5.42 mm larva. Meristics for ossification of fin elements are presented in Table 2.

All neural and haemal spines and centra of the 24 vertebrae (10 abdominal vertebrae, 14 caudal vertebrae) had completed ossification in the 6.25 mm larva. The initial vertebral ossification, indicated by the stain in the neural spines of the first few abdominal vertebrae and in the haemal spines of the caudal vertebrae, was present in the 4.09 mm larva.

Preopercular spines of the omaka larvae were formed along two rows as in the jack mackerel (Ahlstrom and Ball, 1954), viz. the posterior edge of the preoperculum and the "preopercular crest" just anterior to the preopercular edge (as defined by Ahlstrom and Ball, 1954). Those spines situated along the preopercular crest were fewer and smaller than those along the edge of the preoperculum. During the larval development of omaka, the number of spines along the

TABLE 2.—Meristics of cleared and stained *Caranx mate* larvae. Larvae smaller than 4.58 mm are omitted owing to lack of ossification of these fin elements.

SL (mm)	Age (days)	Caudal (principal)	Pectoral	Anal	Dorsal (second)	Dorsal (first)	Ventral
4.58	12	7 + 8					
5.42	14	8 + 7	6	I,6	9		
6.25	16	9 + 8	11	II,13	17	VII	3
7.67	18	9 + 8	18	III,17	I,21	VIII	I,5
8.38	20	9 + 8	20	II-I,18	I,21	VIII	I,5
9.25	22	9 + 8	21	II-I,17	I,22	VIII	I,5
9.88	24	9 + 8	22	II-I,17	I,21	VIII	I,5
10.88	26	9 + 8	I,20	II-I,18	I,22	VIII	I,5
11.63	28	9 + 8	I,20	II-I,19	I,22	VIII	I,5
12.38	30	9 + 8	I,20	II-I,17	I,21	VIII	I,5
13.50	33	9 + 8	I,21	II-I,19	I,23	VIII	I,5
17.00	36	9 + 8	I,21	II-I,18	I,22	VIII	I,5

ascending arm of the preoperculum increased from two (2.9-3.5 mm larvae) to as many as six (7.0-9.0 mm larvae) and from two to seven along the anteriorly projecting descending arm. The apical spine of the preoperculum remained slightly larger and broader-based than the others as in the jack mackerel (Ahlstrom and Ball, 1954), but was still smaller and less prominent than in our other common carangid larva, *Gnathanodon speciosus* (unpublished data), and provides one characteristic for separating the two species.

The omaka larvae showed no serrated dorsal crest at the back of the head which was evident in the jack mackerel (Ahlstrom and Ball, 1954). It is considered to be a rather common feature of carangid larvae (Berry 1959, McKenney, Alexander, and Voss 1958, Okiyama 1970, Shojima 1962) and is present in several of our unidentified species of carangid larvae.

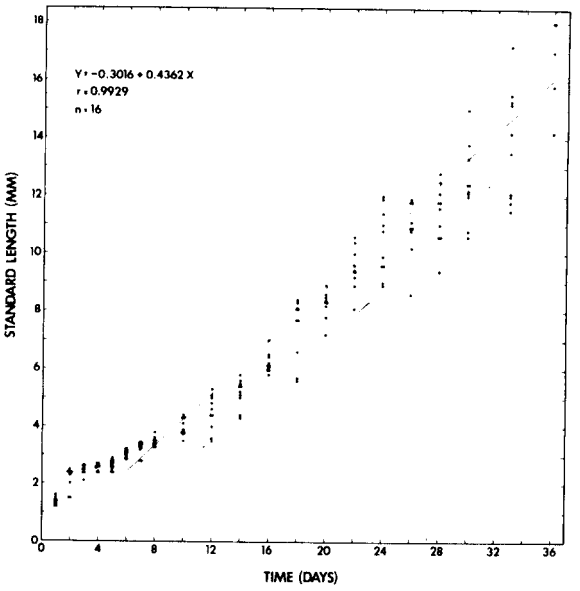

FIGURE 4.—Growth rate of *Caranx mate* in culture. Regression based on mean length after day 6. n = 16.

GROWTH

The growth rate and description of changes in body form are based mainly on specimens reared from eggs taken in surface tows from Kaneohe Bay on 22 February 1971 (Table 1). At that time the bay surface temperature was 24.4°C. Rearing tank temperatures ranged from 22.1° to 25.9°C, with a mean of 24.5°C, so the thermal environments were similar. As stated in the methods section, the salinity and oxygen level in the tank remained similar to those in the bay throughout the experiment. Without data on the quantity and quality of food for any given time of the rearing period, however, it is impossible to assess the reality of the growth rate. The general shape of the curve (a nearly straight line) and the absence of any mass mortality suggests that the rearing environment was at least adequate throughout the experiment. The absence of prolonged lags in growth suggest the absence of periods of major stress.

The growth curve (Figure 4) is composed of at least three segments of differing slope: from hatching through day 2; day 3 through day 5; and from day 6 onward. The inflection in the curve at day 2-3 coincides with the near final absorption of yolk, and perhaps more important, the development of a functional mouth. No major structural change occurs at day 6 which might be linked to that inflection. Among four rearing trials, the change in length from hatching to day 6 (ca. 2.5 mm) was extremely variable. In two of the trials, larvae increased in length through day 3, then shrank. It appears that the variability in early omaka growth rate might be linked to the success of larvae in obtaining their first exogenous energy (Thomas Cooney, pers. comm.—M.A. thesis research). Owing to this variability, the statistical description of the growth rate of larvae through day 5 is of little value. Interpolation between mean (preserved) size at hatching (1.03 mm) and mean size of day 6 (3.05 mm) yields an estimate growth of 0.35 mm/day.

The relationship chosen to express larval growth beyond day 6 was the linear regression: $\overline{SL}$ (in mm) = −0.3016 + 0.4362 (age in days) (Figure 4), as determined from 153 preserved specimens. A slightly better fit would have been obtained with a more complex function, but the improvement in the curve would be slight.

The greatest departures from linear growth occurred at day 14 and day 28 ($\overline{SL}$ = 5.2 mm and 11.4 mm, respectively). No major morphological developments occurred at these sizes, so the causes (if the departures are real) are not known. The generally poorer fit of the data to the curve at the largest sizes is probably attributable to sampling. As the vagility of larvae increases with size, the probability increases that the smaller

larvae in a tank are selected for preservation. This effect is apparent from the larger (than predicted from the curve) mean size of the five fish on day 36, which were the last specimens in the tank when it was emptied.

One source of error in relating early growth rates of larvae to those of larger larvae is their shrinkage upon preservation. Five groups of ten live larvae (one to five days old), ranging in mean standard length from 2.46 to 2.85 mm, ranged in length from 2.13 to 2.55 mm 24 h after preservation. Shrinkage was also observed to begin within seconds after death when larvae died while being observed microscopically. This latter observation suggests that shrinkage was not entirely due to the effects of formaldehyde on body proteins. The percent shrinkage was not correlated in a simple way with size. Although, presumably, this percentage decreases with increased size of larvae, the shrinkage values, which ranged from 8 to 22% in the five groups, can introduce significant error into estimates of early larval growth. Newly hatched larvae shrank as much as 30% when they died.

Farris (1959) described two growth stanzas of the jack mackerel, viz. (A) from hatch to day 3 and (B) from day 3 to 7. If these correspond to our first two segments, then the second segment (day 3-7) of growth in omaka is twice that of jack mackerel (0.195 mm/day compared to 0.10 mm/day). Alternatively, comparing growth from hatching to yolk absorption—day 3 in omaka, day 6 in jack mackerel—yields a similar difference, 0.48 and 0.26 mm/day, respectively. The comparisons suggest that effects of starvation may occur prior to complete yolk absorption. Farris' growth rates for segment B (on starved fish) may be underestimates. Lasker, Feder, Theilacker, and May (1970) found that larvae may begin to feed before complete yolk absorption. Comparisons need to be made between starved and fed yolk-sac larvae of the same species reared in the same physical environment before a definitive answer can be reached.

BODY PROPORTIONS

As Marr (1955) pointed out, expression of relationships between body dimensions as ratios contributes nothing more than plots of the original measurements, so the latter were used. Relationships between standard length and 1) head length, 2) eye diameter, 3) snout to anus length, and 4) body depth at pectoral fin were all adequately described by an equation of the form: $Y = a + b(\overline{SL})$. All of the data used in the regressions are from one series of reared omaka larvae (Table 1). The ratios all adequately describe specimens captured in the field.

In the following discussions of these relationships, comparisons are made between the omaka and jack mackerel (*T. symmetricus*), described by Ahlstrom and Ball (1954). The latter is the only carangid larva for which these kinds of data are published. With similar data for other carangid species, these may prove useful in a key to carangid larvae.

Head Length

Head length was related to standard length according to the equation: HL = −0.2796 + 0.3477 ($\overline{SL}$ in mm) (Figure 5). Unlike *T. symmetricus* (Ahlstrom and Ball, 1954), there was no inflection in the curve at ca. 4 mm. The slope of the regression line for omaka (0.3477) is not very different than that for the jack mackerel (0.378), so this ratio would not be very useful by itself in distinguishing the two species. Ahlstrom and Ball (1954) did find a different slope (0.556) in the jack mackerel larvae smaller than 4.2 mm, but several of our smaller larvae would fit either regression.

Eye Diameter

The relationship between eye diameter and

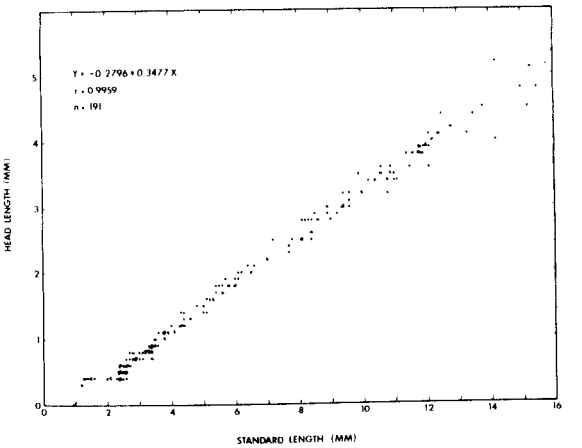

FIGURE 5.—Relationship between standard length and head length of *Caranx mate* larvae.

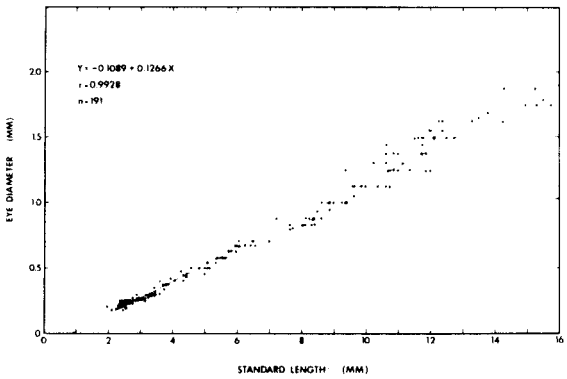

FIGURE 6.—Relationship between standard length and eye diameter of *Caranx mate* larvae.

standard length was described by a straight line of the equation: ED = −0.1089 + 0.1266 ($\overline{SL}$ in mm) (Figure 6). Omaka larvae have almost the same (proportional) eye size as *T. symmetricus* (0.127), reported by Ahlstrom and Ball (1954). Therefore, this ratio is not useful as a distinguishing characteristic.

The omaka eye was somewhat ovoid with the blunt end anterior. The posterior, more acute, end of the eye became more angled up to day 4, then the trend was reversed so the juvenile round eye shape was reached by day 20 ($\overline{SL}$ = 8.27). The "squarish distortion" reported for *T. symmetricus* (Ahlstrom and Ball, 1954) did not occur in omaka.

Snout-to-Anus Length

The snout-to-anus length increased 0.5347 mm for each millimeter increment in standard length throughout larval development (Figure 7). As might be expected from the body depth differences between omaka and jack mackerel, the ratio between snout-to-anus length and standard length of omaka is slightly smaller than that for the jack mackerel (0.581), the latter being a more elongate larva. Again, however, the difference is probably too small to be useful in separating the species.

Body Depth at Pectoral Insertion

The relationship between the body depth and standard length remained constant throughout larval development (Figure 8). No inflection was evident in the omaka, as was reported for *T. symmetricus* by Ahlstrom and Ball, 1954 (larvae smaller than 4.2 mm). The slopes of the regression lines (0.425 for omaka and 0.278 for jack mackerel larvae) are different enough to be used to distinguish these species over 4 mm; omaka larvae are considerably deeper-bodied. The other common carangid in Kaneohe Bay, *G. speciosus*, has a still deeper-bodied larva (our unpublished data); so this ratio appears the most useful of the four discussed to distinguish at least these three species.

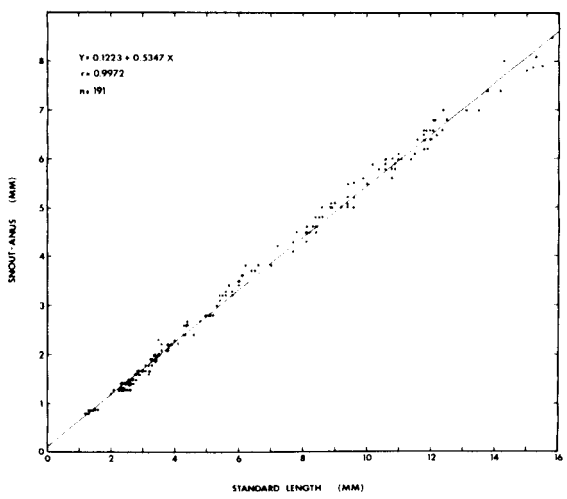

FIGURE 7.—Relationship between standard length and snout-to-anus length of *Caranx mate* larvae.

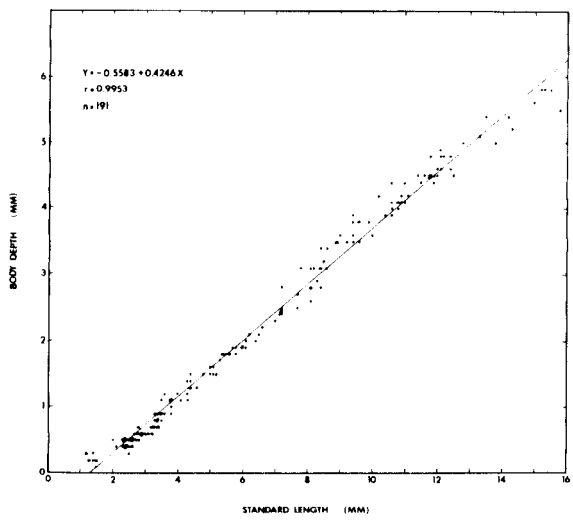

FIGURE 8.—Relationship between standard length and body depth of *Caranx mate* larvae.

SUMMARY

1. Omaka eggs were pelagic and spherical with a single oil droplet and segmented yolk. The diameter was about 700-740 μ.

2. Egg development occurred in three distinguishable stages: early—fertilization to blastopore closure; middle—to tail flexure; and late—to hatching. Respective duration times at 24.5°C were 11-12 hours, 11-12 hours, and 0.5-1 hour.

3. Yolk sac larvae hatched at a length of 1.3-1.7 mm with the oil globule positioned forward in the yolk sac.

4. By the fourth day ($\overline{SL}$ = 2.6 mm), the eyes were pigmented, the yolk and oil globule absorbed, and the mouth functional.

5. Fin development (first appearance of lepidotrichia) occurred in the order: caudal (3.4 mm); pectoral (5.4 mm); anal and soft dorsal (5.4-5.5 mm); spiny dorsal (5.8 mm); and pelvic (6.2 mm).

6. Unlike many carangid larvae, omaka did not develop a serrated crest behind the head.

7. Values for ratios of body proportions to standard length were: head length, 0.3477; eye diameter, 0.1266; snout-to-anus length, 0.5347; body depth, 0.4246. Only the body depth/$\overline{SL}$ ratio was useful in separating omaka from jack mackerel and certain other Hawaiian carangid larvae.

8. The growth of our cultured omaka after day 6 was adequately described by a straight line with slope 0.44. Before day 6, growth was extremely variable, averaging about 0.35 mm/day.

9. Of primary use in separating omaka from jack mackerel larvae (the only other similarly described carangid larva) were pigment pattern, the absence of a serrated dorsal ridge behind the head, and the difference in the ratios of body depth to standard length.

10. Significant decreases in size (up to 33%) and pigmentation of larvae occurred upon preservation. Both of these effects decreased with age of larvae.

11. Although based on larvae reared in the laboratory, our data relating growth and development to time would be expected to simulate those from natural tropical habitats, especially the data for fish eggs and early larva.

ACKNOWLEDGMENTS

Throughout the paper reference is made to the excellent paper by Ahlstrom and Ball (1954), describing the eggs and larvae of the jack mackerel (*T. symmetricus*). The authors acknowledge a debt to Ahlstrom and Ball for their example. Many of their descriptive techniques were used by us, and, in our opinion, should be considered a standard for all larval fish descriptions. Larval fish taxonomy suffers greatly from dissimilarities among descriptive techniques. Thanks are also extended to David Hashimoto, Senior Technician at the Hawaii Institute of Marine Biology, for rearing the larvae. This research was, in part, supported by University of Hawaii Sea Grant No. GH-93. (UNIHI-SEAGRANT-JC-74-02.)

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FOOD HABITS OF GEORGIA ESTUARINE FISHES I. FOUR SPECIES OF FLOUNDERS (PLEURONECTIFORMES: BOTHIDAE)

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ABSTRACT

The food habits of four species of bothid flounders from Georgia coastal waters were examined by means of stomach content analyses. Ocellated flounders, *Ancylopsetta quadrocellata* (Gill); bay whiff, *Citharichthys spilopterus* (Günther); and windowpane, *Scophthalmus aquosus* (Mitchill) fed heavily on the mysid shrimp, *Neomysis americana*, without regard to season of the year or location within the estuary. The food habits of both *A. quadrocellata* and *C. spilopterus* changed to some extent as the fish became larger. Organisms larger than *N. americana* dominated the stomach contents of *A. quadrocellata* larger than 150 mm standard length and *C. spilopterus* larger than 125 mm. *S. aquosus*, in the size range examined, fed almost exclusively on *N. americana*.

Fringed flounder, *Etropus crossotus* (Jordan and Gilbert) primarily consumed the calanoid copepod, *Pseudodiaptomus coronatus*, during the spring, summer, and fall and diversified their food habits during the winter. *P. coronatus* dominated the stomach contents both in the rivers and sounds of Georgia estuarine waters and was the dominant organism in fishes of all sizes up to 100 mm when polychaete annelids became important. The food of *E. crossotus* did not appear to vary with time of day; however, *E. crossotus* did not actively feed at night. The difference in food habits between *E. crossotus* and the other three bothid species appears to be associated with the relative size of the mouth.

Pleuronectiform fishes of the family Bothidae are common in the estuarine waters of the southeastern United States. Otter trawl samples taken within the sounds and rivers of Georgia indicate that fishes of the family Sciaenidae are the most common, with bothids being among the next most common species. Summer flounder, *Paralichthys dentatus* and southern flounder, *P. lethostigma*, are common, but are not present in commercially exploitable quantities. *P. albigutta* has also been reported from Georgia waters, but appears to be relatively rare (Dahlberg and Odum, 1970). Ocellated flounder, *Ancylopsetta quadrocellata*, while not commercially valuable, is occasionally caught by sport fishermen.

Bothid flounders are generally associated with the bottom, either lying on the surface of the substrate or buried to a greater or lesser extent in the sediments. The feeding behavior of flounders under various conditions (both in nature and in culture) has been described (Steven, 1930; Olla, Wicklund, and Wilk, 1969; de Groot, 1970; Olla, Samet, and Studholme, 1972; Stickney, White, and Miller, 1973), but little information on the selective food habits of bothids is presently available. The food habits of *Paralichthys* sp. have been examined by Darnell (1958) in the Gulf of Mexico and by Poole (1964) in New England waters. A limited amount of additional information on *P. albigutta* is also available from samples taken off the southwestern coast of Florida (Topp and Hoff, 1972). Examination of the stomachs from a few specimens of *A. quadrocellata* and *Etropus crossotus*, fringed flounder, demonstrated that both feed on crustaceans in Florida waters (Topp and Hoff, 1972) with *E. crossotus* also utilizing polychaetes and chaetognaths for food (Reid, 1954; Topp and Hoff, 1972). Fourteen species of bothid flounders were examined by de Groot (1971) who found that they divided into three groups by food preference: fish feeders, crustacean feeders, and polychaete-mollusc feeders.

The food habits of bothid flounders along the Georgia coast have not been previously elaborated. For purposes of the present study, four

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species were selected which seasonally account for the majority of bothids captured by otter trawling and were thus judged to be important in the energy flow through the Georgia estuarine ecosystem. The four species chosen were *A. quadrocellata*; bay whiff, *Citharichthys spilopterus*; *E. crossotus*; and windowpane, *Scophthalmus aquosus*. Other important Pleuronectiform fishes of the Georgia coast include *P. dentatus*, *P. lethostigma*, *Trinectes maculatus*, and *Symphurus plagiusa*.

MATERIALS AND METHODS

The coastal region of Georgia consists of a system of barrier islands separated by sounds from which a network of rivers and tidal creeks emanate. The tide range (reaching nearly 3 m on spring tides) coupled with the low relief of the barrier islands and coastal plain results in extensive areas of intertidal marshlands. The marshes are dominated by *Spartina alterniflora*.

Flounders were collected by otter trawl and cast net from Wassaw Sound, Ossabaw Sound, St. Catherines Sound, and Sapelo Sound, and from various locations in rivers above the sound limits (Figure 1). Most of the fish utilized in this study were captured during 1971 and 1972 by personnel from the Savannah Science Museum and Skidaway Institute of Oceanography. Others were donated from collections made by workers at the University of Georgia Marine Institute during 1968. Whole fish were preserved in 10% Formalin[3] after capture.

Location, date of capture, and standard length were recorded for each specimen used in the study. The stomachs were removed, and their contents examined under a dissecting microscope. Organisms found within the stomachs were identified to species when possible and counted. Parasitic nematodes and trematodes were found in many stomachs but were excluded from the food habit data.

In many instances identifications of food organisms were made from pieces of animals found within stomachs. In most cases these pieces provided enough material for specific identification, but in those cases where decomposition made identification to species impossible, the material was identified to the class or family level. Few cases were found in which the stomachs contained completely unidentifiable organic material. Emphasis was placed on correctly enumerating the organisms found in stomachs. Neither biomass nor volumetric displacement data were obtained. Since food items were often identified from parts of an individual (the remainder having been either digested or not actually ingested), it was felt that any estimate of biomass would have little significance.

Many stomachs contained pieces of polychaete annelids which had apparently been nipped off by the fish in their feeding activities. Since it was not possible to reconstruct these fragments into whole animals, heads were counted. Counts based on fragments of organisms cannot be considered completely accurate; however, such food organisms often accounted for a relatively small fraction of the total stomach contents. The organisms which made up the numerical bulk of the food were usually in good condition, facilitating exact counting.

One of the more important organisms found, *Neomysis americana*, has not been reported from as far south as Georgia by many previous authors, although it has been reported from the stomachs of two species of Gadidae, *Urophycis regius* and *U. floridanus* (Sikora, Heard, and Dahlberg, 1972). The reported range of *N. americana* is from the Gulf of St. Lawrence to Virginia (Tattersall, 1951; Wigley and Burns, 1971). This range was extended to near the northern South Carolina border by Williams (1972) who also reported that *N. americana* was common in North Carolina. The range is presently again being extended by A. B. Williams (pers. commun.) who has examined and verified examples of *N. americana* from our collections.

RESULTS AND DISCUSSION

Overall Evaluation

Data summarizing the food of each of the four bothid species are presented in Table 1. Organisms are excluded which were not present in at least 1% of the stomachs examined in any of the four species of fish or which did not account for 1% or more of the total food organisms found in the stomachs of one or more of the species of fish. A complete list of food organisms recovered is presented in the Appendix.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

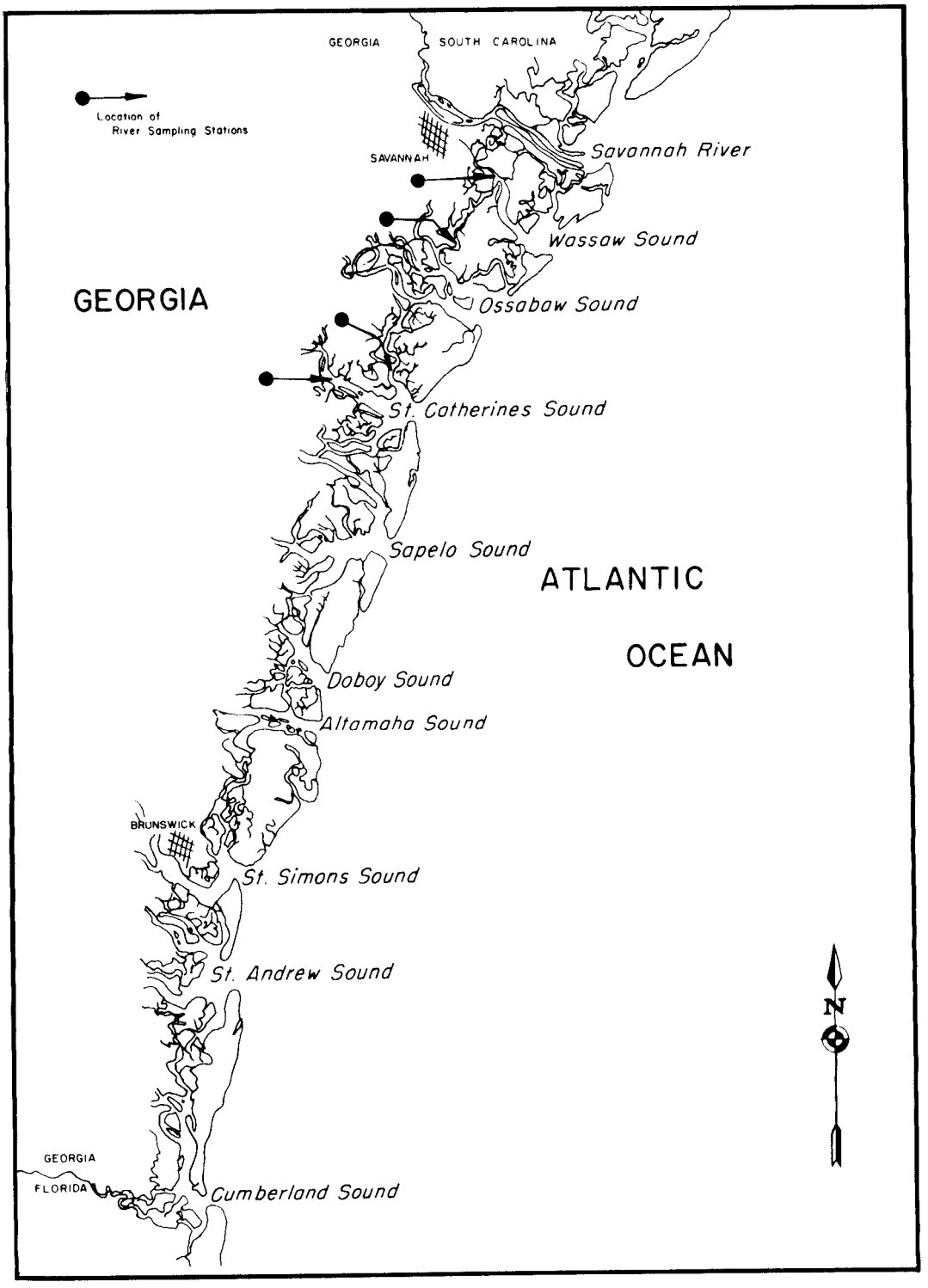

FIGURE 1.—Sampling area along the coast of Georgia indicating the sounds and river locations from which fish samples were obtained.

The food habits of *E. crossotus* are distinct from those of the other three species (Table 1). *Pseudodiaptomus coronatus* dominated the stomach contents of *E. crossotus* but accounted for only an insignificant fraction of the stomach contents of *A. quadrocellata*, *C. spilopterus*, and *S. aquosus*. The stomach contents of each of the latter three species were dominated by *Neomysis americana*.

Of secondary importance in the stomachs of *E. crossotus* were polychaete annelids, especially the spionid, *Paraprionospio pinnata*. The importance of *Pa. pinnata* is extended if the assumption is made that most of the animals listed under Spionidae (Table 1) were, in fact, *Pa. pinnata* in a state of decomposition, making specific identification impossible.

No fish remains were found in any of the stomachs of *E. crossotus* examined, although they were found in *A. quadrocellata*, *C. spilopterus*, and *S. aquosus*. The difference in primary feeding habits between *E. crossotus* and the other three species of bothids appears to be a reflection of relative mouth size (Figure 2). *E. crossotus* has a very small mouth relative to head length (mouth averages about 6 into head), whereas, *A. quadrocellata*, *C. spilopterus*, and *S. aquosus* all have relatively larger mouths in proportion to head length (mouth averages 3 to 4 into head). The small mouth of *E. crossotus* correlates with its selectivity for small organisms (such as *Ps. coronatus*, which range from 1 to 1.5 mm in length) and those of small diameter (such as *Pa. pinnata*). While the remaining three fish species appear to favor *N. americana* as a primary food organism, the diversity of sizes or organisms available to them appears greater. *N. americana* ranged from 6 to 12 mm in length in our collections. This organism was not completely excluded from the food of *E. crossotus* (Figure 3) but was fed upon only to a limited extent.

Table 1 presents the food habit data collected for each species without regard to season of the year, location in the estuary, or size of the fish under investigation. In order to more critically evaluate the data collected on each species, a

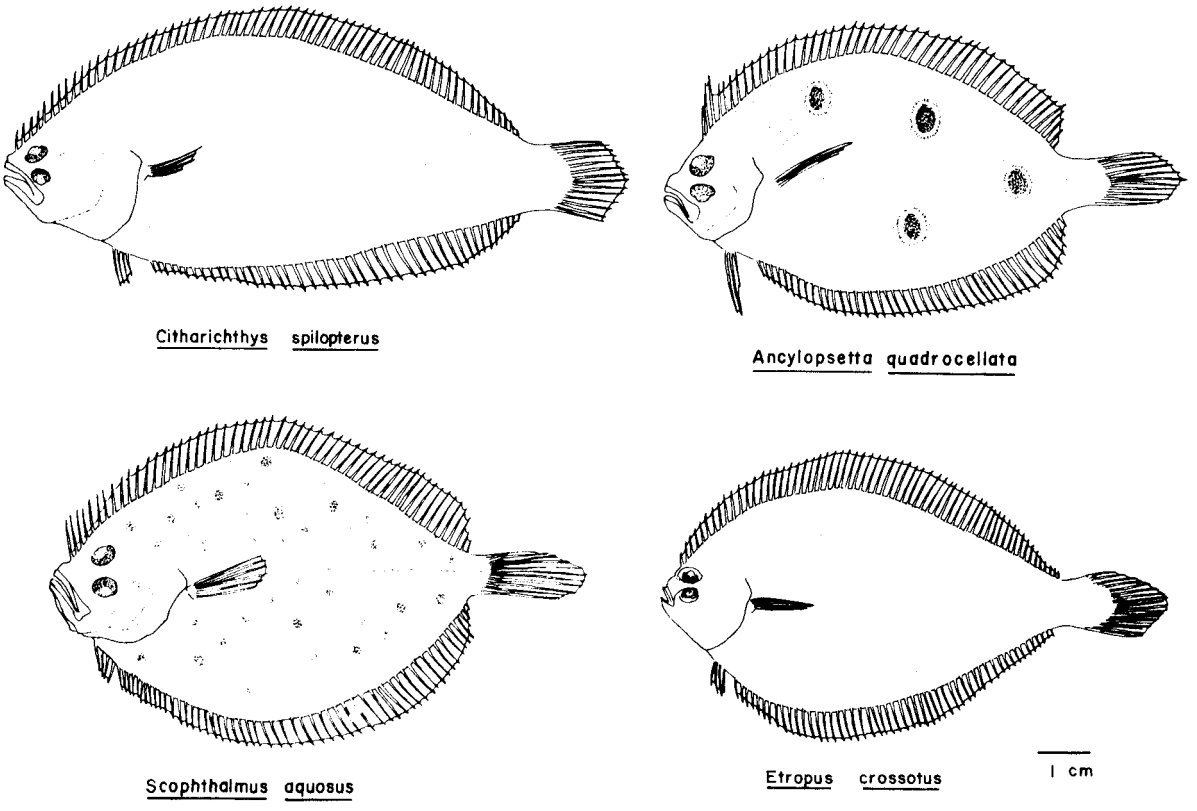

FIGURE 2.—Line drawings of the four species of Bothidae discussed depicting the differences in mouth size relative to body length.

TABLE 1.—Occurrence of organisms appearing in 1% or more of the stomachs examined, or representing 1% or more of the total number of food organisms recovered from the stomachs of one or more of the four species of Bothidae under investigation.[1]

Food organisms	*Etropus crossotus*		*Citharichthys spilopterus*		*Ancylopsetta quadrocellata*		*Scophthalmus aquosus*	
	Percentage occurrence in stomachs	Percentage of total number of organisms	Percentage occurrence in stomachs	Percentage of total number of organisms	Percentage occurrence in stomachs	Percentage of total number of organisms	Percentage occurrence in stomachs	Percentage of total number of organisms
Ectoprocta:								
Bugula neritina	0.2	<0.1	0.0	0.0	0.0	0.0	1.0	0.1
Polychaeta:								
Diopatra cuprea	1.7	0.3	0.0	0.0	0.0	0.0	1.0	0.1
Nereis succinea	4.0	0.2	0.0	0.0	0.5	0.1	1.0	0.1
Nereidae	1.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Paraprionospio pinnata	29.5	2.9	0.5	0.2	0.0	0.0	0.0	0.0
Spionidae	15.9	2.6	0.5	<0.1	0.9	0.2	0.0	0.0
Asabellides oculata	3.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Sabella microphthalma	1.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified remains	1.7	0.1	0.0	0.0	0.5	0.1	0.0	0.0
Mollusca:								
Pelecypod siphons	1.9	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Decapoda—Reptantia								
Pinnixa sp.	2.4	0.1	0.0	0.0	3.2	0.5	0.0	0.0
Portunid megalops and zoea	2.6	0.2	7.1	0.9	0.0	0.0	0.0	0.0
Portunus spinimanus	0.0	0.0	0.5	<0.1	1.4	0.3	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0	1.4	0.4	0.0	0.0
Neopanope sayi	0.0	0.0	0.0	0.0	3.7	1.0	0.0	0.0
Hexapanopeus angustifrons	0.0	0.0	0.0	0.0	1.8	0.5	0.0	0.0
Cancer irroratus	0.0	0.0	0.0	0.0	1.4	0.4	0.0	0.0
Portunid postlarvae	0.2	<0.1	1.4	0.1	2.8	0.8	0.0	0.0
Callinectes sapidus	0.0	0.0	4.3	0.6	0.5	0.1	0.0	0.0
Decapoda—Natantia:								
Acetes americanus carolinae	0.2	<0.1	0.0	0.0	0.0	0.0	1.0	0.1
Palaemonetes pugio	1.4	0.1	16.2	2.8	0.9	0.5	1.0	0.1
Trachypenaeus constrictus	1.0	0.1	35.7	10.4	7.8	5.3	0.0	0.0
Periclimenes longicaudatus	0.0	0.0	1.4	0.1	0.0	0.0	0.0	0.0
Ogyrides limicola	5.2	0.3	10.5	3.3	0.0	0.0	0.0	0.0
Stomatopoda:								
Squilla empusa	0.0	0.0	15.2	2.0	5.5	1.0	1.0	0.1
Amphipoda:								
Ampelisca vadorum	3.8	0.6	1.0	0.1	1.4	0.3	1.0	0.1
Corophium tuberculatum	2.6	0.2	0.0	0.0	0.9	0.1	1.0	0.1
Unciola serrata	0.2	<0.1	0.0	0.0	3.7	4.6	1.9	0.1
Batea catharinensis	0.5	<0.1	0.0	0.0	0.5	0.1	2.9	0.2
Monoculodes edwardsi	7.4	0.6	1.0	0.1	0.5	0.1	1.0	0.1
Erichthonius brasiliensis	0.2	0.1	0.0	0.0	0.5	0.1	2.9	0.1
Caprella equilibra	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.1
Gammarus palustris	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.1
Microprotopus ranei	0.2	<0.1	0.0	0.0	0.0	0.0	1.0	0.1
Listriella barnardi	2.1	0.1	1.0	0.1	0.9	0.1	0.0	0.0
Copepoda:								
Pseudodiaptomus coronatus	34.2	84.6	1.4	0.8	0.5	0.8	1.9	0.5
calanoid copepod remains	0.5	0.1	1.0	0.2	0.9	0.1	3.8	1.0
Cumacea:								
Leucon americanus	6.9	0.5	0.5	<0.1	0.0	0.0	0.0	0.0
Mancocuma altera	2.1	0.2	0.0	0.0	0.0	0.0	4.8	0.2
Oxyurostylis smithi	7.4	1.4	0.0	0.0	0.5	0.1	3.8	0.3
Mysidacea:								
Neomysis americana	19.0	3.1	65.7	72.1	51.6	81.0	59.0	96.3
Isopoda:								
Edotea montosa	5.7	0.4	0.0	0.0	0.5	0.1	0.0	0.0
Osteichthyes:								
Symphurus plagiusa	0.0	0.0	4.8	0.5	1.4	0.2	0.0	0.0
Anchoa mitchilli	0.0	0.0	1.0	0.1	0.9	0.3	0.0	0.0
Cynoscion sp.	0.0	0.0	1.9	0.2	0.0	0.0	0.0	0.0
Sciaenidae remains	0.0	0.0	16.7	2.8	0.0	0.0	0.0	0.0
Gobiidae remains	0.0	0.0	4.3	0.5	0.0	0.0	0.0	0.0
Unidentified remains	0.0	0.0	11.4	1.1	1.8	0.3	1.0	0.1
Others	0.0	0.0	0.0	0.7	0.0	0.5	0.0	0.0
Empty stomachs	26.5	—	7.6	—	30.9	—	35.2	—

[1]The total number of stomachs analyzed for each species were: *E. crossotus*, 421; *C. spilopterus*, 210; *A. quadrocellata*, 217; and *S. aquosus*, 105. The total number of organisms obtained from the stomachs of fishes examined were: *E. crossotus*, 8,734; *C. spilopterus*, 2,442; *A. quadrocellata*, 1,490; *S. aquosus*, 2,209.

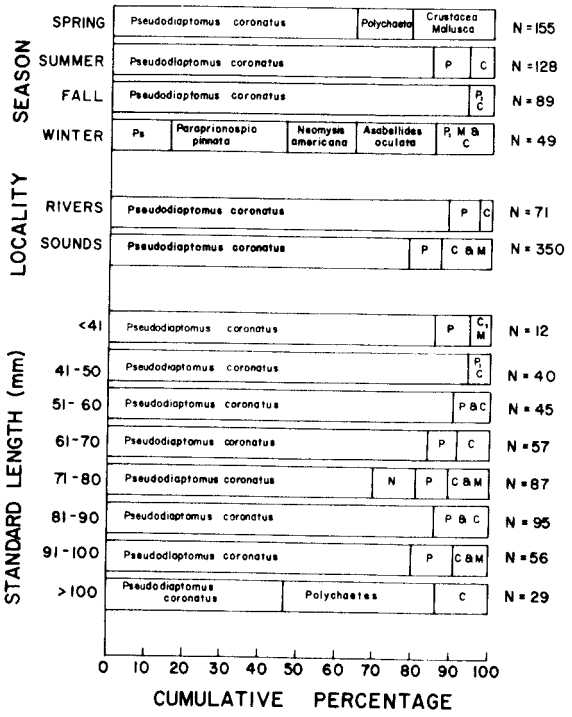

FIGURE 3.—Histogram illustrating the feeding habits of *Etropus crossotus* by season of the year, locality, and standard length. (N = number of stomachs analyzed for each bar, P = Polychaetes, C = Crustacea other than those specifically identified in the bar, Ps = *Pseudodiaptomus coronatus*, M = mollusca, and N = *Neomysis americana*.)

series of figures was prepared which take these parameters into consideration (Figures 3-8).

Etropus crossotus

The food habits of *E. crossotus* related to season of the year, locality within the estuary (rivers as opposed to sounds), and standard length are presented in Figure 3 indicating the percentage of total numbers of food organisms contributed by each taxa. *E. crossotus* was most abundant during the spring and summer months (March through August). *Ps. coronatus* was the dominant organism in the stomachs of *E. crossotus* during the spring, summer, and fall. During the winter, *Ps. coronatus* was displaced to a large extent by the spionid polychaete *Pa. pinnata* and by *N. americana*. Whereas Table 1 indicated that *Pa. pinnata* was of general importance especially in terms of frequency of occurrence in the stomachs, Figure 3 indicates that this organism was more important during the winter (December through February) than during any other season of the year. This change in food habits does not appear to reflect a reduction in the availability of *Ps. coronatus*. Plankton samples taken in conjunction with this and other studies have demonstrated that *Ps. coronatus* is present during the winter in numbers often exceeding those of other seasons of the year. The change in food habits may reflect an increased availability of *Pa. pinnata* rather than a decrease in the availability of *Ps. coronatus*. The increased availability of *Pa. pinnata* may have been a function of an increase in absolute numbers of the polychaetes or may have been due to a change in the behavior patterns of the predator, prey or both. Studies of benthos associated with stations in Ossabaw Sound, from which many of the fishes were collected, indicate that *Pa. pinnata* is the dominant benthic infaunal form throughout the year on mud substrates and exhibits widely fluctuating standing crop levels (Stickney and Perlmutter, unpubl. data).

The possibility that the shift in food habits in winter may have been a function of the size of the fishes occurring in the estuaries during that season was considered. Animals in the larger size ranges did not dominate the winter samples but were generally present during the spring (Figure 4). Fish in the smallest groups were present most often in the summer when *Ps. coronatus* were highly dominant in the stomachs. Suitable numbers of *E. crossotus* were present throughout

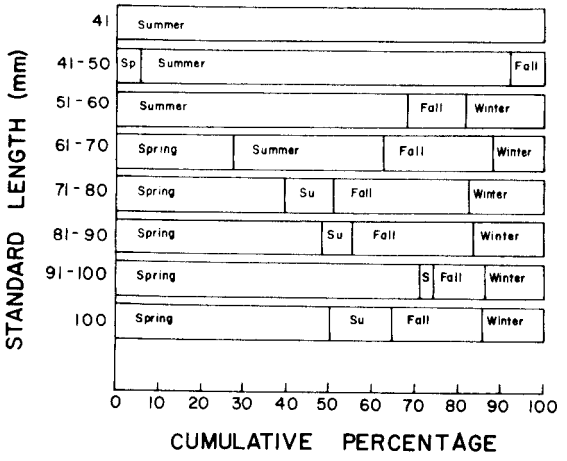

FIGURE 4.—Histogram of percentage of stomachs examined during spring (March through May), summer (June through August), fall (September through November), and winter (December through February) for *Etropus crossotus* of various standard length groups.

each season of the year to provide reliability to the data (Figure 4).

The food habits of *E. crossotus* were similar in both the rivers and sounds of Georgia. There were some alterations in food habits associated with increased standard length, however. While *Ps. coronatus* was present in a greater percentage in the stomachs of *E. crossotus* of all sizes than any other food organism, polychaetes increased in importance in fishes longer than 100 mm. The appearance of polychaetes in stomachs of larger *E. crossotus* may be a function of the increase in mouth size during growth.

Virtually all of the copepods found in the stomachs of *E. crossotus* were *Ps. coronatus*. Plankton samples taken by us during the course of this study verified that the copepod population in Georgia coastal waters is dominated by *Ps. coronatus*.

During October 1972, a series of bihourly trawls over a 24-h period was obtained in Ossabaw Sound. Each trawl was of 10-min duration and covered the same bottom. A total of 121 *E. crossotus* were captured in the 12 samples, and their stomachs were analyzed. Data from these fish were excluded from Figure 3 but are included in Figure 5.

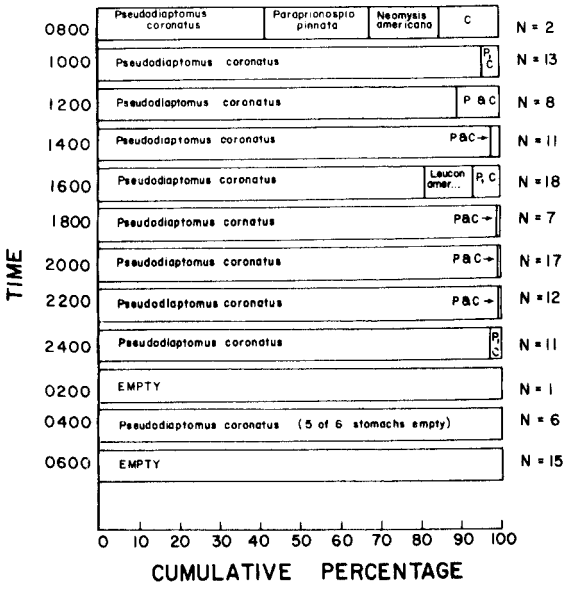

FIGURE 5.—Histogram illustrating the feeding habits of *Etropus crossotus* at 2-h intervals for 24 h. (N = number of stomachs analyzed for each bar, C = Crustacea other than those specifically identified in the bar, P = polychaetes, and Leucon amer. . . = *Leucon americanus*.)

P. coronatus was the numerically dominant organism in the stomachs with the exceptions of samples taken at 0200, 0600, and 0800 h. At 0200 and 0600 h none of the stomachs examined (16) contained food. At 0800 h only two *E. crossotus* were obtained, and a variety of food organisms were identified, with *Ps. coronatus* most abundant. The 0400 h sample contained six *E. crossotus* of which only one contained food (100% *Ps. coronatus*).

Based on this limited information, it appears that *E. crossotus* feeds mainly during the daylight hours with unchanging food habits throughout the day. This observation correlates with the findings of de Groot (1971) which indicate that bothids are visual feeders.

Ancylopsetta quadrocellata

The food habits of *A. quadrocellata* at different seasons of the year, location within the estuary, and standard length are presented in Figure 6. The preponderance of the animals were captured during the spring, reflecting the seasonal availability of this fish in Georgia estuarine waters.

N. americana was the dominant food organism throughout the year. *Trachypenaeus constrictus* became important during the summer and fall. *Neopanope sayi* was present in significant quantities during the winter.

While the food habits of *A. quadrocellata* captured in rivers were nearly identical to those captured in sounds, there were some differences in food habits with size of the fish. *N. americana* exceeded 50% of the total number of organisms found in the stomachs of fishes of less than 150 mm. Fish remains were found in the stomachs of fishes longer than 75 mm, although fish were never the dominant food organism. *T. constrictus* first became important as food in *A. quadrocellata* longer than 100 mm and was the dominant organism in fishes from 150 to 174 mm. Fishes longer than 175 mm fed on a variety of organisms. These data indicate that the diversity of foods increases with the size of the predator. The relatively large mouth of *A. quadrocellata* compared to that of *E. crossotus* may account for some of this variability in food habits with size (Figure 2).

Ps. coronatus, the dominant organism in the stomachs of *E. crossotus*, was virtually absent from the stomachs of *A. quadrocellata* longer than

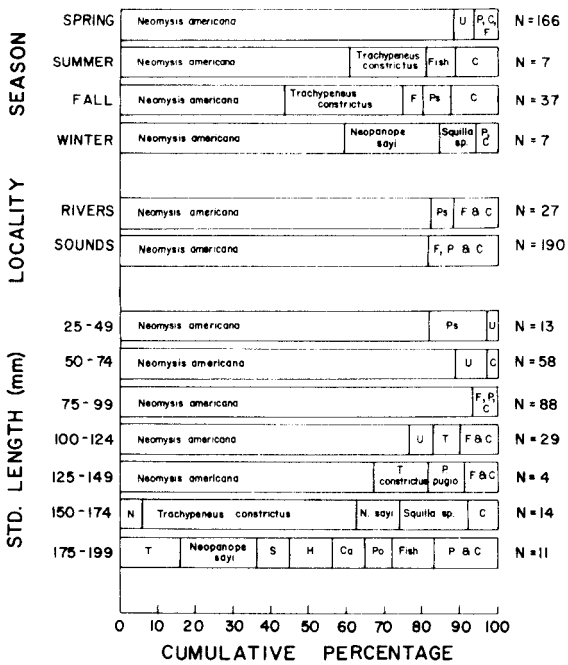

FIGURE 6.—Histogram illustrating the feeding habits of *Ancylopsetta quadrocellata* by season of the year, locality, and standard length. (N = number of stomachs analyzed for each bar, U = *Unciola serrata*, P = polychaetes, C = Crustacea other than those specifically identified in the bar, F = fish remains, Ps = *Pseudodiaptomus coronatus*, and T. constrictus = *Trachypenaeus constrictus*, P. pugio = *Palaemonetes pugio*, N = *Neomysis americana*, S = *Squilla* sp., H = *Hexapanopeus augustifrons*, Ca = *Cancer irroratus*, and Po = *Portunus gibbesii*.

50 mm. This may also relate to mouth size differences between the species. Studies with *Paralichthys lethostigma* and *P. dentatus* reared in the laboratory on brine shrimp, *Artemia salina*, indicate that once the flounders reach sufficient size (in this case about 25 mm), they have difficulty retaining ingested *A. salina* nauplii (Stickney and White, unpubl. data). The nauplii tend to be flushed through the gills and out the operculums. While the fish are still able to hunt the *A. salina* by sight, they do not seem to ingest a great number of nauplii. The relative mouth sizes of *P. lethostigma* and *P. dentatus* are similar to those of *A. quadrocellata, C. spilopterus,* and *S. aquosus*.

Citharichthys spilopterus

The food habits of *C. spilopterus* in relation to season of the year, location, and size are documented in Figure 7. The majority of the fish examined were captured during the summer (June through August). No fish were captured during the winter months (December through February). *N. americana* was the dominant species occurring in the stomachs of *C. spilopterus* during each of the three seasons for which data are available. A greater proportion of *T. constrictus* occurred in fishes captured in sounds than in those taken from rivers. The percentage of *N. americana* and fish remains in the stomachs of *C. spilopterus* from the two localities were nearly identical.

Food habit patterns relative to standard length of *C. spilopterus* were similar to those observed in *A. quadrocellata*. *N. americana* became less important as food with increasing size in *C. spilopterus*. *T. constrictus* became the dominant organism in *C. spilopterus* of 125 mm and above. *N. americana* was absent in the stomachs of fishes longer than 125 mm.

Fish less than 50 mm were not obtained in the trawls. It is possible that all sizes of *C. spilopterus* do not occur in Georgia estuarine waters but merely that they migrate through the southeastern Atlantic coast during certain seasons of the year. Specimens longer than 140 mm were not taken. The seasonal distribution observed agrees with that determined by Dahlberg and Odum (1970).

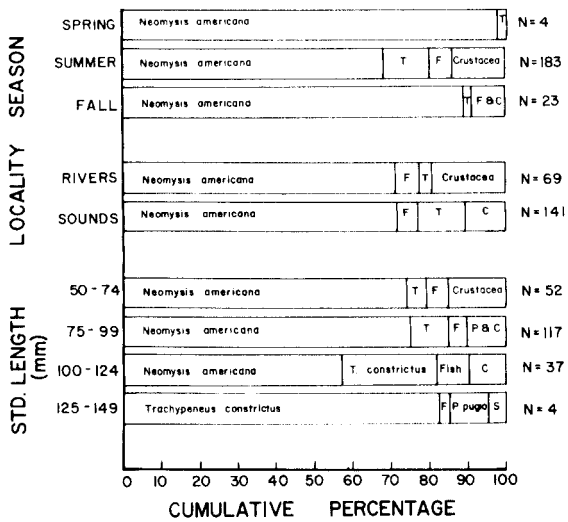

FIGURE 7.—Histogram illustrating the feeding habits of *Citharichthys spilopterus* by season of the year, locality, and standard length. (N = number of stomachs analyzed for each bar, T = *Trachypeneus constrictus*, F = fish remains, C = Crustacea other than those specifically identified in the bar, P = *Palaemonetes pugio*, and S = *Squilla empusa*.)

Scophthalmus aquosus

S. aquosus were present in Georiga coastal waters primarily during the spring (March through May). Few specimens were captured during the remainder of the year (Figure 8). *S. aquosus* fed nearly exclusively on *N. americana* during all seasons and in all locations. Several species of crustacea, fish remains, and an ectoproct made up the remainder of the food organisms found in the stomachs of *S. aquosus* (Table 1).

There was no change in food habits with size as found in *A. quadrocellata* and *C. spilopterus*, even though *S. aquosus* longer than 150 mm were captured. There were few animals in the size ranges above 74 mm, however, and the presumed food habits may reflect a lack of samples. Most of the fish captured were rather small. The relative abundance of small fish compared with the larger sizes is probably a good indication of their relative abundance in nature.

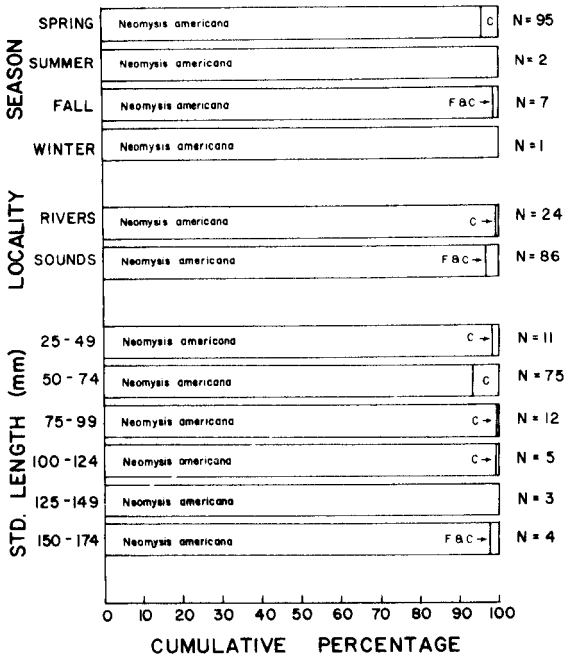

FIGURE 8.—Histogram illustrating the feeding habits of *Scophthalmus aquosus* by season of the year, locality, and standard length. (N = number of stomachs analyzed for each bar, F = fish remains, and C = Crustacea other than *Neomysis americana*.)

CONCLUSIONS

The four bothid fish species examined during this study are all relatively small fishes which feed on a variety of organisms. All appear to be totally carnivorous, since no plant material was recovered from the stomachs. Because of the predominance of certain organisms within the stomachs and the lack of detritus and sand so common in animals which indiscriminately browse off the sediments, they appear to be selective feeders. This selectivity apparently relates to the ability of bothids to feed by sight (de Groot, 1971).

E. crossotus was found to feed heavily on *Ps. coronatus*, and secondarily on spionid polychaetes, especially *Pa. pinnata*. The small mouth relative to body size of *E. crossotus* may play an important role in the food habits of this species. By the same token, the larger mouths of the other species may prohibit them from feeding on small food items.

A. quadrocellata, *C. spilopterus*, and *S. aquosus* fed heavily on *N. americana*, however, *A. quadrocellata* and *C. spilopterus* adjusted their food habits, becoming more diversified and utilizing *T. constrictus* as a primary food organism as they grew larger. The food habits of *S. aquosus* did not change with increasing size within the range of sizes examined. The relatively larger mouths of these three species seem important in allowing them to consume food organisms of larger sizes than those eaten by *E. crossotus*. The three fishes with the larger mouths fed to some extent on other species of fishes, whereas no fish remains were found in the stomachs of *E. crossotus*.

ACKNOWLEDGMENTS

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APPENDIX

List of organisms found in stomachs of Bothidae from Georgia estuarine waters

Rhynchocoela
- *Cerebratulus* sp.

Ectoprocta
- *Bugula neritina* (Linnaeus)

Polychaeta
- *Diopatra cuprea* (Bosc)
- *Paraprionospio pinnata* (Ehlers)
- *Nereis succinea* (Frey and Leuckart)
- *Sabellaria vulgaris* Verrill
- *Sabella microphthalma* Verrill
- *Asabellides oculata* Webster
- *Clymenella torquata* Leidy
- Spionidae
- Nereidae

Mollusca
- Gastropod remains
- Pelecypod siphons
- Pelecypod postlarvae

Crustacea
- Amphipoda
  - *Ampelisca vadorum* Mills
  - *Ampelisca* sp.
  - *Listriella barnardi* (Wigley)
  - *Corophium tuberculatum* Shoemaker
  - *Unciola serrata* Shoemaker
  - *Batea catharinensis* Muller
  - *Melita appendiculata* (Say)
  - *Melita nitida* Smith
  - *Monoculodes edwardsi* Holmes
  - *Erichthonius brasiliensis* Dana
  - *Paracaprella tenuis* Mayer
  - *Microprotopus ranei* Wigley
  - *Corophium simile* Shoemaker
  - *Cerapus tubularis* Say
  - *Lembos websteri* Bate
  - *Gammarus palustris* Bousfield
  - *Caprella equilibra* Say
  - *Corophium lacustre* Vanhoffen
- Copepoda
  - *Pseudodiaptomus coronatus* Williams
  - *Labidocera aestiva* Wheeler
  - Calanoid copepoda
- Cumacea
  - *Leucon americanus* Zimmer
  - *Oxyurostylis smithi* Calman
  - *Mancocuma altera* Zimmer
- Mysidacea
  - *Neomysis americana* (S. I. Smith)
- Ostracoda (unidentified)
- Isopoda
  - *Edotea montosa* Stimpson
- Stomatopoda
  - *Squilla empusa* Say
  - *Squilla neglecta* Gibbes
- Decapoda (Natantia)
  - *Acetes americanus carolinae* Hansen
  - *Penaeus setiferus* (Linnaeus)
  - *Trachypenaeus constrictus* (Stimpson)
  - *Palaemonetes pugio* Holthuis
  - *Palaemonetes vulgaris* (Say)
  - *Ogyrides limicola* Williams
  - *Periclimenes longicaudatus* (Stimpson)
  - *Latreutes parvulus* (Stimpson)
  - *Alpheus normanni* Kingsley
  - Caridean larvae
- Decapoda (Reptantia)
  - *Pagurus pollicaris* Say
  - *Pagurus* sp.
  - *Callinectes sapidus* Rathbun
  - *Portunus spinimanus* Latreille
  - *Portunus gibbesii* (Stimpson)
  - *Callinectes similis* Williams
  - *Cancer irroratus* Say
  - *Hexapanopeus angustifrons* (Benedict and Rathbun)
  - *Neopanope sayi* (Smith)
  - *Pinnixa* sp.
  - *Persephona punctata aquilonaris* Rathbun
  - Megalops and zoea
  - Portunid postlarvae

Osteichthyes
- *Prionotus* sp.
- *Symphurus plagiusa* (Linnaeus)
- *Synodus foetens* (Linnaeus)
- *Bairdiella chrysura* (Lacépède)
- *Anchoa mitchilli* (Valenciennes)
- *Etropus crossotus* Jordan and Gilbert
- *Fundulus heteroclitus* (Linnaeus)
- *Menidia* sp.
- *Cynoscion* sp.
- Bothid postlarvae
- Fish remains

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DISTRIBUTION OF SIPHONOPHORES IN THE REGIONS ADJACENT TO THE SUEZ AND PANAMA CANALS

ANGELES ALVARIÑO[1]

ABSTRACT

These studies are based on the material collected by Israeli cruises in the eastern Mediterranean and the Red Sea (Gulf of Elat), and by Scripps Institution of Oceanography Expeditions in the Caribbean and the Pacific regions adjacent to the Panama Canal. Published information on the distribution of siphonophores in those areas and in adjacent regions is included. Distributional tables and maps are also included.

The eastern Mediterranean collections encompass 21 species of siphonophores. Most of these species have been previously recorded in the western Mediterranean. *Eudoxia russelli* (eudoxid of *Chelophyes appendiculata*), *Sulculeolaria angusta*, and *S. chuni* have not been previously observed in any Mediterranean region. New records for the eastern Mediterrranean are: *Ch. contorta, Diphyes bojani, D. dispar, Lensia campanella, L. meteori, L. subtilis, S. quadrivalvis, S. turgida, Rosacea plicata, Physophora hydrostatica*, and *Apolemia uvaria*. Few species previously observed in the Mediterranean were not present in the collections here analyzed.

Fifteen species of siphonophores appeared in the material from the Gulf of Elat. New records for the Red Sea are *Ch. appendiculata, E. russelli, Diphyopsis mitra*. The other species present (*Ch. contorta, Diphyes dispar, L. subtilis, S. chuni, S. quadrivalvis, Abylopsis eschscholtzi, A. tetragona, Enneagonum hyalinum, Cordagalma cordiformis, Agalma elegans*, and *A. okeni*) have been previously observed in the Red Sea.

New records at both sides of the Suez Canal which could be considered indicative of migration along this waterway are: *Ch. appendiculata* (Mediterranean to the Red Sea), and *S. chuni* (Red Sea to the Mediterranean). However, the species are cosmopolitan in distribution, and the source of the populations in the regions adjacent to the Suez Canal may be in the adjacent oceanic regions.

Thirty species of siphonophores were observed in the Caribbean and Pacific regions adjacent to the Panama Canal. Most of the species are new records for those regions. Twenty one more species, not present in the collections here analyzed, had been previously recorded at either or in both the Caribbean, Gulf of Mexico and/or in regions of the Pacific adjacent to the area surveyed.

Particular attention is devoted to the distribution of closely related pairs of allopatric species, *Muggiaea atlantica–M. kochi*, and *Ch. appendiculata–Ch. contorta*. *Muggiaea kochi* (neritic species) and *Ch. appendiculata* inhabit the Caribbean, Gulf of Mexico and adjacent regions of the western tropical Atlantic. *Muggiaea atlantica* (neritic species) and *Ch. contorta* inhabit the Pacific regions off Mexico and Central America. However, few specimens of *Ch. contorta* and *M. atlantica* were also observed in the Caribbean at locations near the opening of the Panama Canal, and specimens of *Ch. appendiculata* and *M. kochi* occurred at locations in the Pacific close to the Panama Canal. This distributional incidence may suggest that migration or artificial transport is taking place via the Panama Canal. It is also indicated that few specimens of *L. challengeri* (Indo-Pacific species) were observed near the opening of the Panama Canal in the Caribbean.

New data have been published on the siphonophores of the regions adjacent to the Suez Canal (eastern Mediterranean and the Red Sea), as well as for the regions adjacent to the Panama Canal (western Caribbean and the Central American Pacific). Bigelow and Sears (1937) included data on the distribution of the siphonophores in the eastern Mediterranean, and Lakkis (1971) on the Lebanese region. Schneider (1898), Totton (1954), and Halim (1969) presented information on the siphonophores of the Red Sea. Bigelow (1911) analyzed the siphonophores of the eastern tropical Pacific, which included few locations in the regions here surveyed; Alvariño (1968, 1972) studied the siphonophores of the tropico-equatorial oceanic regions, and Alvariño (1971) covered the Central American Pacific including also a compilation of distributional data for the world oceans.

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The present work constitutes a more detailed survey on the siphonophores of the regions adjacent to the above mentioned interoceanic canals. These studies are based on the Siphonophorae material (65 plankton samples) collected by Israel in the eastern Mediterranean during 1967, 1968, 1969, and 18 plankton samples (Red Sea, 1969, 1970) corresponding to two locations in the Gulf of Elat; and the 64 plankton samples from Scripps Institution of Oceanography Expeditions (La Creuse 1962, Bonacca 1963, *Thomas Washington* 1969) in the Caribbean and Pacific regions adjacent to the Panama Canal. The Scripps Institution collections covered larger regions than the area in which the present studies are concentrated, and the total collections of the mentioned expeditions have been analyzed and the results included in Alvariño (1968, 1971, 1972).

The present studies chiefly concern with the distribution and some ecological aspects of the siphonophores. The subject is treated under two parts: 1) distribution of siphonophores in the eastern Mediterranean and the Red Sea, and 2) the siphonophores of the western part of the Caribbean and the Central American Pacific.

The pattern of distribution of the species is presented. Tables with the distribution of the species include also references on previous records for the regions.

Maximum density for most of the species off Israel and around Cyprus can be attributed to the high productivity of the region (Lakkis, 1971).

The present study also indicates the Red Sea includes fewer species than the Indian Ocean. This factor may be related to the high salinity and temperature of the Red Sea, as well as to the shallowness of the sill at Bab el Mandeb.

The incidence of both polygastric and eudoxid forms in most of the samples shows breeding is taking place in those regions, and that reproduction may be an uninterrupted process along the year.

A large number of species of siphonophores are truly cosmopolitan, inhabiting the Arctic, Antarctic, Indian, Pacific, and Atlantic Oceans, whereas other species inhabit only the Atlantic, Pacific, and Indian Oceans (Alvariño, 1971), and some others are restricted to the Indian Ocean, adjacent waters and the southeastern Asiatic regions, while few are restricted to either the Atlantic or the Indo-Pacific regions.

Owing to the above mentioned biogeographic considerations, particular emphasis in the distribution of the species should be dedicated to the pairs of closely related species allopatric in distribution. The pairs to be considered correspond to the Panamanian region: *Chelophyes appendiculata–Ch. contorta* (respectively related to cold-temperate, and warm waters), *Muggiaea atlantica–M. kochi* (inhabiting respectively the neritic temperate and neritic warm waters), and *Lensia challengeri–L. fowleri* (respectively Indo-Pacific and Atlantic species).

The evidence of a two way migration "via" the Panama Canal, as shown by the distribution presented by several species at the regions adjacent to the entrance to the Panama Canal, could be active, by progression of the population along the waterway, or passively transported in the ballast waters or the waters used in the cooling system of ships. Therefore, migrations could be also greatly intensified or enhanced by passive transport along the canal.

METHODS

The plankton samples here analyzed were not collected in uniform manner. The plankton collections from the eastern Mediterranean and the Gulf of Elat were obtained with a standard plankton net of the Villefranche type, as designed and described by Working Party No. 2 (1968). The net has a mouth internal diameter of 57 cm, a total length of 261 cm, and 200-μ mesh. Vertical, oblique, and horizontal tows were taken. The vertical and oblique hauls in the eastern Mediterranean and the Gulf of Elat reached from 200 m to the surface, and the horizontal tows were obtained at various depths in the upper 200 m at a speed of 2-3 knots during 10 min.

The material from the Scripps Institution collections corresponds to 1-m net oblique hauls taken from about 140 m to the surface, and at less than 100 m or less than 50 m in shallow waters; and the ½-m net oblique tows were obtained from about 150 m to the surface and the horizontal hauls at various depths between 50 and 0 m.

Each total plankton sample was analyzed for siphonophores, and the number of specimens determined for both polygastric and eudoxid forms. However, owing to the diversity of the collecting methods used, and the time span

covered by the collections, quantitative data are not considered, and only qualitative data are included in the presentation of the results.

DISTRIBUTION OF SIPHONOPHORES IN THE EASTERN MEDITERRANEAN AND THE RED SEA

Twenty-one species of siphonophores were observed in the eastern Mediterranean collections, and fifteen species in the Gulf of Elat (Red Sea) collections.

Eudoxia russelli (eudoxid of *Ch. appendiculata*), *Sulculeolaria angusta*, and *S. chuni* are new records for the Mediterranean.

Chelophyes contorta, Diphyes bojani, D. dispar, Lensia campanella, L. meteori, L. subtilis, Sulculeolaria quadrivalvis, S. turgida, Rosacea plicata, and *Apolemia uvaria* are first records for the eastern Mediterranean. These species have been previously observed in the western Mediterranean. The only previous records of *Ch. contorta* for the Mediterranean correspond to the Alborán Sea (Alvariño, 1957). Therefore, the presence of the species in the Levant Mediterranean basin could be considered a tracer of Atlantic waters. All the Mediterranean species are also found in the Atlantic. Some of the species have permanently established populations in the Mediterranean, while others may be only remains of the Atlantic flow.

Most of the species previously found in the eastern Mediterranean (Bigelow and Sears, 1937; Lakkis, 1971) were also observed in the collections here analyzed.

Some species previously found in the western Mediterranean (*M. atlantica, L. fowleri, Clausophyes ovata, Ceratocymba sagittata, Vogtia pentacantha, V. spinosa, Praya cymbiformis, Amphicaryon acaule, Anthophysa rosea, Rhizophysa filiformis, Cordagalma cordiformis, Athoribya rosacea,* and *Nanomia cara*) have not been observed in the eastern Mediterranean (Alvariño, 1971; Lakkis, 1971) (Table 1).

The most abundant species in both distributional coverage of the surveyed region and in number of species, *Ch. appendiculata, D. dispar, Hippopodius hippopus, Bassia bassensis* were found along the years, and in December appeared scattered or absent (Figures 1, 2, 6, 8). *Eudoxoides spiralis, S. turgida, S. quadrivalvis*, and *S. angusta* followed in decreasing order of abundance in both space covered and number of individuals (Figures 3, 5). These species appeared abundantly off Israel, Lebanon, Syria and around Cyprus. *Sulculeolaria angusta* and *S. turgida* were also found in the Cretan region.

Species with few scattered records are, *E. russelli* (north of Cyprus), *Ch. contorta* (off Israel and between Syria and Cyprus), *D. bojani, M. kochi, L. campanella, L. multicristata, L. subtilis, S. chuni, A. tetragona, R. plicata, A. uvaria, Agalma elegans*, and *Physophora hydrostatica* (spread along the Levant basin). (Figures 1-8.)

It is worthy of notice that the maximum density for most of the species of siphonophores appeared at the easternmost part of the Mediterranean Sea, off Israel and around Cyprus, which can be attributed to the high productivity of the region (Lakkis, 1971).

The species scattered along the eastern Mediterranean, not previously observed in this sea, could be considered tracers of Atlantic waters (Oren, 1971).

The presence of *L. multicristata* (a mesoplanktonic species) off Tira, Israel, could be an indicator of upwelling.

It is well established that the fauna of the eastern Mediterranean is an impoverished fauna from that of the western basin. Many species do not reach the Levant Mediterranean basin, and only appear accidentally there, and few become established in the area. Por (1971) considered that "The colder areas of the Aegean Sea probably constitute an environment in which the Atlantic fauna is much better represented and better fitted to withstand the competition of the tropic immigrants."

Siphonophorae fauna of the Red Sea is poorer than that of the Indian Ocean, both in number of species and in the density of the respective populations. The Gulf of Elat may also include fewer species than the main Red Sea basin. The Gulf of Elat collections correspond to the winter months. Some of the species observed in the Gulf of Elat constitute new records for the Red Sea (*Ch. appendiculata, E. russelli,* and *Diphyopsis mitra*). Por (1971) stated that siphonophores and other holoplanktonic groups have not been found in the Suez Canal waters.

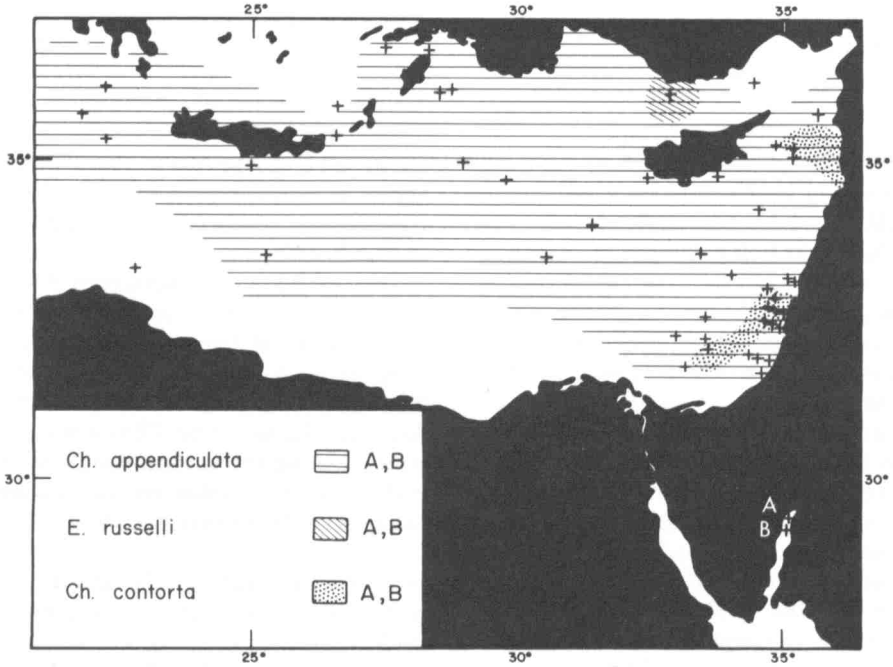

FIGURE 1.—Distribution of *Chelophyes appendiculata*, *Eudoxia russelli*, and *Chelophyes contorta* in the regions adjacent to the Suez Canal.

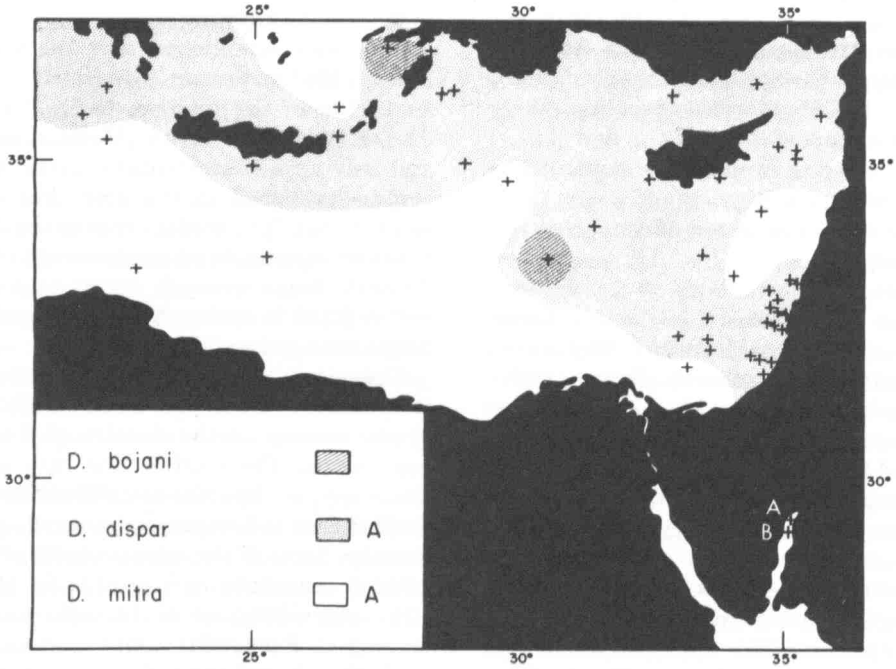

FIGURE 2.—Distribution of *Diphyes bojani*, *Diphyes dispar*, and *Diphyopsis mitra* in the regions adjacent to the Suez Canal.

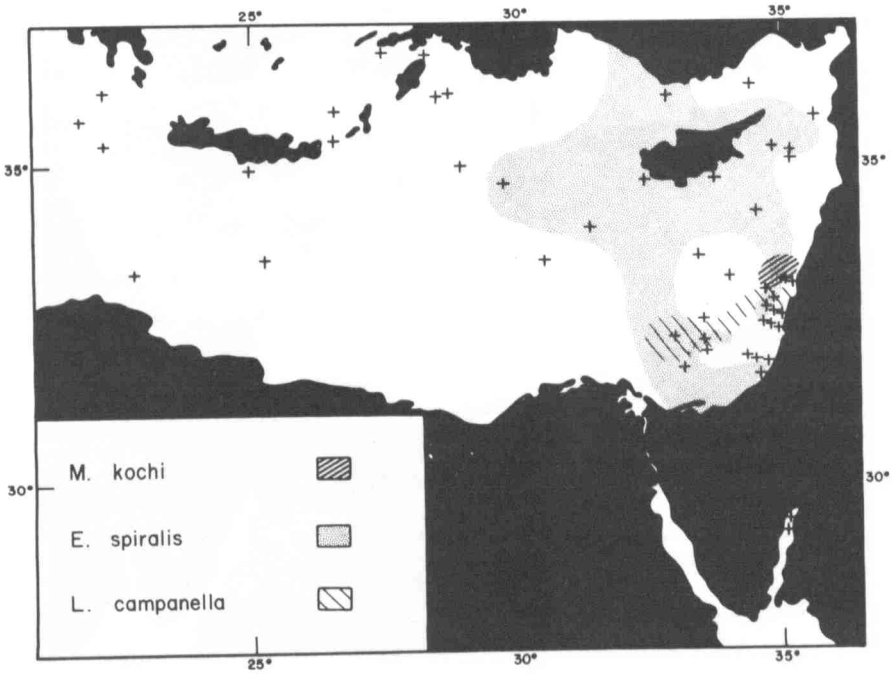

FIGURE 3.—Distribution of *Muggiaea kochi*, *Eudoxoides spiralis*, and *Lensia campanella* in the regions adjacent to the Suez Canal.

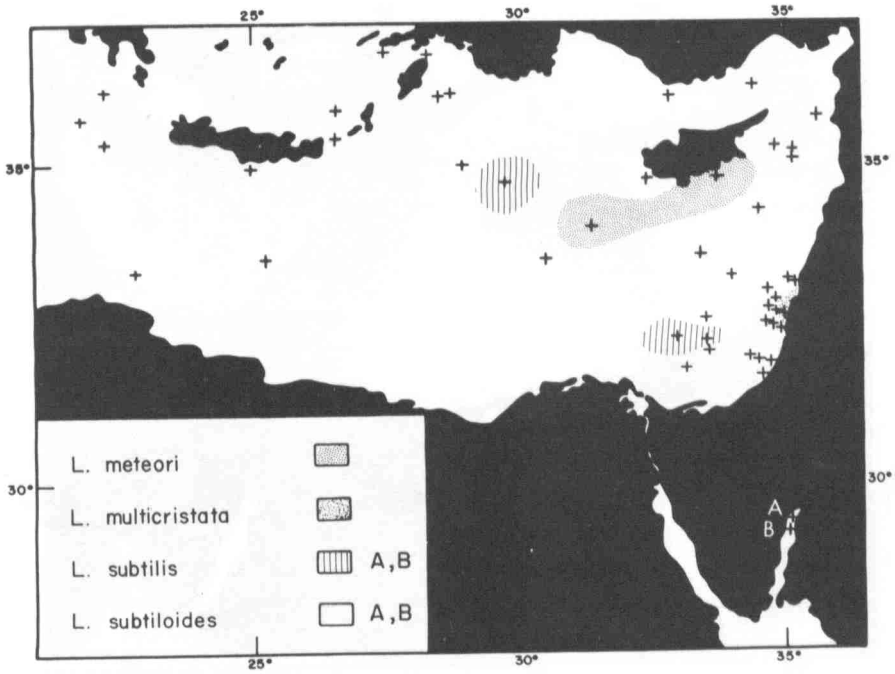

FIGURE 4.—Distribution of *Lensia meteori*, *Lensia multicristata*, *Lensia subtilis*, and *Lensia subtiloides* in the regions adjacent to the Suez Canal.

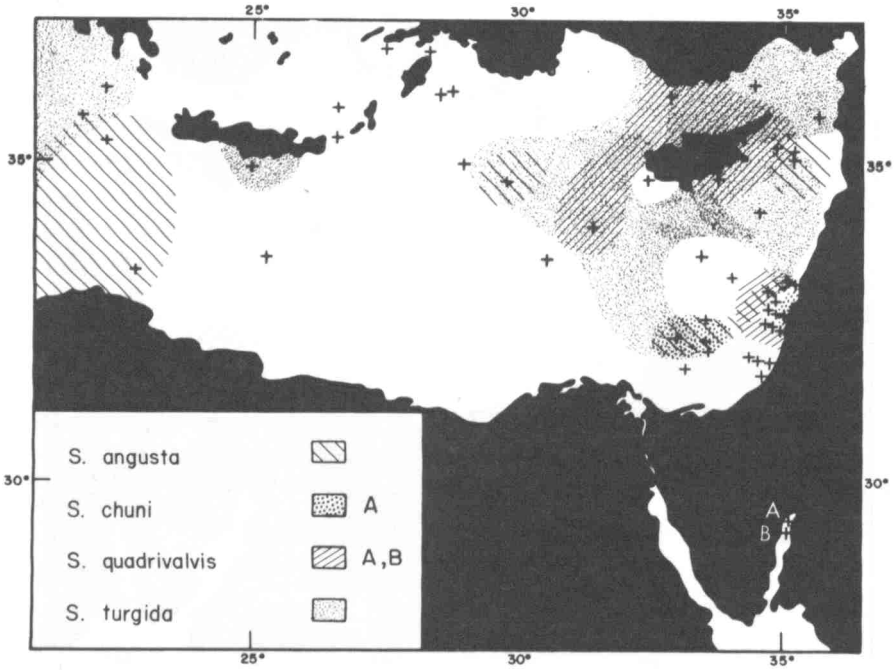

FIGURE 5.—Distribution of *Sulculeolaria angusta, Sulculeolaria chuni, Sulculeolaria quadrivalvis,* and *Sulculeolaria turgida* in the regions adjacent to the Suez Canal.

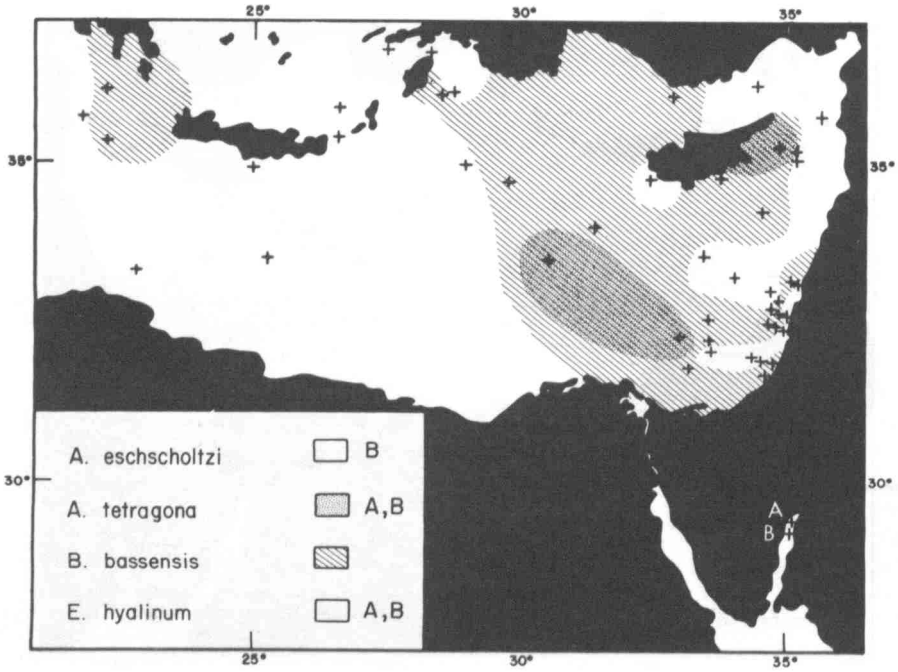

FIGURE 6.—Distribution of *Abylopsis eschscholtzi, Abylopsis tetragona, Bassia bassensis,* and *Enneagonum hyalinum* in the regions adjacent to the Suez Canal.

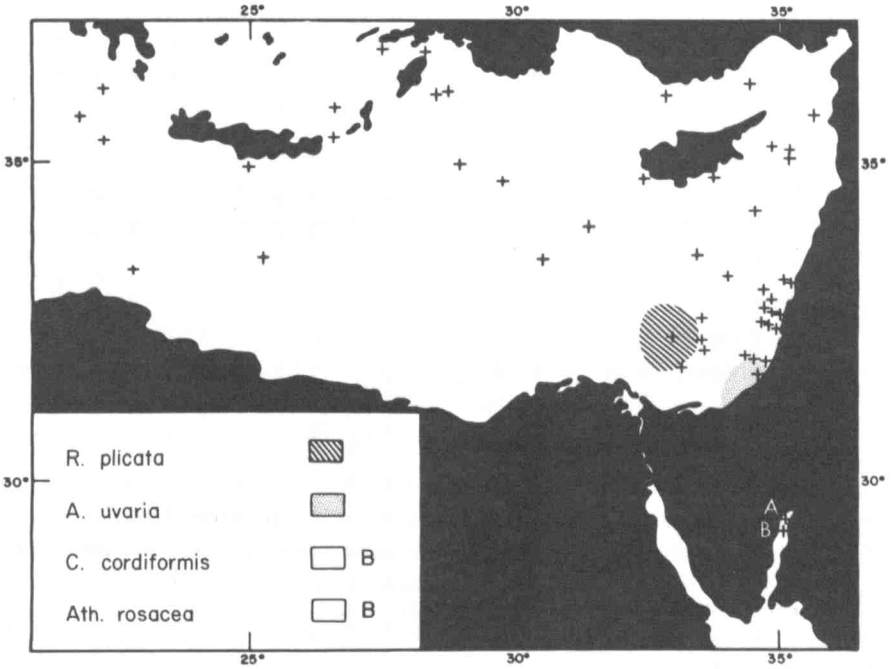

FIGURE 7.—Distribution of *Rosacea plicata, Apolemia uvaria, Cordagalma cordiformis*, and *Athoribya rosacea* in the regions adjacent to the Suez Canal.

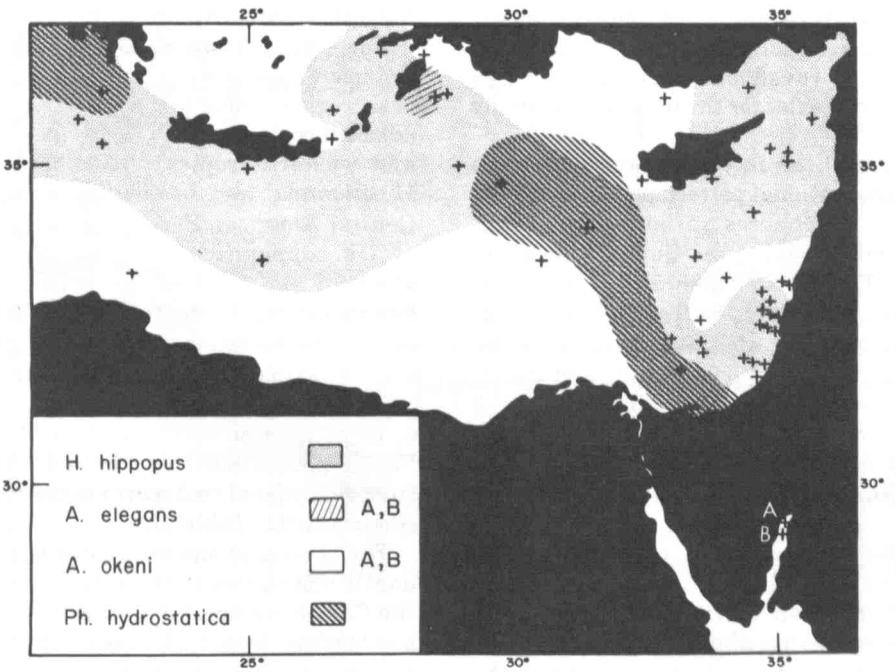

FIGURE 8.—Distribution of *Hippopodius hippopus, Agalma elegans, Agalma okeni*, and *Physophora hydrostatica* in the regions adjacent to the Suez Canal.

Other new records for the Gulf of Elat are *Diphyes dispar, L. subtilis, L. subtiloides, S. chuni, S. quadrivalvis, A. eschscholtzi, A. tetragona, E. hyalinum, C. cordiformis, A. rosacea, A. elegans*, and *A. okeni*. These species, except *Ch. contorta*, were only previously observed in either the central and the southern Red Sea or both (Figures 1, 2, 4-8). *Ch. contorta* was previously observed in the Gulf of Elat (Furnestin, 1958).

The depth of the sill at Bab el Mandeb does not exceed 100 m (Halim, 1969) and consequently meso and bathypelagic species are extensively excluded from the Red Sea. Halim considered the scarcity of species in the Red Sea as due to the "excluding action of the deep outflow over the sill at the southern entrance of the Red Sea on the deep water species; and . . . the effect of the high (21.5°–22°C) minimum temperature of the Red Sea deep water in inhibiting many species. . . ." He also considers excluding features the "high salinity (40.5–41.0‰) and the very low oxygen content (below 1 ml/l in summer and 2 ml/l at the end of the winter) below sill depth."

Similar interpretation could be applied for the paucity of the Mediterranean siphonophores as compared with the Atlantic, because of the sill at Gibraltar.

Thorson (1971) stated that "the physical-chemical conditions for the animals to pass the Canal have improved enormously although there are still obstacles for the migration of many species."

Seasonal variations in occurrence, abundance and in the distributional pattern presented by the species of siphonophores in both the Levant Mediterranean basin and the Gulf of Elat are to be expected. The various populations may show changes in both location and time of year. These changes may be due to the characteristics of the flow through the Strait of Gibraltar, and Bab el Mandeb respectively, and the characteristics of the circulation in the Mediterranean and the Arabian Sea, as well as the aspects of the vertical migration (Halim, 1969), and the ontogeny of the population.

Most of the siphonophores, except for a few species as explained above, present a wide almost cosmopolitan distribution (Alvariño, 1971). However, species abundant in the western Mediterranean and the Atlantic reaching the easternmost Mediterranean region could be considered "indicators" or tracers of the Atlantic waters. This could be similarly applied to some Indo-Pacific or Indian Ocean species reaching the Red Sea.

SIPHONOPHORES OF THE WESTERN CARIBBEAN AND THE CENTRAL AMERICAN PACIFIC

The pairs of closely related species allopatric in distribution, *Ch. appendiculata-Ch. contorta, M. atlantica-M. kochi*, and *L. challengeri–L. fowleri* deserve special attention.

Chelophyes appendiculata inhabits the temperate oceanic regions, and appears scattered along the tropico-equatorial realm, while *Ch. contorta* presents a distribution restricted to the tropico-equatorial regions (Alvariño, 1971).

Muggiaea atlantica inhabits the neritic temperate eastern Pacific, Transition region (band between the Subarctic and Central Pacific), the Japanese neritic waters and the neritic regions of the temperate Atlantic. *Muggiaea kochi* occupies the neritic tropico-equatorial Atlantic and the eastern equatorial Pacific (Alvariño, 1971).

Lensia challengeri is an Indo-Pacific species, and *L. fowleri* is most probably restricted to the Atlantic waters (Alvariño, 1971).

However, *Ch. appendiculata, M. kochi*, and *L. fowleri* appear widely distributed in the Caribbean region annex to the Panama Canal and in adjacent regions of the Caribbean, Gulf of Mexico, and western tropical Atlantic. *Ch. contorta, M. atlantica*, and *L. challengeri* appear in the Central American Pacific region. Few specimens of *Ch. appendiculata* and *M. kochi* were observed at locations near the opening of the Panama Canal in the Pacific, and few specimens of *Ch. contorta, M. atlantica*, and *L. challengeri* occurred at locations near the opening of the Panama Canal in the Caribbean. These observations suggest the Caribbean and the Pacific populations may be able to migrate or survive artificial transport via the Panama Canal (Figures 9-11, Table 2).

The species of siphonophores appearing abundantly distributed in the surveyed region in both the Caribbean and the Central American Pacific are *Diphyes bojani, D. dispar, Diphyopsis mitra*, and *A. eschscholtzi. Diphyes bojani* occurred at all Caribbean stations, except for the close to

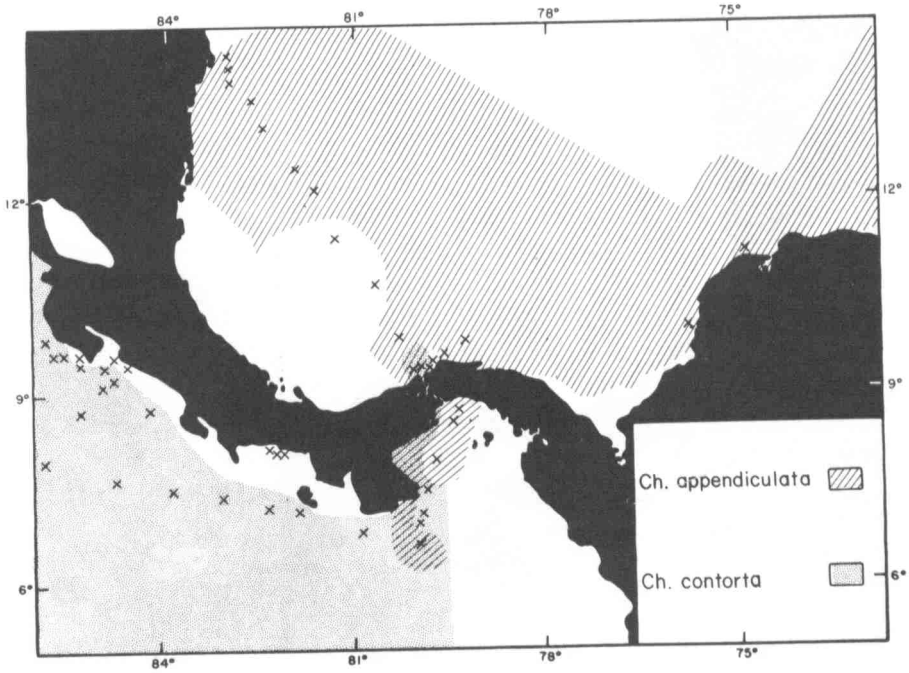

FIGURE 9.—Distribution of *Chelophyes appendiculata* and *Chelophyes contorta* in the regions adjacent to the Panama Canal.

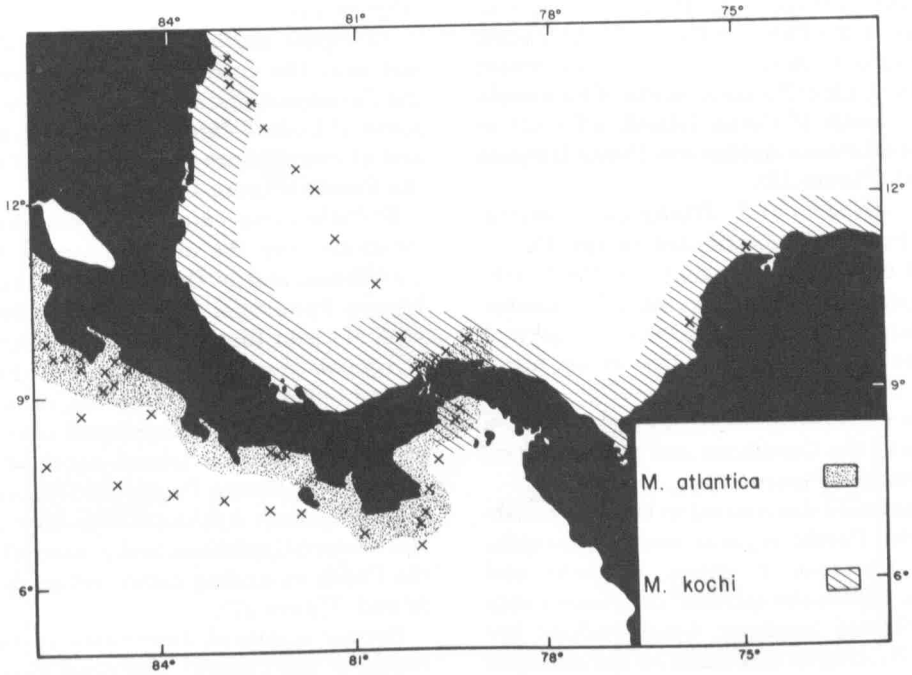

FIGURE 10.—Distribution of *Muggiaea atlantica* and *Muggiaea kochi* in the regions adjacent to the Panama Canal.

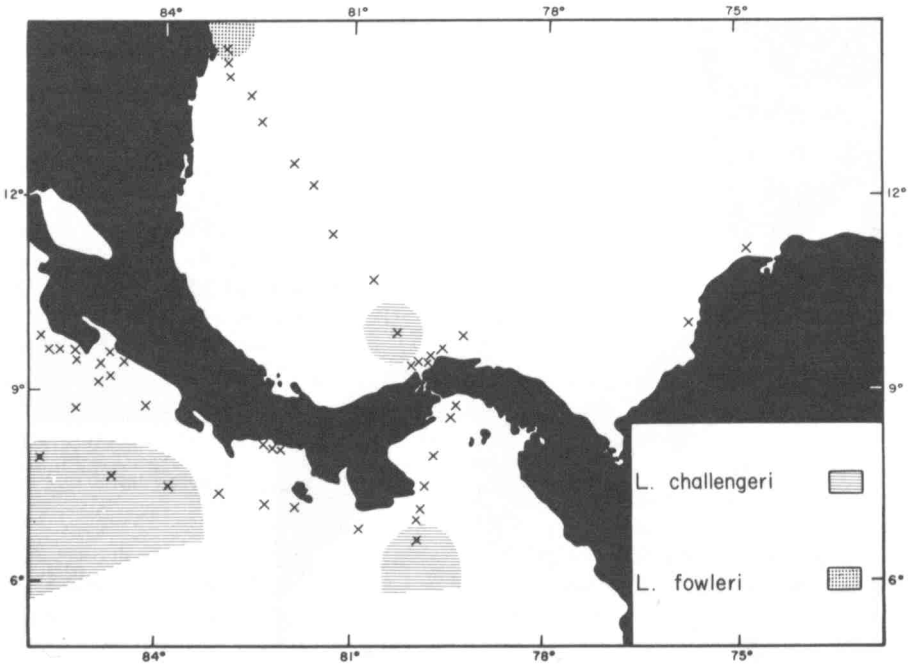

FIGURE 11.—Distribution of *Lensia challengeri* and *Lensia fowleri* in the regions adjacent to the Panama Canal.

shore locations off Huani, Nicaragua, off Puerto Colombia and Cartagena de Indias, and east to the entrance of the Panama Canal. In the Pacific region it was only missing at the northernmost station in the Gulf of Panama, south of Peninsula de Azuero, south of Coiba Island, off Gulf of Nicoya, and off Punta Arenas and Punta Guiones (Costa Rica) (Figure 12).

Diphyes dispar and *Diphyopsis mitra* appeared abundantly distributed in the Pacific region, and only in two locations in the Caribbean. *Diphyes dispar* was present off Colombia and off Laguna Perlas (Nicaragua), and *Diphyopsis mitra* at two locations a few miles north of Panama (Figures 12, 13).

Abylopsis eschscholtzi was only absent at a few stations in the Caribbean and in the Central American Pacific (Figure 14).

Species scattered distributed in both the Caribbean and the Pacific regions were *Eudoxoides spiralis, A. tetragona, S. chuni, A. okeni,* and *E. hyalinum. Eudoxides spiralis* was present only at five Caribbean locations, which include two stations off Nicaragua and three off the entrance to the Panama Canal, and in the Pacific appeared at two stations southeast of Peninsula de Azuero and at two offshore stations west of Costa Rica (Figure 13).

Abylopsis tetragona appeared off Colombia and near the entrance of the Panama Canal in the Caribbean, and south of the Azuero Peninsula, south of Coiba Island, west of Nicoya Peninsula, and at one offshore station west of Costa Rica in the Pacific (Figure 14).

Sulculeolaria chuni was observed at three locations over the deepest part of the western Caribbean, and in the Gulf of Panama, south of Nicoya Peninsula, and at two offshore stations west of Costa Rica in the Pacific (Figure 16).

Agalma okeni was found once in the Caribbean region (off Costa de Mosquitos, Nicaragua), and in the Pacific regions appeared from the Azuero Peninsula to Coiba Island, south of Costa Rica and west of Nicoya Peninsula (Figure 19).

Enneagonum hyalinum was only observed at the western Caribbean, and at several locations in the Pacific extending northwestwards from Coiba Island (Figure 17).

Species scattered distributed in the surveyed region of the Central American Pacific were, *S. quadrivalvis, S. turgida, B. bassensis,* and *H. hippopus* (Figures 16-18).

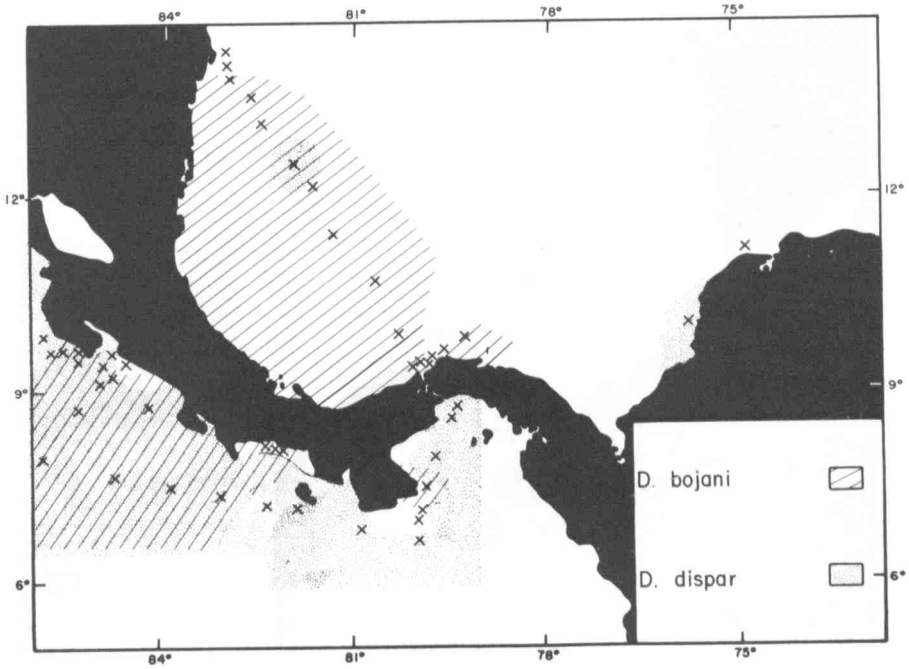

FIGURE 12.—Distribution of *Diphyes bojani* and *Diphyes dispar* in the regions adjacent to the Panama Canal.

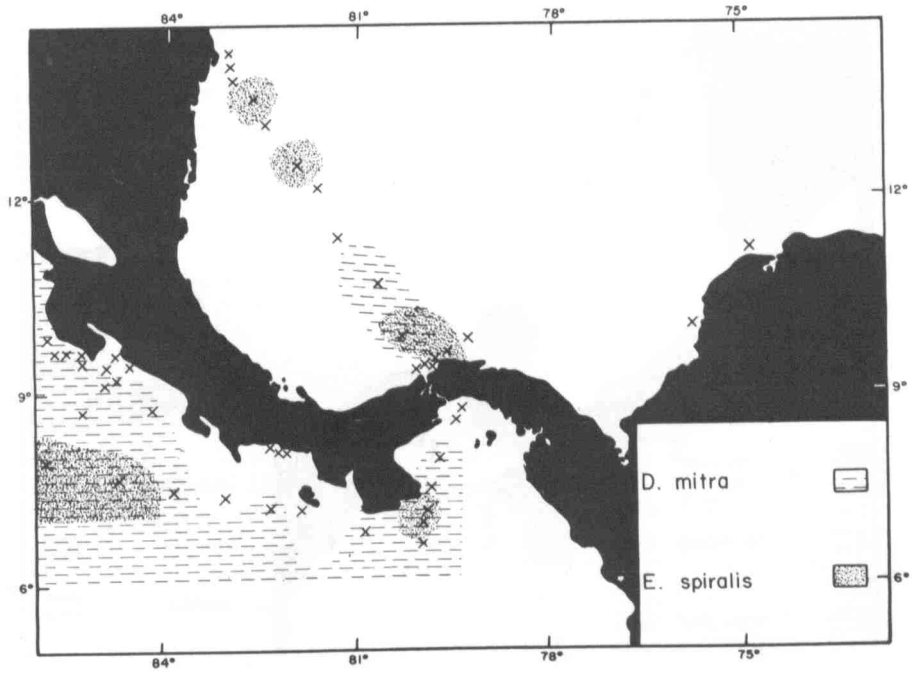

FIGURE 13.—Distribution of *Diphyopsis mitra* and *Eudoxoides spiralis* in the regions adjacent to the Panama Canal.

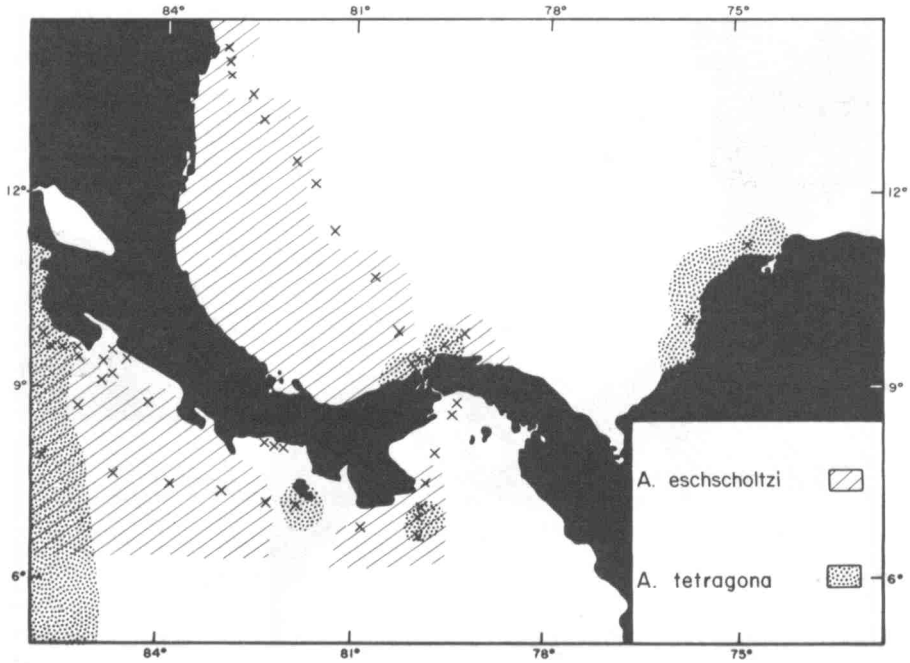

FIGURE 14.—Distribution of *Abylopsis eschscholtzi* and *Abylopsis tetragona* in the regions adjacent to the Panama Canal.

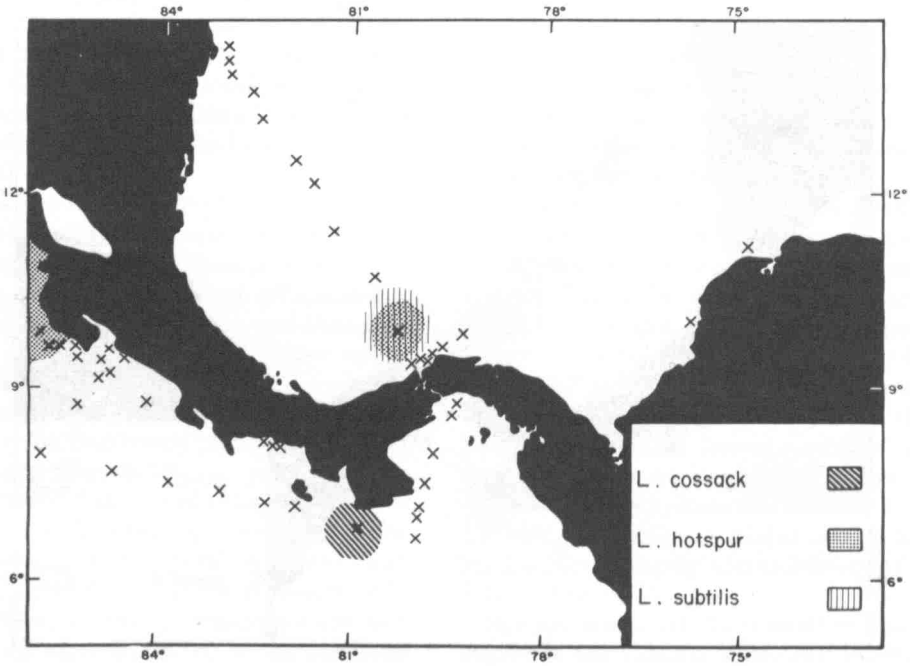

FIGURE 15.—Distribution of *Lensia cossack*, *Lensia hotspur*, and *Lensia subtilis* in the regions adjacent to the Panama Canal.

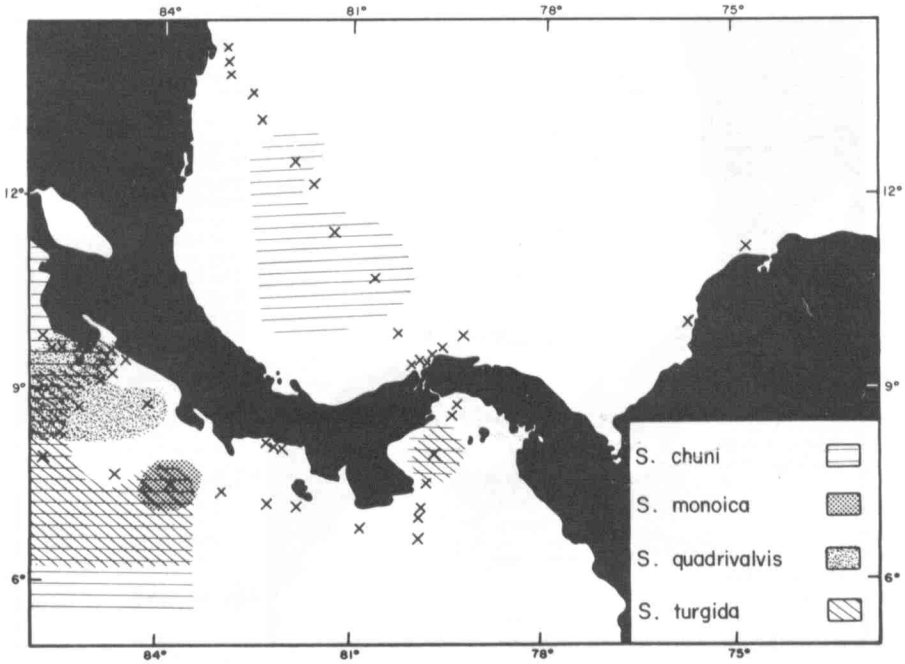

FIGURE 16.—Distribution of *Sulculeolaria chuni, Sulculeolaria monoica, Sulculeolaria quadrivalvis,* and *Sulculeolaria turgida* in the regions adjacent to the Panama Canal.

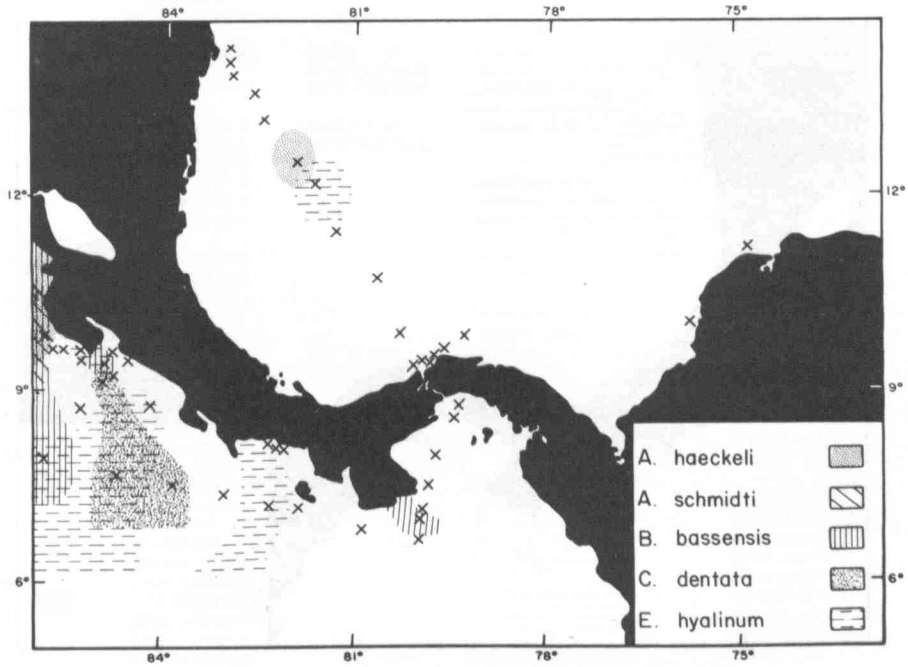

FIGURE 17.—Distribution of *Abyla haeckeli, Abyla schmidti, Bassia bassensis, Ceratocymba dentata,* and *Enneagonum hyalinum* in the regions adjacent to the Panama Canal.

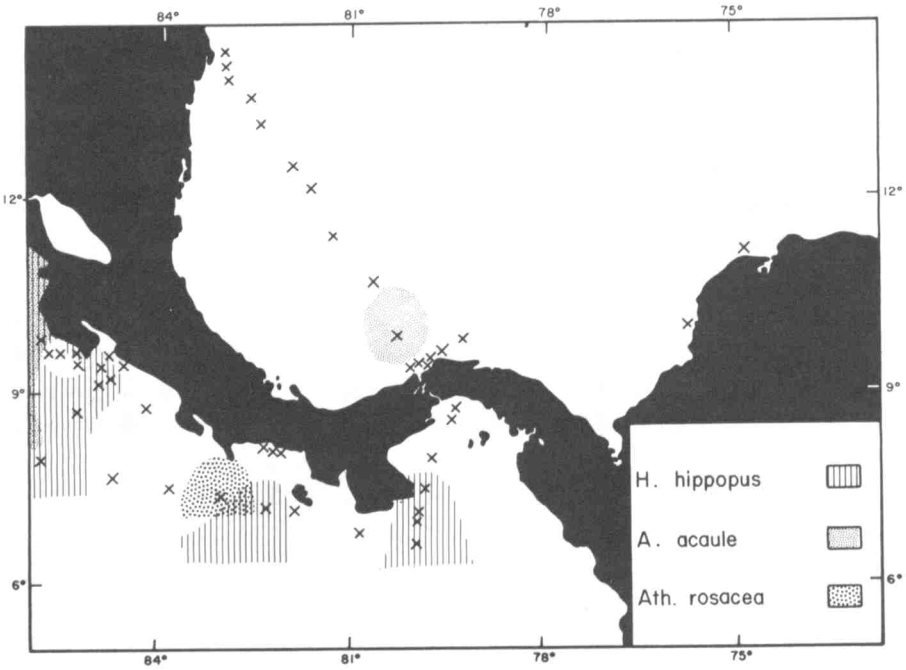

FIGURE 18.—Distribution of *Hippopodius hippopus*, *Athoribya rosacea*, and *Amphicaryon acaule* in the regions adjacent to the Panama Canal.

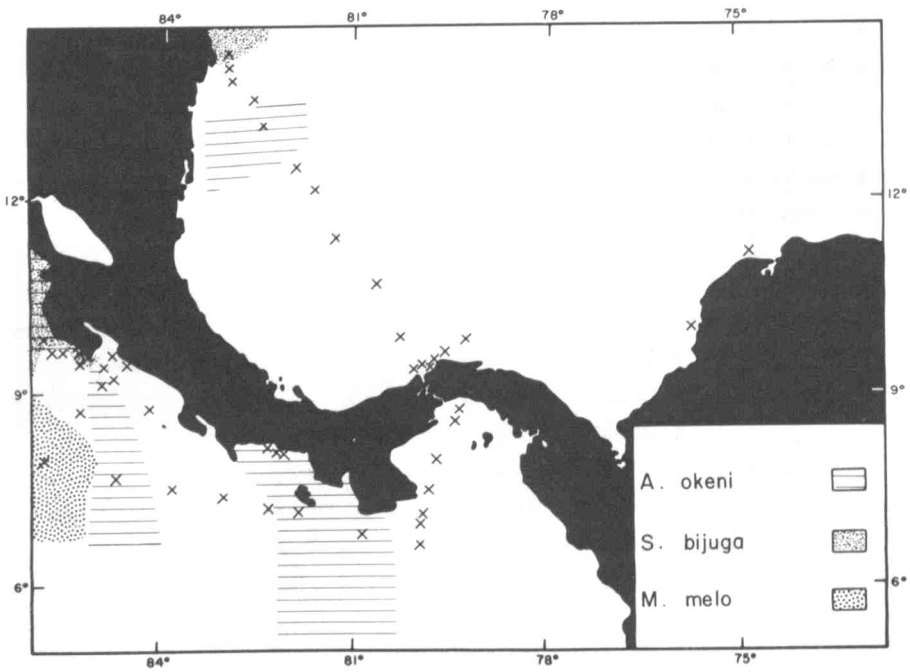

FIGURE 19.—Distribution of *Agalma okeni*, *Stephanomia bijuga*, and *Melophysa melo* in the regions adjacent to the Panama Canal.

TABLE 1.—Siphonophores of the regions adjacent to the Suez Canal.

Species	Eastern Mediterranean	Red Sea
Chelophyes appendiculata Eschscholtz, 1829	• ••	
	32°20′N-34°51′E	Gulf of Elat:
	32°45′N-34°57′E	29°30′N-34°55′E
	33°03′N-34°55′E	29°25′N-34°50′E
	35°05′N-35°00′E	
	33°00′N-35°00′E	
	32°55′N-34°34′E	
	35°35′N-35°26′E	
	34°50′N-28°55′E	
	35°55′N-28°37′E	
	36°30′N-28°13′E	
	36°31′N-27°27′E	
	35°14′N-26°33′E	
	33°25′N-30°20′E	
	33°10′N-33°50′E	
	31°31′N-34°28′E	
	32°23′N-34°37′E	
	34°37′N-32°20′E	
	32°30′N-33°21′E	
	31°42′N-34°28′E	
	32°46′N-34°53′E	
	32°50′N-34°50′E	
	33°25′N-33°14′E	
	32°01′N-33°25′E	
	33°25′N-25°15′E	
	34°47′N-25°10′E	
	35°11′N-22°15′E	
	35°35′N-21°50′E	
	35°57′N-22°15′E	
	34°10′N-34°29′E	
	35°57′N-32°23′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	35°50′N-31°15′E	
	32°43′N-34°38′E	
	32°10′N-32°50′E	
	32°07′N-33°24′E	
	31°42′N-33°00′E	
	35°55′N-28°33′E	
Eudoxia russelli Totton, 1932	35°57′N-32°23′E	Gulf of Elat:
		29°30′N-34°55′E
		29°25′N-34°50′E
Chelophyes contorta (Lens & Riemsdijk, 1908)	••	•+
	32°45′N-34°57′E	Gulf of Elat:
	35°05′N-35°00′E	29°25′N-34°50′E
	32°23′N-34°37′E	
	32°50′N-34°51′E	
	32°01′N-33°25′E	
	32°43′N-34°38′E	
Diphyes bojani (Eschscholtz, 1829)	••	
	36°31′N-27°27′E	
	33°25′N-30°20′E	
Diphyes chamissonis Huxley, 1859		+
Diphyes dispar Chamisso & Eysenhardt, 1821	••	+
	34°50′N-32°47′E	Gulf of Elat:
	35°05′N-35°00′E	29°30′N-34°55′E
	33°00′N-35°00′E	
	32°46′N-34°53′E	
	32°55′N-34°34′E	
	35°35′N-35°26′E	
	35°05′N-34°05′E	
	34°50′N-28°55′E	
	35°55′N-28°37′E	
	36°30′N-28°13′E	
	36°31′N-27°27′E	
	35°14′N-26°33′E	
	33°25′N-30°20′E	
	31°31′N-34°28′E	
	32°23′N-34°37′E	
	34°37′N-32°20′E	
	32°30′N-33°21′E	
	31°42′N-34°28′E	
(Diphyes dispar)	33°25′N-33°14′E	
	32°01′N-33°25′E	
	34°47′N-25°10′E	
	35°35′N-21°50′E	
	35°57′N-22°15′E	
	32°20′N-34°51′E	
	31°37′N-34°32′E	
	31°44′N-34°26′E	
	32°45′N-34°49′E	
	32°50′N-34°50′E	
	35°57′N-32°23′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	33°50′N-31°15′E	
	32°43′N-34°38′E	
	32°10′N-32°50′E	
	32°07′N-33°24′E	
	35°00′N-35°00′E	
	35°55′N-28°33′E	
Diphyopsis mitra Huxley, 1859		Gulf of Elat:
		29°30′N-34°55′E
Muggiaea atlantica Cunningham, 1892	••	+
Muggiaea kochi Will, 1844	••	
	33°03′N-34°55′E	
Eudoxoides spiralis Bigelow, 1911	••	
	35°05′N-35°00′E	
	31°31′N-34°28′E	
	34°37′N-32°20′E	
	32°50′N-34°51′E	
	34°35′N-29°40′E	
	34°10′N-34°29′E	
	35°57′N-32°23′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	33°50′N-31°15′E	
	32°43′N-34°48′E	
	32°10′N-32°50′E	
	32°07′N-33°24′E	
	31°42′N-33°00′E	
Clausophyes ovata Keferstein & Ehlers, 1861	••	
Sphaeronectes spp.	••	+
Lensia campanella Moser, 1925	••	+
	32°43′N-34°38′E	
	32°10′N-32°50′E	
	32°07′N-33°27′E	
Lensia conoidea Keferstein & Ehlers, 1861	••	
Lensia fowleri Bigelow, 1911	••	+
Lensia hotspur Totton, 1954		+
Lensia meteori Leloup, 1934	••	+
	34°35′N-33°35′E	
	33°50′N-31°15′E	
Lensia multicristata Moser, 1925	••	
	32°45′N-34°49′E	
Lensia subtilis Chun, 1886	••	+
	34°35′N-29°40′E	Gulf of Elat:
	32°10′N-32°50′E	29°30′N-34°55′E
	32°07′N-33°24′E	29°25′N-34°50′E
Lensia subtiloides Lens & Riemsdijk, 1908	••	+
		Gulf of Elat:
		29°30′N-34°55′E
Sulculeolaria angusta Totton, 1954	35°05′N-35°00′E	
	32°55′N-34°34′E	
	32°46′N-34°53′E	
	37°17′N-22°47′E	
	35°11′N-22°15′E	
	34°35′N-29°40′E	
	32°07′N-33°24′E	
	35°00′N-35°00′E	
Sulculeolaria biloba Sars, 1846	••	

TABLE 1.—*Continued.*

Species	Eastern Mediterranean	Red Sea
Sulculeolaria chuni Lens & Riemsdijk, 1908		+
	32°10′N-32°50′E	Gulf of Elat:
	32°07′N-33°24′E	29°30′N-34°55′E
	32°45′N-34°49′E	
Sulculeolaria quadrivalvis Blainville, 1834	**	+
	32°21′N-34°48′E	Gulf of Elat:
	32°55′N-34°34′E	29°30′N-34°55′E
	35°57′N-32°23′E	29°25′N-34°50′E
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	33°50′N-31°15′E	
Sulculeolaria turgida (Gegenbauer, 1854)	**	
	32°45′N-34°49′E	
	35°35′N-35°26′E	
	34°47′N-25°10′E	
	35°35′N-21°50′E	
	35°57′N-22°15′E	
	34°35′N-29°40′E	
	34°10′N-34°29′E	
	35°57′N-32°23′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	33°50′N-31°15′E	
	32°43′N-34°38′E	
	32°10′N-32°50′E	
	35°00′N-35°00′E	
Abylopsis eschscholtzi Huxley, 1859	* **	+
		Gulf of Elat:
		29°25′N-34°50′E
Abylopsis tetragona Otto, 1823	* **	+
	33°25′N-30°20′E	Gulf of Elat:
	35°05′N-34°38′E	29°30′N-34°55′E
	32°10′N-32°50′E	29°25′N-34°50′E
Bassia bassensis Quoy & Gaimard, 1834	* **	+
	33°03′N-34°55′E	
	33°25′N-30°20′E	
	31°31′N-34°28′E	
	32°23′N-34°37′E	
	32°30′N-33°21′E	
	35°11′N-22°15′E	
	35°57′N-22°15′E	
	34°35′N-29°40′E	
	34°10′N-34°29′E	
	32°46′N-34°53′E	
	35°57′N-32°23′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	33°50′N-31°15′E	
	32°43′N-34°48′E	
	32°10′N-32°50′E	
	32°07′N-33°24′E	
	31°42′N-33°00′E	
	31°37′N-34°32′E	
	35°55′N-28°33′E	
Ceratocymba sagittata Quoy & Gaimard, 1827	**	
Enneagonum hyalinum Quoy & Gaimard, 1827	* **	+
		Gulf of Elat:
		29°25′N-34°50′E
Hippopodius hippopus Forskal, 1776	* **	+
	32°21′N-34°48′E	
	35°39′N-26°34′E	
	35°05′N-35°00′E	
	32°23′N-34°37′E	
	32°55′N-34°34′E	
	35°35′N-35°26′E	
	35°05′N-34°05′E	
	34°50′N-28°55′E	
	35°55′N-28°37′E	

Species	Eastern Mediterranean	Red Sea
(*Hippopodius hippopus*)	36°31′N-27°27′E	
	32°46′N-34°53′E	
	33°25′N-33°14′E	
	32°01′N-33°25′E	
	34°47′N-25°10′E	
	33°25′N-25°15′E	
	37°17′N-22°47′E	
	35°11′N-22°15′E	
	35°35′N-21°50′E	
	35°57′N-22°15′E	
	34°35′N-29°40′E	
	34°10′N-34°29′E	
	32°50′N-34°50′E	
	32°20′N-34°51′E	
	31°37′N-34°32′E	
	31°42′N-34°28′E	
	31°44′N-34°26′E	
	32°45′N-34°49′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	33°50′N-31°15′E	
	32°43′N-34°38′E	
	32°10′N-32°50′E	
	32°07′N-33°24′E	
	31°42′N-33°00′E	
	35°00′N-35°00′E	
	35°55′N-28°33′E	
Vogtia glabra Bigelow, 1918	* **	
Vogtia pentacantha Kolliker, 1853	**	
Vogtia spinosa Keferstein & Ehlers, 1861	**	
Praya cymbiformis Chiaje, 1841	**	
Rosacea plicata Quoy & Gaimard, 1827	**	
	32°10′N-32°50′E	
Amphicaryon acaule Chun, 1888	**	+
Amphicaryon ernesti Totton, 1954		+
Anthophysa rosea Brandt, 1835	**	+
Apolemia uvaria Lesueur, 1811	**	
	36°31′N-27°27′E	
Rhizophysa filiformis Forskal, 1775	**	
Cordagalma cordiformis Totton, 1932	**	+
		29°25′N-34°50′E
Athoribya rosacea (Forskal, 1775)	**	+
		29°25′N-34°50′E
Agalma elegans Sars, 1846	* **	+
	35°55′N-28°33′E	Gulf of Elat:
		29°30′N-34°55′E
		29°25′N-34°50′E
Agalma okeni Eschscholtz, 1825	* **	+
		Gulf of Elat:
		29°30′N-34°55′E
		29°25′N-34°50′E
Stephanomia bijuga (Chiaje, 1841-42)	* **	+
Stephanomia rubra Vogt, 1852	* **	+
Nanomia cara Agassiz, 1865	**	
Physophora hydrostatica Forskal, 1775	**	
	35°57′N-22°45′E	
	34°35′N-29°40′E	
	35°50′N-31°15′E	
	31°42′N-33°00′E	
Forskalia edwardsi Kolliker, 1853	* **	+

* Previously observed (see Alvariño, 1971; Lakkis, 1971).
\+ Previously observed in the Red Sea (Alvariño, 1971 compilation of distributional data).
**Previously observed in the western Mediterranean (see Alvariño, 1971).

TABLE 2.—Siphonophores of the regions adjacent to the Panama Canal.

Species	Caribbean Sea region	Central American Pacific
Chelophyes appendiculata	* **	
	11°07′N-74°47′W	08°41′N-79°31′W
	10°19′N-75°38′W	08°48′N-79°30′W
	09°46′N-79°20′W	08°00′N-79°43′W
	09°37′N-79°39′W	
	09°27′N-79°48′W	
	14°19′N-83°09′W	
	13°56′N-82°59′W	
	13°38′N-82°38′W	
	13°12′N-82°25′W	
	12°31′N-81°52′W	
	12°11′N-81°38′W	
	10°04′N-80°22′W	
Chelophyes contorta		**
	09°27′N-79°48′W	07°30′N-79°54′W
	09°25′N-79°57′W	08°46′N-84°11′W
		09°13′N-84°45′W
		09°28′N-85°15′W
		09°39′N-85°41′W
		07°12′N-79°54′W
		07°02′N-79°57′W
		06°55′N-80°50′W
		07°12′N-81°48′W
		07°18′N-82°25′W
		07°27′N-83°04′W
		07°30′N-83°54′W
		07°39′N-84°46′W
		07°51′N-85°49′W
		08°48′N-85°17′W
		09°07′N-84°58′W
		09°23′N-84°52′W
		09°51′N-85°43′W
Dimophyes arctica (Chun, 1897)	**	**
Diphyes bojani	**	**
	09°46′N-46°20′W	07°30′N-79°54′W
	09°27′N-79°47′W	08°10′N-82°13′W
	09°27′N-79°38′W	08°10′N-82°15′W
	13°56′N-82°59′W	08°10′N-82°16′W
	13°38′N-82°38′W	08°46′N-84°11′W
	13°12′N-82°25′W	09°13′N-84°45′W
	12°31′N-81°52′W	09°28′N-85°15′W
	12°11′N-81°38′W	09°39′N-85°41′W
	11°27′N-81°15′W	07°27′N-83°04′W
	10°44′N-80°45′W	07°30′N-83°54′W
	10°04′N-80°22′W	07°39′N-84°46′W
		07°57′N-85°49′W
		08°48′N-85°17′W
		09°07′N-84°58′W
		09°23′N-84°52′W
Diphyes dispar	* **	* **
	10°19′N-75°38′W	09°38′N-85°44′W
	08°46′N-84°11′W	08°48′N-79°30′W
	09°13′N-84°45′W	08°00′N-79°43′W
	09°28′N-85°15′W	06°40′N-79°59′W
	09°39′N-85°41′W	06°55′N-80°50′W
	12°31′N-81°52′W	07°12′N-81°48′W
		07°27′N-83°04′W
		07°30′N-83°54′W
		07°39′N-84°36′W
		07°57′N-85°49′W
		08°48′N-85°17′W
		09°07′N-84°58′W
		09°23′N-84°52′W
		09°39′N-84°44′W
		09°32′N-85°10′W
		09°51′N-85°43′W
Diphyopsis mitra	**	**
	10°44′N-80°45′W	07°30′N-79°54′W
	10°04′N-80°22′W	08°46′N-84°11′W
		09°13′N-84°45′W
		09°28′N-85°15′W
		09°39′N-85°41′W
		08°00′N-79°43′W

Species	Eastern Mediterranean	Red Sea
(Diphyopsis mitra)		07°12′N-79°54′W
		07°02′N-79°57′W
		06°40′N-79°59′W
		06°55′N-80°50′W
		07°18′N-82°25′W
		07°30′N-83°54′W
		07°39′N-84°46′W
		07°57′N-85°49′W
		08°48′N-85°57′W
		09°07′N-84°58′W
		09°32′N-85°10′W
		09°51′N-85°43′W
Muggiaea atlantica		**
	09°28′N-84°21′W	09°38′N-85°44′W
	09°46′N-79°20′W	08°41′N-79°31′W
	09°27′N-79°48′W	07°30′N-79°54′W
		08°10′N-82°13′W
		08°10′N-82°15′W
		08°10′N-82°16′W
		09°13′N-84°45′W
		09°28′N-85°15′W
		09°39′N-85°41′W
		08°48′N-79°30′W
		07°12′N-79°54′W
		07°02′N-79°57′W
		06°55′N-80°50′W
		09°07′N-84°58′W
		09°23′N-84°52′W
		09°39′N-84°44′W
		09°32′N-85°10′W
		09°51′N-85°43′W
Muggiaea kochi	**	
	11°07′N-74°47′W	08°41′N-79°31′W
	10°19′N-75°38′W	
	09°46′N-79°20′W	
	09°37′N-79°39′W	
	09°28′N-79°46′W	
	09°27′N-79°47′W	
	14°19′N-83°09′W	
	14°07′N-83°01′W	
	13°56′N-82°59′W	
	13°38′N-82°38′W	
	10°04′N-80°22′W	
	09°25′N-79°57′W	
Eudoxoides spiralis	**	**
	09°37′N-79°39′W	07°12′N-79°54′W
	09°28′N-79°46′W	07°02′N-79°57′W
	13°38′N-82°38′W	07°39′N-84°46′W
	12°31′N-81°52′W	07°57′N-85°49′W
	10°04′N-80°22′W	
Lensia campanella	**	**
Lensia challengeri Totton, 1954		**
	10°04′N-80°22′W	06°40′N-79°59′W
		07°30′N-83°54′W
		07°39′N-84°46′W
		07°57′N-85°49′W
Lensia conoidea		**
Lensia cossack Totton, 1941	**	**
		06°55′N-80°50′W
Lensia fowleri	**	
	14°19′N-83°09′W	
Lensia hotspur	**	**
	10°04′N-80°22′W	09°51′N-85°43′W
Lensia lelouveteau Totton, 1941	**	
Lensia meteori		**
Lensia multicristata	**	
Lensia reticulata Totton, 1954	**	
Lensia subtilis	* **	
	10°04′N-80°22′W	
Sulculeolaria bigelowi (Sears, 1950)		**
Sulculeolaria biloba	**	**

TABLE 2.—*Continued.*

Species	Eastern Mediterranean	Red Sea
Sulculeolaria chuni	**	**
	12°31′N-81°52′W	08°00′N-79°13′W
	11°27′N-81°15′W	07°30′N-83°54′W
	10°44′N-80°45′W	07°57′N-85°49′W
		09°23′N-84°52′W
Sulculeolaria monoica Chun, 1888	**	**
		07°30′N-83°54′W
Sulculeolaria quadrivalvis	**	**
		08°46′N-84°11′W
		09°28′N-85°15′W
		08°48′N-85°17′W
		09°07′N-84°58′W
		09°23′N-84°52′W
Sulculeolaria turgida		**
		08°00′N-79°43′W
		07°30′N-83°54′W
		07°57′N-85°49′W
		09°23′N-84°52′W
Abyla carina Haeckel, 1888	**	
Abyla haeckeli Lens & Riemsdijk, 1908	* **	* **
	12°31′N-81°52′W	09°51′N-85°43′W
Abyla schmidt Sears, 1953	**	
		09°51′N-85°43′W
Abylopsis eschscholtzi	* **	* **
	10°46′N-79°20′W	07°30′N-79°54′W
	14°19′N-83°09′W	08°46′N-84°11′W
	14°07′N-83°01′W	09°28′N-85°15′W
	13°12′N-82°25′W	09°39′N-83°09′W
	12°31′N-81°52′W	07°12′N-97°54′W
	10°44′N-80°45′W	07°02′N-79°57′W
	10°04′N-80°22′W	06°40′N-79°59′W
	09°25′N-79°57′W	06°55′N-80°50′W
		07°18′N-82°25′W
		07°27′N-83°04′W
		07°30′N-83°54′W
		07°39′N-84°46′W
		07°57′N-85°49′W
		08°48′N-85°17′W
		09°07′N-84°58′W
		09°51′N-85°43′W
Abylopsis tetragona	* **	
	11°07′N-74°47′W	09°38′N-85°44′W
	10°19′N-75°38′W	07°02′N-79°57′W
	09°37′N-79°39′W	07°57′N-85°49′W
	09°25′N-79°57′W	09°51′N-85°43′W
Bassia bassensis	**	* **
		07°02′N-79°57′W
		07°57′N-85°49′W
		09°23′N-84°52′W
		09°51′N-85°43′W
Ceratocymba dentata Bigelow, 1918		* **
		07°30′N-83°54′W

Species	Eastern Mediterranean	Red Sea
(Ceratocymba dentata)		07°39′N-84°46′W
		09°07′N-84°58′W
Ceratocymba leuckarti Huxley, 1859	**	**
Ceratocymba sagittata	**	
Enneagonum hyalinum	**	* **
	12°11′N-81°38′W	07°18′N-82°25′W
		08°46′N-84°11′W
		07°39′N-84°46′W
		07°57′N-85°49′W
		09°07′N-84°58′W
		09°23′N-84°52′W
		09°32′N-85°10′W
Hippopodius hippopus	**	**
		07°30′N-79°54′W
		07°12′N-79°54′W
		07°02′N-79°57′W
		06°42′N-79°59′W
		07°18′N-82°25′W
		07°57′N-85°49′W
		08°48′N-85°17′W
		09°07′N-84°58′W
		09°23′N-84°52′W
		09°32′N-85°10′W
		09°51′N-85°43′W
Vogtia glabra	**	
Vogtia pentacantha	**	
Vogtia spinosa		**
Rosacea plicata		**
Nectopyramis natans Bigelow, 1911		**
Amphicaryon acaule	* **	**
	10°04′N-80°22′W	09°51′N-85°43′W
Amphicaryon ernesti	**	
Rhizophysa filiformis	**	
Athoribya rosacea		07°27′N-83°04′W
Agalma elegans	**	
Agalma okeni	**	* **
	13°12′N-82°25′W	06°55′N-80°50′W
		07°12′N-81°48′W
		07°39′N-84°46′W
		09°07′N-84°58′W
		09°32′N-85°10′W
		09°51′N-85°43′W
Stephanomia bijuga	**	**
	14°19′N-83°09′W	09°32′N-85°10′W
		09°51′N-85°43′W
Stephanomia rubra	**	
Physophora hydrostatica		**
Melophysa melo Quoy & Gaimard, 1827		*
		07°57′N-85°49′W

*Previously observed.
**Previously observed in adjacent regions of the Caribbean Sea and/or the Gulf of Mexico, and adjacent regions of the Pacific Ocean (see Alvariño, 1971 compilation of distributional data).

Species present at few locations in the surveyed region of the Caribbean and Pacific were, *L. hotspur*, *Abyla haeckeli*, and *A. acaule*. *Lensia hotspur* and *A. acaule* were only found at one location to the north off the entrance of the Panama Canal in the Caribbean, and west of the Peninsula de Nicoya in the Pacific (Figures 15, 18). *Abyla haeckeli* was observed once off Costa de Mosquitos, Caribbean Sea, and at one location off Punta Guiones in the Pacific (Figure 17).

Species present once or at few locations in the Pacific region were, *L. cossack*, *S. monoica*, *Abyla schmidti*, *C. dentata*, *Melophysa melo*, *A. rosacea*, and *Stephanomia bijuga* (Figures 15-19).

Lensia subtilis and *L. fowleri* were found only once each, respectively at few miles north of the entrance to the Panama Canal, and off Huani in the Caribbean (Figures 11, 15).

The information presented here should be considered only as a basis for future and more

detailed sets of investigations to enlighten further the distribution and the characteristics of the populations of siphonophores, their fluctuations in time and locations, concurrently with the hydrographic, ecological characteristics and other variants.

The author regrets that the pertinent hydrographic data obtained concurrently with the zooplankton collections were not available in time to be included in the discussion of results.

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THREE NEW SPECIES OF THE GENUS *MONOGNATHUS* AND THE LEPTOCEPHALI OF THE ORDER SACCOPHARYNGIFORMES

SOLOMON N. RAJU[1]

ABSTRACT

Three new species of the genus *Monognathus*—*M. isaacsi*, *M. ahlstromi*, and *M. jesse*—are described from the Pacific Ocean, bringing the number of the species to six. *M. isaacsi* differs from the other species in having a relatively large head and dark brown pigmentation on the whole body. *M. ahlstromi* has a characteristic paddle-shaped caudal fin, and *M. jesse* has a lanceolate caudal fin. A key to the six species and their distribution in the Pacific and Atlantic are given. Leptocephali of *Monognathus* sp. are identified and described for the first time. The status and relationships of the Monognathidae are discussed.

Metamorphic forms of *Saccopharynx* and *Eurypharynx* are described. The identity of *Leptocephalus latissimus* to *Saccopharynx* and of *L. pseudolatissimus* to *Eurypharynx* is confirmed. An unknown leptocephalus closely resembling that of *Cyema* is described, and the possibility of a new genus in the Cyemidae is suggested. Relationships of the Cyemidae to the Nemichthyidae are refuted, and relationships of the Cyemidae to the Saccopharyngiformes are supported.

The deepsea gulpers of the order Saccopharyngiformes (Monognathidae, Saccopharyngidae, and Eurypharyngidae) are among the most curious and extremely modified bathypelgic fishes, and very little is known about them. Böhlke (1966) reviewed the literature on the attempts to relate them to diverse groups of fishes.

I describe three new species of *Monognathus* (*M. isaacsi*, *M. ahlstromi*. and *M. jesse*) and four metamorphic stages of *Monognathus* sp. A key to the six known species of the genus *Monognathus* is given. This is the first record of the family from the southern, central, and eastern Pacific. The three species of *Monognathus* described by Bertin (1934, 1938) from the Atlantic and Indo-Pacific regions are only juveniles. The lack of adult monognathids even led Böhlke (1966) to suspect that the then known monognathids might be postlarval saccopharyngids. The specimen named as *M. isaacsi* is in a more advanced stage than any of the other specimens of the six species. Many of its features clearly indicate that this family is distinct from the Saccopharyngidae. A leptocephalus stage in the life history of *Monognathus* is reported for the first time. Information on the ethmoid tooth, food, and distribution of *Monognathus* is given. The status and relationships of the family Monognathidae to the Saccopharyngiformes are discussed.

Two metamorphic forms, one belonging to *Saccopharynx* and the other to *Eurypharynx*, are described, and *Leptocephalus latissimus* Schmidt 1912 is assigned to *Saccopharynx* and *L. pseudolatissimus* Bertin 1934 to *Eurypharynx*.

An unknown leptocephalus closely resembling that of *Cyema* is described from the North Pacific, and the possibility of a new genus in the Cyemidae is suggested. The relationship of the Cyemidae to the Nemichthyidae is questioned, and its relationship to the Saccopharyngiformes is supported.

MATERIALS AND METHODS

The account is based on the study of one fully transformed juvenile, two early juveniles, and four metamorphic forms of the genus *Monognathus* collected from the central and eastern North Pacific during the Tethys (1960), CalCOFI (1962), and Scan (1969) expeditions. One specimen of *Leptocephalus latissimus* was obtained from the San Diego Trough (1950) and its metamorphic form off Baja California. A metamorphic form of *Eurypharynx pelecanoides* was collected from the central North Pacific during the Styx expedition (1968). All the specimens were collected by the 10-foot Isaacs-Kidd midwater trawl (IKMT). Total length and body depth were measured with dial calipers, and measurements of head, snout, and eye were taken by ocular micrometer following the methods of Castle (1963). Some specimens

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were dissected. Drawings were made with the aid of a projector and camera lucida. All the holotypes are presently housed in the Marine Vertebrates Collection of the Scripps Institution of Oceanography.

Names: The new species of the genus *Monognathus* are named for John D. Isaacs of the Scripps Institution of Oceanography (SIO), La Jolla; Elbert H. Ahlstrom of the Southwest Fisheries Center, National Marine Fisheries Service, La Jolla; and Jesse N. Raju, wife of the author (noun in apposition).

KEY TO THE SPECIES OF THE GENUS *MONOGNATHUS*

1a.	Pectoral fin present	2
1b.	Pectoral fin absent	3
2a.	Head large, about 13.3 in total length, caudal fin normal	*M. isaacsi*
2b.	Head small, about 9 in total length, caudal fin lanceolate	*M. jesse*
3a.	Caudal fin normal, vertebrae long	4
3b.	Caudal fin either whiplike or paddle shaped, vertebrae short	5
4a.	Vertebrae 94, teeth in mandible 8, adipose region of dorsal fin with 48-63 rays	*M. jesperseni*
4b.	Vertebrae 88, teeth in mandible 12, adipose region of dorsal fin with 36-48 rays	*M. bruuni*
5a.	Caudal fin whiplike, dorsal commences on myotome 3, two ethmoid teeth	*M. taningi*
5b.	Caudal fin compressed, paddle shaped, dorsal commences on myotome 13, one median ethmoid tooth	*M. ahlstromi*

MONOGNATHUS ISAACSI SP. N.

Figures 1D, I; 2O

Holotype: SIO 69-353, western North Pacific, 32°02.3′N-32°07.9′N, 156°07.0′E-156°06.7′E, depth of capture 0-950 m, IKMT, 1(56 mm), 2 June 1969.

Description: Body elongate, compressed except at head. Trunk clearly marked from tail, 2.9 in total length. Maximum depth at middle of body, 10.3 in total length. Head large, 7.6 in total length. Snout moderately long, 2.4 in head. Olfactory organ rudimentary, a short curved tube open at both ends. Eyes tubular, small, 18.7 in head. Upper jaw soft, maxilla not recognizable, no upper teeth. Skin inside of mouth dusted with melanophores. Median ethmoid tooth projects below level of lips, visible from side. Lower jaw slightly longer than upper jaw, with four small teeth. Mouth large, gape reaching far behind eye. Postorbital distance 1.7 in head. No branchiostegals recognizable. Gill opening small, ventrolateral. About 75 myotomes could be counted and another 25-30 are estimated for a total of about 100. Tail blunt at tip. Stomach bulging, extending beyond trunk as a sac. Dorsal fin high, originating behind gill openings, with 80 unsegmented rays. Predorsal distance 3.7 in total length. Anal fin high, originating behind vent, with 52 unsegmented rays. Preanal distance 1.5 in total length. Pectoral fins small, rays not distinct.

Pigmentation: Uniformly dark brown.

Remarks: This is the first known specimen of the Monognathidae with complete body pigmentation. The absence of an upper jaw and the presence of an ethmoid fang indicate that *M. isaacsi* is properly referable to the Monognathidae. Of all the members of the Saccopharyngiformes so far known, this species represents the most generalized form except for the reduced eye, presence of the enlarged ethmoid fang, and absence of the upper jaw. The shape of the body, the head with its long snout and large mouth, the nature of the median fins, and the presence of pectoral and absence of ventral fins are typical of eels. In *Eurypharynx* and *Saccopharynx* the mouth is enlarged and the suspensorium highly modified, and in *Saccopharynx* the tail is whiplike. The snout in these genera is reduced whereas it is long in *M. isaacsi*.

The meristic and morphometric characters of the three species described by Bertin (1938) and the three new species described in this account are given in Table 1. The relative lengths of the head, cranium, snout, and predorsal distance are the highest in *M. isaacsi*. The head is depressed. The teeth in the lower jaw are different in shape and fewer in number than in other species. The median ethmoid tooth is long and projects into

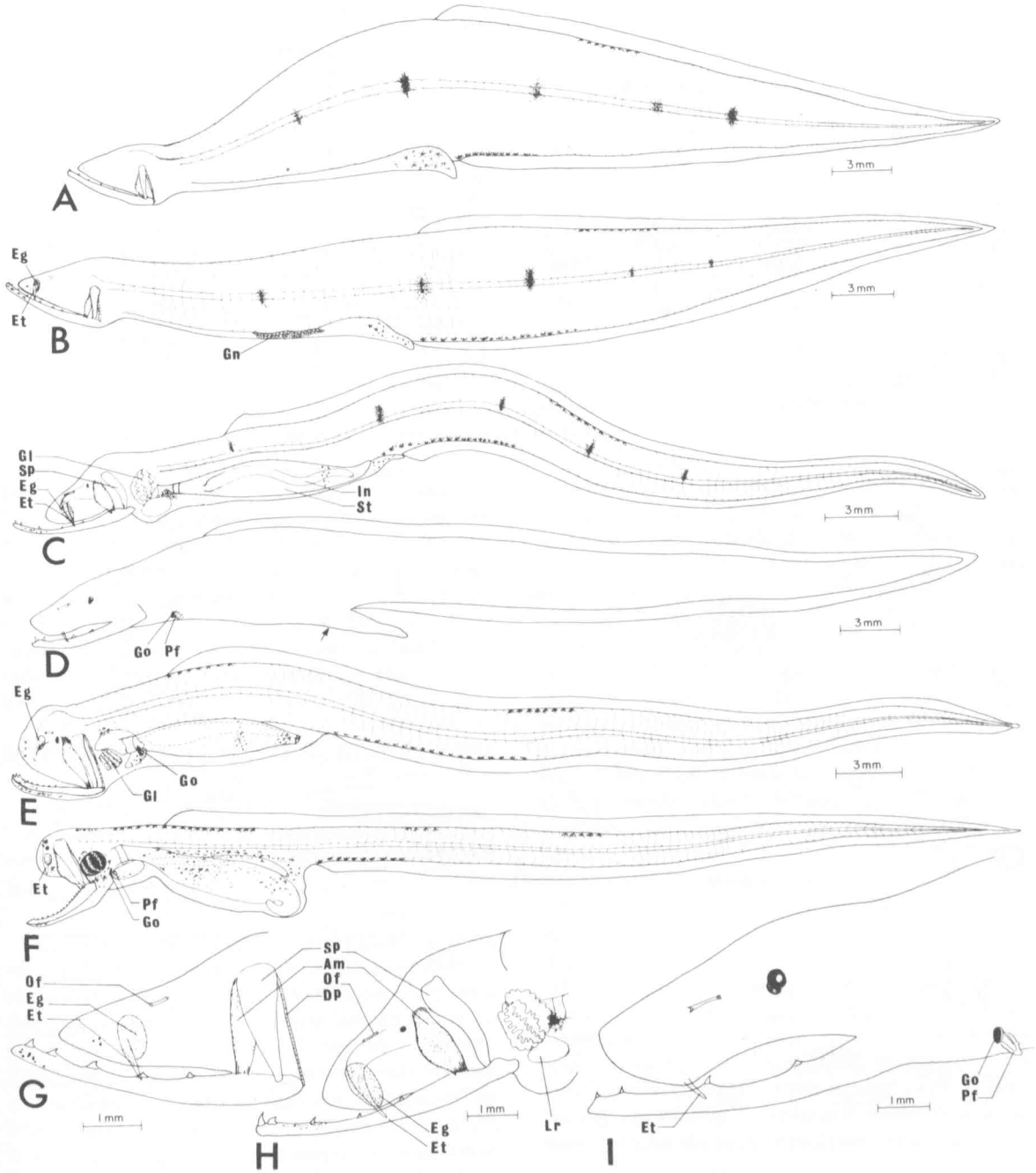


FIGURE 1.—**A-C,** metamorphic stages of *Monognathus* sp.: **A,** 42 mm TL; **B,** 48 mm TL and **G,** its head; **C,** 42.2 mm TL and **H,** its head. **D.** *M. isaacsi* and **I,** its head; **E,** *M. ahlstromi;* **F,** *M. jesse.* **Am,** adductor mandibulae; **Dp,** depressor; **Et,** ethmoid tooth; **Eg,** ethmoid gland; **Ey,** eye; **Gl,** gills; **Go,** gill opening; **Gn,** gonad; **In,** intestine; **Lr,** liver; **Of,** olfactory organ; **Pf,** pectoral fin; **Sp,** suspensorium; **St,** stomach.

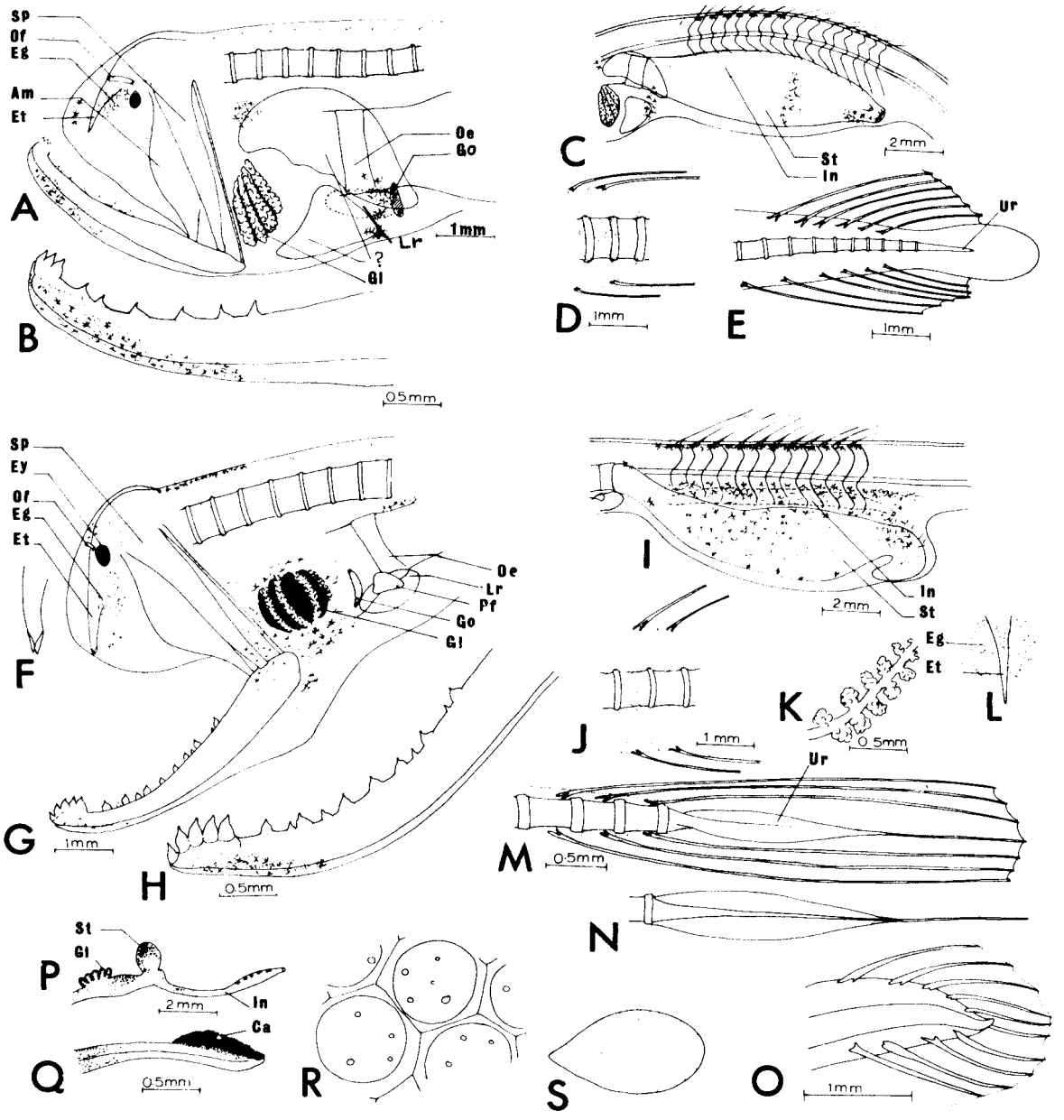


FIGURE 2.—**A-E**, *Monognathus ahlstromi:* **A**, head; **B**, lower jaw; **C**, midbody; **D**, vertebrae and myotomes; **E**, tail. **F-N**, *M. jesse:* **F**, ethmoid tooth; **G**, head, **H**, lower jaw; **I**, midbody; **J**, vertebrae of myotomes; **K**, gill arch; **L**, ethmoid gland and tooth; **M**, tail; **N**, dorsal view of urostyle. **O**, caudal fin of *M. isaacsi*. **P**, gut and **Q**, tail of metamorphic *Eurypharynx*. **R**, portion of the ovary of and **S**, ovary of adult *Eurypharynx*. **Am**, adductor mandibulae; **Ca**, caudal organ; **Dp**, depressor; **Et**, ethmoid tooth; **Eg**, ethmoid gland; **Ey**, eye; **Gl**, gills; **Go**, gill opening; **In**, intestine, **Lr**, liver; **Oe**, esophagus; **Of**, olfactory organ; **Pf**, pectoral fin; **Sp**, suspensorium; **St**, stomach; **Ur**, urostyle.

TABLE 1.—Morphometric and meristic characters of the species of the genus *Monognathus*.

Item	*taningi*	*bruuni*	*jesperseni*	*ahlstromi*	*jesse*	*isaacsi*
Total length (mm)	56	80	109	48.5	63	56
Percentage of total length:						
Depth	3.9	5.9	4.6	9	8	9.6
Predorsal distance	7.7	[1] 35	13.8	13.2	11.9	19.5
Preanal distance	25	38.7	35.8	27.6	25.4	34.0
Head	8	10	9.1	10.7	9	13.3
Cranium	5	3.9	3.2	4.3	4.9	7.9
Percentage of head length:						
Snout	—	—	—	19	21.4	41.3
Eye	—	—	—	5.5	8.9	5.2
Suspensorium	70	56.2	65	63	57	—
Mandible	122	75	85	83	89	84
Number of vertebrae or myotomes	95(23)	88(26)	94(25)	113(31)	104(26)	115(24)
Dorsal fin rays	120	74	97	90	80	80
Anal fin rays	60	42	97	60	54	52
Teeth in mandible	8	12	8	9	16	4
Predorsal myotomes	3	12	11	13	11	—
Preanal myotomes	24	30	29	32	27	—

[1]The predorsal distance given by Bertin is obviously wrong as the dorsal originates on myotome 12.

the mouth, but it does not do so in other species. There is a small pectoral fin. The vertebrae are weakly ossified, not distinct in radiographs, but about 75 myotomes could be counted, and about 30-35 more are estimated on the basis of the size of the myotomes. Differences of this magnitude could well indicate generic separation, but I hesitate to introduce new genera in this poorly known group.

MONOGNATHUS AHLSTROMI SP. N.

Figures 1E; 2A-E

Holotype: SIO 63-405, eastern North Pacific, 34°57.0′N, 129°19.0′W, 0-2,000 m, IKMT, 1(48.5 mm), 29 Mar. 1962.

Description: Body compressed except at head, very delicate, covered with loose semitransparent skin. Preanal region 3.6 in total length, very deep due to voluminous stomach. Tail (postanal region) very narrow, 1.3 in total length, tapering gradually to a point. Maximum depth before anus, 11.0 in total length (may vary according to quantity of contents of stomach). Head deep, large, 9.0 in total length; cranium very small and weak. Snout small, 5.4 in head, membranous. Olfactory organ reduced, a small curved tube open at both ends. Eye rudimentary, oval, vertical length 18.0 in head, lens round, extremely small. Gape of mouth reaching far beyond eye. Region of upper jaw membranous, devoid of teeth, no maxilla distinguishable. Ethmoid tooth short, hollow, tip sharp and bifid, and does not project into mouth as in *M. isaacsi*; it appears as though it is lodged in a sheath and comes out of the sheath through an opening on the membranous palate only when pressed. Ethmoid glands paired, oval (0.8 mm × 0.4 mm) on either side of tooth. Lower jaw long, 9.7 in total length, tip armed with three sharp closely packed teeth followed by series of six pointed, equally spaced, triangular teeth. Opercular bones and branchiostegals absent. Gills four, covered by delicate transparent membrane. Gill filaments short, foliaceous. Gill openings ventrolateral, moderate in size. Pectoral fin absent. Myotomes 28 + 85 = 113, W-shaped. Esophagus short, followed by thickened girdle-like region. Stomach large, bulging with opening just posterior to anus. This opening of the stomach appears to be a structural feature and not a wound associated with capture. Intestine a narrow straight tube on right side of body, opening to exterior on right side. Liver small and lobular. Dorsal fin originating on myotome 14, moderately high, 90 unsegmented rays. Caudal fin represented by an enlarged, paddlelike structure without fin rays. Vertebral centra short.

Pigmentation: No trace of any larval mid-lateral pigmentation. A few dendritic melanophores on snout and lower jaw. Dendritic melanophores around esophageal and liver region inside body and on body wall in stomach and anal

regions. Dendritic, deep pigmentation at base of dorsal fin on myotomes 14-20 and 50-57, and on anal fin on myotomes 32-51.

Remarks: This species differs from all the three species of *Monognathus* described by Bertin (1938) and from *M. jesse* described in this account in having a high myotome count of 113. The structure of the caudal fin also is different. In *M. bruuni* and *M. jesperseni* the urostyle is produced into a needlelike structure forming a false caudal fin along with the dorsal and anal fin rays. In *M. taningi* the urostyle is produced into a very long, whiplike structure. The urostyle in this species is spinelike, surrounded by a large paddle-shaped, compressed structure. The ethmoid tooth is small and does not project into the mouth. If Bertin's (1938) observations are correct, this species differs from the above three species also in having four gills as only one gill was figured in his drawings. There is a series of three closely packed teeth at the tip of the lower jaw, and such a series is not seen in the forms described by Bertin.

MONOGNATHUS JESSE SP. N.

Figures 1F; 2F-N

Holotype: SIO 60-245, central North Pacific, 12°07.1′N-12°23.8′N, 148°35.1′W-148°18.0′W, 0-2,100 m, IKMT, 1(63 mm), 9-10 July 1960.

Description: Body compressed except at head. Preanal region deep due to voluminous stomach, preanal region 3.9 in total length. Postanal region 3.6 in total length, tapering to point. Body covered with loose semitransparent skin. Maximum depth at middle of preanal region, 12.6 in total length. Head deep, large, 8.7 in total length. Snout blunt, membranous, small, 4.7 in head. Olfactory organ a slightly curved short tube, open at both ends. Eye rudimentary, 11.2 in head, oval, lens extremely small. Gape of mouth reaching beyond eye. Upper jaw degenerate, membranous, unsuitable to serve as jaw, no maxilla recognizable, no teeth. Median ethmoid tooth large, pointed, tip calcified and bifid, surrounded and hidden by soft tissue. Ethmoid glands paired oval bodies, one on either side of tooth. Lower jaw long, slightly curved, tip armed by 5 closely packed large teeth followed by 11 teeth of characteristic shape. No opercular bones or branchiostegals recognizable. Gills four, small, but proportionally larger than those of *M. ahlstromi*. First gill slit smallest, second and third largest, last gill slit slightly larger than first. Gill filaments short and foliaceous, alternately on either side. First three gills holobranchs, fourth a hemibranch. All gills covered by membranous operculum. Gill opening vertical, moderate in size, in front of pectoral fin. Myotomes W-shaped, 26 + 78 = 104. Vertebrae heavy, shorter in length in trunk region, slender and elongate in tail region. Esophagus short with opaque girdlelike region. Stomach voluminous, recurved at end. Intestine a straight tube, shorter than stomach, situated on right side of stomach. Liver lobular. Pancreas and heart lost due to damage. Dorsal fin originates on myotome 11, relatively high, with 80 unsegmented rays. Anal fin originates on myotome 30, with 54 unsegmented rays. Urostyle depressed, lanceolate, with middorsal ridge. Pectoral fin small, triangular, rays indistinct.

Pigmentation: Brown chromatophores on snout, tip of lower jaw, at angle of mouth. Dendritic brown chromatophores on head, predorsal region, gill membrane, lateral side of body as far back as anal region. Three deeply seated melanophore patches (seen only if cleared in glycerine) at base of dorsal fin inside myotomes, one long patch on myotomes 5-22, second on myotomes 40-43, and third on myotomes 58-62. Anal fin has similar large patch on myotomes 30-39.

Remarks: This species differs basically from the three species described by Bertin (1938) and from *M. ahlstromi* in the presence of a small pectoral fin, structure of the urostyle, myotome number, dentition of the lower jaw, relatively longer tail, and fin ray counts. Bertin (1938) gave no account of the pigmentation of his specimens, hence it is not possible to compare pigmentation. The pigmentation in this specimen differs from that of *M. ahlstromi* in the following respects. There is additional pigmentation on the head, angle of the lower jaw, and gill membrane, more profuse pigmentation on the lateral side of the body and predorsal region, and three patches at the base of the dorsal fin.

METAMORPHIC FORMS OF *MONOGNATHUS* SP.

Figure 1A, B, C, G, H

SIO 60-241, central North Pacific, 7°25.5'N-7°55.0'N, 144°29.0'W-144°35.0'W, depth of capture 0-2,100 m, IKMT, 1(42.2 mm), 7 July 1960. SIO 60-276, central North Pacific, 24°28.9'N-24°36.9'N, 147°55.5'W-147°27.0'W, 0-3,000 m, IKMT, 1(48 mm), 7-8 Aug. 1960. SIO 60-275, central North Pacific, 23°23.4'N-23°40.0'N, 151°04.0'W-150°38.8'W, 0-3,000 m, IKMT, 1(58 mm), 6 Aug. 1960. SIO 60-283, eastern North Pacific, 28°13.0'N-28°19.1'N, 135°21.8'W-134°54.1'W, 0-3,000 m, IKMT, 1(50 mm), 12 Aug. 1960.

Description (Figure 1B, G): Total length 48 mm, body elongate, compressed, and transparent. Depth 12.0 in total length, maximum depth at middle of body. Head long. Cranium weak, triangular, 10.7 in total length. Snout slightly blunt. Olfactory organ rudimentary, a small curved tube open at both ends. Eyes lost due to damage. Upper jaw membranous, without teeth. Ethmoid tooth long, projecting into mouth. Ethmoid gland paired, well developed. Lower jaw 8.6 in total length. Suspensorium 24.0 in total length. Adductor mandibulae well developed. Gills, liver, and part of gut damaged and lost. Posterior region of gut projects out of body outline. Opisthonephros a coiled tube extending behind vent (not shown in figure). Ovaries tubular, elongate, with few ova (250-300). Dorsal originates on myotome 32 and anal on myotome 30. Myotomes W-shaped, 30 +83 = 113. Midlateral brown, chromatophore patches conspicuous, one on left and four on right side. Brown chromatophores on tip of upper and lower jaws, at base of dorsal fin rays on myotomes 50-60, and anal fin rays on myotomes 31-49. Juvenile pigmentation appears on body as minute, uniformly scattered brown chromatophores (not shown in figure).

Changes during metamorphosis: Most of the morphological changes undergone are similar to those observed in the metamorphosis of the eels. In the smallest specimen (42 mm, Figure 1A) the body is deeper, and the lower jaw and suspensorium are relatively shorter. A median ethmoid tooth is not yet formed. In later stages (48 mm, 50 mm, 42.2 mm; A, B, C of Figure 1, respectively) there is a slight decrease in the length and depth of the body, and increase in the length of the head, snout, lower jaw, and suspensorium. A median ethmoid tooth is formed with its associated gland. Larval midlateral pigmentation begins to fade with the gradual development of juvenile pigmentation. The dorsal and anal fins move slightly forward. Two specimens have developed a pair of tubular ovaries containing about 250-300 spherical ova 0.06 mm in diameter (not shown in figure). An interesting aspect of the metamorphosis of monognathids is the degenerative changes that take place in the head, olfactory organ, and eye. The bones of the head become very weak and membranous. The eye and the olfactory organs are reduced to minute structures. A median ethmoid tooth with a pair of glands develops. The wide W-shaped myotomes become narrower with the decrease in the depth of the body, and in the larval condition they may approach a V-shape as in *Cyema* and *L. latissimus* and *L. pseudolatissimus*.

Remarks: The four metamorphic stages described above are assigned to *Monognathus* sp. on the basis of the characteristic median ethmoid tooth and the absence of an upper jaw. These stages share some features with *M. isaasci* such as general shape of the body, large head, projecting ethmoid tooth, myotome number, and structure of the tail. But *M. isaacsi* has a pectoral fin which is not seen in the metamorphic forms. Assignment to the species is not possible at this time.

The leptocephali of monognathids are not identified as yet. But the features of metamorphic forms (Table 2) indicate that they are small (40-60 mm), elongate larvae with a series of five splanchnic, unequally placed, midlateral melanophores with pigmentation on the gut, and with about 100-120 wide V-shaped myotomes.

GENERAL REMARKS

Upper jaw: The name Monognathidae was given to these fishes by Bertin (1937a), who assumed that only one jaw (lower jaw) was present. But Tchernavin (1947b) pointed out that there is no evidence that a palatopterygoid cartilage is absent in the Monognathidae. As all

TABLE 2.—Number and position of midlateral melanophores in five metamorphic monognathids and Pacific leptocephalus.

Metamorphic monognathids and Pacific leptocephalus	Total number myotomes	Left side melanophores	Right side melanophores	Total number melanophores (pre + postanal)	Distribution of chromatophores on myotomes R = Right, L = Left
42-mm specimen	31 + 80 = 111	2	3	2 + 3 = 5	(15-16)R, (29-30)L, (44-45)R, (59-60)R, (67-68)L
48-mm specimen	30 + 83 = 113	1	4	1 + 4 = 5	(15-16)R, (32-33)R, (45-46)L, (57-58)R, (67-68)R
58-mm specimen	30 + 75 = 115	2	3	1 + 4 = 5	(12-13)L, (31-32)R, (46-48)R, (56-58)R, (70-71)L
50-mm specimen	31 + 82 = 113	3	2	2 + 3 = 5	(15-16)L, (28-29)L, (44-45)R, (55-56)R, (67-68)L
42.2-mm specimen	24 + 81 = 105	4	1	2 + 3 = 5	(9-10)R, (27-28)L, (43-44)L, (55-56)L, (67-68)L
Pacific leptocephalus	56 + 46 = 102	4	1	4 + 1 = 5	(13-14)L, (25-26)L, (40-41)L, (50-51)L, (59-60)R

other known leptocephali possess a maxilla with larval teeth until metamorphosis, monognathid leptocephali also possibly have a maxilla bearing larval teeth. Leptocephali of eels characteristically lose their larval teeth during metamorphosis, and the adult teeth develop after metamorphosis. Hence it is possible that monognathid leptocephali might have possessed the maxilla with its larval teeth which might have been lost during metamorphosis. Due to the extreme degenerative changes and deossification of the skull the maxilla might have lost its identity and the adult set of teeth failed to develop.

Median ethmoid tooth: The median ethmoid tooth is a structure unique to the Monognathidae, and its function is not known. It develops during metamorphosis and persists in the adult. It is larger in *M. isaacsi* than in other species. It is hollow and slightly curved with a minute opening at its sharp tip. There is a pair of glandular masses, one on each side of the tooth. The ethmoid tooth with its gland closely resembles the fangs of a poisonous snake and probably serves a similar function.

Gills: Only one gill arch is present in the monognathids according to Bertin (1937a). But a close examination of *M. ahlstromi* and *M. jesse* showed four distinct gill arches bearing short foliaceous gill filaments arranged alternately as in *Eurypharynx*. The gills and gill openings are very small as are those of *Eurypharynx* and *Saccopharynx*.

Pectoral fin: The pectoral fin is absent in the three species described by Bertin (1937a) and in *M. ahlstromi*. There is a small fleshy pectoral fin in *M. isaacsi* and *M. jesse*.

Caudal organ: A caudal organ, whose function is much disputed, is present at the tip of the tail in *Eurypharynx* and *Saccopharynx*. Although a typical caudal organ is not present in any of the known species of the monognathids, the caudal fin is modified either into a filamentous structure as in *M. taningi*, or into a flattened structure as in *M. ahlstromi* and *M. jesse*, or is relatively unmodified as in *M. isaacsi*.

Food: Fish eggs with a sculptured egg membrane, fish larvae, and copepods were found in the mouth and pharynx of the metamorphic forms, but they might have been taken accidentally while in the net.

Distribution (Figure 3): This family has previously been known only from the Atlantic off the coast of North Africa and from the western Pacific (Bertin, 1938). This study shows that it is widely distributed in the whole tropical and subtropical belt of the Pacific, and it is likely that the family may also be found in the tropical Indian Ocean.

RELATIONSHIPS

Bertin (1937a, 1938) erected the family Monognathidae based on his study of four juveniles.

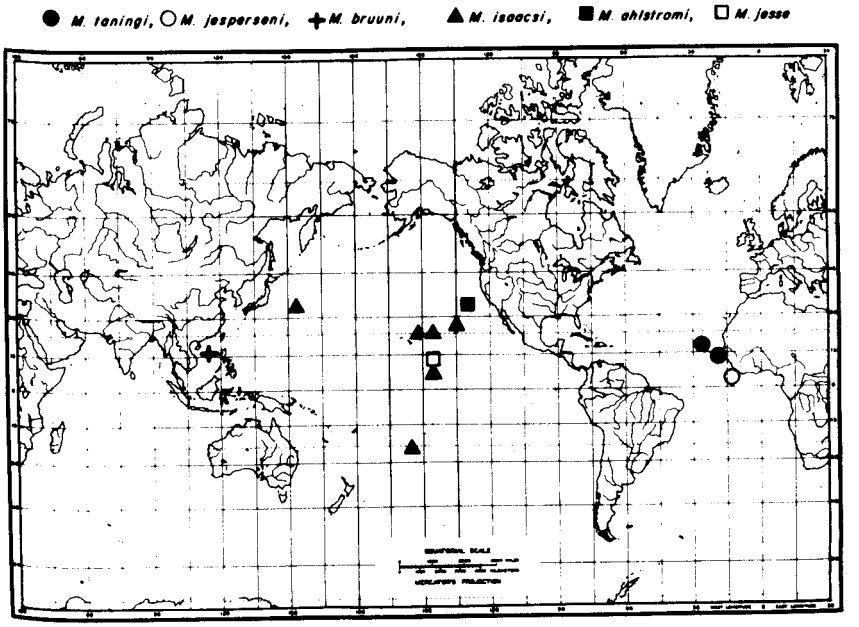


FIGURE 3.—Distribution of the six species of the genus *Monognathus*.

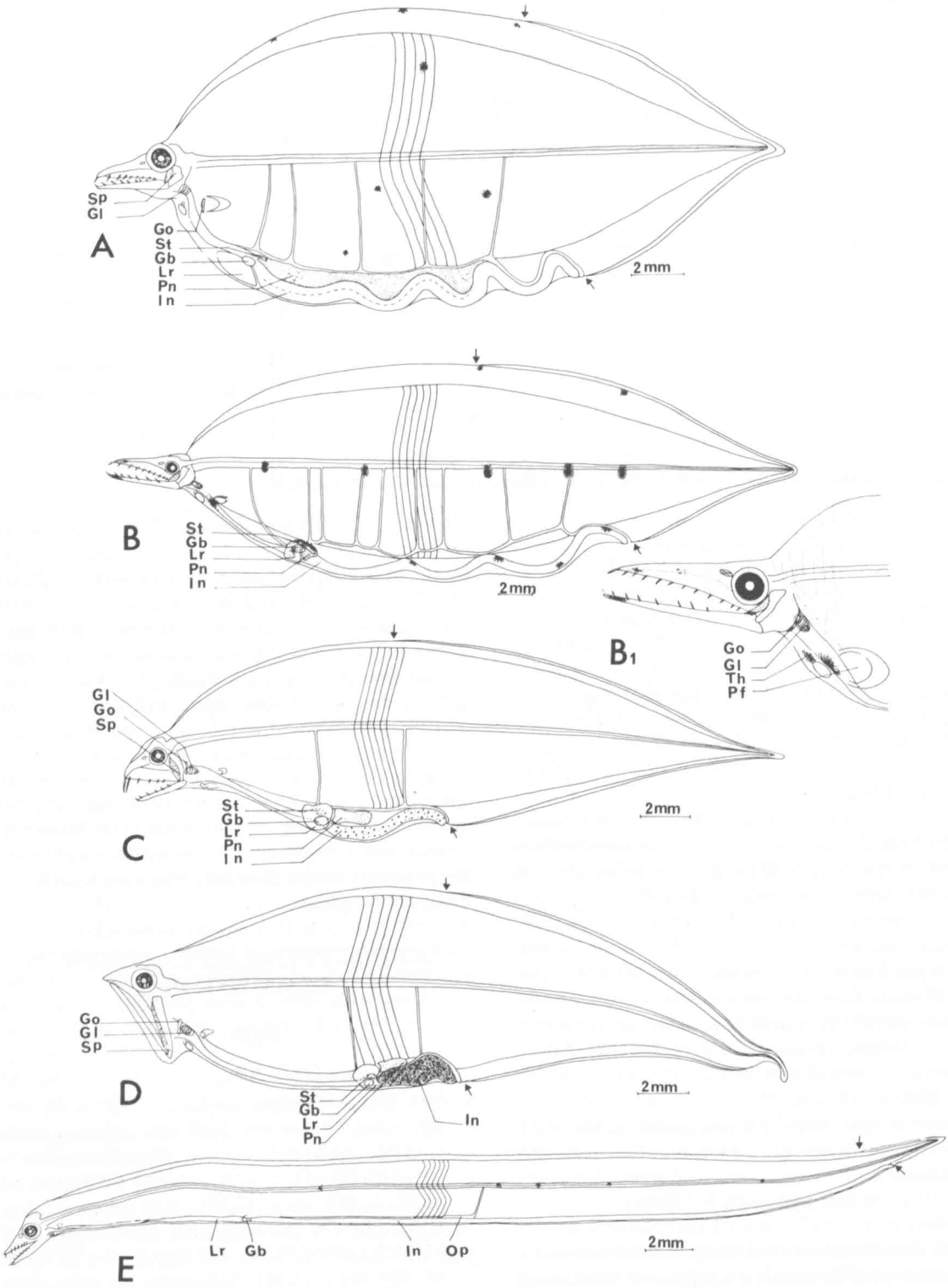
One of the four specimens had been earlier described by Roule (1934) as a semilarva of the Lyomeri. According to Bertin the family Monognathidae consists of a single genus, *Monognathus*, with three species, none of which was designated as the genotype. Myers (1940) recognized two genera, *Monognathus* (genotype *M. taningi* Bertin) and *Phasmatostoma* (new genus; genotype *M. jesperseni* Bertin), on the basis of the number of ethmoid teeth, position of the dorsal fin origin, and nature of the vertebrae and caudal fin. Böhlke (1966) accepted *Phasmatostoma* as a separate genus of the Monognathidae. As already pointed out, *M. isaacsi* may well represent a third genus of the family Monognathidae as the differences between *M. isaacsi* and *M. taningi* are even more pronounced than those between *M. taningi* and *M. jesperseni* or *M. bruuni*, which are separated as *Phasmatostoma*. *M. ahlstromi* and *M. jesse* may also turn out to be new genera as the caudal fin, which is a conservative structure in fishes, varies greatly in the two fishes. However, I would restrain myself to introduce new genera till a detailed study of many adult and larval specimens is undertaken, as the studies on these fishes are based only on very few specimens (1-2 in number), and even these are only juvenile and metamorphic forms.

Tchernavin (1947a) stated that there is no evidence that the Monognathidae are related to the Saccopharyngiformes. His arguments were based on some of the observations of Bertin such as the absence of pectoral fin, presence of only one gill arch, and other osteological characters. Greenwood et al. (1966) and Böhlke (1966) considered monognathids to be related to the Saccopharyngiformes. The general features of *M. isaacsi*—such as the elongated suspensorium, presence of small gill openings and four small gill arches, alternating arrangement of gill filaments on the arch as in *Eurypharynx*, voluminous stomach, occurrence of leptocephalus stage in the life history, the presence of the pectoral fin, and the modified caudal fin—indicate that the Monognathidae are related to the Saccopharyngiformes, more closely to the Saccopharyngidae than to the Eurypharyngidae.

LEPTOCEPHALUS LATISSIMUS SCHMIDT 1912

Figure 4C

Leptocephalus latus Schmidt 1909. SIO 66-353, San Diego Trough, 32°40′N, 117°35′W, 480-366 mwo, Tucker net, 1(30 mm), 23 Aug. 1950. LACM, 6525-16, Santa Catalina Basin, 33°18′27″N-33°24′40″N, 118°44′00″W-118°51′35″W, 0-213 mwo, IKMT, 1(39 mm), 22 Aug. 1963. LACM, 9830-10, No Name Basin, 32°01′30″N-32°04′00″N, 117°59′00″W-117°56′00″W, 600 mwo, IKMT, 1(40 mm), 28 July 1967.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Description: Specimen described (SIO 66-353): Body deep, compressed except at head, total length 30 mm. Maximum depth in middle of body, 3.8 in total length. Posterior end of body attenuate, caudal organ not yet developed. Head short, 7.5 in total length. Skull membranous and transparent. Snout short, 4.0 in head. Olfactory organ rudimentary. Eyes round, dark brown, 5.7 in head. Upper jaw soft, maxilla indistinct. Lower jaw partly damaged. Teeth six in upper jaw, five in lower jaw. Gill opening small, four gill arches. Pectoral fin small, thick. Esophagus a narrow tube, reaching middle of body. Stomach rudimentary. Intestine short, swollen, looped. Liver a small ventral lobe. Pancreas rectangular, dorsal to gut. Opisthonephros a short tube. Myotomes 45 + 125 = 170.

Pigmentation: Minute dark brown chromatophores on swollen part of intestine.

LEPTOCEPHALUS PSEUDOLATISSIMUS BERTIN 1934

Figure 4D

Leptocephalus gastrostomi bairdii Lea 1912.
Leptocephalus pseudolatissimus Bertin 1934.
Material examined: SIO 56-127, Marshall Islands vicinity, western Pacific, 1(32 mm).

Description: Body deep, compressed except at head, posterior end tapering. Maximum depth in the middle of body, 4.0 in total length. Head large, very deep, 7.6 in total length. Skull bones transparent and membranous. Teeth in both jaws lost due to damage. Gill opening small, gill arches five in number. Pectoral rudimentary. Esophagus a narrow tube. Stomach small. Liver a small ventral lobe. Pancreas rectangular. Opisthonephros a short tube. Myotomes 38 + 65 = 103.

Pigmentation: Dense brown pigmentation in the form of small patches on the swollen part of the intestine.

FIGURE 4.—**A**, leptocephalus of *Cyema atrum;* **B**, unknown Pacific leptocephalus; **Bl**, head of unknown Pacific leptocephalus; **C**, *Leptocephalus latissimus;* **D**, *Leptocephalus pseudolatissimus;* **E**, leptocephalus of *Nemichthys scolopaceus.* **Gb**, gall bladder; **Gl**, gills; **Go**, gill opening; **In**, intestine; **Lr**, liver; **Op**, opisthonephros; **Pf**, pectoral fin; **Sp**, suspensorium; **St**, stomach; **Th**, thyroid gland?; **Pn**, pancreas.

Remarks: Leptocephalus latissimus and *L. pseudolatissimus* resemble each other in many characters except for the differences in myotomal count, number of gill arches, length and number of intestinal loops, and pigmentation. *L. latissimus* has a higher myotomal count ranging from 170 to 250 and four gill arches whereas *L. pseudolatissimus* has 103-125 myotomes, five gill arches, a short intestinal loop, and more pigmentation on the loop.

Murray and Hjort (1912) discovered the leptocephalus stage in the life history of Saccopharyngiformes. The larva was later described by Lea (1913), who named it *Leptocephalus gastrostomi bairdii (Gastrostomus bairdii = Eurypharynx pelecanoides)* and suggested that *L. latissimus* Schmidt (1909, 1912) was a larva of another saccopharyngiform. Bertin (1938) described a series of four saccopharyngiforms and assigned both *L. latissimus* and *L. pseudolatissimus* to *Saccopharynx* on the basis of the nature of suspensorium and myotomal counts. The lowest myotomal count in his larvae was 115, and since the highest vertebral count of *Eurypharynx* known to him at that time was 110, he assigned the larvae to *Saccopharynx* as the number exceeded the highest vertebral count of *Eurypharynx*. It is now known that the vertebral count of *E. pelecanoides* ranges from 103 to 125 (Orton, 1963). Tchernavin (1947a) disputed Bertin's allocation of larvae of *Saccopharynx* on the basis of myotomal count and suggested that the low count forms might belong to *Eurypharynx* and the high count forms to *Saccopharynx*. Orton (1963) and Böhlke (1966) also suggested the identity of *L. pseudolatissimus* with *Eurypharynx* on the basis of vertebral counts (97-125).

METAMORPHIC FORM OF *SACCOPHARYNX*

(Not illustrated)

LACM 9579-36, 30°00′00″N-29°30′21″N, 118°40′59″W-118°29′18″W, 2,910 mwo, IKMT, 1(80 mm), 30 Aug. 1966.

Description: Body elongate, posterior region whiplike. Head large, depressed, 14.3 in total length. Snout small, 4.7 in head. Olfactory organ small, two nostrils placed closely one above the other in front of eye. Eye small, 7.0 in head.

Jaws unusually long, with minute recurved teeth on both jaws. Gills plumose. Esophagus short, thin, no girdlelike region. Stomach well developed, empty, white. Intestine long, thick walled, empty, posterior end with series of 12 melanophores on dorsal side till vent. Posterior end of intestine of metamorphic *Eurypharynx* also has similar series of five melanophores on dorsal side. Liver elongate, pale yellow. Gall bladder oval, thin, transparent. About 40 preanal and 110 postanal myotomes can be counted. Myotomes in whiplike portion of tail are not distinct. Tip of tail (caudal organ) enlarged into bulblike structure. Median fin delicate, low. Pectoral fins large, fleshy.

Pigmentation: Microscopic brown dotlike juvenile pigmentation scattered sparsely all over body, but dense on snout and jaws. Larval pigmentation before vent as a row of linear patches. Tip of tail unpigmented.

METAMORPHIC FORM OF *EURYPHARYNX PELECANOIDES*

Figure 2P, Q

SIO 68-451, central North Pacific, Hess Seamount, 17°59.0′N, 174°24.1′W, 0-1,250 m, IKMT, 1(39 mm), 31 Aug.-1 Sept. 1968.

Description: Body elongate, compressed except at head. Depth 8.0 in total length, maximum depth near middle of body, posterior half tapering gradually to whiplike tail with rudimentary caudal organ (Figure 2Q). Head small, broad, depressed, badly damaged. Snout very short, blunt. Eyes large, round, black. Olfactory organ rudimentary. Upper jaw cartilaginous, maxilla toothless, its boundary not clear. Lower jaw lost due to damage. Gills extremely small, five holobranchs, six gill slits, white in color, gills of both sides placed very close together, gill filaments very small, gill arches very soft, and do not appear to have any bony or cartilaginous elements. Esophagus short, slightly bulged, brown, followed by rudimentary stomach (Figure 2P). Stomach bulged, muscular, with brown pigment. Liver lost due to damage. Intestine short, continued as rectum with five black dendritic chromatophores on dorsal side. Opisthonephros lost due to damage. Myotomes about 105. Dorsal and anal fins damaged.

Pigmentation: Body covered uniformly with dark brown juvenile pigmentation. Tip of tail white except for black caudal organ.

Ovary of adult (Figure 2R,S): Examination of the ovary of one large specimen of *E. pelecanoides* (600 mm, vertebrae 31 + 87 = 118) in the Scripps Institution of Oceanography (group 25, H.52.376) gives the following information. Ovary large, oval, paired, brown in isopropyl alochol, two ovaries of same size, 62.2 mm in length, 29 mm in breadth, oval in shape, maximum thickness in center 10 mm, weight of two ovaries 18.4 g, about 33,000 ova in both ovaries, eggs arranged in single layer which is folded into laminae of double layers. Thus, each ovary is a long sheet of ova. Ova embedded in sheet of jellylike mass divided into hexagonal meshes, each mesh enclosing single ovum. Ova well developed, round, average diameter 0.9 mm, yellow, containing 4 or 5 yellow oil globules of varying sizes, diameter of largest oil globule 0.15 mm.

Remarks: The two metamorphic forms *L. latissimus* and *L. pseudolatissimus* were badly damaged and distorted, making it very difficult for illustration. But characters such as pigmentation and the caudal organ provided some information on their identity to the adults.

The metamorphic specimen of *L. pseudolatissimus* has juvenile pigmentation, and the caudal organ is well developed and is more advanced than the larvae described before. The myotomal count, the number of gill arches, the position and structure of the caudal organ, the juvenile pigmentation, and other characters clearly establish the identity of *L. pseudolatissimus* as the larva of the deepsea gulper *Eurypharynx pelecanoides*.

The higher myotomal count of *L. latissimus* certainly indicates its identity with *Saccopharynx*, as suggested by Tchernavin (1947a). Orton (1963), in discussing the relationship of *L. latissimus*, pointed out its possible identity as the larva of *Saccopharynx* but also warned that the then unknown monognathid larva might be a possible candidate for *L. latissimus*. The characters of the metamorphic monognathid and saccopharyngid

larvae described in this account help to identify *L. latissimus* as the larva of *Saccopharynx*. Böhlke (1966) pointed out that the similarities between saccopharyngids and monognathids might warrant consideration of monognathids as postlarval saccopharyngids. The characters of the metamorphic *Saccopharynx* and *M. isaacsi* do not support his contention. The ethmoid tooth persists into the fully transformed stage in monognathids (*M. isaacsi*), but it is absent in the metamorphic *Saccopharynx*. A girdlelike region is present on the esophagus, and the liver is a short lobe in monognathids, whereas no girdlelike region is present; the liver is elongate, and the tail is extremely attenuate and whiplike in metamorphic *Saccopharynx*.

A new type of saccopharyngiform larva has been recently studied (Castle and Raju, unpublished data), and the details will be published elsewhere. This larva (myotomes 62 + 43 = 105) resembles *L. latissimus* and *L. pseudolatissimus* in the shape of the body, myotomes, and other features, but differs from them in having a large eye, absence of long needlelike teeth in the upper jaw, and the structure of the intestine. At present, it is not possible to assign the larva to any of the known families of the Saccopharyngiformes.

UNKNOWN PACIFIC LEPTOCEPHALUS

Figure 4B

Holotype: SIO 70-118, 24°33′S, 154°55′W-154°56′W, IKMT, 1(40 mm), 4 Oct. 1969.

Description: Body elongate, compressed except at head, tapering toward both ends of body. Maximum depth in middle of body, 3.2 in total length. Head long, 3.6 in total length. Snout long, about 4.0 in head. Olfactory organ small, an elongate cup, nostrils not formed. Eye fairly large, 13.7 in head, round, black, surrounded by a transparent area. Upper jaw elongate, maxilla distinct, dentition 1 + 11. Lower jaw elongate, slightly projecting beyond upper jaw, dentition 1 + 7. Suspensorium long. Gill opening wide. Opercular elements present, cartilaginous. Gills very small, four. Branchiostegals absent. Myotomes wide, V-shaped, 56 + 46 = 102, muscle fibers very broad. Dorsal fin origin on myotome 38, fin rays not formed, predorsal distance 2.0 in total length. Anal fin rays not formed. Pectoral fin small, behind gills. Esophagus a straight tube. Stomach a rudimentary, fingerlike process at myotomes 17-19. Intestine long, muscular, thrown into three loops of increasing depth posteriorly opening to exterior at myotome 56. Liver small. Gall bladder and stomach enclosed by liver. Pancreas a small, thick lobe. Opisthonephros tubular, wavy, opening behind vent. First and last blood vessels to viscera at myotomes 8 and 48, respectively.

Pigmentation: A thick black patch at tip of lower jaw, a small black patch at tip of upper jaw on ventral side. Sparse black pigment along midline of snout and olfactory region, a series of midlateral patches, one each on myotomes 13, 25, 40, 50, 59, the last patch on right side and the rest on left, two stellate melanophores on dorsal finfold, and a series of five on heart, liver, and intestinal loops on ventral side.

Remarks: This is the first report of this type of larva from the Pacific. It appears that there is only one record of a similar larva, *L. holti*, from the North Atlantic off the coast of northern Spain (Schmidt, 1909). *L. holti* resembles this larva in most characters such as the shape of the body, head, and snout, in dentition, myotomes, gut, liver, and pigmentation. The preanal and total myotomal counts (67 + 45 = 125 + ca) of *L. holti* are higher than the myotomal counts of this larva, which undoubtedly belongs to a different but closely related species.

Schmidt did not allocate *L. holti* to its adult, but simply suggested that it may belong to some southern warm-water eel. Although it is difficult to establish the identity of the larva conclusively in the absence of successive metamorphic and juvenile stages, certain morphological and anatomical characters of the larva are closer to the larval features of *Cyema*, saccopharyngids, and monognathids, and a comparison of its characters is made with their larval features.

Comparison with Cyema: This larva has striking resemblances to that of *Cyema* in the following features: The shape and the size of the body are similar although less deep; the head is elongate; the teeth are similar in shape; the eye is larger and circular; the myotomes are V-shaped; the intestine is thrown into loops; the gill opening and gills are small. But the larva differs from

Cyema in the following respects: *Cyema* has five intestinal loops (four in early stages) which are more compact and deeper whereas this larva has only three shallow intestinal loops; the liver in *Cyema* is small, laminar, and situated at myotome 6 whereas in this larva the liver is a very thick lobe at myotome 17; the pancreas in *Cyema* is a large and thin film of tissue extending along all the intestinal loops except the last and does not form a bulge with the liver whereas it is a thick lobe forming a bulge with the liver in this larva; the position of the gills in *Cyema* is more anterior than in this larva; the body depth in this larva is less than that of *Cyema*; the pigmentation on the myotomes in *Cyema* is scattered all over the body whereas it is limited to a series of five midlateral melanophore patches in this larva. But the basic characteristics of the larva are so strikingly similar to those of the larva of *Cyema*, I am compelled to relate it to an unknown species of the family Cyemidae. If the larva is a cyemid larva, it will probably belong to a new genus other than *Cyema* as the differences between the larva of *Cyema atrum* and this larva appear to be at generic level.

Comparison with saccopharyngid and eurypharyngid larvae: In all three kinds of leptocephali the size and shape are approximately similar, the myotomes are V-shaped, the suspensorium is elongated, the gills are small and more posterior in position, the liver is a thick lobe, the pancreas is a thick lobe forming a bulge with the liver, the intestine is looped, and the opisthonephros and the last blood vessel are on the last intestinal loop. However, this larva differs from saccopharyngid and eurypharyngid larvae in the shape of the head and the nature of the teeth, in having more intestinal loops and a longer intestine, and in the presence of a midlateral series of pigmentation spots.

Comparison with metamorphic monognathids: This larva resembles the metamorphic forms in myotome shape, the elongate snout, the total number of myotomes and the midlateral melanophores (Table 2), the structure and position of the melanophores in relation to mytome number, and the pigmentation at the tip of the jaws. But this larva has a well-developed eye whereas the metamorphic forms have rudimentary eyes. But degeneration of the eye may take place during metamorphosis as in *Cyema*, which has a degenerate eye in the adult and a very large eye in the larva. The gills, liver, and intestine are lost due to damage in the 42-mm and 48-mm metamorphic specimens, and a comparison of these structures cannot be made. A pectoral fin is absent in metamorphic forms whereas this larva has a pectoral fin. The position of the vent is more anterior in the metamorphic forms than in *Monognathus*, which may be attributed again to metamorphosis. The deep pigmentation at the base of the median fins, which increases progressively in later stages, is obviously juvenile pigmentation. Although the midlateral pigmentation, myotome number and shape, and other characters agree with those of metamorphic forms of *Monognathus*, the differences preclude a close relationship.

AFFINITIES OF SACCOPHARYNGOIDEI WITHIN THE ANGUILLIFORMES

The Saccopharyngiformes have not been successfully related to any family within the Anguilliformes. In the most recent classification of the teleostean fishes (Greenwood et al., 1966), the group is placed next to Aoteidae and Cyemidae as a suborder (Saccopharyngoidei) of the order Anguilliformes. The family Cyemidae has been traditionally regarded as related to nemichthyid eels because of the superficial resemblances of the beak. I suggest that the Cyemidae be considered as related to the Saccopharyngiformes and not to the Nemichthyidae for the following reasons.

The adults of *Cyema* differ from the nemichthyids in morphological and osteological characters. All the nemichthyid eels are extremely elongate, but *Cyema* is very short. The adult *Cyema* has a small degenerate eye and a large stomach (about one-fourth of the total length excluding the beak), as in the Saccopharyngiformes, whereas the nemichthyids have large eyes.

The differences in their larvae are even more basic. The larvae of *Nemichthys scolopaceus* Richardson, 1848 (Bertin, 1937b) and other nemichthyids (Beebe and Crane, 1936, 1937a, 1937b) are also elongate and become extremely attenuate during growth and metamorphosis, but the larva of *Cyema* has a short and deep body.

The myotomes of the nemichthyid larvae are W-shaped whereas those of *Cyema* are V-shaped. The intestine is looped in *Cyema* whereas it is straight in the nemichthyid larvae. On the other hand, the larva of *Cyema* closely resembles those of the Saccopharyngiformes in the size and shape of the body, myotome shape, looped intestine, position of the vent, and elongate suspensorium. Bertin (1937b) has pointed out some of the larval and osteological resemblances between the Cyemidae and the Saccopharyngiformes and attributed the similarities of the beak of the Cyemidae and Nemichthyidae to convergent evolution as the beak in *Nemichthys* is mainly formed by the elongation of the vomer, but in *Cyema* by the two maxillaries.

The four families—Cyemidae, Monognathidae, Saccopharyngidae, and Eurypharyngidae—share some basic characters such as short, deep bodied larvae with V-shaped myotomes, looped gut, elongated suspensorium, and a degenerate eye in the adult condition. The striking similarities of these larvae and their differences with the larva of *Nemichthys* are shown in Table 3 and Figure 4. The gross differences in the adults of the four families are probably due to the drastic changes undergone during metamorphosis and other causes. At present, I can only point out the similarities of the Cyemidae to the Saccopharyngiformes. Further studies may provide information to help include or exclude the Cyemidae in the Saccopharyngiformes.

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TABLE 3.—Comparison of larval characters.

Characters	*Cyema atrum*	Pacific leptocephalus	*Leptocephalus latissimus*	*L. pseudo-latissimus*	*Nemichthys scolopaceus*
Size of body (mm)	Small (20-60)	Small (35-40)	Small (20-40)	Small (20-40)	Large (over 100)
Shape of body	Oval	Oval	Oval	Oval	Ribbonlike
Myotomes	V-shaped (obtuse angle)	V-shaped (obtuse angle)	V-shaped (obtuse angle)	V-shaped (obtuse angle)	W-shaped
Intestine	Looped	Looped	Looped	Looped	Straight
Position of vent	About three-fourths from head	About three-fourths from head	About one-half from head	About one-half from head	Subterminal
Liver	Short lobe	Short lobe	Short lobe	Short lobe	Elongate
Pancreas	Very large	Large lobe	Large lobe	Large lobe	Small and elongate
Suspensorium	Elongate	Elongate	Elongate	Elongate	Small

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OSTEOLOGICAL DEVELOPMENT AND VARIATION IN YOUNG TUNAS, GENUS *THUNNUS* (PISCES, SCOMBRIDAE), FROM THE ATLANTIC OCEAN[1]

THOMAS POTTHOFF[2]

ABSTRACT

The development and variability of osteological and meristic features obtained from 427 juvenile *Thunnus* from 8 to 117 mm SL are described. The juveniles of *T. atlanticus*, *T. thynnus*, and *T. alalunga* can be identified. *Thunnus obesus* cannot be separated from *T. albacares*, but both are separable as the "*Thunnus* spp. complex" from the other three species. Identification methods are discussed with emphasis on the features of the axial skeleton, number of gillrakers over the ceratobranchial bone, pterygiophore pattern under the second dorsal fin, and the shape of the lateral line.

This paper describes the development of osteological features and their variability for the identification of juvenile *Thunnus* from 8 to 100 mm standard length (SL). To date, this has not been attempted in an orderly and systematic fashion for the species in the Atlantic Ocean, mainly because all juveniles have the same general external appearance as *T. atlanticus* shown in Figure 1. Nevertheless, some species have been previously identified by using mostly external characters: Sella (1924), Schaefer and Marr (1948), Wade (1950, 1951), Mead (1951), Padoa (1956), Jones (1960), Matsumoto (1961), Marchal (1963a, b), and Yabe, Ueyanagi, and Watanabe (1966). The identifications were probably correct, although other species of juvenile *Thunnus* could fit these same descriptions. Scaccini (1961) published on a series of juvenile *Thunnus* from the Mediterranean and stated that they were *T. thynnus*, but he did not reveal how he arrived at his identifications. Ueyanagi (1967) mentioned the occurrence of small *T. alalunga* in the North and South Atlantic Oceans, but he gave no identification methods. Klawe and Shimada (1959) and Klawe (1961) examined juvenile *Thunnus* material, using external and osteological characters, but they had doubts as to the correctness of their identifications. Watson and Mather (1961) used the soft X-ray method to distinguish between the species. One of their major characters was the vertebral position of the first ventrally directed parapophysis. I found this character to be of limited value, because the vertebral position of the first parapophyses changes with growth. Potthoff and Richards (1970) used osteological characters to identify two species of juvenile *Thunnus* from bird stomachs, and Juárez (1972) described larvae of *T. atlanticus*, also on the basis of osteological methods. Other researchers have used adult osteological characters on specimens larger than 100 mm (Yabe et al., 1958; Nakamura and Kikawa, 1966).

I was not entirely successful in separating all species. Using osteological characters, *T. albacares* and *T. obesus* were not separable from each other as juveniles (from 8 mm to about 100 mm SL), but together they can be separated from the other three *Thunnus* species in the Atlantic Ocean. Thus, I have lumped them together as the "*Thunnus* spp. complex."

Adult characters from the works of Kishinouye (1923), Frade (1932), Godsil and Byers (1944), de Sylva (1955), Watson (1964), Nakamura (1965), and Gibbs and Collette (1967) formed the basis for my study. At first I identified the largest fish in my collection and then worked down to the smaller sizes, noting changes that occurred.

METHODS

The specimens used in this study were first measured with dial calipers or calibrated ocular micrometers and the standard length (SL) from

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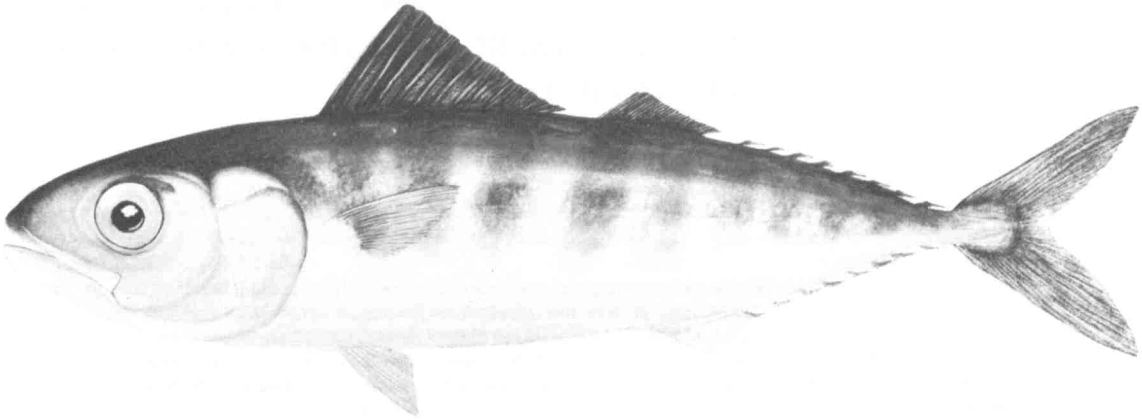

FIGURE 1.—*Thunnus atlanticus*, 85 mm SL. Specimen was cleared and stained later for species determination.

the anterior tip of the upper jaw to the posterior edge of the hypural plate was taken. After determining length measurement the right opercular plates were removed and the specimens were then cleared and stained (Taylor, 1967). All counts were made on cleared and stained material that was preserved in 100% glycerin, using a binocular microscope with 100× magnification. On a few of the larger specimens 25× magnification was used. Counts on the gill arches, fins, and vertebral column were made on the right side of the specimen, except for the pectoral finrays and lateral line scales, which were counted on both sides. The side with the higher count was used for tabulation. Small gillrakers and finrays that were just beginning to appear in their first stage of development were always included in the counts. Structures such as the pterygiophores, neural and haemal spines, zygapophyses, etc., were always counted, although in smaller specimens some of these structures were very small and showed very weak ossification. The hypural complex (parhypural, hypural plates, and ural centrum) was considered as the last vertebra. I was unable to make every count on all of the specimens because of damage or their developmental stage. For these reasons, the number of specimens used for the various counts may vary.

The osteological terms used in this paper are mainly from Eaton (1945) and Gibbs and Collette (1967). The terms transforming and juvenile are defined for scombrid fishes as follows: specimens of the transforming stage can be identified with the aid of larval pigment characters but have attained most adult gross anatomical features, such as number of vertebrae and median fins; juveniles attain the juvenile pigmentation which obliterates the larval pigmentation. The transition from larval to transforming to juvenile stages is gradual in scombrids and allows for individual subjective judgment. In my opinion, the larval stage for *Thunnus* lasts to about 9 mm SL, the transforming stage to about 13 mm SL, and the juvenile stage to sexual maturity.

MATERIAL

Most of the *Thunnus* used in this study were collected with a dip net, using a strong light at night. A few were collected by plankton nets and some were taken from fish or bird stomachs. The numbers and standard lengths of all specimens examined for this study are shown in Figure 2. Their numbers and size ranges for general capture areas are shown in Table 1.

VERTEBRAL COLUMN

Number of Vertebrae
(Figures 3 to 6; Tables 2, 13)

The species of *Thunnus* usually have 39 vertebrae, including the hypural plate: 18 precaudal and 21 caudal vertebrae for all species except the western Atlantic *T. atlanticus*, which usually has 19 and 20, respectively. In juveniles the centra in the anterior two-thirds of the vertebral column are already ossified at 8 mm SL, but are still developing in the posterior third. About 9 mm SL, ossification of all centra is completed. Pleural ribs

start on the 3rd precaudal vertebrae attached to the parapophyses and to the tips of the haemal arches. Caudal vertebrae lack pleural ribs and their haemal arches continue as one haemal spine. In transforming specimens, it is sometimes difficult to distinguish pleural ribs from haemal spines, but one can use the first large anal pterygiophore as a demarkation point because it is always found in the interhaemal space anterior to the first haemal spine.

Knowledge of the variability of precaudal and caudal arrangement and number of vertebrae is important in the identification of specimens, particularly in the 8- to 14-mm-SL size range where fewer characters are available. However, great differences in vertebral variability exist from

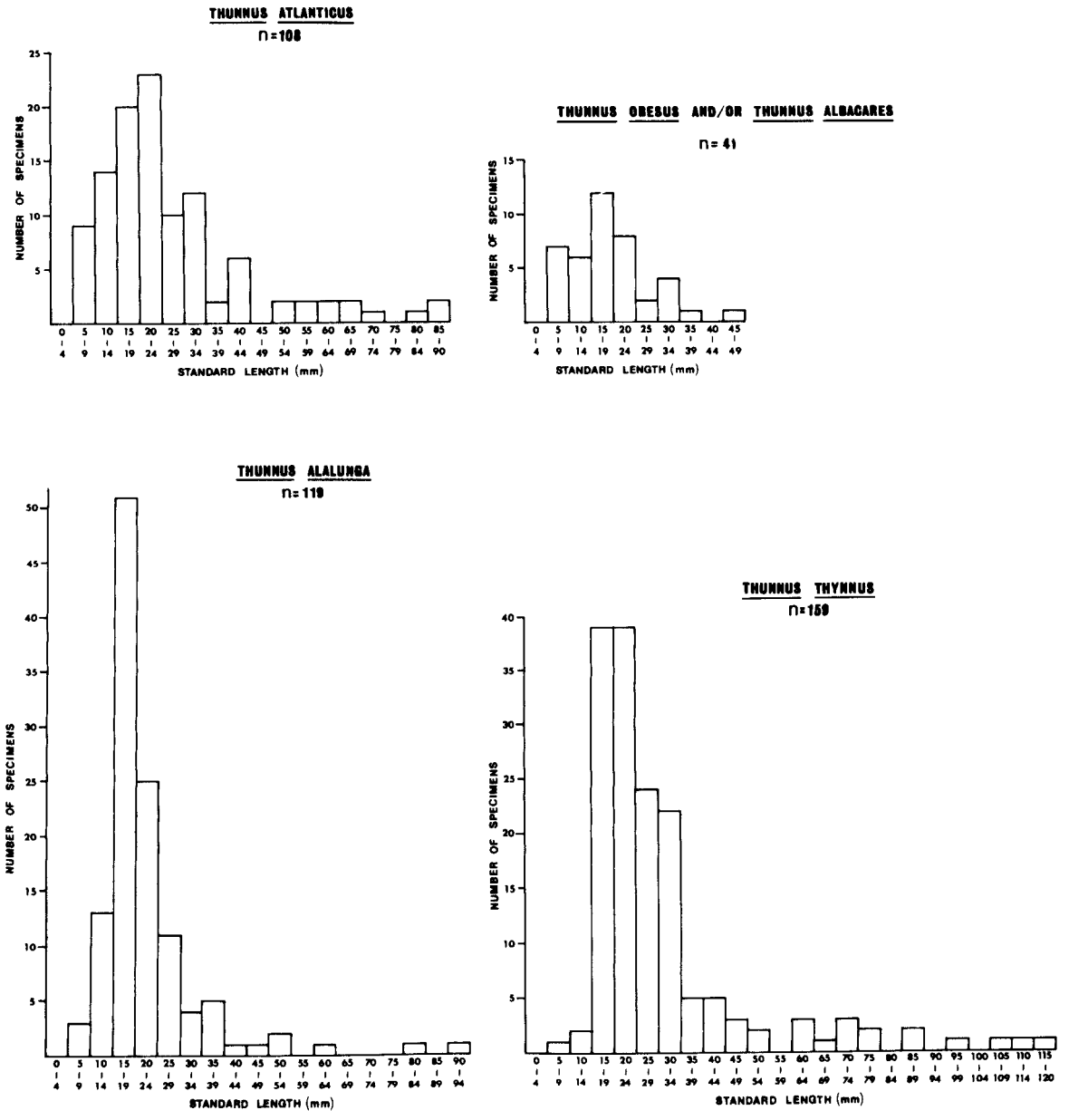

FIGURE 2.—Length distribution by species of all specimens examined for this study.

TABLE 1.—Capture areas, species, number, size range, and mean standard length for specimens studied.

Area	Species	No.	Size range SL (mm)	Mean SL (mm)
Northeast Pacific Ocean	*Thunnus* spp.	23	14-31	19
Northwest Atlantic Ocean	*T. thynnus*	14	8-71	32
Northwest Atlantic Ocean	*T. alalunga*	1	9	
Northwest Atlantic Ocean	*T. atlanticus*	35	9-71	34
Northwest Atlantic Ocean	*Thunnus* spp.	4	18-33	27
Gulf of Mexico	*T. thynnus*	15	17-115	45
Gulf of Mexico	*T. atlanticus*	65	8-87	23
Gulf of Mexico	*Thunnus* spp.	1	32	
Caribbean Sea	*T. alalunga*	9	15-22	19
Caribbean Sea	*T. atlanticus*	7	8-85	35
Mid-North Atlantic Ocean	*T. alalunga*	1	18	
Equatorial East Atlantic Ocean	*Thunnus* spp.	11	8-47	17
Mediterranean Sea	*T. thynnus*	78	14-117	33
Mediterranean Sea	*T. alalunga*	102	9-91	23
Unknown	*T. thynnus*	52	13-44	23
Unknown	*T. alalunga*	6	16-41	24
Unknown	*T. atlanticus*	1	11	
Unknown	*Thunnus* spp.	2	16, 20	

various reports, probably because of insufficient sample size and population differences. I have found variability in precaudal and caudal arrangement, as well as in total vertebrae. Vertebral numbers ranged from 38 to 40, and total variability from the normal counts of 18 + 21 = 39 and 19 + 20 = 39 ranged from 1.9% for *T. atlanticus* to 14.6% for *Thunnus* spp. Frade (1932) found 13.6% variability for *T. thynnus* compared to my 5.1%, and he reported eight specimens with 38, six with 40, and one with 41 vertebrae. Gibbs and Collette (1967) doubted Frade's (1932) high counts of 40 and 41 vertebrae, but they confirmed Godsil and Byers' (1944) specimen of *T. thynnus* with 38 vertebrae. Otherwise, they report no variability in vertebral numbers from more than 200 skeletons, except for three abnormalities where two adjacent centra were fused. I found one such "fusion abnormality" in a *T. thynnus* with 16 + 22 = 38 from more than 400 *Thunnus* specimens examined.

First Ventrally Directed Parapophysis
(Figure 3)

Ventrally directed parapophyses are already present on the anterior centra in the smallest (8 mm SL) specimens. There are two parapophyses per centrum. Posteriorly, these two structures become larger and finally join to form the haemal

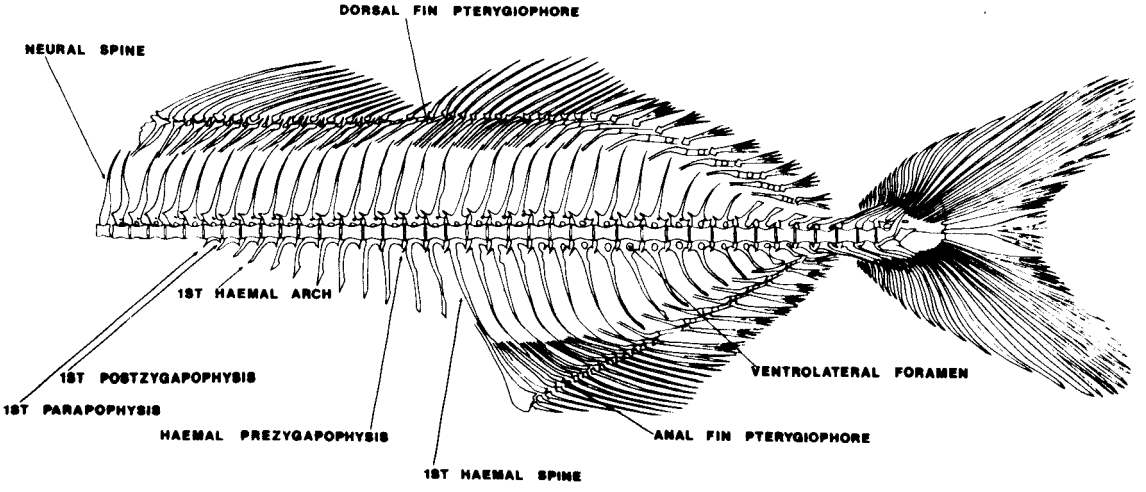

FIGURE 3.—Relationship of the axial skeleton to the fin supports and fins in *Thunnus thynnus*, 24 mm SL.

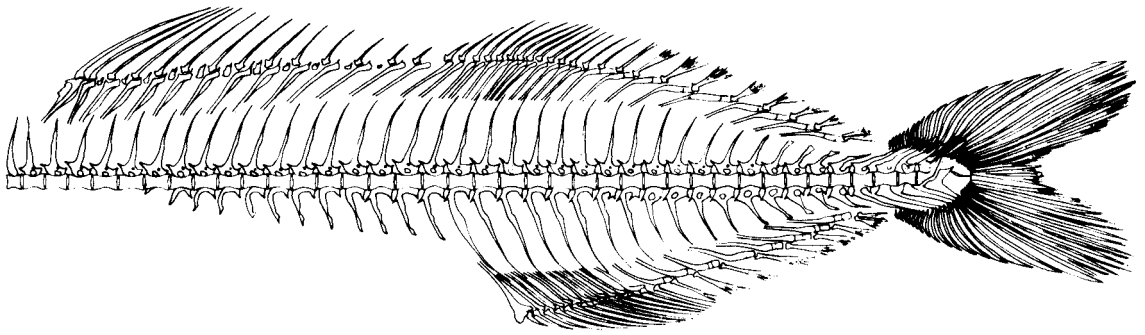

FIGURE 4.—Relationship of the axial skeleton to the fin supports and fins in *Thunnus alalunga*, 22 mm SL.

arches. The first (anteriormost) ventrally directed parapophysis occurred on the 8th or 9th vertebra on specimens 10 mm SL and smaller. In fish larger than 10 mm SL the first ventrally directed parapophysis occurred on the 6th, 7th, or 8th vertebra. I could not determine specific differences in the position of the first ventrally directed parapophysis. Differences reported by Watson and Mather (1961), Watson (1964), and Gibbs and Collette (1967) occur only in specimens larger than 80 mm SL. In juveniles less than 80 mm SL, the first ventrally directed parapophysis is one to three vertebrae anterior to the adult position. As the fish grow, some of the anteriormost parapophyses move to a lateral position on the centra.

First Closed Haemal Arch
(Tables 3, 13)

The closed haemal arches are formed quite early. Even the smallest (8 mm SL) specimens of *Thunnus* that I examined had their first anteriormost closed haemal arch on the diagnostic vertebra. The arch is formed by the fusion of the distal ends of the elongated two parapophyses on each centrum. At times it is difficult to determine whether the parapophyses have actually fused or are only lying close together. Care should be taken to determine this fact. The position of the first closed haemal arch is a character of some value, since it forms at very small sizes. Posteriorly, the arches become more elongated in a dorsoventral direction, forming spines at their distal points (Figures 3 to 6). The vertebral position of the first closed haemal arch separates the species of the genus *Thunnus* into two groups. In *T. thynnus* and *T. alalunga* the first arch occurs on the 10th vertebra; in *T. atlanticus* and *Thunnus* spp. it occurs on the 11th. The variability of this character ranges from 1% to 12% for the various species. *Thunnus alalunga* is the most conservative for this character, and *T. thynnus* is the most variable.

TABLE 2.—Precaudal and caudal arrangement of the vertebrae and total vertebral number in juveniles of *Thunnus*.

Item	*T. thynnus*	*T. alalunga*	*T. atlanticus*	*Thunnus* spp.
Total variability from mode (%)	5.1	3.4	1.9	14.6
Precaudal, caudal, and total number of vertebrae				
16 + 22 = 38	1			
18 + 20 = 38	2			
19 + 19 = 38			1	
17 + 22 = 39	1			5
18 + 21 = 39	149	114	1	35
19 + 20 = 39	2	4	105	
18 + 22 = 40	1			
19 + 21 = 40	1			1

First Ventrally Directed Haemal Postzygapophysis
(Figures 3 to 7; Tables 3, 13)

The haemal postzygapophyses begin to develop a little later than the parapophyses. In 12- to 15-mm-SL fish, they first appear as tiny bony projections on the ventral posterior edge of the centrum. They develop anteriorly and posteriorly from the center of the vertebral column. At about 13 to 16 mm SL, the position of the first haemal postzygapophysis becomes a diagnostic character. A 100× magnification should be used in the

smaller specimens. The species of *Thunnus* can be separated into two groups by the vertebral position of the first haemal postzygapophyses. *Thunnus thynnus* and *Thunnus* spp. have the first haemal postzygapophyses most often on the 7th vertebra; *T. alalunga* and *T. atlanticus* on the 8th. *Thunnus thynnus, T. atlanticus,* and *Thunnus* spp. develop the haemal postzygapophyses on their respective diagnostic vertebrae at about 13 to 14 mm SL; *T. alalunga* develops them at about 15 to 16 mm SL.

I examined seven prepared skeletons from young adults for all species from 400 to 700 mm SL and found that the position of the first ventrally directed haemal postzygapophyses was one vertebra posterior to those of juveniles. I attribute this difference between juveniles and adults to the lateral movement of the structures during growth and also to differential growth between the centrum and the haemal postzygapophyses. The elongate haemal postzygapophyses that characterize the adult *T. atlanticus*, i.e., the longest haemal postzygapophysis is equal to or longer than the centrum (Gibbs and Collette, 1967), develop only gradually in juveniles of that species, and no specimens below 80 mm SL can be separated on the basis of this character. The same is true for adult *T. albacares*, which approach the condition of *T. atlanticus*. I was unable to follow this through on juveniles in the *Thunnus* spp. complex because I lacked specimens in the larger sizes. All my *Thunnus* spp. specimens had haemal postzygapophyses no larger than those of all the other species in their comparable size groups.

Haemal Prezygapophyses
(Figures 3 to 7; Table 3)

The haemal prezygapophyses develop almost at the same time as the haemal postzygapophyses, but later than the parapophyses. They first show up as minute bony projections on the two anterior parts of the haemal arches near the centra in about 10- to 13-mm-SL fish. Development, in order of appearance, proceeds from the anterior to the posterior vertebrae and varies slightly with species and size. Young *T. atlanticus* develop them at 10 mm SL, the remaining species between 12 and 13 mm SL. High magnification (100×) should be used on specimens that just develop this structure. Most specimens of *T. thynnus* and *T. alalunga* have their first haemal prezygapophyses under the 15th or 16th vertebra, *T. atlanticus* under the 16th and 17th, and *Thunnus* spp. under the 14th. There is however considerable overlap with apparent bimodal tendencies for the various species.

In small juvenile *Thunnus*, all haemal prezygapophyses arise from the haemal arches. Only in specimens larger than 80 mm SL are the haemal prezygapophyses on the centra and then only posterior from about the 30th vertebra. In adult *Thunnus* the haemal prezygapophyses arise from the centra posterior from about the 25th vertebra (Gibbs and Collette, 1967).

The position of the anterior haemal prezygapophyses on the haemal arches or centra varies for the species of the adults of *Thunnus*. Adult *T. alalunga* have their more anterior haemal

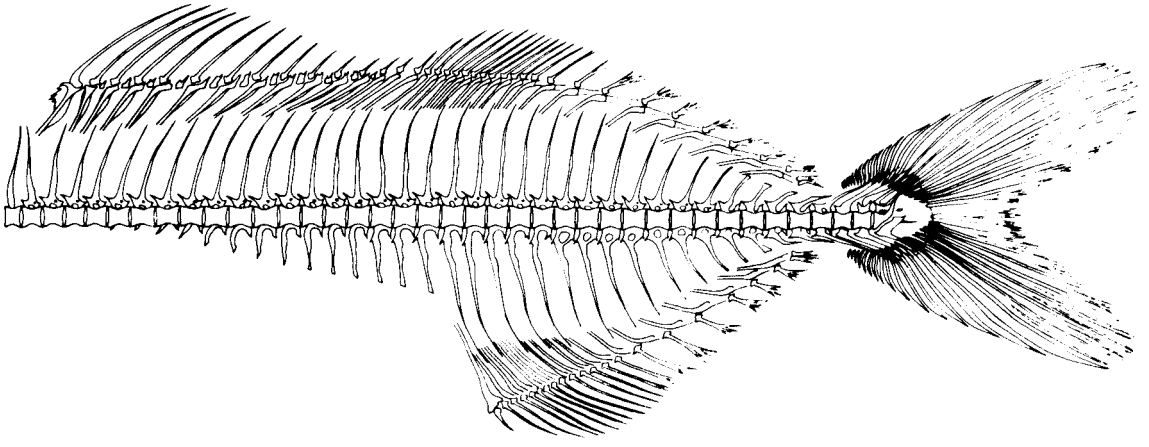

FIGURE 5.—Relationship of the axial skeleton to the fin supports and fins in *Thunnus atlanticus*, 23 mm SL.

TABLE 3.—Vertebral position of the first closed haemal arch, first ventrally directed postzygapophysis, first haemal prezygapophysis, and first ventrolateral foramen for juveniles of *Thunnus*.

Species	Vertebra 6	7	8	9	10	11	12	13	14	15	16	17	18	20	21	22	23	24	25	26	27	Modal variation %	Size range mm SL	
										Position of first closed haemal arch														
T. thynnus				1	137	18																12	8-117	156
T. alalunga				1	115																	1	9-91	116
T. atlanticus					2	101	4															6	8-87	107
Thunnus spp.					2	38	1															7	8-47	41
										Position of first ventrally directed haemal postzygapophysis														
T. thynnus	2	153	2																			3	13-117	157
T. alalunga		3	97	4																		7	15-91	104
T. atlanticus			86																			0	13-87	86
Thunnus spp.	3	28																				10	14-47	31
										Position of first haemal prezygapophysis														
T. thynnus							2	2	16	81	49	6											13-117	156
T. alalunga								1	15	55	32	9	1										12-91	113
T. atlanticus								1	4	7	46	32	5										10-87	95
Thunnus spp.								8	14	7	2												13-47	31
										Position of first ventrolateral foramen														
T. thynnus															1	12	16	20	18	6	2		25-117	75
T. alalunga																	3	13	5	3	1		25-91	25
T. atlanticus															6	12	14	9	—	1			25-87	42
Thunnus spp.														1	3	4							27-47	8

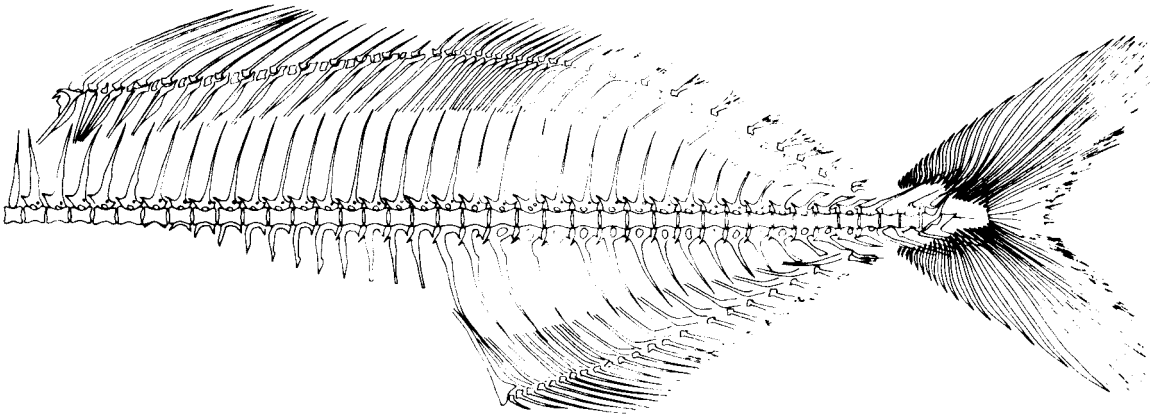

FIGURE 6.—Relationship of the axial skeleton to the fin supports and fins in *Thunnus* spp., 31 mm SL.

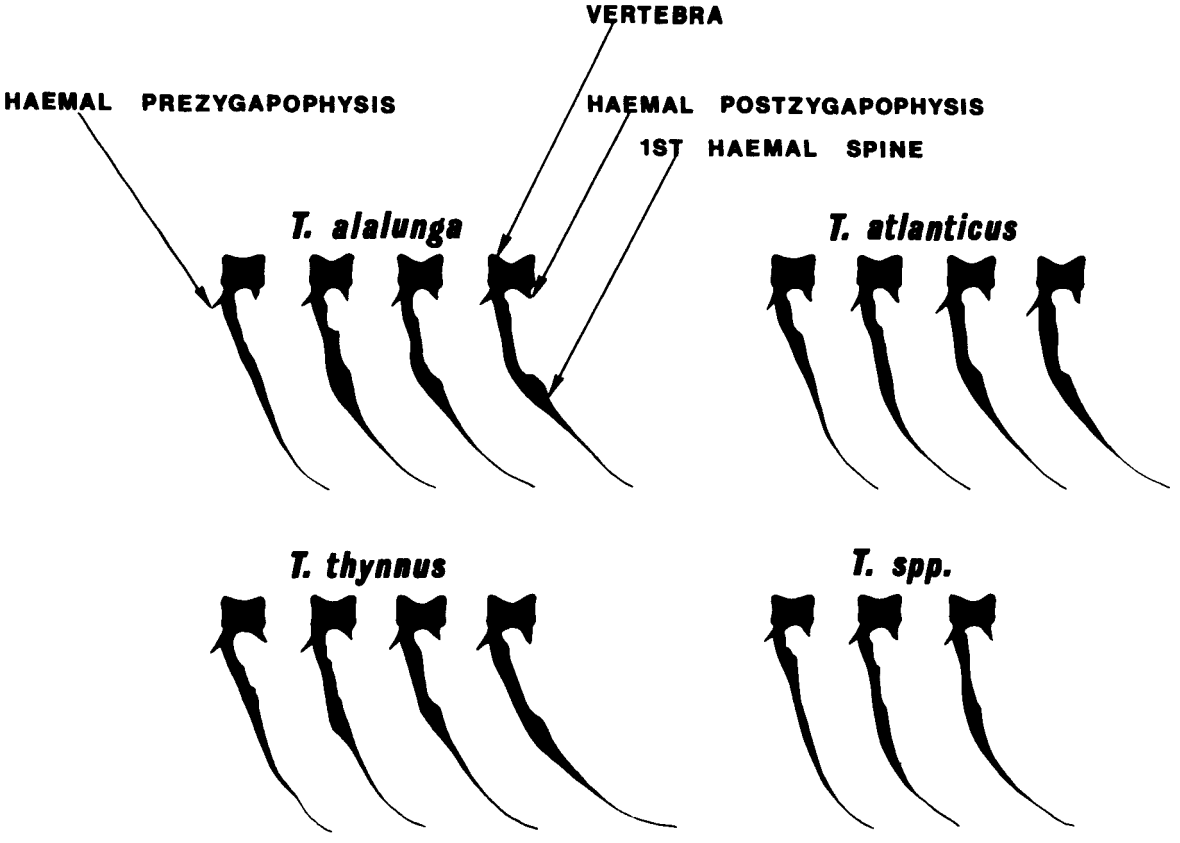

FIGURE 7.—Shape of the first haemal spine for juveniles of the *Thunnus* species. From left to right: *T. alalunga* 17, 34, 61, 91 mm SL; *T. atlanticus* 18, 34, 64, 85 mm SL; *T. thynnus* 17, 33, 65, 100 mm SL; *Thunnus* spp. 16, 33, 47 mm SL.

prezygapophyses on the centra, *T. thynnus* and *T. obesus* have them near the centra but on the haemal arches, and *T. albacares* and *T. atlanticus* have them well ventrad of the centra on the haemal arches (Gibbs and Collette, 1967). In juveniles below 50 mm SL, this specific difference for the adults is not apparent because the more anterior haemal prezygapophyses arise at about the same position on the anterior parts of the haemal arches for all species. In specimens larger than 50 mm SL, the differences between the species can be gradually perceived with increased size.

In my collection not even the largest juvenile *T. alalunga* (91 mm SL) had its anterior haemal prezygapophyses on the centra; instead, they were close to the centra on the haemal arches as in *T. thynnus*. The largest juvenile *T. atlanticus* (87 mm SL) had the anterior haemal prezygapophyses well ventrad on the haemal arches. Consequently, large juveniles of *T. alalunga* and *T. thynnus* cannot be separated by the position of their anterior haemal prezygapophyses, but large juvenile *T. atlanticus* can be separated from *T. alalunga* and *T. thynnus* because the shift of the more anterior haemal prezygapophyses to ventrad is accomplished at a smaller size in *T. atlanticus* than the shift dorsad to the edge of the centra in *T. alalunga*. Lack of larger *Thunnus* spp. specimens prevents their separation by this character. I am certain that large juveniles (>100 mm SL) of the *Thunnus* spp. complex could be separated to the species on the basis of the position of the anterior haemal prezygapophyses since differences have been observed on adult *T. albacares* and *T. obesus* as mentioned above.

Ventrolateral Foramina
(Figures 3 to 6; Table 3)

The ventrolateral foramina are the last gross anatomical feature to develop on the vertebral column. They begin to form as projecting bony bridges from the anterior edges of the haemal postzygapophyses to the posterior edges of the haemal arches in specimens from 19 to 22 mm SL. On rare occasions 17-mm-SL fish may show beginning development of the structure. The very first developing ventrolateral foramen can be located beneath any vertebra from the 27th to 30th, but it is most often found beneath the 28th. During growth, new structures are added beneath the centra, anterior and posterior to the first foramen. All of the ventrolateral foramina are developed at about 25 mm SL, generally from the 22nd to the 36th vertebra. There is considerable overlap for all the species with some modal separation for specimens greater than 25 mm SL in the vertebral position of the first ventrolateral foramen. The ventrolateral foramina can be found posteriorly to the 36th vertebra on all 25- to 35-mm-SL specimens of all species. After 35 mm SL, some posterior openings are gradually filled in by ossification. Juvenile *T. thynnus* from 71 to 117 mm SL had the last ventrolateral foramen on the 32nd and 33rd vertebra, *T. alalunga* from 54 to 91 mm SL on the 31st, and *T. atlanticus* from 52 to 87 mm SL on the 29th or 30th. My largest *Thunnus* spp. specimen (47 mm SL) had the last ventrolateral foramen on the 34th vertebra. In adult *Thunnus* the last foramen is found on the 29th to 30th vertebra according to my own examination of seven skeletons of adults (400 to 700 mm SL). Gibbs and Collette (1967) found it on the 29th to 33rd vertebra.

All species of *Thunnus* have initially circular or nearly circular shaped openings, which gradually decrease in diameter posteriorly. Juveniles larger than 60 mm SL lose the circular shape on the anteriormost foramina, acquiring a more triangular or oval shape. Specific differences in the size and shape of the anterior openings are not distinct for juveniles as they are for adults (Gibbs and Collette, 1967).

First Haemal Spine
(Figure 7)

The first haemal spine is located on the haemal arch of the first caudal vertebra. It is a considerably elongated process. Anterior to this process, in close proximity, are the first two anal pterygiophores (Figures 3 to 6). The preceding haemal processes on the haemal arches of the precaudal vertebrae are shorter than the first haemal spine and also have at their tips flattened parapophyses for rib articulation. Yabe et al. (1958), Matsumoto (1963), and Yoshida (1965) reported on the flattening of the first haemal spine in *T. alalunga* and stated that this character may be unique to the species. I believe that this is true for the adults but not for the juveniles because in all *Thunnus* species the first haemal spine goes through a variety of flattened shapes during

its ontogeny. In addition, there is great individual variability in the shape of the first haemal spine within each species. Nevertheless, *T. alalunga* exhibits the greatest flattening of the first haemal spine during its ontogeny and *Thunnus* spp. the least. *Thunnus thynnus* and *T. atlanticus* generally show less flattening than *T. alalunga* but more than *Thunnus* spp.

In *T. alalunga* the first haemal spine begins to flatten a little at 21 mm SL. Flattening continues to increase to about 35 mm SL. From this size on changes in shape occur, but the degree of flattening remains essentially the same. *Thunnus atlanticus* does not show any flattening before 60 mm SL and *T. thynnus* not before 30 mm SL. *Thunnus* spp. showed slight flattening at 47 mm SL.

As the shape of the first haemal spine is a character of degree and cannot be accurately assessed, I suggest that only persons familiar with the Atlantic species of *Thunnus* juveniles in all sizes use this character.

TABLE 4.—Variability of spine and ray counts of the dorsal and anal fins in the various species for juveniles of *Thunnus*.

Species	Spines, first dorsal fin				Number of specimens	Variability from mode %
	13	14	15	16		
T. thynnus	1	144	1	1	147	2
T. alalunga	—	112	1	—	113	1
T. atlanticus	2	97	1	—	100	3
Thunnus spp.	—	37	—	—	37	0

Species	Rays, second dorsal fin and finlets			Number of specimens	Variability from mode %
	22	23	24		
T. thynnus	4	134	4	142	6
T. alalunga	—	104	4	108	4
T. atlanticus	4	89	1	94	5
Thunnus spp.	—	30	—	30	0

Species	Rays, anal fin and finlets					Number of specimens	Variability from mode %
	20	21	22	23	24		
T. thynnus	—	5	127	6	2	140	9
T. alalunga	—	2	101	5	—	108	6
T. atlanticus	1	85	6	—	—	92	8
Thunnus spp.	—	1	28	1	—	30	7

FINS AND FIN SUPPORTS

First Dorsal Fin
(Table 4)

All species develop the full complement of spines in the first dorsal fin before 8 mm SL. Fourteen spines were regularly counted in the first dorsal, even in the smallest specimens (8 mm SL). The count of 14 spines is remarkably constant for juveniles with a variability of 0% to 3% for the various species. This remarkably constant count of 14 can serve as a generic character to separate juveniles of the genus *Thunnus* from other scombrid genera in the Atlantic Ocean such as *Euthynnus* (15-16), *Katsuwonus* (15-16), and *Auxis* (10-12) (Potthoff and Richards, 1970); *Scomberomorus* (15-19) (W. J. Richards, pers. comm.)[3]; *Scomber* (9-13) (Matsui, 1967); *Acanthocybium* (24-26) (Rivas, 1951); *Sarda* (20-22); and *Orcynopsis* (13) (Collette and Chao, 1973).[4] There is conflict between the consistency of first dorsal fin counts in juveniles and greater variation of counts in adults (Frade, 1931; Rivas, 1951; Bullis and Mather, 1956; Gibbs and Collette, 1967). In some adults the posteriormost spines become embedded in the dorsal groove and surrounding tissue and are consequently overlooked.

The first dorsal fin can be easily separated from the second dorsal fin because the last spine of the first dorsal is always shorter than the first element in the second dorsal (Figures 3 to 6), and the spacing between spines of the first dorsal fin is greater than that between rays of the second dorsal. The space between the last spine of the first dorsal and the first element of the second dorsal is wider than the following spaces between the rays of the second dorsal. This difference in spacing is due to the shape, structure, and spacing of pterygiophores, which support the visible elements of the fins.

Second Dorsal Fin and Finlets
(Table 4)

Eight-mm SL larvae of all species have already acquired the full complement of rays in the second dorsal fin, but lack two or three of the posteriormost finlets. By 11 to 13 mm SL all finlets are developed. *Thunnus atlanticus* develops its second dorsal rays and finlets to a full complement at a slightly smaller size, usually by 10

[3]Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.

[4]Collette, B. B., and L. N. Chao. 1973. Systematics and anatomy of the bonitos (*Sarda* and their relatives). Unpublished manuscript.

to 12 mm SL. A total count of 23 rays was obtained most of the time for the second dorsal fin and finlets of all the species (Frade, 1931; Bullis and Mather, 1956; Gibbs and Collette, 1967). Although the variability was greater than that for the first spinous dorsal fin, it did not exceed 6% in the second dorsal fin. I included the dorsal finlet counts with ray counts of the second dorsal fin because in larvae and juveniles of *Thunnus*, and perhaps with all other scombrid genera, it is impossible to determine precisely the break between the last posterior second dorsal fin softray and the first anterior dorsal finlet even in cleared and stained specimens. Figures 3 to 6 show this gradual intergradation from softrays to finlets. The last ray of the second dorsal fin can be separated from the first finlet by their pterygiophore structure in specimens larger than 50 mm SL. Finlet pterygiophores have two clearly visible bony parts from a lateral view and second dorsal fin pterygiophores have only one clearly visible part. Figures 3 to 6 show specimens that have not yet developed the two clearly visible parts in their finlet pterygiophores.

Anal Fin and Finlets
(Tables 4, 13)

The anal fin develops similarly to the second dorsal fin. At 8 mm SL, all rays in the anal fin are present with three or four of the posteriormost finlets lacking. By 11 to 12 mm SL all finlets are developed. *Thunnus atlanticus* typically has 21 anal elements (rays plus finlets), and the remainder of the species have 22 (Frade, 1931; Bullis and Mather, 1956; Gibbs and Collette, 1967). Variability for this character ranges from 6% to 9%. The counts of the anal finlets were included in the anal ray counts for the same reasons given previously for the second soft dorsal fin.

Pectoral Fins
(Table 5)

Development of rays in the pectoral finfold had already started in my smallest (8 mm SL) specimens. The increase in number of pectoral rays and their sequence of development was similar for all the species. Wide ranges in number of pectoral fin rays were common for equal size groups. These wide ranges narrow in the 25 to 29 mm SL size groups where adult counts of more than 30 rays are attained (Frade, 1931; Bullis and Mather, 1956; Gibbs and Collette, 1967). The rays in the pectoral fins were counted on both sides for each specimen. The side that yielded the highest value was taken for tabulation. In 34% of all specimens counted there was no difference in counts between the two pectoral fins; in 47% of the specimens, a difference of one ray was noted; 11% of the specimens had a difference of two rays; 6% had a three ray difference; and 2% differed by four rays. Only one specimen differed by five rays. At 8 mm SL, 8 to 12 rays were developed on the dorsal side of the finfold. Development of rays proceeded progressively ventrad until the finfold was completely occupied with rays. At 20 mm SL, very few juveniles have the adult count of more than 30 rays. At 23 mm SL, about one-half of the specimens have adult counts, and at 27 mm SL all have adult counts. Adults and all juveniles >27 mm SL have more than 30 pectoral fin rays, usually 31 to 34, sometimes 35, rarely 36 or 37. My data are corroborated by Schaefer and Marr (1948) and Mead (1951).

Pelvic Fins

All the fin elements of the pelvic fins were visible in my smallest (8 mm SL) specimens of *Thunnus*. A count of six fin elements was obtained for each fin throughout the size range sampled. I could not be certain if the first element was a spine but all have I,5 as adults.

TABLE 5.—Range of variation in pectoral fin ray counts for selected sizes in juveniles of *Thunnus* of all the species combined.

Size mm SL	Range of variation, number of pectoral fin rays	Most frequent number of pectoral fin rays
8	8-12	—
9	10-19	10,14
10	9-24	—
11	13-23	18
12	16-20	17
13	15-24	18,19,21
14	18-25	23
19	26-31	27,28
20	26-32	27,29
21	28-31	29,30
22	28-31	29,30
23	28-33	29,31,32
24	29-35	31
25	29-34	31,32
26	29-33	32
27	31-34	31,32
28	32-33	32

Caudal Fin
(Table 6)

At 8 mm SL, a total of 27 to 31 rays is developed on the caudal fin. If the total was an even number then an equal number of rays was found dorsad and ventrad to the midline. If it was an uneven number then the dorsal side of the caudal fin always carried one more ray. As the larvae grow, additional procurrent rays are added equally on the caudal fin to the dorsal and ventral side. The last rays to develop are the anteriormost. There is a difference in caudal ray development between *T. thynnus* and the other species. *Thunnus thynnus* usually has fewer caudal rays than the other species at all sizes, particularly from 14 to 22 mm SL. At 17 mm SL, few *T. thynnus* have the maximum caudal counts of more than 48 rays. At 23 mm SL, about one-half of the *T. thynnus* specimens had maximum counts and only after about 35 mm SL did all but two specimens have maximum caudal counts. Collectively, the remaining species differ from *T. thynnus* in that, at 15 mm SL, a few specimens had already acquired the maximum complement of caudal rays. At 18 mm SL, one-half of the specimens had maximum counts, and all but one specimen had the maximum counts at 24 mm SL. I noted three exceptions to the above statements: one 34-mm-SL *T. atlanticus* had 48 rays and two *T. thynnus* had 47 and 44 rays at 40 and 50 mm SL, respectively. From my data I believe that all *Thunnus* juveniles >24 mm SL have a maximum of more than 48 caudal rays, usually 49 to 51, rarely 52. I also believe the maximum juvenile counts represent the adult complement of caudal rays, although I did not examine any adult fish. Frade (1931) found 46 caudal rays as the most frequent number for adult *T. thynnus*. The difference is likely due to difficulty in counting the anteriormost rays on adults. For this study, I did not attempt a detailed examination of the principal caudal rays or of the hypural complex. A study of the ontogeny of the caudal skeleton in *T. atlanticus* will be published in the future.

Dorsal and Anal Fin Supports
(Figures 8 to 10; Tables 7, 13)

The spines, rays, and finlets of the dorsal and anal fins are supported within the body by pterygiophores. The pterygiophores are made up of two or three bony parts referred to as radials. Spines and rays have a proximal and a distal radial; finlets have an additional middle radial. The distal radials of the posterior rays of the second dorsal fin and finlets and of the anal fin and finlets cannot be seen from a lateral view because they are hidden by the bifurcate bases of

TABLE 6.—Range of variation in total caudal fin ray counts for selected sizes and species groups of juveniles of *Thunnus*.

	Range of variation, number of total caudal fin rays		Most frequent number of total caudal fin rays	
Size mm SL	*T. alalunga, T. atlanticus, Thunnus* spp.	*T. thynnus*	*T. alalunga, T. atlanticus, Thunnus* spp.	*T. thynnus*
8	27-31	—	—	—
9	32-40	—	33,37	—
10	34-43	—	—	—
11	39-46	—	—	—
12	41-43	—	—	—
13	42-45	—	45	—
14	45-47	41	45	—
15	44-49	43	47	—
16	45-49	46-47	46,47,48	47
17	46-49	45-49	47,48,49	47
18	47-50	47	48,49	47
19	48-51	46-49	49	47
20	47-51	47-48	49	47
21	47-51	47-49	49,50	47,48
22	49-51	47-49	49	47
23	47-51	48-50	50	49
24	48-51	47-49	50,51	49
25	49-51	47-50	51	49
26	50-52	49-51	50	50
27	48-50	48-49	50	49

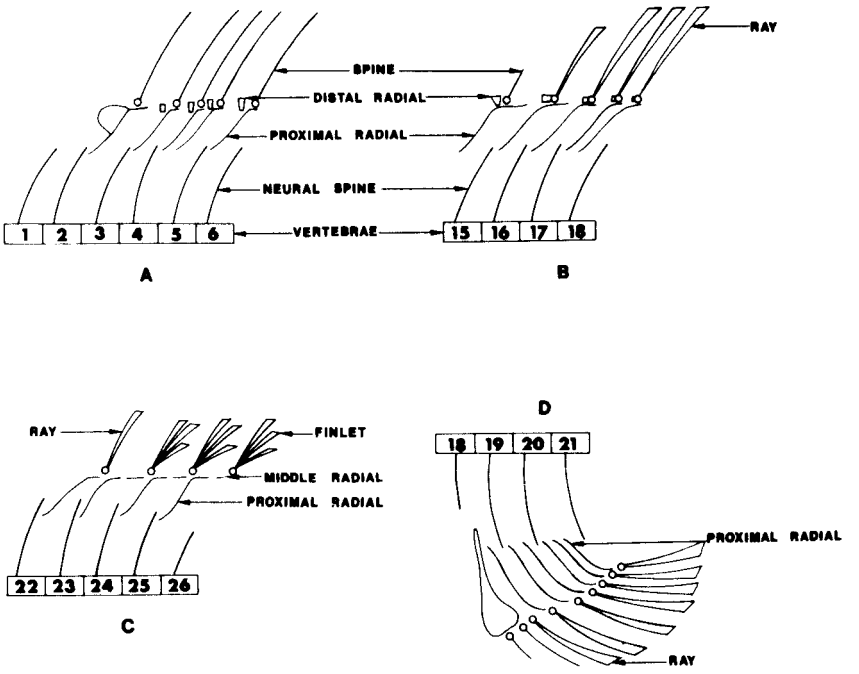

FIGURE 8.—Schematic representation of the relationship between vertebrae, pterygiophores, and fin elements in juveniles of *Thunnus* (lateral view). A. Anterior portion of first dorsal fin, pterygiophores, and vertebrae; B. Last spine of first dorsal fin, anterior portion of second dorsal fin, pterygiophores, and vertebrae; C. Last ray of second dorsal fin, anterior finlets, pterygiophores, and vertebrae; D. Anterior portion of anal fin, pterygiophores, and vertebrae.

the fin elements. Generally, all species of *Thunnus* have 37 dorsal fin elements (XIV-15-8) but only 36 pterygiophores; the first pterygiophore supports the first two spines. In actuality, the first pterygiophore is serially associated with the second spine but has captured and fused to it the distal radial of the first spine (Figure 8A). The proximal radial of the first spine has been lost. The first spine is therefore only secondarily associated with the first pterygiophore. Posteriorly, each fin element is serially associated with a pterygiophore, but each fin element also rests atop the adjacent posterior pterygiophore in a secondary association (Figure 8). Thus, two pterygiophore fin element associations exist. The serial association is most often overlooked. The last fin element (finlet) in the dorsal fin assembly is serially associated with its pterygiophore. It also rests in a secondary association on a very small bone, which I assume to be a reduced proximal radial of a lost finlet without its serial middle and distal radials. The distal radials of the spinous dorsal that, to me, resemble the horns of a moose (Kramer (1960) uses the term "alate"), form in part and rigidly support the dorsal groove and become smaller in size in a posterior direction. The distal radials are still present in the second dorsal fin, although their semblance to moose horns has disappeared ("non-alate"). They decrease in size posteriorly (Figure 8B) until they disappear from the lateral view at about the 9th ray. Dissection of posterior fin rays and finlets revealed the presence of the distal elements between the bifurcate bases of the rays or finlets (Figure 9B, C). Spines, on the other hand, do not have bifurcate bases (Figure 9A). Instead, the distal radials are located anterior to the base of the spine.

The anal fin and finlet pterygiophores are structurally similar to the pterygiophores of the second dorsal fin and finlets with one exception: The first anal pterygiophore in *Thunnus* is derived from two cartilaginous parts which fuse at about 8 mm SL. It has two anal fin elements in serial association and one in secondary (Figure 8D). Thus, all Atlantic species of *Thunnus*,

except *T. atlanticus*, have 22 anal fin elements (15-7) but only 20 pterygiophores. *Thunnus atlanticus* has 21 fin elements (14-7) but only 19 pterygiophores. As in the second dorsal fin, all the anal fin rays and finlets have a bifurcate base that contains a small distal radial (Figure 9B, C). The last anal finlet, as well as the last dorsal finlet, is serially associated with a pterygiophore but has a secondary association with a small bone that I assume to be a greatly reduced proximal radial of a lost finlet.

Pterygiophore development is more or less synchronous with fin spine and ray development. My smallest 8-mm-SL *Thunnus* specimens lacked about two to four posteriormost pterygiophores dorsally and ventrally (see earlier fin sections). At 13 mm SL, all specimens had acquired a full count of pterygiophores. *Thunnus atlanticus* has a full count at the slightly smaller size of 11 to 12 mm SL. In the very small sizes of 8 to 11 mm SL, the pterygiophores cannot be differentiated into proximal, middle, and distal radials. At about 11 mm SL, differentiation first begins under the anteriormost section of the first dorsal fin. A few of the distal radials begin to separate from the main mass of the pterygiophores in tiny nonalate blocks. The separation and development sequence is in a posterior direction. At 20 to 35 mm SL, all the distal radials are separated under the first dorsal fin, are well ossified, and gradually assume an alate shape.

The middle radials under the finlets (usually eight dorsal and seven ventral) begin to separate and ossify over a great size range. Some specimens showed no separation at 30 mm SL, whereas others showed some separation and ossification as small as 22 mm SL. The middle radials of the finlet pterygiophores separate and develop in an anterior direction. First to develop are the posterior middle radials of the last finlets. Most specimens had all their ventral middle radials developed by 40 mm SL, but a few still lacked the first (e.g., anteriormost) dorsal middle radial. By 60 mm SL, all specimens had their eight dorsal middle radials developed.

In juvenile *Thunnus* it is difficult to determine, externally, the exact number of finlets because of the gradual intergradation from fin ray to finlet. A finlet can now be precisely defined as having a middle radial serially associated with it. I think that at 50 mm SL one can, with some certainty, count middle radials to determine finlet number. Caution is warranted, however, because a few specimens may still lack the first (e.g., anteriormost) dorsal middle radial. Table 7 has been compiled from my specimens above 40 mm SL. There was not enough material available in the larger sizes to assess variability and specific differences in the number of middle finlet radials. The most common combination of middle dorsal and ventral radials is 8/7. Variability from this combination seems to be low in *T. atlanticus* and *T. alalunga* and high in *T. thynnus*.

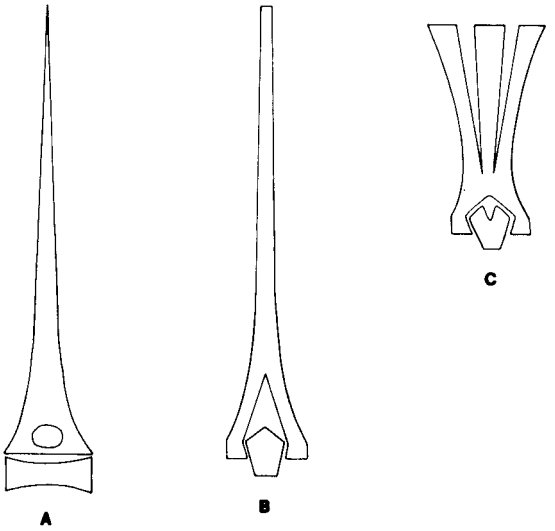

FIGURE 9.—Schematic representation of the relationship between fin elements and distal radials (anterior view) in juveniles of *Thunnus*. A. First dorsal fin spine and distal radial near base; B. Second dorsal fin ray and distal radial within bifurcate base; C. Finlet and distal radial within bifurcate base.

Most of the interneural and interhaemal spaces bounded by the neural and haemal spines are occupied by one or more pterygiophores in *Thunnus* (Figures 3 to 6). The association of pterygiophores with the interneural and interhaemal spaces is limited to smaller juveniles. By 100 mm SL, the anteriormost pterygiophores under the first dorsal fin are already situated above the neural spines and do not insert into any interneural spaces. As the juveniles grow, more pterygiophores lose their association with their respective interneural spaces. I did not examine specimens larger than 117 mm SL and cannot say if all pterygiophores, dorsally and ventrally, pull away by the time the fish become adults. For the identification of juveniles, however, the serially associated pterygiophores of the second dorsal fin can be used successfully in

TABLE 7.—Number of dorsal and ventral middle radials of the finlets in three species of juveniles of *Thunnus* (41-117 mm SL).

Species	Middle radials					
	Dorsal / Ventral	7/7	8/7	9/7	8/8	9/8	*n*
T. atlanticus		1	14	—	1	—	16
T. alalunga		2	5	—	—	—	7
T. thynnus		—	9	2	6	2	19

separating *T. thynnus* from *T. alalunga* and *T. alalunga* from the *Thunnus* spp. complex. All of my *T. alalunga* specimens (n = 116) had their first three second dorsal interneural spaces occupied with only one pterygiophore (Figure 10, Table 13). The following five spaces were filled with two and one with three pterygiophores, and the last posteriormost second dorsal interneural space again had only one pterygiophore. This pattern of pterygiophore insertions under the second dorsal fin is most characteristic of *T. alalunga*, but may occur in the other species to a lesser degree. Figure 10 and Table 13 also show the percentages of occurrence for the second dorsal pterygiophore insertion sequences which are most characteristic for that species. Ninety-five percent of my 148 *T. thynnus* specimens had their first two second dorsal interneural spaces occupied with only one pterygiophore. The following five spaces were filled with two and one with three pterygiophores, and the last two posteriormost second dorsal interneural spaces had only one pterygiophore. The remaining 5% of my *T. thynnus* specimens had the identical *T. alalunga* second dorsal pterygiophore insertion sequence. Ninety-eight percent of my 41 *Thunnus* spp. specimens resembled *T. thynnus* and 2% *T. alalunga*. *Thunnus atlanticus* was the most variable in the second dorsal pterygiophore insertion sequence; 46% of my 92 specimens resembled *T. alalunga*, 19% resembled *T. thynnus*, and 35% had six interneural spaces occupied with two pterygiophores but did not have a space with three pterygiophores (Table 13).

Counting from anterior, the first 12 occupied interneural spaces associate in *Thunnus* with the first dorsal fin. The diagnostic second dorsal interneural spaces are the 13th through the 21st. Following, in the 22nd to 30th spaces are the finlet pterygiophores (Figure 10). The interneural spaces occupied by three or zero pterygiophores for the second dorsal fin and finlets are depicted in Figure 10 on the basis of where they most often occurred, but they could vary as much as two spaces in an anterior or posterior direction. The percentages in Figure 10 refer only to the arrangement under the second dorsal fin.

The distribution of pterygiophores under the anal fin (Figure 10, Table 13) present too much variability to be useful for species separation, except perhaps in *Thunnus* spp. and *T. atlanticus*. The first five anteriormost interhaemal spaces are occupied by two or three pterygiophores in *T. thynnus* and *T. alalunga*. The 6th and 7th spaces, which complete the anal fin association, always have only one pterygiophore. The anal finlet pterygiophores insert into the 8th to 14th spaces, one to a space. The last or 14th interhaemal space that is occupied by the last or

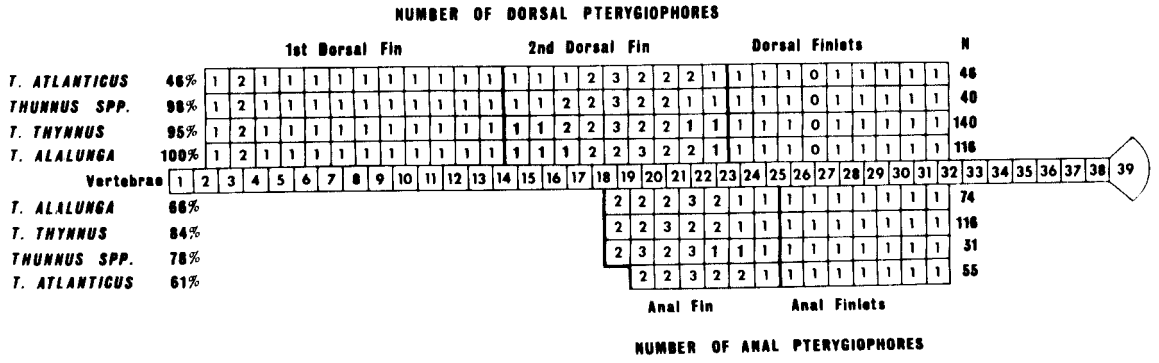

FIGURE 10.—Representative arrangement of pterygiophores in relation to the fins and vertebrae for the juvenile *Thunnus* species. Percentages and number of specimens (N) are for the occurrence of the commonest arrangement under the second dorsal fin only; other arrangements given in Table 12. Modified after Matsui (1967).

posteriormost pterygiophore is directly opposite the last or 30th interneural space that is occupied by the pterygiophore of the last dorsal finlet. *Thunnus* spp. and *T. atlanticus* deviate from this pattern. In 78% of my 40 *Thunnus* spp. specimens, only the first four interhaemal spaces were occupied by more than one pterygiophore, the 5th through 7th spaces had only one. *Thunnus atlanticus* differed by having only six interhaemal spaces available for the anal fin. Thus, 61% of a total of 89 fish had their first five spaces occupied with more than one pterygiophore and the 6th space with one.

BONES AND RAKERS OF THE FIRST GILL ARCH
(Figures 11, 12)

In *Thunnus* the gillrakers develop within the epithelium that overlies the three bones of the first gill arch and their connective cartilage. In its first stage of development, the raker can be observed on cleared and stained preparations, under 100× power, as a tiny speck of weakly stained material within the translucent epithelium. As the speck grows it gradually assumes the triangular shape of a raker. The tip of the raker will finally break through the epithelium, and its broad base remain anchored in the tissue close to the bone. Ankylosed rakers were not observed on the bones of the first gill arch, even in the larger specimens. As the epithelium is opaque in preserved specimens, gillraker counts for smaller juveniles should be made only on cleared and stained material for accuracy. Mead (1951) noted that no gillrakers could be seen in fish smaller than 15 mm. I believe that he referred to untreated specimens, because in my collection all species of *Thunnus* had six or seven rakers at their smallest size (8 mm SL).

The ceratobranchial bone of all species has six to seven rakers at 8 mm SL. Development and acquisition of rakers over the ceratobranchial proceeds distally from the angle towards the hypobranchial bone. The raker in the angle is always included in the ceratobranchial count. It develops at about 8 mm SL.

At 14 mm SL some specimens of all the species develop a raker on the epibranchial bone next to the angle. One exception was noted: an 11-mm-SL *T. atlanticus* with one raker on the epibranchial. Additional rakers over the epibranchial bone develop distally from the angle.

The last bone of the gill arch to acquire rakers is the hypobranchial. The size of the juveniles when this occurs depends on the size at which the ceratobranchial becomes entirely occupied with rakers. In the hypobranchial count I have included the rakers (usually one, sometimes two) found over the cerato-hypobranchial cartilage.

The first rakers to appear are usually located over the cartilage but are considered hypobranchial rakers. Occasionally rakers appear over the hypobranchial bone leaving the cartilage empty. *Thunnus atlanticus* has the lowest adult gillraker counts and completes its entire ceratobranchial complement at the smallest size (9-15

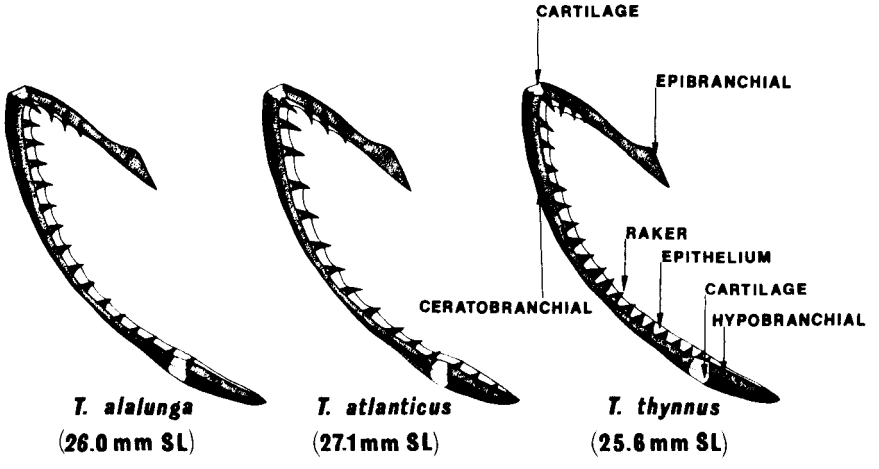

FIGURE 11.—First right gill arches of juveniles of three *Thunnus* species.

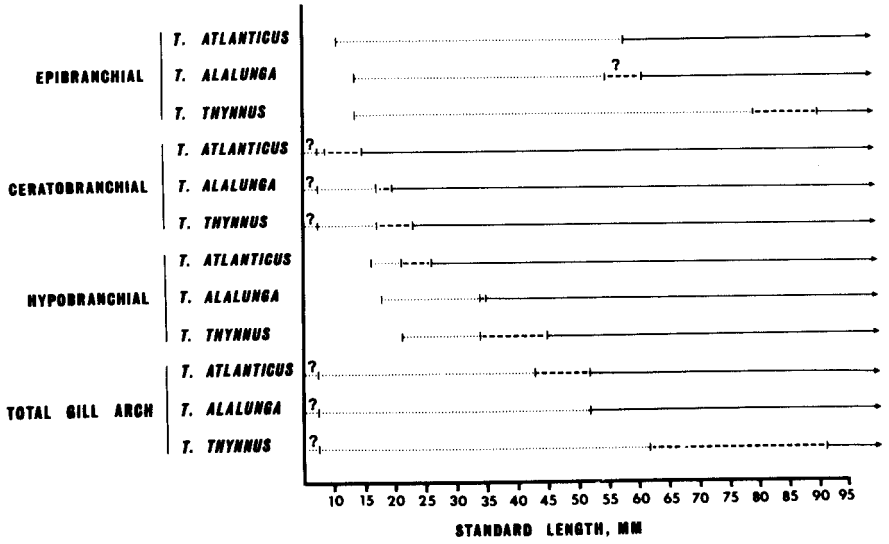

FIGURE 12.—Representative scheme of gillraker development with increase in size over the three bones of the first gill arch for juveniles of three *Thunnus* species. Dotted line: developmental stage, one or more rakers present; dashed line: adult gillraker complement present in some specimens; solid line: adult gillraker complement present in all specimens; question mark: assumed, no data available.

mm SL) of the Atlantic species. Therefore, some juvenile *T. atlanticus* have their first raker over the hypobranchial at 16 mm SL, and all have at least one raker over the hypobranchial at 20 mm SL. Some *T. alalunga* and *Thunnus* spp. juveniles have their first raker over the hypobranchial at 18 mm SL, and all have at least one raker over the hypobranchial at 22 mm SL. *Thunnus thynnus* has the highest adult gillraker counts and adds its first rakers to the hypobranchial at the largest size of all the species; they begin to appear on some of the 21-mm-SL specimens from the western Atlantic and on some of the 23-mm-SL specimens from the Mediterranean. Not until 28 mm SL do all *T. thynnus* have at least one raker over the hypobranchial.

Summarizing the data from Tables 8 to 11, one can conclude that:

1. The species differ in size at which they attain the maximum gill raker counts on each bone of the first gill arch.
2. Each species differs from the others in maximum number of rakers that it can have on some or all of the three bones of the first gill arch.
3. All species of *Thunnus* first attain the maximum complement of rakers over the ceratobranchial bone.
4. The range of the maximum number of rakers over the ceratobranchial bone shows the greatest interspecific difference.

Thunnus atlanticus (Table 8; Figures 11, 12). The maximum gillraker count over the epibranchial bone of 7 to 9 rakers was first present in specimens of 58 mm SL. The diagnostic maximum count of 11 to 13 rakers over the ceratobranchial bone was first present in a 9-mm-SL specimen, but it was not until 15 mm SL that all specimens had the diagnostic count. Maximum counts over the hypobranchial bone (including the cerato-hypobranchial cartilage) of 4 to 6 rakers were first observed on 21-mm-SL specimens, but not before 26 mm SL did all juveniles attain the maximum count. The maximum total count for the first gill arch of 23 to 27 rakers was first observed in a 43-mm-SL specimen and all specimens larger than 52 mm SL had maximum total counts. The maximum total count is attained in some specimens at a smaller size than the maximum epibranchial count. This discrepancy is explained by the range in number of rakers over the ceratobranchial and hypobranchial bone. Gibbs and Collette (1967) give 19 to 25 rakers as the total number over the first arch for *T. atlanticus*. Because all specimens larger than 34 mm SL had more than 20 gillrakers, I believe that

TABLE 8.—Distribution of gillrakers over the branchial bones of the first gill arch for various size groups in *Thunnus atlanticus* juveniles. $n = 104$.

(Total gillraker counts for western Atlantic adults from Gibbs and Collette, 1967, Table 2*.)

N	SL (mm)	Epibranchial										Ceratobranchial								Hypobranchial						
		0	1	2	3	4	5	6	7	8	9	6	7	8	9	10	11	12	13	0	1	2	3	4	5	6
7	5-9	7										1	—	4	1	—	—	1		7						
14	10-14	12	2											3	1	2	5	3		14						
19	15-19		8	8	3												4	15		4	6	7	2			
23	20-24			6	16	1											2	20	1			6	9	8		
10	25-29			1	7	2											2	8					1	8	1	
12	30-34				3	8	1										1	10	1					8	4	
1	35-39						1											1						1		
6	40-44				2	2	1	1										6					1	—	5	
2	50-54							2										2							2	
2	55-59									2							1	—	1						1	1
2	60-64									2								1	1						1	1
2	65-69								1	—	1							2						1	—	1
1	70-74								1								1								1	
1	80-84									1								1							1	
2	85-89									2							1	1						1	1	

N	SL (mm)	Total gillraker count																						
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
7	5-9	1	—	4	1	—	—	1															
14	10-14			3	1	2	5	1	2														
19	15-19								3	7	1	6	—	2									
23	20-24											3	5	9	5	1							
10	25-29													4	4	1	1						
12	30-34														4	3	4	1					
1	35-39																1						
6	40-44																2	3	—	1			
2	50-54																		2				
2	55-59																				1	1	
2	60-64																				1	—	1
2	65-69																		1	—	—	—	1
1	70-74																		1				
1	80-84																				1		
2	85-89																			2			
*120	>300														1	7	29	59	21	2	1		

T. atlanticus may actually not fully develop or may lose some rakers during its later life. Potthoff and Richards (1970) already mentioned this possibility.

Thunnus alalunga (Table 9; Figures 11, 12). The maximum gillraker count over the epibranchial bone of 7 to 8 rakers was first obtained in a 61-mm-SL specimen. Most likely, however, maximum counts over the epibranchial would first show in the 55- to 59-mm-SL size range, but the lack of specimens for those sizes precludes a definite statement. Bullis and Mather (1956) counted 7 to 9 rakers on four adult specimens. The diagnostic maximum count of 14 to 16 rakers over the ceratobranchial bone was first present in a few 17-mm-SL specimens. At 20 mm SL, all specimens had the diagnostic maximum count. This count overlaps with the *Thunnus* spp. complex. Maximum counts over the hypobranchial bone (including the ceratohypobranchial cartilage) of 5 to 6 rakers were first observed on a 34-mm-SL specimen; all specimens larger than 35 mm SL had the maximum count. The maximum total count for the first gill arch of 27 to 29 rakers is attained at 53 mm SL. Gibbs and Collette (1967) give 25 to 31 rakers as the total number over the first gill arch for adult *T. alalunga* from the western Atlantic. Our difference is due to my smaller sample size and population variance.

Thunnus thynnus (Table 10; Figures 11, 12). The maximum total gillraker count over the epibranchial bone of 12 to 13 rakers was first present in one 79-mm-SL specimen. Because I lack data in the larger size ranges, I can only estimate that all *T. thynnus* have a full epibranchial after they have reached 90 mm SL. The diagnostic maximum counts of 17 to 20

rakers over the ceratobranchial bone were first observed in 17-mm-SL specimens from the western Atlantic. It was not until 23 mm SL that all specimens, including the Mediterranean samples, had the diagnostic maximum count. Maximum counts over the hypobranchial bone (including the hypo-ceratobranchial cartilage) of 7 to 9 rakers were first observed on a 34-mm-SL specimen from the western Atlantic, but not before 45 mm SL did all juveniles, including the Mediterranean samples, attain the maximum count. One exception was noted at 71 mm SL with 6 hypobranchial rakers. The maximum total count for the first gill arch of 36 to 41 rakers was first observed in a 62-mm-SL specimen; all juveniles in the 90- to 94-mm-SL size range will probably have the maximum total count. As in *T. atlanticus*, the maximum total gill arch count is reached in some *T. thynnus* specimens at a smaller size than the maximum epibranchial count. This discrepancy is again explained by the range in number of rakers over the ceratobranchial and hypobranchial bone. Gibbs and Collette (1967) give 34 to 43 rakers as the total number over the first arch for the western Atlantic *T. thynnus thynnus*. Our difference is due to my smaller sample size and population variance.

Thunnus spp. (Table 11). Juvenile *T. albacares* and *T. obesus* could not be separated and were grouped together under *Thunnus* spp. Lack of enough specimens in a proper size range prevented me from making observations on gillraker ontogeny. There is considerable overlap between the *Thunnus* spp. complex and *T. alalunga* in number of rakers and their development over the three bones of the first arch. The maximum counts of 14 to 16 rakers over the ceratobranchial bone are identical for *Thunnus* spp. and *T. alalunga*. At 15 mm SL, one *Thunnus* spp. specimen had the maximum ceratobranchial count and at 20 mm SL all

TABLE 9.—Distribution of gillrakers over the branchial bones of the first gill arch for various size groups in *Thunnus alalunga* juveniles. n = 118.

(Total gillraker counts for western Atlantic adults from Gibbs and Collette, 1967, Table 2*.)

		Epibranchial									Ceratobranchial											Hypobranchial						
N	SL (mm)	0	1	2	3	4	5	6	7	8	6	7	8	9	10	11	12	13	14	15	16	0	1	2	3	4	5	6
3	5-9	3									1	—	—	1	—	1						3						
13	10-14	10	3								2	—	—	—	5	2	3	1				13						
50	15-19	5	28	11	6												13	8	11	17	1	38	11	1				
25	20-24		1	6	18														8	16	1	2	9	6	7	1		
11	25-29			1	6	4													2	8	1		2	5	3	1		
4	30-34				2	2													2	2					1	2	1	
5	35-39					1	4												1	3	1						5	
1	40-44						1														1						1	
1	45-49							1											1									1
2	50-54							2												2								
1	60-64								1											1							1	
1	80-84									1										1								1
1	90-94									1										1								

		Total gillraker count																										
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
3	5-9	1	—	—	1	—	1																				
13	10-14				2	5	2	2	2																		
50	15-19							2	12	7	4	11	4	8	1	1											
25	20-24											1	2	5	5	8	3	1									
11	25-29													1	2	4	1	2	1								
4	30-34															1	—	2	—	1							
5	35-39																			2	2	1					
1	40-44																					1					
1	45-49																					1					
2	50-54																						2				
1	60-64																						1				
1	80-84																								1		
1	90-94																								1		
*55	>700																				1	1	10	20	15	6	2

TABLE 10.—Distribution of gillrakers over the branchial bones of the first gill arch for various size groups in *Thunnus thynnus* juveniles. $n=152$.

(Total gillraker counts for western Atlantic adults from Gibbs and Collette, 1967, Table 2*.)

		Epibranchial													
N	SL (mm)	0	1	2	3	4	5	6	7	8	9	10	11	12	13
1	5-9	1													
2	10-14	1	1												
38	15-19	5	30	3											
39	20-24	2	12	18	6	1									
22	25-29			3	15	2	1	1							
20	30-34			1	4	8	4	3							
5	35-39					2	1	1	1						
5	40-44						1	2	1	1					
3	45-49							1	—	2					
2	50-54								1	1					
3	60-64									1	1	1			
1	65-69											1			
3	70-74										2	—	1		
2	75-79											1	—	1	
2	85-89											1	—	1	
1	95-99													1	
1	105-109														1
1	110-114														1
1	115-119														1

		Ceratobranchial									
N	SL (mm)	7	12	13	14	15	16	17	18	19	20
1	5-9	1									
2	10-14		1	—	1						
38	15-19		1	4	10	13	6	3	1		
39	20-24					1	12	15	9	2	
22	25-29							4	18		
20	30-34							5	13	2	
5	35-39							2	1	2	
5	40-44								4	1	
3	45-49								2	1	
2	50-54								1	—	1
3	60-64							2	1		
1	65-69									1	
3	70-74								2	1	
2	75-79							1	1		
2	85-89								1	1	
1	95-99								1		
1	105-109										1
1	110-114								1		
1	115-119								1		

		Hypobranchial									
N	SL (mm)	0	1	2	3	4	5	6	7	8	9
1	5-9	1									
2	10-14	2									
38	15-19	38									
39	20-24	25	8	3	2	1					
22	25-29	2	8	6	2	4					
20	30-34		1	3	7	2	3	3	1		
5	35-39				1	—	1	—	3		
5	40-44						1	3	1		
3	45-49								3		
2	50-54								2		
3	60-64								2	1	
1	65-69								1		
3	70-74							1	—	1	1
2	75-79								1	1	
2	85-89								1	1	
1	95-99								1		
1	105-109									1	
1	110-114									1	
1	115-119									1	

		Total gillraker count																															
N	SL (mm)	7	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
1	5-9	1																																
2	10-14		1	—	—	1																												
38	15-19		1	3	2	9	14	4	3	1	1																							
39	20-24						1	7	9	7	2	6	4	1	1	—	1																	
22	25-29										2	1	8	5	2	2	—	2																
20	30-34												1	3	2	5	2	2	1	2	1	1												
5	35-39															1	1	—	—	1	—	—	1	1										
5	40-44																		1	—	1	1	2											
3	45-49																					1	—	1	1									
2	50-54																							1	1									
3	60-64																						1	1	—	—	1							
1	65-69																										1							
3	70-74																								1	1	—	—	1					
2	75-79																								1	—	—	—	1					
2	85-89																									1	—	—	—	1				
1	95-99																											1						
1	105-109																															1		
1	110-114																													1				
1	115-119																													1				
*288	>300																								3	2	12	32	63	102	40	29	4	1

specimens had it. Therefore, the juveniles of the *Thunnus* spp. complex can only be separated from *T. alalunga* by the vertebral position of the first haemal arch, by the shape of the first haemal spine, by the vertebral position of the first ventral postzygapophysis, and by the pterygiophore pattern of the second dorsal and, perhaps, anal fins. However, caution should be used in applying any separating character because of variability. Percentages for variabilities can be found in the respective tables.

LATERAL LINE SCALES
(Figure 13, Table 12)

All species develop the first lateral line scale at 16 to 18 mm SL. The scale originates near the dorso-posterior edge of the pectoral girdle. It is rectangular in shape, with strong ossifications on the dorsal and ventral sides. These strong ossifications develop into two plates that project vertically to the base of the scale. As growth proceeds, more scales are added posteriorly, forming a distinct broken line, which at first slopes ventrad then dorsad and levels off in a posterior direction. At about 60 mm SL, lateral line scales cannot be counted because the scales fuse to form a continuous line. Fusion of the scales occurs first on the anterior portion of the lateral line and proceeds posteriorly.

Sella (1924) and Watson and Mather (1961) noted specific differences in the shape of the lateral line. I have examined this character in detail and found that *T. thynnus* can be separated from all the other *Thunnus* species. Eighty-one *T. thynnus* from a total of 159 were undamaged and large enough to show the lateral line contour. In all 81 specimens the first three scales formed a posteriorly descending straight line, whereas the following scales formed a posteriorly ascending line at an angle approximately 90° to the first line. At the 8th or 9th scale the line curved in a posterior direction, parallel to the body axis. At 19 mm SL, some *T. thynnus* can be separated on the basis of the lateral line contour because at this size some have acquired four scales. The 4th scale in *T. thynnus* is always aligned at a 90° angle to the preceding three. At 22 mm SL, all *T. thynnus* have acquired four or more scales and are therefore totally separable from the other species.

In the remaining species a descent and ascent in the lateral line is also present, but it forms a smooth curve instead of a right angle. In all specimens (29 *T. alalunga*, 46 *T. atlanticus*, and 14 *Thunnus* spp.) the last scale to descend

TABLE 11.—Distribution of gillrakers over the branchial bones of the first gill arch for various size groups in *Thunnus* spp. juveniles. n = 40.
(Total gillraker counts for western Atlantic adults from Gibbs and Collette, 1967, Table 2*.)

		Epibranchial								Ceratobranchial											Hypobranchial							
N	SL (mm)	0	1	2	3	4	5	6	7	6	7	8	9	10	11	12	13	14	15	16	0	1	2	3	4	5	6	7
6	5-9	6								1	—	4	—	1							6							
6	10-14	3	3											1	2	—	2	1			6							
12	15-19		9	3													2	5	5		8	3	1					
8	20-24			3	4	1												3	5		1	3	1	3				
2	25-29					2													2						1	—	1	
4	30-34					1	2	1											4						1	2	1	
1	35-39								1										1								1	
1	45-49						1													1								1

		Total gillraker count																												
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
6	5-9	1	—	4	—	1																							
6	10-14					1	2	—	—	2	1																		
12	15-19									2	3	4	1	1	1														
8	20-24											1	—	1	3	1	1	1											
2	25-29																		1	—	1								
4	30-34																		1	—	2	—	1						
1	35-39																							1					
1	45-49																							1					
*127	>600 *T. albacares*																						6	11	33	37	30	9	1
*55	>600 *T. obesus*																				5	13	15	17	4				

TABLE 12.—Number of lateral line scales for selected sizes of juveniles of *Thunnus*.

SL (mm)	*Thunnus alalunga*														*Thunnus thynnus*													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	0	1	2	3	4	5	6	7	8	9	10	11	12	13
16		2																										
17	4														2	2	3											
18	2	1	1	1												1	1	1										
19		2													2	—	—	5	3	1								
20			1	4	—	—	—	2										2	5	1	1							
21					2													1	1	4	1							
22								2	1	2	—	1							1	—	3	—	1					
23										1	1										4	—	—	1	—	1	—	1

SL (mm)	*Thunnus atlanticus*														*Thunnus* spp.													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	0	1	2	3	4	5	6	7	8	9	10	11	12	13
16															1	1												
17															1	—	2											
18			1	1											1	1	1											
19			1	1	1															2								
20				1	1	—	1													1	1	1						
21					1	—	—	—	—	1	1	1													1			
22									1	—	1	—	—	1														
23												1	1	4														

posteriorly is the 4th or 5th, never the 3rd as in *T. thynnus*. If the lines of the curve that show descent and ascent were to subtend an angle, it would be larger than 90°. Some specimens of these species have also acquired four or more scales by 19 mm SL. They can be distinguished from *T. thynnus* by their 4th scale that stays in line on a descent with the 3rd. At 21 mm SL, all specimens have four or more scales. Slight differences in the curvature of the lateral line were noted between *T. alalunga*, *T. atlanticus*, and *Thunnus* spp., but these differences were not distinct enough for separating the species.

IDENTIFICATION
(Table 13)

The generic external characters of transforming and juvenile *Thunnus* have been adequately documented by a number of workers as pointed out in the introduction. Richards and Potthoff (in press) concluded that if accurate identifications to species are necessary, the only choice is to use osteological characters, even though this involves the time-consuming task of clearing and staining.

Only three characters are available to separate the species from 8 to 14 mm SL: the number of precaudal and caudal vertebrae, vertebral position of the first closed haemal arch, and the pterygiophore pattern under the second dorsal fin. Assuming a specimen is not a variant in any of the three characters, it can be identified as follows:

Character	*Species separated*
Number precaudal + caudal vertebrae	*T. atlanticus* from *T. thynnus*, *T. alalunga*, *Thunnus* spp.
First closed haemal arch	*T. atlanticus* + *Thunnus* spp. from *T. thynnus* + *T. alalunga*
Pterygiophore pattern	*T. alalunga* from *T. thynnus* + *Thunnus* spp.

Although the vertebrae are not yet developed posteriorly at 8 mm SL, they nevertheless can be counted by noting chondrified neural and haemal spines which are present above and below the notochord. Care should be taken not to count the parhypural bone as a haemal spine. The parhypural belongs to the hypural plate but resembles a haemal spine during early development. The position of the first closed haemal arch is difficult to determine in small specimens but it can be done with diligence and patience. The pterygiophores may not be entirely ossified at 8 mm SL, but they are present as chondrified struts. Varying the substage light, by moving the mirror below the microscope, will bring them into view.

The vertebral position of the first haemal postzygapophysis becomes available as a character on specimens from 15 to 20 mm SL. In this size range, only *T. atlanticus* acquires the diagnostic

TABLE 13.—Comparison of diagnostic characters for juveniles of *Thunnus*. Parentheses indicate rare occurrence.

Character	*T. thynnus*	No.	%	*T. alalunga*	No.	%	*T. atlanticus*	No.	%	*Thunnus* spp.	No.	%
Number of vertebrae, precaudal and caudal	18 + 21 = 39	149	95	18 + 21 = 39	114	97	19 + 20 = 39	105	98	18 + 21 = 39	35	85
	[16-19]+[20-22] = 38-40	8	5	19 + 20 = 39	4	3	[18,19]+[19,21] = 38,39	2	2	[17,19]+[21,22] = 39,40	6	15
First haemal arch on vertebra number	10	137	88	10	115	99	11	101	94	11	38	93
	11, (9)	19	12	(9)	1	1	12, (10)	6	6	10,12	3	7
First haemal post-zygapophysis on vertebra number	7	153	97	8	97	93	8	86	100	7	28	90
	(6),(8)	4	3	7,9	7	7				6	3	10
Number of anal fin elements, including finlets	22	127	91	22	101	94	21	85	92	22	28	93
	21,23,(24)	12	9	(21),23	7	6	(20),22	7	8	21,23	2	7
Pattern of single second dorsal fin pterygiophores for interneural spaces	1,1— — — — —1,1	140	95	1,1,1,— — — — —1	116	100	1,1,1,— — — — —1	42	46	1,1— — — — —1,1	40	98
	1,1— — — — — —1	8	5				1,1— — — — — —1	32	35	1,1,1— — — — —1	1	2
							1,1— — — — —1,1	18	19			
Pattern of single anal fin pterygiophores for interhaemal spaces	— — — — —1,1	116	84	— — — — —1,1	74	66	— — — — —1	55	61	— — — —1,1,1	31	78
	— —1— —1,1 / — — — —1,1,1	23	16	— —1— —1,1	38	34	— — — —1,1	34	39	— — — — —1,1	9	22
Gillraker number over ceratobranchial bone	17,18,(19,20)	102		14,15,(16)	81		11,12,(13)	92		14,15,16	27	
Shape lateral line	right angle			smooth curve			smooth curve			smooth curve		

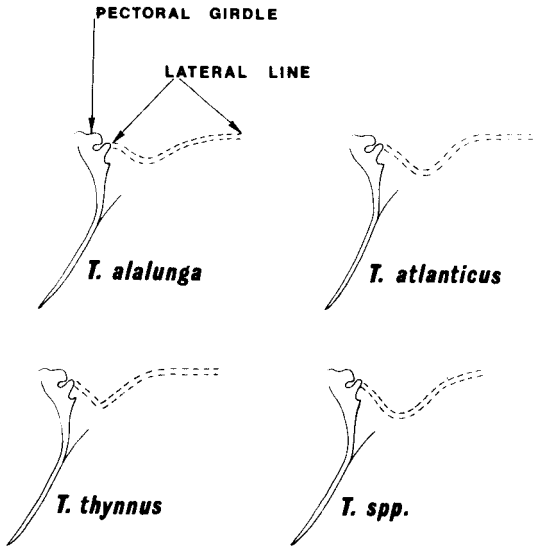

FIGURE 13.—Outline of the lateral line for juveniles of the *Thunnus* species. Each pair of dashes in the lateral line represents one scale.

count of gillrakers over the ceratobranchial. The juveniles can be identified as follows:

Character	*Species separated*
Number precaudal + caudal vertebrae Ceratobranchial filled with 11-12 rakers	*T. atlanticus* from *T. thynnus*, *T. alalunga*, *Thunnus* spp.
First closed haemal arch	*T. atlanticus* + *Thunnus* spp. from *T. thynnus* + *T. alalunga*
Pterygiophore pattern	*T. alalunga* from *T. thynnus* + *Thunnus* spp.
First haemal postzygapophysis	*T. alalunga* + *T. atlanticus* from *T. thynnus* + *Thunnus* spp.

Juveniles in this size range are easier to identify for two reasons. First, they are further advanced in development, they stain better, and the characters are more readily discernible. Second, the availability of two additional characters permit cross-checking so that it is possible to identify "one character" variants. For example, a specimen with 18 + 21 vertebrae and the ceratobranchial filled with 12 gillrakers is a vertebral variant of *T. atlanticus*. Although gill rakers over the ceratobranchial bone can vary over a range, specific ranges do not overlap except for *T. alalunga* with the *Thunnus* spp. complex. Thus, the ceratobranchial count, if available, should take precedence over the vertebral count. The first haemal postzygapophysis may be very small and high magnification should be used when viewing this character.

All characters listed in Table 13 are available for identification on specimens past 21 to 23 mm SL. The following features can be used to identify a specimen:

Character	*Species separated*
Number precaudal + caudal vertebrae	*T. atlanticus* from *T. thynnus*, *T. alalunga*, *Thunnus* spp.
Gillraker number over ceratobranchial	All species separable except *T. alalunga* from *Thunnus* spp.
First closed haemal arch	*T. atlanticus* + *Thunnus* spp. from *T. thynnus* + *T. alalunga*
Pterygiophore pattern	*T. alalunga* from *T. thynnus* + *Thunnus* spp.
First haemal postzygapophysis	*T. alalunga* + *T. atlanticus* from *T. thynnus* + *Thunnus* spp.
Shape lateral line	*T. thynnus* from *T. alalunga*, *T. atlanticus*, *Thunnus* spp.

It is not difficult to identify specimens larger than 21 mm SL. Sufficient characters are available and bones are well ossified and stained. However, variability should be taken into account and characters with the least variability should be relied upon the most. The number of gillrakers over the ceratobranchial bone and the shape of the lateral line should take precedence over the other characters. I have never observed the range for the number of ceratobranchial rakers in one species overlap with that of another, except *T. alalunga* with *Thunnus* spp., and I have never seen a *T. thynnus* with a smoothly curved lateral line.

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A NEW MODEL OF OCEAN MIGRATIONS OF BRISTOL BAY SOCKEYE SALMON

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ABSTRACT

A model is presented that describes the ocean migrations of Bristol Bay sockeye salmon from the time the fish leave the estuary until they return as adults. Bristol Bay sockeye salmon inhabit extensive areas of the ocean during various stages of their life at sea, ranging across most of the North Pacific Ocean from about long. 140°W to near long. 167°E and from near lat. 46°N to lat. 58°N in the central Bering Sea. Initially, their migration route takes the young juveniles from the eastern Bering Sea through the central and eastern Aleutian Islands passes to south of lat. 50°N where in late winter they become broadly distributed across the North Pacific Ocean. In June the immature fish start a northward movement and in summer occupy waters from lat. 50°N to the Aleutian Islands and over an east–west area from long. 160°W to 170°E; part of the population moves north into the Bering Sea. The following winter the sockeye separate into immature and maturing components. Those that will mature remain in waters north of lat. 50°N from whence they will migrate back to Bristol Bay in the spring with the major proportion entering the Bering Sea through passes east of long. 175°W. The immature fish that will remain at sea another year move south of lat. 50°N in the winter and early spring, then essentially repeat the migration they had made the previous summer. These fish as maturing fish the following winter and spring follow the same migration route as the earlier maturing group.

No direct relationship was found between the distribution and migration of the sockeye and defined oceanographic features of the Subarctic Region of the North Pacific Ocean.

A model of the complete ocean migrations of sockeye salmon, *Oncorhynchus nerka*, from Bristol Bay, Alaska, was originally developed by Royce, Smith, and Hartt (1968). Their model suggested that Bristol Bay sockeye during their life at sea make two or three circuits of an elongated east–west course extending from about long. 165°E to 140°W in the North Pacific Ocean and Bering Sea. These migrations were thought to be associated with major currents of this region—the Alaskan Stream and Subarctic Current.

Since formulation of the model by Royce et al. (1968), Bakkala (1971) studied the distribution and abundance of immature sockeye salmon in relation to ocean currents and other features of the Subarctic Region and suggested certain refinements to the earlier model. New information available through continued offshore studies combined with a review of existing tagging data has led us to propose a new model of migration of Bristol Bay sockeye to supplement that proposed by Royce et al. (1968).

Studies of the oceanic distribution of Pacific salmon have shown sockeye salmon from Bristol Bay, Alaska, to be widely distributed in the North Pacific Ocean and Bering Sea. Tagging experiments have shown that Bristol Bay sockeye salmon range from about long. 140°W, approximately 111 km from the coast of southeastern Alaska, to near long. 167°E, approximately 463 km from the coast of Kamchatka, an east–west distance of about 3,700 km. From south to north, Bristol Bay sockeye have been identified near lat. 46°N in the northeastern Pacific Ocean to near lat. 58°N in the central Bering Sea. Notwithstanding their broad distribution and dynamic movements, the basic distribution and seasonal migrations of the sockeye are known.

In this report we examine data from tagging experiments and salmon catches in relation to environmental features to describe the distribution and migration of Bristol Bay sockeye salmon from the time they leave the estuary until they return as maturing fish. Following these discussions, a model of migrations for Bristol Bay sockeye salmon is presented.

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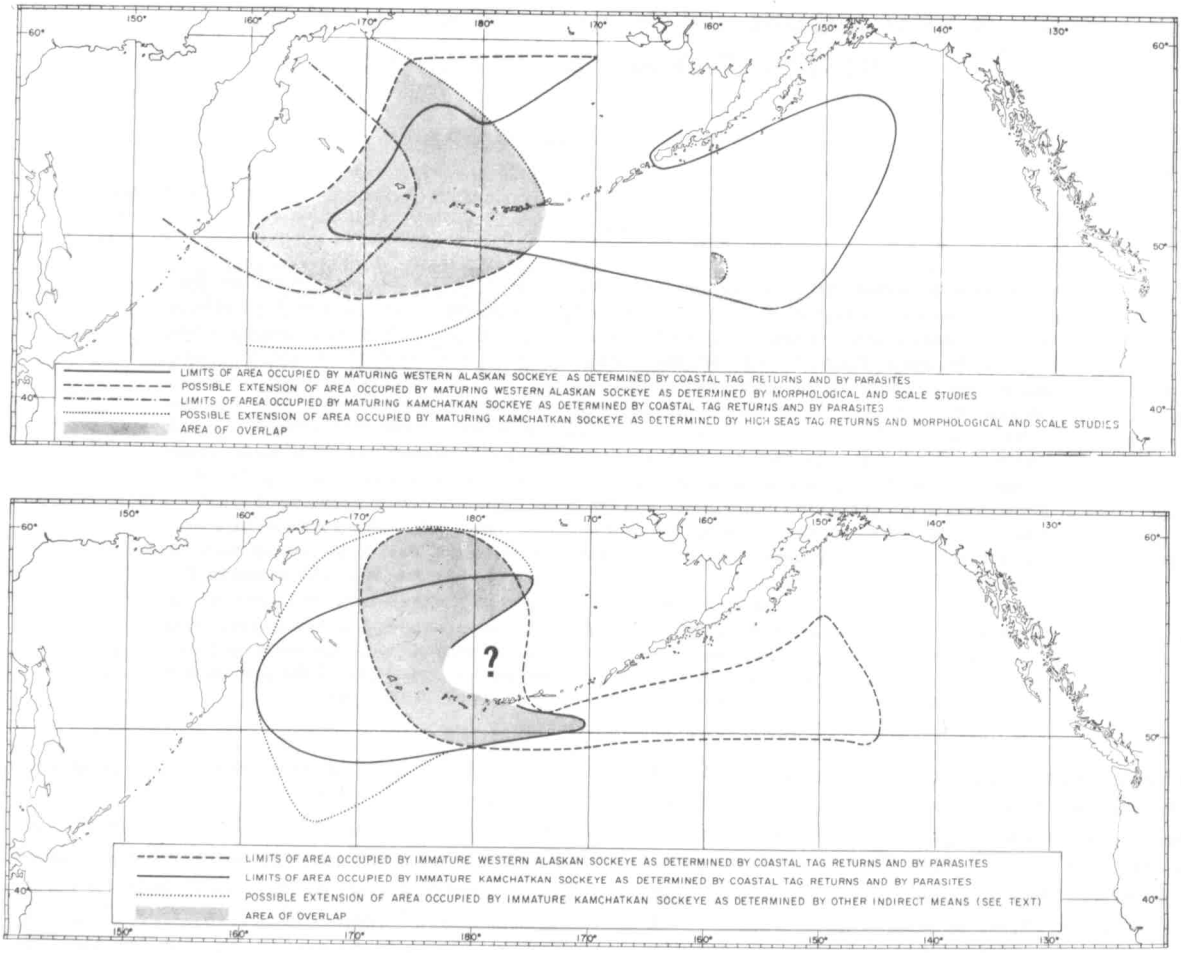

FIGURE 1.—Range and area of overlap for maturing (a) and immature (b) sockeye salmon from Asia and North America (Figures 74 and 76 of Margolis et al., 1966).

REVIEW OF DISTRIBUTION OF BRISTOL BAY SOCKEYE SALMON AS DETERMINED BY COASTAL TAG RETURNS

Numerous researchers, through tagging experiments, morphometric studies, scale studies, and analysis of parasites, have defined certain aspects of the distribution of Bristol Bay sockeye salmon (defined as those sockeye originating in the eastern Bering Sea from Unimak Island northward to the Kuskokwim River). From a comprehensive review and updating of these studies, Margolis et al. (1966) defined the limits of oceanic distribution of maturing and immature western Alaska sockeye salmon (Figure 1). Examination of recent summaries of tag returns[2] for 1956–69 (Figures 2 and 3) corroborates the general distribution pattern of sockeye salmon stocks from western Alaska, from other North American regions, and from Asia as described by Margolis et al. The tag returns show, however, an extension in the range of western Alaska immature sockeye salmon to west of long. 170°E (see Figure 3).

Maturing Bristol Bay sockeye salmon, which had been tagged at sea primarily during April, May, and June, are shown to be distributed

[2]Aro, K. V., J. Arthur Thomson, and Dorothy P. Giovando. 1971. Summaries of salmon tag recoveries in North Pacific coastal and high seas areas from salmon tagging in INPFC statistical areas in the North Pacific Ocean by Canada, Japan, and the United States, 1956 to 1969. Fish. Res. Board Can., Manuscr. Rep. 1148, 641 p. (Unpubl.)

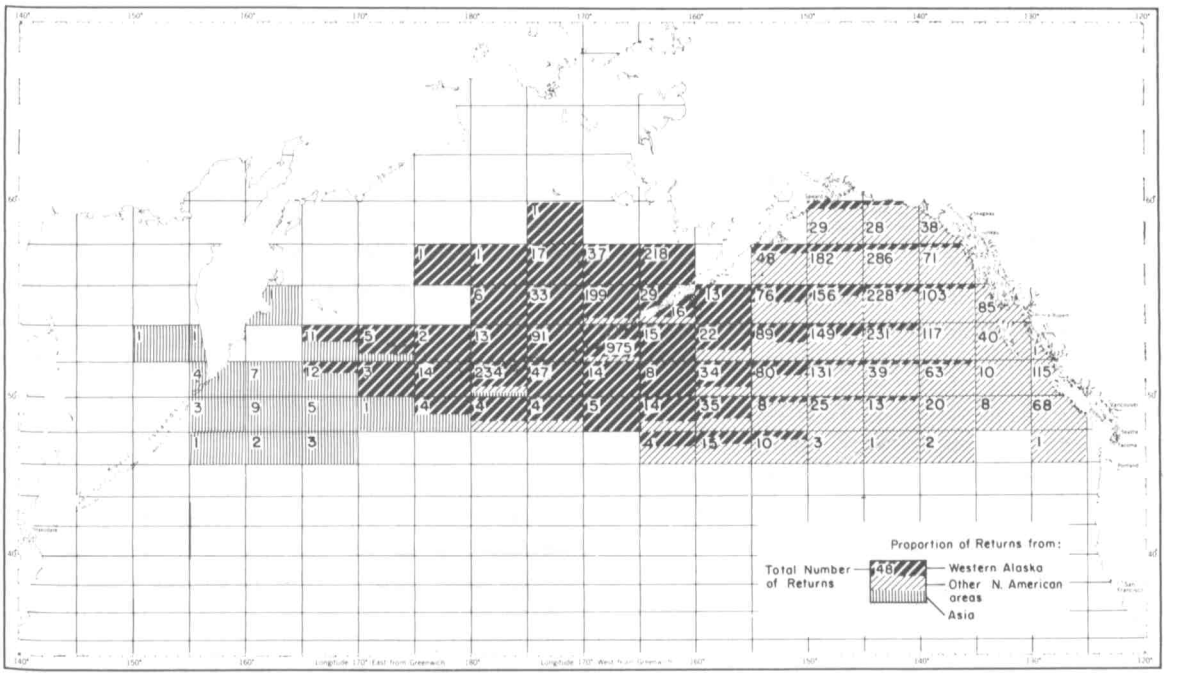

FIGURE 2.—Tagging locations (2° × 5° areas) for maturing sockeye salmon recovered in western Alaska, other North American areas, and Asia, 1956–69. The proportion of returns to these major land areas from each 2° × 5° area of the ocean are shown diagrammatically by having each 2° × 5° rectangle represent 100%. Small percentage returns could not be accurately illustrated, and in some instances percentages are exaggerated to show presence.

across most of the North Pacific Ocean and in the central and eastern Bering Sea south of lat. 60°N (Figure 2).

These tagging data also illustrate areas where Bristol Bay sockeye predominate as well as areas where they overlap with other stocks. Although tagging effort varied between some years and was far from uniform in various parts of the ocean, the return showed Bristol Bay sockeye predominating in the spring from about long. 155°W to 170°E. Their main area of overlap with other North American stocks was from about long. 140° to 160°W. With Asian sockeye, their main area of overlap was between long. 165° and 175°E.

Tag returns from immature sockeye salmon tagged primarily in the summer (late June through August) have been too few to portray their oceanic distribution in detail (Figure 3). The small numbers of tag returns are due to the poor survival associated with tagging small immature fish and the lack of widespread tagging throughout the oceanic areas inhabited by the fish. For limited data, the results show overlap of Bristol Bay sockeye with other North American stocks between about long. 145°W and 175°E. Bristol Bay immatures predominate south of the Aleutian Islands. Total returns of tagged fish for all years indicate that in the area immediately south of Adak Island, approximately 10% of the tag returns were from other North American areas. Very few tag returns were reported from Asian streams. The returns suggest some overlap of immature fish of Asian origin with Bristol Bay fish south of the central and western Aleutian Islands, but they do not indicate areas where Asian sockeye predominate.

Recent studies by the National Marine Fisheries Service (NMFS) have been directed toward understanding the influence of the oceanic environment on distribution and migration of salmon at sea. These studies, primarily concerned with Bristol Bay sockeye salmon, should disclose the causes of change in distribution and movements of the Bristol Bay stock. They should also lead to improved forecasts of run sizes and predictions of the effect of the Japanese high-seas fishery on salmon stocks of the United States. Results of these investigations and conclusions drawn from

coastal tag returns have provided information for describing the migrations of sockeye salmon through most of their life at sea.

DISTRIBUTION AND MIGRATION OF BRISTOL BAY SOCKEYE SALMON INFERRED FROM HIGH-SEAS CATCHES

The apparent relative abundance of sockeye salmon taken in gill nets, purse seines, and longlines from synoptic sampling over periods of time and large areas of the ocean furnish much information on movements and distribution of fish. This information coupled with the age composition of the catches and tagging data provides important links for formulating migration patterns of the stock.

First Year at Sea

Juveniles Age .0 (July-December)[3]

Juvenile salmon, age .0 fish after leaving the rivers of Bristol Bay, move southwest along the north side of the Alaska Peninsula throughout summer, but substantial numbers remain in the eastern Bering Sea until sometime after the middle of September (Hartt et al., 1967; Hartt, Dell, and Smith, 1969; Straty and Jaenicke, 1969[4]). Sampling with purse seines indicates that the juveniles do not make a rapid directional migration at this stage of life but disperse slowly toward the southwest as they move back and forth with the tides. By mid-September the juveniles are still present in large numbers east of long. 165°W extending at least 167 km offshore. The length of time that the juveniles spend in the eastern Bering Sea and their restricted distribution are probably due to the local abundance and availability of food. During this period of late summer, growth is rapid as the fish, averaging 17 to 18 cm long, feed on the abundant supply of zooplankton and larval fish (Hartt et al., 1967).

The migration routes of the juvenile sockeye as they leave the eastern Bering Sea is unknown due to lack of sampling in fall and early winter.

Immatures Age .1 (January-June)

The small sockeye were next taken as age .1 fish (an additional year is added on 1 January regardless of state of annulus formation) in winter catches in the North Pacific Ocean at various locations; a few specimens have been taken in the south-central Bering Sea. Bakkala (1971) has summarized winter gill-net catches of age .1 fish for 1962–67 by research vessels of the Northwest Fisheries Center, NMFS. To his data we have added catches made in the winters of 1969 and 1970 (Figure 4).[5] These data illustrate that main catches of age .1 sockeye were made near lat. 46°30′N in the central North Pacific and between lat. 48° and 51°N in the northeastern Pacific from long. 165° to 155°W. A good catch was also made near lat. 50°N at 175° and 170°W.

Relatively small numbers of fish were taken in the Bering Sea during sampling in late January and early February 1963 and near long. 170°E in February 1965. (Stations shown on long. 170°E represent stations fished as far west as long. 167°18′E.)

There were no tagging data to indicate area of origin of the age .1 fish taken in the winter. We can surmise their origin, however, on the basis of the freshwater age composition of catches, at least for some years. The largest catches of age .1 fish occurred in 1965 (10 and 16 March) near lat. 46°30′N between long. 175°E and 180°. CPUE (see footnote 5 for definition of catch per unit effort) of 16 and 13 were the largest made during the years of winter sampling. Most of these fish (78% of the catch) were age 2.1 (a salmon of age 2.1 has spent two winters in fresh water after hatching and one winter in the ocean). Later in the year in the samples taken south of Adak Island (where tag returns indicate that Bristol Bay fish predominate), the 2.1 age-group made up approximately 75% of the catch of age .1 fish. One year later this same group, now age 2.2 fish, made up about 70% of the mature age .2 fish in the 1966 run to Bristol Bay. That same year the age composition of the mature Asian sockeye

[3]Age designation used are those suggested by Koo (1962). The numeral preceding the dot indicates number of winters in fresh water; the numeral following the dot indicates number of winters at sea.

[4]Straty, R. R., and H. W. Jaenicke. 1969. Estuarine ecology of sockeye salmon in Bristol Bay. Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska. (Unpubl. manuscr.)

[5]In this and other figures the catch per unit of effort (CPUE) of gill nets is the value of the sums of the average catch per shackle of each mesh size. A shackle is approximately 91.5 m long.

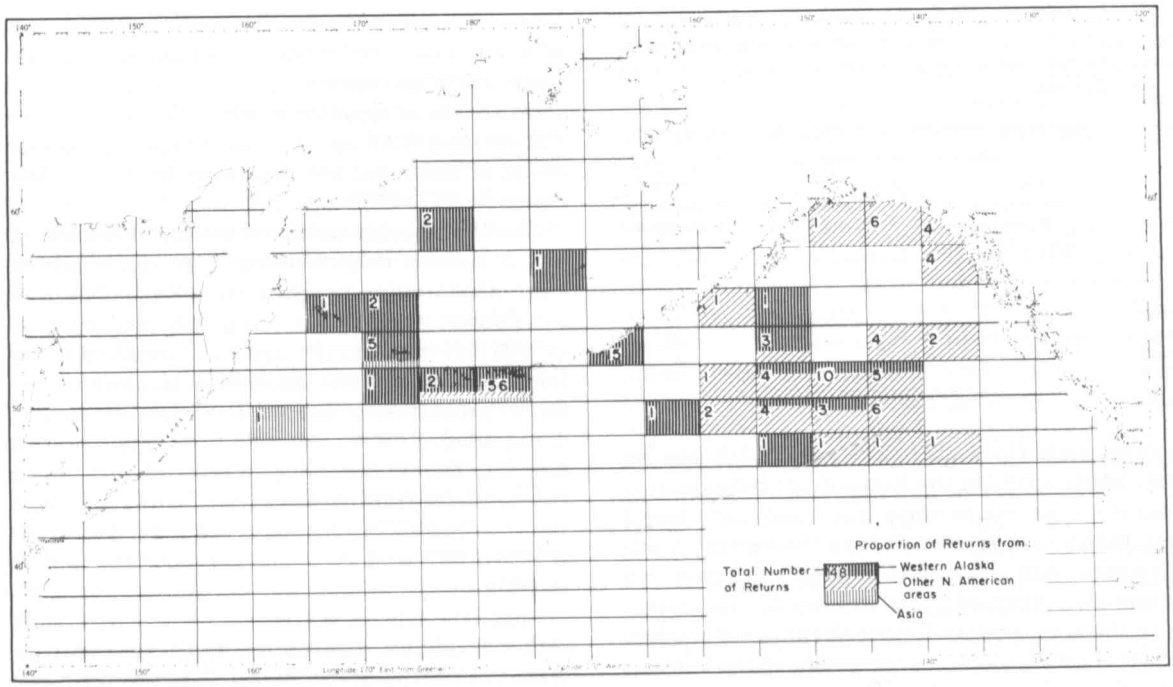

FIGURE 3.—Tagging locations (2° × 5° areas) for immature sockeye salmon recovered in western Alaska, other North American areas, and Asia, 1956-69. The proportion of returns to these major land areas from each 2° × 5° area of the ocean are shown diagrammatically by having each 2° × 5° rectangle represent 100%. Small percentage returns could not be accurately illustrated, and in some instances percentages are exaggerated to show presence.

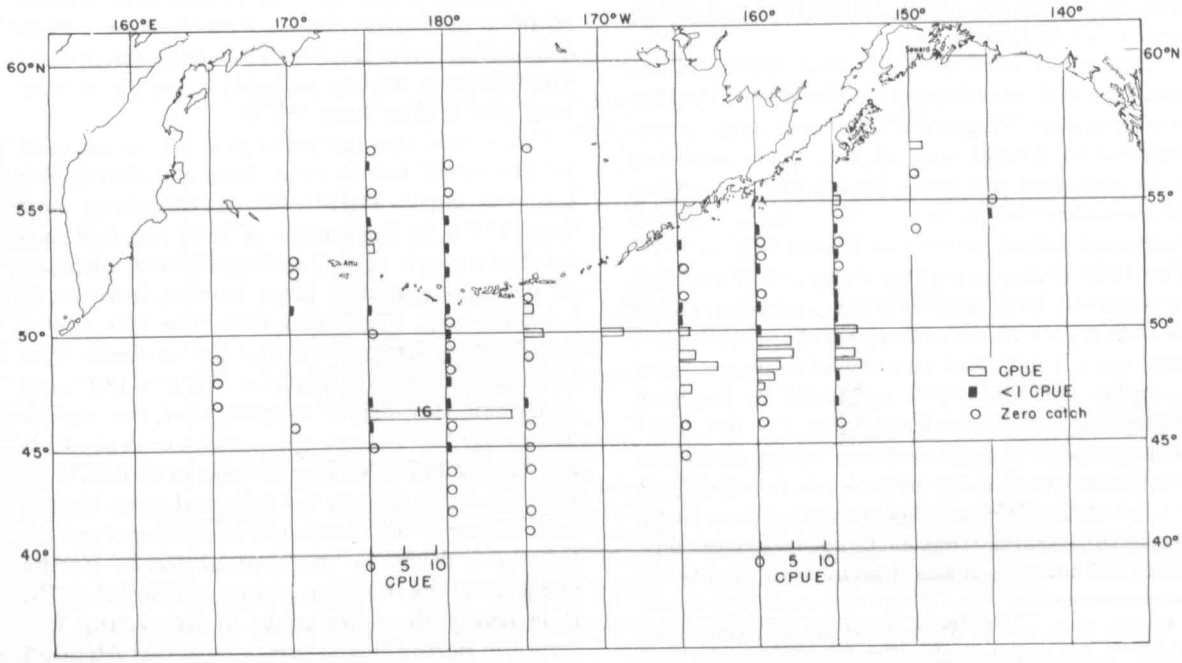

FIGURE 4.—Distribution of age .1 sockeye salmon in February and March 1962–70, with the exception of 1964, 1966, and 1968.

TABLE 1.—Proportion of age 2.1 sockeye salmon in samples from the northeastern Pacific and south of Adak Island in 1962, 1967, and 1969 and of age 2.2 sockeye in the following year's Bristol Bay run.

Year	Area and time of sampling				
	Northeastern Pacific winter (age 2.1)			Adak Island summer (age 2.1)	Bristol Bay in following year (age 2.2)
	155°W	162°W	165°W		
	Percent				
1962	35	—	—	53	50
1967	53	34	—	43	37
1969	60	—	83	79	90

was estimated to be about 24% age 2.2 fish (Fredin and Worlund).[6] On the basis of age composition, therefore, we can surmise that most of the small fish taken near lat. 46°30′N in the central Aleutian area were of Bristol Bay origin and that this is one area occupied by Bristol Bay fish in winter.

In the northeastern Pacific Ocean, good catches of age .1 sockeye salmon were made in the winters of 1962, 1967, and 1969. The proportions of age 2.1 fish in these catches are shown in Table 1. Also shown are the proportions of age 2.1 fish in the catches made the following summer south of Adak Island (where Bristol Bay fish traditionally predominate as shown by tag returns) and the proportions of age 2.2 fish in the following year's run to Bristol Bay.

Catches in 1969 probably best illustrate the presence of Bristol Bay fish in the area during the winter season. Progeny of the record–size spawning run to Bristol Bay in 1965 were expected to be abundant and predominate among samples of immature fish at sea in 1969 and as age 2.2 maturing fish in returns to Bristol Bay in 1970. The 1969 winter sampling along 155°W resulted in relatively large catches of age .1 sockeye salmon in January which were composed of approximately 60% age 2.1 fish (73% in areas of largest catches near lat. 49° and 50°N) as would be expected if they originated from Bristol Bay. The few age .1 sockeye taken in more northern waters along this longitude (near lat. 52° to 55°N) were mainly age 1.1 fish (82%); they possibly originated from North American coastal areas eastward of Bristol Bay. The 1969 samples of age .1 sockeye salmon taken along long. 165°W had an even higher proportion of age 2.1 fish (83%) than samples taken along long. 155°W and compared more closely to the age composition of samples south of Adak Island in the summer (79% age 2.1) and to the age composition of maturing fish returning to Bristol Bay rivers in 1970 (90% age 2.2).

The 1967 winter sampling produced catches of age .1 sockeye salmon along long. 162°W which were also similar in age composition (34% age 2.1 fish) to that of maturing fish returning to Bristol Bay in 1968 (37% age 2.2). Sampling along long. 155°W in 1967 showed a somewhat different proportion of age 2.1 fish (53%) from that along long. 162°W. In 1962 the proportion of age 2.1 fish along long. 155°W also differed substantially from that of maturing fish in Bristol Bay in 1963 (35% age 2.1 along long. 155°W in winter 1962 and 50% 2.2 fish in Bristol Bay in 1963).

From the above relations, we surmise that sockeye salmon originating from Bristol Bay reach the northeastern Pacific Ocean by January and February of their first year at sea. It appears from age comparisons that they probably predominate eastward to about long. 160°W and possibly to long. 155°W in years of high abundance such as in 1969. Their range may extend even farther to the east. Catch data thus demonstrate that Bristol Bay sockeye become widely distributed across the North Pacific Ocean in their first winter at sea and probably extend from near long. 175°E to at least 155°W.

Catch data also indicated possible routes used by the young fish to move from the Bering Sea into the North Pacific Ocean. Sampling near long. 170°E in the winter of 1965 resulted in a catch of a single age .1 sockeye salmon whereas, as previously shown, large catches were made between long. 175°E and 180°. The lack of age .1 fish along long. 170°E and the evidence from age composition that fish from 175°E to 180° were of Bristol Bay origin suggest that the waters near long. 170°E may represent an area separating Asian and Bristol Bay sockeye in winter. Most Asian sockeye salmon are assumed to be located west of long. 170°E. Inasmuch as catches of age .1 fish were made in the central North Pacific Ocean from the Aleutian Islands to near lat. 45°N, it is likely that one route of the young fish from the Bering Sea is through central Aleutian Islands passes. In sampling on long. 165°, 160°, and 155°W, we caught few age .1 sockeye north

[6]Fredin, R. A., and D. Worlund. Catches of sockeye salmon of Bristol Bay origin by the Japanese mothership salmon fishery, 1956–70. Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, Wash. (Unpubl. manuscr.)

of about lat. 51°N compared to catches south of this latitude. It appears, therefore, that the young salmon migrate through passes between long. 169°W and 179°E (the area bordered by Umnak Island on the east and Amchitka Island on the west) and then move eastward. A possible pathway from the Bering Sea to the North Pacific may be Amchitka Pass where a branch of the Alaskan Stream in September flows northward into the Bering Sea (Favorite and Ingraham, 1972).

Depending on routes followed, the migration from the eastern Bering Sea to the central North Pacific near lat. 46°N or south of the Alaska Peninsula between lat. 48° and 51°N would require migrations of from about 700 to 1,000 miles (1,300–1,850 km) and travel rates of at least 8 to 10 miles (14.8–18.5 km) per day. This rate is entirely reasonable for it has been estimated that juvenile salmon travel about 10 miles (18.5 km) per day in the Gulf of Alaska (Royce et al., 1968).

Salmon research cruises have also included oceanographic studies which have defined major oceanographic features of the Subarctic North Pacific (McAlister et al., 1970). These are permanent features of the Subarctic Region and are defined by surface and subsurface characteristics (generally between 100 and 400 m). Salmon catches have been related to these features in an attempt to determine their influence on distribution and movements of salmon. Bakkala (1971) related winter catches of age .1 sockeye salmon in 1962, 1963, 1965, and 1967 to the major water masses and indicated that the salmon were usually associated with the Oyashio Extension Area (Figure 5).

Catches in winter 1969 and 1970, however, show that the age .1 fish were not always associated with this water. The eastward-moving water between the Ridge and Transition Areas was previously separated into Oyashio and Subarctic Current Areas, but more recent terminology combines the two areas into a single feature called the Western Subarctic Intrusion (Favorite, Ingraham, and Fisk, 1972). In Figure 6 are shown four years of winter catch data and associated oceanic features in the northeastern Pacific. In 1962 and 1967, age .1 fish were associated with the Western Subarctic Intrusion. In 1969 and 1970, this water mass shifted northward (in 1970 it formed only a relatively narrow tongue stretching east of long. 160°W) but was not accompanied by a corresponding shift in distribution of the age .1 sockeye salmon. These fish remained at much the same latitudes as in the earlier years, and their winter distribution was not affected by changes in location of the specific water mass. Because this particular water mass is defined by weak eastward flow and temperature conditions between 200 and 400 m, it

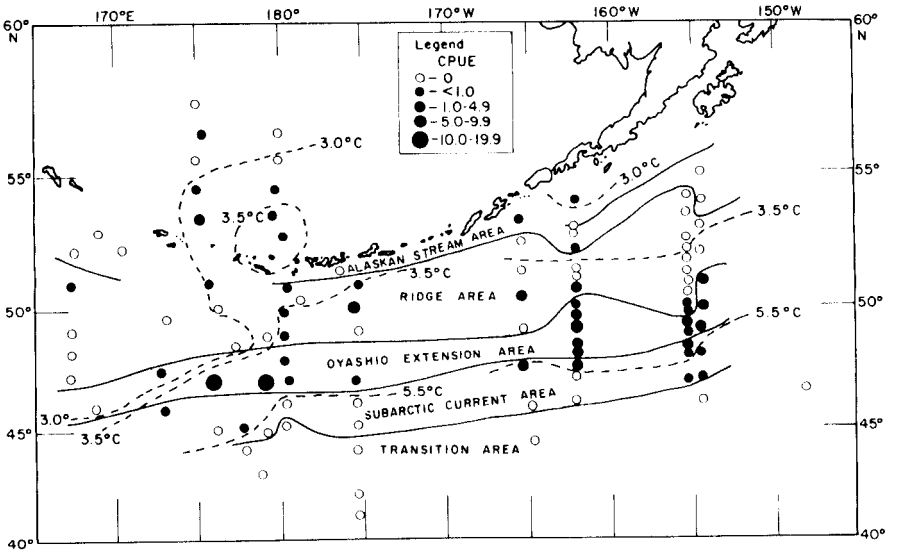

FIGURE 5.—Distribution of age .1 sockeye salmon in the winters of 1962, 1963, 1965, and 1967 in relation to oceanographic features of the Subarctic Region of the North Pacific Ocean.

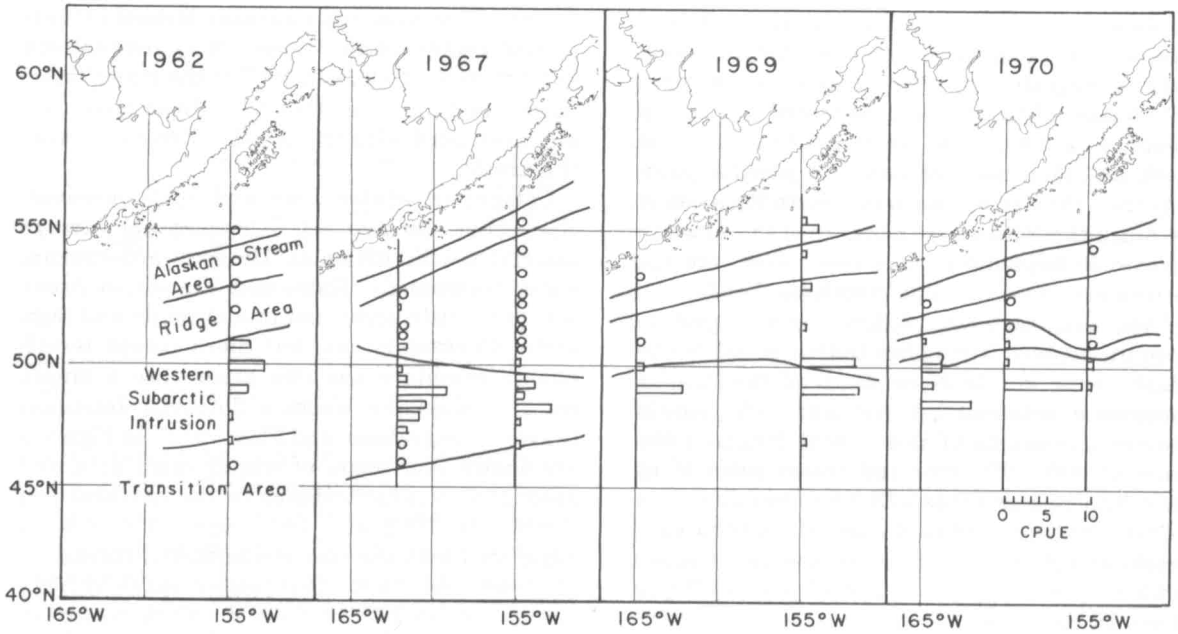

FIGURE 6.—Distribution of age .1 sockeye salmon from winter catches in the northeastern Pacific Ocean in relation to defined oceanographic features.

is possible that other surface conditions may have greater bearing on the distribution and movements of salmon.

Examination of surface water temperatures in relation to winter catches of age .1 sockeye (Figure 5) revealed that the largest catches were in the temperature range of 3.5° to about 5.5°C. The young fish were not generally taken in the extremes of cold or warm surface waters. This was clearly illustrated in 1965 by sampling near long. 170°E. Only a single age .1 sockeye was taken between long. 165° and 170°E in surface water temperatures of 1.8°C. No fish were caught at other stations where surface temperatures ranged from 1.6° to 2.4°C. Areas in the Bering Sea, where age .1 sockeye were caught, generally had surface temperatures of 3°C or more. The low surface water temperatures or the subsequent reduction in abundance of food forms may cause age .1 sockeye to move out of the Bering Sea and seek warmer water in the North Pacific Ocean. The highest water temperature at which age .1 fish were taken was 6.8°C.

By April and May the age .1 sockeye salmon reach their southernmost limits of distribution (Figure 7). Japanese research vessels caught relatively large numbers of age .1 sockeye in gill nets from lat. 44° to 46°N along long. 175°W illustrating their occurrence south of the central Aleutian Islands. Samples taken in 1969 were composed of about 70% age 2.1 fish, which was comparable to the age composition of age .1 sockeye salmon taken south of Adak Island that same summer in purse seines by the Fisheries Research Institute (79% age 2.1).

A few age .1 sockeye salmon were taken in early May 1968 by a Japanese research vessel along long. 175°E (Figure 7). The small sample of readable scales (10 fish) was 50% age 2.1, 40% age 3.1, and 10% age 1.1. This was quite unlike the age composition of age .1 sockeye caught south of Adak Island during summer 1968 by the Fisheries Research Institute (71% age 1.1 fish), indicating that the immature sockeye along long. 175°E in early May might have been Asian fish.

In the northeastern Pacific, sampling with gill nets along long. 165°W in the spring of 1969 resulted in small catches of age .1 fish as far south as lat. 46°N, the limit of sampling. Longline fishing surveys provided some data on the distribution of age .1 sockeye salmon to the east of long. 165°W.

During 1964, 1965, and 1966, longline surveys by the Fisheries Research Institute (FRI) were made in the northeastern Pacific including the Gulf of Alaska to obtain salmon for tagging. Although longline gear is not considered as

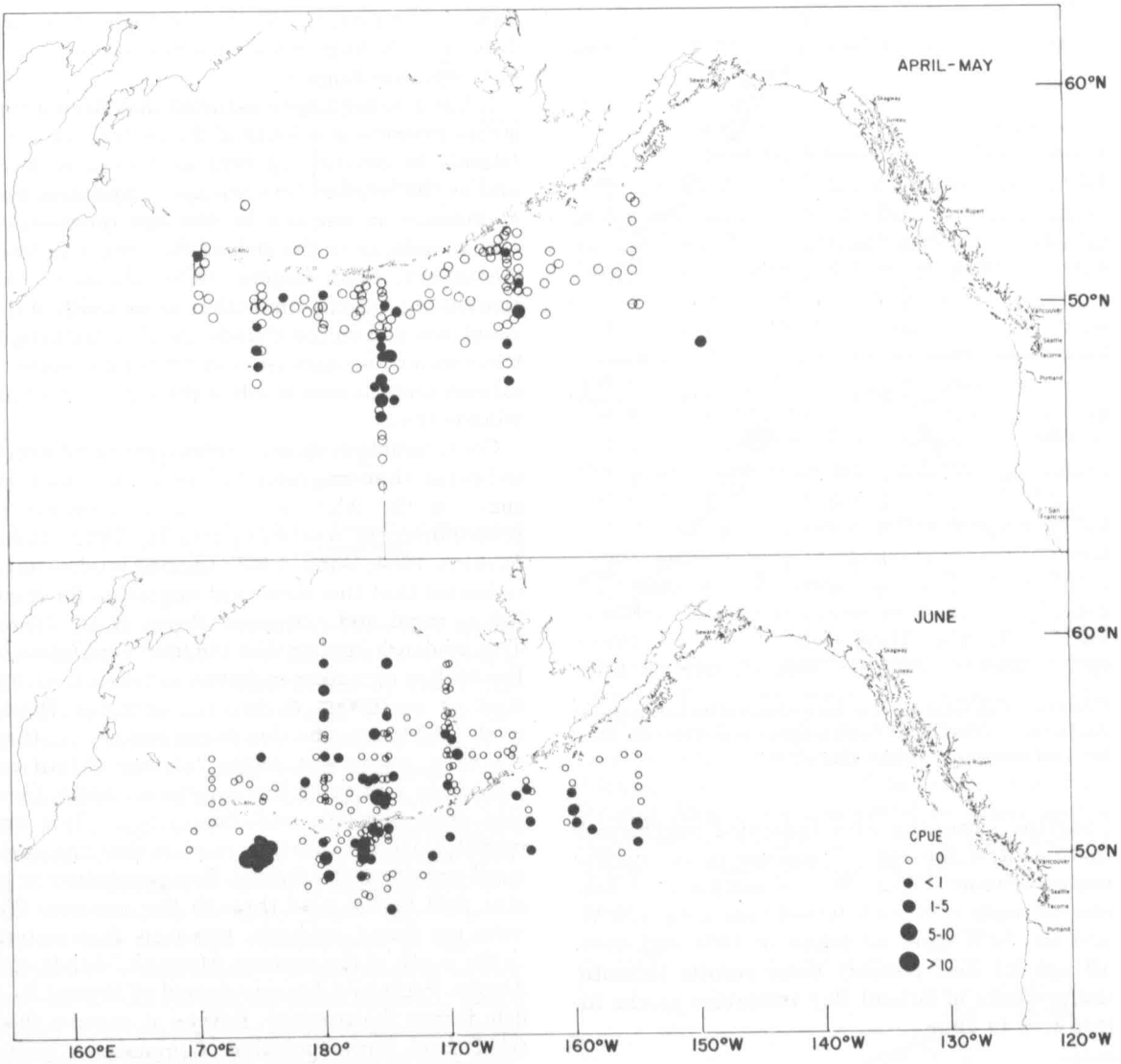

FIGURE 7.—Distribution of age .1 sockeye salmon in the spring (data from 1956–61 and 1966–70).

efficient for age .1 salmon as for older age-groups, some age .1 fish were taken, and these catches at least reflected the presence of the immature fish. In April and May (Figure 8) age .1 sockeye salmon were primarily found south of lat. 52° to about 46°N and extended eastward to about 140°W.

Most of the age .1 sockeye salmon caught by FRI during the 3 yr of longline surveys were taken in 1964. These fish in the area of the largest catches (long. 160° to 145°W, south of lat. 52°N) were mainly age 2.1 fish (75%), the age-group which predominated among samples taken in the central Aleutian Islands area during the summer and which were likely of Bristol Bay origin, and fish which made up part of the record run of age 2.2 sockeye to Bristol Bay in 1965. Thus it appears that Bristol Bay stocks in April and May could extend eastward in the northeastern Pacific at least as far as long. 145°W.

By June the age .1 sockeye have started a northward movement along a broad east-west front and in late June have even reached the central portions of the Bering Sea (Figure 7).

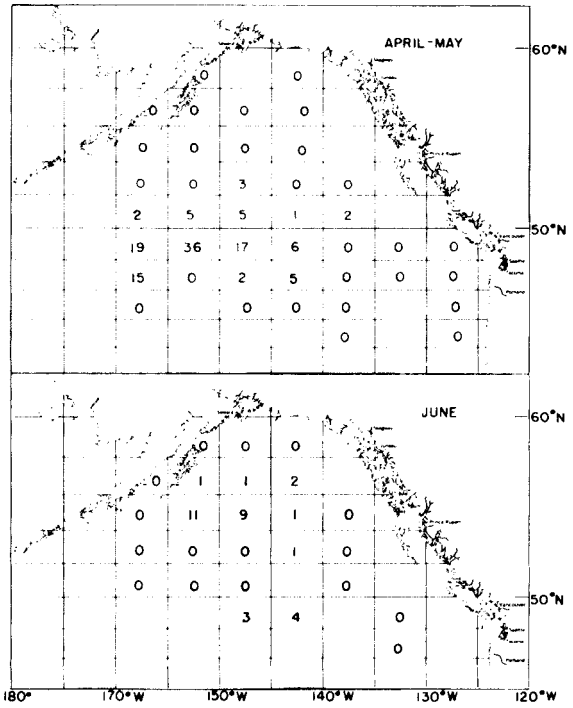

FIGURE 8.—Catches of age .1 sockeye salmon in the northeastern Pacific (in numbers of fish) with longline gear, 1964–66. Data are total catches not weighted for effort.

Longline sampling also indicated northward movement of the age .1 sockeye in the northeastern Pacific (Figure 8). The sample of 11 fish caught south of Kodiak Island near long. 150°W and lat. 54°N were all taken in 1964 and were all age 2.1 fish; possibly these results indicate the presence of Bristol Bay immature stocks in this area in June.

Second Year at Sea

Immatures Age .1 (July–December)

In the summer, July–September, the distribution and migration of immature sockeye salmon south of the Aleutian Islands has been well documented (Hartt, 1962, 1966; French, 1964; French, Craddock, Bakkala, Dunn, and Thorson, 1967; Royce et al., 1968; Bakkala, 1971; Rothschild et al., 1971).

An example of the distribution in late July is shown in Figure 9. This typifies the distribution of immature sockeye salmon south of the Aleutians in July and August; the relative abundance of immatures is usually highest in late July or early August and at lower levels in early July and late August.

It has also been demonstrated that Bristol Bay stocks predominate south of the central Aleutian Islands by coastal tag returns 1 or 2 yr later and by the relation between age composition and abundance at sea and by the age composition and abundance in the Bristol Bay run 1 yr later (Ossiander, 1965; Rogers, 1970). Based on the limited tag returns from other areas south of the Aleutians and on the abundance of immatures in these waters, we surmise that Bristol Bay sockeye salmon predominate south of the entire Aleutian Islands chain.

Considerable evidence has been produced which indicates that migration of immature sockeye south of the Aleutian Islands in summer is predominantly westward (Hartt, 1962, 1966; Larkins, 1964; Dunn, 1969); tagging studies have indicated that this westward migration for some fish is rapid and extensive (Royce et al., 1968). This evidence implies that the total population of Bristol Bay immature sockeye salmon shifts to the west or northwest during the summer. Royce et al. (1968) describe this migration as ". . . they migrate westward south of the Aleutian Islands in a more or less continuous band, from late June through mid-September." This apparent movement further implies that the eastward extent of the Bristol Bay population may also shift to the west through the summer. We have not found evidence, however, that waters to the south of the eastern Aleutian Islands and Alaska Peninsula become devoid of Bristol Bay fish during the summer. Rather, it appears that the Bristol Bay population of immatures main-

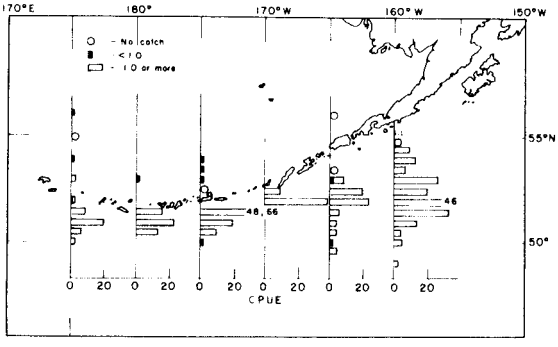

FIGURE 9.—Distribution of immature sockeye salmon, 21–31 July (from Bakkala, Figure 12, 1971).

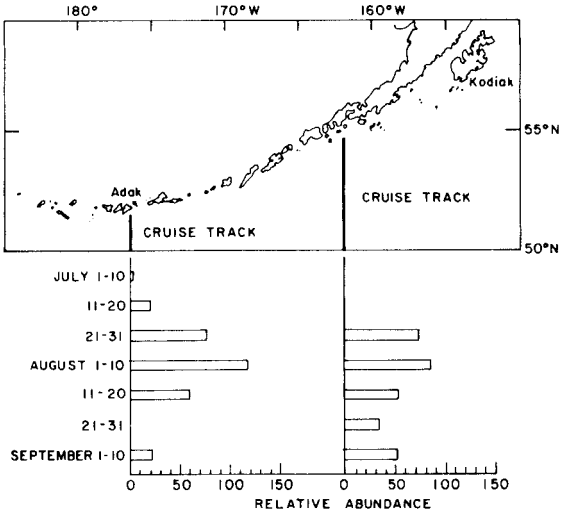

FIGURE 10.—Relative abundance of age .1 sockeye salmon along cruise tracks fished in summer 1963.

tains a broad east–west distribution throughout the summer. Definition of the eastward limit of this distribution is complicated by the intermingling of Bristol Bay and other North American stocks of immature sockeye salmon in the northeastern Pacific. Some evidence of the eastward range of Bristol Bay fish is provided by the age composition of age .1 fish sampled between long. 176° and 158°W in 1963 and 1966. In 1963 systematic sampling along long. 176° and 162°W from July to early September (Figure 10) showed that age composition of age .1 fish was very similar for the two areas as shown in Table 2. Sockeye salmon in the following year's Bristol Bay run was composed of approximately 66% age 1.2 fish and 34% age 2.2 fish or very similar to the dominant ages of age 1.1 and 2.1 fish, noted in each area the previous summer. This suggests that in the summer of 1963, Bristol Bay sockeye were distributed as far east as long. 162°W throughout the summer.

TABLE 2.—Freshwater age composition of age .1 sockeye salmon from samples along long. 162°W and 176°W in summer 1963.

Sampling area	Age-group				
	0.1	1.1	2.1	3.1	4.1
	Percent				
176°W	0.7	65.2	31.9	2.3	0.03
162°W	1.3	67.9	27.7	3.1	0

The age composition for the three lines fished in 1966 (Figure 11) varied considerably as illustrated in Table 3. Substantial differences were shown between samples at long. 176°W and samples to the east. The FRI purse seine samples south of Adak Island were approximately 33% age 1.1 and 67% age 2.1 fish—very similar to the age composition observed from gillnetting in this area. The following year's run to Bristol Bay, however, was composed of about 17% age 1.2 fish and 83% age 2.2 fish (Rogers, 1970). This indicates that Bristol Bay sockeye (or age-groups within the Bristol Bay stock) were distributed differently in 1966 compared to 1963. Other possibilities were that non-Bristol Bay fish made up a higher proportion of the catches in 1966 or that there were differential maturity schedules for the two major age-groups.

Although age composition of the samples did not clearly demonstrate the predominance of Bristol Bay sockeye in the northeastern Pacific in 1966, it seems likely that a large proportion of the fish taken in this area as well as south of the Aleutian Islands generally were of Bristol Bay origin. This assumption is based on the relative high abundance of sockeye shown by catches south of the Alaska Peninsula and Aleutian Islands, in view of the relative size of the Bristol Bay stock compared to other North American stocks and the evidence from tagging studies on immatures (see Figure 3).

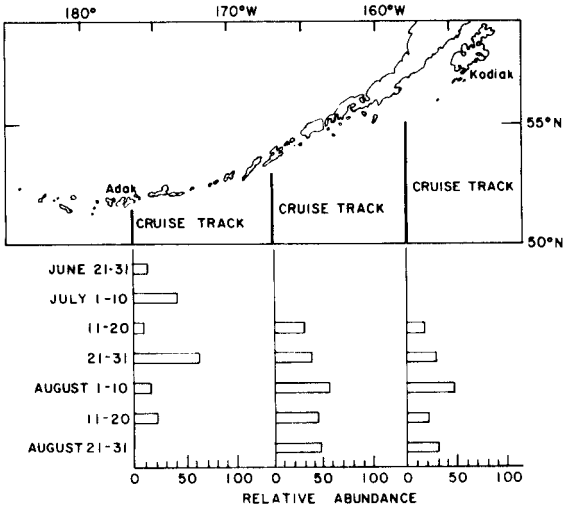

FIGURE 11.—Relative abundance of age .1 sockeye salmon along cruise track fished in summer 1966.

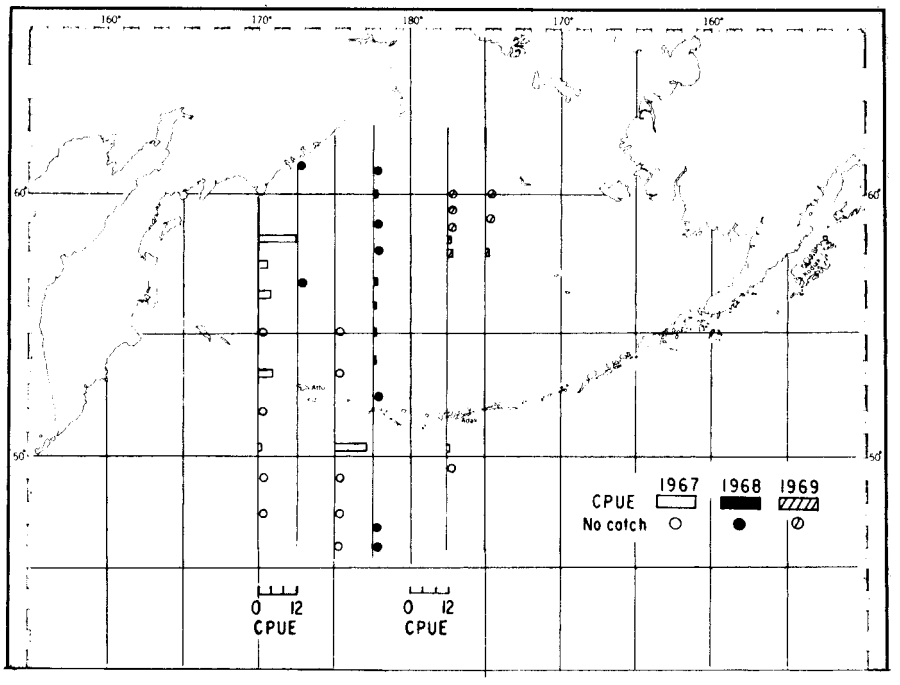

FIGURE 12.—Distribution and abundance of age .1 sockeye salmon in July 1967, 1968, and 1969 as shown by catches of Japanese research vessels.

TABLE 3.—Freshwater age composition of age .1 sockeye salmon from samples along long. 158°W, 167°W, and 176°W in summer 1966.

Sampling area	Age-group				
	0.1	1.1	2.1	3.1	4.1
	Percent				
176°W	0.1	29.6	68.5	1.8	0
167°W	0.6	52.7	43.7	3.0	0
158°W	0	68.1	29.5	2.4	0.16

Further evidence that a considerable proportion of the Bristol Bay immature sockeye salmon remain in the northeastern Pacific Ocean through the summer is indicated by catch data from research vessels fishing simultaneously along various longitudes in July and August (Bakkala, 1971). These data (Figures 10 and 11) showing peaks in relative abundance followed by a decline in abundance in two or three areas at similar time periods indicated that the major proportion of immatures from the eastern areas did not migrate westward and move through the area south of the central Aleutian Islands at a later time period.

Royce et al. (1968) suggested that many age .1 sockeye salmon from Bristol Bay migrate northward into the Bering Sea in late summer. The fact that some Bristol Bay sockeye occupy waters of the western Bering Sea has been established by the recapture of 5 sockeye in Bristol Bay tagged as immatures in the Bering Sea west of 180°. Recent catch data indicate that the abundance of Bristol Bay immatures in the Bering Sea varies depending upon the abundance of the stock and perhaps on other factors. Machidori (1970)[7] reported on catches of age .1 sockeye salmon in the Bering Sea during research cruises in 1967, 1968, and 1969. His data are shown in Figures 12, 13, and 14 as converted from tans (one tan of gill net is 50 m long) to CPUE in equivalent shackles of gear. Although fishing effort was not equal in all areas in July, August, and September, the data suggested lack of substantial numbers of salmon in the Bering Sea east of long. 175°E in July, but show large catches in August indicating a movement of

[7]Machidori, S. 1970. On summer distribution of immature sockeye salmon in the northwestern North Pacific and its adjacent waters. [In Japanese] Fish. Agency Jap., Tokyo (Int. North Pac. Fish. Comm. Doc. 1311), 59 p. (Transl., 15 p.)

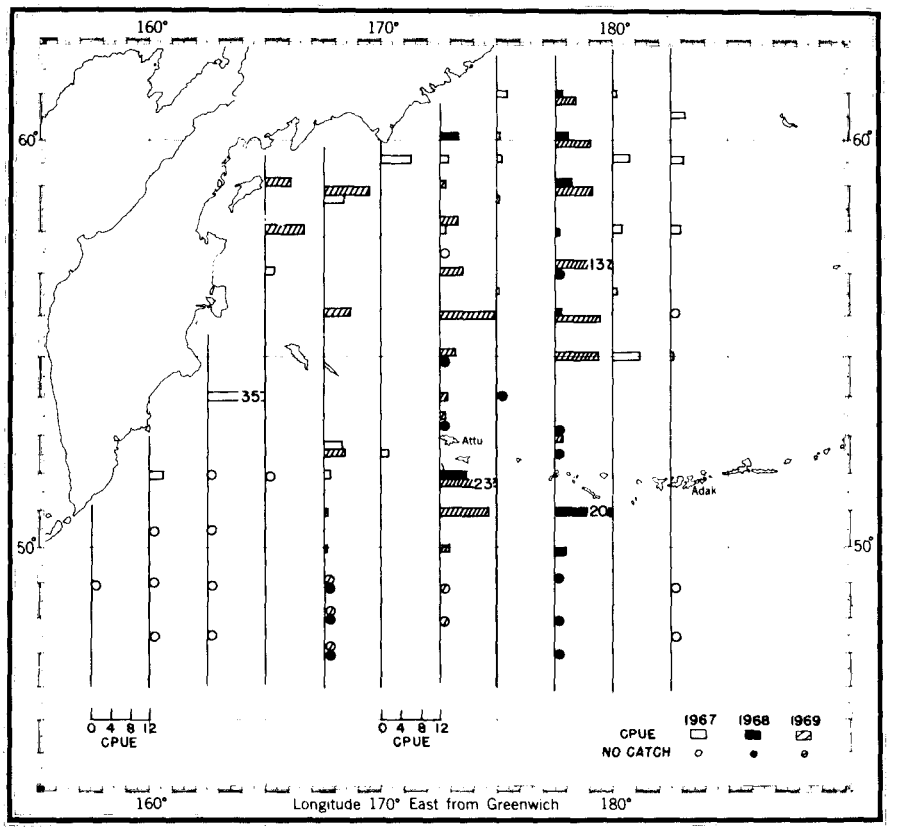

FIGURE 13.—Distribution and abundance of age .1 sockeye salmon in August 1967, 1968, and 1969 as shown by catches of Japanese research vessels.

immatures into the Bering Sea in August. In 1969 catches were much larger in August from long. 172°30′ to 177°30′E than in 1967 or 1968, suggesting the presence of large numbers of age .1 fish that were progeny of the 1965 record run to Bristol Bay. Evidence from age composition of these catches (mainly age 2.1 fish) also indicated that they were predominantly Bristol Bay fish as originally suggested by Machidori. The location of these fish in the central and western Bering Sea indicates that routes of travel from the North Pacific to the Bering Sea were through passes west of Adak Island. Large numbers of age .1 fish, probably of Asian origin, were taken in the Bering Sea west of long. 175°E in September (Figure 14), but sampling did not extend far enough eastward to determine if Bristol Bay fish still remained in the Bering Sea.

From the above analysis we conclude that some proportion of the age .1 fish from Bristol Bay inhabit the central and western Bering Sea in August and that their abundance in the Bering Sea varies with the abundance of the total stock.

Although some of the Bristol Bay immatures move north into the western Bering Sea, the large numbers of immatures remaining south of the Aleutians indicate that many of the Bristol Bay sockeye remain in the North Pacific Ocean and maintain a broad east–west distribution throughout the summer. At the time large catches of age .1 sockeye were taken in the Bering Sea —from 12 to 30 August 1969—large catches were also being made south of Adak Island from 1 to 15 August (French, Bakkala, Dunn, and Sutherland, 1971). Catches by Japanese and United States research vessels in August 1970 better illustrate this point (Figure 15). The relative abundance of age .1 sockeye was generally higher throughout the area south of the Aleutian Islands than it was at stations fished in the Bering

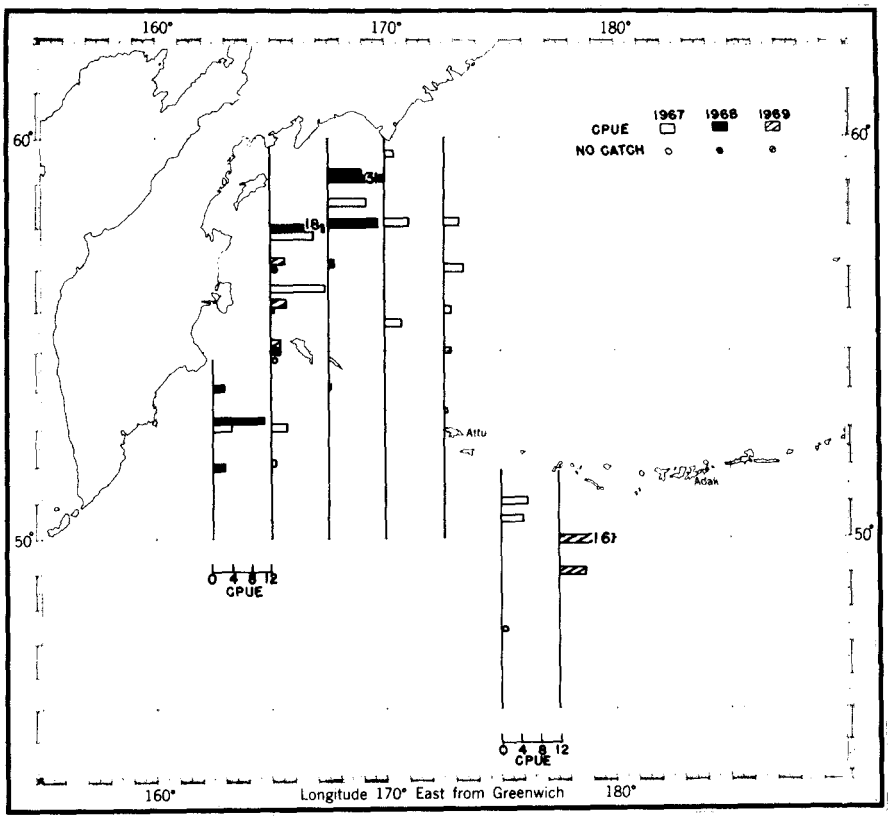

FIGURE 14.—Distribution and abundance of age .1 sockeye salmon in September 1967, 1968, and 1969 as shown by catches of Japanese research vessels.

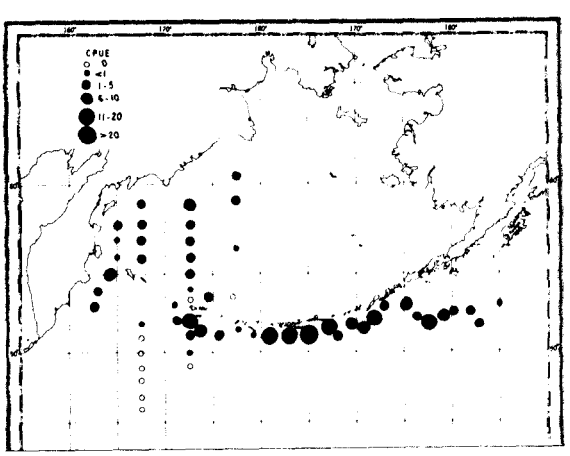

FIGURE 15.—Distribution and abundance of age .1 sockeye salmon in August 1970 as shown by catches of United States and Japanese research vessels.

Sea; the CPUE averaged about four times higher in the North Pacific than in the Bering Sea (sets with no catch were disregarded).

Further evidence of fish remaining in the North Pacific Ocean is provided by tag recoveries in 1964, as reported by Bakkala (1971). His summary of FRI tagging experiments (Figures 16 and 17) shows that immature sockeye, mainly age .1 (129) but including 16 age .2 fish, were recaptured in the North Pacific from 1 to 43 days after tagging. Recovery locations indicated that direction of movement from the tagging site was diverse and that recaptures were made to the south, southwest, west, and north. Four immature sockeye salmon were recaptured in the Bering Sea near lat. 60°N, apparent further evidence of movement of some Bristol Bay immatures into the western Bering Sea.

Because tag recoveries were dependent on the location and effort of the Japanese mothership fleet, the degree of movement to certain areas, as illustrated in Figure 16, may not have been

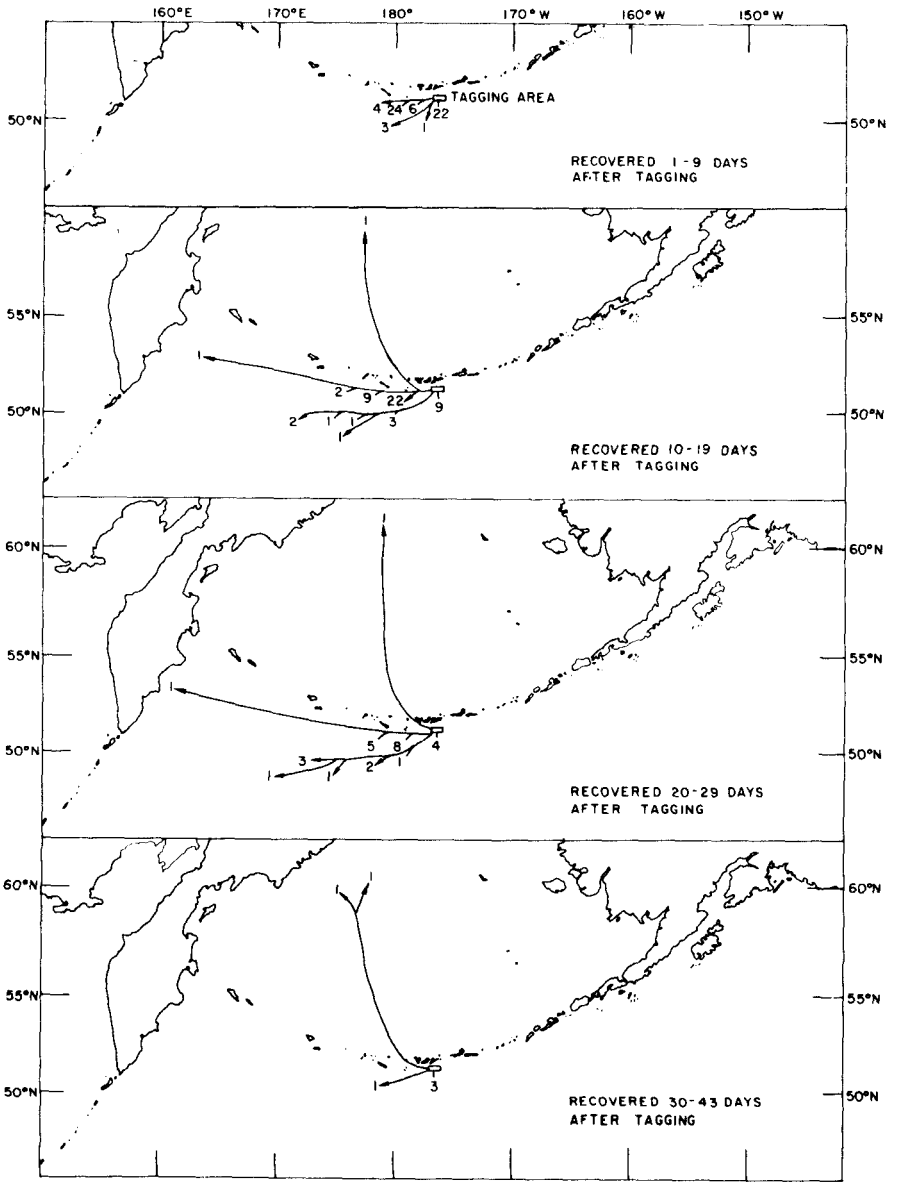

FIGURE 16.—Recovery locations for immature sockeye salmon tagged near Adak Island from 16 June to 24 July 1964 and recovered in the North Pacific Ocean from 12 July to 9 August 1964 (data from Fisheries Research Institute, 1964).

accurately reflected. Effort was concentrated south of the Aleutian Islands (near, west, and southwest of the release location) and in the Bering Sea near lat. 60°N (Figure 17). Movement of tagged fish to the east could not be detected, and movement north and northwest in the area between the Aleutian Islands and lat. 58°N would have a low probability of being detected compared to movement in the North Pacific Ocean. A substantial portion of the recoveries occurred in the North Pacific Ocean over an extended period; 36% of the recoveries were taken 10 to 19 days after tagging, 19% 20 to 29 days after tagging, and 4% 30 or more days after tagging. These recoveries indicated that substantial numbers of the releases remained in the North Pacific Ocean.

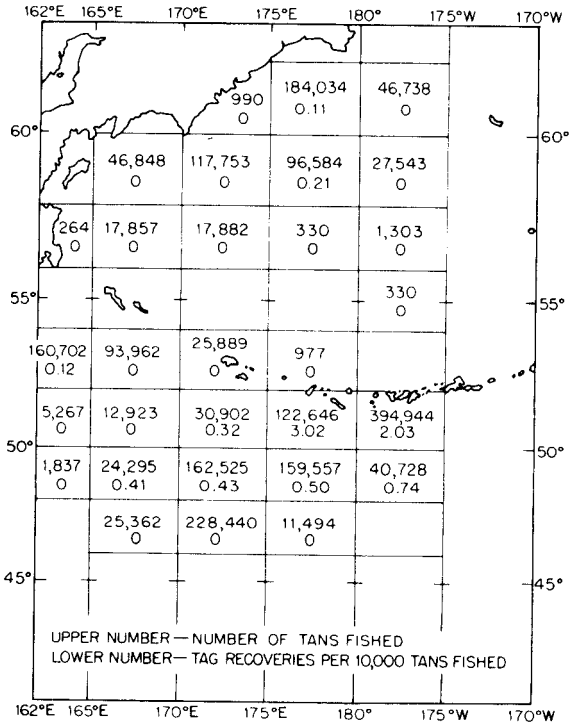

FIGURE 17.—Fishing effort and tag recoveries per unit of effort by the Japanese mothership fleet in 2° by 5° areas and for the period of 21 July to 10 August (data from Fisheries Agency of Japan, 1966 and Fisheries Research Institute, 1964).

There is some doubt about the true proportion of immature sockeye salmon remaining in the North Pacific Ocean in comparison to those moving to the Bering Sea. The rates of return from the high-seas fleet was 3.5% of age .1 fish and 5.1% of age .2 fish, rather low rates considering the total fishing effort, although the small age .1 fish even with tags affixed may not be vulnerable to the fishery with its large-mesh gill nets. By way of comparison tag returns of 8.9% were made on the high seas of maturing fish from tagging experiments in the central and western Aleutian Islands area in 1960 (Hartt, 1966).

Because of the dynamic nature of the ocean migration of salmon (the rate of travel of those recovered in 1964 ranged from 2 to 50 nautical miles per day and averaged 17 nautical miles per day), it is possible that the fish recovered in the North Pacific Ocean after an extended period had migrated extensively and reentered the fishing area south of the Aleutian Islands. We do not know if the immature salmon make such a migration in the summer. It is known, however, that immature sockeye salmon become more widely distributed in the Bering Sea in August compared to their distribution in July (see Machidori, footnote 7), a pattern which might argue against the possibility of a return migration to the North Pacific Ocean in July or even by early August.

In relation to oceanographic features, the age .1 fish in summer were found primarily in the Ridge Area water south of the Alaska Peninsula and eastern Aleutian Islands but were located in both the Ridge Area and the Alaskan Stream south of the central and western Aleutian Islands (Bakkala, 1971). Ridge Area waters in summer were also found to have greater concentrations of food organisms than other water areas of the Subarctic Pacific Region (McAlister et al., 1969, 1970).

In summary, the evidence from distribution studies indicates that movements of Bristol Bay immatures in June are northward from areas they occupy in spring to waters they occupy in summer—generally between lat. 50°N and the Aleutian Islands and Alaska Peninsula. The majority of Bristol Bay fish appears to remain in these waters through the summer, but some smaller proportion continues northward or northwestward into the Bering Sea. Thus, the distribution of immatures is seen to shift northward from spring to summer but not extensively on an east-west plane.

Conflicting with this hypothesis of summer distribution is other evidence which has indicated that migrations in the North Pacific are predominantly and continuously westward throughout the summer (Royce et al., 1968), implying that the population of Bristol Bay immatures is displaced to the west during the summer and leaves waters of the northeastern Pacific Ocean. Direct evidence of immature sockeye salmon migrating long distances across the North Pacific from the northeast Pacific is provided by tag recoveries on the high seas of age .2 immature fish. Three immature sockeye salmon were tagged in the northeast Pacific near long. 145°W in May and recovered in the central Aleutian Islands area in July and August of the same year. Similarly, two immature sockeye tagged south of Unalaska Island in late June were recovered in the western Aleutian Islands area, one near 171°E in late July and one near 173°E in early August of the same year. Such long migrations across the North Pacific have not been demonstrated by the age .1 fish. The apparent contradiction of the two lines of evidence cannot satisfactorily be resolved at

present. It may be that the Bristol Bay population of immatures actually shifts to the west in the summer but to a limited degree, or the movements of the fish are not constant from year to year. Our inability to readily identify stocks of sockeye at sea and the limited sampling make such movements difficult to detect. Another possibility is that migrations are not as directional as some evidence would imply but rather more variable; a yet undetected recirculation (or eastward movement) of immatures may also be occurring to maintain a broad east–west distribution of immatures throughout the summer.

Information on the distribution and movements of age .1 fish in the fall and early winter is limited. The only catch data available are from south of the western Aleutian Islands (Figure 18). Age .1 fish were still abundant in this area in October and November. It is unknown whether these sockeye had remained in the North Pacific Ocean through the summer and fall or were, at least in part, fish that had returned from the Bering Sea.

Immature and Maturing Age .2 (January–June)

During their second winter at sea, the sockeye (now age .2 fish) either remain in the northern part of the North Pacific Ocean or move into southern areas depending on their maturation schedule (if they mature as age .2 fish the following summer or not). Generally most age .2 sockeye mature; the percentage maturing has been estimated as ranging from 60 to 80% each year (Royce et al., 1968). Separation of the immature age .2 fish is evident at least by midwinter. Catch data from winter cruises show a partial separation of the two groups of age .2 sockeye in most areas fished (Figures 19 and 20). This may represent the period when the immature component of the age .2 group are in the process of separating from the maturing group by moving south, leaving the matures in the more northerly waters.

By spring, separation of immature and maturing age .2 sockeye is much more pronounced (French, Bakkala, Osako, and Ito, 1971). It was shown that in the northeastern Pacific Ocean immature sockeye were not taken north of about lat. 49° in April and only appeared in catches in this area in late May and June. Maturing sockeye, however, were taken throughout the area from lat. 49° to 54°N. In the western and central Aleutian area along long. 175°E and 175°W, immatures were primarily south of lat. 48°N, and matures were caught mainly north of this latitude in May.

On the basis of the winter and spring catch data, we surmise that in winter, age .2 immature sockeye start migrating to southern waters and by spring become well separated from the maturing fish. Maturing sockeye tend to remain in northern waters throughout the winter and spring. They are found primarily in Ridge Area water and waters of the Western Subarctic Intrusion Area (Bakkala and French, 1971).

Most of the maturing Bristol Bay population probably shifts eastward in Ridge or Western Subarctic Intrusion Area waters during the fall or winter. Evidence of eastward movement is provided by comparing results of sampling south of Adak Island in summer 1969 with those from south of the Aleutians in spring 1970 (Figure 21). On the basis of age composition, magnitude of catches, and historical tagging data from this area, we conclude that the large numbers of sockeye taken near long. 176°W in July and August were primarily Bristol Bay fish; some of these sockeye undoubtedly moved even farther west, and others were probably already to the west of Adak Island. In spring 1970, sampling demonstrated that most maturing sockeye were east of long. 175°W indicating that many of the fish located west of long. 175°W in the previous summer had returned east of long. 175°W by spring.

The location of concentrations of Bristol Bay sockeye in spring (which is influenced by the extent of their eastward movement in fall or winter) determines the main migration routes taken to reach Bristol Bay; probably the largest part of the population is located east of long. 175°W, and the main migration is through passes east of long. 175°W. This conclusion was also indicated by Kondo et al. (1965). (We do not know the relative abundance or distribution of Bristol Bay sockeye that may be in the Bering Sea in late winter or early spring prior to the time of migration.) The intrusion of the Western Subarctic Gyre or northward shift of the Western Subarctic Current may affect the westward distribution of Bristol Bay sockeye or the eastward distribution of Asian sockeye in some years. For example, the percentage of Bristol Bay fish in catches by the Japanese mothership fleet in the area where Asian and Bristol Bay sockeye salmon

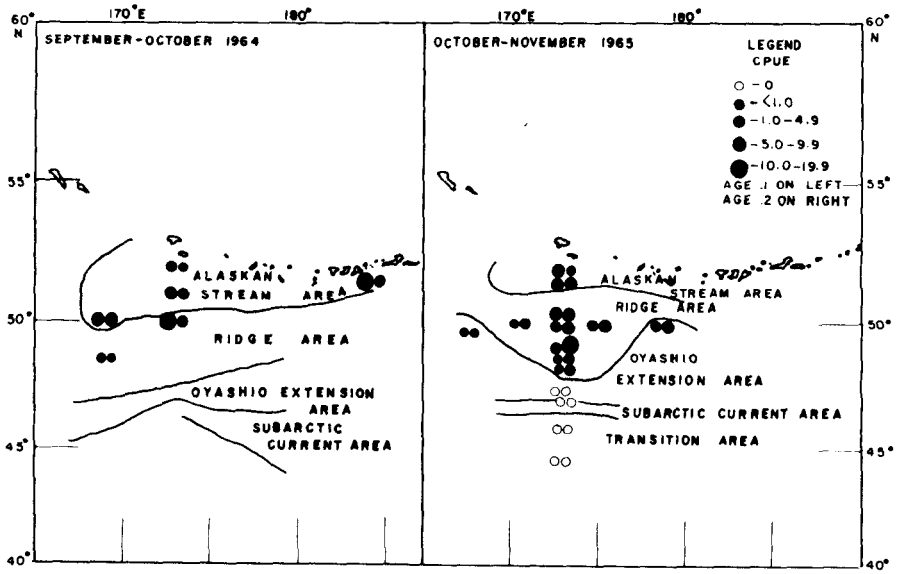

FIGURE 18.—Distribution of immature sockeye salmon in the fall in relation to oceanographic features of the Subarctic Region of the North Pacific Ocean (from Bakkala, Figure 48, 1971).

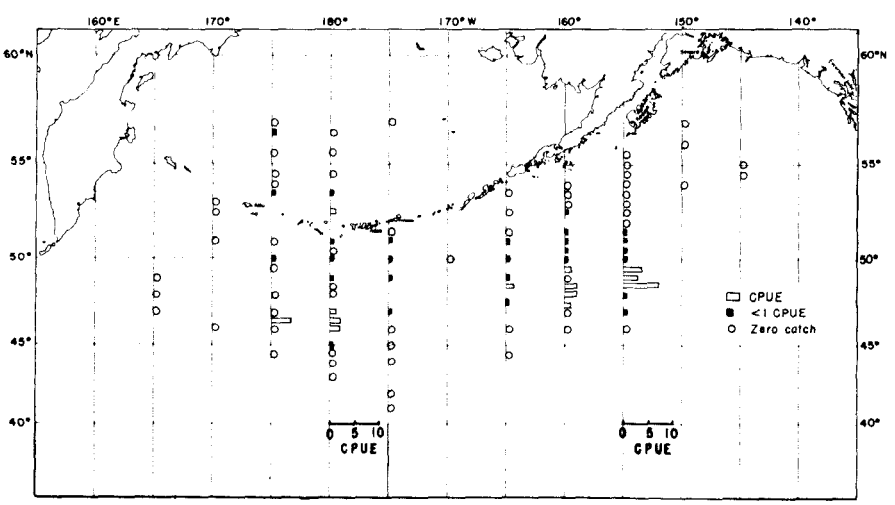

FIGURE 19.—Distribution of immature age .2 sockeye salmon in winter (data from 1962–70 with the exception of 1964, 1966, and 1968).

intermingle (long. 170° to 175°E, lat. 46° to 52°N) was estimated to be 5.8% in 1967 and 49.4% in 1968 (Fredin and Worlund[6]). In spring 1967, cold water (2°C) from the Western Subarctic Domain intruded well east of long. 170°E at lat. 47°N, whereas in 1968 the cold water was farther west than in 1967 (French et al., 1971). This change in the environment may have limited the westward distribution of Bristol Bay fish and in turn the catch of Bristol Bay sockeye by the Japanese in 1967.

Tagging data indicate that salmon west of long. 170°W in April and May will pass through Aleutian Islands passes west of Adak Island; fish east of long. 170°W will pass through Aleutian passes east of long. 175°W. In Figure 22,

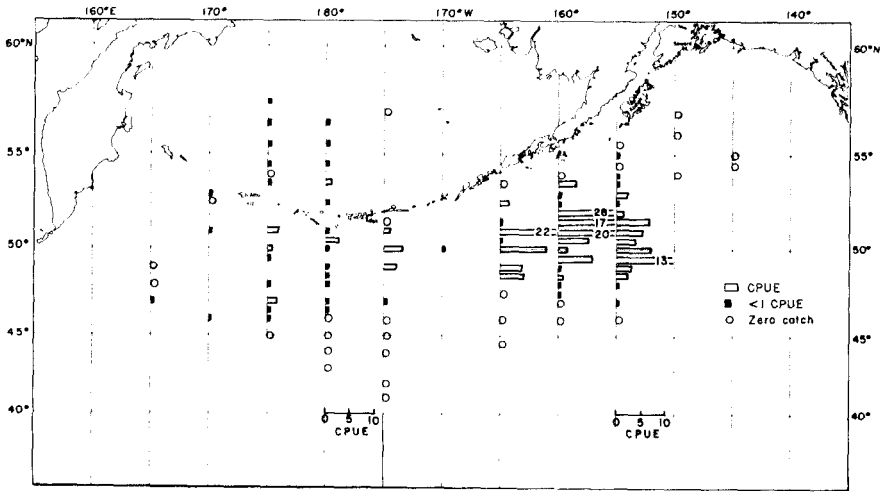

FIGURE 20.—Distribution of maturing age .2 sockeye salmon in winter (data from 1962–70 with the exception of 1964, 1966, and 1968).

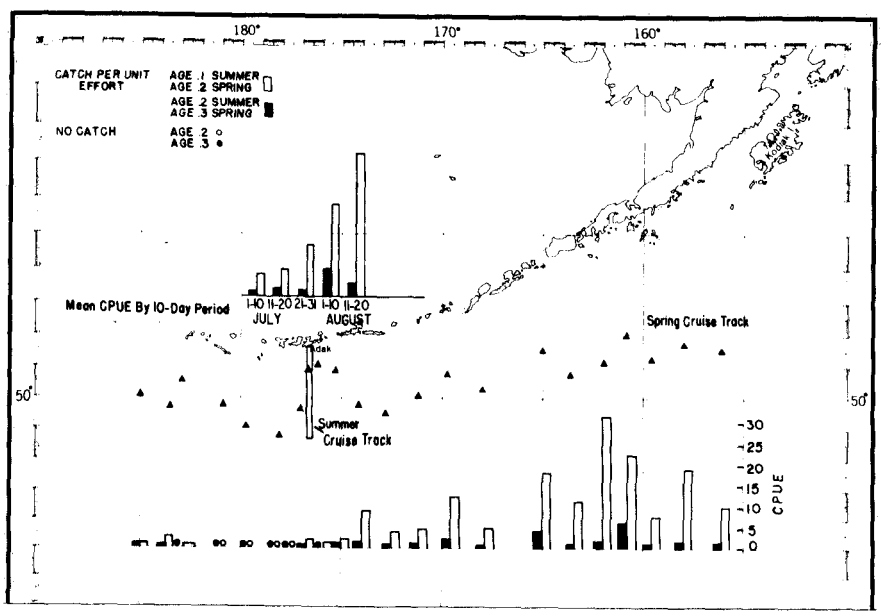

FIGURE 21.—Fishing stations and relative abundance of immature sockeye salmon during summer 1969 near Adak Island (shown above station line) and maturing sockeye salmon in spring 1970 (shown below stations).

recoveries of tagged salmon by the mothership fishery (which were made only west of long. 175°W) show a marked decline in recoveries for tagging locations east of long. 175°W. For tagging locations east of long. 170°W, recoveries were almost all from Bristol Bay and only a very few recoveries were made in the mothership fishery. Thus, primary routes to Bristol Bay for the salmon located east of long. 170°W must have been through Aleutian Islands passes east of long. 175°W (primarily Amukta Pass).

Routes of maturing sockeye salmon moving eastward in the Bering Sea may be variable and over a broad front. Largest catches by the

Japanese mothership fleet between long. 180° and 175°W in the Bering Sea in June occur from the Aleutian Islands to lat. 56°N, and fairly good catches may extend to lat. 58°N (Peterson, 1971). U.S. research vessels have made large catches of maturing sockeye salmon in June near the Pribilof Islands—which indicate migrations far north of the Aleutian Islands. The entry of most sockeye into Bristol Bay, however, is apparently off the southern coast of the bay. Gill-net sampling near Bristol Bay, before the fishing season, between long. 165° and 160°W indicated that the largest concentration of sockeye salmon was about 40 miles (74 km) from the Alaska Peninsula (French, Craddock, and Dunn, 1967). Paulus (1968)[8] reported the largest catches in this area to be from 40 to 60 miles (74 to 111 km) offshore.

Third Year at Sea

Most age .2 sockeye that do not mature after their second year at sea remain an additional year in the ocean and then return to Bristol Bay to spawn as age .3 fish. A few fish will stay at sea still another year to return as age .4 fish, but they make up a very small percentage of the Bristol Bay run. From 1960 to 1965 the estimated number of age .4 fish in the spawning run ranged from 2,300 fish to 25,600 fish or from 0.01% to 0.22% of the total run.

[8]Paulus, R. D. 1968. Bristol Bay intermediate high seas inshore test fishing program, Project AFC-6-2, 1968 field season. Alaska Dep. Fish Game, Annu. Tech. Rep. Anadromous Fish Proj., 61 p.

Immatures Age .2 (July–December)

The immature age .2 sockeye were shown to move south and separate from the concentrations of maturing fish of age .2 in the winter. In the winter and spring, they become intermixed with the newly arrived age .1 immatures. In the summer, they probably repeat the migration they made the previous summer as age .1 fish since age .2 immatures are intermixed with age .1 fish in all areas sampled. Machidori (see footnote 7) shows the immature age .2 sockeye in the Bering Sea in the same general areas as the age .1 sockeye.

Maturing Age .3 (January–June)

The maturing age .3 sockeye, in the winter, are generally distributed in northern areas of the North Pacific Ocean, and in January and February they were also found in the Bering Sea (Figure 23). In these areas, the distribution of age .3 fish overlaps considerably with that of

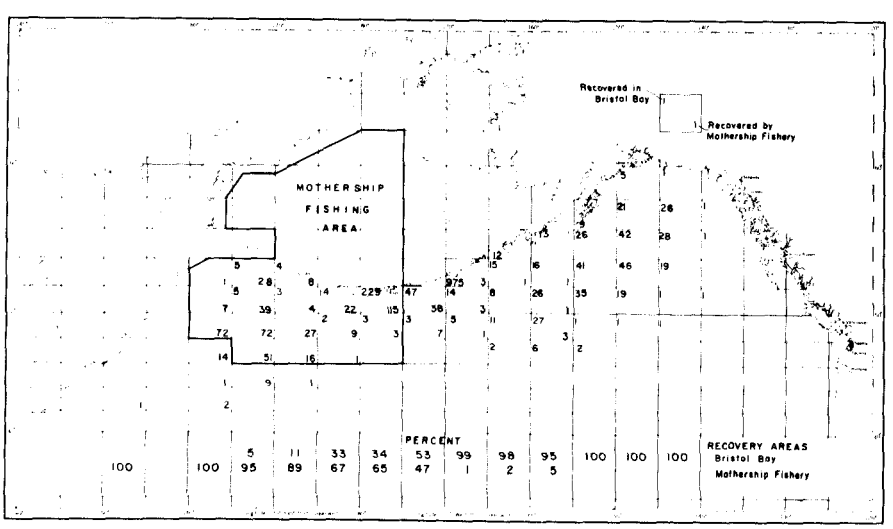

FIGURE 22.—Tagging location for maturing sockeye salmon tagged in the North Pacific Ocean in April, May, and June 1956–67 and recaptured in Bristol Bay or the Japanese mothership fishery. Percentage recovery for each 5° of longitude is shown below.

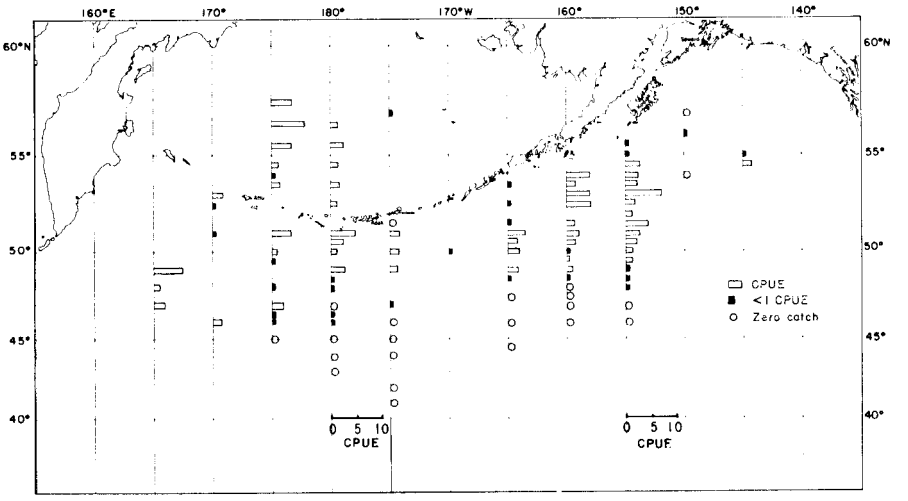

FIGURE 23.—Distribution of age .3 sockeye salmon in winter (data from 1962–70 with the exception of 1964, 1966, and 1968).

maturing age .2 fish but is somewhat north of the latter group. We do not know if these fish remain in the Bering Sea throughout winter and early spring.

By spring, the age .3 sockeye are distributed across the North Pacific Ocean primarily in the Ridge Area and the northern part of the Western Subarctic Intrusion Area waters. Their movements toward Bristol Bay in late spring are assumed to be similar to those described for age .2 sockeye.

INFLUENCE OF WATER AREAS AND CURRENTS ON SALMON MIGRATIONS

In the previous sections we have inferred from various research results the migrations of Bristol Bay sockeye salmon from the time they leave the estuary until they return as maturing fish. We have also shown their distribution in relation to water masses which can be summarized as follows: After leaving the Bering Sea, possibly in Alaskan Stream Area water extruding through Aleutian Islands passes, (Favorite and Ingraham, 1972), the young salmon move southward in winter through the Alaskan Stream and Ridge Areas into the Western Subarctic Intrusion Area waters. In spring they usually are in Transition waters. In early summer they move northward (a reversal of the winter movement) through the Western Subarctic Intrusion Area to Ridge and Alaskan Stream Area waters. Some components of the population move into central and northern parts of the Bering Sea. The salmon that will mature the following spring remain in northern waters, the Ridge Area primarily, over the winter and spring until they commence the spawning migration. Immature age .2 fish repeat the southward movement they made a year earlier and join the new group of age .1 fish. The matures, in late spring, migrate from the Ridge Area and the northern part of the Western Subarctic Intrusion Area waters through the Alaskan Stream and into the Bering Sea through various passes of the Aleutian Islands.

The influence of these water masses on distribution and migrations of sockeye salmon is not evident from our observations. As demonstrated, sockeye salmon in all life history stages appear to move readily in and out of the various water masses. Although salmon at certain life history stages appeared to associate with certain water masses in some years, a shift in location of water masses in other years was not accompanied by a corresponding shift in salmon distribution. Examples of this were shown in Figure 6; in 1962 and 1967, immatures were mainly found near or south of lat. 50°N and in the Western Subarctic Intrusion Area; but in 1970 when this oceanographic feature was located north of 50°N, most immatures were in the same general location

(near or south of lat. 50°N) but were now mainly in the Transition Area. Bakkala (1971) noted a similar situation in the summer; immatures were usually found in the Ridge Area south of the eastern Aleutian Islands and Alaska Peninsula, but when the Alaskan Stream extended farther offshore, the geographical distribution of salmon was unchanged and the immature salmon were in both the Alaskan Stream and Ridge Areas. His data also demonstrated that whereas immatures south of the eastern Aleutian Islands and Alaska Peninsula were found mainly in the Ridge Area, those south of the central Aleutian Islands were most abundant in the Alaskan Stream. The Alaskan Stream was previously thought to be the major route of westward migration for salmon, but westward migration occurred in the Ridge Area as well. The Subarctic Current, a term used to describe the faster moving waters near the boundary of the Western Subarctic Intrusion and Transition Areas, was also hypothesized to be a route of eastward movement by maturing sockeye salmon in fall and winter, but most maturing fish are far north of this current and probably move east in Ridge Area waters.

In summary, it could not be demonstrated that defined oceanographic features of the North Pacific Ocean had any direct influence on the north–south movements and distribution of sockeye salmon. Their movements and distribution may be governed by other environmental conditions such as water temperature or food abundance.

Research vessel catch data and the variable numbers of Bristol Bay sockeye available to the Japanese mothership fishery indicate that maturing Bristol Bay sockeye make eastward migrations in the North Pacific Ocean in the fall or winter and that the proportion of Bristol Bay fish making this migration or the extent of these migrations vary between some years. This is perhaps influenced by the interaction of the Alaskan and Western Subarctic Gyres and possibly by the recirculation of Alaskan Stream waters. Maturing Bristol Bay sockeye are found mainly in the Alaskan Gyre in spring, and if the westward extent of this gyre is limited by the strength of the Western Subarctic Gyre, the westward distribution of maturing sockeye may also be limited. (See Figure 24 for the location of the two gyres.) We have no direct evidence to support this possibility.

MODEL OF MIGRATION OF BRISTOL BAY SOCKEYE SALMON

From the accumulated knowledge of distribution and migration of Bristol Bay sockeye salmon, we have diagrammed a model of their movements from the time they leave the estuary until they return. The model differs from that given by Royce et al. (1968), but the two models are in agreement in regard to the major areas in which the salmon are found.

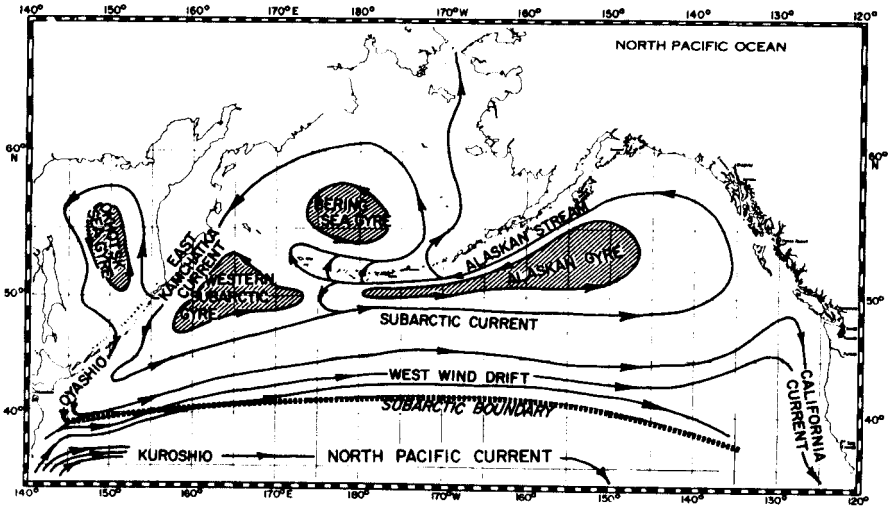

FIGURE 24.—Schematic diagram of surface circulation in the Subarctic North Pacific to illustrate the general location of the Alaskan and Western Subarctic Gyres (from Dodimead, Favorite, and Hirano, Figure 109, 1963).

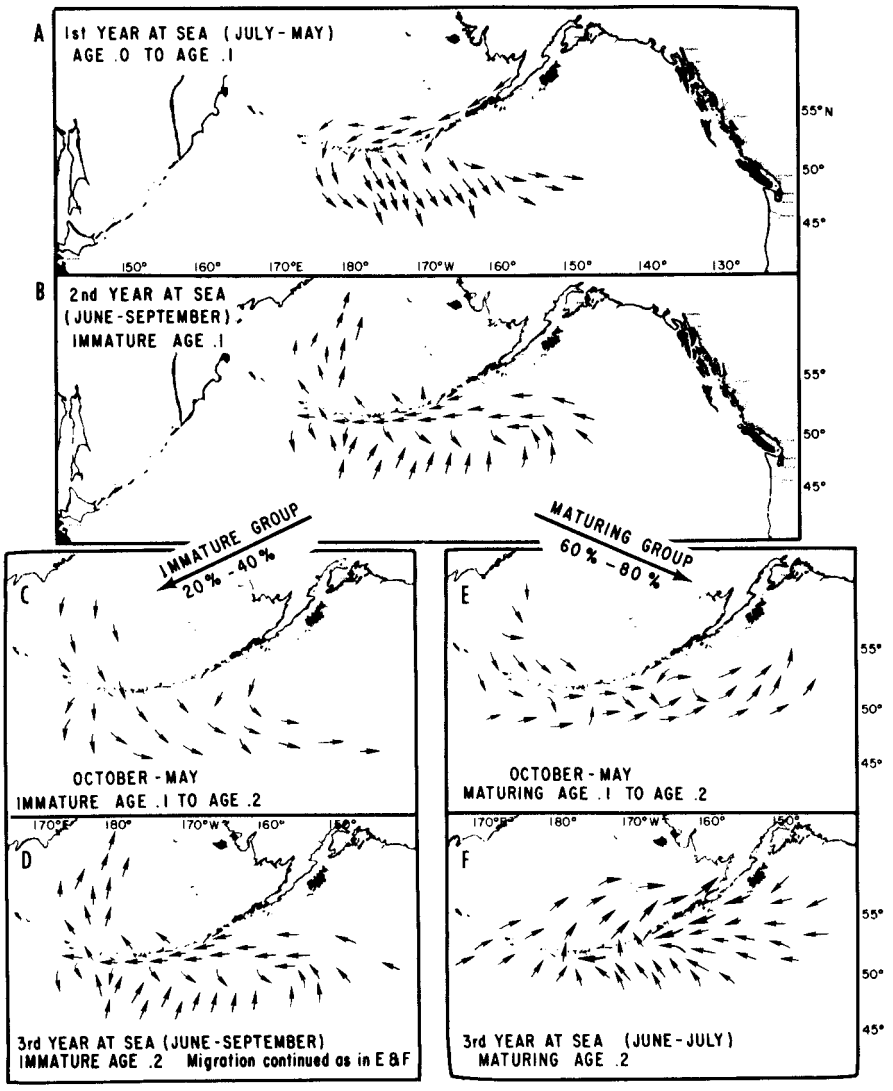

FIGURE 25.—Model of migration of Bristol Bay sockeye salmon.

The new model calls attention to changes in migration or distribution patterns from year to year—which could affect indices of abundance that are based on data from only one area or time period.

A graphical illustration of the model appears in Figure 25, and a brief narrative account follows.

First Year at Sea

Juveniles Age .0 (July–December)

Juveniles, age .0 fish, after leaving the rivers of Bristol Bay, move southwest along the north side of the Alaska Peninsula, and by mid-September many still remain east of long. 165°W and within 90 miles (167 km) of shore. In late fall or early winter the juveniles move southwestward along the Aleutian Islands and then proceed south through various passes, most likely between long. 179°E and 169°W. The migration out of the Bering Sea may be motivated by lowered surface water temperatures and reduced food supplies—juveniles generally are not found in surface waters with temperatures less than 3°C. Principal routes of migration may be through Aleutian Islands passes where the Alaskan Stream branches into the Bering Sea.

Immatures Age .1 (January–May)

The immatures (age .1 on 1 January), after reaching the North Pacific Ocean, move southward through the Alaskan Stream and Ridge Area and by midwinter become located primarily south of lat. 50°N in Western Subarctic Instrusion or Transition Area waters. There is no evidence that the young fish follow major currents during the southward movement; they move southward over a broad east–west area. The young immatures are probably in search of food sources and favorable water temperatures (3.5–6.0°C) that prevail in more southern waters.

In early spring the immatures shift somewhat farther south and become more sharply separated from the matures (sockeye salmon from an earlier brood year). By April and May the immature age .1 fish have reached their southern limit of migration over a broad area from about long. 175°E to 145°W and are found from about lat. 45° to 50°N in Transition and Western Subarctic Intrusion waters—an area of favorable water temperatures, 4.5–6.0°C, and food sources.

Second Year at Sea

Immatures Age .1 (June–September)

In June the immatures start a return northward movement over a broad east–west area. This movement may be related to the increase in surface water temperatures and subsequent zooplankton blooms from south to north.

By July, the age .1 fish have moved north from areas occupied in the spring and are mainly located north of lat. 50°N in the Alaskan Stream and Ridge Areas. These waters in summer have more abundant food than other water areas of the Subarctic Pacific Region, which probably accounts for the distribution of sockeye on the north–south plane. On an east–west plane, the immature sockeye are distributed over a wide area, from about long. 170°E to about 160°W. Most of the fish are moving in a westerly direction during the summer, but recirculation of immatures or limited westerly movement maintains the wide east–west distribution through the summer. Some elements of the population move north into the Bering Sea in summer and become distributed in the central Bering Sea to at least lat. 60°N. The majority of the population remains south of the Aleutian Islands.

The continuity of the Alaskan Stream and Alaskan Gyre or the eastward intrusion of the Western Subarctic Gyre are oceanic features that may influence the western limits of distribution of Bristol Bay immature sockeye.

Separation of Immature and Maturing Sockeye (October–May)

In January and February of this period (the sockeye now become age .2 fish), they separate into immature and maturing components. The immature group will remain at sea a third year before maturing and will follow a somewhat different migration pattern (as shown in Figure 25 C) than the maturing group (Figure 25 E). The remaining period at sea for the immature group will be discussed following the description of movements of the maturing fish.

Maturing Age .1 to Age .2 (October–May)

The age .1 sockeye which will mature the following spring remain in the more northerly waters of the North Pacific Ocean (primarily north of lat. 50°N in the Alaskan Stream and Ridge Areas) throughout fall, winter, and spring until they begin their inshore migration. The extensive east–west distribution of sockeye (which was noted previously) is maintained. Evidence of varying catch rates of Bristol Bay sockeye by the Japanese mothership fishery west of long. 175°W (rates have varied between years from 2.2 to 35.2% of the total run) suggests that the distribution of maturing sockeye shifts to the east in fall and winter and that the magnitude and extent of this movement governs the availability of sockeye to the Japanese fishing fleet.

During this period, the maturing sockeye salmon are associated with the Alaskan Gyre—primarily the Ridge Area, but they are also found in the Western Subarctic Intrusion and Transition Areas, depending upon the location of these oceanic features.

The areas from which the maturing Bristol Bay fish initiate their inshore migration essentially have been established by April as a result of previous migrations. At that time their routes of inshore migration (and the proportion of the population available to the Japanese mothership fishery) have been determined, and variations in oceanographic features are assumed to have little effect on these inshore routes of migration.

Maturing Age .2 (June–July)

In June the spawning migration toward Bristol Bay is northward through Alaskan Stream waters and through various Aleutian Islands passes into the Bering Sea. Maturing age .2 fish move eastward over a broad south–north area extending from the Aleutian Islands to about lat. 58°N. As they approach Bristol Bay the schools of fish become more concentrated, and their main route of migration is about 40–60 miles (74–111 km) from the north side of the Alaska Peninsula.

Third Year at Sea

The fish that remain immature through their second year at sea separate from the maturing component in midwinter and move into more southern waters of the North Pacific (Figure 25 C). Here they are joined by the new group of age .1 fish; the two age groups repeat the migrations already described and shown in Figures 25 D, E, and F.

ACKNOWLEDGMENTS

We are indebted to the Oceanographic Unit (F. Favorite, Program Leader) of the Northwest Fisheries Center (NWFC), National Marine Fisheries Service, NOAA, for definition of oceanographic features and stimulating discussions on the oceanography of the Subarctic Pacific Region. The Stock Identification and Aging Unit of the NWFC (R. Major, Program Leader) provided all salmon age readings from scale samples obtained during the various research cruises. W. Royce, L. Smith, and A. Hartt of the Fisheries Research Institute, University of Washington, authors of a paper on the ocean migrations of Bristol Bay sockeye (Royce et al., 1968), kindly read the manuscript and, although they view the migrations somewhat differently than the present authors, offered many useful suggestions that were incorporated into the paper.

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NOTES

MIGRANT GRAY WHALES WITH CALVES AND SEXUAL BEHAVIOR OF GRAY WHALES IN THE MONTEREY AREA OF CENTRAL CALIFORNIA, 1967-73

This paper presents evidence modifying two statements in the monographic study of the gray whale, *Eschrichtius robustus*, by Rice and Wolman (1971):

1. "The route taken by females with calves during the spring [northward] migration is unknown [page 14]." They arrived at this conclusion after being able to cite only three records of cows with calves over a 10-yr survey period inshore and offshore, at San Francisco and on aerial censuses from San Francisco, Calif., to Cape Flattery, Wash.
2. "Non-pregnant adult females regularly ovulate in late November and early December . . . while still north of central California on the southward migration [page 61]." and "Almost all of the adult females (except those carrying near-term fetuses) taken during southward migration [end of page 73] probably had already conceived, although none was visibly pregnant. . . . The mean conception date calculated from the fetal growth curve . . . is 5 December. . . . The calculated conception dates fall between 27 November and 13 December, except for one on 22 December and one on 5 January [pages 73–74]."

Whales with Calves on Northward Migration

The known breeding grounds of the northeastern Pacific Ocean population of gray whales were described in detail by Gilmore (1960). Rice and Wolman (1971) reviewed in their monograph the seasonal migratory cycle of this species. Leatherwood (1973)[1] reported 23 observations of northbound females with calves sighted during aerial censusing from 1969 to 1972, off southern California. The majority were "well inshore."

[1]Leatherwood, J. S. 1973. Aerial observations of migrating gray whales, *Eschrichtius robustus*, off southern California (1969–1972). California Gray Whale Workshop, 21–22 Aug. 1972. (Unpubl. manuscr.)

At 1400 h on 12 May 1967, at Point Lobos State Reserve near Carmel, Calif., a group of six or seven killer whales, *Orcinus orca*, attacked a gray whale and its 6-m calf, killing the latter as it took refuge in beds of giant kelp, *Macrocystis pyrifera*, (Baldridge, 1972). This was considered to be the same group of killer whales that unsuccessfully attacked two adult gray whales and a calf just outside the surf at Moss Landing, Monterey County on 2 May 1967 (Morejohn, 1968).

At 1350 h on 27 March 1970, at Lucia, Monterey County, 70 km south of Carmel, together with W. B. Gladfelter, I observed an adult and calf, with a second adult in close attendance. All were resting at the surface in open water on a day of remarkable calm. One adult frequently rolled on its side, raising a flipper and half of the tail flukes above the surface. The distance from the point of observation was too great to confirm whether or not the calf nursed. They remained in the same location for 30 min and were still there when observation was terminated.

From 0715 to 0800 h on 16 April 1970, two adults accompanied by their calves with an estimated length of 6–7 m remained in a sheltered cove at Hopkins Marine Station in Pacific Grove, Monterey County, where the water depth is 12 m. Both calves appeared to nurse when the adults rolled on their longitudinal axes, each with a flipper and half fluke raised. Although the calves were mottled in pigmentation, no barnacle incrustations could be seen on the dorsal areas. Upon completion of the nursing behavior the adults, very closely accompanied by their calves, swam off on a course following the shore of Monterey Bay. Northbound whales unaccompanied by calves for the most part follow a direct course from the vicinity of Point Pinos, Monterey County, toward Davenport, Santa Cruz County, 48 km to the north.

At 0900 h on 15 May 1971, at Julia Pfeiffer Burns State Park, 40 km south of Carmel, Judson E. Vandevere and I observed two adults, one very closely accompanied by a half-grown calf. They swam steadily north very close to, and in some instances through, the outer edges of the kelp beds.

At 1200 h on 3 May 1973, at Hopkins Marine Station in Pacific Grove, an adult and calf, closely attended by two more adults, the four in very close formation and almost touching, followed a course identical with that of the animals seen on 16 April 1970. They did not appear to stop and nurse although there was much splashing and rolling on their sides as they proceeded.

In addition to these observations, L. G. Ingles (1965:329) recorded an instance of nursing behavior observed "early one April a few miles south of Carmel." P. Sund of the National Marine Fisheries Service reported (pers. commun.) that on 23 January 1973, during aerial censusing of southbound gray whales, he observed an adult with a small nursing calf just north of Pt. Sur, Monterey County. This is the first instance which has come to the attention of this author, of a calf born north of San Diego, Calif.

Hubbs (1959) in describing the northwar migration off southern California stated "the cows with calves seem to take a more offshore path." With the possible exception of the 1970 record, my own observations suggest that females accompanied by calves keep very close to shore, often moving through the outer fringes of the extensive beds of giant kelps. In all of these observations the very close proximity of calves to females when swimming was apparent. J. S. Leatherwood (pers. commun.) indicated that his aerial observations showed the calves "all nearly touching the mother."

Sexual Behavior of Courting and Possibly of Mating Pairs and Trios

Published reports of sexual activity in gray whales outside the known calving areas in western Mexico were reviewed by Rice and Wolman (1971:97). They are of a fragmentary nature and include a single observation in Humboldt County in northern California (Houck, 1962) and several summer reports of courtship behavior and apparent copulation from the Bering Sea (Tomilin, 1937; Sauer, 1963; Fay, 1963). In addition, Gilmore (1960:12) stated that gray whales "occasionally calve and more often mate in waters off San Diego." The species bred in large numbers in San Diego Bay until the 1870's (Gilmore, 1960).

It would therefore seem worthwhile to indicate that such activity is not unknown in the Monterey Bay area of central California. It has been observed during both the southbound and the return migration (See Table 1).

In all cases the attention of the observer was first drawn to these whales by behavior unlike that of the normal activity of migrating whales. The whales remained in one particular place for long periods and frequently exposed flukes and flippers in a manner not typically seen in actively migrating individuals.

Because Sauer (1963) provides the only detailed published description of courtship behavior in this species, I have used the same terminology in the present account. After cessation of migratory swimming, the whales remained for the most part within a very small area, with one individual, thought to be the ♀, proceeding to swim almost imperceptibly, with an "exaggerated arching" (Sauer's phrase) out of the water of the back and caudal area. This was repeated several times, following which the ♂ appeared to maneuver to get beneath the ♀, by rolling on his side with one flipper and half of the fluke raised vertically above the water surface. After one or more attempts in this manner, the "♀ rolled around the longitudinal axis" (Sauer's phrase) and in apparent genital contact the whales proceeded to "swim in line" (Sauer's phrase) for periods of up to 30 s. In this position the left flipper of the ♂ and the right flipper of the ♀, together with the left half of the male's flukes and the right half of that of the female were raised above the surface as the two whales moved very slowly forward.

The ♀ in the initial stages, and prior to rolling around the longitudinal axis, often raised her head from the water at a 35° angle. The swimming in line sometimes began or ended with both animals apparently in genital contact vertically in the water column, both with their heads raised above the water surface and some 3—4 m apart.

The fact that this was copulatory behavior of considerable intensity was apparent from the erect penis of the male, which was clearly visible on many occasions. When the ♀ failed to roll on her side, the ♂ then appeared at the surface ventral side uppermost with penis erect in an approximate semicircle. Gilmore (1954) illustrates this posture. On one occasion (28 January 1971) while the ♂ swam in this way, the penis was seen to be extruded and withdrawn. The sequence of events leading to copulation was repeated as many as three times within a 2-h period.

It is of interest to note that on six of the eight occasions on which courtship behavior was observed, there were three whales involved. The

TABLE 1.—Sexual behavior, indicating date, water depth, locality, migration direction and remarks.

Date time water depth	Location[1]	Direction of migration	Remarks
27 Jan. 1968 1520–1720 h 18 m	300 m off Lover's Point, Pacific Grove	south	2 whales attempting copulation (see text for description).
27 Mar. 1970 1230–1300 h 40 m	850 m offshore at Lucia, 70 km south of Carmel	north	3 whales lay at the surface and rolled on their sides. Water surface much agitated and 2 animals seen to surface with heads vertically thrust from the water as far as the eye, in close enough contact to be attempting copulation. No penis observed. 0.5 km away another pair behaving similarly. Water exceptionally calm.
28 Jan. 1971 1445–1600 h 32 m	400 m off Hopkins Marine Station, Pacific Grove	south	3 whales made repeated attempts at copulation (see text for description).
3 Feb. 1971 0700–1200 h 30 m	400 m off Cannery Row, Monterey	south	2 whales repeatedly attempted copulation.
18 Mar. 1972 0925–1000 h 30 m	near Point Pinos, Pacific Grove	north	3 courting whales observed by Margot Nelson. Erect penis of ♂ clearly seen during attempted copulation.
21 Mar. 1972 1230–1430 h 40 m	400 m north of Point Pinos, Pacific Grove	north	3 courting whales. Still in progress when observation terminated (see text for description).
24 Mar. 1972 1700 h 40 m	1 km north of Lover's Point, Pacific Grove	north	3 courting whales observed. Too far off for details to be observed, although behavior pattern similar to that observed on other occasions.
4 Apr. 1972 1800–1830 h 20 m	Close to Point Pinos, Pacific Grove	north	3 courting whales. Behavior similar to that observed on other occasions, although no penis observed. For whole period of observation 3–4 California sea lions *Zalophus californianus* cavorted around the whale trio, about their heads, moving under and over the whales, often "porpoising." On occasion the sea lions would remain vertically in the water, heads down beneath the surface, presumably observing the whales, while their hind flippers protruded from the surface.

[1]All locations in Monterey County, Calif.

third whale was always in very close attendance and apparently in bodily contact with the pair attempting mating. Gilmore (1960:16; 1968:12) observed such trios in Mexican waters and speculated that the third whale was another ♂. "With half of the females unavailable each winter 'for mating', there are two eligible males for each female." He described the apparent lack of aggression between ♂♂, and this appeared to be so in the present observations. Walker (1971:403) believed the second male in such trios helps to stabilize the mating pair. More detailed aerial observation will be needed to clarify the role of the second male.

In comparing the Monterey observations with Sauer's detailed Bering Sea account, the following differences were noted:

1. His observations appear to have involved pairs rather than trios, although Fay (1963) reported three whales involved in "courtship play" some 30 km from the site of Sauer's observations.

2. Sauer does not mention seeing the penis displayed.

3. Sauer's animals repeatedly swam in circles 50–200 m in diameter. Such circling was not discernible in Monterey, where the activity took place in the open sea rather than within the confines of a small bay.

4. His description of the female initiating and achieving copulation (Sauer, 1963:166) by means of a "touch display" could not be verified in Monterey, where the observers' viewpoint was usually only 7–8 m above the water surface and the whales from 300 to 600 m distant. Sauer (1963:159) also described the whales as sensitive to his silhouette on the cliffs above and liable to break off courtship activity. This contrasts with behavior in Monterey, where courting pairs and trios were seen on three occasions to be approached by powered boats to within a few meters without apparent interruption of their activity. No "post-copulatory shake" was observed among the Monterey animals.

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NET FILTERING EFFICIENCY OF A 3-METER ISAACS-KIDD MIDWATER TRAWL

The errors associated with quantitative sampling of open ocean populations of zooplankton and epipelagic nekton have received considerable attention. Net selectivity, net sampling efficiency, and patchiness have been examined by Barkley (1964), Murphy and Clutter (1972), and Wiebe and Holland (1968), respectively. Studies of the error caused by avoidance have been summarized by Clutter and Anraku (1968) and further advanced by Barkley (1972). Aron and Collard (1969) have reported on the effects of net speed on catch. Extrusion of organisms through the net, the degree of mesh retention, and the effects of net clogging have been summarized by Vannucci (1968), and a review of filtration problems has been presented by Tranter and Smith (1968).

Somewhat less effort has been directed toward problems encountered in sampling the midwater fish fauna. Harrison (1967) reported on the reliability of trawl data, the bias that may result from using various types of gear, and the problems associated with sampling mesopelagic fishes. These fishes are commonly sampled with an Isaacs-Kidd Midwater Trawl (IKMT) (Isaacs and Kidd, 1953) and results of such sampling, which include considerations of net performance, have been reported by Pearcy and Laurs (1966), Gibbs et al. (1971), Friedl (1971), Backus (1972) Krueger and Bond (1972), and others.

Net performance is critically dependent on the filtering efficiency of the net. Filtering efficiency is a measure of the total volume of water filtered by the net and enables a better quantitative estimate to be made of the actual population density of organisms sampled. Pearcy and Laurs (1966) reported a filtering efficiency of 85% for a 2-m IKMT. To the authors' knowledge, no comparable figure has been published for the 3-m IKMT. This paper investigates the efficiency of this larger net.

Methods

In conjunction with studies of macroplankton and midwater fishes of an area off Bermuda called Ocean Acre (Brooks, 1972), experiments were conducted in January 1973 to determine the net filtering efficiency of a 3-m IKMT.

Although the design and shape of the 2- and 3-m IKMTs in general use are similar, it is obvious from the literature that net construction may vary considerably. The size of the mesh and the thread of the outer net may differ widely, as may the pattern of a graded mesh. Liner mesh size, type, and placement within the outer net, as well as size, shape, and mesh of the cod end of the net, may also differ. As shown in Table 1, the cross-sectional area of the net mouth may also vary.

Since the influence of such factors on the filtering efficiency of a given net can be considerable, the net used in the present experiment is described in detail. Dimensions and material specifications are shown in Table 2. The net was made of No. 21 thread nylon and has outer walls of 6.36-cm stretch mesh. The entire inner surface of the net was lined with No. 42 thread knotless nylon having a 0.95-cm stretch mesh, which was sewn to the outer walls of the net at every foot.

The aft tube of the IKMT was fitted with four rings made of 0.95-cm-diameter stainless steel rod spaced as follows: one 0.81-m-diameter ring at the aft end of the funnel, one 1-m-diameter ring at the aft end of the tube, and two 0.66-m-diameter rings in the aft tube centered between the other rings. The mouth of the net was hung on 1.59-cm-diameter Polydac[1] net rope with four legs extending 0.61 m and the center bosom leg extending 0.41 m. Riblines, composed of 0.95-cm-diameter nylon rope, were rigged down each of the five seams from the mouth opening to the cod end. A standard 1-m conical nylon plankton net (1-m mouth diameter tapering to 19 cm over its length of 3 m) of No. 00 mesh (0.752-mm aperture) was attached to the aft end of the main body of the IKMT. Dimensions of the IKMT mouth are shown in Figure 1; cross-sectional area was 7.08 m^2, and principal dimensions of bridle and paravane were as specified for the 3-m IKMT in Aron (1962).

TABLE 1.—Mouth area of Isaacs-Kidd midwater trawl.

Reference	2-m IKMT (m^2)	3-m IKMT (m^2)
King and Iversen (1962)[1]	3.21	8.19
Aron (1962)	—	7.44
Pearcy and Laurs (1966)	2.89	—
Friedl (1971)	2.94	7.68

[1]Calculated from dimensions given in Figures 7 and 9, respectively.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Dimensions and material specifications of 10-foot IKMT net used for filtering-efficiency studies.

Item	Dimension
Mesh size	
Forward section	[1]0.95 cm
Intermediate section	[1]0.95 cm
Cod end	0.75 mm
Cross-section area	
Mouth	7.08 m^2
Intermediate section	
Forward end	0.52 m^2
Mid section	0.34 m^2
Aft end	0.79 m^2
Cod end	0.79 m^2
Filtering area	
Forward section	52.39 m^2
Intermediate section	12.12 m^2
Cod end	2.27 m^2

[1]Knotless nylon liner—stretched mesh size

When the net is in regular use, a Mark III (15-cm-diameter) GM discrete-depth plankton sampler (DDPS) (Aron et al., 1964) is attached to the aft end of the 1-m plankton net.

Estimates of the filtering efficiency of the 3-m IKMT described here were obtained by two different methods. In the first method, a calibrated TSK (Tsurumi-Seiki Kosakusho) flowmeter was mounted in the net mouth as shown in Figure 1. The meter (A) was tautly suspended by 0.32-cm steel cable (B) inside a 1-m-diameter ring of 1.9-cm-diameter brass rod (C). The 1-m ring, in turn, was suspended in the net mouth by three legs of 0.95-cm-diameter shock cord (D). Each leg of the shock cord was tensioned so that the ring and suspended flowmeter were positioned in the approximate center of the net mouth and maintained at right angles to the water flow during net towing. During the tows, the shock cord stretched, positioning the ring and flowmeter about 1 m inside the net mouth. It is assumed that the water flow at the center of the net mouth was representative of the average flow through the entrance. A second TSK meter of identical design and calibration characteristics was mounted on the spreader bar outside the net. The difference in the number of revolutions registered by the two meters was used in arriving at the estimate of filtering efficiency. The four-bladed impeller of each meter was restrained from turning until after the net was launched and in its towing position.

In the second method used to determine filtering efficiency, a Clarke-Bumpus (C-B) plankton sampler (Clarke and Bumpus, 1950), with shutter

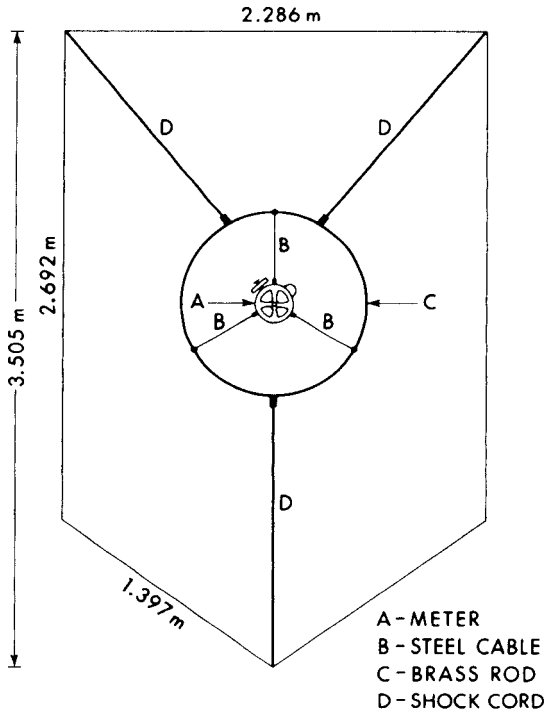

FIGURE 1.—Diagrammatic view of 3-m IKMT mouth with mounted flowmeter.

and net removed, was suspended in the IKMT mouth. This sampler had been calibrated by carefully controlled tows over distances of 2 and 6 nautical miles before being installed in the IKMT. Start and end positions for each tow were determined by radar, LORAN, and shore fixes.

The three legs of shock cord used in the previous trial were attached directly to the frame of the C-B sampler so that the flowmeter could pivot freely within its frame. During launch and again as soon as the flowmeter cleared the water during retrieval, the flowmeter automatically pivoted, causing the axis of the impeller to lie perpendicular to the direction of the tow; i.e., the meter did not register. The impeller blade housing protected the blades from winds, thus preventing rapid spinning of the impeller and erroneous flow readings. As soon as the net was lowered and in towing position, proper aspect of the impeller axis (parallel to the flow) was maintained by water pressure acting on the stabilizing fins attached to the impeller blade housing.

Two net tows were carried out using this apparatus, with the shock cord again stretching to place the C-B sampler just inside the net mouth. Start and end positions were obtained, as during the calibration runs, by radar, LORAN, and shore fixes. Previously determined calibration information allowed calculation of the number of revolutions that would have resulted if the sampler had been towed by itself over the same known distances covered during the two tows.

All net tows were made at ship speeds ranging between 3 and 4.5 knots over distances of 6 and 10.75 nautical miles. The direction of the tows was approximately perpendicular to the prevailing current flow. Very little biological material was captured during these net tests, hence clogging was considered a negligible factor.

Results and Discussion

The two methods used to determine filtering efficiency yielded similar results (Figure 2). For method 1, the total number of revolutions (N′) registered by the meter in the net mouth is plotted against the number of revolutions (N) registered by the meter on the spreader bar for the two net lowerings. These results are shown as squares. For method 2, the number of revolutions (N′) registered by the calibrated C-B meter

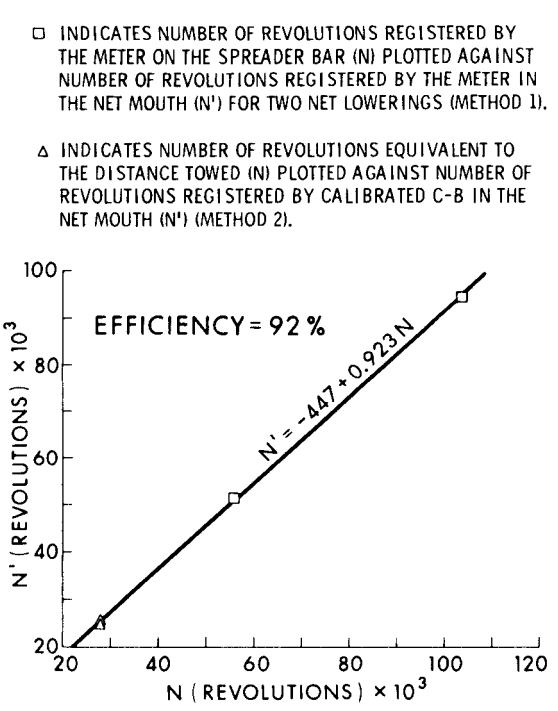

FIGURE 2.—Filtering efficiency of 3-m IKMT.

in the net mouth is plotted against the number of revolutions (N) obtained in the calibration distance tow. These data are shown as triangles.

A linear regression analysis performed on the data points produced the regression line shown in Figure 2. The slope of the line (regression coefficient) was taken as a measure of the filtering efficiency of the 3-m IKMT and had a value of 92%. Although the filtering efficiency determined by this study applies to the specific net described in this note, it can probably serve as a guide to the filtering efficiency of most 3-m IKMTs and enable a better quantitative estimate to be made of the actual population density of organisms sampled.

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AMERICAN LOBSTERS TAGGED BY MAINE COMMERCIAL FISHERMEN, 1957-59

In 1957 at the suggestion of C. Owen Smith, then editor of the "Maine Coast Fisherman," several commercial lobster fishermen volunteered to tag illegal American lobster, *Homarus americanus*, with tags furnished by the Maine Department of Sea and Shore Fisheries. The purpose of the tagging was to obtain additional information on the migratory behavior of lobsters.

Between April 1957 when the first lobster was tagged and October 1959 when the last of the recaptures was reported, 162 lobsters ranging from 78 to 200 mm in carapace length (CL) were tagged and released under this cooperative program. No legal lobsters were tagged. The lobsters consisted of four illegal classifications: 1) those with extruded eggs, 2) those less than the legal minimum size, 3) those larger than the legal maximum size, and 4) those which had had a V-shaped notch cut into the telson to signify successful motherhood. Seventy-three were tagged in Penobscot Bay (72 in 1957 and 1 in 1958) and 89 in Sheepscot Bay (all in 1958).

The small number of lobsters involved does not permit definitive conclusions regarding their behavior. The evidence furnished by the results does not agree with tagging reports before and since (Harriman 1952,[1] Cooper 1970) of an area which apparently is more isolated and the lobster population more static.

Of the lobsters tagged, 75 or 46% were 127 mm or larger in carapace length. Only 23 or 14% of the total tagged were recaptured (2 were recaptured twice), 14 were recaptured after more than 1 mo of freedom, and the remaining 9 were recaptured within 1 mo. Although only 18 or 24% of large lobsters (127-200 mm) were recaptured, they represented 78% of all lobsters recovered (Table 1). Four or 22% of large lobsters recaptured, all from Penobscot Bay, traveled 75 or more nautical miles from the point of release to the place of recovery (Table 2, Figure 1). In addition, one V-notched female of 111 mm CL tagged near Tom Rock, Sheepscot Bay, was recaptured 7 mo later near Race Point Light off Provincetown, Mass.

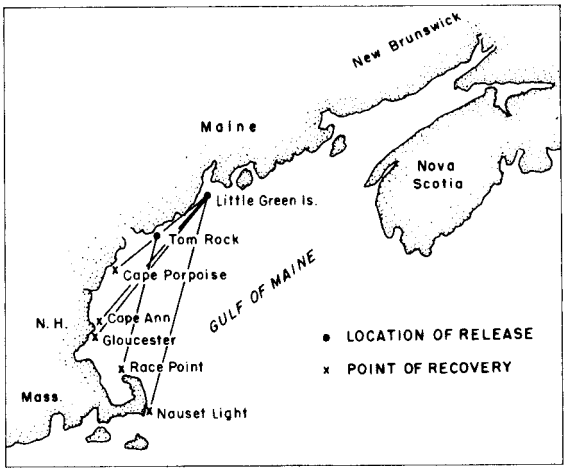

FIGURE 1.—Location of release and point of recovery of the five major wandering lobsters.

The four from Penobscot Bay included a large female tagged near Little Green Island and recaptured near Timber Island, Cape Porpoise, 2 mo later; another large, sexually unidentified lobster also tagged near Little Green Island in April 1957 and recaptured near Gloucester, Mass., 14 mo later; and a 133-mm CL male tagged 12 September 1957, near Little Green Island and recaptured 19 March 1959, near Cape Ann Light, Mass. The longest migration was from Penobscot Bay to Nauset Light, Mass., an estimated straight-line distance of 138 nautical miles (250 km) made in 13 mo by a lobster greater than 127 mm CL and of unidentified sex.

Of the five major wandering lobsters, four exceeded the Maine maximum legal size of 127 mm, suggesting that large mature lobsters are more prone to major migration than are smaller lobsters.

Before they were recaptured, 6% of the 68 Penobscot Bay tagged lobsters between 127 and 151 mm CL traveled between 75 and 138 nautical miles from the release area. This compares with an average 7% recovery of all sizes reported by Cooper and Uzmann (1971) of their tagging from April 1968 to June 1969.

One 79-mm CL female, the smallest lobster recaptured, traveled less than 6 nautical miles (10.9 km) in 9 mo. All other recaptures were lobsters 90 mm or larger. One of these traveled

[1]Harriman, D. M. 1952. Progress report on Monhegan tagging—1951-1952. Maine Dep. Sea Shore Fish., Augusta. (Unpubl. Rep.)

TABLE 1.—Tagging and recovery data.[1]

Carapace Length (mm)	Tagged lobsters							Recovered lobsters				
	Penobscot Bay			Sheepscot Bay				Penobscot Bay			Sheepscot Bay	
	M	F	Unk	M	F	Unk	Total	M	F	Unk	F	Total
178-200	1	3					4	1				1
127-151	40	25	3	3			71	10	5	2		17
102-126		1			14		15				2	2
78-101				31	39	2	72				3	3
Total	41	29	3	34	53	2	162	11	5	2	5	23

[1]M = male, F = female, Unk = not determined.

TABLE 2.—Information on the five major wandering lobsters.

Tagging site	Sex[1]	Carapace length (mm)	Tagging date	Recapture site	Recapture date	Elapsed time (mo)	Approximate distance traveled	
							Nautical miles	km
Little Green Isl. Penobscot Bay, Me.	Unk	>127	4/57	Nauset Light, Mass.	5/26/58	13	138	250
Little Green Isl.	F	>127	5/10/57	Cape Porpoise Maine	7/16/57	2	75	136
Little Green Isl.	Unk	>127	4/57	Gloucester Mass.	6/5/58	14	113	205
Little Green Isl.	M	133	9/12/57	Cape Ann Mass.	3/19/59	18	113	205
Tom Rock Sheepscot Bay, Me.	F	111	11/4/58	Race Point Light, Mass.	6/5/59	7	113	205

[1]Unk = not determined, F = female, M = male.

8 nautical miles (14.5 km); the remainder less than 4 nautical miles (7.3 km). Movements appeared to be random in contrast to the southwesterly trend of the major migrants.

Preliminary conclusions resulting from this study are supported by the frequent comments of Massachusetts lobster fishermen who profess appreciation for Maine's maximum size limit which permits lobsters, telson V notched in Maine, to migrate to Massachusetts where they are legal.

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EFFECTS OF OIL ON MARINE ECOSYSTEMS: A REVIEW FOR ADMINISTRATORS AND POLICY MAKERS

DALE R. EVANS[1] AND STANLEY D. RICE[2]

ABSTRACT

A broad selection of recent literature on the effects of oil on marine ecosystems is reviewed. The focus is on studies on crude oil, and the results are discussed with the purpose of providing a summary of findings that will be a useful reference for administrators and policy makers involved in decisions concerning petroleum developments and related activities. The characteristics of crude oil and factors modifying its impact on the marine environment are discussed. Most research on the toxicity of oil has dealt with acute effects and data on long-term impacts at the community level are inconclusive. It is concluded that chronic low-level pollution is potentially more damaging to ecosystems than isolated catastrophic spills. Decision makers are forced to rely on interpretative judgments rather than conclusive data.

Much of the material in this report was gathered as background material for use in preparing the marine section of the final environmental impact statement on the proposed trans-Alaska pipeline system (U.S. Department of the Interior, 1972). Some of the statements are essentially unchanged from the way they were presented in the appendix to volume IV of the impact statement. The impact statement made it clear that not enough data are available to analyze conclusively all of the potential environmental impacts of operation of the pipeline marine terminal facilities at Port Valdez, Alaska, and the transshipment of crude oil by tankers to west coast ports. A conclusion that can be drawn, however, and a message of the impact statement, is that oil poses a significant hazard to marine ecosystems, and a good deal of intensive research is necessary if these hazards are to be quantified and fully understood.

Research on oil pollution published since the impact statement on the pipeline was issued reveals that scant progress has been made, particularly with regard to the effects of chronic low-level oil pollution. Current and projected demands for energy in the United States are prompting accelerated development of offshore petroleum reserves, expanded oil tanker traffic, and proposals for construction of deepwater port facilities to handle the increasing number of supertankers. These developments will not wait for conclusive answers to questions on oil pollution. Recognizing this, we feel it is important that public administrators and policy makers be made aware of the inferences and trends evident in the research findings to date. These findings present a persuasive case that decisions regarding the handling of crude oil and petroleum products should be conservative and in favor of protecting the natural environment. While this report is by no means a complete review of the literature, it is sufficient to illustrate the potential danger of oil pollution to marine ecosystems and provide some guidance for policy decisions.

History is replete with examples of man's scientific and technological advances carrying him into situations he did not fully comprehend and with consequences he could not evaluate. Bella (1970) noted that "our ability to change this world is going to increase faster than our ability to predict what that change is going to be." He concludes that our management procedures must recognize the degree of ignorance we have about this world in which we live.

Pollution of the ocean by oil is a worldwide problem of growing concern to many nations. Spills like the *Torrey Canyon*, the *Arrow*, the Santa Barbara Channel blowout, and other spectacular incidents have helped stimulate international organizations of governments and industry to react to the problem. Viewed pragmatically, international response has been at least as adequate as domestic programs. Predicting the impact of an oil spill on the environment requires an understanding of the complex interactions involved. What

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appears to be universally lacking is the difficult research leading to an understanding of chronic and sublethal effects of oil at the biological community level. The following discussion outlines these complexities and points out how they make most generalizations invalid and the extrapolation of most data dangerous.

DESCRIPTION OF OIL

Crude oil is a complex mixture of many different specific hydrocarbons and a variety of compounds containing sulfur, oxygen, nitrogen, and some trace metals. Hydrocarbons make up the bulk of crude oil and can roughly be placed into one of three classes: paraffinic, naphthenic, and aromatic. From one area to another, crude oils vary in their composition and in density, volatility, and solubility. Their relative toxicity will vary (Ottway, 1971) but is roughly proportional to their aromatic content.

Paraffinic (or aliphatic) hydrocarbons are straight or branched carbon chains and are saturated (thus no carbon-carbon double bonds) with hydrogen or other groups. These hydrocarbons are the least toxic, although they may have an anesthetic or narcotic effect if concentrations are great enough.

Naphthenic compounds (cycloparaffins) contain at least one ring structure that is saturated. With this base, more rings or chains may be attached to form a variety of complex molecules.

Aromatic hydrocarbons also contain a ringed structure, but the ring is unsaturated with hydrogen and contains carbon-carbon double bonds (benzene ring). The simplest aromatic is benzene, which is very toxic and relatively water soluble in comparison to most hydrocarbons found in crude oil. Benzene and other low-boiling aromatics are the most toxic petroleum fractions. High-boiling aromatics act as slower poisons than low-boiling aromatics, but they are equally severe in their effect. In addition, some are known to induce cancer; 3,4-benzpyrene, 1,2-benzanthracene, and some alkylbenzanthracenes have been isolated from crude oil, and their carcinogenic effects on animals and man have been demonstrated (Blumer, 1970).[3]

Olefinic hydrocarbons (paraffinlike but unsaturated and containing reactive carbon-carbon double bonds) are not generally found in crude oils but are plentiful in certain gasolines and other refined products. The fate of olefins in the marine environment is poorly understood, but this class of compounds may be quite reactive under certain conditions and may combine readily with hydrogen, oxygen, chlorine, sulfur, and other elements to produce toxic substances. Once incorporated into organisms, olefins may remain intact for surprisingly long times (Blumer, 1967). The full range of olefinic hydrocarbons probably interferes with the reception of chemical messengers, or odors, in the sea by certain marine organisms (Blumer, 1970, see footnote 3).

When crude oil is processed ("cracked"), olefins and other compounds for gasoline and fuel oils may be formed or separated. Fuel oils, commonly involved in spills, are rated from 1 to 6. Those rated 1 are the lightest, most volatile, and most toxic and have the greatest aromatic concentrations; those rated 6 are the least volatile, least soluble, and least toxic and are asphaltic (tarlike).

Hydrocarbons are not foreign to the marine environment; normal paraffins are synthesized by most, if not all, living organisms. Blumer, Guillard, and Chase (1971) characterized the natural hydrocarbon content of 22 species of phytoplankton and cited literature for zooplankton. There are certain characteristic differences, however, between hydrocarbons native to organisms and the hydrocarbons in petroleum, particularly in the relative distribution of the various hydrocarbons. Crude oils and certain petroleum products are complex mixtures that contain molecules of different sizes in ratios not found in any one species of organism. Certain specific paraffins, and some naphthenic and aromatic compounds, are rarely found in organisms not exposed to oil pollution. These characteristic differences have been the basis for several scientific papers (Blumer, Souza, and Sass, 1970; Ehrhardt, 1972; Clark and Finley, 1973; and others).

FACTORS INFLUENCING THE IMPACT OF OIL

The impact of oil on the marine environment is governed by several factors—physical, chemical, and biological—in addition to the inherent complexity of crude oil and refined products. The behavior, effects, and fate of an oil spill involve all of

[3]Blumer, M. 1970. Scientific aspects of the oil spill problem. Presented at NATO Conference, Brussels, 6 Nov. 1970, 21 p., Woods Hole Oceanogr. Inst., Woods Hole, Mass.

these factors; and because they are interdependent, the reliability of our predictions concerning the impact of a spill is limited by our knowledge of the least understood variable.

Straughan (1972) noted our general inability to predict the environmental impact of a spill because of the complexity of the matter, and identified several factors that govern biological damage caused by a spill: 1) type of oil spilled, 2) dose of oil, 3) physiography of the area of the spill, 4) weather conditions at the time of the spill, 5) biota of the area, 6) season of the spill, 7) previous exposure of the area to oil, 8) exposure to other pollutants, and 9) treatment of the spill. Several of these factors are touched upon below.

Natural Physical Processes Affecting Oil in the Water Column

Once oil is spilled, it is dissipated by evaporation, dissolution, and mixing or dilution in the water column. The natural processes are speeded by wind action and by waves and currents that increase spreading and vertical mixing. Various fractions respond differently to these processes, and the weathered residue behaves differently than the material originally spilled. A contaminated bay may be flushed by freshets, tidal action, or longshore currents. Some oil sinks directly to the bottom, especially in fresh water, where some oil fractions have densities approaching that of fresh water, and in water with high sediment loads. Certain fractions may undergo autoxidation.

Conover (1971) reported that sedimentation of fecal-bound oil that had been ingested by zooplankton may have accounted for up to 20% of the spilled oil entering the water column at Chedabucto Bay, Nova Scotia. Oil can also be removed from the water column by absorption within organisms and accumulation within the food chain. Suspended sediments carried by runoff from a major flood entered the Santa Barbara Channel area immediately before and after the well blowout (Kolpack, 1971). Kolpack noted that adsorption of oil on the flocculated suspended particles followed by decomposition was a major factor in carrying much of the oil to the sea floor. Kinney et al. (1970) reported, however, that in Cook Inlet, Alaska, glacial silt from the inlet had no apparent effect on the emulsion properties or the sinking of the type of crude oil found in that area.

Forrester (1971) noted the extensive distribution of oil particles stirred into the water by wave action after a bunker C oil spill in Chedabucto Bay. Oil particles were found to a depth of 80 m inside the bay and to depths of 45 m at a distance of 65 km outside the bay. Near-surface distribution of particles extended 250 km southwest along Nova Scotia in a band extending up to 25 km offshore. Berridge, Thew, and Loriston-Clark (1969) indicated that the stabilization of emulsions like those observed at Chedabucto Bay and elsewhere was caused by complex chemical components in the nonvolatile residues and not by bacterial activity, marine organisms, or suspended solid matter.

Environmental Differences

The fate and effects of oil spilled in the marine environment are difficult to generalize because several types of environments may be involved. Some extreme comparisons are tropics versus arctic, open ocean versus estuaries, and the differences between the intertidal and subtidal zones.

Within these environments are several diverse physical conditions such as temperature, salinity, oxygen, and nutrient concentrations, as well as biological differences such as species composition, diversity and density, and community metabolic rate. The prediction or assessment of pollution effects on the basis of observations extrapolated from one environment to another is seldom supported by adequate data. Unfortunately, however, few data on pollution effects exist for most areas and species, which has led to the use of information from areas that may be dissimilar in critical respects.

There are arguments as to which environment is the most stable and capable of withstanding attacks by additional pollution stresses. Copeland (1970), discussing the response of ecological systems to stress, suggested the principle that "...those systems already subjected to energy-requiring stresses are more likely to resist the changes than those (such as tropical systems) adapted to relatively constant environments." He concluded that estuarine ecosystems composed of organisms capable of wide adaptations and generalizations, such as north temperate systems, would be relatively unaffected by the same magnitude of disturbance that would drastically alter

a tropical system. Odum (1970) noted, however, that many estuarine species are living near the limit of their tolerance range and that any alteration in the environment, such as additional stresses caused by low levels of pollution, could exclude these animals permanently from the estuary.

All healthy balanced ecosystems are generally functioning at or near some critical tolerance limit. In an ecosystem with a variable environment, such as a north temperate estuary, responses to additional stress might not always be the same. For example, even though factors surrounding an oil pollution incident might be outwardly similar in most respects to another spill in a comparable area, the biological impacts may differ. The ability of the local community to absorb the additional stress will be influenced by the coincidence of seasonal variability of natural stresses, the differences in vulnerability of stages in an organism's life cycle, and many other dynamic features of the ecosystem.

Biological Differences

The effects of oil pollution on many different organisms in various habitats may vary from no effect to responses of avoidance and decreased activity, to nonadaptive responses of panic and physiological stress. What kills one species may have little or no effect on another. Affected organisms vary from single cells, to sedentary clams, to highly mobile predators, each of which has different behavioral and physiological interactions with the environment.

Just as different species are affected differently, so may individuals within a species be affected differently. In particular, different life stages such as eggs, hatched larvae, and newly molted individuals may have different sensitivity to the same level of pollution. Mironov (1968), for example, reported that prelarval stages of barnacle, *Balanus* sp., were 100 times more sensitive to oil pollution than the adult form. This contrasts with the relative lack of sensitivity to crude oil by pink salmon eggs and sac fry, which were 10 times more tolerant than older fry (Stanley D. Rice and Adam Moles, Auke Bay Fisheries Laboratory, National Marine Fisheries Service (NMFS), NOAA, Auke Bay, AK 99821, pers. commun.).

Renzoni (1973) conducted a series of experiments on the toxicity of several crude oils and petroleum products to the sperm, eggs, and larvae of the oysters *Crassostrea angulata* and *C. gigas* and the mussel *Mytilus galloprovincialis*. He found a relatively high degree of tolerance by eggs and larvae but reported that the fertilizing capacity of sperm was markedly affected by similar exposures.

Biodegradation

Quantitative data describing the biodegradation of various components of crude oil, especially in arctic and subarctic areas, are limited.

ZoBell (1973a) briefly reviewed the current understanding of microbial degradation of oil, including interactions, limiting factors, problems, and perspectives. Ahearn (1973) stated that research on microbial utilization of hydrocarbons for treatment of oily pollutants in the environment, though more intensive in recent times, is still in an early stage of development. It is known that microorganisms can degrade much of a crude oil, particularly the less toxic paraffinic compounds. No single species can degrade all the compounds, but many different species together can metabolize a large number of the compounds, if not all. The rate of microbial degradation, which is principally aerobic, decreases with a decrease in temperature. Large quantities of oxygen are needed. It has been estimated, for instance, that complete oxidation of 1 gallon of crude oil would require all of the dissolved oxygen in 320,000 gallons of water. This comparison may be unrealistic because most oil is at the surface of water in contact with air and only the outer surfaces of oil can be attacked at any one time. It is reasonable to assume, however, that an oxygen-deficient environment may well occur under some oil slicks and in oil-contaminated sediments.

Glaeser and Vance (1971) studied the behavior of Prudhoe Bay crude oil in controlled spills in the Chukchi Sea but were not able to isolate any microorganisms which could degrade hydrocarbons at the ambient temperatures of the Arctic, although some emulsification of the crude oil was observed. However, ZoBell and Agosti (1972) collected oil-oxidizing bacteria near natural oil seeps from the Alaska North Slope and observed oxidation rates of mineral oil at −1°C and above. They noted that the solid surfaces of the ice crystals appeared to facilitate bacterial growth, because the rate at −1°C was substantial and near the 4°C rate.

The apparent contradiction between the studies is probably best explained by ZoBell's (1973b) continued observations with North Slope bacteria. He

found that the nine different crude oils were not degraded as rapidly as purified mineral oil. Glaeser and Vance's studies were with microorganisms from the surface water of the Chukchi where small numbers of bacteria may have been present. Furthermore, the observations of Straughan (1971), who noted the apparent lack of biological damage by the Santa Barbara blowout, may apply here. She discussed the possibility that the fauna had an unusually high tolerance for oil, probably because of adaptation from chronic low-level oil exposures from local natural seepages. The observations of ZoBell and Agosti (1972) on the oxidation rates of oil at −1°C may be an example of similar adaptive response by the North Slope bacteria collected near natural seeps. These oxidation rates and other adaptive responses might not occur from organisms that have not been preacclimated to chronic low-level exposures of oil and may explain why Glaeser and Vance obtained reports of negligible oxidation rates at 0°C from microorganisms from surface water of the Chukchi Sea. Robertson et al. (1973) estimated hydrocarbon-oxidizing bacteria populations were in the order of 1/ml in Cook Inlet and Port Valdez, but less in the Arctic Ocean. Numbers decreased with salinity in Cook Inlet and with depth in Port Valdez.

ZoBell (1963) reported that oil is readily adsorbed by clay and silt and suggests that although adsorption of oil by solids renders the oil more susceptible to autobial and microbial oxidation, almost no bacterial decomposition occurs after burial in the bottom sediments, probably because the environment is anaerobic. Blumer and Sass (1972) found that some paraffinic hydrocarbons remained in bottom sediments 2 yr after the West Falmouth oil spill and aromatic hydrocarbons were prominent, which suggests that these more toxic compounds are utilized by bacteria to a minimum degree.

Oil in Sediments

The effect of oil in sediments is poorly understood, although several authors have quantitated oil concentrations and noted its persistence. Scarratt and Zitko (1972) observed little diminution of bunker C oil concentration from soft sediments 26 mo after the wreck of the tanker *Arrow*. The oil reached maximum concentrations in coarse sediments 1 yr after the spill, but the concentrations reduced thereafter. Chemical degradation can occur but is normally restricted to the surface layer of the bottom penetrated by ultraviolet light. Blumer and Sass (1972) noted that "The preservation of hydrocarbons in marine sediments for geologically long time spans is one of the accepted key facts in current thought on petroleum formation." However, in spite of the stability of hydrocarbons in marine sediments, there are characteristic differences between the hydrocarbons in polluted and unpolluted areas. Tissier and Oudin (1973) found that hydrocarbons in polluted sediments differed from those of unpolluted sediments by having lower percentages of heavy components, by not having an odd carbon dominance in the n-alkanes, and by having polycyclic aromatic hydrocarbons with alkyl chains.

Oil residues were observed on sandy beaches by ZoBell (1963) and in marshes and in sediments of the deepest area (15.3 m) near the West Falmouth spill by Blumer, Sass, Souza, Sanders, Grassle, and Hampson (1970).[4] About 2 wk after fuel oil was spilled at Resolute Bay, Northwest Territory, in August 1970, casual sampling revealed that oil penetrated into beach material to a depth of about 3 inches (7.6 cm) (Barber, 1971). Oil may be buried and stay intact for a considerable time, even at the higher temperature of the California coast (ZoBell, 1963). During laboratory experiments, Johnston (1970) determined oil decay rates in sand columns contaminated with various concentrations of oil. Ten percent of the oil was oxidized over a period of several months; the remaining 90% decayed much slower.

The West Falmouth spill provided a unique opportunity for a study of the immediate and long-term effects of an oil spill on an area where the previously existing environmental base was well known (Blumer, Sanders, Grassle, and Hampson, 1971). One effect of the oil was to reduce the cohesion of bottom sediments of tidal marshes and the estuary by killing the benthic plants and animals (Blumer, Sass, Souza, Sanders, Grassle, and Hampson, 1970, see footnote 4). The resulting erosion spread hydrocarbons to new areas, where the process was repeated. Because of the stability and persistence of the hydrocarbons in marine bottom sediments, Blumer, Souza, and Sass (1970) noted that hydrocarbons may be returned to the biosphere by organisms living and feeding in the sediments. This redistribution of hydrocarbons can be

[4]Blumer, M., J. Sass, G. Souza, H. Sanders, F. Grassle, and G. Hampson. 1970. The West Falmouth oil spill. Unpubl. manuscr. Woods Hole Oceanogr. Inst., Ref. No. 70-44, 32 p.

the source of a chronic pollution problem near that spill.

It is quite possible that normal functions of sediments will be disrupted when contaminated by oil. Changes in the sediments that are subtle and difficult to detect, such as decreased nutrient recycling and community metabolism, could result in the loss of significant contributions to the productivity and stability of an area. Although oil in sediments has been monitored and measured after several spills, other aspects of the oil–sediment relation have yet to be studied.

BIOLOGICAL EFFECTS OF OIL POLLUTION

Blumer (1970, see footnote 3) summarizes the potential damage to organisms from pollution by crude oil and oil fractions as follows:

1. Direct kill of organisms through coating and asphyxiation.
2. Direct kill through contact poisoning of organisms.
3. Direct kill through exposure to the water-soluble toxic components of oil at some distance in space and time from the accident.
4. Destruction of the generally more sensitive juvenile forms of organisms.
5. Destruction of the food sources of higher species.
6. Incorporation of sublethal amounts of oil and oil products into organisms (resulting in reduced resistance to infection and other stresses—the principal cause of death in birds surviving immediate exposure to oil).
7. Incorporation of carcinogenic and potentially mutagenic chemicals into marine organisms.
8. Low-level effects that may interrupt any of numerous events (such as prey location, predator avoidance, mate location or other sexual stimuli, and homing behavior) necessary for the propagation of marine species and for the survival of those species higher in the marine food web.

Some of the potential effects described by Blumer may be obvious, such as the direct deaths from acute exposures. Less obvious indirect deaths may occur from effects at either the individual or population level. Individual organisms subjected to sublethal exposures may undergo an "ecological death" if they are less capable of adjusting to and responding to natural changes (stresses) in their physical and biological environments. For example, postmolt Tanner (snow) crab, *Chionoecetes bairdi,* lost legs during short exposures to crude oil (Karinen and Rice, in press). Even though the crabs lived through the exposure, they probably could not have survived in the natural environment because some of them lost as many as seven legs, including both chelae. Moreover, crabs or other adversely but sublethally affected organisms would be more likely to be eliminated by natural selection.

Effects from chronic exposure may be adverse to a population over a period of time if exposed but normal-appearing adults have their ability to reproduce seriously impaired. This loss may be due to physiological changes such as reduced fecundity and delayed ovary development or to impaired behavioral mechanisms which could prevent mate location and identification or homing and timing of spawning. Although the effects at this level might not result in death of the adult, they could induce a trend of decreasing numbers that might eventually eliminate the population or race.

Hydrocarbons in the Marine Food Web

Blumer (1967, 1969) and Blumer, Guillard, and Chase (1971) studied the fate of organic compounds in the marine food web. They found that certain hydrocarbons, even highly unsaturated ones, are stable once they are incorporated into a particular marine organism and that they may pass through many members of the marine food web without alteration and may actually be concentrated in tissue. Most hydrocarbons are lipid soluble and thus may accumulate in food webs to the point where toxic levels are reached. This pathway is illustrated by the well-documented chlorinated hydrocarbon group of pesticides.

The entrance of oil-derived hydrocarbons into marine food webs has been observed several times at several trophic levels. Conover (1971) reported that 10% of the bunker C oil in the water column after the Chedabucto Bay spill was combined with zooplankton and that their feces contained up to 7% oil. Mironov (1968) also noted the ability of some zooplankters to accumulate hydrocarbons. The incorporation of hydrocarbons into the food web at these primary levels assures exposure at all higher trophic levels.

Blumer, Souza, and Sass (1970) and Ehrhardt (1972) reported pollution-derived hydrocarbons in shellfish. Uptake and retention of labeled hydrocarbons of several classes by a marine mussel,

Mytilus edulis, was noted by Lee, Sauerheber, and Benson (1972). Smith (1968) reported the presence of oil and benzene-ring compounds in the feces of limpets browsing on an oily deposit, and in top shells, *Monodonta*, and limpets, *Patella*, living on oiled rocks. He reported that analysis of the gut indicated "the proportion of oil in material ingested by these animals was estimated as about 20-30 percent in *Patella* and 5-50 percent in *Monodonta*."

Organisms at the highest trophic levels may be affected directly by the oil itself or indirectly by hydrocarbons that have reached them through the food web. Horn, Teal, and Backus (1970) found large amounts of tar in the stomachs of three saury, *Scomberesox saurus*, from a sample of ten in the Mediterranean Sea near Gibraltar. Although saury are generally considered to be carnivorous, the occurrence of tar and also of "vegetable debris" in one of the stomachs examined by Horn et al. (1970) suggests that the species is not a very discriminate feeder. Although all ingested oil was obviously not incorporated into the tissues (some oil was found in feces), such feeding behavior does describe a pathway for hydrocarbons to be directly taken up into the tissues of the organism. Thus, oil ingested, absorbed, and even adsorbed may enter the food chain when contaminated organisms are eaten.

Carcinogenicity

Some doubt may remain as to the direct carcinogenicity to man of crude oil and crude oil residues in marine organisms (Blumer, 1969), but evidence pointing toward this is accumulating (Blumer, 1970, see footnote 3; 1972). A literature search and evaluation conducted for the U.S. Coast Guard by Battelle Memorial Institute (1967) noted that shellfish, although alive, may have been unfit for consumption because of the carcinogenic hydrocarbon 3, 4-benzpyrene in their bodies. Oysters that were heavily polluted and contaminated with ship fuel oil were reported to contain 3,4-benzpyrene. The Battelle review also reported that barnacles attached to creosoted poles contained the same carcinogenic hydrocarbon (3,4-benzpyrene). Sarcomas were elicited when extracts from the barnacles were injected into mice. The endemic occurrence of papillary tumors around the rectal opening of soft-shell clam, *Mya arenaria*, was reported, but the author (Battelle Memorial Institute, 1967) did not feel these were due to oil pollution, even though the clams were taken from waters adjacent to areas highly polluted by ship fuel oil. Hyperplasia in reproductive cells of a bryozoan in response to coal tar derivatives was observed by Powell, Sayce, and Tufts (1970). They noted that similar abnormalities may also have occurred in coastal faunas exposed to spills such as the *Torrey Canyon* and the Santa Barbara blowout. However, most observations on these spills were concerned with gross mortality and may not have detected the sublethal effects.

ZoBell (1971) reported the natural synthesis and metabolism of carcinogenic hydrocarbons by several marine organisms. Thus, oil pollution is certainly not the only source for carcinogenic hydrocarbon introduction into marine food webs. Suess (1972) recognized that carcinogens were in seafoods but concluded that they would probably not be dangerous unless the foods contained an excess amount of polynuclear aromatic hydrocarbon carcinogens. Carcinogenesis from oil-contaminated marine organisms has not been proved, but Ehrhardt (1972) expressed a need for carcinogenic testing of hydrocarbon fractions extracted from marine organisms contaminated by exposure to oil.

Observed Toxic Effects

A study of the available information on potential toxic effects of oil pollution reveals more unknowns than proven conclusions. Only a decade ago, ZoBell (1963) reviewed the literature on the effects of oil on bacteria and higher organisms and concluded that oil pollution had no great adverse impact on fishery resources in general. He did point out, however, a few reports of toxic effects, tainting of flesh, and damage to vessels and fishing gear.

The quantity of literature on effects of oil spills has increased since the *Torrey Canyon* incident of 1967. Most of the recent work has depended on onsite visual surveys after occurrence of an oil spill rather than on experiments and detailed study. The surveys have been limited mostly to the effects of oil and of cleaning or dispersing agents on primarily adult intertidal organisms and populations. These observations on a restricted segment of the affected ecosystem include only a few of the factors that influence the total impact of oil. Wilson, Cowell, and Beynon (1973) noted that the absence of results from studies at the commu-

nity level make the interpretation, extrapolation, and use of many observations very difficult. Further, the differences between various crude oils and between the hundreds of petroleum products in their physical and biological effects must always be kept in mind. Comparative data generally are far too few to permit attaching any relative significance to production area or product formulation in this review.

Field Investigations

The utility of many "after-the-fact" studies is limited because of the lack of knowledge of prespill conditions. Data are often collected without proper controls for comparison, and knowledge of natural local fluctuations and species composition of animal populations is usually quite limited. For these reasons conclusions about the impact of a particular spill may vary.

Ehrsam (1972) reported substantial immediate kills of marine life from a fuel oil spill at Anacortes, Wash., and concluded that if larval and juvenile forms of certain organisms were killed, the full impact of the spill may not be known for some time. Katz (1972) observed intertidal transects of the same affected area and concluded that the effects were minor and long-term effects would be unlikely. Webber (1972) pointed out, however, that these after-the-fact studies observed only a small wedge of the total biota. Knowledge of subtidal and benthic organisms as well as larvae and juveniles was lacking.

Other large spills have been studied in greater detail and have contributed significantly to our understanding of the gross effects of oil. Yet, they have been unable to answer many important questions on the effect of pollutant hydrocarbons in the marine environment, and generalizations learned from one spill may not apply to another because each is different.

Field observations of behavior and effects of oil in Arctic ice environments are few. The U.S. Coast Guard investigations in the Arctic have primarily been directed toward gaining knowledge to improve cleanup methods (Glaeser and Vance, 1971; McMinn and Golden, 1973). Campbell and Martin (1973) discussed possible large-scale movements and persistence of oil spilled in the Beaufort Sea. They suggested that the surface waters of the Arctic Ocean and the winter waters of Chedabucto Bay, Nova Scotia, might be comparable, particularly with regard to the physical behavior of oil. Chedabucto Bay is the site of the grounding of the tanker *Arrow* in February 1970 with 2.8 million gallons of bunker C oil aboard. Campbell and Martin (1973) found that highly stable oil-water emulsions formed to a depth of 50 m throughout Chedabucto Bay. They described conditions by which oil reaching the edge of the pack ice could be distributed under the ice.

Thomas (1973) also suggested that results of the studies at Chedabucto Bay might in some respects be applicable to spills in the Arctic. He observed remobilization of oil from beneath the weathered surface of deposits during the summers following the *Arrow* spill and the subsequent re-oiling of some intertidal areas, adding a chronic pollution aspect to the spill. Extensive mortalities of soft-shell clams and salt marsh cord grass, *Spartina alterniflora*, resulted where this occurred. In other areas, clams were visibly contaminated with oil and clam fishing was closed, at least through the summer of 1972 (Thomas, 1973).

When the *Torrey Canyon* broke up near the southwest coast of England in 1967, 15 million gallons of Kuwait crude oil with a high aromatic content were released. Efforts to cope with this first super disaster depended principally upon 2 million gallons of toxic dispersant, which probably caused more damage than the oil, most of which had weathered at sea for a week or more before reaching the shores. Many techniques for oil containment and control on the seas were attempted during the time oil leaked from the tanker; the fact that they all failed reveals the inadequacies of our technology and preparedness for such emergencies.

Extensive investigations of the West Falmouth spill by Blumer and his associates at Woods Hole provide one of the best documentaries of an oil spill. A total of 185,000 gallons of no. 2 fuel oil (41% aromatic content) were spilled in 1969 from a ruptured barge. Intertidal and subtidal benthic organisms of all phyla were killed during the first few days (Blumer and Sass, 1972). Blumer, Souza, and Sass (1970) showed that the uptake of fuel oil hydrocarbons by shellfish left them unfit for human consumption. Later, Blumer and Sass (1972) reported the continued persistence of fuel oil hydrocarbons in the sediments after 2 yr. Although there had been some degradation, the boiling range and composition of the hydrocarbon mixture was basically unchanged.

The 1969 Santa Barbara blowout released an estimated 5,000 barrels of crude oil per day ini-

tially (Foster, Charters, and Neushul, 1971), yet biological damage was not reported widespread and the area has started to recover. Foster, Neushul, and Zingmark (1971) observed that much of the damage to intertidal areas corresponded to sand movement, probably from storm damage. Cimberg, Mann, and Straughan (1973) concluded that the blowout had less effect on intertidal marine organisms than did sand movement and substrate stability. Straughan (1971), reporting on investigations at Santa Barbara, noted factors unique to that accident: 1) the long history of natural oil seepage in the Santa Barbara Channel and 2) the unusually heavy winter runoff at the time of the spill, which reduced salinities, increased sedimentation, and possibly increased pesticides in the channel. R. L. Kolpack (pers. commun. cited by Kanter, Straughan, and Jessee (1971)) noted that Santa Barbara crude oil is relatively insoluble in seawater and contains a very low percentage of the toxic aromatic compounds. Thus, information gathered on the effect of the Santa Barbara spill or any other is of limited utility in predicting the ecological effects of crude oil spills or of other oils in other areas.

Several studies have provided encouraging reports of varying degrees of recovery after some of the recent larger spills. Investigations about 1½ yr after the *Torrey Canyon* spill revealed that at least the affected shoreline areas were recolonizing and recovering, although recovery was not yet complete at that time (Spooner, 1969). The areas affected by the 1969 Santa Barbara blowout were recently reported to be recovering (Cimberg et al., 1973), as was a reef affected by bunker C oil spilled from a tanker collision in San Francisco Bay in January 1971 (Chan, 1973).

Too few of the controlled field investigations have been designed to bridge the gap between field surveys after spills and simulative laboratory experiments. Perkins (1970) exposed periwinkles and other intertidal organisms to the oil dispersant BP1002 in the laboratory and then released marked individuals in the natural environment. After recapture of the individuals exposed, he found that survival from doses as low as one three-thousandth of the 24 h LC_{50}[5] was lower than among the recaptured controls. Crapp (1971a) conducted field experiments by applying crude oil and oil emulsifiers to the intertidal zone. Physical damage by the oil was observed, but toxicity damage was not great because the oil had previously been exposed to air; in contrast, the oil-emulsifier mixtures were toxic. Baker (1970) applied a crude oil to salt–marsh plots at different times of the year and monitored the effects on plants. Summer applications of oil severely affected annuals but not perennials.

Laboratory Studies

Experiments in the laboratory also do not provide all the answers about how an oil spill will affect a marine organism or its environment. Laboratory research has demonstrated the toxicity of various crude oils and petroleum products on several forms of marine life. Much of this research has focused on the planktonic life history stages of pelagic and benthic animals. Many of these planktonic larvae are phototactic at their earliest stages and concentrate in the surface layer of the sea. This community of the surface 5 cm, the neuston, is the first affected by most oil entering the water. Thus, many organisms are most sensitive to oil pollution at the time of their greatest likelihood of exposure.

Studies by Mironov (1968) on the development of fertilized eggs of the plaice, *Rhombus macoticus*, showed extreme sensitivity of the eggs to the influence of the oil products in seawater. He noted that injury to the eggs occurred at concentrations of 10^{-4} to 10^{-5} ml/liter (0.1 to 0.01 ppm). In these concentrations of oil products, 40 to 100% of the hatched prelarvae showed some signs of degeneration during development and perished. Mironov (1969a) also demonstrated that 0.001 ml of crude oil per liter was toxic to the eggs of anchovy, scorpionfish, and sea parrots from the Black Sea.

Newly set spat of *Elinius modestus*, an Australian barnacle introduced to Europe, were tolerant of 100 ppm crude oil but showed reduced cirral activity and retarded shell growth (Corner, Southward, and Southward, 1968). Adults of this species also showed reduced activity at 100 ppm (Corner et al., 1968).

Mironov (1969b) tested crude oil on several copepods and a cladoceran, and found that 0.001 ml/liter accelerated death in all forms and that 0.1 ml/liter caused death in less than 1 day. *Acartia* and *Calanus* died at 0.01 ml/liter oil in seawater in 72 to 96 h (Mironov, 1968). Larvae of crab and shrimp died at 1 ppm (Mironov, 1969c).

Little is known of the mechanisms of various

[5]24 h LC_{50} equals that dose of toxicant that resulted in 50% survival after 24-h exposure.

toxic effects. Damage to cell membranes and the cellular contents of planktonic larvae may occur. Goldacre (1968) demonstrated such cytological damage and death to the freshwater protozoan, *Amoeba proteus*, exposed to crude oil fractions. Brocksen and Bailey (1973) measured increased respiratory response of striped bass and chinook salmon to sublethal concentrations of benzene. The fish recovered to normal activity when they returned to noncontaminated water for several days. Rice and Short were unable to demonstrate changes in the enzyme activity of cholinesterase or Na-K stimulated ATPase in juvenile pink salmon, *Oncorhynchus gorbuscha*, after in vivo and in vitro exposures to Prudhoe Bay crude oil (Stanley D. Rice and Jeffrey Short, Auke Bay Fisheries Laboratory, NMFS, NOAA, Auke Bay, AK 99821, pers. commun.). This is somewhat surprising because various hydrocarbon pesticides have been shown to affect both enzymes.

Cellular membranes of phytoplankton are also damaged by the penetration of hydrocarbon molecules: the cellular contents are extruded, and oil penetrates into the cell. Detergents administered in a concentrated solution also penetrate the plant cells and cause the dissolution of cellular membranes and the extrusion of cellular fluid (Ruivo, 1972). The effects of oils on plant respiration are variable, but an increase of respiration is frequently observed, probably because of an alteration of the mitochondria. This could result in an uncoupling of the oxidative phosphorylation enzymes from the electron transport enyzmes, and the energy release would be lost as heat.

All marine animals ultimately depend on the photosynthetic activity of phytoplankton and algae for the production of biomass. Baker (1971), reviewing the literature, noted that weathered *Torrey Canyon* oil had no apparent effect on the photosynthetic activity of green algae. He did find, however, that green algae treated with fresh crude oil died and that photosynthesis in kelp, *Macrocystis* sp., was reduced when the kelp was exposed to various petroleum products. Kauss et al. (1973) determined the effects of crude oil on several species of freshwater algae in both field and laboratory experiments. In their field studies, response of the algae to a spill varied from suppression of growth to its stimulation. In their laboratory studies, they noted depressed photosynthetic rates in one algal species after it had been exposed to aqueous crude oil and other selected aromatics.

Growth of phytoplankton from axenic cultures and mixed cultures of natural populations was inhibited by water-soluble extracts from no. 2 fuel oil in a laboratory study by Nuzzi (1973). Mironov and Lanskaya (1968) demonstrated that marine phytoplankton vary several orders of magnitude in sensitivity to crude oils and kerosene in oil concentrations ranging from 0.1 to 1,090 ppm. Of the 20 species tested, a diatom, *Ditylum brightwellii*, was the most sensitive. The wide variation in susceptibility may account for the statements in other reviews of low toxicity of crude oils to phytoplankton (Føyn, 1965; Nelson-Smith, 1970) and supports the premise that biological response will differ among species.

Sublethal and Chronic Effects of Oil Pollution

While data are scarce in some of the areas previously discussed, information on the ecological effects of chronic sublethal oil pollution is essentially nonexistent. Observing these effects is difficult because they are not dramatic and may pass unnoticed by the casual observer. A full description would require observations extending over a long period of time.

Lewis (1972), commenting on approaches to the study of chronic pollution, contends "... that without a massive expansion of ecological and reproductive data by simultaneous multidisciplinary studies not only will we be unable to detect the significant long-term changes, but we will even remain unaware of the most suitable or important species and methods to build into a monitoring program."

A few studies concerning sublethal effects on organisms have appeared in the literature. Wells (1972) reported deaths of lobster larvae to exposures of 0.1 ml of Venezuelan crude oil per liter, while larvae exposed to 0.01 ml/liter had poor survival rates and were unable to molt to the fourth stage. Decreased limb (cirral) activity of marine larvae exposed to oil has been reported (Smith, 1968). Kuhnhold (1972), while observing toxic effects of crude oils to eggs of cod and to larvae of cod, plaice, and herring noted that the larvae exposed to oil-contaminated water were unable to avoid well-defined milky clouds of toxic oil dispersions. Blanton and Robinson (1973) observed damage to the gills of specimens of seven species of fish that had apparently been exposed to an oil spill off the Louisiana coast.

Crapp (1971b) observed that fucoid algae replaced barnacle and limpet populations near an outfall where the effluent contained about 20-25 ppm oil from treated ballast water of tankers unloading at Milford Haven. Although the relative oil content was low, the cumulative volume discharged was large (20,000 gallons of oil per year), a situation similar to that which may occur at Port Valdez, Alaska, when the trans-Alaska pipeline is completed.

Blumer (1972) discussed how low-level chronic effects of oil may damage marine organisms because of their dependence on natural organic chemical clues for a variety of functions. Salmon and other fishes utilize organic chemical clues in migrations; predators are attracted to prey by organic compounds at the parts-per-billion level (Whittle and Blumer, 1970); and other organisms may use chemical clues for predator avoidance, selection of habitat, and sex attraction. Blumer (1972) discussed the fears that oil pollution may interfere with these fundamental biological processes by masking or blocking, or by mimicking natural stimuli (resulting in false responses). He cited literature discussing the attraction of lobsters to kerosene and to purified hydrocarbon fractions derived from kerosene and noted that many dead lobsters were washed ashore after the West Falmouth spill. Blumer's fears about interference with chemoreception are further substantiated by the observations of Takahashi and Kittredge (1973) on crab behavior. Crabs, *Pachygrapsus crassipes*, exposed to water-soluble extracts of crude oil failed to exhibit feeding behavior or mating behavior responses when given appropriate chemical stimuli. Inhibition of chemoreception of some motile marine bacteria by a crude oil and several other hydrocarbons has been demonstrated by Walsh and Mitchell (1973).

Rice (1973) performed laboratory tests of avoidance of pink salmon fry to Prudhoe Bay crude oil and observed avoidance of oil at concentrations as low as 1.6 mg/liter. He concluded that salmon fry had the capability of detecting sublethal concentrations of oil and that they might avoid areas contaminated with sublethal levels of oil, which would result in confused and nonadaptive migratory behavior. The effect of chronic low-level pollution in areas such as Port Valdez, the terminus of the trans-Alaska oil pipeline, could be as severe as the total loss of all salmon runs in the local area because of altered behavioral responses to sublethal oil pollution.

CONCLUSIONS

Although crude oil generally should be considered toxic to marine organisms and harmful to their environment, most ecosystems can tolerate some pollution because oil can be dissipated or removed by processes like evaporation, autoxidation, dilution, and biodegradation. However, each organism and environment has a limit to how much oil can be absorbed and metabolized. Catastrophic spills are obviously pollution at a level that ecosystems cannot tolerate without damage. However, if the spills are not continued, the oil will slowly be removed and recovery of the area, at least to some degree, will likely occur. There is some evidence for recovery of some affected individuals.

Assessments of the impact of oil pollution cannot depend solely on evaluation of immediate kills of organisms from acute exposures. Chronic low-level oil pollution can cause subtle changes in organisms and is potentially more dangerous to the ecosystem than dramatic catastrophic spills. For this reason, the effects of chronic pollution warrant intensive study so that they will not be underestimated. The cumulative impact of "ecological death" of individuals which have impaired functions may be quite significant, yet difficult to assess because the death is not tied directly to an acute oil exposure. Equally as dangerous is the potential impact on populations where reproductive processes, adversely affected through physiological or behavioral mechanisms, result in fewer progeny. Chronic pollution may eliminate a species from an area entirely, and once eliminated that species may remain suppressed and may not repopulate the area because of continuing pollution or because its niche has been filled by a more tolerant, possibly less desirable, species.

The adverse effects of oil on animal populations has been of wide concern when stocks of special interest, such as those providing the basis of a sport or commercial fishery, have been involved. It should be remembered that changes in populations of lesser apparent significance will also cause changes in the community because each species population interacts with and is dependent on the rest of the community.

The foregoing review of information does little to simplify or ease the problems of policy makers concerned with marine production and transportation of oil and petroleum products. The weight of

the evidence leaves little doubt that oil poses a serious hazard to living marine resources, that spills and chronic pollution have happened and will continue to occur, and that the interests of the marine environment are best preserved if marine transportation of oil and petroleum products is minimized. The continuing need for new sources and increased amounts of energy, however, limits many of the conservative and prudent alternatives to these hazards. Until research has provided conclusive data, policy makers must continue to rely on these interpretative judgments for much of their guidance in making decisions that can profoundly affect the well being of marine ecosystems.

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ON THE DISPERSAL OF LOBSTER LARVAE INTO THE EAST PACIFIC BARRIER (DECAPODA, PALINURIDEA)

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ABSTRACT

The seaward drift of phyllosoma larvae of lobsters occurring along the coast and adjacent islands of the eastern tropical Pacific Ocean was studied from plankton collections made jointly by the Scripps Institution of Oceanography, Tuna Oceanography Research Program, and the National Marine Fisheries Service, La Jolla, Calif.

Numerous samples taken with trawl and plankton nets were made across the Equatorial current system in two areas: lat. 15°N-5°S, long. 115°-125°W, and lat. 5°N-15°S, long. 95°-115°W. Many late developmental stages of *Panulirus penicillatus* and *P. gracilis* and a few *Scyllarides astori* were found, all apparently having drifted mainly with the South Equatorial Current over a distance of 1,800 to 2,000 or more nautical miles from their likely origin, the Galapagos Islands or the coast of Central America. A few larvae were found in the North Equatorial Countercurrent. This is at times a possible route for return to the adult habitat, but it is doubtful that any of the larvae that have drifted to the most western survey area will be returned by countercurrents in time for metamorphosis or that they can successfully negotiate the remainder of the expanse of the East Pacific Barrier to reach the mid-Pacific islands.

The present report is essentially a follow-up of a previous survey in which a large plankton collection made by the multiship eastern tropical pacific (EASTROPAC) Project in 1967-68 was used in part to ascertain the systematics and geographic distribution of the pelagic phyllosoma larvae of all of the spiny lobsters (Palinuridae) and slipper lobsters (Scyllaridae) known to inhabit the west coast and offshore islands of Central America, Colombia, and Ecuador (Johnson, 1971). In that survey an extensive area was covered along the coast and seaward both north and south of the Equator to about long. 126°W. It therefore forms the basic groundwork drawn upon in the present report dealing with the phyllosoma larvae taken during a more restricted offshore survey within the same area by the Scripps Tuna Oceanography Research Program (STOR) in cooperation with the National Marine Fisheries Service at La Jolla, Calif., and Honolulu, Hawaii. This offshore "skipjack survey" was designed and initiated in 1970 to study the migrations of young skipjack tuna, *Katsuwonus pelamis*, in the eastern tropical Pacific Ocean (Williams, 1971, 1972). A comprehensive review of the current system and water masses so important to pelagic larvae of the area is given by Wyrtki (1967).

From Point Conception southward to the Gulf of Guayaquil, Ecuador a total of four species of palinurid and two species of scyllarid lobsters occur. In the present survey only the larvae of *Panulirus penicillatus* (Olivier, 1811), *P. gracilis* (Streets, 1871), *P. inflatus* (Bouvier, 1895), and *Scyllarides astori* Holthuis, 1960 were found as expatriate larvae from the coast or coastal islands. *Panulirus interruptus* (Randall, 1840) occurs off the coast of southern and Baja California, too far north for its larvae to be expected to enter into the current system covered here except as rare stragglers in the North Equatorial Current. *Evibacus princeps* Smith, 1869 (the second scyllarid) although common to the eastern tropical Pacific, apparently has a larval period too short to be carried far from the coast (Johnson, 1971). The larvae of *P. gracilis* and *P. inflatus* are difficult to separate specifically if the fourth pereiopods have been lost. However, adults of only *P. gracilis* occur in the southern range including the Galapagos Islands and all but two larvae could be referred to that species. The larvae of *Jasus frontalis* (H. Milne Edwards, 1837) and *Scyllarus delfini* (Bouvier, 1909), the two lobsters found in the Juan Fernandez Islands off Chile, were not found in the equatorial currents or in the Peru Current to lat. 24°S during the EASTROPAC survey and none were taken in the present survey.

The duration of the phyllosoma larval period as derived from studies of different species in

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nature indicate about 8 to 11 mo for palinurids (Johnson, 1960; Lazarus, 1967; Chittleborough and Thomas, 1969). In some scyllarids shorter periods are indicated (Saisho, 1962; Robertson, 1968), but in others, including *Scyllarides astori*, a length comparable to that of palinurids is suggested by the wide dispersal of the larvae.

These long drifting periods provide ample time for far and wide dispersal. Coincident with this, the number of larvae caught in a plankton tow is always small especially for the later stages and this precludes close statistical analysis for short surveys. But the presence of even small numbers of larvae when scattered over a large area or period of time are significant in indicating major outlines of the type of drift and dispersal by currents from adult spawning areas.

PROCEDURE

In view of the scarcity of larvae and the presence of only later developmental stages VI-XI (the final phyllosoma stage) in far offshore waters, the collections most generally useful were those from nets filtering large quantities of water: a 15 × 15 m mid-water trawl with a section of 3-mm bar mesh and towed obliquely in steps from 100 to 0 m or from 30 to 0 m for about 1 h 30 min; and a Blackburn micronekton net 5.8 m long constructed of nylon with mesh apertures of about 5.5 × 2.5 mm, and cod end of no. 56 XXX grit gauze. This net attached to a 5 × 5 foot (1.52 × 1.52 m) frame was towed about 60 min obliquely from 200 to 0 m. Samples were also analyzed from tows taken with a 5-m long "neuston" net constructed of nylon with mesh apertures of about 0.65 mm, and cod end of no. 56 grit gauze. This net was attached to a 1-m ring bent to form a narrow opening and buoyed to tow at the immediate surface for 15 min. For *David Starr Jordan* cruise 65, analyses were also made of all samples taken with a similar net attached to a regular 1-m ring towed obliquely from 200 to 0 m for 20-25 min simultaneously with the neuston net.

RESULTS

David Starr Jordan Cruise 57 and *Townsend Cromwell* Cruise 51 5 Nov.-21 Dec. 1970

In Figure 1 is shown the station pattern

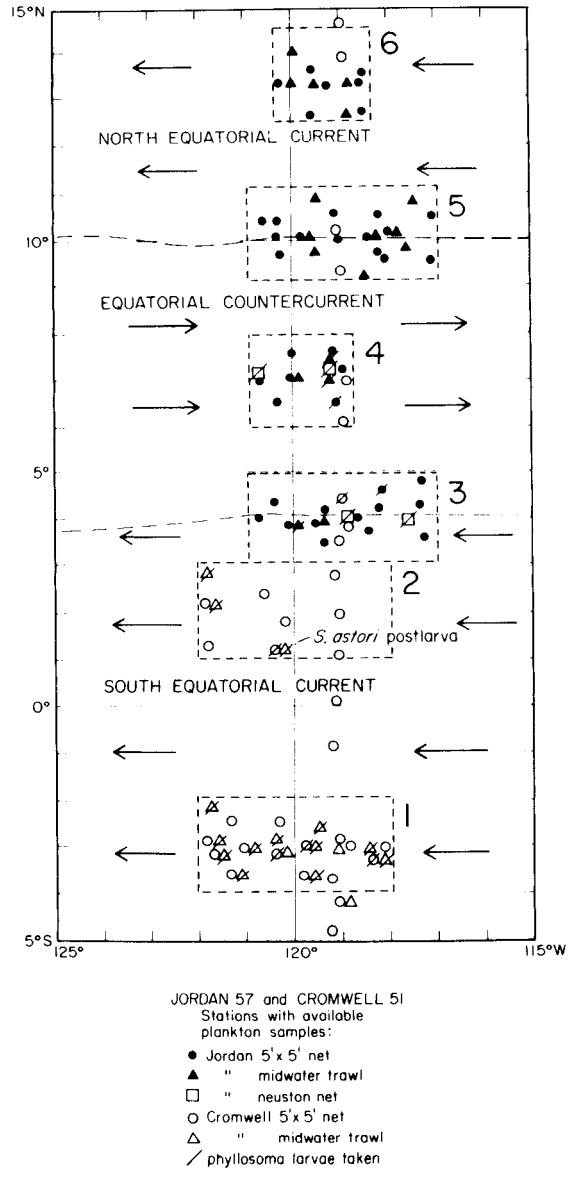

FIGURE 1.—RV *Townsend Cromwell* cruise 51 and RV *David Starr Jordan* cruise 57 station pattern in unit areas 1-6. Neuston net tows are shown only where larvae were taken.

where net tows, positive or negative for phyllosoma larvae, were taken by the trawl or the 5 × 5 foot net. The stations occupied fall into more or less distinct unit areas as designed for the tuna study to correlate with the prevailing major elements of the Equatorial Current System.

The number and stages of larvae caught in the various nets are given in Table 1 for each of

the unit areas. Because of the scarcity of specimens, no attempt is made to give figures based on unit volume of water filtered.

In unit area 1, 52% of 27 tows (other than with the neuston or 1-m net) yielded a total of 87 larvae in this 8° square area in the South Equatorial Current. Nine neuston net tows caught no larvae.

The three stations below 4°S were negative and approach or fall into a large expanse of water that yielded no larvae during the EASTROPAC cruises (Johnson, 1971, Chart 12).

Unit area 2 also in the South Equatorial Current was less well sampled, but 36% of 11 tows with the trawl and 5 × 5 foot net yielded a total of 35 phyllosoma larvae and one scyllarid postlarva (nesto). The five neuston tows were negative.

The large number of larvae caught by the trawl in unit areas 1 and 2 when compared with the more northern unit areas is striking in indicating the tendency of the South Equatorial Current to retain its load of phyllosoma larvae in their long drift from the adult area.

In unit area 3 overlapping into the North Equatorial Countercurrent, which was well developed at the time (Williams, 1971), 20% of 15 tows with the trawl and 5 × 5 foot net were successful but yielded only seven larvae in these nets. However five additional larvae were caught in 2 of 11 neuston tows.

Unit area 4 comprises only a 2° square area within the North Equatorial Countercurrent. Here two of three trawls and one of nine 5 × 5 foot net tows yielded 3 and 1 larvae respectively while the neuston net caught a total of 10 larvae in two of eight tows. The successful neuston tows in this area and in unit area 3 were taken during evening or nighttime tows.

Unit areas 5 and 6 provided no phyllosomas although both areas were comparatively well sampled.

The relatively large number of larvae taken during these two cruises compared with the following cruises reflects more intensive sampling, especially with the trawl, but a seasonality in release of larvae in the adult area may also have contributed.

David Starr Jordan Cruise 60 6 Mar.-11 Apr. 1971

The stations occupied for plankton were more scattered and very few larvae were caught,

TABLE 1.—*David Starr Jordan* cruise 57 and *Townsend Cromwell* cruise 51. Types of gear, total number of tows taken (the successful number of which is shown in parenthesis) and the number of larval species caught with different gear in unit areas 1-6.

Unit areas No. of tows Successful no. in parentheses	Species taken and type of gear	Phyllosoma stages VII	VIII	IX	X	XI	Total larvae in unit area
1	*P. gracilis*, 5′ × 5′		1				
5′ × 5′, 14 (3)	*P. gracilis*, trawl	1	11	18	2		
Trawl, 13 (11)	*P. penicillatus*, trawl			7	16	16	
Neuston, 9 (0)	*S. astori*, trawl	1	1	3	4	6	87
2	*P. gracilis*, 5′ × 5′	1	1				
5′ × 5′, 8 (1)	*P. gracilis*, trawl	2		1	1		
Trawl, 3 (3)	*P. penicillatus*, trawl	1	10	11	6		
Neuston, 5 (0)	*S. astori*, 5′ × 5′		1				
	S. astori, trawl			1			35 + 1 nesto
3	*P. gracilis*, 5′ × 5′	1	2				
5′ × 5′, 13 (2)	*P. gracilis*, trawl	1		1	1		
Trawl, 2 (1)	*P. gracilis*, neuston	1	3	1			
Neuston, 11 (2)	*P. penicillatus*, trawl		1				12
4	*P. gracilis*, 5′ × 5′	1					
5′ × 5′, 9 (1)	*P. gracilis*, trawl			1			
Trawl, 3 (2)	*P. gracilis*, neuston	1	4	5			
Neuston, 8 (2)	*P. penicillatus*, trawl			1	1		14
5							
5′ × 5′, 13 (0)	none						
Trawl, 8 (0)							
Neuston, 11 (0)							0
6							
5′ × 5′, 8 (0)	none						
Trawl, 5 (0)							
Neuston, 8 (0)							0

hence the data on larval distribution, species, and stages taken are entered directly on the chart (Figure 2). The successful tows indicate at least a presence of larvae in all of the major currents traversed. The North Equatorial Current at this time showed a few stage VII *P. penicillatus* with Clipperton Island a likely source of origin.

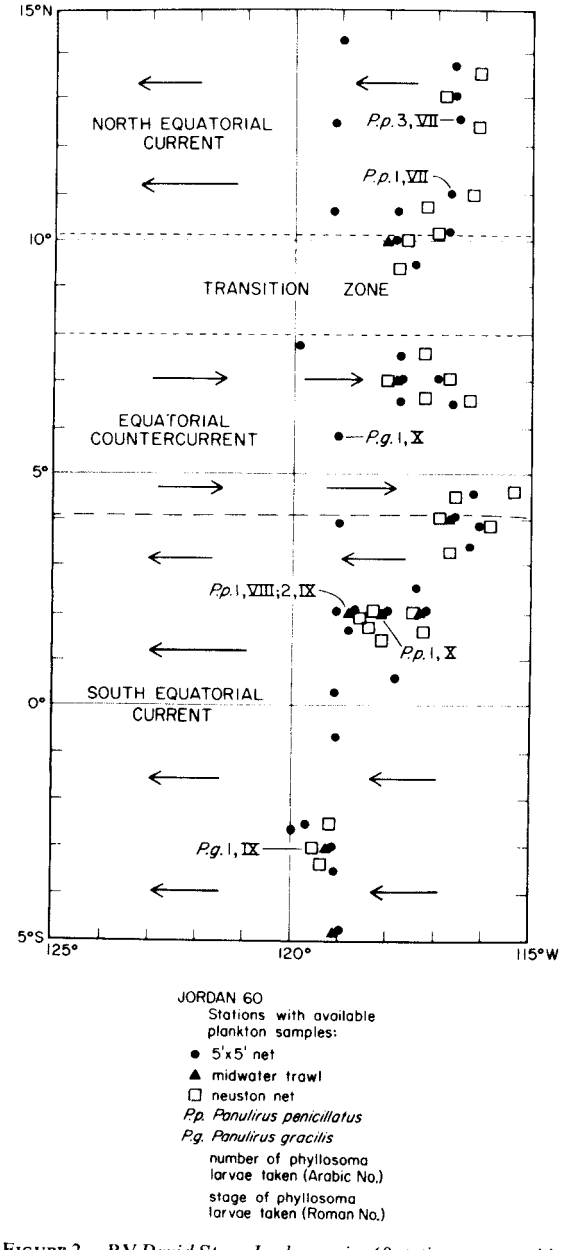

FIGURE 2.—RV *David Starr Jordan* cruise 60 station pattern with number and stage (Roman numeral) of phyllosoma larvae taken at station indicated.

David Starr Jordan Cruise 65 24 Aug.-30 Sept. 1971

As shown in Figure 3, this cruise covered an area much nearer the Galapagos Islands, from which most of the phyllosomas taken probably originated. It also extended less to the north and farther to the south. The data will again be presented here by unit areas (2° squares).

Unit 1 falls below lat. 11°S and yielded no larvae in a total of eight tows (Table 2). It is probable that the area is within the influence of the northern boundary of the western extension of the Peru Current which as already mentioned had few or no phyllosomas during the EASTROPAC cruises.

In unit 2 within the South Equatorial Current, a total of 16 tows with the various nets yielded 19 larvae, mainly by the trawl.

Units 3 and 4 although within the South Equatorial Current had only two and four larvae respectively in a total of 18 mixed tows.

Unit 5 directly west of the Galapagos was the most productive of larvae where five of eight neuston hauls yielded a total of 33 specimens.

Unit 6, still within the South Equatorial Current, was less productive of larvae although three of eight neuston net tows took five larvae.

A total of 35 tows taken with the 1-m net simultaneously with the neuston net during the cruise yielded no larvae whatever (see Discussion).

David Starr Jordan Cruise 77 8 Jan.-17 Feb. 1973

Figure 4 depicts the station pattern across the current system. As in cruise 60 there were so few phyllosoma larvae that it will suffice to record the data relative to these directly on the chart. There were a few scattered palinurid larvae in the North Equatorial Current. The nearest likely source of these being Clipperton Island. A few also occurred in the northern part of the South Equatorial Current. That these probably came from the Galapagos Islands is indicated by the accompanying larvae of *Scyllarides astori*, the adult of which is relatively rare except in that area.

Of special interest however is the occurrence of a single, late stage *Parribacus* sp. phyllosoma in this group of stations. No adult species of this genus has been reported from the west

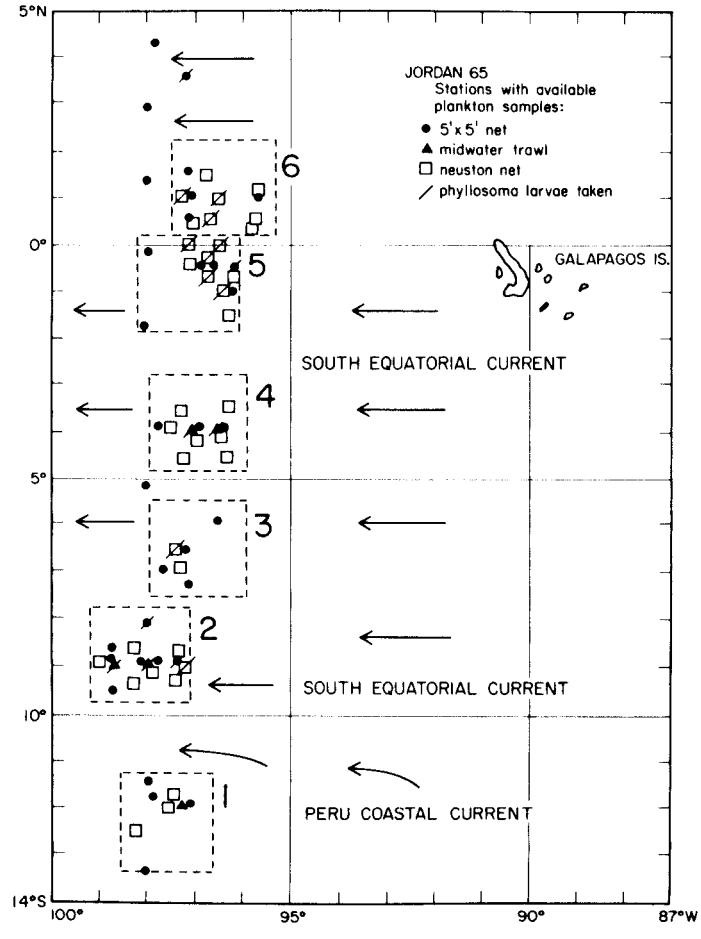

FIGURE 3.—RV *David Starr Jordan* cruise 65 station pattern in unit areas 1-6; 1-m net tow also made at neuston stations.

coast of the Americas. Hence one is forced to conclude that it most likely had drifted from islands to the southwest where the genus is known to occur. It should be mentioned here also that a late larva of this genus was taken at lat. 14°13.6′S, long. 126°00′W near the southern limit of the most distant offshore stations of EASTROPAC. Nothing is known regarding the duration of the entire floating period of this genus.

Saisho (1962) included *Parribacus antarcticus* in his generalization stating that the free-swimming life of scyllarids is shorter than for palinurids. This was based on laboratory studies of only the first three larval stages. However, if the present observations of the two late, but not yet the last, stage is characteristic of the genus they suggest that, like *Scyllarides astori*, the free-swimming life is not abbreviated.

DISCUSSION

This survey is of special interest in substantiating the earlier findings of the EASTROPAC survey relative to the far offshore drift of planktonic stages of lobster larvae in the Equatorial Current System. As in the earlier survey, only species known to occur in the east tropical area were found with one exception (*Parribacus* sp.) referred to above.

Assuming that the Galapagos Islands are the main source of the larvae encountered, it is evident that the westward transport with the South Equatorial Current involves at least a distance of about 1,800 nautical miles. In *Townsend Cromwell* cruise 51 larvae of each of the prevailing species *Panulirus penicillatus*, *P. gracilis*, and *S. astori* were netted in trawl tows at the western-most stations at long. 121°32′-121°54′W between lat. 02°45′N and

TABLE 2.—*David Starr Jordan* cruise 65. Types of gear, total number of tows taken (the successful number of which is shown in parenthesis) and the number of larval species caught with different gear in unit areas 1-6.

Unit areas No. of tows Successful no. in parentheses	Species taken and type of gear	Phyllosoma stages VI	VII	VIII	IX	X	Total larvae in unit area
1							
5′ × 5′, 4 (0)	none						
Trawl, 1 (0)							
Neuston, 3 (0)							0
2	*P. gracilis*, neuston		1	1			
5′ × 5′, 7 (1)	*P. penicillatus*, 5′ × 5′			1	1		
Trawl, 2 (2)	*P. penicillatus*, trawl		5	5	3		
Neuston, 7 (1)	*S. astori*, trawl		1	1			19
3	*P. gracilis*, neuston		2				
5′ × 5′, 4 (0)							
Neuston, 2 (1)							2
4	*P. gracilis*, trawl			4			
5′ × 5′, 3 (0)							
Trawl, 2 (2)							
Neuston, 7 (0)							4
5	*P. gracilis*, neuston	6	14	10	2	1	
5′ × 5′, 6 (1)	*P. penicillatus*, 5′ × 5′		1				
Neuston, 8 (5)							34
6	*P. gracilis*, neuston	2		2	1		
5′ × 5′, 4 (0)							
Neuston, 8 (3)							5
North of unit 6							
Isolated Stn. 229	*P. gracilis*, 5′ × 5′			1			1

02°57′S. During the EASTROPAC survey only *P. penicillatus* was found at the western-most stations at about long. 126°W near the equator, a distance of about 2,000 nautical miles. These *P. penicillatus* larvae might conceivably have drifted eastward from the oceanic islands of the south Pacific where the adult is known to occur. But no other species common to the mid-Pacific islands has ever been found in any part of the eastern tropical Pacific survey areas except for the two specimens of *Parribacus* sp. mentioned previously. Obviously one sees here the working of the East Pacific Barrier towards maintaining a specific separation of west American and Indo-Pacific lobster faunas. *Panulirus penicillatus*, which occurs all the way through the Pacific and Indian Oceans to the Red Sea, is unique among lobsters in having successfully overcome this barrier to become established on offshore islands, but appears to have found additional barriers that prevent establishment on the coast of the mainland. George (1969) interprets this as a failure to compete successfully with the east Pacific mainland species that have evolved there by natural selection. The absence of *P. penicillatus* in the coastal environment may result largely from elimination of the larvae by an admixture of inimical coastal water as they approach the coast. This supposition is suggested by the fact that no larvae of this species have thus far been found at stations near the coast despite their capability of wide dispersal offshore.

Other crustacea with relatively shorter planktonic lives appear also to have migrated eastward across the East Pacific Barrier (Chace, 1962; Garth, 1966).

The countercurrents within the Equatorial Current System provide possible routes for return of east Pacific species that have either fortuitously or through instinctive behavior shifted into countercurrents, possibly through habits of diurnal migrations, and that have not drifted westward to a point of no return determined by requirements inherent in their life cycle.

To evaluate how effective these return routes may be needs further study based on plankton collections designed to elucidate the vertical distribution of the larvae and the diurnal migrations that they undergo in relation to light, etc., and to the depths of prevailing countercurrents in relation to adjacent currents. In this connection it is

useful to examine the results of certain neuston and 1-m net tows, especially those taken during *David Starr Jordan* cruise 65 where 28.5% of 35 neuston tows yielded one or more larvae, and two tows contained eight and nine larvae respectively. All but two of the neuston tows that were positive for larvae were taken during dusk or darkness. The 1-m net tows taken simultaneously from 200 to 0 m yielded no larvae in either the nighttime or daytime tows. This discrepancy is rather surprising and the cause is not clear. But it may indicate that larvae are so scarce and widely dispersed vertically at depth that the 1-m net does not filter enough water to be effective at depth and its passage through the immediate surface layer is very brief, whereas the neuston net, although filtering less water, caught larvae because of their active concentration in a very narrow horizon at the very surface during conditions of reduced light. Other observations in the field (Chittleborough and Thomas, 1969) and in laboratory experiments (Ritz, 1972) demonstrate this behavioral response of phyllosoma leading to a migration into surface layers at night.

In *David Starr Jordan* cruises 57 and 60 the trawl and neuston tows show that larvae do get into the North Equatorial Countercurrent (Figures 1 and 2). This is an expected correlation with the physical studies of the countercurrent which indicate that some variable transverse circulation does occur across the current such that water is drawn in at the surface along the southern boundary and a loss occurs across the northern boundary (Wyrtki, 1967). The Equatorial Undercurrent at the Equator is another possible route for return to the Galapagos and surrounding area.

Williams (1972), in presenting a hypothetical model of an eastward passive migration of skipjack tuna from the central Pacific spawning area in recruitment of the fisheries in the eastern Pacific, has reviewed hydrographic details relative especially to the position, speed, and seasonal interruptions of the North Equatorial Countercurrent. The seasonal fluctuations of this current could aid or retard the passive migration of tuna larvae and juveniles from the spawning grounds depending upon the degree of coordination with the season of spawning. Much of this transport mechanism might apply also to the return of the long-lived lobster larvae. But it is not known if there is a significant seasonality in the release of the larvae in the adult habitat that might fortuitously correlate with the North Equatorial Countercurrent and thus enhance the likelihood of return of larvae that have drifted to the west. Data from EASTROPAC suggest a very long breeding season for the tropical species as judged by the persistent occurrence of early larval stages (III-IV) in

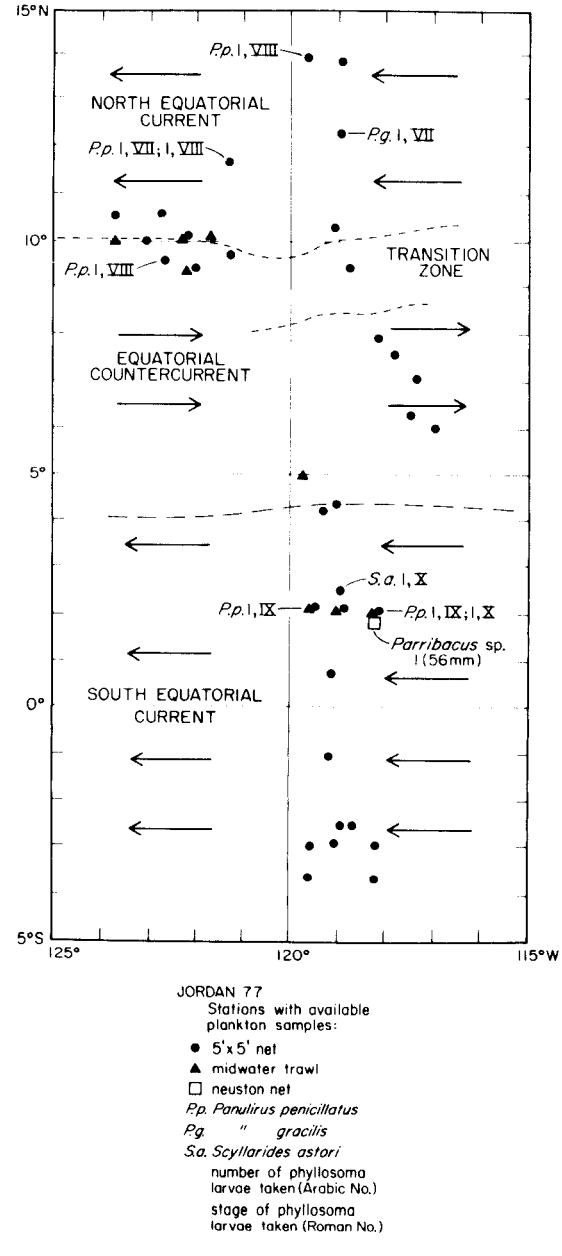

FIGURE 4.—RV *David Starr Jordan* cruise 77 station pattern with number and stage (Roman numeral) of phyllosoma larvae taken at station indicated. Neuston net tow is shown where larva was taken.

the more coastal waters. Larvae that have shifted into the countercurrents from the South Equatorial Current in the eastern part of its course may well be returned in time for metamorphosis near the coast or at offshore islands. It seems probable, however, that safe return from the area of the more westward stations surveyed is doubtful in view of the great distance covered and the expected attrition through predation, etc. Assuming, as before, that the larvae occurring below about lat. 10°N near long. 120°W, originated in the Galapagos Islands area and allowing an average of 20 nautical miles per day westward flow of the South Equatorial Current it would require 3 mo sustained drift to cover the 1,800 nautical miles involved. If shifted promptly at this point into the North Equatorial Countercurrent with an average speed of 15 nautical miles per day another 4 mo of sustained transport would be required to reach an adult area suitable for metamorphosis. It should be noted, however, that only larval stages VII to XI (final stage) were taken at the more distant stations on all skipjack cruises except *David Starr Jordan* cruise 65, the one nearest to the Galapagos Islands. This would indicate that even the youngest larvae taken near long. 120°W were probably older than 3 mo and the likelihood of much additional delay in returning by way of countercurrents militate against a safe return unless metamorphosis can be delayed pending encountering conditions favorable to metamorphosis and assumption of the benthic habit. Recruitment must depend mainly on larvae that have been retained relatively near the coast by coastwise currents, eddies, and backwashes.

None of the east Pacific larvae taken in the far offshore areas show any tendency to gigantism such as was believed to occur in some Crustacea when settlement has been postponed (Bruce, 1970).

To what extent metamorphosis of the phyllosoma larvae to the postlarval stage may take place in the far offshore waters is not known. No palinurid postlarvae were found in any of the cruises. However, a single specimen of *Scyllarides astori* postlarva (known as a nesto) was taken in a trawl at lat. 01°17′N, long. 120°06′W during *Townsend Cromwell* cruise 51 (Johnson, in press).

The chances of the larvae continuing to float successfully westward all the way to the mid–Pacific islands is unlikely and the absence of the species, except for *P. penicillatus*, in these islands substantiates this supposition and clearly manifests the East Pacific Barrier functioning against westward migration of the east Pacific species.

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REPRODUCTIVE CYCLE OF THE SOFT-SHELL CLAM, *MYA ARENARIA*, AT SKAGIT BAY, WASHINGTON

RUSSELL G. PORTER[1]

ABSTRACT

The annual reproductive cycle of the soft-shell clam, *Mya arenaria* L., was studied at Skagit Bay in northern Puget Sound, Wash. Spawning occurred from late May to early September in both 1971 and 1972 with peak spawning in July and June respectively. Small clams (less than 60 mm in length) had a spawning peak that coincided with other size classes although the spawning period was shorter in duration. The single yearly spawning period at Skagit Bay corresponds with east coast populations in Canada and Maine.

The soft-shell clam, *Mya arenaria* L., is found on virtually all coastlines in the northern hemisphere (Hanks, 1963) and is still extending its range as evidenced by its recent movement into the Black Sea (Zambriborshch, Marchenko, and Telegin, 1968; Ivanov, 1969). On the North American continent, it is native to the east coast from which it reportedly was accidentally introduced into San Francisco Bay, Calif., about 1874 (Fitch, 1953). However, there is some evidence from Indian middens that the soft-shell clam is also native to the west coast (Craig, 1927). Its range on the west coast presently extends from California to Alaska (Morris, 1966).

The reproductive cycle of the soft-shell clam has been described from a variety of locations on the east coast, but no data have been presented for west coast populations except for one brief note from Oregon (Edmondson, 1920). The first detailed study on the histology of the gonad of *Mya arenaria* was conducted by Coe and Turner (1938) in New England. They found that spawning occurred in the summer. At Martha's Vineyard in Massachusetts spawning was found to occur over a 6-mo period from spring through early fall (Deevey, 1948). In northern Massachusetts, spawning occurs in late summer and early fall (Ropes and Stickney, 1965), while in New Jersey, spawning takes place in the spring (Belding, 1930; Nelson and Perkins, 1931). Two spawnings per year (spring and fall) have been reported for the Chesapeake Bay in Maryland (Pfitzenmeyer, 1962, 1965) and for Narragansett Bay, R.I. (Landers, 1954). Ropes and Stickney (1965) have tabulated the results of most east coast studies for easy comparison.

This paper describes the annual reproductive cycle for a soft-shell clam population from Puget Sound, Wash. Skagit Bay was selected as the study area since it has a potential for commercial operations, a commercial soft-shell clam fishery is in the beginning stages, and it appears to be the area with the greatest abundance of soft-shell clams in Puget Sound.

DESCRIPTION OF AREA

Skagit Bay, Wash., is located in northern Puget Sound 60 miles north of Seattle. The Skagit River, which has an average discharge of 16,560 ft^3/s (U.S. Department of Interior, 1971:190),[2] empties into the end of the bay via the South Fork and at the northern entrance of the bay via the North Fork. The northern side of the bay is made up of a large broad mud flat approximately 13 square miles in area. The study area was located on the mud flat off Fir Island between Hall Slough and Browns Slough.

The mean tide range at Skagit Bay is 6.5 feet, and the diurnal range 10 feet. The soft-shell clam beds are located at a tidal level of approximately +3.5 feet.

Water temperatures and salinities in the vicinity of Skagit Bay may vary widely on both an annual and a diurnal basis due to river discharge and tidal effects. During 1971, surface temperatures at Strawberry Point varied from 4.79° to 15.68°C, while salinities ranged from 2.54 to 24.53‰. The maximum recorded daily variation

[1]Washington Cooperative Fishery Unit, University of Washington, Seattle, WA 98195.

[2]Thirty-year period—maximum recorded flow: 144,000 ft^3/s, minimum recorded flow: 2,740 ft^3/s.

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in surface water temperature at Strawberry Point was 4°C.

METHODS AND MATERIALS

The study began in November 1970 and was completed in November 1972. Samples were collected once a month from November thru February and twice a month from April thru October in 1971 and March thru October in 1972. The bimonthly samples were taken at 2-wk intervals: generally during the first and third weeks of the month. No sample was collected in January 1971 because river flooding prevented access to the study area. Each sample consisted of 50 clams which was separated from a larger random sample to represent five size classes: clams less than 60 mm in length, those in the 60-, 70-, and 80-mm length ranges, and those larger than 90 mm. As far as possible the 50 clams selected for each sample were equally distributed between the five size classes. The samples taken during the first 3 mo of the study consisted of only 10, 10, and 15 clams respectively. A total of 1,785 clams were collected which ranged from 22 to 105.5 mm in length. Of this total 2.6% were immature, leaving a total of 1,739 mature clams that were utilized in the analysis of the reproductive cycle.

The samples were returned to the laboratory where they were measured and weighed and the gonadal mass removed and preserved in Davidson's acetic acid fixative (Shaw and Battle, 1957). In smaller clams the entire visceral mass was preserved and sectioned; for larger clams a cube of gonadal tissue was removed from the mid-lateral portion of the visceral mass. Usually dissection and preservation were accomplished the day of collection. Clams not dissected until the following day were held in a refrigerated saltwater system overnight.

Slides were prepared by standard histological techniques: tissues were dehydrated in alcohol, cleared in xylene, embedded in paraffin, sectioned at 5–8 microns, and stained with Mayer's hematoxylin and alcoholic eosin (Galigher and Kozloff, 1971).

The number of gonadal stages used to describe bivalve reproductive cycles varies widely. Lammens (1967) distinguished 11 stages and measured the nuclear-cytoplasmic ratio. Previous investigations on *Mya* reproductive biology generally have recognized five phases of development (Shaw, 1962, 1965; Ropes and Stickney, 1965); therefore the following five phases were used: inactive, active, ripe, spawning, and spent. These five phases were distinguished by the following characteristics.

Males

Inactive (Figure 1a)

During this phase the alveoli are filled with follicle cells which contain the typical male type inclusions as described by Coe and Turner (1938). Primary spermatocytes may be visible along the alveolar wall, but are not abundant.

Active (Figure 1b–d)

This phase is typified by the proliferation and maturing of the spermatocytes. In staging the slides, an early active, middle active, and late active stage were identified. The early active stage (Figure 1b) is characterized by the proliferation of primary spermatocytes at the basal membrane of the alveoli and the appearance of some spermatids. The middle active stage (Figure 1c) is characterized by the disappearance of the follicle cells and the migration of spermatids toward the center of the alveoli where they begin aligning in radial columns. The late active stage (Figure 1d) is characterized by the greatly increased number of radially aligned spermatids and the formation of a central lumen in the alveoli.

Ripe (Figure 1e)

In the ripe male clam, the sperm are distinctly bunched in radial columns around the alveoli with their tails, which stain pink with eosin, projecting into the central lumen.

Spawning (Figures 1f and 2a)

When spawning commences a single row of follicle cells form at the alveolar membrane (Figure 1f). These follicle cells contain the typical inclusions of the male, and the number of rows increases as spawning proceeds (Figure 2a).

Spent (Figure 2b)

In the spent clam most all sperm have been discharged, but a few may remain. The alveoli are almost completely filled with follicle cells.

Females

Inactive (Figure 2c)

In the inactive phase the alveoli are filled with follicle cells which contain the distinctive female

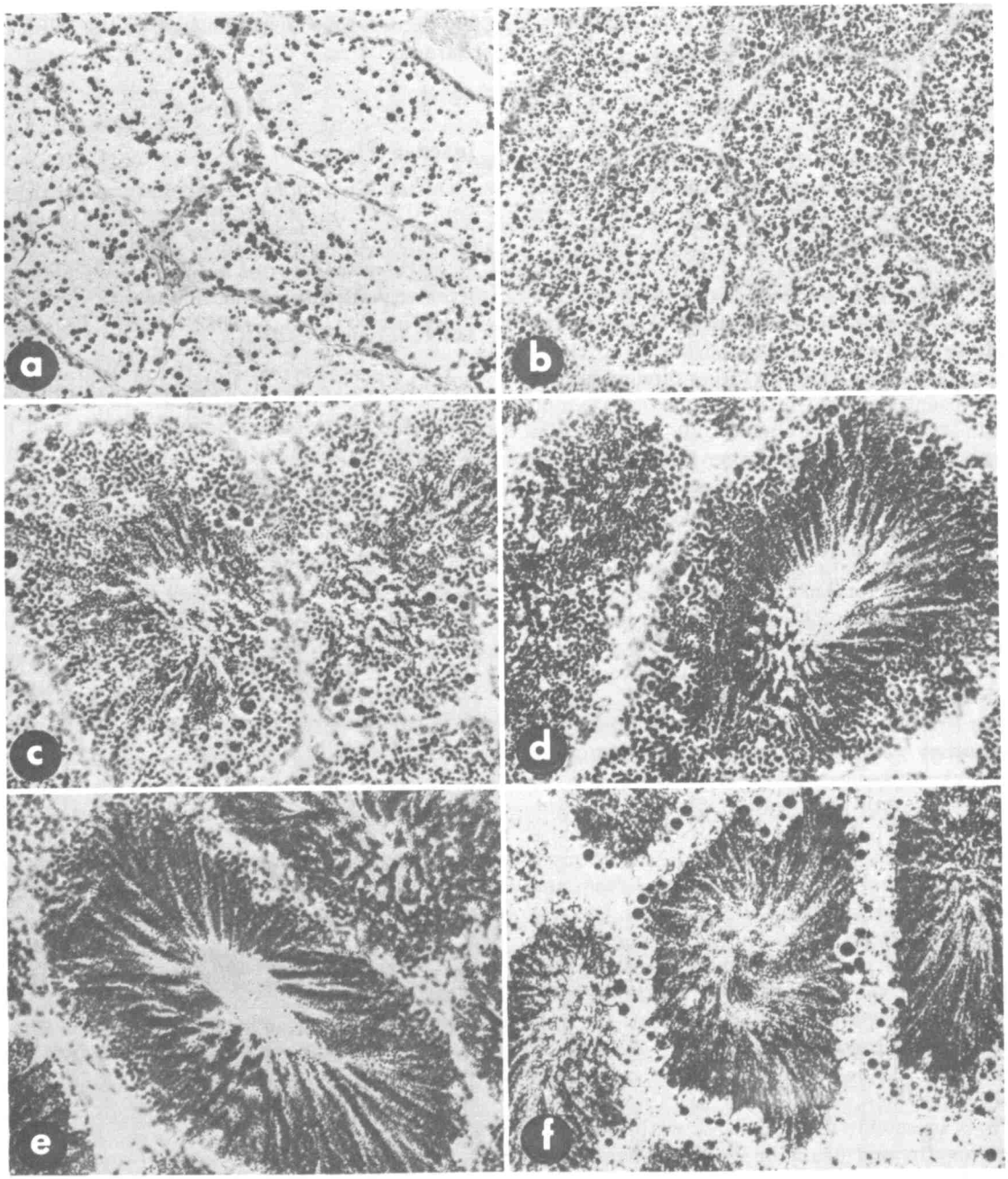

FIGURE 1.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Inactive male (160×), 22 Sept. 1972. Follicle cells with inclusions fill the alveoli. b) Early active male (160×), 17 Feb. 1972. Proliferation of the primary spermatocytes is visible along the basal membrane of the alveoli. c) Active male (250×), 30 Apr. 1971. Spermatids begin aligning in radial columns toward the central lumen of the alveoli. A few sperm balls are visible near the periphery of the alveolus. d) Late active male (250×), 14 May 1971. e) Ripe male (250×), 11 June 1971. The sperm are aligned in radial columns, their tails projecting into the central lumen. f) Early spawning male (250×), 1 June 1972. A single row of follicle cells containing inclusions forms at the basal membrane of the alveoli.

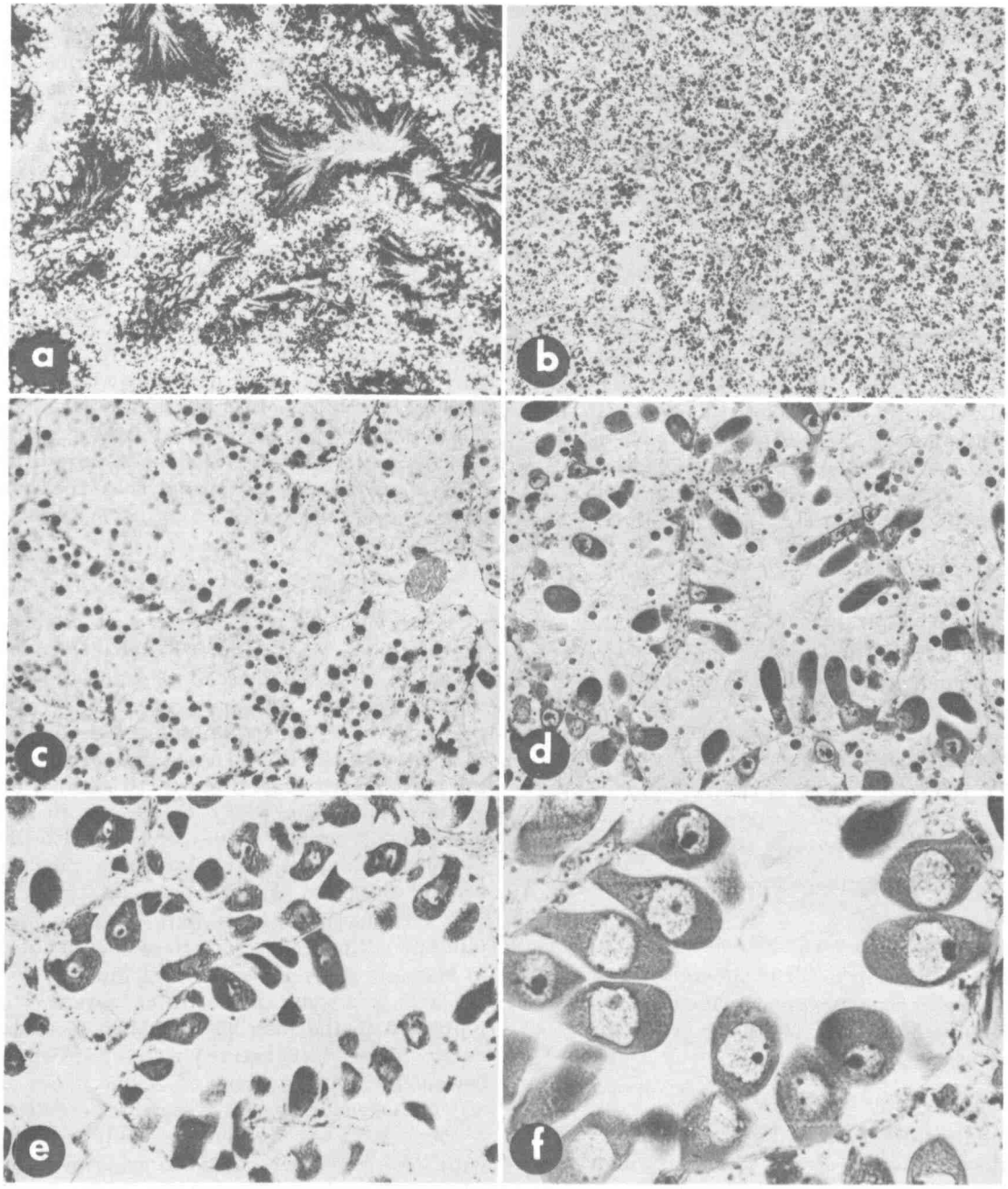

FIGURE 2.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Spawning male (100×), 6 Aug. 1971. The follicle cells reappear as spawning progresses. b) Spent male (100×), 8 Sept. 1972. c) Inactive female (100×), 12 Oct. 1971. Follicle cells containing the typical female inclusions fill the alveoli. d) Early active female (145×), 3 Mar. 1972. The primary ovocytes begin enlarging forming stalked ovocytes. e) Active female (136×), 8 May 1972. The follicle cells and their inclusions have disappeared. f) Late active female (240×), 14 June 1972. The nucleolus and amphinucleolus of the ova have appeared, but most ova are still attached to the basal membrane of the alveoli.

type inclusions (Coe and Turner, 1938). A few primary ovocytes are visible along the alveolar membrane.

Active (Figure 2d–f)

As in the male, three stages were identified for this phase: early, middle, and late active. The early active stage (Figure 2d) is characterized by the proliferation of primary ovocytes and their elongation producing stalks which protrude toward the center of the alveolus between the follicle cells. In the middle active stage (Figure 2e) the follicle cells and their inclusions have disappeared leaving a central lumen in each alveolus. An increasing number of stalked ovocytes attached to the alveolar wall protrude into this lumen. In the late active stage (Figure 2f) the ovocytes are beginning to become spherical with slender stalks, and in many the nucleolus and amphinucleolus are readily visible.

Ripe (Figure 3a, b)

In the ripe phase a majority of the ova are free of the alveolar wall and have taken on spherical shape (Figure 3a). In some individuals the ova are quite abundant, and almost all will be free of the alveolar wall (Figure 3b).

Spawning (Figure 3c)

The spawning phase is characterized by the emptying of the alveoli of ripe ova, leaving behind a few ovocytes that are still attached to the alveolar wall.

Spent (Figure 3d)

In the spent clam the alveoli are empty, and follicle cells begin to fill in the alveoli from the basal membrane inward. Inclusions reappear with the follicle cells, and some of the primary ovocytes are visible.

Immature

The immature gonad (Figure 3e) has a much smaller number of alveoli which are filled with follicle cells devoid of any inclusions.

Each clam was identified as to sex and staged in accordance with the above phases. The percentage of clams in each phase was then calculated. For the purposes of analyzing the reproductive cycle (Figure 4), the three stages of the active phase: early, middle, and late were combined under the single term active phase. In addition, mean monthly percentages were utilized in analyzing the reproductive cycle (Figure 4) for those months during which two samples were collected.

In the presentation of results, the terms 1971 and 1972 reproductive cycle refer to the cycle whose spawning phase occurred during that respective calendar year. However, the reproductive cycle as a whole does not necessarily coincide with, nor is it restricted to, a particular calendar year. The reproductive cycle was assumed to begin with the active phase and end with the inactive phase.

RESULTS

The histological examinations revealed a single yearly spawning period which occurred from late May to early September. This was true for both sexes and for both the 1971 and the 1972 reproductive cycles although the period of peak spawning varied slightly (Figure 4). The sex ratio of the 1,739 clams utilized in the analysis of the reproductive cycle was 48% males (837) and 52% females (902).

1971 Reproductive Cycle

During the 1971 reproductive cycle (Figure 4) clams in the active phase were encountered from February through July for males and February through June for females. Active clams were undoubtedly first present in January although no samples were collected that month. Individuals in the early active stage (Figures 1b and 2d) first appeared in February for both sexes, while those in the middle active stage (Figures 1c and 2e) first appeared in March and the late active stage (Figures 1d and 2f) in early April.

Ripe clams of both sexes were first observed in late April. Ripe males (35%) were most abundant in May and ripe females (47%) in June.

Clams in a spawning condition were first encountered in the later part of May, peaked in July, and were last observed in the early September sample. During July 75% of the males and 55% of the females were in a spawning condition.

Spent clams were present from July to October with the highest percentage occuring in August when 38% of the males and 65% of the females were in this phase.

There was no observed difference in reproductive cycle with size class, except for clams under 60 mm in length. In general the period of peak spawning for those clams was the same as other size classes, but the duration of the spawning period was shorter. It began about 1 mo later than other size classes and ended a month earlier.

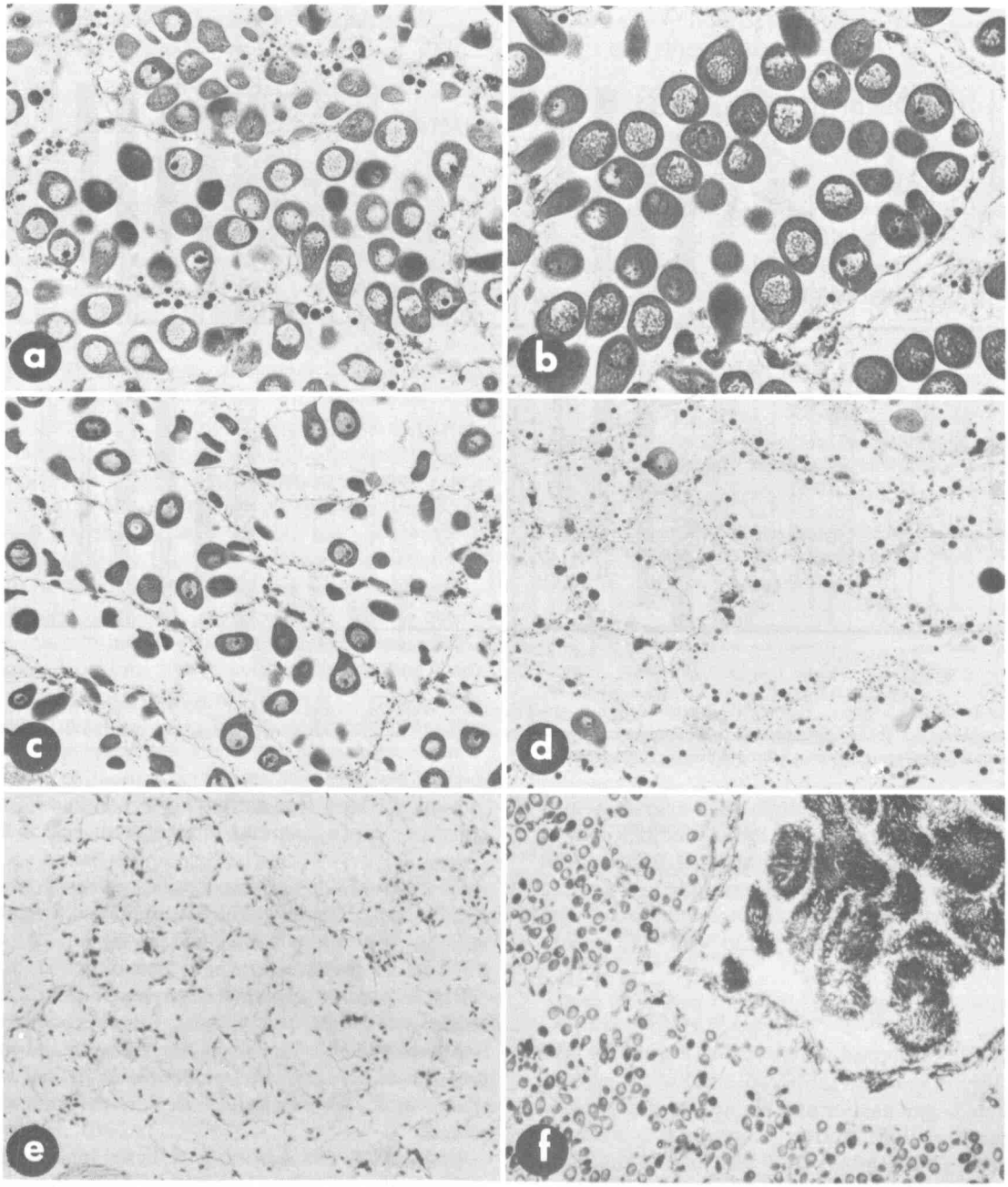

FIGURE 3.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Ripe female (180×), 14 June 1972. The ova are now free of the alveolar wall and have taken on a spherical shape. b) Ripe female (145×), 14 June 1972. c) Spawning female (180×), 1 June 1972. d) Spent female (100×), 24 Aug. 1972. The ova have been discharged, and follicle cells with inclusions are forming along the basal membrane of the alveoli. e) Immature clam (160×), 24 Aug. 1972. Follicle cells devoid of inclusions, but containing the small black follicular nucleii, fill the alveoli. From an individual 38.4 mm in length. f) Hermaphrodite (40×) in a spawning condition (14 June 1972).

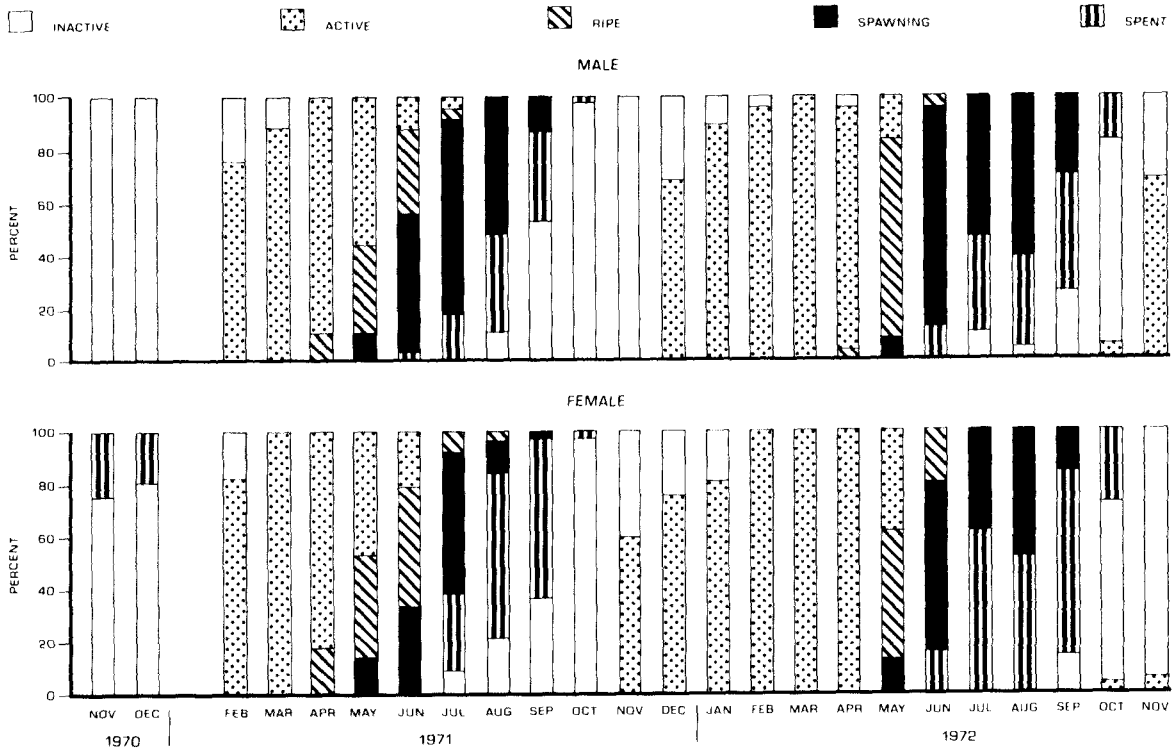

FIGURE 4.—Male and female reproductive cycles of the soft-shell clam, *Mya arenaria*, during 1971 and 1972 from Skagit Bay, Wash. The length of each shaded area represents the percentage frequency of clams in each reproductive phase. A total of 1,739 clams (48% males and 52% females) were examined during the 2-yr study.

The smallest mature male clam examined during the 1971 reproductive cycle was 22.9 mm in length, and the smallest female 31.0 mm. Both were taken in the September sample and were in the inactive phase. The largest immature clam was collected in late May and was 45.2 mm in length.

1972 Reproductive Cycle

The 1972 reproductive cycle (Figure 4) was similar to 1971 with the exception that the cycle as a whole began earlier and the active phase was of longer duration. Active female clams first appeared in November 1971 and active males in December 1971. The active phase lasted until May 1972. During the period from February until April the majority of all clams sampled of both sexes were in the active phase.

Ripe male clams first appeared in April and ripe females in May. Ripe clams of both sexes, 78% of the males and 49% of the females, were most abundant in May.

Spawning commenced in late May and peaked in June for both males (86%) and females (65%) and then continued at a diminished rate until September.

Spent clams of both sexes were present from June through October. They were most abundant in September when 45% of the males and 72% of the females were in the spent phase.

Inactive male clams first appeared in July (10%), while inactive females first appeared in September (13%). The highest percentage of inactive clams occurred in October with 79% of the males and 70% of the females in the inactive phase.

As in 1971, the spawning cycle for most of the clams under 60 mm in length commenced about 1 mo later than the normal cycle and ended 1 mo earlier. The smallest mature clam collected was a 36.3-mm spawning male obtained in July. The smallest mature female was 38.9 mm in length and was in the active phase in March. The largest immature clam was 51.5 mm in length and was collected in March.

In 1971 spawning was quite complete in both

sexes, while in 1972 many of the females failed to spawn completely although the discharge of male sex products seemed complete.

DISCUSSION

The gonadal inclusions of male and female soft-shell clams are distinctive. Coe and Turner (1938) state that the origin of these inclusions is partly from cytoplasmic activity of follicle cells and partly from cytolysis of gametes. The fact that all immature clams in the process of sexual differentiation were found to be developing inclusions characteristic of their sex seems to verify cytoplasmic activity of the follicle cells as one origin of these inclusions. In older male clams, the method of formation of the multinucleated cells first described by Coe and Turner (1938) as pycnotic nucleii and later by Shaw (1965) as sperm balls, needs further study. If the unspawned sperm are retained by the male clam as sperm balls as reported by Shaw (1965) and as my observations indicate (Figure 1c), then perhaps cytoplasmic activity of the follicle cells is the major method by which the inclusions are formed. In female clams the exact relationship between cytolysis of unspawned ova and the formation of inclusions is not known. The single row of follicle cells which form almost immediately at the basal membrane of the alveoli in spent female clams already contain a number of inclusions (Figure 3d) before any of the unspent ova have undergone cytolysis. The origin and function of gonadal inclusions in both sexes requires further investigation.

The gametogenic cycle of the soft-shell clam at Skagit Bay is identical to that reported for clams from the east coast (Coe and Turner, 1938; Shaw, 1962, 1965; Pfitzenmeyer, 1965; Ropes and Stickney, 1965). The single spawning cycle per year, from late May to early September, is similar to that described for studies in eastern Canada (Stafford, 1912; Battle, 1932; Sullivan, 1948) and the New England area (Welch, 1953[3]; Ropes and Stickney, 1965).

The slight variations noted between the spawning cycles of 1971 and 1972 and the incomplete spawning of females in 1972 cannot be explained at present.

Few hermaphroditic *Mya* are reported from other areas (Coe and Turner, 1938; Shaw, 1965). A single hermaphroditic specimen was collected at Skagit Bay (Figure 3f).

[3]Welch, W. R. 1953. Seasonal abundance of bivalve larvae in Robinhood Cove, Maine. Fourth Annual Conference on Clam Research, U.S. Fish and Wildlife Service, Clam Investigations, Boothbay Harbor, Maine, p. 4-6.

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IN SITU EXPERIMENTS WITH COASTAL PELAGIC FISHES TO ESTABLISH DESIGN CRITERIA FOR ELECTRICAL FISH HARVESTING SYSTEMS[1]

WILBER R. SEIDEL[2] AND EDWARD F. KLIMA[3]

ABSTRACT

In situ experiments to test the efficacy of a scale electrical harvesting system were conducted off Panama City, Fla. with both captured and wild coastal pelagic fishes. Six species of fish were exposed to preselected combinations of pulse rate, pulse width, and voltage by either attracting wild fish or placing captured fish between electrodes. Both captured and wild fish could be effectively controlled with a minimum field strength of 15 V/m, 20 to 35 pulses/s, and a pulse width of more than 0.5 ms. Voltage, pulse width, and pulse rate were equally important for controlling the species tested. Based on these results, resistance measurements were calculated and a potential netless harvesting system specified which would require a minimum energy output of 120 kVA dissipated into an electrode configuration 10 × 5 × 5 m with a load resistance of 0.01558 ohms. The basic design specifications for a prototype pulse generator are provided for netless fish harvesting applications and mid-water trawling.

Commercial fishing for the small, fast-swimming fish schools characterizing much of the pelagic fishery resource in the Gulf of Mexico has been hampered due to a lack in harvesting technology (Bullis and Thompson, 1970). The Southeast Fisheries Center, Pascagoula Laboratory, National Marine Fisheries Service has been engaged in the design and development of an electrical harvesting system capable of economically exploiting this resource. Results from laboratory experiments (Klima, 1972) provided design criteria for a 12-kVA (kilovolt ampere) pulse generator which was used to field test and validate the electrical control parameters and to provide design criteria for a pulse generator capable of commercially harvesting marine fishes from the Gulf of Mexico. This paper describes the results of the electrical in situ experiments using captured and wild fish.

Fishing with electricity was first used in fresh water during the latter part of the 19th century by Ishan Baggs, who was granted a British patent in 1863. Electrical fishing remained in obscurity until after World War I, when McMillan (1928) began to use electricity to systematically guide and lead fish. The use of electrical fishing in the sea has lagged considerably behind that in fresh water because of the high conductivity of salt water, which results in extremely low load resistance and therefore very high current and power requirements for generation of significant field strengths. Kreutzer (1964) showed pulsed direct current could be utilized economically to harvest fish in the sea provided that the field voltage gradient and shape, duration, and rate of impulses are suitable. Electrical stimulation produces either fright, taxis, tetanus, or eventually death, depending upon the electrical field pulse characteristics (Viber, 1967; Halsband, 1967; Lamarque, 1967).

The reaction to various combinations of characteristics varies with species, fish size, and probably other factors (Riedel, 1952; Collins, Volz, and Trefethen, 1954; Bary, 1956; Higman, 1956; Monan and Engstrom, 1963; Kessler, 1965; Halsband, 1967; Klima, 1968); hence, a combination of electrical factors which will induce electrotaxis in one species may induce a fright response or no response in another. As a result, it is critical to know the combination of electrical field characteristics which will produce the desired reaction for each species of interest.

Success of electrical fishing equipment depends upon use of optimum electrical combinations for

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inducing fright, taxis, or even tetanus. These various responses have successfully been used to commercially harvest marine animals. The principal applications include an electrical fish pump for *hardening* menhaden in a purse seine (Kreutzer, 1964), an electrical fish trawl (McRae and French, 1965), and an electrical shrimp trawl (Klima, 1968; Seidel, 1969).

MATERIALS AND METHODS

Test Procedure

Field experiments were performed in the nearshore waters off Panama City, Fla. The test equipment used in evaluating fish response to an electrical field consisted of a deck-mounted pulse generator and an electrode array deployed in the water alongside the vessel. Salinity and temperature ranged from 29.5 to 33.8 ‰ and 28.0° to 29.6°C, respectively.

Two separate groups of experimental animals were used in the experiments and are referred to as captured fish and wild fish, respectively. The first group consisted of 393 Spanish sardines, *Sardinella anchovia* Valenciennes; 397 round scad, *Decapterus punctatus* (Agassiz); 390 scaled sardines, *Harengula pensacolae* Goode and Bean; 228 Atlantic thread herring, *Opisthonema oglinum* (Lesueur); and 37 Atlantic bumper, *Chloroscombrus chrysurus* (Linneaeus). They were attracted by lights at night and caught with a 5-m lift net in the northern Gulf of Mexico and held in a tank of circulated seawater. Prior to testing, each fish was inspected for damage, and only fish in good condition were used. Each fish was exposed to a preselected combination of pulse rates, voltage, and pulse widths by carefully dropping them into the electrical field facing toward and within 1 m of the negative electrode.

The second group (wild fish) was not handled by the investigators but rather was attracted by lights at night to an area between the electrodes positioned next to the boat. When five or more fish were between the electrodes, they were exposed to preselected combinations of pulse rates, pulse widths, and voltage. Visual observations were used to estimate species composition, approximate size, and responses.

To evaluate the in situ effectiveness of the pulse characteristics tested, we measured the percent of fish which escaped from the electrical field and the percent which swam the length of the field to the positive electrode. The captured fish were introduced into the field in such a way that they were forced to turn 180° in order to swim to the anode, whereas the wild fish schools were randomly oriented. Fish not electrically stimulated when placed between the electrodes exhibited immediate escape movement toward the cathode, the side, or down, but usually did not escape by swimming toward the anode since they were dropped into the electrode array facing the cathode. Test fish would occasionally mill between the electrodes for several seconds before slowly moving away and to the side. Wild fish not electrically stimulated would mill between the electrodes. Consequently, the reactions of the electrically stimulated fish were evaluated in terms of electrotaxis or a positive response by their directed behavior to the anode. We considered swimming to the anode a positive response. All other responses were designated negative.

Description of Test Equipment

The pulse generator providing electrical energy to the electrode array had an output capability of 12 kVA at a pulse rate of 50 pulses/s with a peak output voltage of approximately 150 V at a pulse width of 0.8 ms (millisecond). The pulse rate could be varied from 4 to 55 pulses/s, and three different output widths were available with the unit; 0.3, 0.5, and 0.8 ms measured at the 10% power points. Pulse rise time was around 0.05 ms with a sloped decay. The pulse generator output was designed to operate into load resistance of either 0.05 or 0.2 ohm, since the operational array resistance could not be predicted for all variations in field conditions. At these loads, the output pulse was relatively smooth and undistorted, exhibiting only slight imperfections in the decay portion of the waveform. The waveform was distorted with other array resistances (Figure 1).

In Figure 1D, both the output pulse and the recharging compensating pulse are shown.[3] The compensating pulse is an important feature of the pulse generator and is designed to significantly reduce both electrode electrolysis and electrolysis of any incidental metal within the electrical field, such as a ship's hull. Essentially, the same

[3]Kreutzer, Patent No. 3,363,353; 16 January 1968.

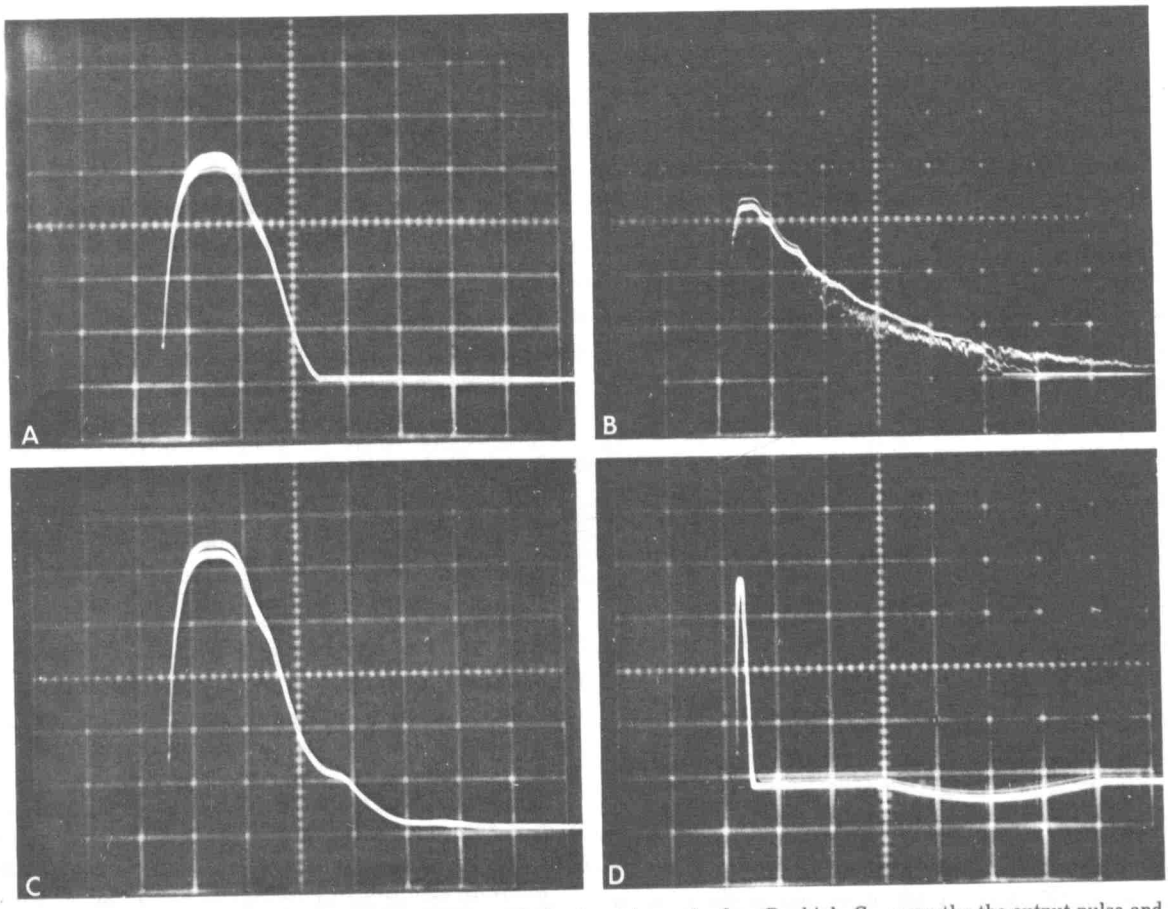

FIGURE 1.—Pulse generator output pulse matched into the load resistance A – low, B – high, C – correctly; the output pulse and compensating pulse are shown in D.

amount of electrical energy is contained within the envelope of the compensating pulse as is within the main pulse except the compensating pulse is of an opposite polarity. The compensating pulse has no effect on fish reaction, since its amplitude is many times less than the main pulse and is below the threshold level of the fish.

The electrode array and pulse generator were designed to effectively energize a minimum volume of water at least 2 m in cross section and 4 m long, and provide a selection of minimum electrical field concentration from 15 to 30 V/m. Each electrode of the array consisted of a copper tube frame with copper strips arranged in a grid pattern. The strips of copper were 15.2 cm wide (6 inches) with square grid openings of 45.7 cm (18 inches) between strips. It has been experimentally demonstrated that the surface of an electrode can be reduced to approximately 10% of the total area and the surface will function electrically as if it were a solid plate (C. Kreutzer,[4] pers. commun.). Our electrode design reduced the conducting surface of the electrode to approximately 53% of the total area. Therefore, this grid technique was utilized to allow the fish to be led to and pass through the anode for easier evaluation of their response. The cable connecting the electrode array to the pulse generator was a 12-m length of 1/0 coaxial conducting cable and represented a total resistance of approximately 0.01 ohm, or a total power loss of 20% in an overall array resistance of 0.05 ohm. Coaxial cable was utilized to eliminate pulse distortion and losses caused by inductance in parallel conductors.

Field strengths listed in volts per meter are averages based on measured electrode-to-electrode values and separation distance between electrodes rather than an in situ field strength

[4]Smith Research and Development Company, Lewes, Del.

measurement, because the density of an electrical field in seawater is not uniform. For ease of measurement, the electrode-to-electrode voltage was measured at the output of the pulse generator and did not take into account cable and connection losses. Also, due to the hookup restriction in the research vessel's instrumentation room, short lengths of parallel conductors were utilized, resulting in a 40% total cable loss. Therefore the true electrode-to-electrode voltages and average field strengths are related to measured values as follows:

A. 150 V = 90 V electrode to electrode = 22.5 V/m.

B. 120 V = 72 V electrode to electrode = 18.0 V/m.

C. 90 V = 54 V electrode to electrode = 13.5 V/m.

D. 60 V = 36 V electrode to electrode = 9.0 V/m.

The configuration of the electrical field at a pulse generator output of 120 V along with actual measured field strengths (expressed as voltage drops measured across 10 cm) at various positions within the field are shown in Figure 2A. The measurements are fairly close in value but not exact. The pickup probe was attached to a long pole and the measurements taken from the side of the RV *George M. Bowers*. Because of water current and boat movement, it was difficult to hold the probe parallel to the electric field in exactly each position shown.

Laboratory tests indicated a field strength of about 15 V/m was required to properly produce electrotaxis in fish 10 cm long. Field strengths throughout the volume of water within the electrode envelope could be maintained equal to or greater than the 15 V/m requirement.

Based on initial field tests, the general zones of fish response produced by the electrode array are 1) effective control, 2) possible control, depending on fish size and its orientation, and 3) fright zone (Figure 2B). The zone of control also extends to the back side of the positive electrode.

RESULTS

Captured Fish

Voltage, pulse width, and rate are equally important for controlling the species tested (Figures 3–5, Table 1). Comparison between the pulse widths indicates that a higher percentage of experimental animals were controlled at the wider pulse widths (0.8 ms). The lower and intermediate stimulation voltages (60 and 90 V) were not as effective in controlling the animals as the higher voltage (120 V). Furthermore, the combination of 0.8 ms pulse width with 120 V appeared to be adequate for inducing electrotaxis at the widest range of pulse rates (20 to 35/s).

The ideal pulse rates for inducing electrotaxis varied for each species. Spanish sardines and scaled sardines were under good control at 20 to 35 pulses/s and round scad at 25 to 35

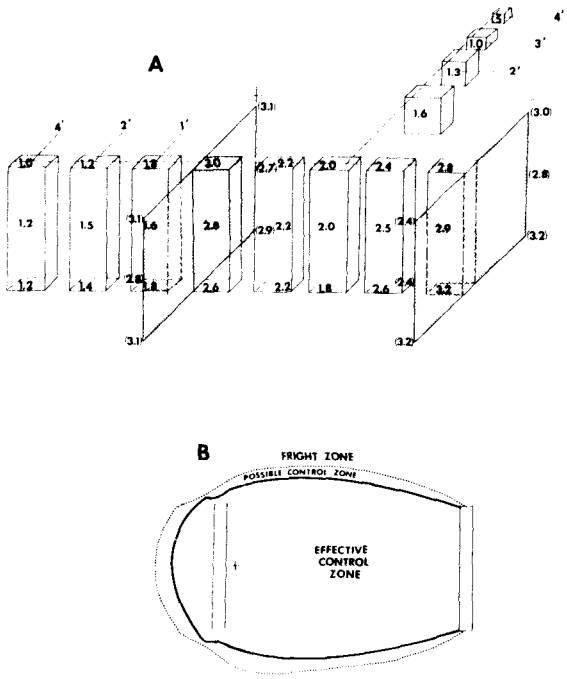

FIGURE 2.—A. Field strength configuration at 72 V electrode to electrode. B. General zones of fish response.

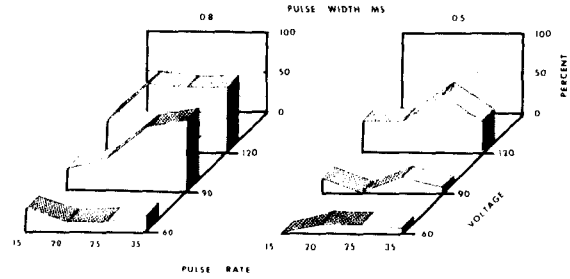

FIGURE 3.—Percent positive response of scaled sardines to various combinations of voltage, pulse rate, and pulse width.

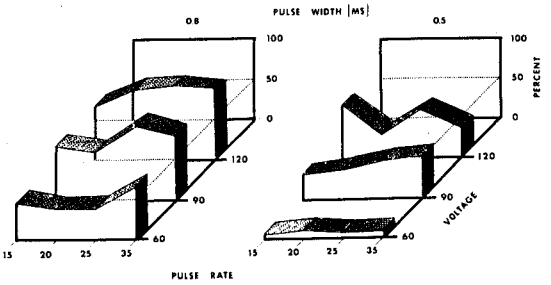

FIGURE 4.—Percent positive response of Spanish sardines to various combinations of voltage, pulse rate, and pulse width.

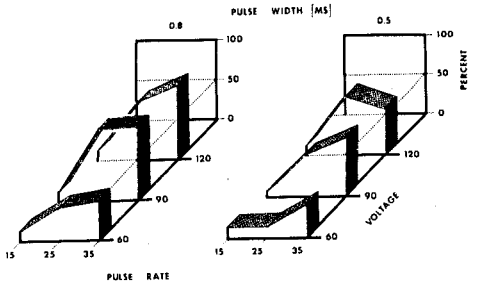

FIGURE 5.—Percent positive response of round scad to various combinations of voltage, pulse rate, and pulse width.

TABLE 1.—Percent of thread herring and bumpers at various stimulation parameters. Each observation consisted of 15 individuals except where noted.

Voltage and pulse width	Pulse rate: Thread herring 15	Thread herring 25	Thread herring 35	Bumper 25
60 V; 0.5 ms	56	53		[1]50
90 V:				
0.3 ms	20	67		
0.5 ms	[2]61	63		80
0.8 ms		100	85	
120 V:				
0.3 ms	27	47		
0.8 ms	41	67		75
150 V; 0.3 ms	33	53	73	

[1]7 individuals.
[2]31 individuals.

pulses/s. Based on the limited data for thread herring and bumper, the best pulse rates were 25 to 35 pulses/s.

A factorial analysis was used to determine the most effective combination of pulse rate, width, and voltage for controlling Spanish sardines, scaled sardines, and round scad (Table 2). This analysis demonstrates that selection of the proper level of voltage, pulse width, and pulse rate are clearly important for controlling these species. Another important aspect may be the interactions between the three main effects, although the meaning behind this significance is uncertain. It can be seen from Table 2 that these interactions vary between species. Interdependence was observed for all tested electrical combinations in scaled sardines and Spanish sardines. Surprisingly, this was not observed for the round scad. Voltage and pulse rate interact for scaled sardines and round scad.

General observations for the first (captured) group of fish indicated if the electrical combination was not adequate, these fish would immediately escape to the side or towards the cathode. However, at times when the pulse width was 0.3 ms, thread herring would elicit a jump and skip on the surface of the water and dart out of the field. This escape behavior was never observed at the wider pulse widths. Controlled fish would swim to the anode and circle between the plates of the electrode from the inside of the field to the back of the field and back again in a circular swimming motion, and were held until the power was turned off.

The most effective electrical combinations for each species are listed in Table 3. We felt that if 70% or more of the experimental group responded positively, the combination was effective. Output voltages of 60 V or less were ineffective for controlling fish regardless of the pulse rate or pulse width. Effective fish control required an output voltage of at least 90 V with a pulse rate of 25 or more, and except for bumper the pulse width had to be 0.8 ms. An overall effective electrical combination was 120 V at 25 to 35 pulses/s at 0.5 to 0.8 ms, and 90 V at 25 to 35 pulses/s at 0.8 ms.

Wild Fish

The second group of fish was attracted into the electrode configuration by a surface nightlight positioned above the electrodes and then stimulated. Usually we were successful in attracting sufficient quantities of fish to evaluate a specific combination of electrical parameters. However, their exact position between the electrodes was never the same, especially when a large school of 30 to 50 fish were positioned between the electrodes. We only used electrical field characteristics which appeared to be successful during our daytime experiments with individual captured

TABLE 2.—Multivariant analysis of variance to determine which parameters are most useful to control Spanish sardine, scaled sardine, and round scad with probability levels (* significant at $P = 0.15$; ** significant at $P = 0.05$).

	Spanish sardine				Scaled sardine				Round scad			
Source of variation	Degrees of freedom	Mean square	F	Level of significance	Degrees of freedom	Mean square	F	Level of significance	Degrees of freedom	Mean square	F	Level of significance
Voltage	2	6,172.8	24.92	0.001**	2	8,827.1	36.25	0.001**	2	3,970.5	34.83	0.001**
Pulse width	1	17,328.0	69.95	0.001**	1	8,938.0	36.71	0.001**	1	2,809.0	24.64	0.001**
Pulse rate	3	578.1	2.33	0.099*	3	1,263.7	5.19	0.007**	2	8,149.5	71.49	0.001**
Voltage/pulse width	2	15.8	0.06	0.939	2	1,508.8	6.19	0.007**	2	110.6	0.97	0.398
Voltage/pulse rate	6	360.2	1.45	0.236	6	491.3	2.02	0.103*	4	633.1	5.55	0.004**
Pulse width/pulse rate	3	104.3	0.42	0.740	3	574.9	2.36	0.097*	2	50.6	0.44	0.648
Voltage/pulse width/pulse rate	6	496.5	2.00	0.105*	6	494.6	2.03	0.101*	4	435.7	3.82	0.020
Error	24	247.7			24	243.5			18	114.0		

TABLE 3.—Effective electrical combinations based on a minimum of 70% eliciting a positive response (Group 1 fish).

Species	Volts	Pulse rates	Pulse width
Spanish sardine	90	25-35	0.8
	120	20-35	0.8
Round scad	90	25-35	0.8
	120	25	0.5
	120	25-35	0.8
Scaled sardine	90	25-35	0.8
	120	25	0.5
	120	20-35	0.8
Thread herring	90	25-35	0.8
Bumper	90	25	0.5
	120	25	0.5

fish. The wild fish were only exposed to a pulse width of 0.5 ms, as the time between tests did not permit a change in pulse width. Since this pulse width provided satisfactory results, we felt that either 0.5 or 0.8 ms would be satisfactory, as indicated from our captured fish experiments. Visual observations indicated that the larger fish (>10 cm) reacted more quickly and swam to and from the anode before the smaller fish (<10 cm) did. Table 4 provides details and summaries of our nighttime observations with wild fish. In general, Spanish sardines and round scad were controlled adequately at 120 V and a pulse rate of 25 to 35 pulses/s at a pulse width of 0.5 ms. When large schools were attracted between the electrodes, it was not always possible to control all of the animals. Our visual observations indicated that fish in the fringe area would escape since the voltage gradient was insufficient to control fish in the fringe areas. The number of fish escaping probably varied with their position in the electrical field and their size, since smaller fish require higher voltage gradients for control than large fish. At 35 pulses/s and 120 V, we were able to pull or force fish into the electrode array from the back side of the positive electrode. Positive reactions were elicited in all species at the prime voltage of 120 and pulse rates between 25 and 35. The results from the wild fish experiment conclusively demonstrate that coastal pelagic fish of the species tested can be controlled and led with combinations of 120 V, 25 to 35 pulses/s, and a pulse width of 0.5 ms.

DISCUSSION

Effective electrical combinations for controlling coastal pelagic species determined during our field experiments compared favorably with the parameters determined by Klima (1970) in labora-

TABLE 4.—Responses of wild fish attracted to electrode configuration at preselected electrical combinations (pulse width — 0.5 millisecond).

Species	Approximate school size	Volts	Pulse rate	Reactions
Spanish sardine, round scad and bumper	10-15	120	25	Positive; pulled into anode and held.
Spanish sardine, round scad and bumper	10-15	120	35	Positive; pulled into anode and held.
Spanish sardine and round scad	30-50	120	35	Positive 50 to 90% led to anode and held; only fish in fringe area escaped.
Thread herring and bumper	5-8	120	35	Positive; led to anode.
Spanish sardine	10	90	15	3 had positive response.
Spanish sardine and round scad	10	100	50	Turn fish to anode—all escaped.
Spanish sardine and round scad	10	100	25	Turn fish to anode—all escaped.
Round scad	20-40	120	35	Positive and held at electrode.
Blue runner, *Caranx crysos*	15	120	25	Positive and held at anode.
Blue runner	10	120	35	Positive and held at anode.
Blue runner	30	120	35	20-25 positive response and held at anode.

tory studies. The range of pulse widths was slightly narrower in the field than in the laboratory where the experiment tank maintained a uniform field, test animals could not escape, and in which narrow pulse widths were not possible. Since wide pulse widths require more electrical energy, it is desirable to select the narrowest pulse width possible which will allow proper control of the species. This in situ investigation clearly demonstrates that pulse widths between 0.5 and 0.8 ms can be effectively employed in open water situations in conjunction with proper field strengths and pulse rates. Our results demonstrate that the effective control of the fishes tested requires no less than 15 V/m at pulse widths of 0.5 ms or greater and pulse rates ranging between 20 and 35/s. A pulse width of 0.3 ms was completely ineffective within the proper field strength and pulse rate range used in our experiment.

A review of the field test data suggests an additional parameter, minimum pulse control power for a specific pulse width and field strength, should be determined during future field experiments. Obviously a minimum output voltage and current is necessary to maintain the established 15 V/m in any particular electrode configuration and resulting load resistance. However, once the minimum power to maintain 15 V/m is reached, if future research can establish that a pulse envelope of minimum total power within a minimum and maximum set of values for pulse rate and pulse width is the important criterion for proper fish control, much greater latitude would be possible in designing a pulse generator for a particular fishing system. This would permit a designer to better select pulse rate, pulse width, and maximum values for voltage and current to provide better equipment reliability and possibly cheaper construction.

The power required to control fish is presented in the following discussion based on the parameters of pulse width, pulse rate, and field strength which we used as criteria during the field tests. Power for each pulse (P_p) is described as:

$$P_p = V_e \times I \times P_w \qquad (1)$$

where V_e = electrode voltage
I = current at load resistance in amperes
P_w = pulse width, milliseconds.

The total load resistance equaled 0.05 ohm with an electrode-to-electrode resistance of 0.033 ohm and a cable loss of 0.017 ohm. Slight daily variations of 0.006 ohm were noted in electrode-to-electrode resistance due to small changes in salinity and temperature. For computations, we rounded the resistance values slightly and the electrode-to-electrode voltage was established as 60% of the output voltage. The current (I) and electrode-to-electrode voltage (V_e) at selected output voltages using an array resistance of 0.03 ohm and a loss resistance of 0.02 ohm were:

Output voltage	V_e	I
150	90	3,000
120	72	2,400
90	54	1,800

The total power (kW) delivered into the electrode array after cable losses can be computed as follows:

$$P_t = V_e \times I \times P_w \times P_r \quad (2)$$

where P_r = pulse rate, pulses per second
P_t = total power in kilovolt ampere.

Using the above values, the total power for effective electrical control values used was:

V_e	P_r	P_w	P_t
54	25	0.8	1.94
72	25	0.5	2.16
72	25	0.8	2.77
90	35	0.3	2.84

The preceding results suggest there is a minimum requirement of total power *(P_t)* to properly control the fish which would be a constant regardless of the specific combinations of pulse width, pulse rate, and field strengths. Once the effective field strength of 15 V/m is exceeded, it appears that different minimum values of pulse rate and pulse width can be obtained to produce equally effective fish response. Unfortunately, there are too few data points to support this conclusion. To properly substantiate such a hypothesis, we would have to determine either a minimum pulse width for a constant electrode voltage at each pulse rate or a minimum pulse rate for a constant electrode voltage at each pulse width. Without this, we cannot definitely state that a parameter of total power *(P_t)* can be used as a control specification rather than various combinations of electrode voltage, pulse width, and pulse rate. Many more tests would be needed to substantiate the hypothesis, although this approach would be advantageous from a designer's standpoint.

120-kVA Pulse Generator Design

The primary objective in the design of our pulse generator was to produce a system which, based on the results of the 12-kVA pulse generator electrical fish control experiments, would provide the capability for prototype development and effective harvest of fish in several modes of system operation. The output power of the pulse generator and pulse control characteristics were established to satisfy requirements for automatic fish harvesting without nets (Klima, 1970), electrical mid-water and bottom trawling for fish, and to provide the potential for prototype development of possible future applications such as fish barriers, electrical aquaculture cages, or other such applications.

Netless Fish Harvesting Mode

The initial reason for our development efforts in the field of electrical fishing was to eventually achieve the automatic fish harvesting system. Since this application imposed the most serious power demands, the design specifics were established around that set of conditions and results of this study were used to calculate the power requirements for a netless fishing system. Allowances were made, however, for application of the system to other electrical control applications. One, a mid-water trawl mode, is described later in the paper.

Use of lights at night concentrate fish (Wickham, 1971) in a volume of water which can then be electrified. The minimum volume of water within a light field which needs to be effectively covered electrically to produce commercial quantities of fish would be 5 m in cross section and 10 m in length. An equation for resistance of seawater between the electrodes is:

$$R = \frac{\rho L}{A} \quad (3)$$

where L = distance between electrodes in meters
A = surface area of the electrodes in square meters
ρ = resistivity of seawater in ohm-meters.

According to this equation the load resistance of two parallel plates is:

$$R = \frac{0.213 \times 10}{25} = 0.0852 \text{ ohm}$$

where ρ at 30‰ and 24°C = 0.213 ohm-m.

However, this formula only describes the resistance of the volume of water between two electrodes as if the electrode array was a finite conductor. In actual practice, a significant spreading of the electrical field occurs in seawater. If the size of an electrode is small in comparison to the

separation distance, the configuration of the electrode in the array is the principal factor in determining the resistance value, as would be the case with small balls or cables for electrodes. For our situation, the size of the electrodes and separation distance are equally important. Since the load resistance of the array in seawater is extremely low, the resistance value used to calculate power requirements becomes extremely important. A small error in the resistance could result in a large miscalculation of the necessary power requirements. For this reason we took great care in computing resistance accurately. Resistance measurements for this situation can be calculated by two methods referred to as Kreutzer and empirical technique. Kreutzer developed a formula for calculating spread resistance for one electrode:

$$R_s = \frac{K_o\,(1 + T \times 0.02)}{\sqrt{A}} \qquad (4)$$

where R_s = spread resistance of one electrode, including field fringing
K_o = a constant at a specific salinity
T = temperature in centigrade
A = area, square meters.

(C. Kreutzer, pers. commun.) The constant K_o varies with different salinity values and must be recalculated for each new salinity. It can be obtained by solving for K_o in Equation (4) which requires knowledge of resistance, surface area, and temperature. Once the value of K_o is determined for a specific salinity, Equation (4) can be used to calculate R_s for varying electrode surface areas. Because the value of K_o varies with different salinity and is difficult to determine since in situ resistance measurements are required, we decided to establish an empirical ratio which compares the theoretical calculated resistance from Equation (3) to an actual measured electrode resistance. The calculated resistance according to Equation (3), using the 2 × 2 × 4 m electrodes of one test was:

$$R = \frac{0.189 \times 4}{4} = 0.189\,\text{ohm}$$

with a salinity of 32.9‰ and a temperature of 28.7°C (ρ = 0.189 ohm-m). The measured resistance was actually 0.039 ohm. An index of difference between the calculated and measured resistance provides a ratio of 4.85. The ratio of calculated to measured resistance ranged from 4.85 to 5.2 throughout the study period, with the measured resistance of the electrode array varying from 0.035 to 0.04 ohm. Hence, a midrange value of 5.0 seems the most practical and resistance value one-fifth of the Equation (3) calculated value is used to compute total spread resistance as shown in the following equation:

$$R_t = \frac{\rho L}{5A} \qquad (5)$$

where R_t = total spread resistance including both electrodes.

As a cross-check to Equation (5) we also computed the spread resistance from Equation (4) using a value of K_o derived from the sample test. The measured resistance of the electrode array in seawater was 0.039 ohm. Since each electrode contributes one-half the resistance, the spread resistance for Equation (4) is 0.0195 ohm. In addition, since both sides of each electrode in our tests were exposed, the surface area for the equation is twice that of one side. Using these values, K_o is determined to be:

$$0.0195 = \frac{K_o(1 + 28.7 \times 0.02)}{\sqrt{2(2)^2}}$$

where K_o = 0.035 ohm-m.

For a 5 × 5 × 10 m electrode array using Equations (4) and (5), the following load resistances are determined at 28.7°C and 32.9‰:

Equation (4)

$$R_t = \frac{0.189 \times 10}{5(5)^2} = 0.01512 \text{ ohm},$$

Equation (5)

$$R_s = \frac{0.035\,(1 + 28.7 \times 0.02)}{\sqrt{2(5)^2}} = 0.00779,$$

where $R_t = 2R_s = 2(0.00779) = 0.01558$,
$R_t = 2R_s$ since R_s is the resistance of one electrode.

As can be seen, the value for the load resistance of a 5-square meter by 10-m array compares favorably when determined by the two different equations. The higher value of 0.01558 ohm was used in making power calculations since any electrode array will have some additional resistance due to connection losses.

Results from our field study thus provided the following set of basic design specifics for our prototype pulse generator for use with attracting lights in a netless fish harvesting application:

1. Minimum field strength – 15 V/m.
2. Pulse rate – 20-35 pulses/s.
3. Pulse width – ≥0.5 ms.
4. Array size – 5 × 5 × 10 m.
5. Load resistance of array – 0.01558 ohm.

Using these specifications, we determined the output capability of the pulse generator which would satisfy our requirements by the following equation:

$$P = VI \times fl \qquad (6)$$

where P = power, watts
V = output voltage, volts
I = current, amperes
f = pulse rate, pulses per second
l = pulse length or width, seconds.

To insure an adequate field strength throughout our electrode array, we chose a value of 20 V/m for the power calculations. We also selected a maximum pulse rate of 50/s and pulse widths of 0.5, 0.75, and 1.0 ms to give the pulse generator more versatility. Using Equation (6), the power requirement is:

$$V = 20 \times 10 = 200 \text{ V for 10-m array}$$

$$I = \frac{V}{R_l} = \frac{200}{0.01558} = 12{,}837 \text{ A},$$

and at 50 pulses/s and 0.75 ms pulse width

$$P = (200)(12{,}837)(50)(0.75 \times 10^{-3})$$
$$P = 96{,}278 \text{ W}.$$

In an applied system, a cable and connection loss will be experienced. Because of the very low load resistances of seawater, a 25% cable loss can easily be expected. Rounding off our requirement to 90 kVA and after allowing for a 25% loss, we need a pulse generator of 120-kVA output to satisfy the system requirements we established.

As a crosscheck of the above designed system, the following formula (Kreutzer, 1964) is used to calculate the effective fish control range of one electrode:

$$R = \sqrt{\frac{I \times L \times \rho}{G \times 2 \times \pi}}$$

where R = effective range, meters
I = current into the water, amperes
L = length of fish, meters
ρ = water resistivity, ohm-meter
G = body voltage of fish.

To determine the effective range of 20 V/m, a value of 1 m is used for the fish length, fish body voltage is 20 V, and the resistivity is again 0.189 ohm-m.

Allowing a 25% cable loss requires a total input voltage of 267 V at a total load resistance of 0.0208 ohm, and the current in the water is found to be:

$$I = \frac{V}{R} = \frac{267}{0.0208} = 12{,}837 \text{ A}.$$

Using these values, range (R) is found to be:

$$R = \sqrt{\frac{12{,}837 \times 1 \times 0.189}{20 \times 2 \times 3.14}}$$
$$R = 4.40 \text{ m}.$$

Since this value is computed for one electrode, the 20 V/m range of two electrodes will be 8.8 m. In actual practice, however, the range of two electrodes paired together is greater than twice the reach of one, and we can supply a 5 × 5 × 10 m array with 20 V/m. At our minimum specification of 15 V/m, the calculated reach of one electrode is 5.08 m.

Since the configuration of the electrode array determines array resistance, various combinations of electrode size and separation distance can change the pulse voltage and current requirements. For this reason, a certain degree of flexibility was designed into the netless fish harvesting mode of the pulse generator. The system is

capable of delivering up to 1,000 V to an electrode array. However, at this voltage, the array shape has to be changed to produce a much higher load resistance to maintain the current at a value which is within the 120-kVA rating of the system and the current and voltage carrying capability of various components in the unit. For instance, at 1,000 V the electrode array has to have a total resistance of 0.3 ohm.

Mid-Water Trawling Mode

The pulse generator was also designed for application to electrical trawling. This use of the system requires a significantly different configuration than in netless harvesting. Since the pulse generator components are far too large to consider underwater mounting of the system on a trawl, it was necessary to design the unit for operation through a long power cable. The cable transmits the pulsed power from the vessel to the trawl. A cable length of 2,200 feet (670.1 m) was chosen to allow trawling to depths of 100 fm (fathoms) (182.9 m) with a cable to depth ratio of at least 3:1. The length of the cable is important because as it gets longer its direct current resistance increases and therefore either the cable losses become greater or the size of the conductors has to be increased to prevent excessive losses. Since a large power loss is not acceptable, conductor size and the resulting cable diameter eventually become too large and are limiting factors in the total length and therefore the power then can be transmitted down the cable.

The operation of a pulse generator into a long cable requires careful design in order to work. First, the impedences of the pulse generator, cable, and electrode array have to be properly matched through step-up and step-down transformers to accomplish transmission of the pulse down the cable. Unless impedences are properly matched, the pulse will become very distorted or can be totally lost in the cable. Another serious limiting factor in the operation of a pulse generator through a long cable for trawling is the underwater transformers which match the power supply cable to the electrode array. The delivery of significant levels of power, such as 120 kVA, through a single transformer would require a transformer that is quite large and would weigh several hundred pounds to handle the pulse current into an array with a load resistance of 0.05 ohm.

Our first intended application of the pulse generator in a trawling mode was with a mid-water trawl. The standard mid-water trawl being used at the Pascagoula Laboratory was a net that opened approximately 9 × 9 m under water. In actual field measurements, it has been found that the net generally opens between 7.5 and 9.0 m in height. Therefore we required the pulse generator to accomplish effective electrical trawling on a vertical opening of 7.5 to 9.0 m and a horizontal opening of approximately 9.0 m. In the mid-water trawl application we expect the electricity to provide a combination of fright, leading, and some tetanus to aid in harvesting of fish. Past experiments at the Pascagoula Laboratory demonstrated that fish generally accumulate in the mouth and forward body of the trawl. Therefore an electrical field applied periodically should force the fish back into the cod end.

Because of component ratings, loading of underwater transformers, and design restrictions, a power of 80 kVA was chosen as the maximum which could be supplied to our electrode array in a mid-water trawling mode. Since the application of 80 kVA through a single transformer is difficult under water, we chose four electrode pairs and four underwater transformers matched to each electrode pair to cover the 9.0 × 9.0 m net. It was found that a reasonable electrode size could be used which would provide a load resistance of 0.2 ohm for each pair and deliver 20 kVA from each transformer. This meant that by connecting the electrode pairs in parallel, each transformer would carry one fourth the current which would be required of a single transformer at the same total output. In addition, the four parallel electrode pairs would represent a total load resistance of 0.05 ohm which could easily be matched to the other impedences of the system.

Within the impedence matching requirements of the pulse generator, cable, and electrode array, and using the maximum output voltage of 2,500 V that the unit is capable of supplying in this mode, 450 V can be supplied to each electrode pair through the matching transformers. The surface area of each electrode pair must be adjusted to provide a resistance value of 0.2 ohm. Therefore, the pulse current of this condition is:

$$I = \frac{V}{R} = \frac{450}{0.2} = 2{,}250 \text{ A.}$$

Using Equation (7) at 15 V/m, the range of an electrode is:

$$R = \sqrt{\frac{2{,}250 \times 1 \times 0.189}{15 \times 2 \times 3.14}}$$

$$R = 2.13 \text{ m.}$$

However, to accomplish at least a fright reaction required 10 V/m or less, depending on fish size. We feel that a fright reaction, although not as effective as positive control of fish, will accomplish disorientation and therefore harvest of some fish in an electrical trawling mode. Since the temperature of below-surface water will be colder, we can use higher resistivities than 0.189 in calculations as shown in the following calculation for field reach at 100 fm water depth. In addition, Kreutzer's Equation (7) states that the factor in the denominator goes from 2 to 4 as the electrodes are placed in mid-water. Using these values, we calculate the maximum variation of values from the surface to 100 fm in the 10 V/m range of one electrode to be:

Surface:

Salinity 32.9‰, temperature 28.7°C, $\rho = 0.189$

$$R = \sqrt{\frac{2{,}250 \times 1 \times 0.189}{10 \times 2 \times 3.14}}$$

$$R = 2.60 \text{ m.}$$

100 fm:

Salinity 30‰, temperature 10°C, $\rho = 0.3$

$$R = \sqrt{\frac{2{,}250 \times 1 \times 0.3}{10 \times 4 \times 3.14}}$$

$$R = 2.32 \text{ m.}$$

Again, the range of two electrodes is found to be greater than twice the range of one electrode. In addition, since each electrode pair based on their required size for 0.2 ohm, will be separated by about 1.22 m, field strength adding will occur. Therefore, the effective range of an electrode pair is significantly more than twice the range of one electrode. By installing one polarity electrode on the headrope and the opposite on the footrope, we should be able to cover a 9 × 9 m area with the weakest part of the field having at least enough strength to frighten fish. We can also use pulse rates higher than 35/s, which will immobilize fish more rapidly. In addition, it must be remembered that at distances closer to the electrodes, the field strength increases and reaches values which will effectively lead or stun the fish. Because the size of each electrode is relatively small, current densities capable of stunning fish will be found at some minimum distance from the electrodes. This is not desirable for leading fish in a netless harvesting application and is avoided by using large electrodes, but it is very desirable in a trawling mode where the electrodes are inside the body of the net.

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ECOLOGY AND NATURAL HISTORY OF A STAND OF GIANT KELP, *MACROCYSTIS PYRIFERA*, OFF DEL MAR, CALIFORNIA

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ABSTRACT

The assemblage of plants and animals living within a stand of *Macrocystis pyrifera* off the coast of southern California was studied from July 1967 through February 1973. *Macrocystis* is a perennial kelp, with some individuals living as long as 7 yr; however, the average life span in this bed was approximately 3 to 4 yr. Physical disturbances associated with storms were the major mortality causes of adult *Macrocystis* in this area. Once detached, these plants drift through the bed and become entangled with other plants which results in extensive mortality. The fact that germination was greatest after the surface canopy was thinned by natural attrition and commercial harvesting suggests that light is a critical factor influencing the recruitment of *Macrocystis*. There was little indication to show that sea urchin grazing contributed to kelp mortality.

Faunal species identified included 38 fish species and 98 invertebrate species. Of these, 14 species of macroinvertebrates were chosen for more intensive study as they represented common or characteristic species in the kelp bed. Patterns of distribution and abundance were recorded during the study period. Most species had aggregated distribution patterns and the populations of most remained reasonably constant over 4.25 yr. *Styela montereyensis* (ascidian) fluctuated annually and the *Muricea californica* (octocoral) population slowly decreased during this time. Conversely, *Diopatra ornata* (polychaete) displayed a numerical increase, such that in August 1972 it was the most abundant macroinvertebrate in the Del Mar kelp bed. A qualitative food web is presented based on limited trophic information.

Many large kelp stands historically have either undergone dramatic oscillations in areal cover and standing crop or completely disappeared (see North, 1971, for history and data). Nearshore kelp stands are found in many scattered locations along the mainland of California and fringe most of the state's offshore islands; in southern California kelps are often conspicuous when the dominant plant, *Macrocystis pyrifera* (Linnaeus) C. Agardh, forms a floating canopy or bed along the sea surface. This kelp community contains many plant and animal species which contribute aesthetic as well as diverse recreational and commercial resources. The loss and deterioration of these stands is correlated with many man-caused perturbations and natural events such as reduced water quality, the over-harvest of numerous important component animal populations, and fluctuations in seawater temperature.

There is widespread concern regarding effects of increasing human perturbations to these nearshore kelp communities which include increasing recreational and commercial usage as well as many projected sewer and thermal outfalls into or in the proximity of kelp beds. Despite this concern, there is little information regarding natural temporal variation of populations inhabiting these assemblages. Furthermore, natural history data such as food web interactions critical to a functional understanding of this community are in a very rudimentary state. This information is obviously vital to the proper management of this resource.

The objectives of this paper are to: 1) describe patterns of distribution and abundance, 2) record long term population fluxes, and 3) note food web and other natural history observations of conspicuous members of a relatively undisturbed kelp association. Such data are essential to the growth of a functional understanding of this community.

The study site (Figure 1) was located in a bed of *Macrocystis pyrifera* about 1 km offshore from Del Mar, Calif. (lat. 32°57′N, long. 117°16′W). The majority of the observations were made at

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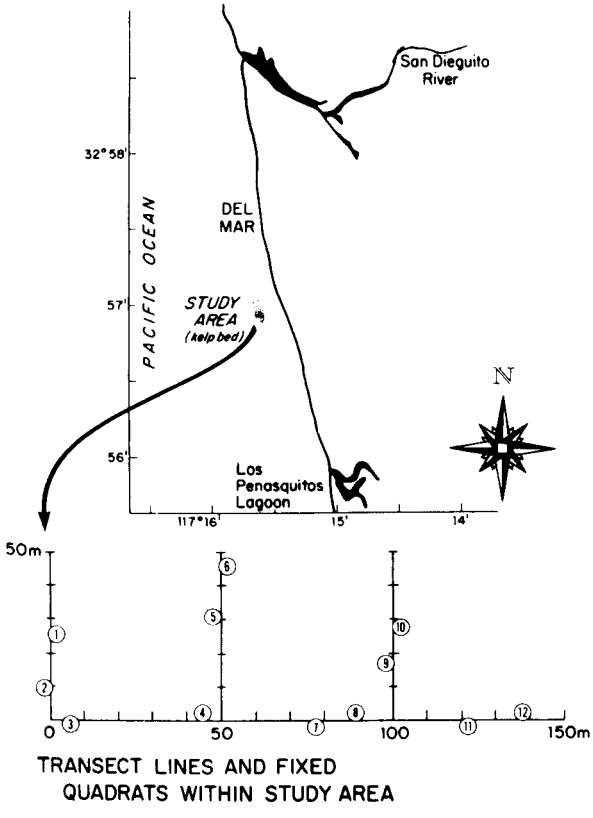

FIGURE 1.—Location of the subtidal study area off Del Mar, Calif. The drawing shows the layout of the transect lines and the position of each fixed quadrat.

depths between 14 and 20 m in the most seaward *Macrocystis* stand directly off 8th Street in Del Mar. These continuing studies were begun in June 1967.

Within the perimeter of the study area the substratum is composed primarily of sedimentary mudstones and siltstones, coarse sand, and silt. The sea floor is somewhat flat in appearance, although low (<1.5 m) consolidated mounds and shallow ledges break up the overall visual uniformity of the bottom.

The monthly mean surface water temperatures recorded off the pier at Scripps Institution of Oceanography, approximately 24 km south of the study site, varied from a minimum of 10.1°C to a maximum of 24.6°C between June 1967 and December 1971 (Scripps Institution of Oceanography, 1968-1971). The annual mean temperature during this same period was 16.3°C. Since the water column in this area is thermally stratified, it is essential to consider bottom temperatures as well. To this end, 70 bottom temperatures were recorded at a depth of 17 m in which the mean temperature was 13.0°C with the minimum recorded temperature being 10.5°C, and the maximum being 16.0°C.

A great deal of water movement is typical to this environment (Inman and Brush, 1973) and water transparency or underwater visibility is greatly affected by the resulting sediment disturbance. Over the 5.7-yr study, the underwater visibility ranged from 0 to 20 m, the average visibility being about 3 to 4 m. However, on many dives the underwater visibility was so reduced that it was impossible to see along the bottom in the vicinity of the kelp bed.

METHODS

The study was initiated in June 1967 after several months of exploratory observations. All of the in situ observations were made while scuba diving and more than 300 h were spent underwater in this location. Most observations were made during daylight hours, however about 5 h were spent in this location between 2000 and 2200 h. The observations reported in this paper span more than 5 yr, from June 1967 through February 1973.

Initially a 100-m transect consisting of 20 brass stakes (75 cm in height) was placed along the sea floor in June 1967. One stake was placed every 5 m, and the entire array was perpendicular to the shoreline. During July 1967 the position of each attached *Macrocystis* plant growing within 1 m on either side of the 100-m transect was recorded. The condition (i.e., number of living stipes, appearance of the holdfast, etc.) of each plant was noted at various times from the beginning of the study until the plant disappeared. Also, juvenile *Macrocystis* were recorded as they appeared along the 2 m × 100 m strip.

In the fall of 1967, the main transect was extended 50 m shoreward, and during March 1968 three additional lines running parallel to the coastline were added (Figure 1). Sectioned 25-m polypropylene lines (0.60 cm in diameter) were staked into the bottom alongside of the brass stakes. The lines were sectioned so that fouling or detachment of any part would not necessitate replacement of the entire transect. All lines were marked at meter intervals with tape, and the brass stakes were numbered with line and plastic

tags. This marking system made it possible to sample any point on the transect and return to the same position even during days of marginal underwater visibility.

The entire transect area was stratified into six 2 × 50 m areas. Two sample points were randomly selected per stratum; at each of these 12 locations a 4-m^2 quadrat was placed in September 1968. Each quadrat consisted of polypropylene line, arranged in a square 2 m on a side, and held in place at each corner with galvanized spikes. Two additional 4-m^2 quadrats (no. 13 and 14) were added in August 1969, but in this case the locations were selected by the presence of juvenile *Macrocystis* in this part of the kelp bed. The latter two quadrats were not included in the evaluation of density or aggregation.

During September 1968 a drawing or map of each fixed quadrat was made underwater on a sheet of plastic recording natural history information and the position of each individual macroorganism. A brass meter square quadrat divided into 0.25-m^2 sections was used while mapping the quadrats in order to reduce the visual area being examined. Quadrats were examined at irregular intervals (i.e. monthly, bimonthly, or quarterly) by the same observer.

Data regarding density, frequency of occurrence, and distribution patterns were calculated from observations in the 12 4-m^2 fixed quadrats and from 48 1-m^2 quadrats placed at randomly chosen points along the transects. All quadrat analyses are from observations taken in August 1972. The distribution patterns of the conspicuous species were analyzed with the index of dispersion, variance/mean × (number of observations −1), described by Greig-Smith (1964). If the variance to mean ratio is significantly less than 1.0, the distribution is considered even, while an index significantly greater than 1.0 indicates an aggregated pattern of distribution. Significance is tested in a Chi square table with $n - 1$ degrees of freedom. Lack of significance indicates a random distribution. Since the results of most such indices depend upon quadrat size, we compared independently the 4-m^2 quadrats and the 1-m^2 quadrats. The only differences in the two analyses of pattern were minor and involved slight loss of significance in three of the 4-m^2 quadrat analyses; in each case this was a result of small numbers of individuals in the 12 larger samples. The results of the pattern analysis are given in Table 5 and are based on the 48 1-m^2 quadrats.

THE ALGAL ASSOCIATION

The floristic components of southern California kelp beds have been described by Limbaugh (1955); Dawson, Neushul, and Wildman (1960); North (1971); and Neushul (1971). Many of the mainland and insular kelp stands that we have surveyed in southern California appeared dissimilar with respect to the algal species present or their relative abundances. Therefore a generalized list of the algae known to inhabit these kelp communities is inadequate when describing a particular stand or comparing two or more kelp stands (Dawson, Neushul, and Wildman, 1960). The one characteristic of all mainland southern California beds appear to share is the overall domination of *Macrocystis*, in terms of both biomass (McFarland and Prescott, 1959) and apparent competition for the available light. The kelp bed at Del Mar is two layered, with the floating portion of *Macrocystis* suspended over an algal turf composed primarily of encrusting corallines. There is also a thinly scattered undergrowth of *Pterygophora californica*, *Laminaria farlowi*, and *Rhodymenia pacifica*. These species are taller than the corallines, but they occur so sparsely in this area that they cannot be considered a separate canopy. The algal association at Del Mar consisted of only a few species of attached macroalgae (Table 1); most of these plants were found along the margins of the *Macrocystis* bed.

TABLE 1.—The attached macroalgae found in the Del Mar kelp bed.

Bossiella orbigniana (Decaisne) Silva
Corallina officinalis var. *chilensis* (Harvey) Kutzing
Cystoseira osmundacea (Turner) C. Agardh
Desmarestia munda Setchell and Gardner
Desmarestia tabacoides Okamura
Laminaria farlowii Setchell
Lithophyllum sp.
Lithothamnium sp.
Macrocystis pyrifera (Linnaeus) C. Agardh
Pterygophora californica Ruprecht
Rhodymenia arborescens Dawson
Rhodymenia pacifica Kylin
Tiffaniella snyderae Farlow

OBSERVATIONS ON *MACROCYSTIS PYRIFERA*

The giant kelp was the most abundant and conspicuous species of brown algae within the study area. It is perennial and usually grows attached to solid substratum anchored into place

by the holdfast. In July 1967, 35 attached *Macrocystis* plants which contributed fronds to the surface canopy were recorded along the 2 × 100 m transect band (Figure 2). For convenience we have arbitrarily lumped all plants with fronds (stipe and blade) reaching the sea surface into a category as canopy adults. With the passage of time, the number of adult *Macrocystis* growing within this 100-m transect band was gradually reduced from 35 plants to a single survivor in June 1970. In addition to the plants along this part of the transect we followed 14 adult *Macrocystis* that grew along the 50-m shoreward extension of the transect (Figure 3). This shallower portion of the kelp bed displayed a similar reduction in the number of adult *Macrocystis*. In April 1968, 14 plants were recorded along this 2 × 50 m belt, however by April 1970 the last survivor had disappeared.

The dramatic fluctuations in the number of adult *Macrocystis* within this kelp stand can be detected from both in situ counts and kelp harvesting records over the past 32 yr (Figure 4). North (1971) stated "that beds five and six, lying between Del Mar and Oceanside, California have often fluctuated in this manner. These beds actually consist of approximately eight major kelp areas along about 15 km of coastline. They flourish and disappear more or less in unison, typically but not invariably with a four year period."

The general pattern for the Del Mar *Macrocystis* population seemed to be gradual attrition of the adult plants with little or no replacement over a 3-yr period, followed by recruitment after most of the adult plants had disappeared. With the addition of 40 young adult *Macrocystis* along the 100-m transect (Figure 2) during the summer of 1971 the study area again supported a density of kelp plants similar to July 1967.

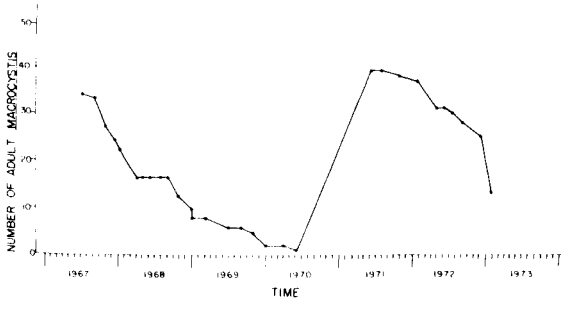

FIGURE 2.—Occurrence of adult *Macrocystis pyrifera* in the 2 m × 100 m transect (0-100 m).

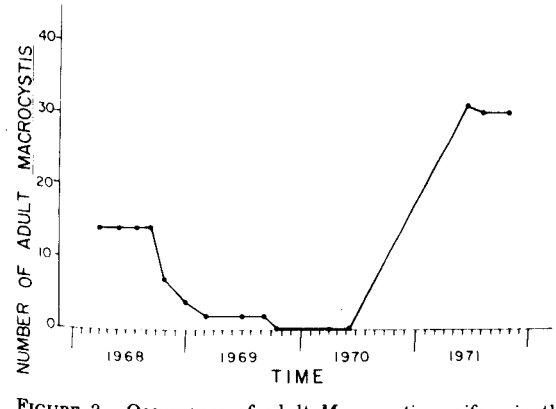

FIGURE 3.—Occurrence of adult *Macrocystis pyrifera* in the 2 m × 50 m transect (100-150 m).

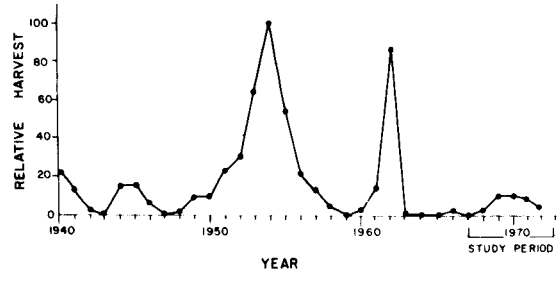

FIGURE 4.—Relative kelp harvest from bed number 5 (Del Mar). After North (1971) and Kelco Company.

Causes of Plant Mortality

Severe grazing of *Macrocystis* by sea urchins, as described by Leighton (1971) off southern California, has not been observed within this kelp stand. The two conspicuous sea urchins in this area, *Strongylocentrotus franciscanus* and *S. purpuratus* were usually observed on consolidated sedimentary mounds, under rocks, or within ledges. During both daylight and nocturnal hours the sea urchins remained in these locations, and in most instances their feeding was restricted to detritus and detached pieces of drift algae. However, *S. purpuratus* was occasionally noted within the deteriorating holdfasts of aging *Macrocystis*. In general, it appeared that there was enough drift algae for the sea urchin population to make foraging unnecessary, and we gathered no evidence that the urchins were exerting much grazing pressure on *Macrocystis*.

Fish damage to *Macrocystis* was minimal in mature plants. Most of the grazing by fishes was directed towards juvenile plants. Quast (1968b, 1971) investigated the stomach contents of fishes collected at Del Mar and found *Macrocystis* fragments in the stomachs of the labrid *Oxyjulis californica*, the kyphosid *Medialuna californiensis* and the embiotocid *Phanerodon furcatus*. He also found macroalgae as a predominant item in terms of frequency and volume in the stomachs of *Girella nigricans*. During daylight hours in this area *O. californica, Embiotoca jacksoni*, and *G. nigricans* were observed biting off portions of adult and/or juvenile *Macrocystis*. Some of the fish grazing may have been directed at the invertebrates associated with the algae, but for whatever reason, the plants were damaged by these feeding activities.

Most adult *Macrocystis* attrition recorded over the 5.7 yr was caused by detachment of the holdfast and thereby elimination of the entire plant. Plants with weakened or decaying holdfasts were particularly vulnerable to physical stress. Three factors probably accounted for most of the plant mortality in this location: 1) storms and strong surge, 2) entanglement of drifting plants with attached *Macrocystis*, and 3) kelp harvesting. Many of the kelp stands in San Diego County have been greatly thinned or almost torn away by the effects of storms (Brandt, 1923; ZoBell, 1971). Brandt (1923) reported that the La Jolla and Pt. Loma kelp beds were reduced nearly 40% in area by storms in the late winter and early spring of 1915. When *Macrocystis* plants become detached they drift along in the water column, often becoming entangled with other kelps (Figure 5). Drifting or dislodged plants thus present a potential source of mortality for attached *Macrocystis*. The stipes, blades, and holdfasts of entangled plants become so entwined that separation becomes almost impossible. We have observed as many as 18 adult *Macrocystis* entwined in one cluster near the transect. In almost every case the entanglement resulted in the mortality of the attached plant. This is a partial explanation why *Macrocystis*

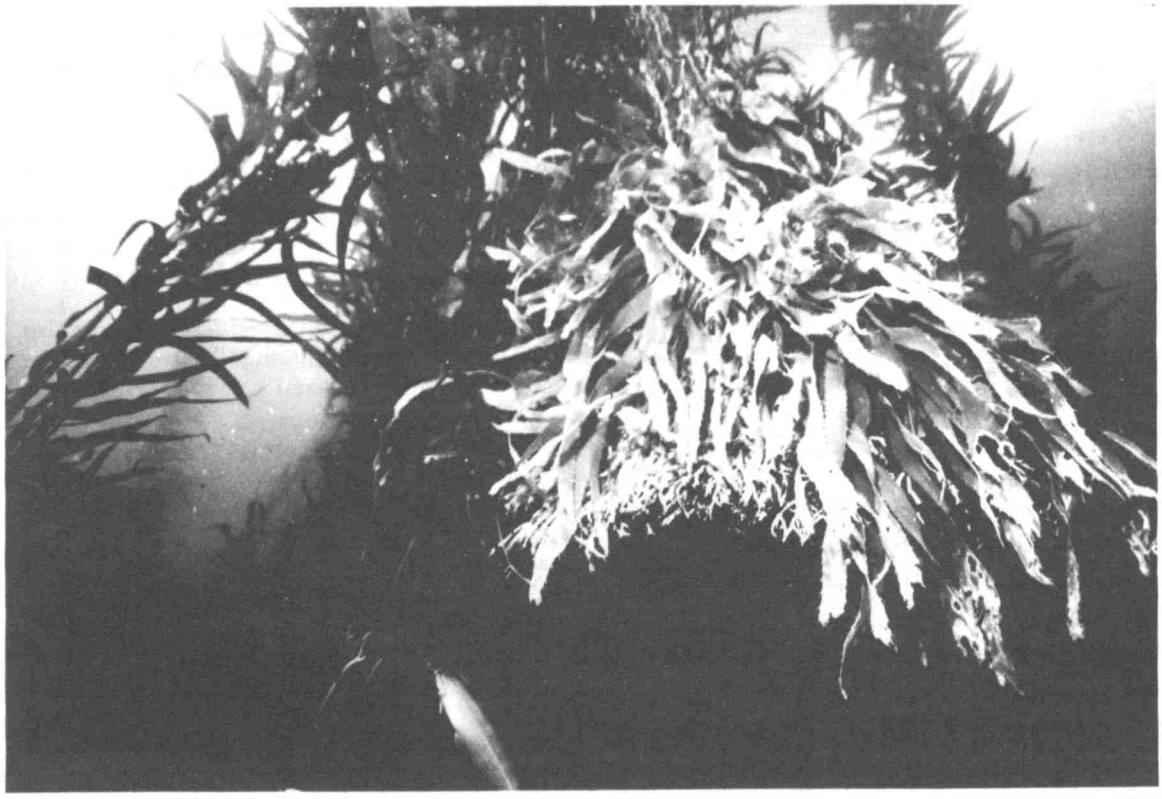

FIGURE 5.—A detached *Macrocystis* drifting through the kelp bed.

growing along the transect were frequently removed in clumps of two or three plants at a time (Table 2).

The effect of harvesting on individual plants is still inconclusive. ZoBell (1971) concluded from observations of drift seaweeds on San Diego beaches that there is no consistent relationship between kelp harvesting operations and the amount of seaweed on beaches. However, at Del Mar we found adult *Macrocystis* pulled free of the substratum following harvesting. On 6 January 1969, 10 marked plants were growing along the 100-m transect (Figure 2) and 4 plants remained in the 50-m extension (Figure 3). The seas were calm and there were no loose or drifting *Macrocystis* observed along the entire transect. The kelp bed was harvested on 7-8 January 1969. Returning to the study area on 9 January 1969 we found unattached *Macrocystis* which were either drifting in the water column or entangled with other attached *Macrocystis*. Two of the marked plants on the 100-m transect were detached from the substratum, and one plant from the 50-m extension was missing. Also, one adult *Macrocystis* from fixed quadrat number 1 was removed. These detached plants probably caused additional mortalities by entangling with other plants in the kelp bed. In summary, strong water movement, plant entanglement, and harvesting probably act in a synergistic manner on attached *Macrocystis*.

Germination, Recruitment, and Survivorship

Macrocystis undergoes a life cycle that alternates between an asexual macroscopic stage termed the sporophyte, and a sexual microscopic gametophyte stage (Brandt, 1923; Neushul and Haxo, 1963). Because of the difficulties inherent in microscopic investigation underwater we recorded recruitment only when the young sporophytes became visible. Although *Macrocystis* spores and gametophytes were probably present at different times of the year (Neushul, 1959; North, 1964), we were primarily concerned with the plants when they visually became part of the epibenthic community. A few young plants (<1 m in height) were observed in the study area during the early summer of 1967, however by the fall of that same year all of these juvenile sporophytes had disappeared. For the next 23 mo, no *Macrocystis* recruits were observed in the vicinity of the transect. During this time the overlying canopy was expanding to a point when, in December 1968, it covered approximately 90% of the 150-m transect line. Thus, insufficient light penetration resulting from shading by adult plants and water turbidity may have been key reasons for the absence of juvenile *Macrocystis* during 1967 and 1968. However, the bed was harvested in January 1969, which apparently reduced the surface canopy to about 15% cover

TABLE 2.—Stipe counts of individually tagged plants through study period. Plant number 1 survived with 7-8 stipes until August 1972. "G" means that the plant was completely gone and "O" signifies that there were no stipes but that the holdfast was still attached. Note the tendency for groups of plants to disappear together; in each case this resulted from mutual entanglement.

	Plant number																												
Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
July 1967	18	34	20	30	22	36	18	16	53	9	34	20	30	54	28	11	55	97	90	—	30	—	71	25	30	41	74	—	58	22
Sept. 1967	21	38	20	12	22	44	13	2	54	7	27	15	40	60	30	14	67	108	98	53	37	34	64	27	58	40	93	80	53	24
Dec. 1967	22	34	26	G	O	43	13	O	57	O	22	6	30	56	32	6	67	96	86	62	42	41	58	22	52	39	80	81	68	O
Jan. 1968	28	38	O			64	17		64		23	6	37	72	35	6	75	88	106	O	48	45	63	23	52	34	71	72	68	
Apr. 1968	32	31					16		60		27	G	32	G	30	4	67	63	102		46	44	G	22	42	35	74	60	G	
May 1968	34	28					10		63		28		35		31	G	73	82	115		42	53		22	52	34	78	62		
June 1968	29	22					10		49		25		36		35		81	84	123		42	52		22	46	31	75	57		
Aug. 1968	25	17					11		58		30		34		34		70	64	116		43	40		22	44	37	77	54		
Sept. 1968	30	14					9		47		30		32		38		80	70	114		42	39		24	50	36	87	64		
Nov. 1968	29	11					G		G		29		23		42		93	27	114		43	43		26	G	G	92	62		
Jan. 1969	23	12									24		22		40		—	G	127		43	40		24			G	65		
Mar. 1969	27	6									14		15		24		65		108		50	G		G				G		
July 1969	23	G									17		22		G		77		130		51									
Sept. 1969	22										14		27				66		126		54									
Oct. 1969	21										13		30				G		90		50									
Jan. 1970	25										G		23						G		G									
Apr. 1970	20												34																	
June 1970	12												G																	

along the 150-m transect. In addition to the harvesting effect, the kelp bed was aging and the canopy was being reduced through the natural attrition of older plants. More areas of the bed were gradually opened to receive increased light penetration.

The first visible germination of *Macrocystis* sporophytes occurred during August-September 1969, when plants approximately 1 to 3 cm in height appeared on or near the survey lines. Although juvenile plants were found in scattered locations throughout the kelp bed, the most dense concentrations appeared around the shoreward (eastern) end of the transect, from about 100 m to 150 m (Figure 1). Only two adult plants remained within this 2 × 50 m band transect during the summer of 1969 (Figure 3); therefore, shading of the underlying sea floor was probably minimal. Also, this shoreward edge of the bed is approximately 5 m shallower than the seaward portion and there may have been more ambient light in this part of the kelp bed. Juvenile sporophyte density ranged from 0 to 32 plants/m^2 within the fixed quadrats. *Macrocystis* recruitment was especially pronounced in the 100- to 150-m area on the transect. For this reason two additional 4-m^2 quadrats (no. 13 and 14) were added in this location when the first sporophytes appeared in August 1969. In September 1969, a total of 387 single-bladed *Macrocystis* were counted within the fixed quadrats (Figure 6). After the first month only 156 plants survived, and by June 1970 the young sporophyte population was reduced to only 5 survivors.

Most of the juvenile plant mortality was believed to be caused by plant entanglement, fish grazing, physical scouring, and/or actual burial of the plants by moving sand. Many of the young sporophytes were damaged, primarily in the region of the apical tip. These plants were inspected for invertebrate grazers, but none were found. It seems likely that the grazers were positioned in the water column because most of the grazing was located around the terminal ends of each blade. On two occasions the labrid *Oxyjulis californica* and the embiotocid *Embiotoca jacksoni* were seen nibbling on juvenile *Macrocystis*. However, because of marginal underwater visibility in this area, it was generally not possible to observe the grazing activities of fishes directly.

Physical scouring and burial is another cause of juvenile plant mortality. For example, one group of young plants (n = 36) growing within a shallow depression along the sea floor became completely covered with sand during the late fall of 1969 and never reappeared. The stipes of *Macrocystis* are quite sensitive to being enclosed or covered (North, 1971), and apparently the young plants can not tolerate burial for any length of time. In kelp beds such as Del Mar, the juvenile *Macrocystis* appear to be highly vulnerable to this physical phenomenon.

The five surviving *Macrocystis* plants that grew within the fixed quadrats continued to mature and eventually the stipes reached the sea surface. One plant perished in September 1972; however, the other four were still present within the quadrats in December 1972, 3 yr and 3 mo after germination.

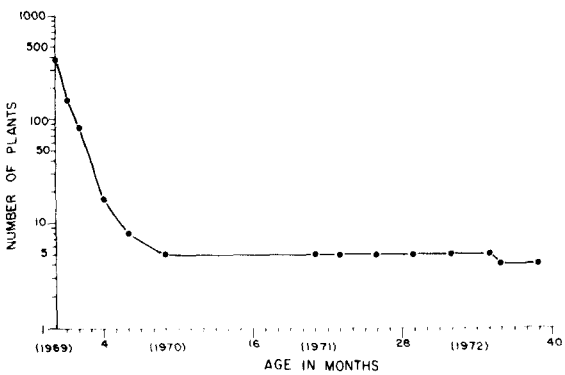

FIGURE 6.—Survivorship curve of individual *Macrocystis* which were observed to recruit in September 1969.

Plant Longevity

At the present time there is little information available in the literature on the life span of *Macrocystis* because most of the data have been collected on the longevity of individual fronds. The maximum life span of a *Macrocystis* frond was found to be about 6 mo (Brandt, 1923; Cribb, 1954; North, 1961). North (1968) reported that 3 yr were required to totally eliminate tagged mature plants within a stand of kelp off La Jolla, Calif. Most of the plants were very large at the beginning of the study, "so they probably were at least 5 years of age when they vanished, or quite likely older." (North, 1968:224).

Of the 49 adult *Macrocystis* plants originally marked along the Del Mar transect no survivors

persisted in August 1972. The oldest surviving plant lived until July 1972, an elapsed time of 5 yr. During July 1967 this plant (number 1) had 18 living stipes (Table 2). The number of stipes growing from this plant reached a maximum of 34 during May 1968; thereafter, the number of stipes slowly decreased. Based on data derived from the fixed quadrats, a *Macrocystis* plant growing in this bed with 18 stipes is at least 2 yr old. Therefore, by July 1972 plant number 1 was probably at least 7 yr of age. In addition, three other tagged plants were believed to be more than 5 yr of age at the time of their dislodgement, and four of the *Macrocystis* that grew up within the fixed quadrats were still alive after 3 yr and 3 mo (Figure 6).

Counting the number of living stipes on selected *Macrocystis* plants does not necessarily indicate the age of a kelp bed or ages of plants within the bed. For example, the number of stipes found on individual plants at Del Mar usually fluctuated with the season and the condition of the plant (Table 2). Most of the adult *Macrocystis* displayed a period during which each plant maintained a maximum number of stipes, followed by a gradual decline in the total number of stipes. At some point in the life of a Del Mar *Macrocystis* the plant no longer appears to be able to actively support a peak number of stipes.

TABLE 3.—A list of fishes observed in the kelp bed by Quast (1968a) and during this study. ++ signifies those species seen in both studies; — signifies those species seen in our study, but not reported by Quast (1968a).

Anisotremus davidsoni (Steindachner)	—
Atherinops affinis (Ayers)	++
Brachyistius frenatus Gill	++
Chromis punctipinnis (Cooper)	++
Coryphopterus nicholsi (Bean)	—
Embiotoca jacksoni Agassiz	++
Engraulis mordax Girard	++
Girella nigricans (Ayres)	++
Gymnothorax mordax (Ayres)	—
Halichoeres semicinctus (Ayres)	—
Heterostichus rostratus Girard	++
Hyperprosopon argenteum Gibbons	++
Hypsurus caryi (Agassiz)	++
Leiocottus hirundo Girard	++
Medialuna californiensis (Steindachner)	++
Oxyjulis californica Günther	++
Oxylebius pictus Gill	—
Paralabrax clathratus (Girard)	++
Paralabrax maculatofasciatus (Steindachner)	—
Paralabrax nebulifer (Girard)	—
Paralichthys californicus (Ayres)	—
Phanerodon furcatus Girard	++
Pimelometopon pulchrum (Ayres)	++
Pleuronichthys coenosus Girard	++
Pneumatophorus diego (Ayres)	—
Rhacochilus toxotes Agassiz	++
Rhacochilus vacca (Girard)	++
Scorpaena guttata Girard	++
Scorpaenichthys marmoratus (Ayres)	—
Sebastes atrovirens (Jordan and Gilbert)	++
Sebastes auriculatus Girard	—
Sebastes chrysomelas (Jordan and Gilbert)	—
Sebastes rastrelliger (Jordan and Gilbert)	++
Sebastes serriceps (Jordan and Gilbert)	—
Seriola dorsalis (Gill)	—
Sphyraena argentea Girard	—
Torpedo californica (Ayres)	—
Urolophus halleri (Cooper)	—

FAUNAL ASSOCIATION

Components of the Epifauna

Within the study area 38 species of fishes were sighted (Table 3), and 98 species of epibenthic invertebrates have been identified (Table 4). Many of the macroinvertebrates listed in the table were rarely observed, but 39 were seen on over half of the dives. A number of these species were numerically uncommon in this area, while other animals were infrequently seen because of differences in activity periods. For example, the gastropod *Cypraea spadicea* was rarely observed in exposed positions during daylight hours, but was one of the most abundant mollusks during the three nocturnal surveys made in this location. Of the 38 species of fish which we recorded, 20 species were collected in 1958 by Quast (1968a).

Epibenthic Invertebrates

Invertebrates considered in this study consisted of those species living along the sea floor that could be counted without disturbing the underlying substratum. Visually and numerically conspicuous macroinvertebrates were selected for study after data were collected on presence of species and their relative abundance in 1967. Of the 98 invertebrate species seen, only 14 species appeared to comprise the "characteristic" assemblage of epibenthic invertebrates in this kelp bed (Table 5). Characteristic epifauna were those "species that were always seen and that dominated the habitat, both numerically and in terms of their demand and impact on it." (Fager, 1968). Table 5 lists the frequency of occurrence, numerical density, pattern of distribution, and habit of each of the 14 species. Because of the importance of natural history information to an eventual synthesis of the organization of the kelp community, the following observations are presented for the 14 species. The species are discussed in order of their relative abundance.

The most abundant and frequently encountered epifaunal invertebrate in the study site during

TABLE 4.—Epifaunal invertebrates collected within the perimeter of the study area.

Porifera
- *Leucilla* (= *Rhabdodermilla*) *nuttingii* Urban
- *Leucosolenia* sp.
- *Tethya aurantia* (Pallas)
- *Verongia thiona* de Laubenfels
- *Cliona celata* Grant

Cnidaria
- *Aglaophenia* spp.
- *Corynactis californica* Carlgren
- *Epiactis prolifera* Verrill
- *Pachycerianthus* sp.
- *Tubularia* sp.
- *Balanophyllia elegans* Verrill
- *Paracyathus stearnsi* Verrill
- *Lophogorgia chilensis* (Verrill)
- *Muricea californica* (Aurivillius)
- *Muricea fruticosa* (Verrill)
- *Tealia coriacea* (Cuvier)
- *Harenactis attenuata* Torrey
- *Parazoanthus lucificum* Cutress and Peguegnat
- *Sertularia* sp.
- *Plumularia* sp.
- *Anthopleura elegantissima* (Brandt)

Annelida
- *Diopatra ornata* Moore
- *Salmacina tribanchiata* (Moore)
- *Phyllochaetopterus prolifica* Potts
- *Eudistylia polymorpha* Johnson
- *Dexiospira spirillum* (Linnaeus)
- *Spirobranchus spinosus* Moore

Arthropoda
- *Paguristes ulreyi* Schmitt
- *Loxorhynchus grandis* Stimpson
- *Taliepus nuttallii* Randall
- *Synalpheus* spp.
- *Alpheus dentipes* Guerin
- *Panulirus interruptus* (Randall)
- *Betaeus harfordi* (Kingsley)
- *Cancer anthonyi* Rathbun

Arthropoda—*Continued*
- *Hippolysmata californica* Stimpson
- *Parapleustes oculatus* Barnard
- *Balanus tintinnabulum* Pilsbry
- *Balanus pacificus* Pilsbry
- *Pachycheles rudis* Stimpson
- *Idothea resecata* (Stimpson)
- *Acanthomysis sculpta* (Tattersall)
- *Lophopanopeus frontalis* (Rathbun)
- *Ampithoe humeralis* Stimpson

Mollusca
- *Kelletia kelletii* (Forbes)
- *Mitra idae* Melville
- *Bursa californica* (Hinds)
- *Conus californicus* Hinds
- *Norrisia norrisi* (Sowerby)
- *Astraea undosa* (Wood)
- *Trivia californiana* (Gray)
- *Megathura crenulata* Sowerby
- *Cypraea spadicea* Swainson
- *Haliotis rufescens* Swainson
- *Haliotis corrugata* Wood
- *Shaskyus* (= *Jaton*) *festivus* Hinds
- *Simnia vidleri* Sowerby
- *Maxwellia gemma* (Sowerby)
- *Crassispira semiinflata* (Grant and Gale)
- *Acteon punctocaelatus* (Carpenter)
- *Mitrella carinata* (Hinds)
- *Crepidula adunca* Sowerby
- *Anisodoris nobilis* (MacFarland)
- *Glossodoris californiensis* (Bergh)
- *Dendrodoris fulva* (MacFarland)
- *Cadlina flavomaculata* MacFarland
- *Flabellinopsis iodinea* (Cooper)
- *Hinnites multirugosus* (Gale)
- *Platyodon cancellatus* (Conrad)
- *Parapholas californica* (Conrad)
- *Adula* (= *Botula*) *falcata* (Gould)
- *Lithophaga plumula* (Hanley)

Mollusca—*Continued*
- *Leptopecten latiauratus* (Conrad)
- *Lima hemphilli* Hertlein and Strong
- *Saxidomus nuttalli* Conrad
- *Octopus bimaculatus* Verrill
- *Penitella penita* (Conrad)
- *Chaeceia ovoidea* (Gould)

Bryozoa
- *Diaperoecia californica* (d'Orbigny)
- *Membranipora membranacea* (Linnaeus)
- *Membranipora serrilamella* Osburn
- *Bugula neritina* (Linnaeus)
- *Antropora tincta* Osborn
- *Thalamoporella californica* (Levinson)

Echinodermata
- *Dermasterias imbricata* (Grube)
- *Astropecten armatus* Gray
- *Astrometis sertulifera* (Xantus)
- *Henricia leviuscula* (Stimpson)
- *Patiria miniata* (Brandt)
- *Pisaster brevispinus* (Stimpson)
- *Pisaster giganteus* (Stimpson)
- *Ophioplocus esmarki* Lyman
- *Ophiothrix spiculata* Le Conte
- *Parastichopus parvimensis* (Clark)
- *Eupentacta quinquesemita* (Selenka)
- *Amphipholis* sp.
- *Ophioderma panamensis* Lutken
- *Ophiopteris papillosa* (Lyman)
- *Strongylocentrotus franciscanus* (A. Agassiz)
- *Strongylocentrotus purpuratus* (Stimpson)

Chordata
- *Styela montereyensis* (Dall)
- *Polyclinum planum* (Ritter and Forsyth)
- *Pyura haustor* (Stimpson)
- *Eudistoma diaphanes* Ritter and Forsyth

TABLE 5.—The conspicuous macroinvertebrates in the Del Mar kelp bed.

Species	Habit	Frequency[1]	Density[2]	Distribution pattern	Probability[4]
Diopatra ornata	Sessile	87/96	12.95	Aggregated	$P<0.001$
Styela montereyensis	Sessile	79/96	3.40	Aggregated	$P<0.001$
Muricea californica	Sessile	67/96	2.53	Aggregated	$P<0.001$
Kelletia kelletii	Motile	35/96	0.62	Aggregated	$0.001<P<0.01$
Parapholas californica	Sessile	22/96	0.47	Aggregated	$P<0.001$
Paguristes ulreyi	Motile	9/96	0.39	Aggregated	$P<0.001$
Muricea fruticosa	Sessile	18/96	0.27	Aggregated	$0.05>P>0.02$
Strongylocentrotus franciscanus	Motile	2/96	0.16	Aggregated	$P<0.001$
Tealia coriacea	Sessile	11/96	0.16	Aggregated	$0.001<P<0.01$
Tethya aurantia	Sessile	10/96	0.14	Random[3]	$0.05<P<0.10$
Astrometis sertulifera	Motile	12/96	0.13	Aggregated	$0.05>P>0.025$
Lophogorgia chilensis	Sessile	4/96	0.04	Random[3]	$0.70>P>0.50$
Strongylocentrotus purpuratus	Motile	2/96	0.03	Aggregated	$0.001<P<.01$
Pisaster giganteus	Motile	3/96	0.01	Random[3]	$0.30<P<0.50$

[1] Occurrence in 96 1-m² quadrats.
[2] Per m².
[3] n is small — index of dispersion inadequate.
[4] Probability of a random distribution.

August 1972 was the tubicolous polychaete *Diopatra ornata* (Table 5). *Diopatra* was seen along the transect during the early years of the study (1967-68) however, it was not until the summer of 1971 that the species was considered to be common. During August 1972, *Diopatra* occurred in all 12 of the fixed quadrats, and quadrat number 7, which contained only a few individuals in 1968, had many clumps of *Diopatra* tubes. The tubes covered an estimated 25-30% of the total area (4 m²) in the quadrat. Unpublished work of Ray Emerson (pers. commun.)[4] demonstrates that approximately 90%

[4]Emerson, R. In preparation. Reproductive biology and population dynamics of the polychaete *Diopatra ornata*. Ph.D. thesis, Univ. of Southern Calif.

of *Diopatra* tubes represent living worms. Emerson considers *Diopatra* a selective but omnivorous deposit feeder. We have seen fragments of *Macrocystis* attached to its tube apparently serving a dual function of camouflage and food reserve. The gastropod *Kelletia kelletii* and the sea star *Pisaster giganteus* were the only invertebrates seen eating *Diopatra* in this area. *Kelletia* was frequently observed penetrating either the sides or opening of the *Diopatra* tube with an extensible proboscis, and *Pisaster* was found with its stomach everted into the opening of the tube.

The solitary ascidian *Styela montereyensis* usually grows attached to rocks, shells, and *Macrocystis* holdfasts. *Styela* was found to live approximately 12 to 20 mo; however, one individual lived for more than 30 mo. Usually there is a heavy recruitment in the late summer and heavy mortality late the next spring (Figure 7). The fall *Styela* population remained reasonably constant over 4 yr (1968-72), despite the fluctuations in the population during a calendar year. A major cause of mortality in the fixed quadrats was sediment movement and strong water motion that either buried or detached the ascidians from the substratum. Three predators of *Styela* were observed: *Pisaster giganteus* and *Kelletia kelletii* frequently were seen feeding on *Styela*. On five occasions these two species were encountered feeding simultaneously on the same *Styela* (Rosenthal, 1971). In addition, we found the sea star *Astrometis sertulifera* eating *Styela* in this location.

The gorgonian *Muricea californica* was the most visually conspicuous and the third most abundant (2.53/m^2) macroinvertebrate in the assemblage (Table 5). It is a colonial animal usually found growing erect from solid substratum. *Muricea californica* recruits become visible to the unaided eye when the colony is approximately 1 cm high; at this stage they appear to be at least several months old (Grigg, 1970). A decline in the *M. californica* population was recorded during the time period of this study. A total of 192 individual colonies were living within the 48-m^2 area in September 1968, but by December 1972 the population had declined to 119 colonies. During this time interval there were 147 mortalities and 74 recruitments recorded in the fixed quadrats (Figure 8). Grigg (1970) found a similar decrease in the *M. californica* population off Del Mar in which he recorded a relatively heavy mortality with no replacement or recruitment during a 1-yr period of observation in 1968. There are several physical factors contributing to the mortality of *M. californica* in this area. Scouring, holdfast detachment, and burial by sand are important examples. Grigg (1970) felt that two-thirds of the mortality recorded at Del Mar during 1968 resulted from physical abrasion by suspended particles, and one-third from colony detachment. Occasionally, *M. californica* growing either between the holdfasts of adult *Macrocystis* or in close proximity to an established plant died when the plant became detached and drifted away. In such cases the *M. californica* were entangled and pulled from the sea floor or were

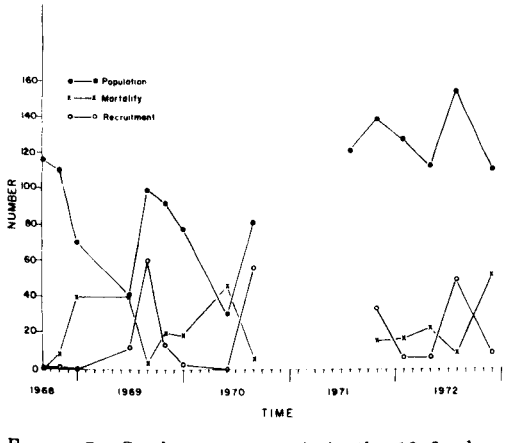

FIGURE 7.—*Styela montereyensis* in the 12 fixed quadrats (48 m^2).

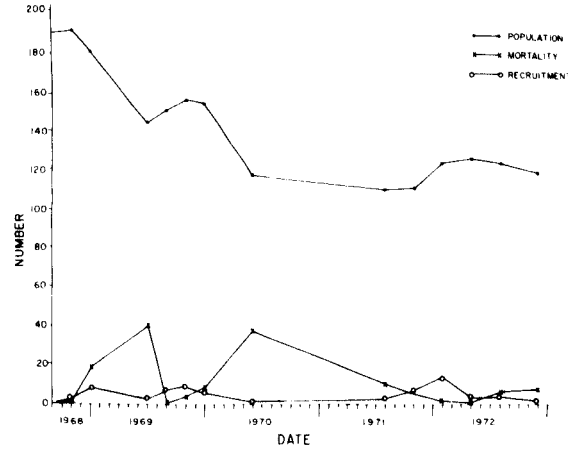

FIGURE 8.—*Muricea californica* in the 12 fixed quadrats (48 m^2).

killed by increased scouring and sediment burial in the absence of the large *Macrocystis* holdfast.

The Kellet's whelk, *Kelletia kelletii*, is usually found on rocky substrata or in sand areas adjacent to more solid substratum. During August 1972 we observed a mean density of 0.62/m^2 in the combined samples (Table 5). On other occasions the density along the transect ranged from 0.42 to 0.75/m^2. Movement off Del Mar is apparently not random, for individual snails were often found in aggregated patterns of distribution. Such aggregations may reflect feeding and reproductive behavior. For example, during the height of the April-May spawning period (Rosenthal, 1970), mixed aggregations of both male and female *Kelletia* were repeatedly encountered. A few of these spawning aggregations contained between 200 and 300 individuals; however, the average spawning cluster was about 15 to 20 snails.

Kelletia is basically a carnivorous scavenger; however it does feed on live sedentary polychaetes and solitary ascidians. It has been observed eating 22 species of invertebrates and 3 species of dead or moribund fish in the subtidal waters off San Diego County (Rosenthal, 1971).

Predators of *Kelletia* include the asteroids *Pisaster giganteus*, *P. brevispinus*, and *Astrometis sertulifera*, and the cephalopod *Octopus bimaculatus* (Rosenthal, 1971). Few other predators are known, although Limbaugh (1955) reported finding juvenile *Kelletia* in the stomachs of pile perch, *Rhacochilus vacca*.

Parapholas californica, a bivalve clam, was the most conspicuous terrigenous borer off Del Mar. It primarily bores into sedimentary rocks consisting of consolidated mudstones and siltstones. Within the 12 fixed quadrats the *Parapholas* population density was 0.54/m^2. During the monitoring period there were two recruitments and three mortalities recorded in these quadrats. *Pisaster giganteus* and *P. brevispinus* occasionally prey upon *Parapholas* in this location, as they do in other nearshore areas off San Diego County (Rosenthal, 1971). Predation by sea stars often has the additional effect of breaking the substratum surrounding the clam.

Paguristes ulreyi is a relatively large, pubescent hermit crab. Almost all were found in discarded *Kelletia* shells; however, a few crabs were also seen in the shells of *Bursa californica*. *Paguristes* was seen throughout the study area, although its most frequent habitat appeared to be the siltstone ledges and consolidated sedimentary mounds located towards the seaward edge of the bed. Each year large aggregations (to 220/m^2) of *Paguristes* were observed in this area from August through October, the crabs often being stacked several layers thick. *Paguristes* is a scavenger (Pequegnat, 1964), a conclusion supported by our observations of it feeding upon dead invertebrates and pieces of detached algae. *Octopus bimaculatus* was the only known predator of *Paguristes* in this location. On two occasions, *O. bimaculatus* was observed moving shells inhabited by *Paguristes* and one individual was encountered while feeding on a *Paguristes*.

Muricea fruticosa is similar in appearance to *M. californica*, but is usually bushier with a rusty-brown coenenchymal layer and white polyps. Both species of *Muricea* were observed growing on similar or identical substrata. The mean of 0.27 colonies/m^2 in this area (Table 5) is in agreement with the estimate of 0.25 colonies/m^2 of Grigg (1970). The *M. fruticosa* population was almost balanced with respect to mortality and recruitment. Fourteen *M. fruticosa* were recorded in the fixed quadrats during September 1968, and 13 individual colonies were found in these same quadrats during December 1972, but during this period 17 mortalities and 16 recruitments were noted. No predators of *M. fruticosa* were observed in the study area, and causes of mortality are believed to be similar to those reported for *M. californica*.

Tealia coriacea is a solitary, medium sized (4 to 7 cm) sea anemone. It attaches to solid substratum and usually the column is partially buried or enclosed by sediment. Two mortalities and three recruitments were recorded in the fixed quadrats. One *Tealia* was eaten by a leather star, *Dermasterias imbricata*, and the other died from an unknown cause. *Dermasterias* has been reported to eat *Tealia* spp. and other sea anemones in the Pacific Northwest (Mauzey, Birkeland, and Dayton, 1968), and may on occasion be an important source of mortality in California kelp beds.

The largest and most conspicuous sea urchin seen off Del Mar was *Strongylocentrotus franciscanus*. Individual test diameters ranged from 5.5 to 18.2 cm. Most of these animals inhabited the sedimentary mounds and boulders located towards the seaward edges of the kelp stand.

The trophic role displayed by *S. franciscanus* in southern California kelp communities has been adequately described (Limbaugh, 1955; Leighton, 1971; North, 1971). *Strongylocentrotus franciscanus* is important because it often overexploits its algal resources in areas of high sea urchin density. Despite the fact that this species is highly motile, foraging movements on attached kelps were not witnessed in this kelp bed. The *S. franciscanus* population appeared to be sustained by snagging detached pieces of macroalgae that drifted along the sea floor. The only predator we observed feeding upon live *S. franciscanus* in this area was the labrid *Pimelometopon pulchrum*.

Tethya aurantia, a hemispherical shaped sponge, attains a circumference of at least 25 cm and is usually found attached to rocks and consolidated sediments. There were two mortalities and three recruitments recorded in the fixed quadrats. One mortality was attributed to sediment burial, and *Dermasterias imbricata* was observed feeding on *Tethya* in the vicinity of the transect. Rosenthal and Chess (1972) reported *Dermasterias* to be a predator of *Tethya* in the sublittoral zone off Pt. Loma, Calif.

Astrometis sertulifera was the most abundant (0.13/m^2) sea star encountered off Del Mar (Table 5). This estimate of abundance is probably conservative because *Astrometis* is relatively small (4 to 6 cm in radius) and individuals are somewhat cryptic in habit. The most frequent habitat of *Astrometis* off Del Mar was the undersides of rocks and the interstices of *Macrocystis* holdfasts. It appears to be ideally suited for preying upon the assemblage of organisms found associated with the holdfasts of *Macrocystis*. *Astrometis* was observed eating juvenile *Kelletia kelletii* (gastropod), *Conus californica* (gastropod), *Mitrella* sp. (gastropod), *Styela montereyensis* (ascidian) and juvenile *Strongylocentrotus purpuratus* (echinoid) in this study. Leighton (1971) mentioned that *Astrometis* feeds heavily on juvenile sea urchins off southern California. No predators of *Astrometis* were observed in the study area; however, Rosenthal and Chess (1972) found that 4% of 437 feeding *Dermasterias* were eating *Astrometis*.

The gorgonian *Lophogorgia chilensis* is one of the most exquisite macroinvertebrates in this region. It usually grows in an upright manner attached to solid substratum. A few small colonies were found growing attached to *Muricea californica*. *Lophogorgia* was not nearly as abundant as *M. californica* or *M. fruticosa*; the mean density during August 1972 was 0.04/m^2 (Table 5). There was one mortality and one recruitment recorded in the 48-m^2 quadrat area during 1968-72. No predators of *Lophogorgia* were observed in this kelp bed and causes of colony mortality are probably similar to those of *Muricea* spp.

The purple sea urchin, *Strongylocentrotus purpuratus*, ranged in size from 15 to 68 mm, with a median size of 42 mm (n = 82). In contrast to the low density in this location (0.03/m^2), other kelp stands off southern California have been found to contain as many as 77 *S. purpuratus*/yd^2 (Leighton, 1971). The most frequent habitat of *S. purpuratus* off Del Mar was the undersides of rocks; however, individuals were also found on consolidated mounds and siltstone ledges. A few individuals were noted within the holdfasts of adult *Macrocystis*; however, we believe the incidence of holdfast infestation is low in comparison to other San Diego County kelp beds. *Strongylocentrotus purpuratus* is a herbivore well known to overexploit its algal resources (Leighton, 1971; North, 1971). In the Del Mar area most of the purple sea urchins were observed eating detritus and drift algae; rarely were the attached macroalgae grazed upon.

Dermasterias imbricata (Rosenthal and Chess, 1972), *Astrometis sertulifera* (Leighton, 1971; pers. observation), and *Pimelometopon pulchrum* (Limbaugh, 1955; pers. observation) are three known *S. purpuratus* predators which inhabited the study area.

Pisaster giganteus is one of the most abundant and widely distributed sea stars found off southern California. Although visually conspicuous at Del Mar, *Pisaster* was not nearly as abundant (0.01/m^2) as it was in some of the other kelp beds (i.e. Pt. Loma, La Jolla, Catalina Island) we surveyed between 1968 and 1972. The diet of *Pisaster* has been partially quantified (Rosenthal, 1971). Although it was occasionally observed scavenging, it primarily feeds on live animals which, in this area, include *Astraea undosa* (gastropod), *Conus californicus* (gastropod), *Kelletia kelletii* (gastropod), *Botula falcata* (pelecypod), *Hinnites multirugosus* (pelecypod), *Lithophaga plumula* (pelecypod), *Parapholas californica* (pelecypod), *Pennitella penita* (pelecypod),

Diopatra ornata (polychaete), and *Styela montereyensis* (ascidian).

DISCUSSION

During the years of this study (1967-73) there was a pronounced oscillation in the number of adult *Macrocystis* in the study area. Partially concurrent with these in situ observations has been a fluctuation in the amount of kelp harvested in this area since 1940 (Figure 4). The disappearance or detachment of adult *Macrocystis* along the transect was usually related to physical stress from an increase in water motion and/or entanglement with detached, drifting kelp plants. Storms, particularly during the months of October through April, seem to be the major cause of plant mortality in this bed. For example, during a 2-mo period (December-February 1973), 46% of the adult *Macrocystis* were lost along the transect (Figure 2). There is historical evidence of severe storm mortality as Brandt (1923) reported the La Jolla and Pt. Loma kelp beds were severely diminished in area by storms in 1888-89 and 1915. Doty (1971) also reports that storms have important effects on the standing crop of algae in Hawaii.

Another cause of plant attrition was commercial harvesting. Four tagged *Macrocystis* representing 21% of the marked plants in the study area were detached from the substratum during a kelp harvesting operation in January 1969. However, this rate of mortality could be higher than the harvesting attrition rate in other beds because of the relatively unstable substratum of the north San Diego County kelp beds. Certainly a preharvest consideration should be given to the actual cutting technique best suited to each individual stand of kelp.

The vulnerability of adult *Macrocystis* to entanglement and detachment would appear to result in the development of a multiage class kelp bed in which there are patches of cohorts or plants of the same age class. That is, the drifting and entanglement is rather localized and results in distinct patches of the canopy being cleared. Thus, germination and recruitment take place not only around the periphery of the bed, but also within central portions. This spatial heterogeneity of different aged *Macrocystis* may add stability to a particular kelp bed as mature, perhaps more secure plants are growing adjacent to both young and senile plants. During February 1972, it was estimated that the Del Mar bed was composed of at least four age classes of *Macrocystis*.

The paucity of juvenile *Macrocystis* sporophytes during the first 23 mo of the study was believed to be related to the establishment of a well-developed adult canopy, turbidity of the water column, and the relatively unstable substratum. These factors are interrelated since they contribute to the absorption and scattering of the available light necessary for germination and sporophyte development. A layer of fine sediment (silt) remained along the bottom during the entire study period, and this silt was usually suspended by increased water motion. The Los Penasquitos salt marsh located approximately 2 km southeast of the study site could be a source of much silt. Whatever the source, this sediment layer seems to be a general feature of most north San Diego County kelp beds, and as it contributes to a reduction in the submarine light and physically scours the substratum, it probably has a strong negative effect on *Macrocystis* recruitment. Despite these limiting factors, young *Macrocystis* sporophytes appeared in the Del Mar bed during August 1969. The reduction of the kelp canopy from natural attrition and harvesting probably paved the way for the late summer germination and recruitment. Following recruitment of these young plants there continued to be a strong attrition as only 4 of the original 387 sporophytes growing within the fixed quadrats survived the 3.25 yr (to December 1972).

Many of the same physical parameters that influence the *Macrocystis* population at Del Mar appear to effect the distribution, frequency of occurrence, and abundance of the fauna. Quast (1968a) determined from three fish collection sites off Del Mar, Bathtub Rock (San Diego County), and Papalote Bay, Baja California that Del Mar was lowest in fish species diversity, despite the fact that it covered the greatest area. He concluded that the differences between the three areas were due to differences in the amount of shifting sediment and the durability of the rocky substratum. Furthermore, he found a positive correlation between the degree of bottom relief and the abundance and species diversity of fish.

The epibenthic invertebrates are similarily affected by the physical characteristics of the habitat. The aggregated distribution patterns of

such sessile species as *Muricea californica, Styela montereyensis*, and *Parapholas californica* (Table 5) probably reflect physical heterogeneity within the Del Mar study site. The aggregated distribution patterns of motile species (*Kelletia kelletii, Paguristes ulreyi*, and *Strongylocentrotus franciscanus*) are probably related to aspects of their foraging and/or reproductive behavior as well as to the physical heterogeneity of the habitat.

The species composition of the epifauna was reasonably constant, however, the abundances of some species has undergone change during the 5.7 yr. The most pronounced population change occurred with the tube dwelling polychaete *Diopatra ornata.* Although this species was recorded within the study area during 1967-68, it was somewhat rare and individuals were not noted within the 12 fixed quadrats until 1971. By August 1972 however, *Diopatra* was the most abundant and most frequently encountered macroinvertebrate in the Del Mar kelp bed (Table 5). Reasons for the *Diopatra* population increase are unknown at this time.

During the same time period the *Muricea californica* population decreased from 192 to 119 colonies during 4.25 yr (Figure 8), despite considerable recruitment of small identifiable colonies. In contrast to the decline in the *M. californica* population at Del Mar, Grigg (1970) studied a population of *M. californica* off La Jolla which was relatively stable with respect to mortality and recruitment. Differences between these two sea fan populations were believed to be due to the physical characteristics of each habitat (Grigg, 1970).

The *Styela montereyensis* population had a reasonably predictable seasonal oscillation, usually reaching a peak during the late summer and fall (Figure 7). The maximum annual population ranged from 81 to 153 individuals. The average life span of *S. montereyensis* is shorter (12 to 20 mo) than some of the other members of this community such as *Muricea californica*, which is thought to reach at least 50 yr of age (Grigg, 1970). Three species: *Pisaster giganteus, Astrometis sertulifera*, and *Kelletia kelletii* feed upon *Styela* in this area; however, natural predation is slight in proportion to the heavy mortality caused by strong water motion and sediment burial. Other Del Mar invertebrate populations were somewhat more constant. For example, the *Muricea fruticosa* population remained relatively constant over the monitoring period (changing from a total of 14 to 13), despite 17 mortalities and 16 recruitments recorded in the fixed quadrats.

There is sufficient evidence of trophic interaction to present a very qualitative food web (Figure 9). Two of the predators, *Pisaster giganteus* and *Astrometis sertulifera* feed upon living members of the community; the diet of the former species is probably better understood (Rosenthal, 1971), because it is seen more often. While both asteroid species attack a variety of prey, mollusks appear to be the major food items off Del Mar. In addition, *Dermasterias imbricata, Pisaster brevispinus, Octopus bimaculatus*, and *Pimelometopon pulchrum* have been added to this food web. We have only qualitative data on the diets of these four species. Two other carnivores, *Kelletia kelletii* and *Paguristes ulreyi*, generally feed upon moribund or decaying animal matter, but they occasionally eat live organisms (Rosenthal, 1971). The rest of the generalized food web represents lower trophic levels.

The biotic components and temporal population changes recorded off Del Mar should not be interpreted as "characteristic" of all southern California kelp beds. Although the Del Mar bed closely resembles kelp stands off northern San Diego and Orange Counties, it appears to be different from those at La Jolla and Pt. Loma.

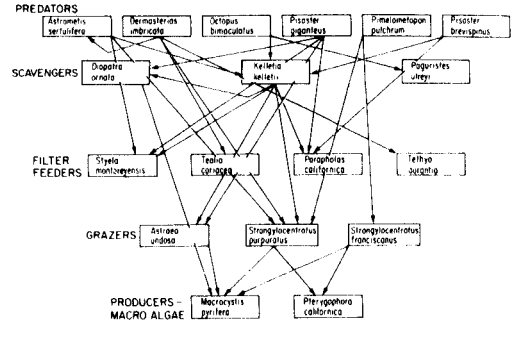

FIGURE 9.—A qualitative food web that depicts trophic interaction in the Del Mar kelp bed.

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THE SWIMMING CRABS OF THE GENUS *CALLINECTES* (DECAPODA: PORTUNIDAE)

AUSTIN B. WILLIAMS[1]

ABSTRACT

The genus *Callinectes* and its 14 species are reevaluated. Keys to identification, descriptions of species, ranges of variation for selected characters, larval distribution, and the fossil record as well as problems in identification are discussed. Confined almost exclusively to shallow coastal waters, the genus has apparently radiated both northward and southward from a center in the Atlantic Neotropical coastal region as well as into the eastern tropical Pacific through continuous connections prior to elevation of the Panamanian isthmus in the Pliocene epoch and along tropical West Africa. Eleven species occur in the Atlantic, three in the Pacific. *Callinectes marginatus* spans the eastern and western tropical Atlantic. *Callinectes sapidus*, with the broadest latitudinal distribution among all the species (Nova Scotia to Argentina), has also been introduced in Europe. All species show close similarity and great individual variation. Both migration and genetic continuity appear to be assisted by transport of larvae in currents. Distributional patterns parallel those of many organisms, especially members of the decapod crustacean genus *Penaeus* which occupy similar habitats.

The blue crab, *Callinectes sapidus* Rathbun, a staple commodity in fisheries of eastern and southern United States, is almost a commonplace object of fisheries and marine biological research, but its taxonomic status has been questionable for a long time. Other members of the genus also have questionable taxonomic status, and they are difficult to identify. In a time when expanding interest in species easily exploitable for food has generated new research, we can benefit from a fresh look at the component species of this important genus in order that major areas of study such as fisheries biology, ecology, zoogeography, embryology, and physiology can proceed on a stable nomenclatural basis. The purposes of this paper are to: 1) synonymize nomenclature, 2) characterize the species, 3) discuss variation in morphology, 4) provide illustrations and keys to identification, 5) delineate geographic distribution of species, 6) provide remarks on ecological associations, 7) contribute to resolution of the fossil record, and 8) document evidence and provide a list of identified specimens in major museums of the world.

HISTORY

Crabs of the genus *Callinectes* have an anecdotal record dating from early explorations of the Western Hemisphere. Perhaps the earliest listing among natural assets in the New World is Thomas Hariot's (1588) mention of "*Sea crabbes*, such as we have in England." A similar record is Marcgrave's account in 1648 (Lemos de Castro, 1962) of a South American *Callinectes* [= *danae* Smith (1869)], one of the common portunids used for food. D. P. de Vries in 1655 (Holthuis, 1958) referred to the eating qualities of blue crabs in the New York area and likened the white and orange color of their chelipeds [females] to colors of the House of Orange. Lawson (1714), recounting his years among the Indians in the Carolinas, may have initiated the tale of raccoons fishing for crabs in marshes with their tails, but more factually he wrote [undoubtedly of the blue crab, *C. sapidus* Rathbun (1896)], "the smaller flat Crabs I look upon to be the sweetest of all Species . . . the Breadth of a lusty Man's Hand . . . . These are inumerable, all over the salts of Carolina . . . taken not only to eat, but are the best Bait for all sorts of Fish, that live in the Salt-Water."

Holthuis (1959) thought that de Geer (1778) probably represented *Callinectes bocourti* A. Milne Edwards (1879) under the name "Crab de l'ocean" when he described a swimming crab from Surinam in general terms as *Cancer pelagicus*. Ordway (1863) considered de Geer's species synonymous with *Lupa sayi* Gibbes (1850), and Rathbun (1896:350) stated "Figures 8, 9 and 11 correctly represent neither of these species, nor are they applicable to any species of *Callinectes*, while, on the other hand, Figure 10 shows the narrow abdomen characteristic of that genus." Since *C. bocourti* is the commonest portunid in Surinam, abundant enough to be marketed, and

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certain of de Geer's figures can be interpreted as *Callinectes*, Holthuis's conclusion seems reasonable.

Bosc (1802) gave a thumbnail natural history sketch for *C. sapidus* in South Carolina comparing crudely in its accuracy with some modern accounts, but he used the name *Portunus hastatus* along with a description taken from J. C. Fabricius which applied to a European species.

Thomas Say (1817) was the first naturalist to give a description of the common blue crab of the eastern United States, calling it *Lupa hastata*, in what he intended as a redescription of *Lupa hastata* (Linn.), a species known from the Mediterranean (Rathbun, 1896).

A few years later Latreille (1825) gave the name *Portunus diacantha* to the common blue crab of eastern United States accompanied by a poor description that applied to more than one species. Say and Latreille, plus perhaps De Kay (1844) who published a description and beautifully colored plate of what he called *Lupa dicantha* [= *C. sapidus*] from New York, account for the main early treatments of *Callinectes* by naturalists.

Search of newspaper and popular journal files could yield a harvest of fact and fiction about these crabs culminating perhaps in accounts of the "crab derbies" held in recent years to promote marketing in crab producing states of the eastern seaboard of the United States. Crab stories abound and crab fishing techniques are similar in all countries where *Callinectes* occurs. It is not surprising, therefore, that this profusion has carried over into the scientific literature where scholars have bequeathed a complex nomenclature in numerous contributions.

Scholarly systematic work on the whole genus was last presented by Rathbun in 1896 as a general revision and amended in 1897. There is no need to clutter the text here by recalling the parade of specific epithets employed in the game of taxonomic musical chairs played by a succession of authors. Each built on the foundation of previous work, usually as collections substantially increased in museums, but many minor papers were reports on expeditions extending the bounds of known geographic ranges for certain species. Details of these histories may be followed in the synonymies, but the principal studies should be placed in perspective as an introduction, and in reviewing them I repeat part of Rathbun's (1896) review.

William Stimpson (1860) created the genus *Callinectes* to contain portunids in which the males have a T-shaped abdomen and the merus of the outer maxillipeds is short, sharply prominent, and curved outward at its antero-external angle. He regarded as one species "the common American *Lupa diacantha* (Latreille)" in his new genus, and doubtfully distinguished a second, *L. (= Callinectes) bellicosa*, which he had described (1859) from the Gulf of California. We now know that the second of Stimpson's generic characters is nearly valueless because other portunids have similar third maxillipeds, but the narrow sixth segment of the T-shaped abdomen of males holds and is reinforced by absence of an internal spine on the carpus of the chelipeds in *Callinectes*.

The limited view of the genus held by Stimpson was soon broadened by Ordway (1863) who recognized nine species distinguished in part by structure of the male first pleopods. Ordway restricted the name *diacanthus* to a Brazilian form described by Dana (1852) which we now know as *C. danae*. The common blue crab of the eastern United States was given Say's (1817) name *hastatus*, Stimpson's *bellicosus* retained, and six new species named. Ordway's study of crustaceans was diverted by the Civil War, and he remained in military life until his death in 1897. Poor communication may have led to Ordway's confusion in nomenclature, but his concept of species based on material then available was remarkably clear.

Latreille's (1825) *diacantha*, though valid, was never widely recognized because of its poor definition. Various *"diacanthas"* were employed for 139 yr finally ending in official suppression of Latreille's ill-starred name in 1964 for purposes of nomenclatural stability. Smith (1869) substituted *C. danae* for Dana's Brazilian *C. diacantha*.

Then followed an interval dominated by A. Milne Edwards's revision of the Portunidae (1861) and his review of the Crustacea of Mexico (1879). Milne Edwards at first did not recognize *Callinectes* as a distinct genus but later accepted it. He conservatively viewed *Callinectes* species as "varieties" of *diacanthus* (adding five new ones to Ordway's nine in 1879), and the influence of his ideas pervaded the field for a long time, leading eventually to Rathbun's revisionary papers. Milne Edwards's reasoning was not without merit for the genus is close to other portunids. Indeed, its validity as a distinct unit was again challenged for a time by Stephenson and Campbell (1959) and Stephenson (1962) during reassessment of

Indo-Pacific Portunidae, but later left intact (Stephenson, Williams, and Lance, 1968).

In 1896 Rathbun recognized the following numbers of species: western Atlantic, six species and one subspecies (Rathbun never treated the nominal subspecies as anything but a full species); eastern Pacific, four species; eastern Atlantic off Africa, one species and one subspecies. The list was almost immediately altered (1897) by name recombinations, elevation of subspecies, description of a new species, and extension of known geographic ranges. This brought the numbers to: western Atlantic, six species and one subspecies; eastern Pacific, four species; eastern Atlantic off Africa, four species. There the inventory rested until 1921 when Rathbun revised the African species, reducing them to three but noting a doubtful subspecies reported from Europe (Bouvier, 1901) greatly resembling *C. sapidus* of the United States. In 1930 Rathbun published the third of a four-volume work that serves as the standard reference on American crabs. In this she reduced the recognized species in the eastern Pacific by one. Collaterally she treated fossil members of the genus, describing three new species from the Oligocene and Miocene of Middle America (1919b), and two more species from similar ages in North America (1935). One of these from the Miocene (=?) of Virginia and Florida was considered identical with living *C. sapidus*.

By 1930 the genus seemed stabilized, but Rathbun herself had introduced confusion in 1907 by describing a juvenile *Portunus* from the South Pacific as *Callinectes alexandri*. This error bore fruit years later in helping to generate doubt concerning validity of the genus (Stephenson and Campbell, 1959). During the same year that Rathbun's cancroid treatise appeared, Contreras (1930) described two new species in a little known paper, one from the Gulf of California and another from the Gulf of Mexico. Capart (1951) and Monod (1956) both supported Rathbun's analysis of West African forms, and in shedding more light on the introduction of *C. sapidus* into European waters (first noticed in 1901) erased Rathbun's doubts about a poorly documented subspecies from that area. They also pointed out difficulties in identifying some specimens. The introduction of *C. sapidus*, documented by numerous authors, was reviewed by Holthuis (1961, 1969). Following petition of Holthuis (1962), the International Commission (1964), to avoid confusion in nomenclature of such a well-known species, made *Callinectes sapidus* Rathbun the type species of the genus and suppressed the long dormant *Portunus diacantha* Latreille, 1825. Garth and Stephenson (1966) confirmed Rathbun's interpretation of the eastern Pacific *Callinectes*, and Williams (1966) described a new species from the Carolinian Province of North America.

Such was the status of the species problem when the present study was undertaken. Numerous authors had expressed difficulty in making identifications, especially of juvenile material. Geographic limits for species seemed ill defined. Few attempts to analyze large series systematically had been attempted, but results of work in fisheries management indicated that populations within species might be distinct. Mindful of this and aware of series of specimens in museums, a review of the group seemed profitable. Simultaneously, Taissoun (1969, 1972) began study of *Callinectes* in Venezuela finding a form endemic to Lake Maracaibo. It is likely that new approaches such as ecological and larval studies may continue to elucidate variation in the genus.

CHARACTERS OF SYSTEMATIC VALUE

The gross features of morphology having greatest usefulness in distinguishing species of *Callinectes* are (Figures 1, 2): viewing dorsally, 1) the number, shape, and arrangement of frontal teeth, 2) shape of the metagastric area, 3) shape and curvature of the anterolateral teeth and the lateral spine, 4) granulation of the dorsal surface; viewing ventrally, shape of male and mature female abdomen. Shape of the chelipeds is also useful, as are the colors in fresh specimens. In addition to gross features, male first pleopods (Figures 18-21) are diagnostic, and shapes of female gonopores (Figures 22-23) are aids to identification.

Body proportions.—Proportions of the body in both sexes change with growth until a characteristically male or female form develops. The carapace of males becomes relatively broader than that of females, with lateral spines accentuated; in especially large individuals of some species the metagastric region tends to be somewhat sunken at its side and rear margins. Females have a dorsally tumid appearance, with the carapace more uniformly inflated and granulated and relatively not so broad nor with lateral spines so accentuated

as in males. Body heights are alike in the two sexes.

Spines.—All spiniform characters, poorly developed and rounded at the apices in juveniles, gradually assume conformation characteristic of the species as growth progresses.

Chelipeds.—All species in the genus have the hands of the chelipeds (Figures 3-17) modified into a major chela (crusher, usually on right side) and a minor chela (cutter, usually on left side)—heterochelic and heterodont (Schäfer, 1954; Ševčić, 1971). Loss of the major chela induces a well-known reversal at the next molt with the new hand becoming a minor chela. A few individuals have two minors, but almost none exhibit two major chelae. Size and strength of the major hand vary a good deal, each species having a sometimes ill defined but characteristic shape. In all, especially among males, the dactyl of the major chela has a strongly developed proximal tooth which closes against a molariform complex on the propodus (Schäfer, 1954). A decurved lower margin near the base of the propodal finger opposite the proximal crushing apparatus on opposed edges of the fingers accompanies development of the complex, and in huge males of some species is a prominent feature. Teeth distal to the molariform complex of the major chela are more sectorial in structure, but not so sharp as those on the minor hand. Sectorial teeth of both hands tend to be arranged in triads, a large central tooth flanked by smaller ones, but there is much variation. In old individuals no longer molting or molting infrequently, the proximal crusher teeth become worn, occasionally almost obliterated. Size and wear vary with species and are undoubtedly associated with feeding habits. *Callinectes sapidus,* for example, is known to feed on the American oyster, *Crassostrea virginica,* and other mollusks. Other species of *Callinectes* probably have similar feeding habits, but these are not well documented.

Secondary sexual structures.—Immature females have a triangular abdomen (Figure 2) with most segments indistinguishably fused, but at the terminal maturation molt (Churchill, 1919) all segments become free. The abdomen of mature females has a variable but roughly characteristic shape in each species. Distal portions of the abdomen in immature males also have a developing shape which becomes characteristic of the species in adults.

Primary sexual structures.—The copulatory apparatus of male *Callinectes* has been recognized as a good separator of species since the time of Ordway (1863), but until recently no one used fine structure of these organs as serious aid to identification. Snodgrass (1936) and Cronin (1947) both described the external male sexual apparatus, and I here adopt Snodgrass's term "first gonopod" for the first male pleopod. The first gonopod is essentially a narrow flat plate rolled longitudinally into a cylinder that may be variously curved and twisted, terminating in a tip varying from nearly tubular to a simply flared trough. First gonopods of each species have characteristic shapes, but there is individual variation reinforced by age, molt stage, wear, and irregularity in preservation. The distal portion of each first gonopod is armed with retrogressive articulated spinules, exceedingly tiny and rather unevenly distributed in one set of species having short first gonopods—*C. gladiator* Benedict (1893), *marginatus* A. Milne Edwards (1861), *ornatus* Ordway (1863), and *similis* Williams (1966) (Figures 18a-d, 20a-d), as well as in a second set with relatively longer first gonopods—*C. arcuatus* Ordway (1863), *danae,* and *exasperatus* (Gerstaecker, 1856) (Figures 18e-g, 20 e-i), but larger and arranged in longitudinal bands among species with long curved first gonopods in a third set—*C. bellicosus, bocourti, latimanus* Rathbun (1897), *maracaiboensis* Taissoun (1972), *rathbunae* Contreras (1930), *sapidus,* and *toxotes* Ordway (1863) (Figures 18h-j, 19, 20j-p, 21). In the last group, the spinules are irregular in size showing evidence of breakage and replacement during growth. Moreover, first gonopods of certain species bear slender setae. In *C. arcuatus* and *danae,* with first gonopods of moderate length, the setae are subterminal (Figure 20e-h) but in others with longer first gonopods [*C. bellicosus, latimanus, maracaiboensis, rathbunae, sapidus,* and *toxotes* (Figures 20j-p, 21)] they are arranged along the shaft at levels between the fifth to seventh thoracic sternites in a single sternomesial row following the twist of the appendage. The setae are relatively largest in *bellicosus* (Figure 20j, k).

Structure of the female gonopores covered by the abdomen and located near the midline on the sixth thoracic somite (Snodgrass, 1936) is less useful as a specific character than that of the male first gonopod, but even here there are some conformational types. Each gonopore leads via a spermathecal duct (vagina) to a spermatheca

which in turn is connected to oviduct and ovary, but it is the gonopore alone that shows crude structural specificity. Hartnoll (1968) showed that the gonopore of portunids is an uncovered structure often rounded laterally and pointed mesially, whose margin is the "rigid integument of the sternum, while the lumen is normally blocked by bulges of the flexible integument which comprises the lining of the vagina." In the set of species having males with long first gonopods, the gonopores of females are paraboloid in outline (Figures 22i-l, 23a-c). Parallels with the other two sets of male gonopod types are less pronounced. Of the intermediate second set, female *C. arcuatus* and *danae* have asymmetrically ovoid gonopores (Figure 22e, f); *exasperatus* has an elongate sinuous gonopore with shelflike overgrowth on the cephalic border (Figure 22g), and *bellicosus* fits into this group (Figure 22h). Females corresponding to the set of males with short first gonopods have gonopores varying from broadly open paraboloid in *C. ornatus* (Figure 22d) to increasingly narrowed openings in *C. gladiator* and *marginatus* (Figure 22b, c), culminating in the narrow transverse slit of *C. similis* (Figure 22a).

MEASUREMENTS

The foregoing discussion shows that measurements must be taken from adults if they are to have systematic usefulness because the young are proportionally different from adults as well as being incomplete for secondary sexual characters. Some species are larger than others and certain proportions are considered useful in keys for identification (Rathbun, 1930; Garth and Stephenson, 1966). Certain populations within species may deviate from the "typical." Initially I thought that analysis of morphometric characters might help to define differences among species as well as among populations within species.

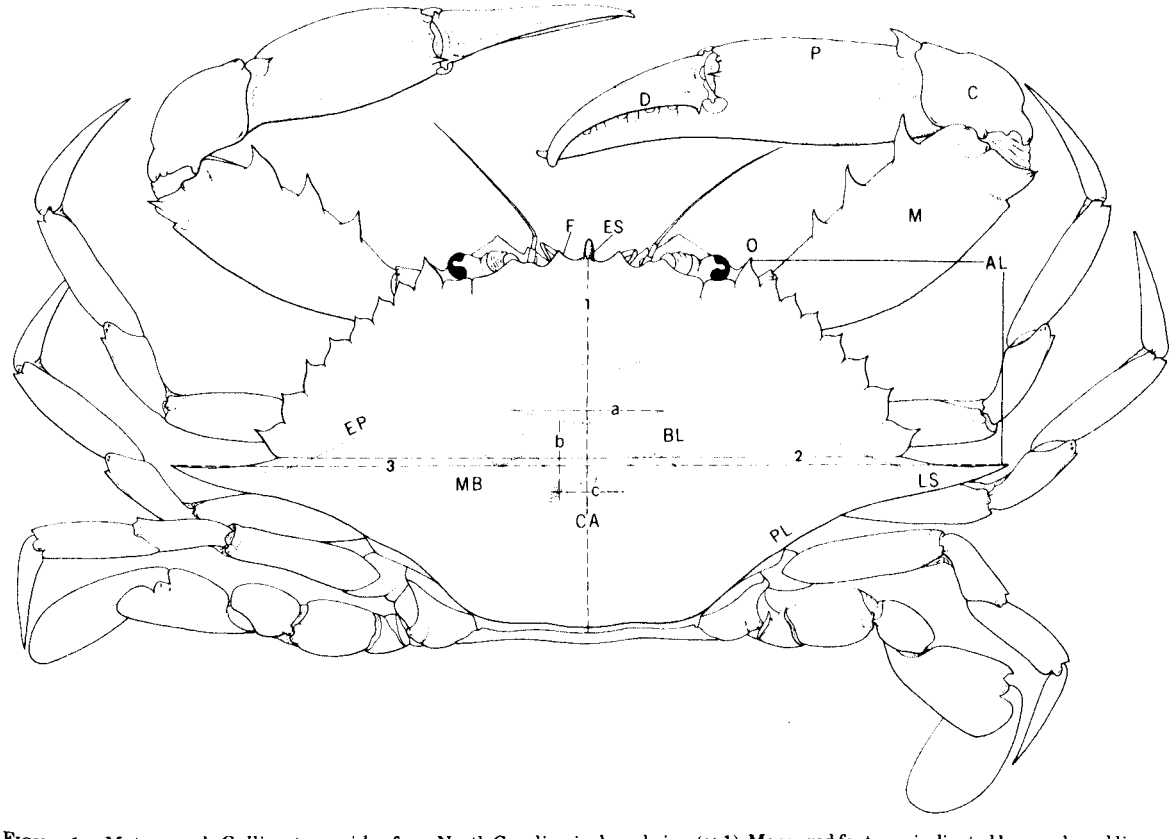


FIGURE 1.—Mature male *Callinectes sapidus* from North Carolina in dorsal view (× 1). Measured features indicated by numbered lines: 1, length; 2, width to base of lateral spines; 3, width including lateral spines; dimensions of metagastric area — a, anterior width, b, length, c, posterior width. Other features included in descriptions: (carapace) F, frontal teeth; O, outer orbital tooth; AL, anterolateral teeth; LS, lateral spine; PL, posterolateral margin; EP, epibranchial line; ES, epistomial spine; MB, mesobranchial area; CA, cardiac area; BL, branchial lobe; (cheliped) M, merus; C, carpus; P, propodus; D, dactyl.

Measurements taken included 18 characters for mature males, 21 for mature females (Figures 1, 2). These characters comprise two sets, one associated with the carapace or general body form, and another with sexual characters. Measurements for both sexes included:

1. Length of carapace including epistomial spine.
2.* Length of carapace excluding epistomial spine.
3.* Width of carapace including lateral spines.
4.* Width of carapace at base of notch between lateral spine and preceding anterolateral tooth.
5.* Width between tips of outer orbital spines (first anterolateral teeth).
6. Width between tips of suborbital spines.
7. Width between tips of lateral interorbital spines.
8.* Maximum height of body.
9.* Anterior width of metagastric area.
10.* Posterior width of metagastric area.
11.* Length of metagastric area.
12.* Angular (lateral) length of metagastric area.

Measurements of elements in the T-shaped male abdomen included:

13. Greatest width of fused segments 3-5.
14. Median length of fused segments 3-5.
15. Median length of narrow segment 6.
16. Narrowest width of narrow segment 6.
17.* Length of telson.
18.* Width of telson.

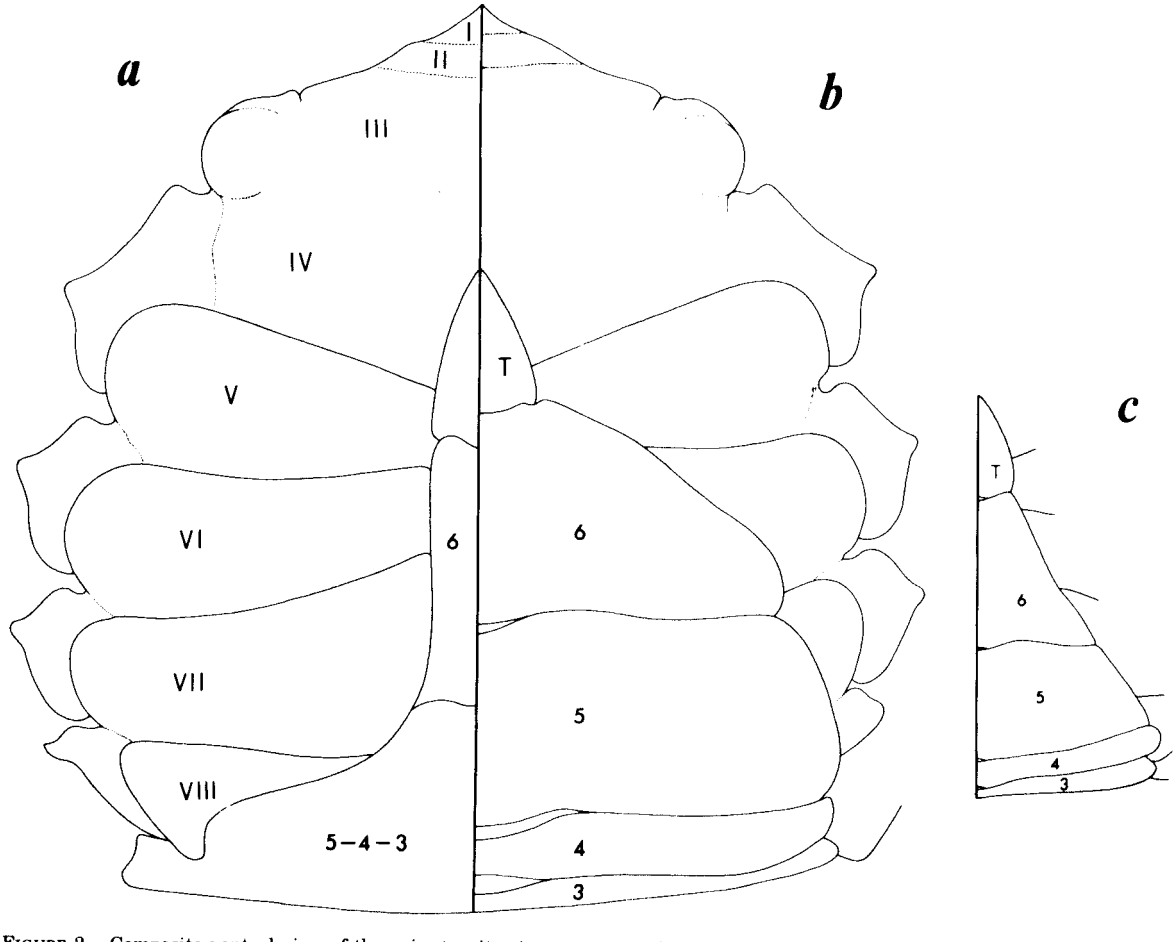


FIGURE 2.—Composite ventral view of thoracic sternites (roman numerals), abdomen (arabic numerals), and telson (T) in situ. **a**, mature male; **b**, mature female; **c**, immature female. Measurements: lengths in midline, widths maximal for structure.

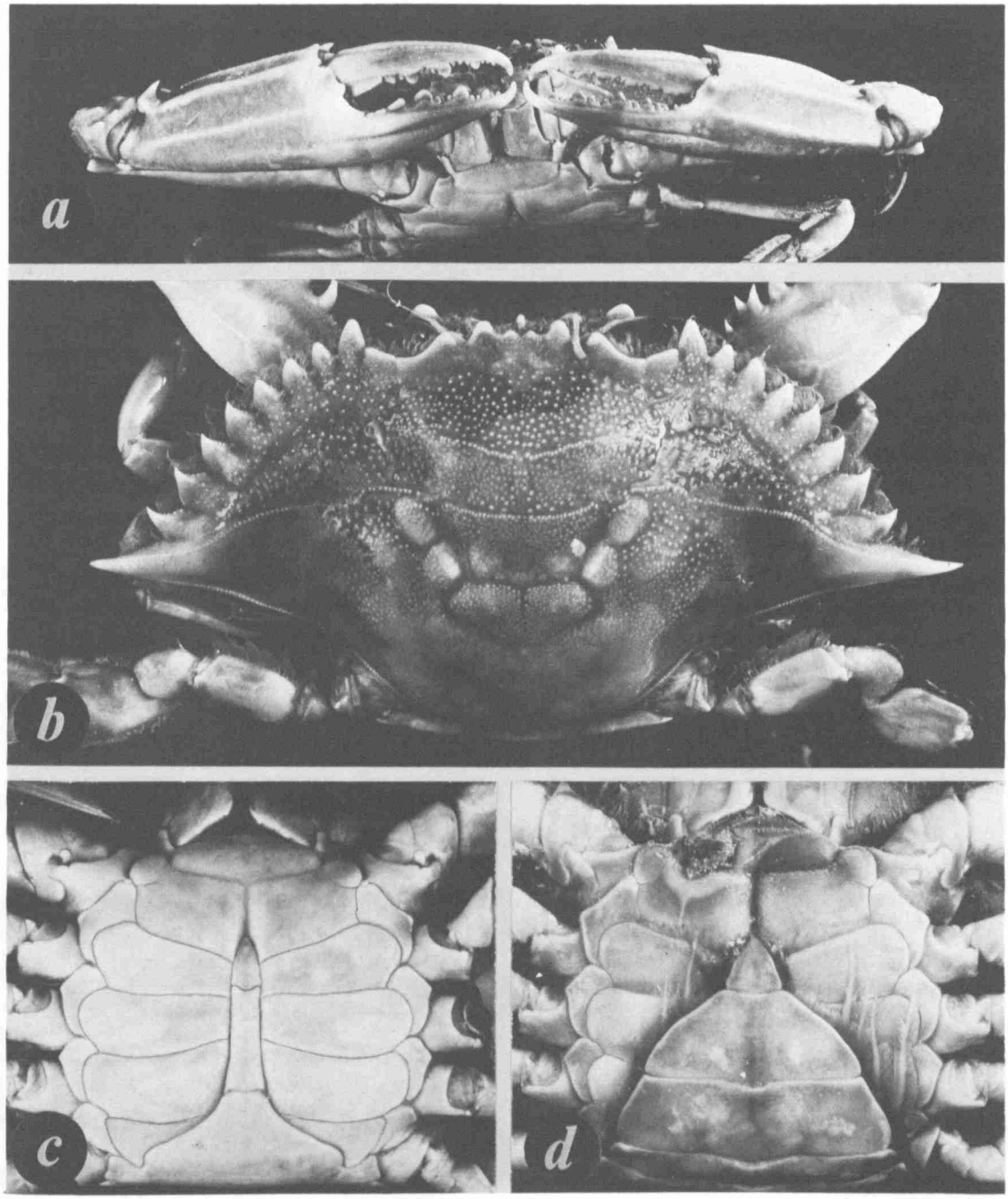


FIGURE 3.—*Callinectes marginatus* (A. Milne Edwards): **a,** chelae in frontal view; **c,** abdomen and sternal area, male, USNM 72351, Salt River Bay, St. Croix, V.I.; **b,** carapace; **d,** abdomen and sternal area, female, USNM 73285, W end San Juan Island near Ft. San Gerónimo, P.R.; **a** × 1; **b** × 1.5; **c** × 1.4; **d** × 1.7.

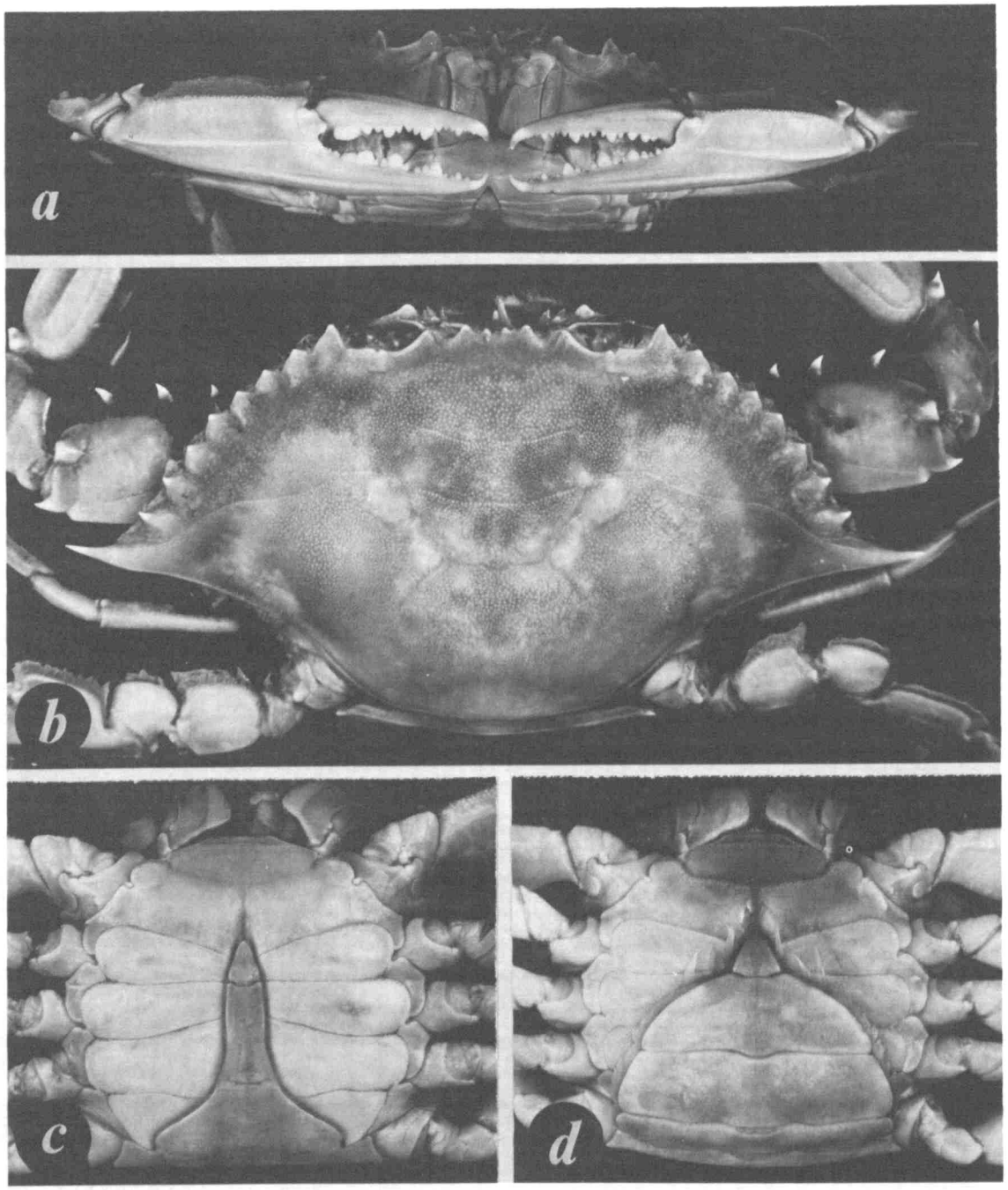


FIGURE 4.—*Callinectes similis* Williams: **a,** chelae in frontal view; **b,** carapace; **c,** abdomen and sternal area, male; **d,** abdomen and sternal area, female; paratypes, UNC-IMS 1556, Beaufort Inlet, Carteret County, N.C.; **a** × 1; **b** × 1.4; **c** × 1.2; **d** × 1.3.

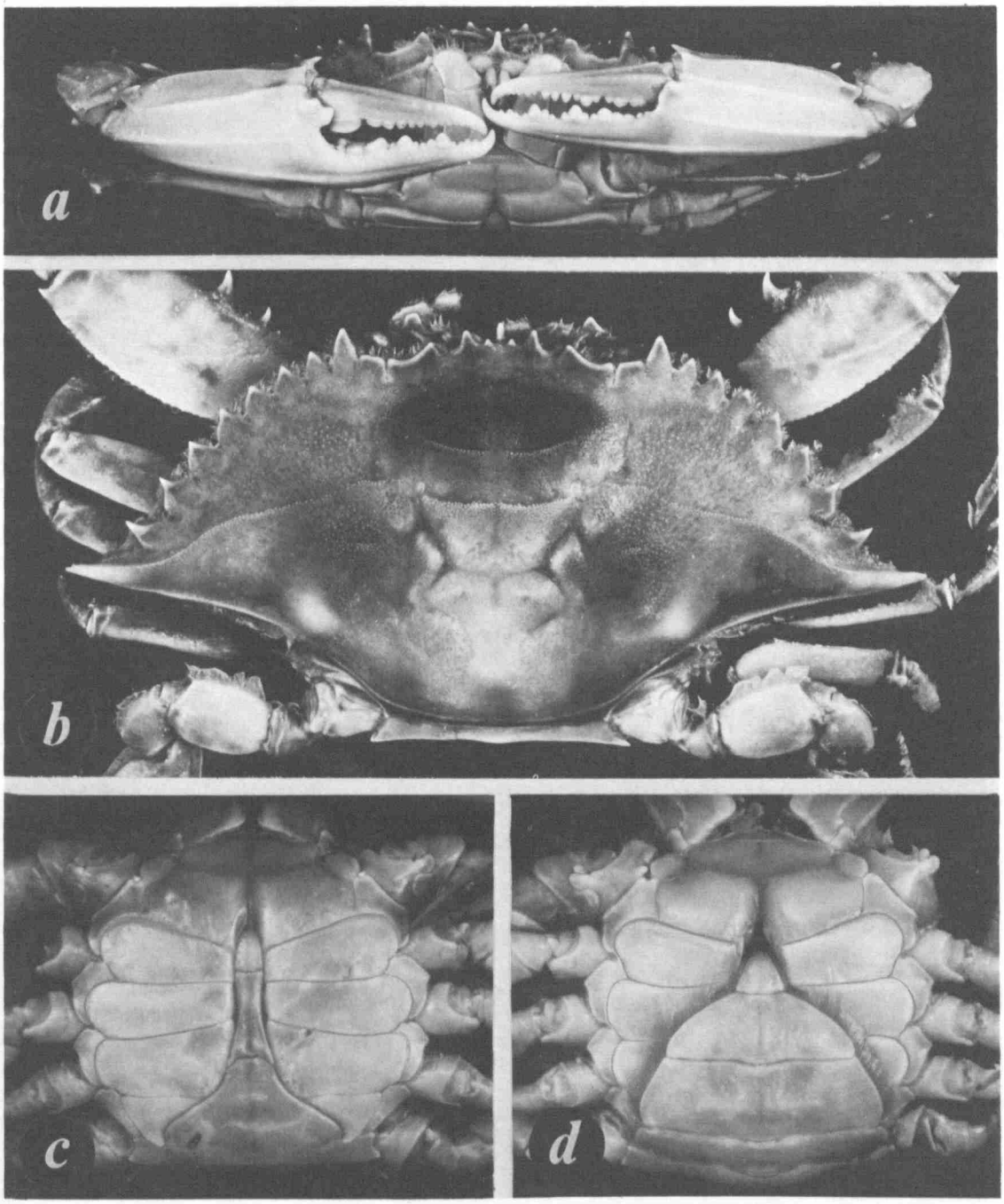


FIGURE 5.—*Callinectes gladiator* Benedict: **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male; **d**, abdomen and sternal area, female, USNM 120940, Nigeria; **a** × 0.9; **b** × 1.4; **c**, **d** × 1.6.

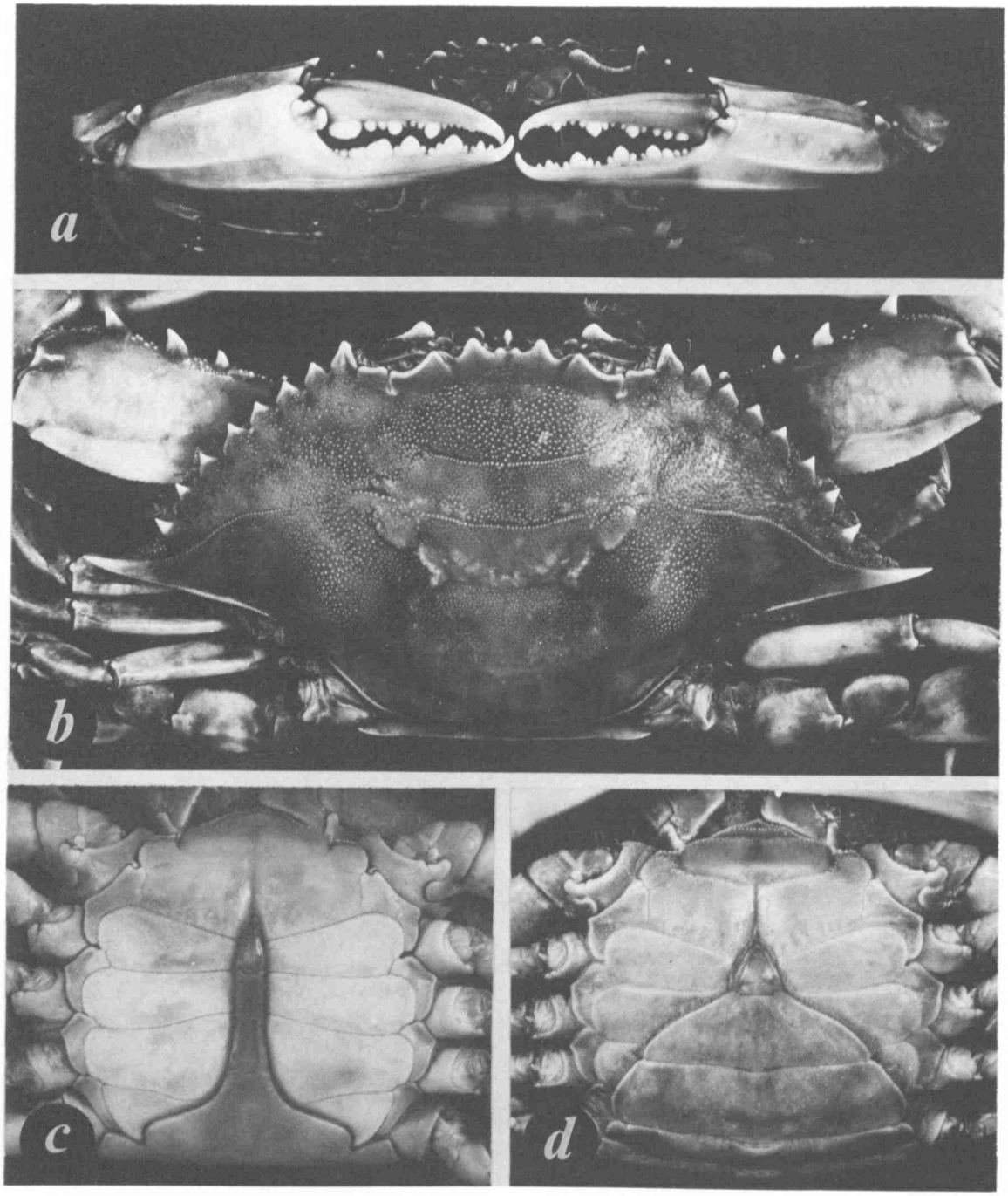


FIGURE 6.—*Callinectes ornatus* Ordway: **a,** chelae in frontal view; **b,** carapace; **c,** abdomen and sternal area, male, 48401, Punta [= Cabo] Cajón, Cuba; **d,** abdomen and sternal area, female, 7584, Curaçao; **a** × 1; **b, d** × 1.3; **c** × 1.5.

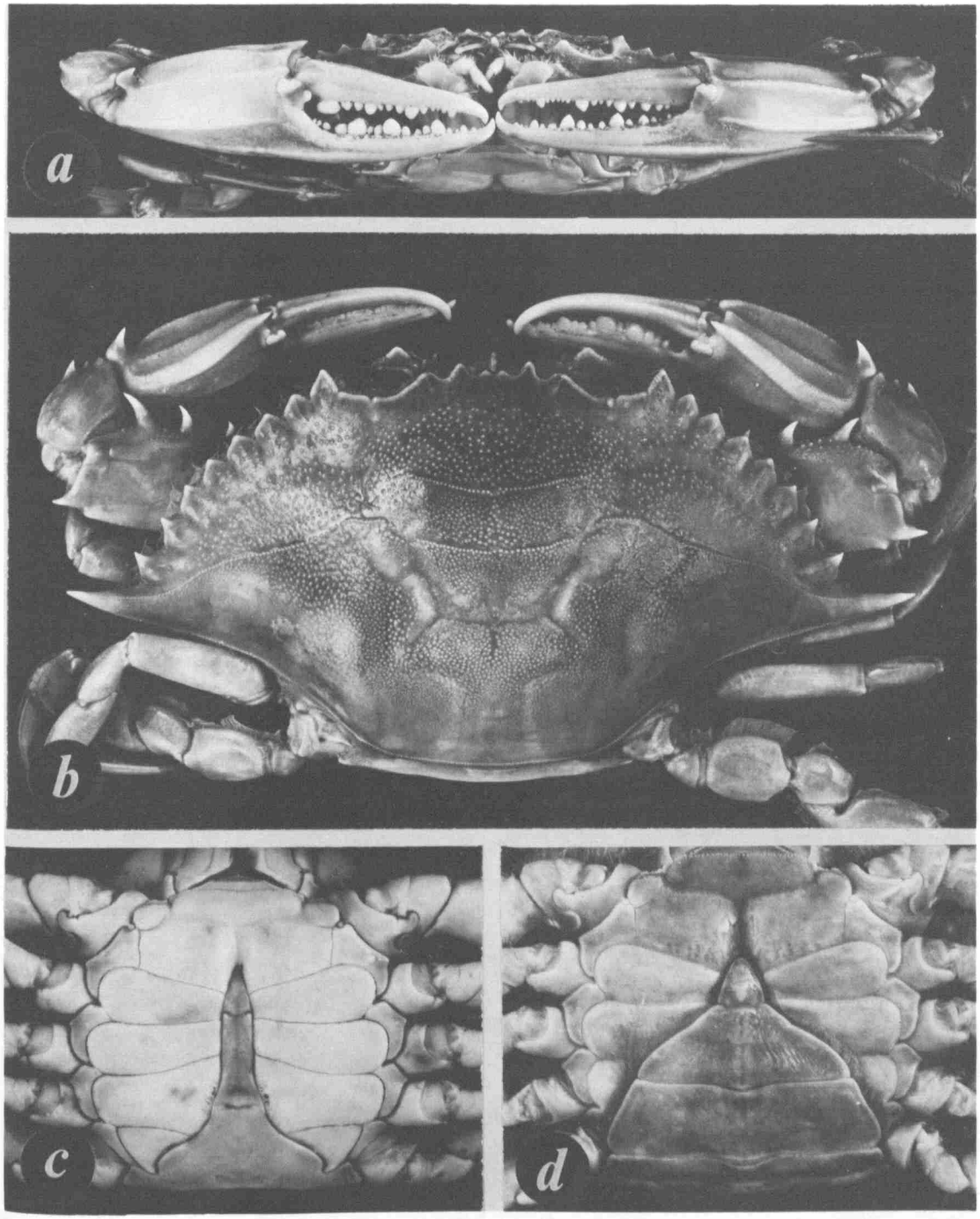


FIGURE 7.—*Callinectes danae* Smith: **a,** chelae in frontal view, male, USNM 60983, São Francisco, Niterói, Brazil; **b,** carapace; **d,** abdomen and sternal area, female, USNM 48400, Los Arroyos, Cuba; **c,** abdomen and sternal area, male, UNC-IMS 2128, Bahía de Mayagüez, P.R.; **a, c** × 1; **b** × 1.4; **d** × 1.5.

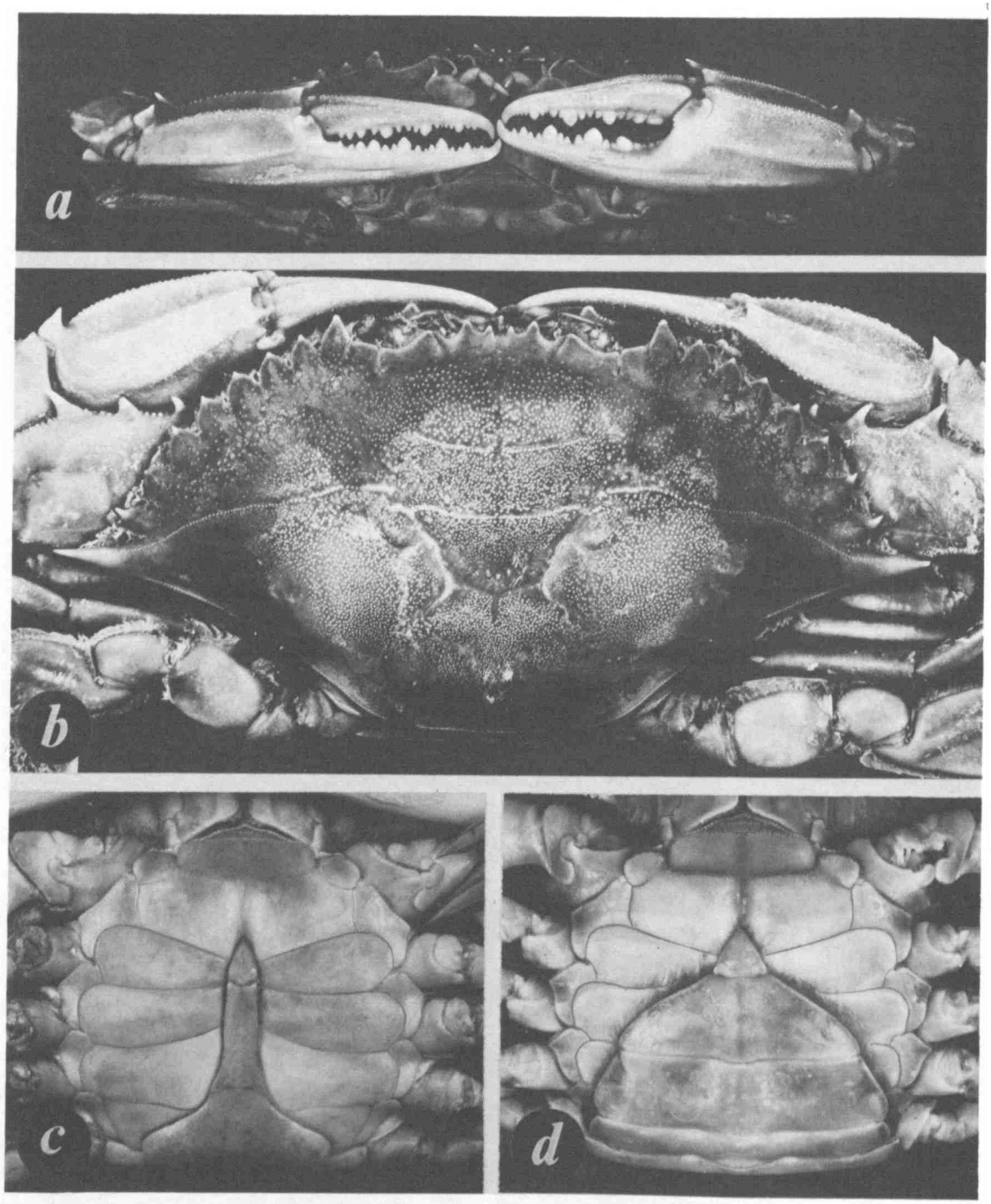


FIGURE 8.—*Callinectes arcuatus* Ordway: **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male, USNM 33417, Isla Magdalena, Baja California, Mexico; **d**, abdomen and sternal area, female, USNM 15431, Estero de los Algodones, SE Guaymas, Sonora, Mexico; **a** × 1; **b**, **c** × 1.2; **d** × 1.4.

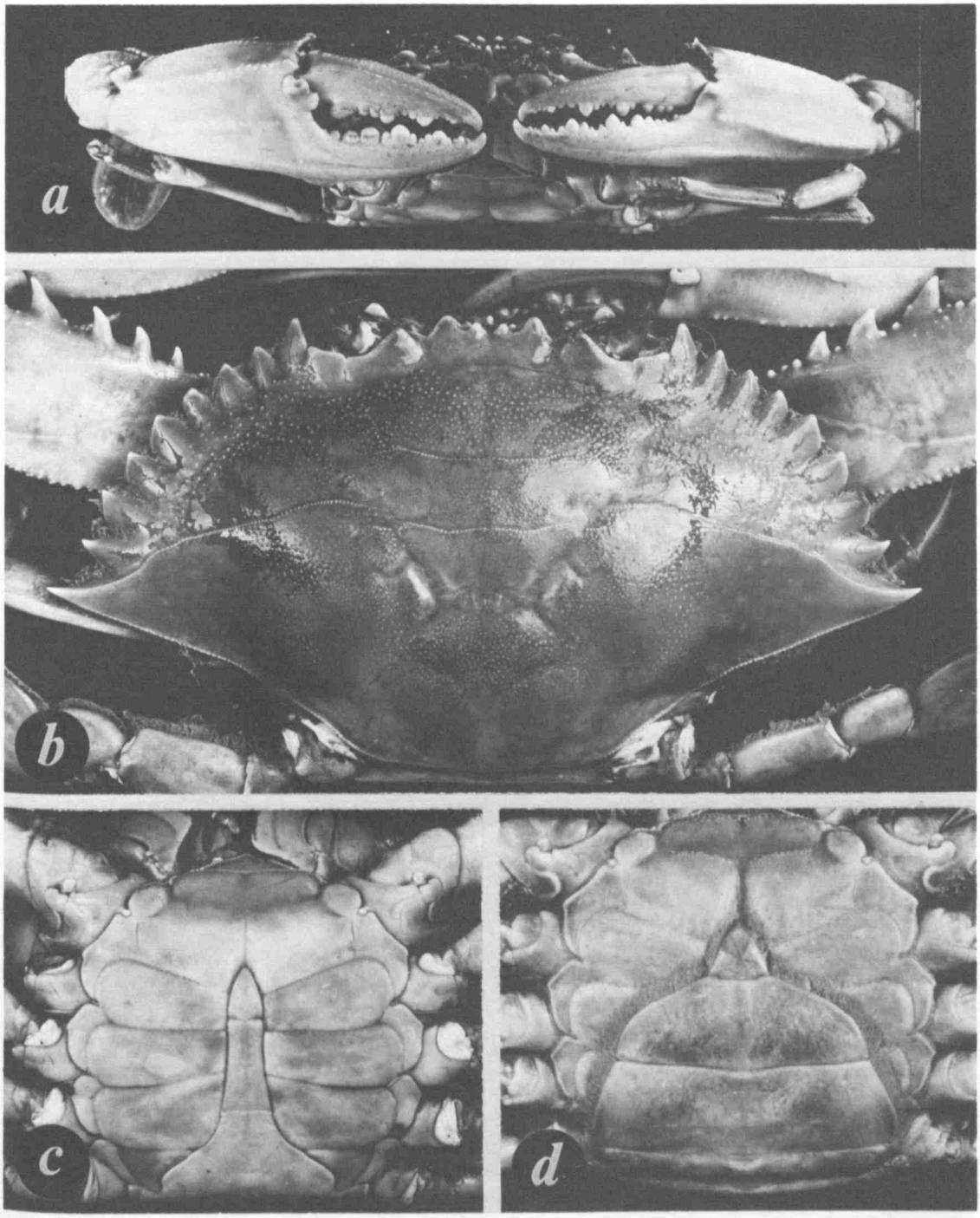


FIGURE 9.—*Callinectes exasperatus* (Gerstaecker): **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male, USNM 19428, Vitória, Estado Espírito Santo, Brazil; **d**, abdomen and sternal area, female, USNM 24467, Puerto Real, P.R.; **a** × 0.8; **b** × 1.1; **c** × 1; **d** × 1.4.

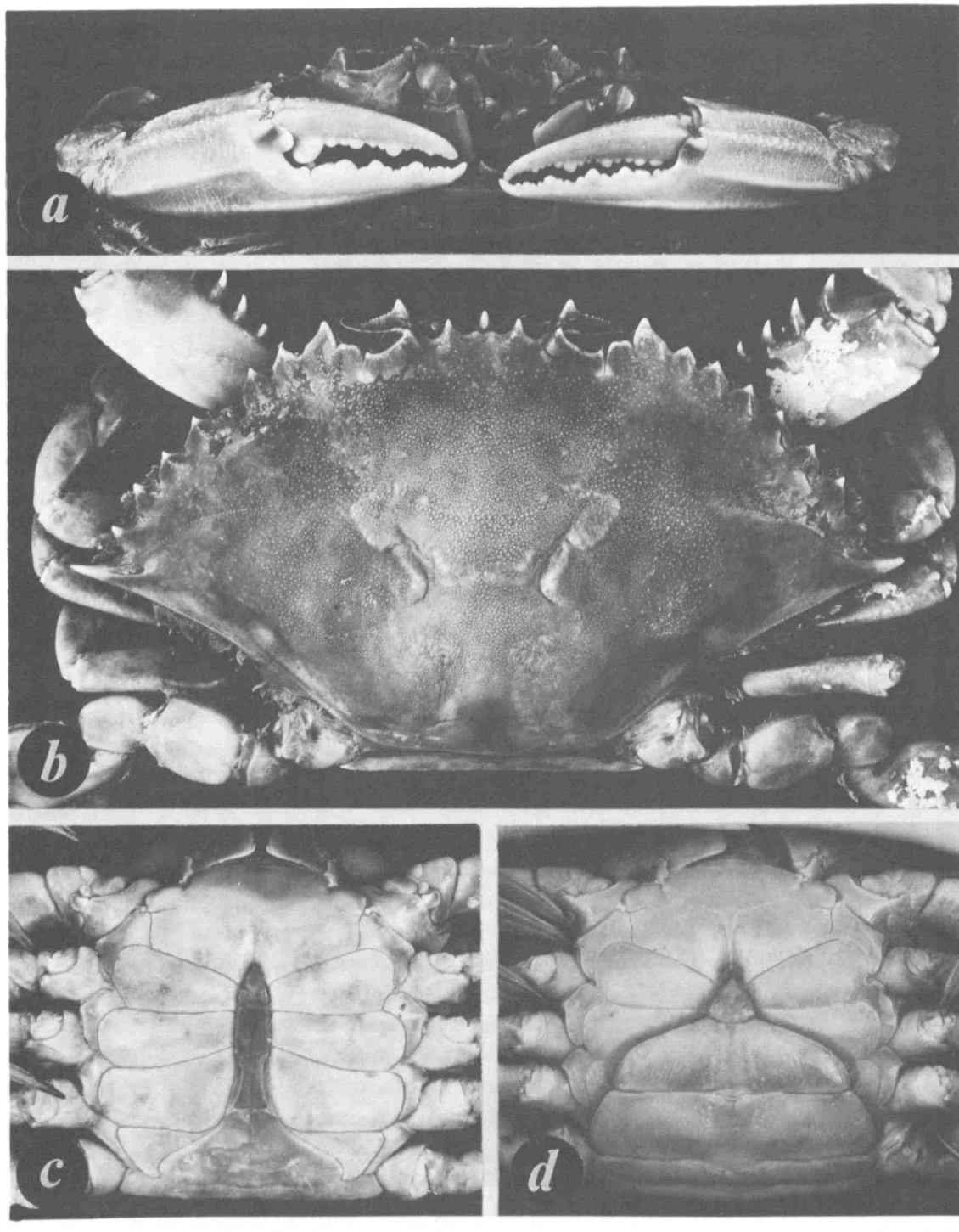


FIGURE 10.—*Callinectes bellicosus* (Stimpson): **a,** chelae in frontal view; **d,** abdomen and sternal area, female, USNM 60010, Pt. Abreojos, Bahía Ballenas, Baja California, Mexico; **b,** carapace; **c,** abdomen and sternal area, male, USNM 15436, La Paz Harbor, Baja California, Mexico; **a, c, d** × 1; **b** × 1.1.

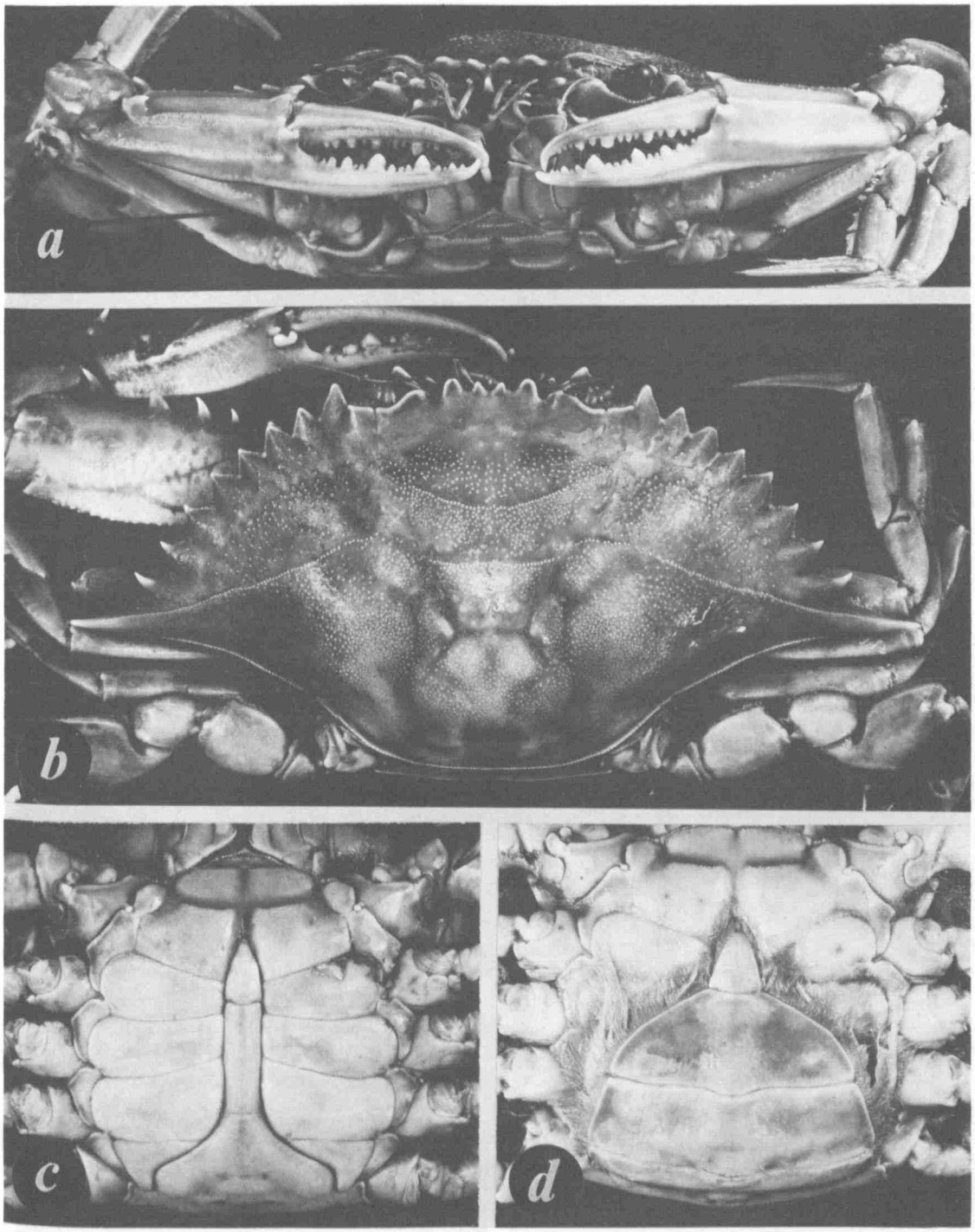


FIGURE 11.—*Callinectes toxotes* Ordway: **a,** chelae in frontal view; **b,** carapace; **c,** abdomen and sternal area, male; **d,** abdomen and sternal area, female, USNM 18507, Acapulco, Guerrero, Mexico; **a** × 1.1; **b** × 0.8; **c, d** × 1.

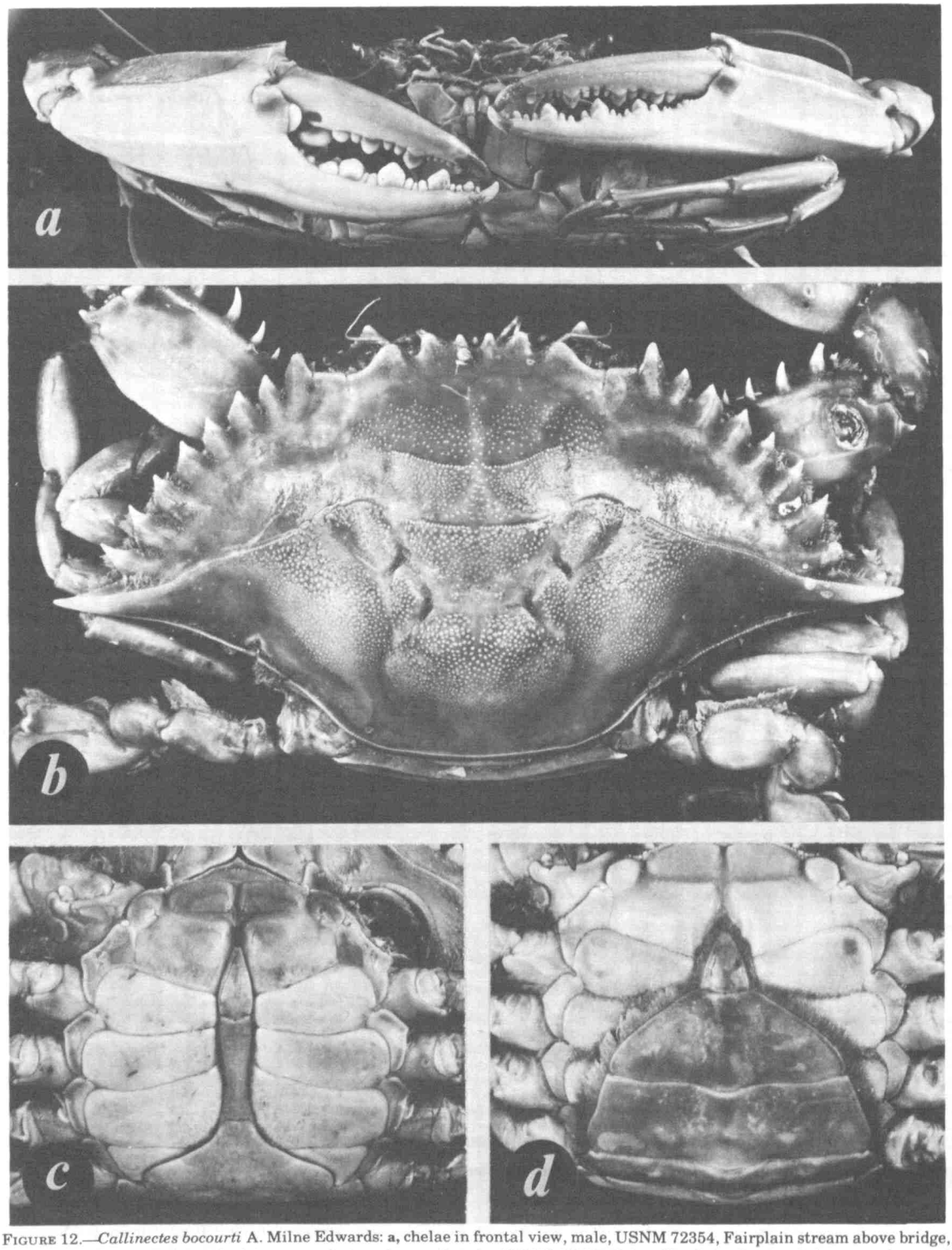


FIGURE 12.—*Callinectes bocourti* A. Milne Edwards: **a,** chelae in frontal view, male, USNM 72354, Fairplain stream above bridge, St. Croix, V.I.; **b,** carapace; **d,** abdomen and sternal area, female, USNM 18235, Sabanilla, Colombia; **c,** abdomen and sternal area, male, USNM 18233, São Luis, Estado Maranhão, Brazil; **a, c** × 1; **b** × 1.2; **d** × 1.4.

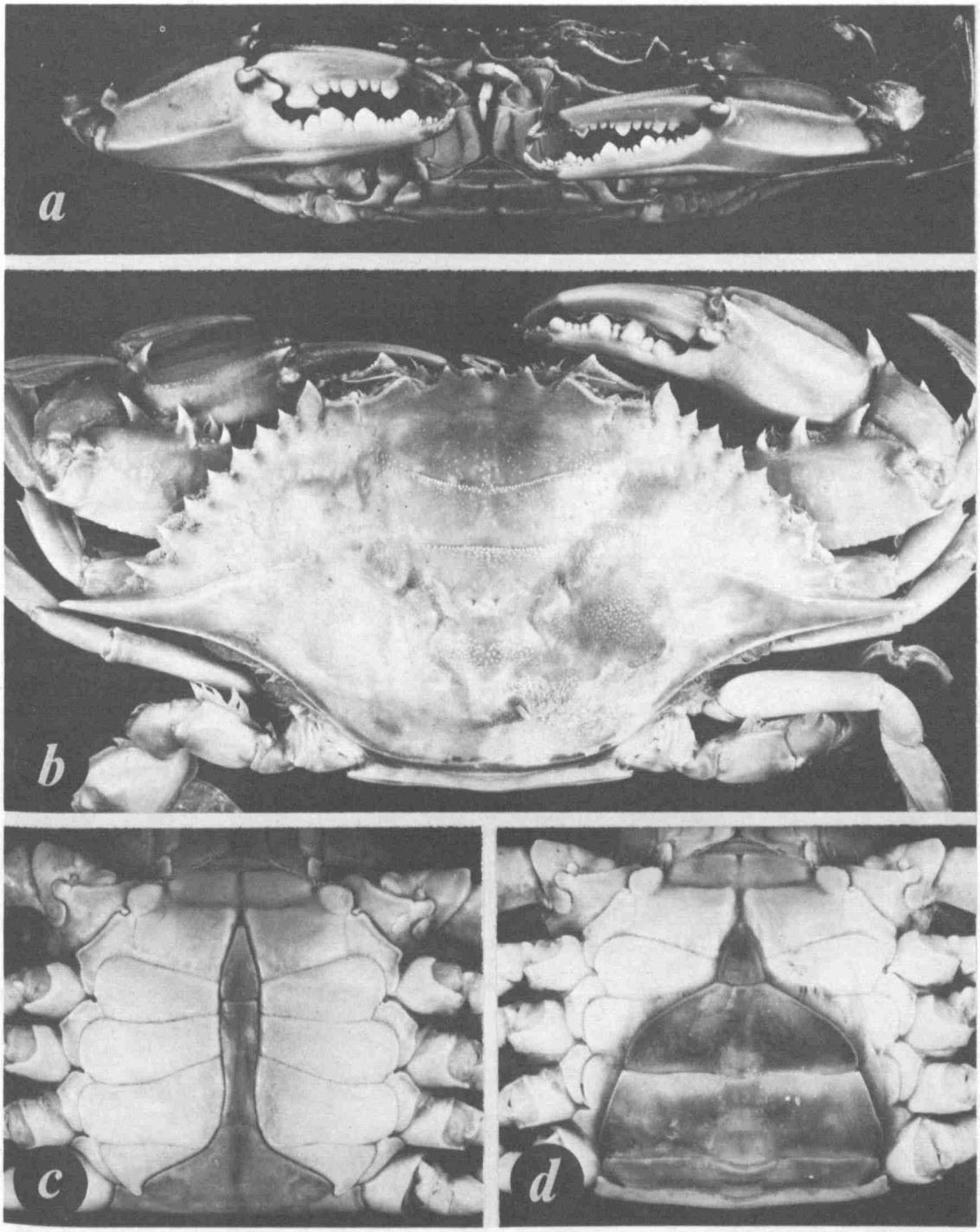


FIGURE 13.—*Callinectes rathbunae* Contreras: **a,** chelae in frontal view; **b,** carapace; **d,** abdomen and sternal area, female; **c,** abdomen and sternal area, male, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; **a, b** × 1; **c, d** × 1.1.

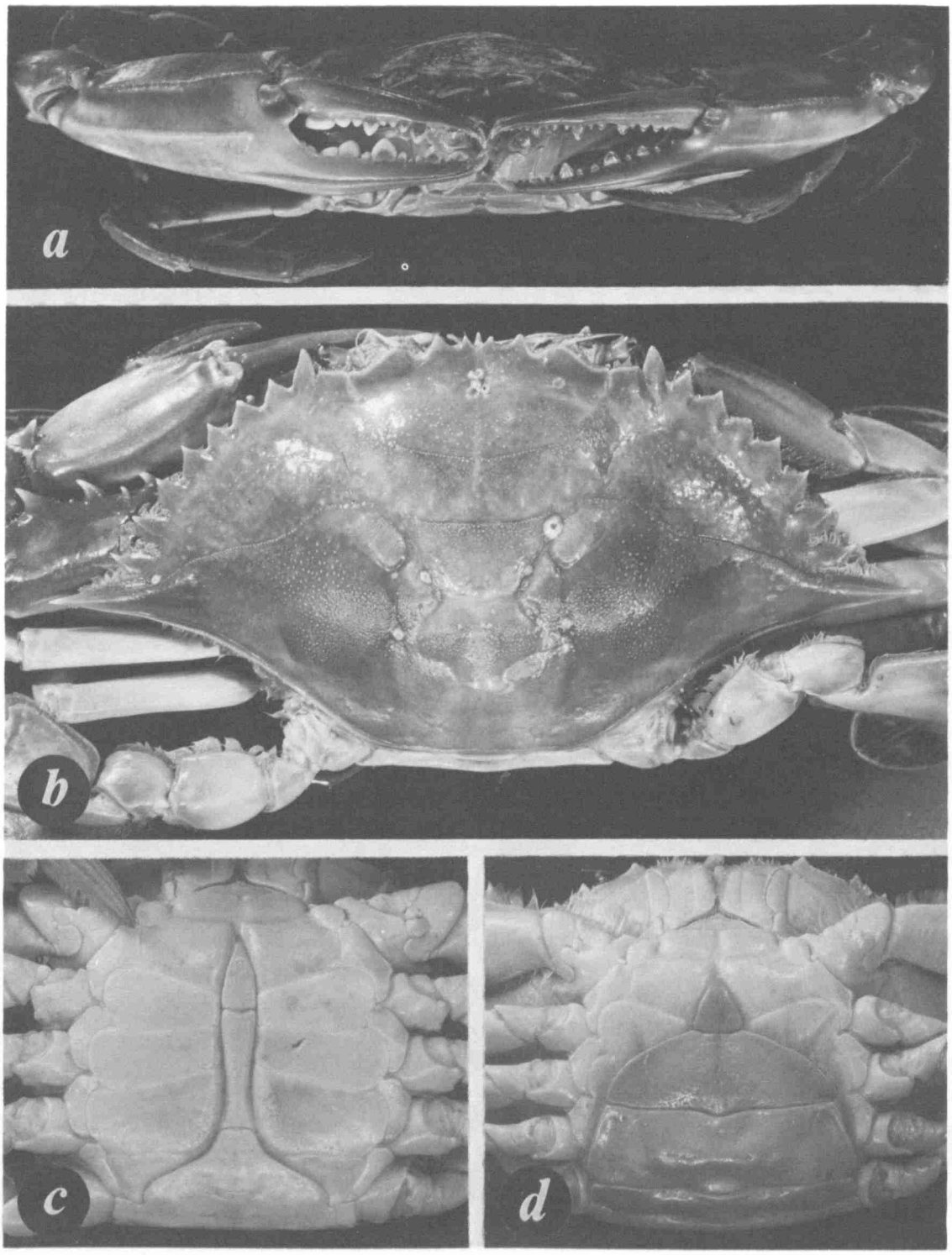


FIGURE 14.—*Callinectes maracaiboensis* Taissoun: **a,** chelae in frontal view, male, USNM 143392, Lago de Maracaibo; **b,** carapace, male, USNM 143393, Puerto Caballo, Maracaibo; **c,** abdomen and sternal area, male; **d,** abdomen and sternal area, female, USNM 139621, Lago de Maracaibo, Venezuela; **a** × 0.95; **b** × 0.85; **c, d** × 1.

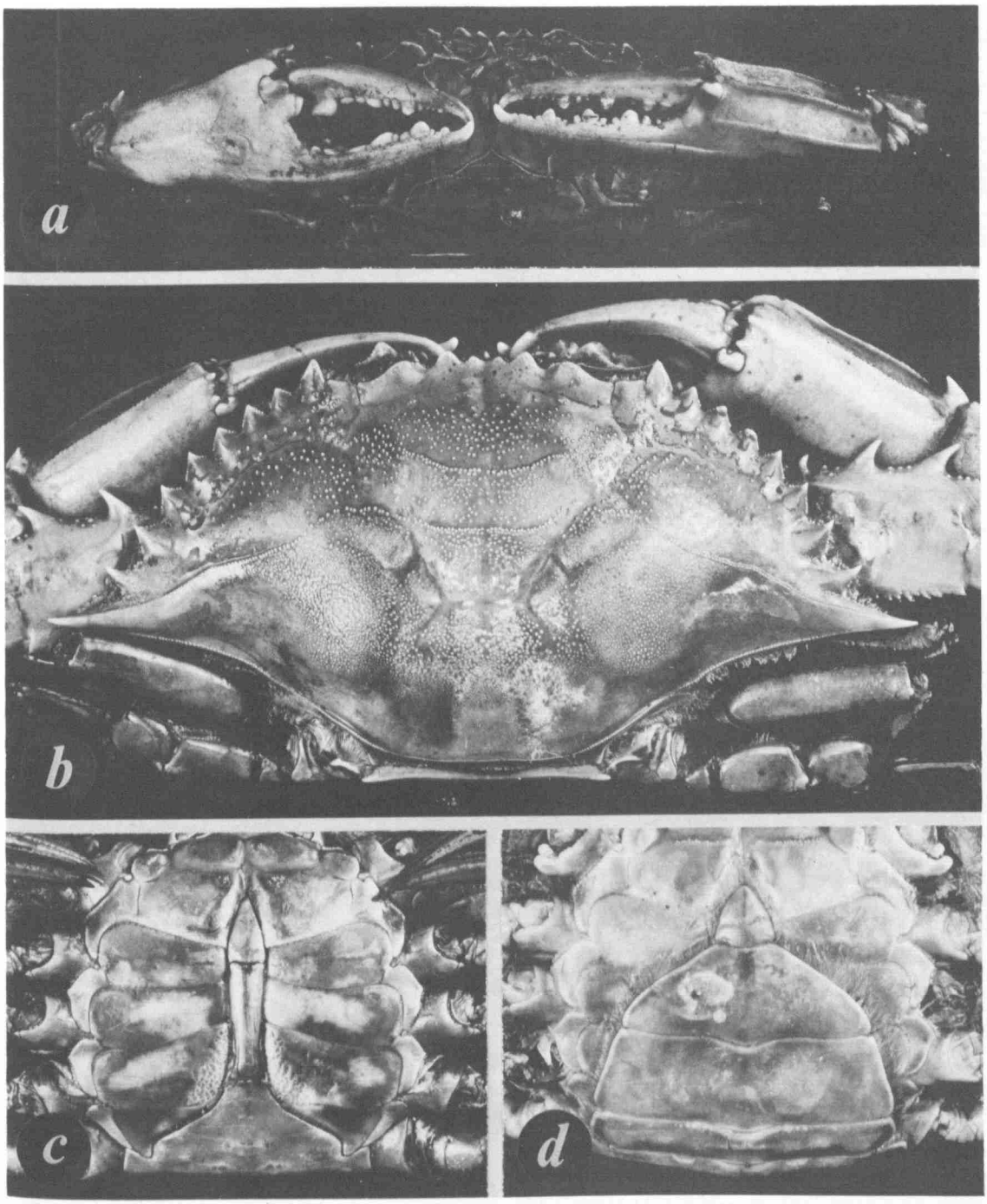


FIGURE 15.—*Callinectes latimanus* Rathbun: **a,** chelae in frontal view; **b,** carapace; **c,** abdomen and sternal area, male; **d,** abdomen and sternal area, female, USNM 54310, Banana, Zaire [= Belgian Congo] **a** × 0.8; **b, c** × 1; **d** × 1.9.

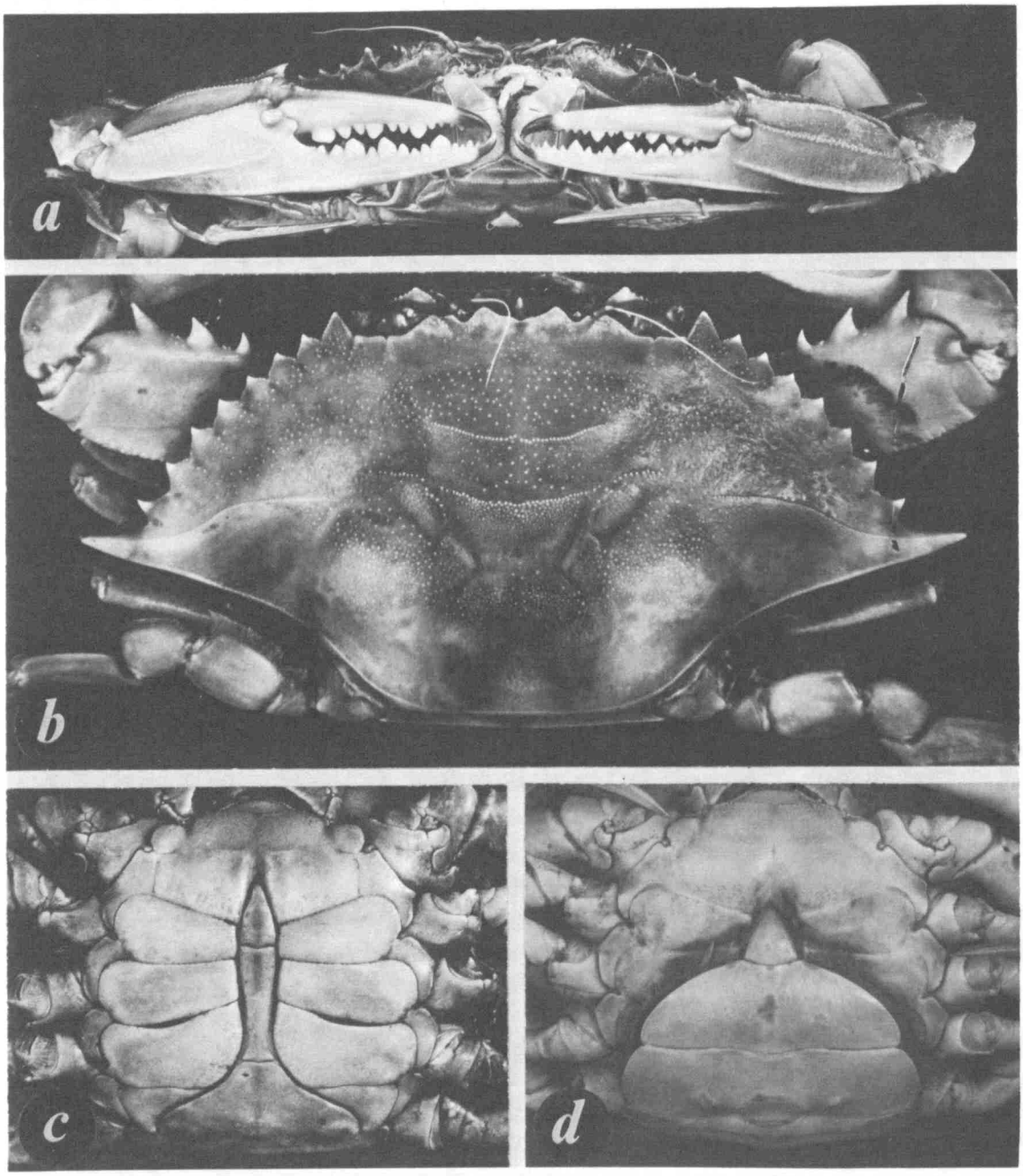


FIGURE 16.—*Callinectes sapidus* Rathbun, forma typica: **a,** chelae in frontal view, male, UNC-IMS 2136, 5 km S Lajas, P.R.; **b,** carapace, male, UNC-IMS 741, North River, Carteret County, N.C.; **c,** abdomen and sternal area, male, USNM 92452, Wye River, Md.; **d,** abdomen and sternal area, female, USNM 30567, Cameron, La.; **a** × 0.8; **b** × 1.3; **c** × 0.6; **d** × 0.85.

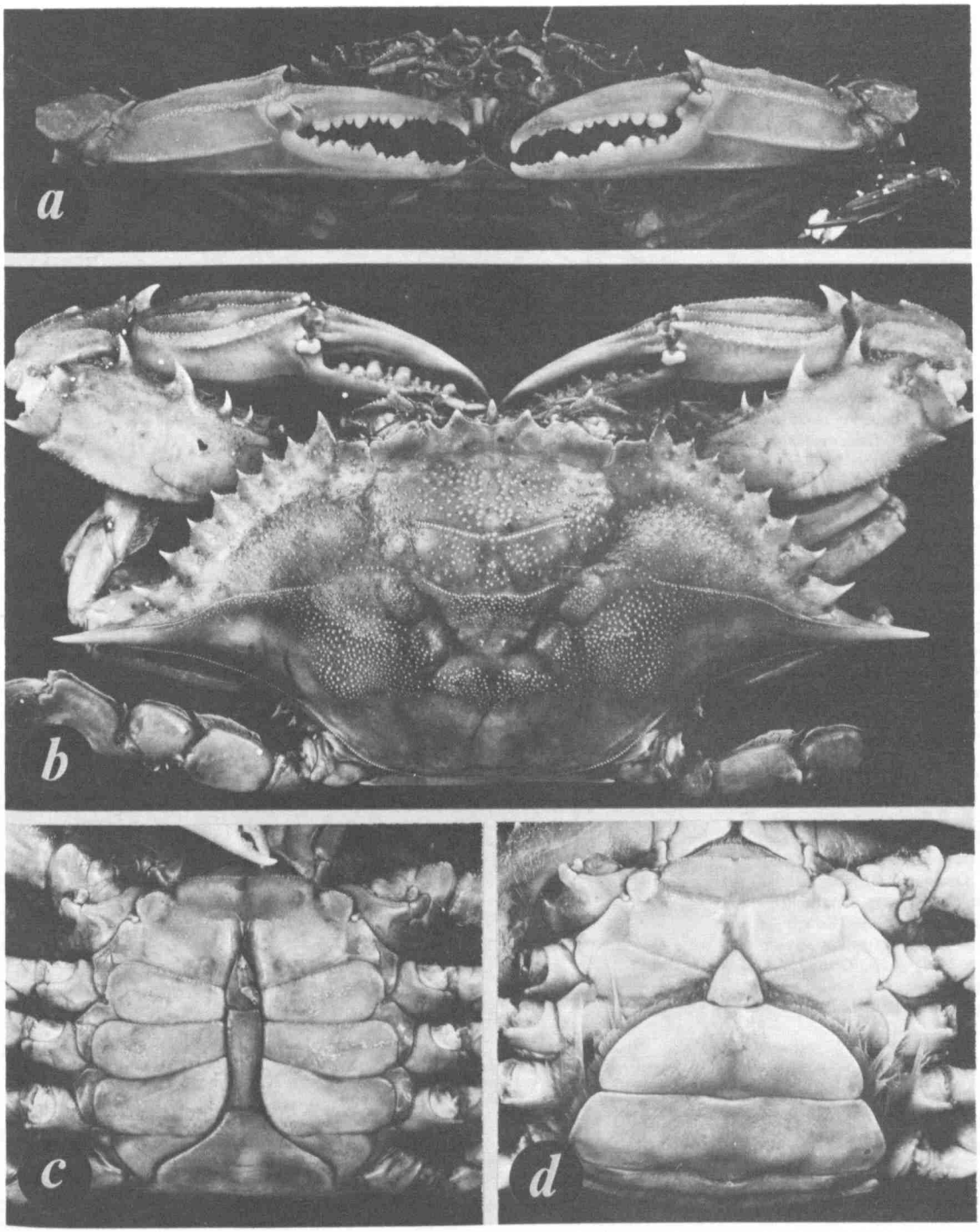


FIGURE 17.—*Callinectes sapidus* Rathbun, forma acutidens: **a,** chelae in frontal view; **b,** carapace; **c,** abdomen and sternal area, male, USNM 18630, Río Escondido, Nicaragua; **d,** abdomen and sternal area, female, USNM 99848, Roca Arroyo Balizas [= Arroyo de Valizes?], Uruguay; **a** × 0.9; **b, c** × 1; **d** × 1.1.

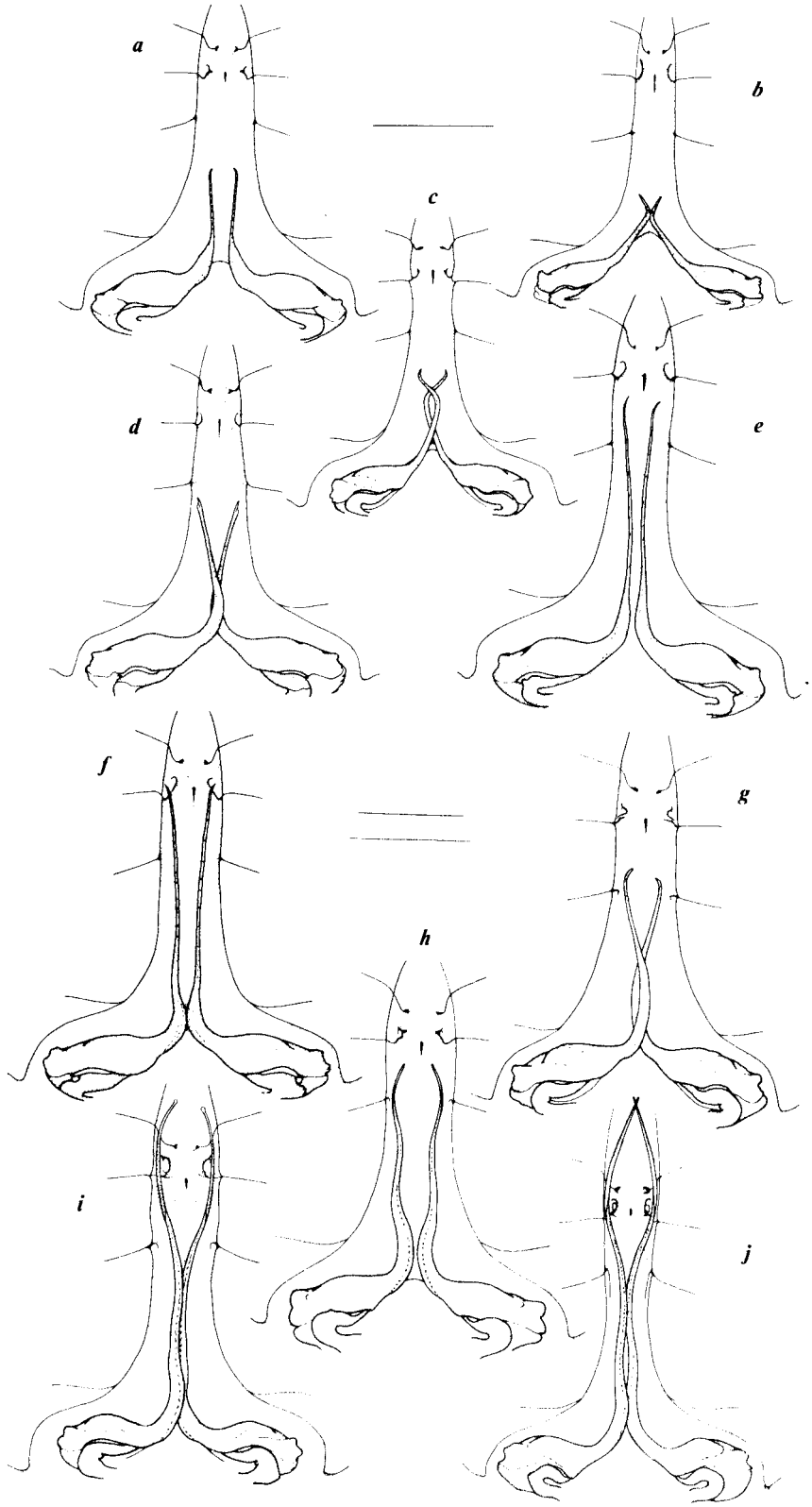


FIGURE 18.—Male, first gonopods in situ with abdomen removed; portions of thoracic sternites IV-VIII: **a**, *Callinectes marginatus* (A. Milne Edwards), USNM 72351, Salt River Bay, St. Croix, V.I.; **b**, *C. similis* Williams, paratype, UNC-IMS 1556, Beaufort Inlet, Carteret County, N.C.; **c**, *C. gladiator* Benedict, Côte du Dahomey, 6°19′N, 2°24′E; **d**, *C. ornatus* Ordway, USNM 48401, Punta [= Cabo] Cajón, Cuba; **e**, *C. danae* Smith, USNM 60983, São Francisco, Niterói, Estado de Rio de Janeiro, Brazil; **f**, *C. arcuatus* Ordway, USNM 33417, Isla Magdalena, Baja California, Mexico; **g**, *C. exasperatus* (Gerstaecker), UNM-IMS 2137, Bahía Fosforescente, P.R.; **h**, *C. bellicosus* (Stimpson), USNM 15436, La Paz Harbor, Baja California, Mexico; **i**, *C. toxotes* Ordway, USNM 18507, Acapulco, Guerrero, Mexico; **j**, *C. bocourti* A. Milne Edwards, USNM 72354, Fairplain stream above bridge, St. Croix, V.I. Scales = 1 cm; **a-f** have higher magnification.

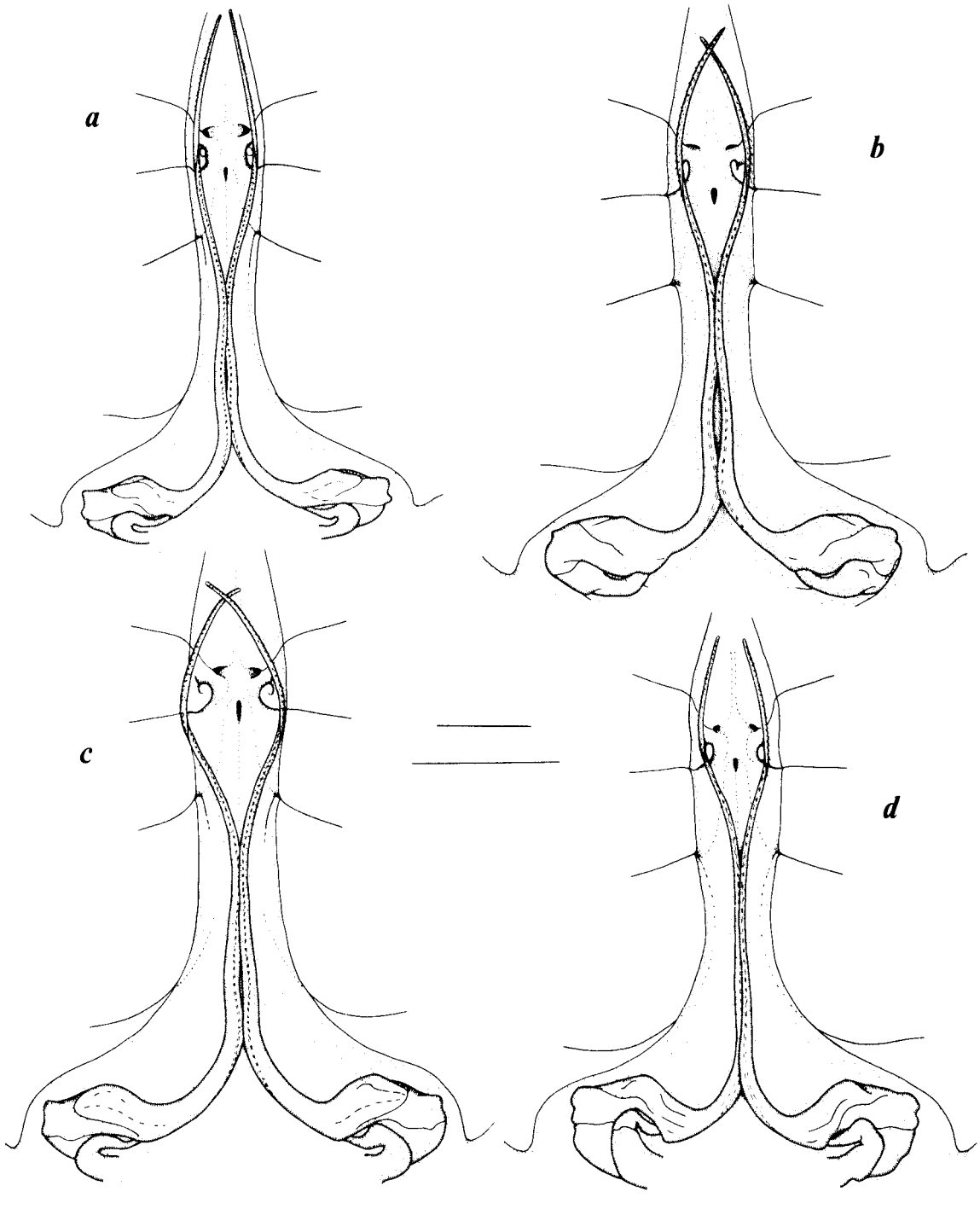


FIGURE 19.—Male, first gonopods in situ with abdomen removed; portions of thoracic sternites IV-VIII; **a**, *Callinectes rathbunae* Contreras, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; **b**, *C. maracaiboensis* Taissoun, Lago de Maracaibo, Venezuela; **c**, *C. latimanus* Rathbun, Plage de Pointe Noire, Congo; **d**, *C. sapidus* Rathbun, USNM 92452, Wye River, Chesapeake Bay, Md. Scales = 1 cm; **d** has lower magnification.

FIGURE 20.—Male, right first gonopod, distal portion in posterior view unless otherwise indicated: **a,** *Callinectes marginatus* (A. Milne Edwards), USNM 72351, Salt River Bay, St. Croix, V.I.; **b,** *C. gladiator* Benedict, Coast of Dahomey, 6°19′N, 2°24′E; **c,** *C. similis* Williams, paratype, UNC-IMS 1556, Beaufort Inlet, Carteret County, N.C.; **d,** *C. ornatus* Ordway, USNM 7584, Curaçao; **e, f,** *C. danae* Smith, USNM 60983, São Francisco, Niterói, Estado de Rio de Janeiro, Brazil; **g, h,** *C. arcuatus* Ordway, USNM 33417, Isla Magdalena, Baja California, Mexico (reconstructed tip of **h** from USNM 60977, Salinas, Ecuador); **i,** *C. exasperatus* (Gerstaecker), UNC-IMS 2137, Bahía Fosforescente, P.R.; **j,** *C. bellicosus* (Stimpson), USNM 15436, La Paz Harbor, Baja California, Mexico; **k,** same, sternal view; **l,** *C. toxotes* Ordway, USNM 18507, Acapulco, Guerrero, Mexico; **m,** *C. bocourti* A. Milne Edwards, USNM 72354, Fairplain stream above bridge, St. Croix, V.I.; **n,** *C. rathbunae* Contreras, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; **o,** *C. maracaiboensis* Taissoun, paratype, USNM 139621, Lago de Maracaibo, Venezuela; **p,** *C. latimanus* Rathbun, Plage de Pointe Noire, Congo. Scales = 1 mm; **a-c** have higher magnification.

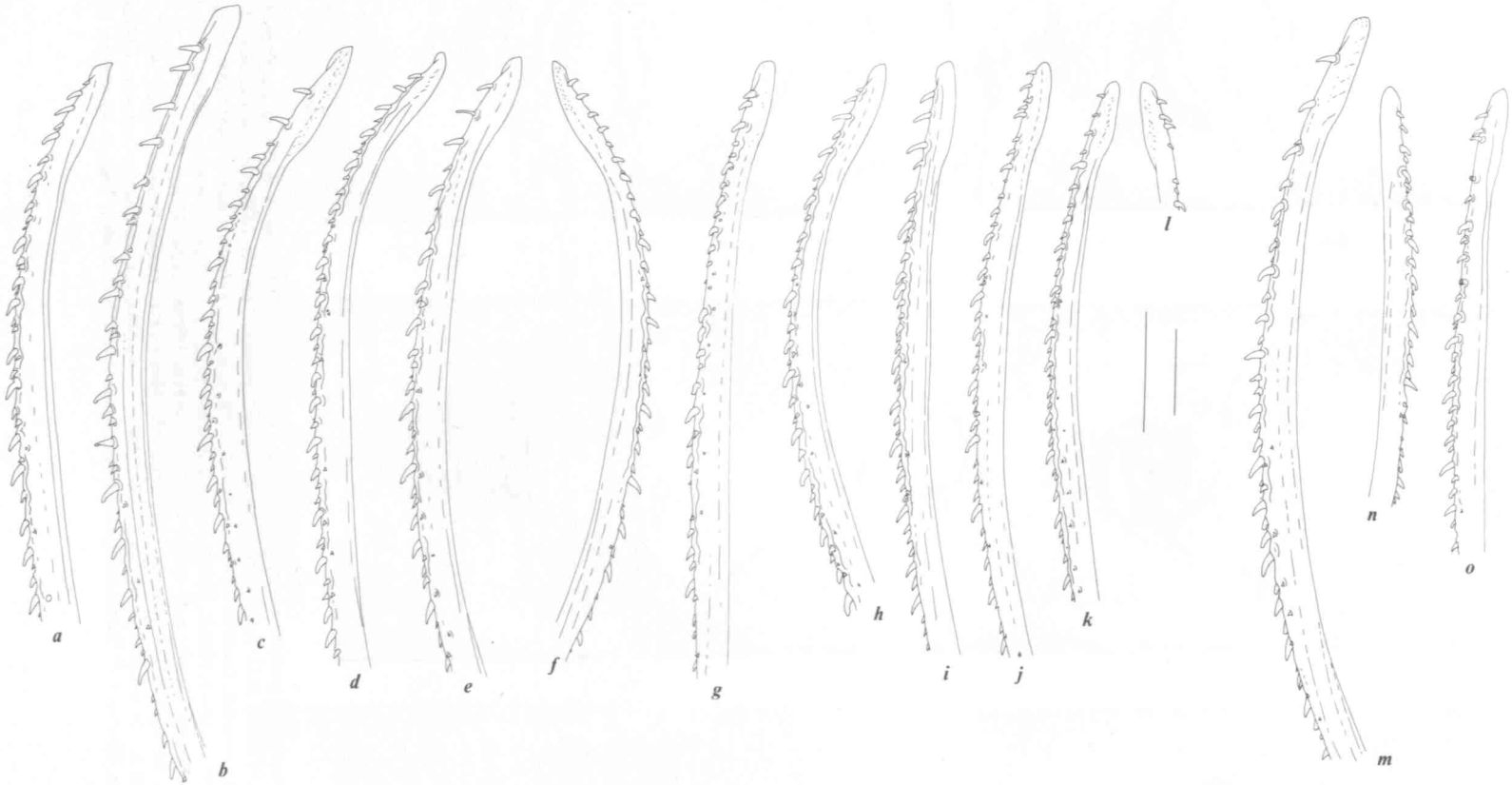


FIGURE 21.—*Callinectes sapidus* Rathbun, male, right first gonopod, distal portion in posterior view unless otherwise indicated: **a,** typical form, USNM 41457, Hudson River at West Point, N.Y.; **b,** typical form, USNM 92452, Wye River, Chesapeake Bay, Md.; **c, d,** typical form, USNM 60601, Cape Hatteras, N.C.; **e,** acutidens form, USNM 122944, Deep Lake, Miami, Fla.; **f,** typical form, right first gonopod, USNM 7679, Jamaica; **g,** acutidens form, USNM 72356, Fairplain stream below bridge, St. Croix, V.I.; **h,** acutidens form, USNM 113278, Tortuguero, Costa Rica; **i,** acutidens form, USNM 43921, Mindi Cut, C. Z., Panama; **j,** acutidens form, Lago de Maracaibo, Venezuela; **k,** typical form, USNM 80650, Lago de Maracaibo, Venezuela; **l,** same specimen, right side; **m,** acutidens form, holotype, MCZ 4696, Santa Cruz, Estado de Bahia, Brazil; **n,** acutidens form, paratype, right first gonopod, USNM 19083, Rio de Janeiro, Brazil; **o,** acutidens form, SADZ-B 3234, Praia de Torres, Estado de Rio Grande do Sul, Brazil (tip straightened in preservation). Scales = 1 mm; **a, g, n** have higher magnification.

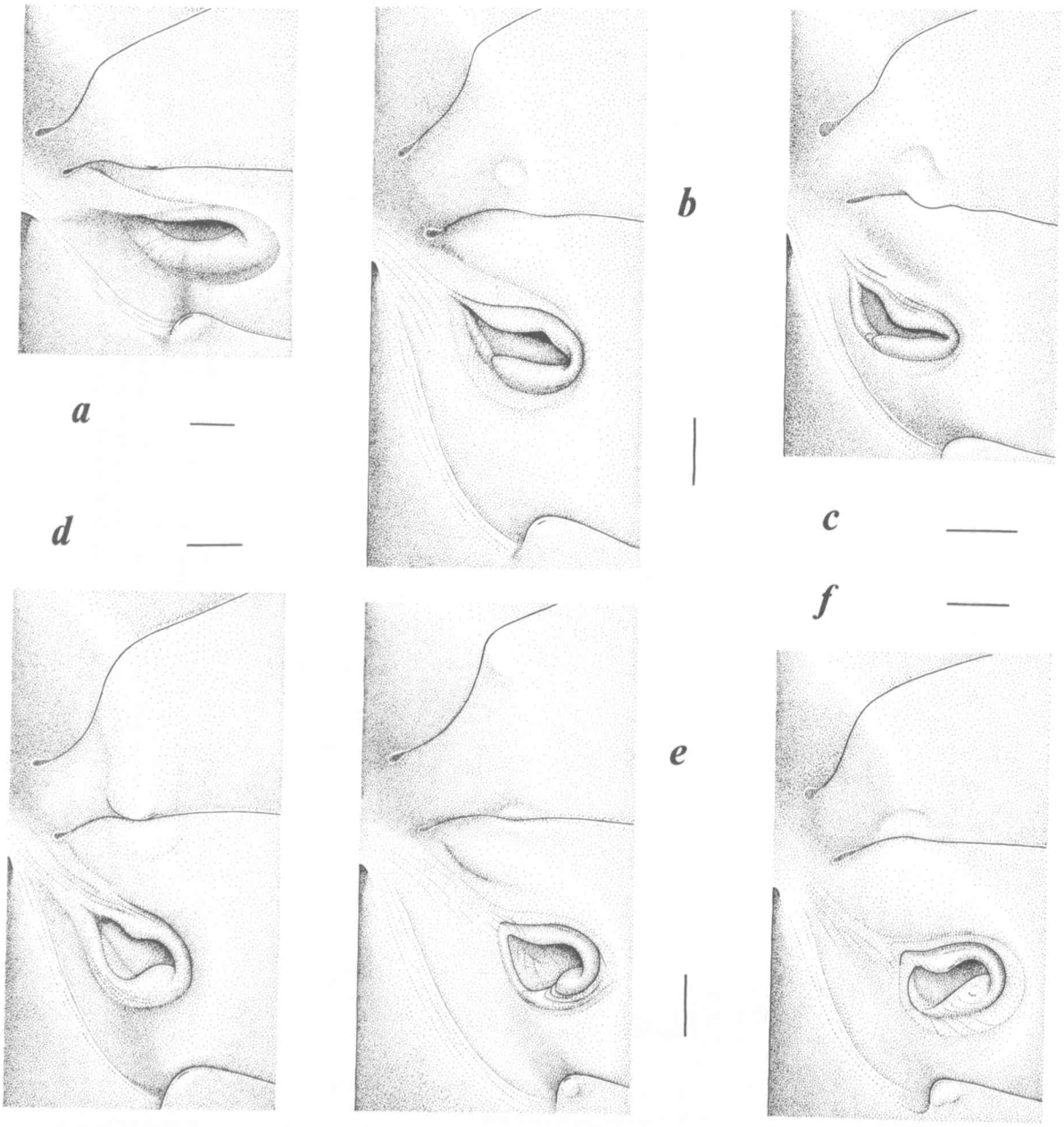
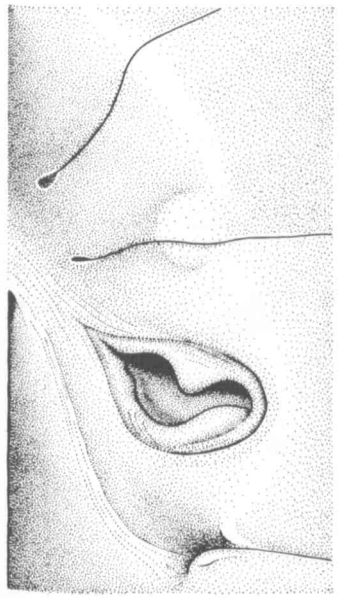


FIGURE 22.—Female, left gonopore and portions of thoracic sternites IV-VII: **a,** *Callinectes similis* Williams, paratype, UNC-IMS 1556, Beaufort inlet, Carteret County, N.C.; **b,** *C. marginatus* (A. Milne Edwards), USNM 73285, W end San Juan I. near Ft. Gerónimo, P.R.; **c,** *C. gladiator* Benedict, Coast of Cameroon, 3°32′N, 9°35′E; **d,** *C. ornatus* Ordway, USNM 7584, Curaçao; **e,** *C. danae* Smith, USNM 60983, São Francisco, Niterói, Estado de Rio de Janeiro, Brazil; **f,** *C. arcuatus* Ordway, USNM 15431, Estero de los Algodones near Guaymas, Sonora, Mexico; **g,** *C. exasperatus* (Gerstaecker), USNM 24467, Puerto Real, P.R.; **h,** *C. bellicosus* (Stimpson), USNM 60010, Pt. Abreojos, Bahía Ballenas, Baja California, Mexico; **i,** *C. toxotes* Ordway, USNM 18507, Acapulco, Guerrero, Mexico; **j,** *C. bocourti* A. Milne Edwards, USNM 18235, Sabanilla, Colombia; **k,** *C. rathbunae* Contreras, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; **l,** *C. maracaiboensis* Taissoun, paratype, USNM 139621, Lago de Maracaibo, Venezuela. Scales = 1 mm.



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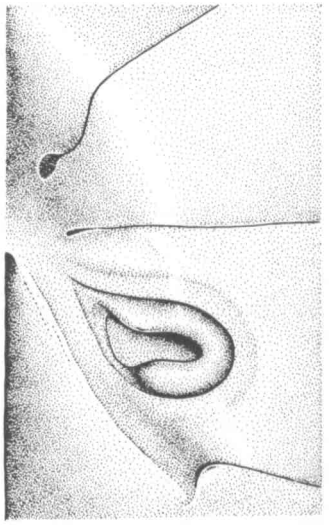

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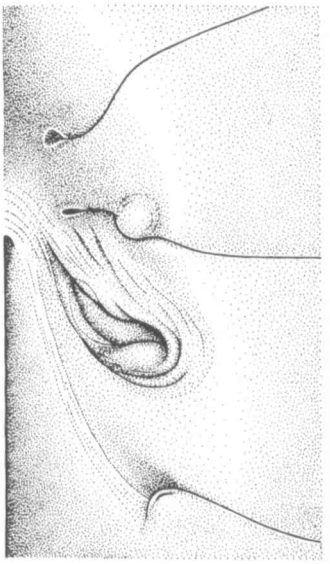

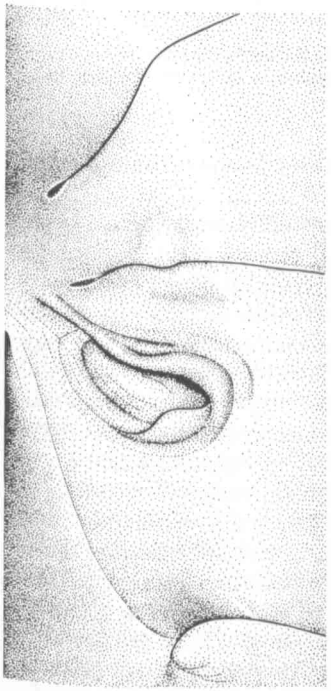

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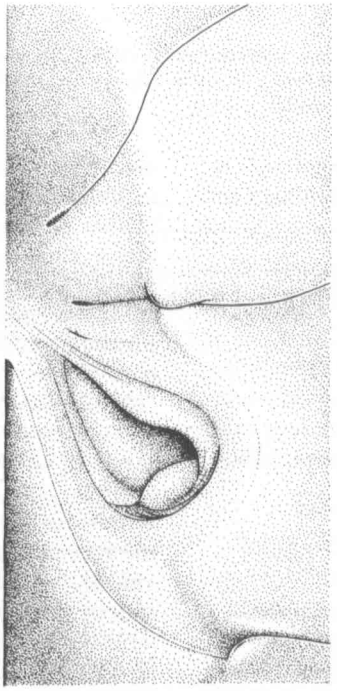

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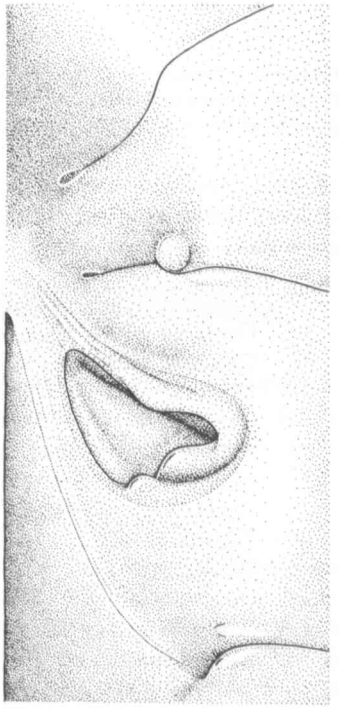

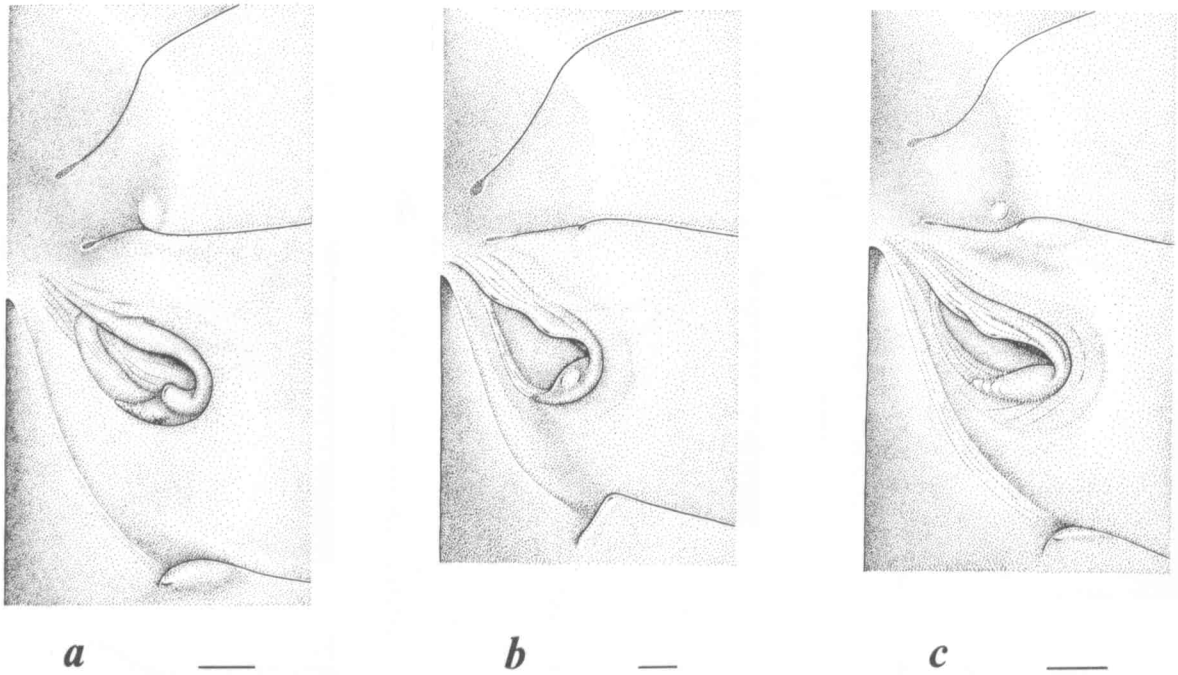

FIGURE 23.—Female, left gonopore and portion of thoracic sternites IV-VII: **a,** *Callinectes latimanus* Rathbun, Plage de Pointe Noire, Congo; **b,** *C. sapidus* Rathbun, typical form, USNM 30567, Cameron, La.; **c,** *C. sapidus* Rathbun, acutidens form, USNM 99848, Roca Arroyo Balizas [= Arroyo de Valizes?], Uruguay. Scales = 1 mm.

Measurements of elements in the broad apron-shaped abdomen of sexually mature females included:

13. Greatest width of segment 2.
14. Greatest width of segment 3.
15. Greatest width of segment 5.
16. Median length of segment 5.
17. Greatest width of segment 6.
18. Median length of segment 6.
19. Median length of segment 3 (proximal edge) to tip of telson.
20.* Length of telson.
21.* Width of telson.

Analysis of selected nonsexual characters.—Study showed that some of these measurements were more valuable than others at the specific level and 11 (marked with asterisks), generally considered useful in verbal description, were chosen for cluster analysis. Unfortunately, they neither clustered as species nor as species groups when analyzed. Results indicated that specific morphological differences in this genus are based on characters other than, or in addition to, those measured and analyzed in this test. Measurements therefore were judged to have limited value in identification.

This finding is supported strongly by evidence other than results of the attempt at cluster analysis. Female *Callinectes* attain sexual maturity in a terminal metamorphic molt. Males attain an adult conformation at sexual maturity but may continue to molt at reduced frequency. Van Engel (1958) and others have shown that *C. sapidus* females molt 18 to 20 times in attaining maturity, males 18 or 19 before becoming mature and 3 or 4 times beyond that stage. The range of variation in number of molts may be much greater than this, for both dwarf and giant sexually mature individuals are known. Allometric changes accentuated at the two ends of this continuum attest to wide variability in form. Estévez (1972) emphasized variability in *C. arcuatus* and *C. toxotes*. Tables 1 and 2 show means, standard deviation, and sample size for selected characters from adult male and female *Callinectes* species. For almost all species the coefficient of variation ($V = 100s/x$) is high for all characters shown, an indication that morphometrically there is great variation in the group. Simpson, Roe, and Lewontin (1960:91) stated that V values greater than 10

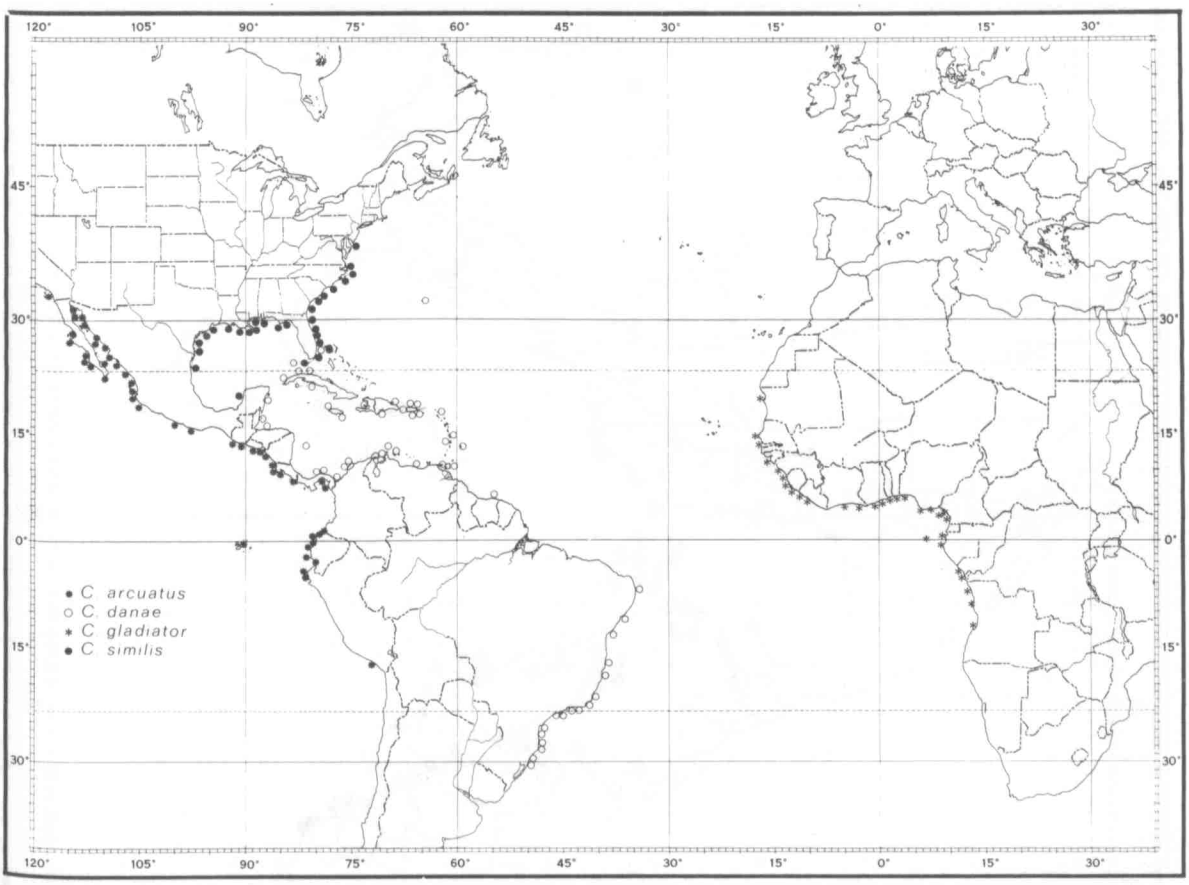

FIGURE 24.—Respective geographic distributions of *Callinectes arcuatus* Ordway, *C. danae* Smith, *C. gladiator* Benedict, and *C. similis* Williams in the Atlantic and eastern Pacific oceans based on specimens studied and verified published records.

indicate that a sample is not reasonably unified. Throughout the genus great variation in morphometry of the body makes keys for identification involving proportions almost impossible to devise unless qualified by exceptions.

From a different viewpoint, Stephenson et al. (1968) applied methods of numerical analysis to 44 species and putative subspecies of *Portunus* (mainly from America, but certain Indo-Pacific species for comparison), *Callinectes, Arenaeus,* and *Scylla,* relying on presence or absence of 57 characters to build up a data matrix from which character assessments could be made. The method nicely demonstrates that *Callinectes* is a very homogeneous group, but the internal relationships implied do not correspond harmoniously with classical interpretation. This is not a matter of conflict, but simply one of judgment, the method seeming to be limited by interpretation of character states, weighting being one serious problem and choice of characters another. Were the analysis run with different emphases, results might reflect those to some extent.

LARVAL DEVELOPMENT

Among *Callinectes* species, larval development of only *C. sapidus* and *C. similis* has been determined by hatching eggs and rearing in the laboratory. Costlow, Rees, and Bookhout (1959) and Costlow and Bookhout (1959) described seven zoeal stages, atypically an eighth, and a megalopa for *C. sapidus*. Larvae and megalopae of the two species are apparently almost identical, the stages being similar to those of other portunids (Costlow and Bookhout, pers. commun.). Importantly, the megalopae of *Callinectes* lack an internal carpal spine on the chelipeds whereas megalopae of *Portunus* have a well-developed spine on this member

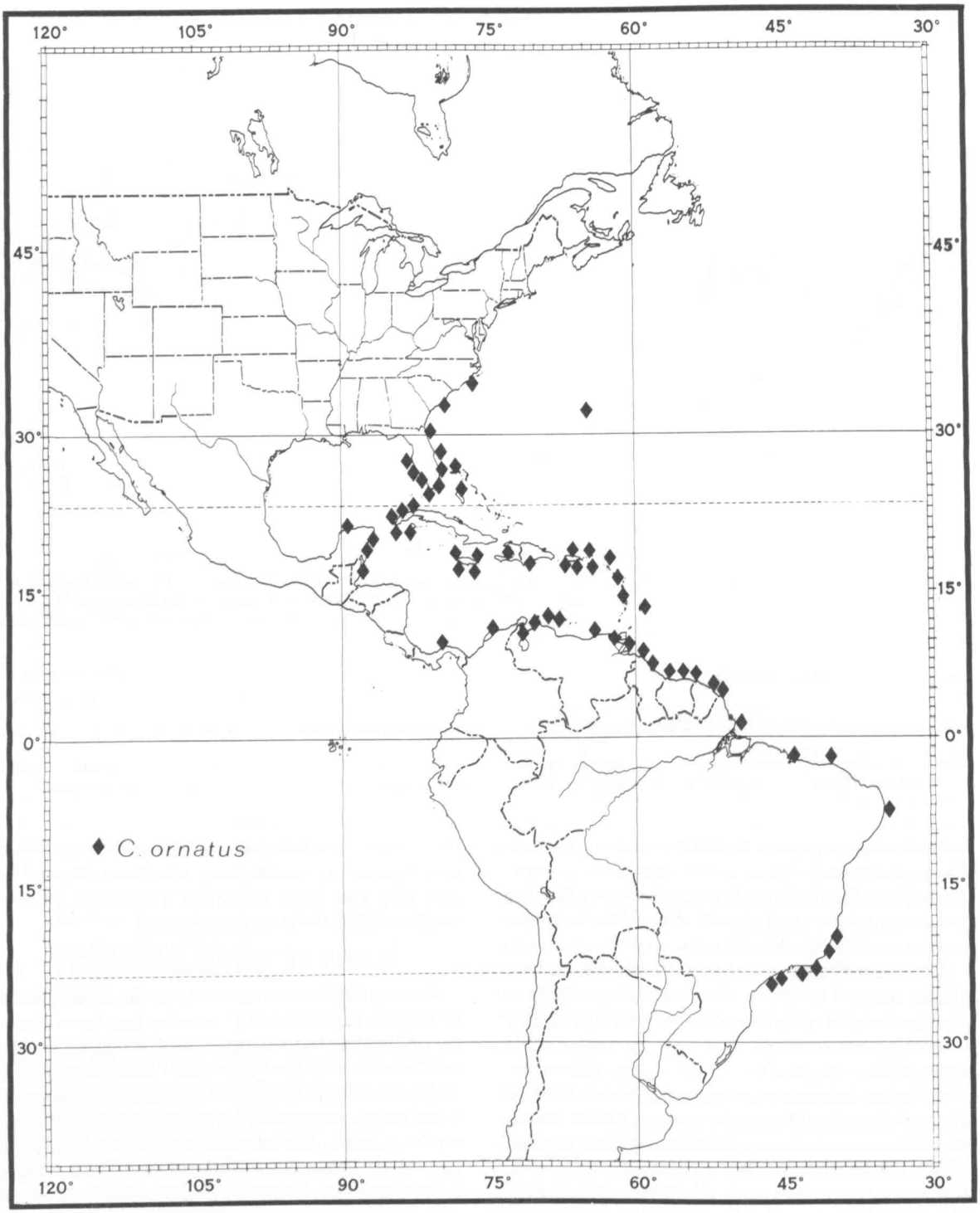

FIGURE 25.—Geographic distribution of *Callinectes ornatus* Ordway in the western Atlantic Ocean based on specimens studied and verified published records.

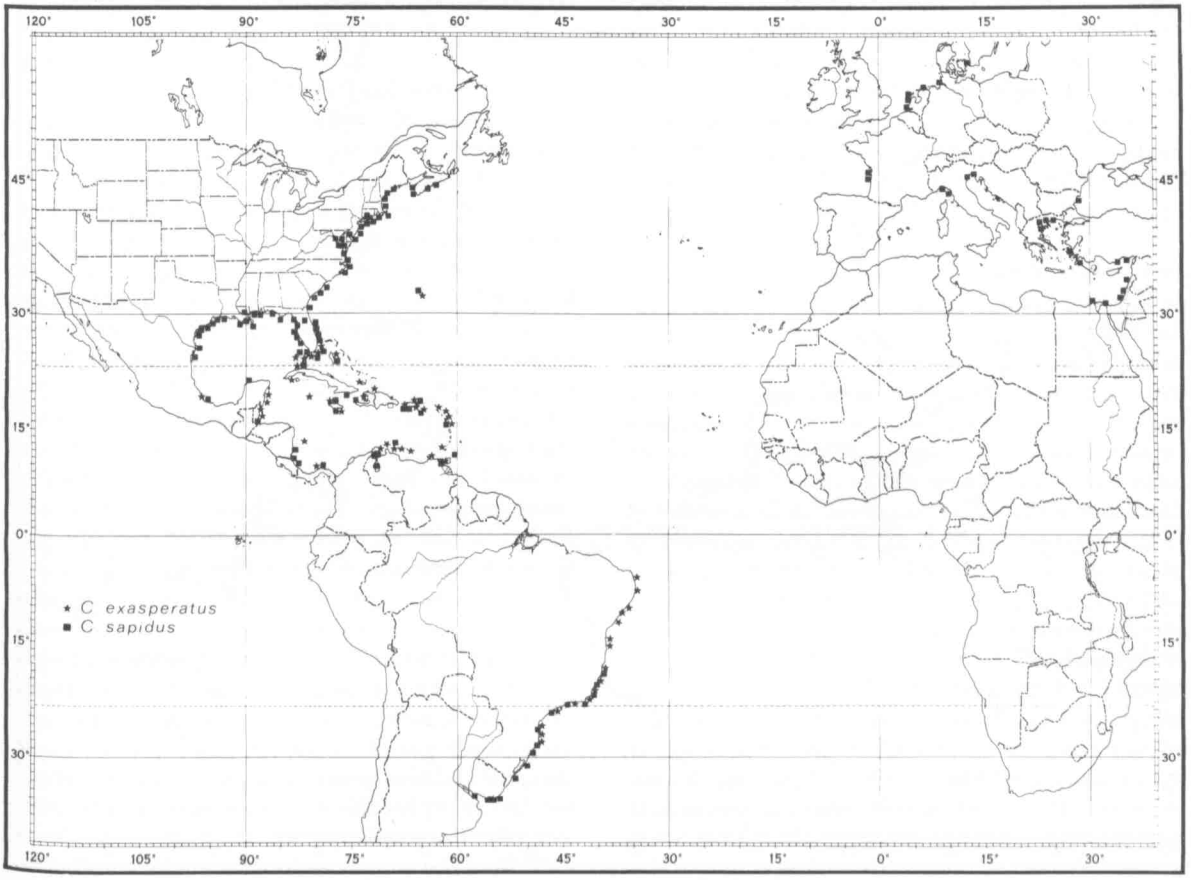

FIGURE 26.—Respective geographic distributions of *Callinectes exasperatus* (Gerstaecker) and *C. sapidus* Rathbun in the western Atlantic Ocean with introductions to the eastern Atlantic and Mediterranean Sea, based on specimens studied and verified published records.

(Williams, 1971), showing one of the generic distinctions at an early phase of development.

Costlow (1965, 1967) followed the early work on larvae with a series of experimental studies showing that development of *C. sapidus* is subject to variation both in staging and duration. Total development time of *C. sapidus* from hatching of egg to transformation of the megalopa to first crab stage has varied from 31 to 69 days in the laboratory in various combinations of salinity and temperature, but duration of individual stages is variable even in a single salinity-temperature combination. The stages are constant enough, however, that Van Engel (1958), Cargo (1960), Nichols and Keney (1963), Pinschmidt (1964), Tagatz (1968), More (1969), and Williams (1971) were able to identify zoeae or megalopae from nearshore oceanic and estuarine plankton. In nature as in experiments, development time may be extended by environmental conditions. Megalopae have been found throughout the year in North Carolina estuaries.

FOSSIL RECORD

Hard parts of portunids most abundant as fossils in Tertiary formations in eastern North and Middle America are portions of the chelipeds, usually the dactyls and portions of the propodi. Some deposits contain remains of carapaces and/or sterna, occasionally almost whole exoskeletons of crabs, but any of the remains are scarce. It was largely on the basis of cheliped fragments that Rathbun (1919a, b, 1926, 1935) listed and described *Callinectes* species from formations attributed to ages as old as the Oligocene. Withers (1924) described a fragment of chela from the Eocene of Jamaica as *Callinectes*, and Blake (1953) added information

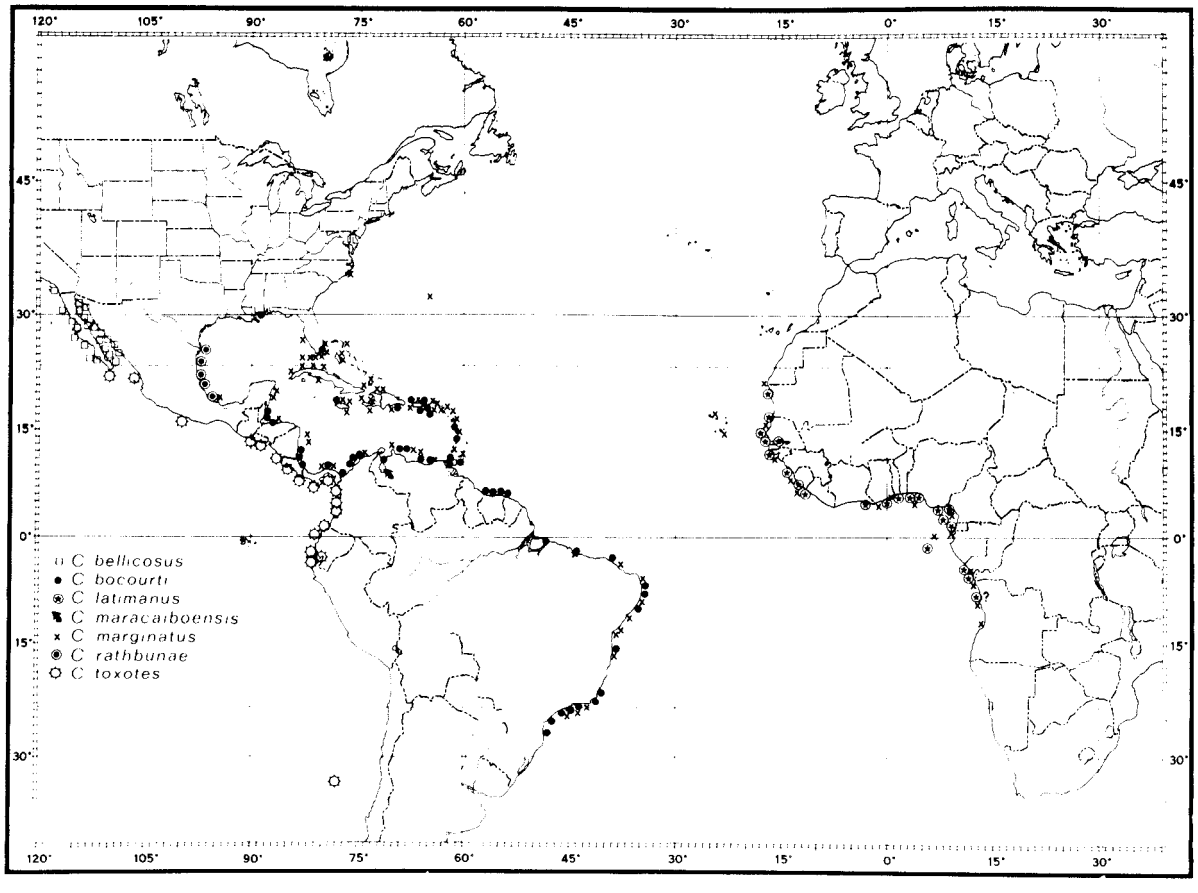

FIGURE 27.—Respective geographic distributions of *Callinectes bellicosus* Stimpson, *C. bocourti* A. Milne Edwards, *C. latimanus* Rathbun, *C. marginatus* (A. Milne Edwards), *C. maracaiboensis* Taissoun, *C. rathbunae* Contreras, and *C. toxotes* Ordway in the Atlantic and eastern Pacific oceans based on specimens studied and verified published records.

on remains from the Quarternary. Williams (1965) uncritically accepted determinations for Atlantic and Gulf Coastal Plain records from the Miocene to Recent, but study of this material, even though its interpretation is beyond the scope of the present paper, leads to an attitude of restraint.

The characters by which *Callinectes* is distinguished from other portunid genera, shape of male abdomen and lack of an internal carpal spine on the chelipeds, are rarely evident in the fossil material, the only undoubted specimens (treated in species accounts below) coming mainly from Pleistocene and a few Miocene horizons. All others studied lack characters for positive first order identification and therefore their determinations rest on secondary features such as shape of the chelae or other nondiagnostic parts of the body. Although the numerous cheliped fragments most resemble these parts in living species of *Callinectes,* they also resemble those of *Ovalipes* and certain *Portunus,* especially the large *P. pelagicus* and *P. sanguinolentus* distributed widely in the Indo-Pacific region today (Stephenson, 1962), as well as the robust *Arenaeus cribrarius* and *A. mexicana,* respectively from Atlantic and Pacific shores of the Western Hemisphere (Rathbun, 1930). A single propodal finger of a form attributed to *P. sayi* reported from the Miocene of Florida (Rathbun, 1935) greatly resembles other remains attributed to *Callinectes.* Margins of warmer seas of early and mid Tertiary (Ekman, 1953; Hazel, 1971) could have favored such forms or others like contemporary *Scylla* of Indo-Pacific waters, fossil representatives of which were described [=?] by Rathbun (1919b, 1935) from the Miocene of Florida, Dominican Republic, and Mexico. Judging by ecological requirements of living species, *Callinectes* would have been well

adapted to such an environment, but fossil evidence for its existence in the Paleocene remains indirect.

There are constant structural differences between the early fossil series and modern *Callinectes*. The palms of chelae of *C. jamaicensis* Withers, 1924 (Eocene), *C. alabamensis* Rathbun, 1935 (Oligocene), *C. declivis* Rathbun, 1919a (lower Miocene), and *C. reticulatus* Rathbun, 1919a (Oligocene-lower Miocene) are short and faceted more like *Callinectes* than other living genera of portunids, but they are relatively thinner than in living members of the genus. The fingers in these early forms have length-width proportions and tooth arrangements that resemble modern *C. sapidus*, but the tooth rows are relatively narrower proximally on propodal fingers and less inclined toward development of a molariform crushing surface. Of the four external facets on the palm, the upper mesial one in the fossil series is always inclined downward toward the inner surface in major chelae whereas in modern *Callinectes* species it is nearly horizontal in the major chela and noticeably inclined downward only in the minor one; moreover, the third or dorsolateral facet is relatively wider in living *Callinectes* species than in any of the early fossils. Compression and erosion may have altered relief but not uniform angle of inclination of facets in the fossils. Generally, fossils older than early-mid Miocene attributed to *Callinectes* have less powerful chelae than living species and these differences in structure seem significant enough to warrant generic separation of the two series when more material comes to light.

MODERN DISTRIBUTION

Confined almost exclusively to shallow, often brackish coastal waters as adults, the genus *Callinectes* is represented by six species distributed (Figures 24-27) around the Caribbean Sea and southward to southern Brazil: *C. marginatus, ornatus, danae, exasperatus, bocourti,* and *sapidus*. A seventh species, *C. maracaiboensis*, is localized in estuaries of Venezuela. One of these species, *C. marginatus*, bridges the Atlantic, ranging with *C. gladiator* and *C. latimanus* from Mauritania to Angola in West Africa. It also reaches the Cape Verde Islands. Only three species occur in the Gulf of Mexico, exclusive of the southeastern part off Florida: *C. rathbunae*, an isolated relative of *C. bocourti* in the western Gulf, *C. similis*, an essentially Carolinian form ranging northward along the coast, and *C. sapidus*, which ranges far beyond, occasionally to the Maritime Provinces of Canada. In the eastern Pacific, disregarding distant island occurrences, *C. arcuatus* is distributed from extreme southern California to Peru, sharing its range with *C. bellicosus* in the region of Baja California and with *C. toxotes* from there south.

If one relies on structure of male first gonopods alone for estimation of morphological similarity, the following zoogeographical associations emerge. The set of species with short first gonopods (*C. marginatus, gladiator, ornatus,* and *similis*) has separate eastern and western Atlantic components, and one member on both sides of the tropical Atlantic. The second set with longer first gonopods (*C. arcuatus, bellicosus, danae,* and *exasperatus*) occurs in the tropical western Atlantic and eastern Pacific. The third set with quite long first gonopods (*C. toxotes, bocourti, rathbunae, maracaiboensis, latimanus,* and *sapidus*) has representatives in all regions. Distributions of all species fit patterns accepted by Ekman (1953:30, ff.) as representative of many along the tropical-subtropical Atlantic and east Pacific coasts, but one, *C. sapidus*, has a latitudinal range that seems to exceed this pattern. In this species, development of a northern and southern form may be in progress.

The amphi-Atlantic distribution of *C. marginatus*, records of *C. exasperatus, marginatus, ornatus,* and *sapidus* from Bermuda, *C. arcuatus* from the Galápagos Islands, *C. toxotes* from Juan Fernández, as well as less removed northern marginal records for essentially southern species along the North American continent (*C. bocourti* in southern Florida and Mississippi; *C. marginatus* in North Carolina; *C. similis* in New Jersey; *C. sapidus* in Nova Scotia) all point to extensions of range by larval transport in currents (Verrill, 1908b; Garth, 1966). Investigators working with larval stages (reviewed in Williams, 1971) suggest that larvae and megalopae can move considerable distances; zoeae have been found off St. Johns River, Fla., at stations up to 160 km, and megalopae in the same area up to 128 km from shore. In Chesapeake Bay and Pamlico Sound, N.C., megalopae have been found 170 and 100 km respectively from presumed points of entry to the estuarine systems. Most of this off-and-onshore movement of larval stages appears to be a homeostatic developmental feature in the life

histories of the species. Among spiny lobsters, whose larvae are seemingly better fitted for temporary pelagic existence than crab larvae because of leaflike shape, up to 6 mo or greater duration of larval life occurs (Lewis, 1951; Austin, 1972). Phyllosomas of some spiny lobsters are rarely found beyond the latitudinal geographic limits of the coastal adult population. George and Main (1967) attributed this result to behavioral responses of the larvae, vertical migration, etc., within prevailing current systems which act to preserve integrity of distribution, but Austin (1972) held open the idea of long distance transport over considerable lengths of time. Some dispersal of larvae at the fringes of less pelagic *Callinectes* populations obviously occurs, but the wanderers are at a competitive disadvantage in establishing temporary range extensions. Nevertheless, larval dispersal of *Callinectes* coupled with movement of adults, judged to be minor except within an estuarine system (Fischler and Walburg, 1962; Tagatz, 1968), seems to assure genetic continuity over broad areas.

If one accepts the tenet that the center of evolution for a group contains the largest number of species, Neotropical Atlantic American shores seem to be the primary center in which the genus *Callinectes* developed and from which it radiated. Fossil evidence indicates that this radiation took place in the Tertiary, a period of time in which land-water relationships of that region diverged widely from their positional and areal extent today (Woodring, 1966, 1971). Olsson (1972) regarded the Miocene as the time when Panamanian molluscan biotas related to those of today evolved under conditions of general subsidence and when parts of present day Central America were reduced to an archipelago of large islands separated by straits between the Caribbean and east Pacific. Ekman (1953), Fell (1967), and others regarded the marine fauna that evolved in this region as an impoverished western outpost of the Tethyan fauna, related most closely to that of the eastern Atlantic and southern Europe. Though the tropical Atlantic and neighboring east Pacific regions both shared in the radiation of *Callinectes*, the conservatism of this offshoot contrasts remarkably with the far richer divergence of its parent stock. Stephenson (1962) considered the Indo-Pacific, with 175 living species, as the germinal center for the Portunidae. It seems reasonable to view *Callinectes* as a portunid group evolving at the geographic limits of the family, specializing in occupation of estuaries, and paralleling in many ways the heavy-bodied Indo-Pacific *Scylla serrata* (Stephenson, 1962).

If *Callinectes* evolved mainly in the Caribbean faunal province, the present distribution of species in essentially three isolated centers raises questions concerning dispersal. Separation of the east Pacific from the Caribbean by elevation of the Panamanian isthmus near the close of the Tertiary understandably isolated certain elements of the genus and may have promoted further radiation, but close relationship of species in the two areas is emphasized by an obvious geminate pair —*danae-arcuatus*—similar in a number of morphological features, which occurs today on east and west coasts of Middle and South America. Separation of the east and west Atlantic fragments of the genus is harder to resolve because not only does one species bridge this gap, but two species groups (short and long first gonopods) are represented on both sides of the ocean, seemingly specialized along the same general lines. Which is the ancestral stock? Were pelagic larvae the mechanism of transport, as Fell (1967) proposed for analogous but cold-tolerant echinoderms, perhaps aided by island stepping stones in the mid Atlantic? (Fell rejected continental drift as a plausible explanation for transport, an idea more acceptable today than it was in 1967, but involving a time span greater than concerned here [McKenzie, 1972].) Length of life of the larvae of most species of *Callinectes* under pelagic conditions remains unknown. West Africa is upstream from the Western Hemisphere in prevailing equatorial surface currents. It seems unlikely that the larvae could move counter to this current from a center in the west or survive the much longer (and today, colder) northern transit from the West Indies via the Gulf Stream beyond Bermuda to the Azores, Canaries, and finally to west Africa. So far as known, all *Callinectes* utilize estuaries during part of their lives. Populations on small islands may be nonbreeding, transitory implants, or unsuccessful breeders. Means and paths of long-distance transport, and effectiveness of transients in colonization, among these forms will remain unknown until more data are collected.

Finally, the clustering of species by numerical methods employed by Stephenson et al. (1968) does not reflect the three groups suggested by first gonopod types, but it does support classical interpretation setting *C. marginatus* and perhaps *C. gladiator* aside as the most peripheral morpholog-

ically. It suggests that the three west American species, *C. arcuatus, bellicosus,* and *toxotes* differ appreciably from each other and that they arose from eastern American ancestors. It also supports the idea that most of the postulated "central" species occur in the Atlantic and that "it is conceivable that the group originated from an eastern American ancestor." Beyond this the results are less compatible with conclusions reached here, but the analysis was done without including *C. similis* which may be a linking form that would have changed the interpretation.

SPECIES ACCOUNTS

In the species accounts that follow, the synonymies include only citations of works that primarily are concerned with descriptive, taxonomic, or zoogeographic information. The reason for this limitation is that commercially valuable species often have a voluminous literature. All inclusive synonymies for them become so unwieldy that the real purpose—taxonomic history of the species—becomes obscured. The descriptions also are limited because full descriptions are elsewhere in the literature.

Two features included in the descriptions need clarification. The term "metagastric area" is employed for the central trapezoidal area of the carapace in the sense Chace and Hobbs (1969) used it rather than the term "intramedial area" employed by others (cf. Rathbun, 1930; Williams, 1966). Strictly speaking, this region of the carapace includes the undifferentiated metagastric (over 90%) and at least part of the shortened urogastric (less than 10%) areas, but for all practical purposes the first term is sufficiently explicit. The number of anterolateral teeth in *Callinectes* is nine (Rathbun, 1930), but the first of the series is also known as the outer orbital tooth and the last as the lateral spine. This partition of the series is observed here. The first and last teeth are always named and the small teeth are numbered.

Abbreviations adopted for institutions loaning study material are: AHF, Allan Hancock Foundation, University of Southern California; AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; MCZ, Museum of Comparative Zoology, Harvard; MNB, Museu Nacional, Rio de Janeiro; MNHNP, Museum National d'Histoire Naturelle, Paris; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SADZ-B, Secretaria da Agricultura, Departamento Zoologia, São Paulo; UNC-IMS, University of North Carolina, Institute of Marine Sciences, Morehead City; USNM, National Museum of Natural History, Washington, D.C.; YPM, Peabody Museum of Natural History, Yale University, New Haven, Conn.

Supplementary literature records are occurrences not represented by specimens studied, but accepted on basis of supporting data.

GENUS *CALLINECTES* STIMPSON, 1860

Callinectes Stimpson, 1860, p. 220 [92].- Rathbun, 1896, p. 349 (revision).- 1921, p. 394 (review of African species).- 1930, p. 98 (review of Western Hemisphere species).- not Chen, 1933, p. 95 (=*Portunus*?).- Monod, 1956, p. 204 (review of African species).- Garth and Stephenson, 1966, p. 42 (review of eastern Pacific species).

Description.—Portunid crabs lacking an internal spine on carpus of chelipeds. Abdomen of males broad proximally, narrow distally, roughly T-shaped; first segment broad, almost hidden; second segment broad, slightly overlapping coxae of fifth pereopods at each side; third-fifth segments fused and tapering sinuously from broad third to distally narrow fifth; sixth segment elongate and narrow; telson ovate with acute tip. Abdomen of females exhibiting two forms: immature females with abdomen triangular from fourth segment to tip of telson, segments fused; mature females with abdomen broadly ovate (excluding telson), segments freely articulated; first segment almost hidden; second and third segments slightly overlapping coxae of fifth pereopods at each side; fifth and sixth segments with greatest sagittal length; sixth segment narrowing distally in irregular broad arc to articulate with triangular telson. Abdomen and telson of both sexes reaching anteriorly beyond suture between thoracic sternites IV and V.

Type species.—*Callinectes sapidus* Rathbun, 1896, by designation of International Commission of Zoological Nomenclature (1964:336).

Gender.—Masculine.

Number of species.—Fourteen, which may be distinguished by the following keys.

KEY TO SPECIES OF *CALLINECTES* (EXCLUDING JUVENILES)

Figures 3-17

1. Front with two prominent, broad based, triangular teeth between inner orbitals; each with or without rudimentary submesial tooth on mesial slope (Atlantic; Western Hemisphere, introduced in Europe) ..... *sapidus.*

1′. Front with four teeth between inner orbitals, or two prominent lobulate or narrowly triangular teeth separated by a nearly plane space often bearing a pair of rudimentary submesial teeth 2

2. Submesial pair of frontal teeth well developed and more than half as long as lateral pair (measuring from base of lateral notch between teeth) 3

2′. Frontal teeth decidedly unequal in size, submesial pair no more than half as long as lateral pair (measuring from base of lateral notch between teeth), or vestigial 8

3. Four frontal teeth reaching nearly common level 4

3′. Submesial frontal teeth definitely falling short of lateral pair 7

4. Four frontal teeth lobulate, not triangular (Pacific; Baja California–Juan Fernández) *toxotes.*

4′. One or both pairs of frontal teeth triangular 5

5. Four frontal teeth with rather rounded tips, lateral pair more broadly triangular than submesial pair and with mesial side having more oblique slope than lateral side .. 6

5′. Four frontal teeth acute, lateral pair usually broader than submesial pair (Atlantic; Mexican Gulf coast) ..... *rathbunae.*

6. Anterolateral teeth trending forward, their anterior margins shorter than posterior; vestiges of reddish color usually persisting in preserved specimens (except long-preserved ones); distal border of sixth abdominal segment in mature females broadly triangular (Atlantic; Caribbean-South America) ..... *bocourti.*

6′. Anterolateral teeth directed outward, their tips acuminate and margins shouldered at least in anterior portion of row; vestiges of greenish color usually persisting in preserved specimens (except in long-preserved ones); distal border of sixth abdominal segment in mature females semiellipsoid (Atlantic; Venezuelan estuaries) ... *maracaiboensis.*

7. Granules on ridges and crests of chelae coarse and well separated (Atlantic; Caribbean-South America) ..... *exasperatus.*

7′. Granules on ridges and crests of chelae moderate to fine and closely crowded, often worn smooth in adults (Atlantic; West Africa) ..... *latimanus.*

8. Carapace remarkably smooth, lines of granules visible but barely perceptible to touch (except epibranchial line variably prominent) 9

8′. Carapace not so smooth, scattered granules and lines of granules quite evident to sight and touch 10

9. Submesial pair of frontal teeth vestigial (Pacific; Baja California and Golfo de California) *bellicosus.*

9′. Submesial pair of frontal teeth small but definitely formed (Atlantic; United States-Gulf of Mexico) ..... *similis.*

10. Carapace coarsely granulated; all anterolateral teeth except first two curved forward, without shoulders (Atlantic; Bermuda-Florida–South America-West Africa) .... *marginatus.*

10′. Carapace finely granulated; only last or last two anterolateral teeth curved forward, remainder with shoulders 11

11. Submesial pair of frontal teeth absent or vestigial (Atlantic; Bermuda-North America-South America) ..... *ornatus.*

11′. Submesial pair of frontal teeth never vestigial, but no more than half length of lateral pair 12

12. Lateral spine almost always less than three times length of preceding anterolateral tooth; tips of anterolateral teeth forming a decided arc; males with distal portion of first gonopods almost straight 13

12′. Lateral spine almost always three or more times length of preceding anterolateral tooth; at least second to fifth anterolateral teeth with tips in a nearly straight line; males with distal portion of first gonopods S-curved (Atlantic; West Africa) ..... *gladiator.*

13. First gonopods of mature males with subterminal dorsal setae never more than four in number, often inconspicuous or missing (Atlantic; Caribbean-South America) ..... *danae.*

13′. First gonopods of mature males with subterminal dorsal row of setae numbering more than four (Pacific; Southern California-Peru; Galápagos Islands) ..... *arcuatus.*

KEY TO MATURE OR NEARLY MATURE MALE *CALLINECTES* BASED PRIMARILY ON FIRST GONOPODS

Figures 18-21

1. Tips of gonopods falling well short of suture between thoracic sternite VI and mesially expanded sternite VII 2

1′. Gonopods reaching to, almost to, or beyond suture between thoracic sternite VI and mesially expanded sternite VII 5

2. Gonopods well separated from each other, never touching or crossed 3

2′. Gonopods overlapping each other, often crossed 4

3. Gonopods slender distally, nearly straight, tips bent slightly mesad (Atlantic; United States-Gulf of Mexico) ..... *similis.*

3′. Gonopods fairly stout distally, angled toward midline, then abruptly bent forward in a short slender terminal extension (Atlantic; Bermuda-Florida-South America-West Africa) ..... *marginatus.*

4. Tips of gonopods lanceolate, continuing in line with shaft, portion proximal to tip armed with short backward pointing spines quite visible at low magnification (Atlantic; Bermuda-North America-South America) ..... *ornatus.*

4′. Tips of gonopods not lanceolate, curved mesad, spines on S-curved shank exceedingly small at low magnification (Atlantic; West Africa) ..... *gladiator.*

5. Tips of gonopods curved abruptly mesad (Atlantic; Caribbean–South America) .... *exasperatus.*

5′. Tips of gonopods not curved abruptly mesad 6

6. Slender portion of gonopods almost straight, minutely spined (under magnification), tips almost always bent ventrolaterally, never extending beyond abdominal locking tubercle on thoracic sternite V 7

6′. Slender portion of gonopods definitely curved or sinuous, variously spined, tips never bent ventrolaterally 8

7. Gonopods with subterminal dorsal setae never more than four in number, often inconspicuous or missing (Atlantic; Caribbean–South America) ..... *danae.*

7′. Gonopods with subterminal dorsal row of setae numbering more than four (Pacific; Southern California-Peru; Galápagos Islands) ..... *arcuatus.*

8. Tips of gonopods reaching well beyond abdominal locking tubercle on thoracic sternite V 9

8′. Tips of gonopods not reaching beyond abdominal locking tubercle on thoracic sternite V (Pacific; Baja California and Golfo de California) ..... *bellicosus*

9. Slender portion of gonopods with spinules small under magnification and most dense near middle, absent near tip (Pacific; Baja California-Juan Fernández) ..... *toxotes.*

9′. Slender portion of gonopods with spinules readily visible at low magnification and distributed to tip 10

10. Gonopodal spines arranged in a broad dorsolateral band 11

10′. Gonopodal spines arranged in a single, rather uneven dorsolateral row (a few tiny spines lying outside row) (Atlantic; Western Hemisphere, introduced in Europe) ..... *sapidus.*

11. Tips of all frontal teeth reaching same level 12

11′. Submesial pair of frontal teeth definitely shorter than lateral pair (Atlantic; West Africa) *latimanus.*

12. Four frontal teeth with rather rounded tips, lateral pair more broadly triangular and with mesial side having more oblique slope than lateral side 13
12'. Four frontal teeth acute, lateral pair usually broader than submesial pair (Atlantic; Mexican Gulf coast) ..... *rathbunae.*
13. Anterolateral teeth trending forward, their anterior margins shorter than posterior; vestiges of reddish color usually persisting in preserved specimens (except long-preserved ones); (Atlantic; Caribbean-South America) ..... *bocourti.*
13'. Anterolateral teeth directed outward their tips acuminate and margins shouldered at least in anterior portion of row; vestiges of greenish color usually persisting in preserved specimens (except in long-preserved ones); (Atlantic; Venezuelan estuaries) ..... *maracaiboensis.*

CALLINECTES MARGINATUS (A. MILNE EDWARDS)

Figures 3, 18a, 20a, 22b, 27

Neptunus marginatus A. Milne Edwards, 1861, p. 318, pl. 30, fig. 2 (syntypes: 3 ♀ dry, MNHNP 895-1S, 895-2S, 896, Gabon).

Callinectes larvatus Ordway, 1863, p. 573 [8] (syntypes: 1 ♂, MCZ 5147, Tortugas, Fla., USA; 3 ♂, 1 ♀, MCZ No. 5151, Key West, Fla., USA; 3 ♂ MCZ 5152, Bahamas; 1 ♂, 1 juv ♀ [not ♂], MCZ 5155, Jeremie, Haiti).- Smith, 1869, p. 9.- A. Milne Edwards, 1879, p. 225 (var. of *C. diacanthus*).- Rathbun, 1896, p. 358, pl. 18, pl. 24, fig. 5; pl. 25, fig. 4; pl. 26, fig. 4; pl. 27, fig. 4.- Rankin, 1898, p. 232.- Young, 1900, p. 188 (var. of *C. diacanthus*).- Doflein, 1904, p. 99.

Neptunus diacanthus.- Brocchi, 1875, pl. 16, fig. 76 [?].- de Man, 1883, p. 150.- Pfeffer, 1890, p. 5, pl. 1, figs. 5, 6.

Callinectes africanus A. Milne Edwards, 1879, p. 229 (var. of *C. diacanthus*) (syntypes: MNHNP, Cape Verde Islands, not found in 1968).- A. Milne Edwards and Bouvier, 1900, p. 71 (var. of *C. diacanthus*) (not pl. 4, fig. 5 = *C. sapidus*).

Callinectes larvatus var. *africanus?* Benedict, 1893, p. 537.

Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part; specimen b, Cuba).

Callinectes marginatus.- Rathbun, 1897, p. 149.- 1900a, p. 291.- 1900b, p. 142.- 1901, p. 48.- 1921, p. 395, text-fig. 2, pl. 19, fig. 1; pl. 20, fig. 1.- 1930, p. 123, figs. 15e, 16d, 17d, 18c, pl. 53.- 1933, p. 49.- 1936, p. 383.- de Man, 1900, p. 41, pl. 1, fig. 5 (juv ♀, not ♂).- Nobili, 1906, p. 305.- Gruvel, 1912, p. 3, 6, pl. 2, fig. 1.- Balss, 1921, p. 58.- Odhner, 1923, p. 21.- Boone, 1927, p. 32.- Contreras, 1930, p. 235, fig. 6.- Vilela, 1949, p. 59.- Capart, 1951, p. 134, fig. 48.- Chace, 1956, p. 154.- Chace and Hobbs, 1969, p. 131, fig. 37d.- Monod, 1956, p. 208, figs. 238, 239.- Rossignol, 1957, p. 82.- Guinot and Ribeiro, 1962, p. 48.- Forest and Guinot, 1966, p. 65.- Taissoun, 1973, p. 39, figs. 4A, 5B, photo 7.

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Callinectes marginatus var. *larvatus*.- Verrill, 1908a, p. 368, text-fig. 22b, pl. 18, fig. 1.

Description.—Carapace (Figure 3) bearing four frontal teeth, submesial pair no more than half length of lateral pair. Central trapezoidal (metagastric) area short, anterior width about 2.4 times length, posterior width about 1.5 times length. Anterolateral margins arched slightly; anterolateral teeth exclusive of outer orbital and lateral spine without shoulders, usually trending forward and anterior margins of all except first two concave, last two teeth spiniform. Lateral spine moderately long and slender. Surface coarsely granulate anterior to prominent epibranchial line and over mesobranchial regions, more finely and closely granulate on proto- and mesogastric areas, prominent branchial lobes, and especially on cardiac lobes; posterior and posterolateral margins smooth.

Chelipeds with smoothly granulate prominent ridges on propodi and reduced ones on carpi; fingers compressed but broadened dorsoventrally producing a pointed spatulate shape; major chela with usual enlarged proximal tooth on dactyl opposing propodal molariform complex, propodus often with decurved lower margin.

Male abdomen and telson narrow, reaching slightly beyond suture between sternites IV and V; telson about 1.8 times longer than wide; sixth

TABLE 1.—Mean measurements ($\bar{x}$) in mm, with standard deviations (s) and sample sizes (N), of selected characters for adult male *Callinectes*. Refer to Figures 1 and 2 for illustration of measurements.

Measurements	*arcuatus*			*bellicosus*			*bocourti*			*danae*			*exasperatus*			*gladiator*			*latimanus*		
	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N
Length	42.3 ±	7.4	74	58.5 ±	17.0	28	55.0 ±	9.0	46	46.5 ±	5.8	84	52.6 ±	7.0	54	35.0 ±	6.3	23	53.9 ±	10.4	27
Width																					
incl. lat. spines	94.0	18.7	75	118.3	33.7	28	109.3	20.0	45	108.7	14.7	84	101.6	14.0	54	87.0	15.4	23	112.8	23.2	26
base lat. spines	74.5	13.9	75	104.5	31.0	28	94.5	15.7	45	83.4	10.7	84	89.2	12.2	54	65.3	11.7	23	96.3	22.6	27
Max. height	24.6	4.5	74	33.4	9.5	25	31.9	5.2	45	25.8	3.4	84	31.6	4.4	54	20.8	4.2	23	32.1	12.0	27
Metagastric																					
ant. width	17.18	3.08	74	24.59	7.22	25	19.73	3.48	46	18.91	2.48	84	21.40	2.96	54	14.4	2.70	23	20.10	4.28	27
length	7.08	1.38	74	8.97	2.85	25	9.95	1.74	46	7.71	1.12	84	9.03	1.39	54	5.52	1.10	23	9.74	2.12	27
post. width	9.41	1.72	74	14.16	3.96	26	10.42	1.85	46	10.92	1.50	84	11.25	1.66	54	8.34	1.65	23	10.35	2.13	27
Telson																					
length	5.12	0.89	66	6.97	1.88	27	9.82	1.84	44	5.51	0.83	82	6.63	1.04	52	4.39	0.72	23	9.72	1.88	26
width	3.37	0.51	67	4.57	0.92	27	4.86	0.61	44	3.73	0.62	81	4.40	0.82	52	2.73	0.41	23	5.13	0.83	26

Measurements	*maracaiboensis*			*marginatus*			*ornatus*			*rathbunae*			*sapidus*			*similis*			*toxotes*		
	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N
Length	57.8 ±	7.8	11	42.6 ±	6.4	82	41.6 ±	7.8	81	52.8 ±	5.2	5	63.2 ±	13.9	65	43.3 ±	5.8	26	71.3 ±	11.6	24
Width																					
incl. lat. spines	113.7	16.8	11	93.8	14.7	82	91.2	16.4	80	112.8	13.4	5	142.8	35.2	65	97.6	13.1	26	153.1	27.5	24
base lat. spines	97.8	12.7	11	77.5	12.5	82	72.5	14.0	81	92.2	9.4	5	115.1	26.3	65	75.7	10.4	26	125.9	21.9	24
Max. height	33.1	4.2	11	24.6	3.8	81	23.6	4.8	81	30.4	3.4	5	36.4	8.5	61	23.5	3.2	26	39.8	6.3	24
Metagastric																					
ant. width	21.21	2.64	8	17.05	2.74	82	18.75	3.95	81	18.92	2.73	5	23.60	5.32	65	18.64	2.94	26	25.53	4.25	24
length	8.81	3.66	9	7.11	1.22	82	6.57	1.30	81	9.30	1.09	5	10.60	2.59	65	6.81	1.04	26	12.14	2.07	24
post. width	8.15	4.04	8	10.60	1.49	82	11.49	2.07	81	9.80	1.54	5	12.85	2.89	65	11.09	1.55	26	12.11	2.12	24
Telson																					
length	14.08	1.23	11	5.74	1.18	79	4.99	1.02	78	9.56	0.95	5	9.95	2.42	65	5.25	0.75	26	10.91	1.71	23
width	6.07	0.44	11	3.19	0.59	79	3.04	0.54	78	4.74	0.44	5	5.66	1.23	65	3.65	0.37	26	5.93	0.68	23

TABLE 2.—Mean measurements ($\bar{x}$) in mm, with standard deviations (s) and sample sizes (N), of selected charaters for adult female *Callinectes*. Refer to Figures 1 and 2 for illustration of measurements.

Measurements	*arcuatus*			*bellicosus*			*bocourti*			*danae*			*exasperatus*			*gladiator*			*latimanus*		
	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N
Length	36.5 ±	8.1	30	56.4 ±	6.6	16	51.6 ±	6.7	30	40.8 ±	3.9	52	49.5 ±	5.0	32	29.9 ±	5.7	45	53.5 ±	4.9	19
Width																					
incl. lat. spines	78.9	16.8	30	110.8	14.2	16	106.2	14.0	31	92.9	9.0	52	97.1	10.6	32	73.3	12.6	45	117.2	10.5	18
base lat. spines	62.9	14.0	30	97.0	12.1	16	88.1	11.3	31	71.7	7.1	51	82.8	8.6	32	54.8	10.1	45	94.5	9.0	19
Max. height	22.0	5.2	29	33.6	4.4	16	31.0	4.2	30	23.7	2.3	52	30.8	3.4	31	18.7	3.5	45	32.3	3.1	18
Metagastric																					
ant. width	16.02	3.34	29	24.70	2.85	15	19.76	2.90	30	17.57	1.78	52	21.90	2.18	32	13.03	2.11	44	20.94	3.99	19
length	6.34	1.46	29	9.43	0.96	15	9.72	1.27	30	7.00	0.81	52	8.85	1.01	32	4.93	1.10	44	10.05	1.06	19
post. width	9.14	1.98	29	14.38	1.30	15	10.90	1.75	30	10.47	1.13	52	11.85	1.30	32	7.65	1.21	44	11.67	1.10	19
Telson																					
length	4.19	1.01	30	6.92	0.97	16	7.76	1.19	29	4.94	0.56	50	6.25	0.79	31	3.65	0.94	45	8.03	0.97	19
width	4.39	0.95	30	7.02	0.75	16	6.53	0.83	29	5.04	0.50	50	6.54	0.80	31	3.77	0.92	45	7.12	0.63	19
Abd. seg. length																					
5th	7.04	1.75	30	11.84	1.69	16	10.70	1.56	30	8.03	1.37	51	10.63	1.28	32	6.14	1.59	45	11.09	1.18	19
6th	7.38	1.86	29	11.76	1.49	16	11.23	2.15	29	8.16	0.96	48	9.89	1.10	30	5.68	1.42	45	13.89	7.36	19

Measurements	*maracaiboensis*		*marginatus*			*ornatus*			*rathbunae*			*sapidus*			*similis*			*toxotes*		
	$\bar{x}$	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N
Length	53.3	3	38.7 ±	3.8	42	36.5 ±	8.4	43	57.0 ±	7.4	5	54.7 ±	12.7	69	35.4 ±	5.2	39	66.9 ±	3.9	13
Width																				
incl. lat. spines	114.3	3	83.5	8.5	42	77.7	12.5	43	126.6	12.6	5	131.0	34.3	69	76.9	11.8	39	148.9	11.5	13
base lat. spines	91.7	3	68.9	6.9	42	29.5	4.8	43	101.6	12.0	5	99.4	24.1	68	60.9	9.0	39	117.9	7.6	13
Max. height	31.3	3	23.3	2.5	42	20.5	4.3	42	34.0	5.0	5	31.8	7.9	64	19.8	2.9	39	39.4	2.6	13
Metagastric																				
ant. width	20.40	3	16.23	2.46	41	16.86	2.96	42	22.88	3.36	5	21.66	4.97	69	15.77	3.09	39	25.80	1.92	13
length	9.53	3	6.69	0.80	41	5.88	1.04	42	10.12	1.34	5	9.38	2.39	69	5.70	0.89	39	12.00	0.69	13
post. width	11.23	3	10.24	1.33	41	10.46	1.97	42	12.64	2.46	5	12.13	2.67	69	9.67	1.41	39	13.10	1.03	13
Telson																				
length	8.20	3	5.11	0.56	40	4.24	0.86	43	8.24	1.51	5	7.94	1.91	67	4.08	0.70	39	9.48	0.64	13
width	7.10	3	4.91	0.53	40	4.27	0.81	43	7.36	1.06	5	7.03	1.52	67	4.48	0.55	39	8.16	0.76	13
Abd. seg. length																				
5th	11.27	3	7.93	0.93	41	6.70	1.46	43	12.52	1.86	5	12.09	2.99	66	7.10	1.11	39	13.88	1.32	13
6th	11.57	3	8.06	0.90	39	7.04	2.93	41	16.86	8.79	5	11.96	3.14	65	7.30	1.18	38	14.24	3.01	13

segment nearly parallel sided but somewhat broadened proximally. Mature female abdomen and telson reaching same level as in male, length slightly exceeding width (1.05 times); sixth segment longer than fifth. First gonopods of male (Figures 18a, 20a) short, reaching about mid-length of sternite VII, approximating each other or occasionally overlapping at level of sharp distal curve, distal portion abruptly curved laterad, tapered to a rather sharp point, twisted one-fourth turn on axis and, except for membranous spout-like tip, armed with minute scattered retrogressive spinules tending to arrangement in rows, a few spinules proximal to flexure. Gonopores of female (Figure 22b) ovate with apex on long axis directed anteromesad, aperture of each with margin irregularly rounded and sinuous except on mesial side where it slopes from surface laterad under superior anterior border.

Size of carapace in mm.—Largest male: length 67, width at base of lateral spines 118, including lateral spines 142. Largest female: length 49, width at base of lateral spines 82, including lateral spines 95. Mature size of females varies considerably, the smallest examined having a carapace length of 33 and width including lateral spines of 70. Summary of selected measurements is given in Tables 1 and 2.

Color.—Carapace brown with areas of bluish black. Chelae brown above; fingers dark on external face except for tips and proximal portion, internal face dark in distal two-thirds; dark color of fingers retained in preservation (in part from Rathbun, 1930, and pers. commun. from Charles A. Johnson). Milne Edwards and Bouvier (1900) gave essentially the same impression, characterizing the entire carapace, abdomen, external face of chelipeds, posterior legs, some areas of the walking legs with their marginal hairs as greenish brown and other parts of the appendages as a beautiful blue, but there is some confusion here because the colored plate accompanying this description (Plate 4, Figure 5) represents *C. sapidus*. Rossignol (1957) described the carapace as marbled, and recently preserved material in alcohol sometimes does give an impression of mottled gray and white on the carapace.

Variation.—The carapace in *C. marginatus* shows a number of individual variations. The small anterolateral teeth generally trend forward, but there is enough individual departure from this pattern to cause confusion. Teeth in the mesial part of the row trend forward more than those in the lateral part, the first three often being rounded while the last four are pointed. Small anterolateral teeth on syntype females in MNHNP do not definitely trend forward, and those on the syntype of *C. larvatus* (MCZ 5155) are well separated, with apices directed outward rather than hooked forward. There are differences, too, in width of the anterolateral teeth, a suggestion of narrower teeth in Brazil than in Florida, and broad teeth on some African material. Occasionally there is some iridescence along the anterolateral border, and often hairiness along the lower anterolateral border.

The inner orbital fissures are usually tightly closed, sometimes with a slight notch on the orbital border, but open in some African and Dutch West Indies (Aruba) material.

The anterolateral slopes have an arching concavity proximal to the bases of the anterolateral teeth and extending transversely behind the orbitofrontal region that is more pronounced than in other species of the genus. This is especially evident in mature females. The abdomen of immature males is flush with the sternum and relatively wider than in adults in which it is somewhat recessed. Among mature males, calcification is weak in the articulation between the fifth and sixth abdominal segments allowing definite flexure in this joint, but transverse ridges ("stops") on external exposed edges of the joint prevent doubling backward. The calcification pattern is well demonstrated in two mature males in USNM 4172 from Dominican Republic. Abdominal segment 6 is constricted at mid-length in some males. The abdomen of adult females resembles that of *C. ornatus*.

Sexual differences include a more tumid appearing body among females than males, an effect resulting partly from less produced lateral spines, as well as granulations on the carapace that are relatively more prominent than on males. Granules on the carapace sometimes are very coarse in front of the epibranchial line, but seldom as coarse behind as in front of this line. Inconspicuous spination on the male first gonopods in specimens from the Canal Zone of Panama, Honduras, Colombia, and Venezuela is not so strong nor dense as that in males from Florida where there is a suggestion that the scattered spines are in rows proximal to the distal bend; spination

seems entirely lacking in some Brazilian material.

This is the species that should be named "latimanus" because broad, spatulate, often strongly asymmetrical chelae occur on both juveniles and adults. The chelipeds often seem heavy for the size of the animal bearing them, but pronounced asymmetry is not universally present. Some individuals have both chelae basically alike except for size, and in almost all except juveniles the ventral side of the propodus (especially the major) is decurved in a wide sweep giving emphasis to the "spatulate" character. The proximal tooth on the dactyl of the major chela may be moderate but is often large in size and worn as shown in Figure 3a. Some juveniles with worn chelae have a gape between fingers of the minor as well as major chela along with development of a strong proximal tooth on the dactyls. Although similarity in chelae may indicate regeneration, there is no evidence that replacement has occurred.

Habitat.—Meager data recorded with specimens suggests that this species lives in a variety of shallow littoral environments probably seldom exceeding 15 m (rarely to 25 m [?]) and usually in much shallower water from intertidal pools to 3 m deep. Most specimens have been collected by hand, seine, dip net, etc., from sand and mud flats, algae and grass flats, sandy beaches, rocky pools, eroded coral bases, oyster bars, shallows at edge of mangroves, and at the surface under lights at night. A number of authors (Milne Edwards and Bouvier, 1900; Monod, 1956; Rossignol, 1957; Forest and Guinot, 1966; Coêlho, 1967a, b, 1970) have noted that *C. marginatus* is a coastal species limited to depths of a few meters, often in brackish water, but rather rare and never as abundant as other species of *Callinectes*. Capart (1951) found it on shallow mud bottoms in salinities varying from 7.43-14.85‰ at the surface to 19.29-32.56‰ in 5-m depths and in a bottom temperature range of 22.5° to 27.42°C; he never found it in the ocean. Buchanan (1958) similarly found it in 5.5-14-m depths in a temperature range of 27° to 30°C off Accra, Ghana, in what he termed the inshore fine sand community. Chace (1956) recorded it in 27.5°C water off Los Roques, Venezuela.

Spawning.—Both the museum material studied and records in literature yield only fragmentary evidence on spawning. Ovigerous females are recorded from December to July in various parts of the geographic range on both sides of the Atlantic. Specifically the records are: Congo and St. Thomas, December; St. Thomas, January; Grenadines and Cuba, March; Haiti, April; Jamaica and Senegal, May; Colombia, Curaçao and São Tomé (Forest and Guinot, 1966), June; Florida and Puerto Rico, July.

Distribution.—Off southern Florida through Caribbean Sea to south central Brazil off Estado de São Paulo; Bermuda and Cape Verde Islands; Senegal to central Angola (Figure 27). A recent record from North Carolina is regarded as a temporary range extension.

Economic importance.—Gravel (1912), describing fisheries for *C. latimanus* along the Gulf of Guinea, noted that *C. marginatus* is also caught all along the coast from Senegal to the Congo under a variety of local names.

Remarks.—The populations on each side of the Atlantic seem indistinguishable by means of external morphological characters. Different names applied to the populations on each side reflect the discontinuity of early collections, Verrill (1908a) for instance considering *larvatus* the American and *africanus* the African variety, but with the progress of exploration and inventory it is evident that the whole is a genetic continuum with minor local variations already pointed out. Most modern workers (Capart, 1951; Monod, 1956) accept this idea although deploring the difficulty in identifying juveniles.

Verrill (1908b) early recognized the significance of larval transport in oceanic currents, applying it to populations of *C. marginatus* in Bermuda that have their origin in the West Indies. It is tempting to make the generalization that this species in its moderate size, short, simply ornamented male first gonopods, and amphi-Atlantic pattern of geographic distribution possibly represents an unspecialized and primitive member of the genus, but such ideas are qualified by the specialization of chelae seemingly well adapted by their dorsoventrally broadened but rather thin fingers for reaching into crevices, perhaps into mollusk shells after they are cracked. In short, generalized structure is hard to assess.

Some specimens show evidence of massive fouling by the barnacle *Chelonibia*. A male (dry) from Brazil (BMNH 48.86) measuring 89 mm between

tips of lateral spines bears the basal disc of a barnacle measuring 24.9 × 26.2 mm, or an oval area covering all of the metagastric and a portion of the right branchial lobe forward to the base of the frontal margin and edge of the right orbit. A second and still intact barnacle covers all of the left mesobranchial region (11.7 × 13.0 mm).

Material.—Total. 242 lots, 615 specimens.

Specimens listed in Rathbun (1930) from USNM (31091, 4172, 24445, 24446, 24447, 24448, 24449, 24450, 24454, 43905, 62684, 54255 not found; 32514 = *C. ornatus*, 33103 = *C. similis*, 61364 = *C. danae*) and MCZ.

USNM. 99 lots, 282 specimens, including the following not cited above:

UNITED STATES

Florida: 80624, Lake Worth, 1945, 1 ♂, A. H. Verrill. 113458, Pigeon Key, Monroe Co., 7 Aug. 1965, 1 ♂, R. B. Manning. 123063, Bahia Honda Key, Monroe Co., 14 June 1964, 2 ♂, 2 juv, Foster and Kaill, No. 64-11-I. 71635, Key West, 1934, 1 ♂, H. H. Darby. 76972, Key West, no date, 5 ♂, 1 ♀ (ov), C. J. Maynard. 123075, Key West, no date, 3 ♂, 2 ♀, U.S. Bur. Fish. The following from Dry Tortugas—62156, 25 July 1928, (juv) 2 ♀, A. S. Pearse. 76968, Fort Jefferson, Aug. 1930, 1 ♂, W. L. Schmitt. 62155, Loggerhead Key, 6 Aug. 1928, 2 ♂ (juv), A. S. Pearse. 76967 and 76970, Long Key, 25 June 1931, 1 ♂, 5 juv, W. L. Schmitt. 76969, Long Key-Bush Key, 18 June 1932, 1 ♂, W. L. Schmitt. 71636, Bush Key, 4 Aug. 1934, 1 ♀, H. H. Darby. 71655, Sarasota Bay, summer 1930, 1 juv, W. W. Wallis.

BAHAMAS

101130, Bimini Bay, 27 Nov. 1951, 1 ♂ (juv), F. Frieders.

CUBA

99977, E Xanadú, Hicacos Pen., Matanzas Prov., 24-27 Jan. 1957, 1 carapace, W. L. Schmitt.

JAMAICA

123060, N shore, 18°24.5′N, 77°07′W, 20 May 1965, 1 ♀ (ov), *Oregon* Stn. 5405. 123062, Kingston Harbor, 17 May 1965, 1 ♀, B. B. Collette.

HAITI

65859, Ile a Vache, 29 Apr. 1930, 1 ♀ (ov), W. M. Parish. 81481, I. opposite Bayeaux, 23 June 1941, 1 ♂, H. H. Bartlett.

DOMINICAN REPUBLIC

62828, near Montecristi, winter 1928-29, 1 chela, H. W. Kreiger.

PUERTO RICO

73282, off Fort San Gerónimo, San Juan, 30 Apr. 1937, 3 ♂, W. L. Schmitt. 73285, near Fort San Gerónimo, W end San Juan I., 27 Mar. 1937, 1 ♀, W. L. Schmitt.

VIRGIN ISLANDS

St. Croix: 72351 and 72359, Salt River Bay, 1935-36, 2 ♂, H. A. Beatty. 73284, Christiansted, 9 Apr. 1937, 1 ♂, W. L. Schmitt. 76964 and 76965, Envy Bay, no date, 1 ♂, 2 ♀, H. A. Beatty. Prickly Pear I. 123070, Vixen Pt., Gorda Sound, 15 Apr. 1956, 1 ♀ (juv), Nicholson, Schmitt, and Chace.

BARBUDA

123069, near Oyster Pond Landing, 6 Apr. 1956, 1 ♂, Schmitt, Chace, Nicholson, and Jackson.

ANTIGUA

123068, Tank Bay, English Harbor, 3 Apr. 1956, 3 ♂, Schmitt, Chace, Nicholson, and Jackson.

GUADELOUPE

123067, between Monroux and Rat Is., Pointe à Pitre, 30-31 Mar. 1956, 21 ♂, 5 ♀, 13 juv, Chace and Nicholson.

ST. LUCIA

123066, shore of bay outside Marigot Lagoon, 21 Mar. 1956, 1 ♂, Chace, Nicholson, and crew.

GRENADINES

123064, Tyrrell Bay, Carriacou I., 15 Mar. 1956, 3 ♀ (ov), Schmitt and Nicholson. 123065, Tyrrell Bay, Carriacou I., 16 Mar. 1956, 1 ♀, D. V. Nicholson.

MEXICO

Quintana Roo: 123072, Cozumel I., near lighthouse at Punta Molas, 9 Apr. 1960, 5 ♂, Rehder and Bousfield. 123071, Bahía del Espíritu Santo, north shore near Lawrence Pt., 6 Apr. 1960, 1 ♂, Rehder, Daiber, and Haynes. 123073, Pt. Santa María [20°19′N, 86°59′W], 22 Apr. 1960, 1 ♂, Schmitt and Rehder.

HONDURAS

78107, Utila I., Sept. 1938, 1 ♂, L. Mouquin.

COLOMBIA
123061, Isla de San Andrés, 5 June 1964, 1 ♀ (ov), B. A. Rohr.

PANAMA
61427, Margarita I. [09°23′N, 79°53′W], June 1924, 1 ♀, E. Deichmann.

BRAZIL
Bahia: 123074, Plataforma, 1875-77, 1 ♂, 1 ♀ (ov), Hartt Exped. Rio de Janeiro: 123076, São Francisco, 25 Aug. 1925, 1 ♂, W. L. Schmitt.

ZAIRE
54255, Banana, mouth of Congo River, July-Aug. 1915, 1 ♀, H. Lang.

AHF. 7 lots, 12 specimens.

UNITED STATES
Florida: Key Largo S Gordons Landing at Rock Harbor, 19 Sept. 1950, 2 ♂, 1 ♀, Stn. LM52. Hawk Channel, Plantation Key, 3 mi S Tavernier bridge, 25 May 1949, 1 ♀, A126-49, Stn. LM20-49. Hawk Channel off Lower Matecumbe Key, 9 June 1949, 2 ♂, 1 ♀, A140-49, Stn. LM34-49. Hawk Channel, Lower Matecumbe Key, 23 Sept. 1950, 2 ♀, Stn. LM57. Long Key, Florida Bay, 10 June 1949, A141-49, Stn. LM35-49.

TOBAGO
Bucco Bay, 11°10′42″N, 60°48′07″W, 20 Apr. 1939, 1 ♂, *Velero III,* Stn. A40-39.

TRINIDAD
Port of Spain, 10°38′12″N, 61°32′08″W, 18 Apr. 1939, 1 ♀, *Velero III,* Stn. A37-39.

AMNH. 30 lots, 81 specimens.

UNITED STATES
Florida: Lake Worth, July and Aug. 1945, 1 ♂ (juv), W. G. Van Name. 9789, Lake Worth, June 1945, 1 ♂, A. H. Verrill. 2290, Key Largo, no date, 1 ♂, C. W. Beebe.

BAHAMAS
11222, North Bimini, June 1939, 7 ♂, W. Beebe Bermuda Exped. 11288 and 11289, Bimini, 5 Sept. 1947, 2 ♂, J. C. Armstrong. 9343, Nassau, Mar. 1930, 1 ♂, R. W. Miner. 3297, no date, 1 ♂, col. unknown. 11290, Dicks Point, New Providence, 1946-47, 1 ♂, H. Dodge. 11297, Octagon Point, New Providence, 1946-47, 1 ♀, H. Dodge. 2252, Andros, no date, 3 ♂, B. E. Dahlgren and H. Müeller. 959, Andros, Apr. 1908, 7 ♂, 1 ♀, B. E. Dahlgren and H. Müeller.

CUBA
3158, 6 mi SW Cienfuegos, off Cayo Carenas [22°05′N, 80°28′W], 18 June 1918, 1 ♂, B. Brown. 3165, Cayo Cristo [23°03′N, 80°00′W], 4 mi N Isabela, 2-3 July 1918, 1 ♀, B. Brown.

HAITI
11219, Bizoton Reef [18°32′N, 72°23′W], 4 Mar. 1927, 1 ♂, 2 ♀, W. Beebe Exped.

PUERTO RICO
2671, near San Antonio Bridge, San Juan, 10 July 1914, 1 ♂, 1 ♀, R. W. Miner. 2674, Landing place in Candado Bay, San Juan, 9 July 1914, 1 ♀, R. W. Miner. 2682, San Juan Harbor, 21 July 1914, 1 ♀ (ov), R. W. Miner. 2672, rocks at entrance of Condado Bay, San Juan, 14 July 1914, 1 ♀, R. W. Miner.

ZAIRE
3455, no date, 1 ♂ (dry), H. Lang and J. Chapin. 3272 and 3329, Banana, Aug. 1915, 4 ♂, 5 ♀, H. Lang and J. Chapin. 3340, Banana, no date, 6 ♂, 5 ♀, H. Lang and J. Chapin. 3428, Manuba, Banana, July 1915, 2 ♂, H. Lang and J. Chapin. 3476, Banana, July 1915, 1 ♀ (juv), H. Lang and J. Chapin.

ANGOLA
3443, Luanda, 23 Sept. 1915, 1 ♀, H. Lang and J. Chapin. 5895 [Angola ?], 1925, 6 ♂, 2 ♀ (1 ov), Vernay Angola Exped. 5901, [Angola ?], 1925, 3 ♂, Vernay Angola Exped. 5884, Lobito Bay, Apr. 1925, 1 ♀, H. Lang and R. Boulton. 5882, Lobito Bay, May 1925, 7 juv (frags.), H. Lang and R. Boulton.

ANSP. 4 lots, 4 specimens.

UNITED STATES
Florida: 3569, Manatee R. [Manatee Co.], no date, 1 ♂, S. Ashmead.

VIRGIN ISLANDS
St. Croix: 3485, no date, 1 ♀ (dry), R. E. Friffith.

ST. MARTINS
1316, no date, 1 ♂, Van Rijgersma.

[ST. BARTHÉLEMY]
621, Bartholemew I., no date, 1 ♂, A. Goes.

BMNH. 10 lots, 18 specimens.

UNITED STATES
Florida: 1938.3.19.21, Dry Tortugas, 2 ♂, Colman and Tandy.

JAMAICA
1960.8.25.1, Portland Bight, 18 May 1956, 1 ♀ (ov), H. M. S. *Vidal.*

MEXICO
65.29, 2 ♂, (dry), vi/9.

BRAZIL
48.86, 1 ♂, (dry), vi/6/7. Pernambuco, unreg. 1 ♂, D. Wilson Barker.

GAMBIA
Unreg., Gunjur beach, 13 Nov. 1950, 1 ♂ (juv), M. H. Routh. 1952.9.9.21/22, 1 mi N Gunjur, 3 Mar. 1951, 1 ♀, and Rock pool N end Gunjur beach, 11 Dec. 1950, 1 juv, M. H. Routh.

SIERRA LEONE
1920.9.21.1/5, Murray Town, 2 ♂, 3 ♀, W. P. Lowe.

FERNANDO PÓO
53.1, 1 ♂ (dry), vi/9, Cuming.

ANGOLA
1911.2.28.14/15, Luanda, 1 ♂, 1 ♀, W. P. Lowe.

MCZ. 27 lots, 71 specimens.

UNITED STATES
Florida: 5208, July 1859, 1 ♀ (ov), Capt. Woodbury. 5148, 13 Feb. 1861, 2 ♂, Capt. Woodbury. 8747, no date, 1 ♂, Maynard. 5149, Key West, Feb. 1859, 1 ♂, T. Lyman. 5150, Key West, no date, 2 ♂, C. E. Faxon. 5209, Fort Jefferson, Tortugas, no date, 2 ♂ (part of Ordway's material).

BAHAMAS
8665, E Great Abaco I., 1904, 1 ♀, Allen, Brant, and Barbour. 11672, Alicetown, North Bimini, May 1941, 1 ♂, 1 juv, R. W. Foster and J. Huntington. 8635 and 8646, Mangrove Cay, Andros I., 1 Aug. 1904, 1 ♂, 1 juv, O. Bryant. 9425, Simms, Long I., 7 July 1936, 1 ♂, Harvard Bahama Exped. 10359, Salt Pond canal, 1.5 mi SE Matthew Town, Great Inagua I., 24 June 1938, 1 ♂, R. A. McLean and B. Shreve.

CUBA
2893, Bahía Honda, 1877-78, 2 juv, *Blake* Exped.

HAITI
5156, near Jérémie, no date, 1 ♂, D. F. Weinland.

DOMINICAN REPUBLIC
9841, Santa Barbara de Samaná, Aug. 1937, 1 ♀, W. J. Clench.

VIRGIN ISLANDS
St. Thomas: 5153 and 8864, Dec. 1871, 20 ♂, 10 ♀ (2 ov), *Hassler* Exped.

TOBAGO
9917, Pigeon Point, 17-18 Aug. 1937, 2 ♂ (juv), E. Deichmann.

CAPE VERDE ISLANDS
6530. La Praia, July 1883, 1 ♀, *Talisman* Exped.

MNB. 4 lots, 8 specimens.

BRAZIL
Ceará: 333, Fortaleza, Praia de Mucuripe, 1945, 1 ♀, A. Carvalho. Pernambuco: 55, [no other data], 3 ♂, 2 ♀. 331, Recife, Praia do Pina, Sept. 1944, 1 ♂. 330, Recife, Praia do Pina, Aug. 1944, 1 ♂.

MNHNP. 13 lots, 18 specimens.

GUADELOUPE
No date, 2 ♂, (dry), M. Beaupertuis.

CAPE VERDE ISLANDS
La Praia, July 1883, 1 ♂, *Talisman,* 41-42. No date, 1 ♂, M. Barboradu Bocage 587-66. No date, 1 ♀, M. Bouvier.

SENEGAL
Beach at Dakar, May 1895, 1 ♀ (ov), M. Chaper.

GUINEA
Fotoba, Isles des Guinée, [6 mi W Conakry], 9-10 Mar. 1947, 2 ♂, 1 ♀, Inst. d'Afrique Noire.

SÃO TOMÉ
Golfe de Guinée, 1956, 1 ♀, *Calypso* Stn. T 28. Golfe de Guinée, 1956, 1 ♀ (ov), *Calypso* Stn. T 9.

GABON
Types, 3 ♀ (dry). 3 juv, M. Duparquet 181.63 (dry).

CONGO
1892-94, 2 ♀, Dybowski.

RMNH, 38 lots, 105 + specimens.

UNITED STATES
Florida: 23268, Bear Cut, Key Biscayne, 1 Jan. 1965, 2 ♂ (juv), J. A. Cabreru and L. B. Holthuis. 18719, Bear Cut, Key Biscayne, 1-9 Sept. 1963, 1 ♂, L. B. Holthuis. 15003, Tortugas, July 1925, 1 ♂ (juv), H. Boschma.

BAHAMAS
6911 and 11859, Nassau, New Providence I., 1887, 1 ♂, 1 ♀, A. de Haas. 1860, Bahama Is., 1887, many adults, A. de Haas.

VIRGIN ISLANDS
15009, St. Croix, Krause Lagoon, 15 June 1955, 2 juv, P. W. Hummelinck.

ST. MARTIN
11861, coast near Philipsburg, 16-17 Feb. 1957, 1 ♂, 4 juv, L. B. Holthuis. 11866, Freshwater pond W of Philipsburg, 17 Feb. 1957, 6 ♂, 2 ♀, 9 juv, L. B. Holthuis. Unnumbered, mouth freshwater pond W of Philipsburg, 17 and 20 Feb. 1957, dry carapace, L. B. Holthuis. 10720, Great Bay, 7 June 1950, 1 ♂, T. W. Hummelinck. 8121, Great Bay, Ft. Blanche, 26 June 1949, 1 juv, T. W. Hummelinck. 11864, Oyster pond on E coast, 22 Feb. 1957, 1 ♂, 1 ♀, L. B. Holthuis. 1128, NE shore Great Bay, 16 May 1949, 2 ♀, P. W. Hummelinck.

GUADELOUPE
23423, Grande Anse by bridge, La Desirade, 23 Jan. 1964, 1 ♂, P. W. Hummelinck.

ARUBA
11863, Lagoon W Savaneta, 19 Mar. 1957, 2 ♂, L. B. Holthuis. 15008, Lagoon NW Savaneta, 21 Mar. 1957, ♂ juv, L. B. Holthuis. 557, 1881-1882, 6 ♂, 3 ♀, A. J. van Koolwijk. 11862, 1883, 1 ♀, K. Martin. 1872, July 1883, 3 ♂, 1 ♀ (juv), de Haas. 2273, June 1920, 1 ♂ (juv), Prof. col.

CURAÇAO
15006, Santa Cruz Baai, 13 Nov. 1956, 1 ♀ (juv), L. B. Holthuis. 15004, Piscadera Baai, 14 Nov. 1957, 2 ♀ (juv), L. B. Holthuis. 11865, Piscadera Baai, 11-13 Feb. 1957, 2 ♂, 1 ♀, L. B. Holthuis. 23422, SE part Piscadera Baai, 25 Oct. 1963, 1 ♂, P. W. Hummelinck. 23401, S part Piscadera Baai, 25 Oct. 1963, 1 ♀, P. W. Hummelinck. 11860, Mouth of Piscadera Baai, 19 Dec. 1956, 1 ♀, 2 juv, L. B. Holthuis. 23459, Mouth of Piscadera Baai, 14 Dec. 1963, 1 ♀ (paper shell), P. W. Hummelinck. 15015, Mouth of Spanish Water near Nieuwpoort, Santa Barbara beach, 25 Nov. 1956, 1 ♂, L. B. Holthuis. 15005, Mouth of Spanish Water near Nieuwpoort, Santa Barbara beach, 8-13 Nov. 1957, 1 ♂, 4 juv, L. B. Holthuis. 18644, Boca Grandi, St. Jean, 6 Feb. 1955, 2 ♂, J. S. Zaneveld. 15007, S shore St. Joris Baai near Choloma, 3 Jan. 1957, 2 ♂, 1 ♀, 1 juv, L. B. Holthuis. 18646, back part Playa Grandi, Boca Wacao, 30 Jan. 1955, 1 ♂, juv, J. S. Zaneveld. 15010, Spanish Water near Jan Zoutvat, 18 Nov. 1956, 1 ♂, juv, L. B. Holthuis. Unnumbered, reefwater, June 1920, 1 ♀ (ov?), Boeke.

BONAIRE
Lagoon, 27 Mar. 1955, dry carapace, mature, J. S. Zaneveld and R. W. Hummelinck. 11867, Lagoon on E coast, 10 Mar. 1957, 3 ♂, 1 ♀, 4 juv, L. B. Holthuis.

NIGERIA
Lagos Harbor, 23 May 1964, 1 carapace (dry), *Pillsbury* Stn. 1.

SADZ-B. 7 lots, 11 specimens.

UNITED STATES
Florida: 878, Key West, 1885, 1 ♂, Smithsonian.

BRAZIL
Ceará: 3231, Fortaleza, Praia de Iracema, 21 Jan. 1964, 3 ♂, A. L. Castro. Bahia: 3215, Ilha Madre de Deus [12°44′S, 38°37′W], 1932, 1 ♂, Oliviera Pinto. 1731, Ilha Madre de Deus, Jan. 1933, 1 ♂, Pinto e Camarão. 3224, Ilhéus, 1919, 3 ♂, E. Garbe. Rio de Janeiro: Unnumbered, Angra dos Reis, Praia Mombaca, 1 ♀. São Paulo: 890, São Sebastião, 1915, 1 ♂, E. Garbe.

UNC-IMS. 4 lots, 6 specimens.

UNITED STATES
North Carolina: Back Sound off mouth of Taylor Creek, Carteret Co., 20 Nov. 1971, 1 ♀, C. A. Johnson III.

CONGO

2740, Pte. Indienne, env. de Point-Noire, 12 May 1964, 1 ♂, 1 ♀, A. Stauch. 2741, Pte. de Tchitembc, 31 Dec. 1963, 1 ♀ (ov), A. Stauch. 2742, W de Pointe-Noire, 1 ♂, 1 ♀, A. Crosnier.

Supplementary literature records.— Bermuda (Verrill, 1908a); Veracruz, Mexico (Contreras, 1930); Aruba (de Man, 1883); Los Roques and La Orchila, Venezuela (Chace, 1956); Barra das Jangadas, S of Recife, Brazil (Coêlho, 1966); near Rio de Janeiro, Brazil (Oliveira, 1956); Ilha da São Sebastião, Brazil (Luederwaldt, 1929); Port Etienne, Mauritania, and Apam, [Ghana], plus a long list of localities duplicated in material examined and other literature (Monod, 1956); Cape Verde Islands (2 localities), and Angola (3 localities) (Guinot and Ribeiro, 1962); Bissau, Portuguese Guinea (Osorio, 1887, 1888, 1898); Gold Coast (Buchanan, 1958); São Tomé (Forest and Guinot, 1966); Pointe Noire, Congo (Rossignol, 1962).

CALLINECTES SIMILIS WILLIAMS
Lesser Blue Crab

Figures 4, 18b, 20c, 22a, 24

Callinectes ornatus.- Ordway, 1863, p. 572 (part, the Texas specimen).- Rathbun, 1896, p. 356 (part).- 1930, p. 114 (part).- Hay and Shore, 1918, p. 433, pl. 34, fig. 2.- Contreras, 1930, p. 231 (part), fig. 4 (?).- Pounds, 1961, p. 42, pl. 7, fig. 2c.- Williams, 1965, p. 172, fig. 152.

Callinectes danae.- Rathbun, 1930, p. 118 (part).- Pounds, 1961, p. 42, pl. 7, fig. 2b.

Callinectes similis Williams, 1966, p. 87, figs. 3, 4E, F (type: ♂, USNM 113341, 2-3 mi off beach between St. Johns River jetties and Jacksonville Beach, Fla.).

Description.—Carapace (Figure 4) with four frontal teeth, submesial pair small but definitely formed. Central trapezoidal (metagastric) area short and wide, anterior width about 2.75 times length, posterior width about 1.6-1.7 times length. Anterolateral margins broadly arched; anterolateral teeth exclusive of outer orbital and lateral spine short and broad, tips of first five nearly rectangular, sixth and especially seventh acuminate; first five teeth with anterior margins shorter than posterior and separated by narrow based rounded notches. Lateral spine strong, slender, and curved forward. Surface of carapace even, lightly and quite uniformly granulate except smooth along posterolateral and posterior slopes, and nearly smooth along anterolateral and anterior margins, especially between teeth and along orbits; smooth areas with tendency to iridescence.

Chelipeds with very fine granulations on ridges; carpus bearing two obsolescent granulate ridges and suggestion of others, inferior lateral ridge terminating anteriorly in a low tooth occasionally followed by a low flattened eminence; chelae strong, not greatly dissimilar in size.

Male telson longer than wide; sixth segment of abdomen slightly sinuous sided but broader at all levels than telson, proximal half slightly constricted laterally and less indurated than other parts, flush with sternum in retracted position. Mature female telson slightly wider than long. First gonopods of male (Figures 18b, 20c) reaching anteriorly two-thirds length of sternite VII, or beyond; distal portion slender, extending straight to tips curved slightly mesad, armed with scattered minute retrogressive spinules, most dense distally and laterally and largest distally. Gonopores of female (Figure 22a) narrowly ellipsoid with long axis in transverse plane; aperture of each with simple rounded borders except at mesial end where it slopes from surface laterad under superior anterior margin.

Size of carapace in mm.—Largest male: length 55, width at base of lateral spines 97, including lateral spines 122. Largest female: length 45, width at base of lateral spines 76, including lateral spines 95. Summary of selected measurements is given in Tables 1 and 2. Franks et al. (1972) reported an individual with carapace width of 171.

Color.—Adult male: "Carapace green dorsally, irregular areas of iridescence at bases of, and between, anterolateral teeth, and on posterior and posterolateral borders. Chelipeds and portions of legs similar in color or more tannish green dorsally, with iridescent areas on outer and upper edges of carpus and hands; chelae white on outer face, blue to fuchsia on inner surface, with fuchsia on tips of fingers and teeth of opposed edges. Lateral spines and some anterolateral teeth, as well as spines on chelipeds, white tipped. Walking legs grading from fuchsia distally through violet blue to light blue mottled with white proximally,

pubescence on legs beige. Swimming legs variably mottled with white; all legs with stellate fuchsia markings at articulations. Underparts white and blue." (Williams, 1965).

Ovigerous female: "Similar to male except with more violet blue on inner surface of chelae; fingers either with white teeth or fuchsia colored teeth. Legs with dactyls reddish orange grading abruptly to blue on propodi, pubescence brown to beige. Abdomen with iridescent areas." (Williams, 1965).

Carapace of juveniles sometimes with a maculate light olive pattern.

Variation.—Borders of the metagastric area are somewhat more deeply defined on young individuals than adults, and the shape of this area tends toward that in *C. danae* (USNM 123015, Mississippi) in the young. Differentiation of the major and minor chelae resembles that in other members of the genus although the two chelae on most individuals tend to be similar sized. In some specimens the major chela has a strong proximal tooth on the dactyl.

Habitat.—Franks et al. (1972) gave a good summary of habitat for this species. In Mississippi they caught it year round in trawl samples from 9- to 92-m depths at temperatures ranging from 13.2° to 29.0°C and in salinities ranging from 24.9 to 37.4‰, but it was most abundant in 37-m depths and showed a slight preference for 29.0 to 31.9‰ salinities. The same environment exists in northeastern Florida where Tagatz (1967) found the species most abundant in the ocean near shore and in the lower 25 miles of St. Johns River, mainly in salinities greater than 15‰; also in North Carolina it is seldom found in estuaries beyond lower limits of 15‰ salinity. In all areas studied the species is associated with *C. sapidus*, often in large numbers, but it is usually culled out of commercial catches because of its small size (Lunz, 1958; Pounds, 1961; Williams, 1966; Franks et al., 1972).

Spawning.—Published data on spawning in Texas and South and North Carolina summarized by Williams (1966) suggested a spring and fall spawning season for *C. similis*, and Tagatz (1967) found this true for northeastern Florida as well where females spawn in the ocean from March to July, peaking in May when 75% of them are ovigerous, and again from October to November. Ovigerous females in the collection of the USNM indicate that these limits are somewhat broader elsewhere and may be correlated with temperature, for there are representatives from Louisiana and Texas in February and Campeche Banks in December.

Distribution.—Off Delaware Bay to Key West, Fla.; northwestern Florida around Gulf of Mexico to off Campeche, Yucatán (Figure 24).

Remarks.—Small- to medium-sized juveniles are extremely difficult to identify in parts of the range where *C. danae* and *C. ornatus* also occur (southern Florida).

The few specimens from off Delaware Bay are all juveniles, suggesting that northern limits for this species, as for many others from the Carolinian Province, vary seasonally and are extended northward during favorable warm years.

Among unusual specimens seen, a female taken off Cape San Blas, Fla. (USNM 101429) with carapace measuring 37 mm long × 64 mm wide, exclusive of lateral spines, bears dorsally the largest *Chelonibia* seen fouling the species. The barnacle measures 18.5 × 21.3 mm at base × 18.3 mm height of sidewall. An immature female crab taken off Timbalier Bay, La. (USNM 123026) has that part of the front bearing frontal teeth produced forward.

Closely resembling *C. danae* and *C. ornatus*, *C. similis* seems to be the Carolinian member of the complex. *Callinectes similis* has the smoothest and most uniformly granulated carapace among the three, and the shortest, broadest anterolateral teeth. These teeth are not equilaterally triangular, having shorter anterior than posterior borders, and are more directed forward in the anterior portion than in the remainder of the row. Central teeth in the row have the anterior border extending almost straight laterad. The carapace of mature females has very little sculpture and remarkably uniform granulation overall. Granulations on the ridges of the chelipeds are among the finest of any species of *Callinectes*. Because of simplicity in structure of the male first gonopods, the relatively broad male abdomen and relatively generalized structure of the chelae and frontal teeth, it is tempting to regard this species as one of the most primitive or unspecialized members of the genus and I have arranged it so in the order of presentation, knowing full well that such evidence is highly subjective.

Material.—Total: 117 lots, 354 specimens.

USNM. 104 lots, 329 specimens, including the following listed in Rathbun (1930) as *C. danae* (20115, 22817), *C. marginatus* (33103), and *C. ornatus* (8863, 62460, 58366, 3185, 51029, 61428, 21631).

UNITED STATES

New Jersey: 62674, Cape May, 8 Sept. 1928, 1 ♂ (juv), H. G. Richards. 64257, near Brandywine Lightship, Delaware Bay, 29 July 1930, 1 ♂ (juv), H. G. Richards. 77009, off New England Creek, Delaware Bay, 25 Aug. 1931, 1 ♀ (juv), H. G. Richards.

Delaware: 77008, off Slaughter Creek, 4 Aug. 1931, 1 juv, H. G. Richards.

North Carolina: 123058, Beaufort, recd. 19 Nov. 1959, 1 ♀ (ov), J. D. Costlow, reared larvae. 123059, Beaufort Harbor, Aug. 1946, 1 ♂, D. H. B. Ulmer.

South Carolina: 97699, N Edisto R., 22 Apr. 1953, 1 ♂, 7 ♀, G. R. Lunz. 123012, S Creek near entrance into N Edisto R., 31 May 1966, 1 ♂ (juv), J. C. McCain. 123011, off mouth N Edisto R., 31 May 1966, 1 ♀, J. C. McCain.

Georgia: 123054, Jointer R. [near Jekyll I.], 17 Mar. 1932, 2 ♀, W. W. Anderson.

Florida: 123034, [off mouth St. Johns R.], 30°26.5′N, 81°23′W, 17 Apr. 1940, 9 ♂, 9 ♀ (6 juv), *Pelican* Stn. 215-1. 123047, [off mouth St. Johns R.] 30°26′N, 81°20.5′W, 17 Apr. 1940, 1 ♂, 1 ♀, *Pelican* Stn. 215-2. 113345, off St. Johns R. jetties, 14 Aug. 1962, 8 ♂, 6 ♀, M. E. Tagatz and G. P. Frymire. 113341, 113342, 113343, 113344, 2-3 mi off beach between St. Johns R. jetties and Jacksonville Beach, 18 June 1962, 8 ♂, 9 ♀, A. B. Williams et al. 123014, [off Jacksonville Beach] 30°21′N, 81°20.5′W, 19 Nov. 1963, 2 ♂, 2 ♀, *Silver Bay* Stn. 5381. 123101, [off St. Augustine] 29°54.5′N, 10°10′W, 9 Feb. 1965, 2 ♀, *Oregon* Stn. 5234. 123018, [off SE St. Johns Co.] 29°28.5′N, 81°04.5′W, 28 Mar. 1940, 2 ♂, *Pelican* Stn. 202-6. 99917, Matanzas R. at Crescent Beach, 1 Dec. 1954, 1 ♂, D. K. Caldwell. 123017, [N Daytona Beach] 29°18.5′N, 81°01.5′W, 6 Apr. 1940, 1 ♀, *Pelican* Stn. 212-3. 123046, [off Daytona Beach] 29°14.5′N, 80°59.5′W, 6 Apr. 1940, 1 ♂, 1 ♀ (ov), *Pelican* Stn. 212-2. 123020, [off Daytona Beach] 29°07.5′N, 80°55′W, 5 Apr. 1940, 5 ♂, 2 ♀, *Pelican* Stn. 211-5. 123021, [off Daytona Beach] 29°11′N, 80°43′W, 19 Jan. 1940, 1 ♀, *Pelican* Stn. 172-3. 123008, 123009, Ponce de Leon Inlet, Volusia Co., 13 Apr. 1946, 2 ♂ (juv), DePalma and Strickland. 123045, [off New Smyrna] 29°00′N, 80°47.5′W, 19 Jan. 1940, 1 ♂, *Pelican* Stn. 171-7. 101686, NE off Cape Canaveral, 29°15′N, 80°13′W, 1 June 1957, 2 ♀ (1 ov), *Combat* Stn. 334. 123016, [off Cape Canaveral] 28°24′N, 80°32.5′W, 4 Apr. 1940, 1 ♂, *Pelican* Stn. 207-3. 123022, [SE Cape Canaveral] 28°23′N, 80°27.5′W, 18 Jan. 1940, 1 ♂, *Pelican* Stn. 169-2. 99902, Sewall Point, Martin Co., 27 Feb. 1955, 2 juv, D. K. Caldwell et al. 113460, Bear Cut Key, Biscayne side Miami, 17 Aug. 1965, 1 ♂, 1 ♀ (juv), R. B. Manning. 77103, Coral Gables, 7 July 1932, 1 ♂, J. F. W. Pearson. 76984, Key West, 26 May 1918, 1 ♂ (ov), 3 juv., D. R. C. 76980, Key West, no date, 2 ♀, C. H. Maynard. 123103, mud cove 2 mi from tip of Alligator Harbor, Franklin Co., 27 Oct. 1967, 4 ♂, 5 ♀, C. Swift and J. Rudloe. 101429, off Cape San Blas, 29°16′N, 85°08′W, 15 July 1957, 1 ♀ (ov), *Oregon* Stn. 1755. 123102, St. Andrews Bay Shipyard area, Bay Co., 18 Aug. 1967, 1 ♂, L. Abele and C. Swift. 99914, Choctawhatchee Channel, Okaloosa Co., no date, 1 ♀, K. Caldwell. 99896, Intracoastal Waterway 3.5 mi E Interarity Point, Pensacola, 15 Aug. 1953, 1 ♂, F. Berry and A. Mead.

Alabama: 92425, 30°15.5′N, 88°10′W, 22 June 1951, 3 ♂, 1 ♀, 1 juv., H. M. Hefley, *Oregon* Stn. 387.

Mississippi: 123015, inside Petit Bois Island, Mississippi Sound, 20 Apr. 1967, 27 ♂, 10 ♀, *George M. Bowers* Stn. 4. 123010, off N side Little Deer Island, Ocean Springs, 1 Sept. 1965, 3 juv, J. C. McCain.

Louisiana: 123040, 28°22.5′N, 91°44.5′W, 12 July 1938, 1 ♂, *Pelican* Stn. 84-1. 123057, 28°31′N, 91°09′W, 13 July 1938, 3 ♂, 1 ♀ (juv), *Pelican* Stn. 86-4. 123029, 28°38′N, 91°05′W, 18 Mar. 1938, 1 ♂, *Pelican* Stn. 31. 123019, 28°39.5′N, 91°06′W, 11 Nov. 1938, 1 ♂, 2 ♀ (1 juv), *Pelican* Stn. 90-2. 123039, 28°40′N, 90°51.5′W, 10 July 1938, 1 ♂ (juv), *Pelican* Stn. 80-7. 123035, 28°41.5′N, 91°10′W, 11 Nov. 1938, 2 ♂, 2 ♀ (1 juv), *Pelican* Stn. 90-3. 123050, 28°42′N, 92°15.5′W, 13 Nov. 1938, 4 ♂, 4 ♀, *Pelican* Stn. 93-6. 101428, 28°46′N, 90°47′W, 6 Mar. 1957, 7 ♀ (ov), *Oregon* Stn. 1749. 123033, 28°46.5′N, 91°18.5′W, 11 Nov. 1938, 1 ♂, *Pelican* Stn. 90-5. 123037, 28°48′N, 89°51′W, 13 May 1938, 3 ♀ (2 ov), *Pelican* Stn. 69-6. 123048, 28°49′N, 91°23′W, 11 Nov. 1938, 3 ♂, 1 ♀, *Pelican* Stn. 90-6. 92350, 28°50′N, 89°33′W, 7 May 1951, 1 ♂, *Oregon* Stn. 342. 91432, 28°53.3′N, 89°36.5′W, 13 Sept. 1950, 1 ♀ (juv), *Oregon* Stn. 107. 123038, 25 mi S Grand Isle, 28°55′N, 90°02′W, 17 Feb. 1938, 1 ♂, *Pelican* Stn. 22. 123041, 28°55′N, 92°15.5′W, 13 Nov. 1938, 3 ♂, *Pelican* Stn. 93-3.

123025, 28°55.5′N, 89°59′W, 10 Nov. 1938, 2 ♀ (1 ov), *Pelican* Stn. 87-7. 123028, 28°56′N, 91°52′W, 29 Mar. 1938, 1 ♂, 2 ♀, *Pelican* Stn. 37. 123056, 28°56.5′N, 91°50′W, 11 July 1938, 2 ♂, 2 ♀, *Pelican* Stn. 82-5. 91939, 28°57′N, 89°36′W, 14 Sept. 1950, 1 ♀, *Oregon* Stn. 110. 123036, 28°57′N, 89°43′W, 10 Nov. 1938, 4 ♀ (1 ov), *Pelican* Stn. 87-4. 123024, 28°58′N, 89°28.5′W, 10 Nov. 1938, 1 ♂, *Pelican* Stn. 87-1. 123026, 28°58′N, 90°17′W, 10 July 1938, 1 ♀ (juv), *Pelican* Stn. 79-7. 123023, 28°59′N, 92°15.5′W, 13 Nov. 1938, 1 ♂, 2 ♀ (juv), *Pelican* Stn. 93-2. 123049, 28°59.5′N, 91°44.5′W, 12 Nov. 1938, 1 ♂, *Pelican* Stn. 91-4. 64148, off Breton Island, Nov. 1930, 1 ♂, Stewart Springer. 91954, 29°22′N, 88°49′W, 24 Sept. 1950, 3 ♂, *Oregon* Stn. 132. 123027, 29°01.5′N, 89°33′W, 8 July 1939, 1 ♂, 1 ♀, *Pelican* Stn. 77-2. 91433, 29°12′N, 88°50′W, 12 Sept. 1950, 1 ♂, *Oregon* Stn. 103. 123055, 3-6 mi ESE SW Pass, 16 Feb. 1934, 1 ♀ (ov), T. C. P., M. J. Lindner, and W. W. Anderson.

Texas: 123030, 29°00′N, 94°38.5′W, 21 Jan. 1939, 1 ♀, *Pelican* Stn. 104-5. 123031, 29°10.5′N, 94°50.5′W, 3 May 1938, 5 ♂, 2 ♀, *Pelican* Stn. 56-5. 123005, Galveston, 11 Aug. 1940, 4 ♂, 1 ♀, from J. L. Baughman. 123006, Galveston, 7 July 1940, 1 ♂, 2 ♀ (juv), from J. L. Baughman. 123007, Galveston, 11 Aug. 1940, 9 ♂, 2 ♀ (1 soft), from J. L. Baughman. 80662, Galveston, no date, 5 ♂, 4 ♀, J. L. Baughman. 123013, 17 mi S, 7 mi E Alvin, Brazoria Co., 28 July 1952, 1 ♀ (juv), S. Alvin. 22817, Alligator Head, Matagorda Bay, no date, 1 ♂ (dry), from J. D. Mitchell. 123051, 27°59′N, 95°20.5′W, 22 Jan. 1939, 1 ♀, *Pelican* Stn. 107-3. 123032, 28°20.5′N, 96°13′W, 2 May 1938, 1 ♀ (juv), *Pelican* Stn. 54-2. 101678, 28°20′N, 94°97′W, 25 Sept. 1957, 2 ♀, *Silver Bay* Stn. 187. 123044, 27°40′N, 96°34′W, 22 Apr. 1938, 1 ♂, 2 ♀ (ov), *Pelican* Stn. 42. 123043, 27°51′N, 96°55.5′W, 2 May 1938, 3 ♂, 2 ♀ (1 ov), *Pelican* Stn. 53-1. 80663, Port Aransas Pass, 5 June 1941, 1 ♀, G. Gunter. 80664, Port Aransas Pass, no date, 10 ♂, 11 ♀, G. Gunter. 123042, 26°48.5′N, 96°40′W, 4 Feb. 1939, 1 ♀ (ov), *Pelican* Stn. 115-3. 123052, 26°05′N, 97°05′W, 5 Feb. 1939, 1 ♀ (juv), *Pelican* Stn. 118-4.

MEXICO

Tamaulipas: 94452, 24°12′N, 97°17′W, 13 Oct. 1952, 1 ♀, *Oregon* Stn. 662. 123053, off Soto la Marina, 140 mi S Rio Grande R., 15 Mar 1947, *Pelican*. Campeche Bank: 94453, 19°54.1′N, 91°43′W, 10 Dec. 1952, 1 ♀ (ov), *Oregon* Stn. 719. 94454, 20°12′N, 91°40′W, 11 Dec. 1952, 2 ♂, 1 ♀ (ov), *Oregon* Stn. 720.

AHF. 4 lots, 13 specimens.

UNITED STATES

Florida: Choctawhatchee Bay entrance W end Destin bridge [Okaloosa Co.], 19 June 1949, 6 ♂, 4 ♀, LM42-49.

Louisiana: Breton Sound, Mississippi Delta, 21 Oct. 1951, 1 ♂, R. H. Parker.

Texas: 1.25 mi off Mustang Island, 31 Aug. 1951, 1 ♀, E. Puffer, J498. Off Padre Island, 9 June 1956, 1 ♀, R. H. Parker, J482.

AMNH. 3 lots, 4 specimens.

UNITED STATES

Florida: 11298, Lake Worth, July and Aug. 1945, 1 ♀, W. G. Van Name and A. H. Verrill.

Texas: 2755, Galveston, no date, 2 ♂ (juv), col. unknown.

BAHAMAS

2445, Nassau, 1899, 1 ♂, R. P. W.

BMNH. 1 lot, 1 specimen.

UNITED STATES

Texas: 11.1.1946, 1 ♀, Baughman.

MCZ. 4 lots, 5 specimens.

UNITED STATES

North Carolina: 11352, 2 mi SE Roanoke Island, 19 Dec. 1940, 1 ♂ (juv), R. Foster.

Florida: 5207, 1859, 2 ♂, G. Wurdemann. 5129, Cape Florida (S end Biscayne Bay), no date, 1 ♂ (juv), G. Wurdemann.

Texas: 5134, 13 Feb. 1861, 1 ♂, G. Wurdemann.

RMNH. 1 lot, 2 specimens.

UNITED STATES

Mississippi: 17825, 29°38.5′N, 88°30′W, 21 Aug. 1962, 1 ♂, 1 ♀, *Oregon* Stn. 3713.

UNC-IMS. 7 lots, 74 specimens + many uncatalogued.

UNITED STATES

North Carolina: 1556, (Paratypes), off Beaufort Inlet, Carteret County, 31 Oct. 1962, 5 ♂, 4 ♀ (2 ov), E. Bayer, from *Ensign*.

Florida: 2140, Clapboard Creek, trib. of St. Johns River, 7 June 1964, 7 juv, col. unknown.

2237, Sisters Creek at Fort George River?, Duval County, 2 ♂, 2 ♀, G. P. Frymire and G. C. Williams. 2138, Mouth of Sisters Creek off St. Johns River, M. E. Tagatz and G. P. Frymire. 1995 (Paratypes), off St. Johns River jetties, 5 ♂, 4 ♀, 3 juv, M. E. Tagatz and G. P. Frymire. 1990 (Paratypes), 2 to 3 mi off beach between St. Johns River jetties and Jacksonville Beach, 17 ♂, 16 ♀ (10 ov), 8 juv, G. P. Frymire, M. E. Tagatz, and G. C. Williams.

Texas: 2139, Galveston Bay, June 1964, 1 ♂, col. unknown.

Supplementary literature records.—Laguna Madre de Tamaulipas (as *danae,* Hildebrand, 1957).

CALLINECTES GLADIATOR BENEDICT

Marine Blue Swimming Crab

Figures 5, 18c, 20b, 22c, 24

Lupa smythiana Leach (nomen nudum) in White, 1847, p. 27.

Callinectes tumidus var. *gladiator* Benedict, 1893, p. 537 (type: ♂, USNM 14879, Baya River, Elmina, Ashanti [Ghana]).

Callinectes tumidus gladiator.- Rathbun, 1896, p. 360.

Callinectes gladiator.- Rathbun, 1897, p. 150.- 1900a, p. 291.- 1921, p. 397, fig. 3; pl. 19, fig. 2.- Balss, 1921, p. 58.- Monod, 1927, p. 606.- 1956, p. 205, figs. 236-237.- Irvine, 1932, p. 15, fig. 9.- 1947, p. 298, fig. 203.- Vilela, 1949, p. 58, fig. 6.- Capart, 1951, p. 130, fig. 46.- Rossignol, 1957, p. 82.- 1962, p. 116.- Guinot and Ribeiro, 1962, p. 48.- Crosnier, 1964, p. 32.- Forest and Guinot, 1966, p. 64.

Description.—Carapace (Figure 5) bearing four frontal teeth, submesial pair almost never more than half length of lateral pair. Metagastric area short, anterior width about 2.5 times length, posterior width about 1.5 times length. Anterolateral margins arched slightly; teeth, exclusive of outer orbital and lateral spine, with tendency to arrangement in a 3-2-2 pattern; proximal three narrow-acute and separated by narrow sinuses; middle two broader, acuminate, and more widely separated; lateral two spiniform and trending forward. Lateral spine usually long and slender. Surface finely or moderately and evenly granulate except for variably smooth portions at periphery, especially on posterior and posterolateral slopes. Tendency toward ridging or heaping of granules on branchial and cardiac lobes. Epibranchial line prominent and nearly uninterrupted.

Chelipeds with propodus sharply ridged, ridges granulated; carpus often with granulated ridges evident dorsally; major chela with strong tooth at base of dactyl.

Male abdomen and telson narrow, reaching slightly beyond suture between thoracic sternites IV and V; telson about 1.6 times longer than wide; sixth segment constricted at midlength, sides markedly divergent proximally. Mature female abdomen and telson reaching same level as in male, telson a bit wider than long, sixth segment slightly shorter than fifth. First gonopods of male (Figures 18c, 20b) reaching slightly beyond midlength of thoracic sternite VII; curved sigmoidally in distal half, overlapping, divergent except at extreme tip and twisted mesioventrally on axis; armed distally with minute retrogressive spinules, scattered or occasionally arranged in rows. Gonopores of female (Figure 22c) irregularly lunate with superior limb of each directed anteromesad; aperture of each with rounded margin becoming lowest mesially where it slopes from near surface level laterad under posteriorly arched anterior border.

Size of carapace in mm.—Largest male: length 48, width at base of lateral spines 92, including lateral spines 117. Largest female: length 60, width at base of lateral spine 108, including lateral spines 138. Summary of selected measurements is given in Tables 1 and 2.

This species shows considerable variability in size but is, on the whole, the smallest in the genus. Females are often quite delicate, maturing at sizes as small as a length of 23, width at base of lateral spines 41, and width including lateral spines of 54. Irvine (1947) noted that large individuals measure 6 inches or more (155 mm) across the carapace.

Color.—Uniform gray-green or gray-blue with spot of blue on palm and proximal internal part of fingers of chela (Rossignol, 1962). Beautiful mottled carapace with bright blue legs, called the marine or deep sea blue swimming crab (Irvine, 1932, 1947). Preserved specimens often have an oval dark mahogany colored spot, variable in size, on the gastric and metagastric areas.

Variations.—In some ways *C. gladiator* resembles the "acutidens" form of *C. sapidus,* surpassing it in development of even more acute, slender spination, and showing variable ridging or cresting of granulations on branchial lobes and mesobranchial regions as well as formation of a transverse ridge of granules on each cardiac lobe. The peaking of granules is apparent at quite small size. In addition, these lobes and regions are often prominent and thrown into somewhat angular planes bordering the contrastingly sunken metagastric area. The second abdominal segment terminates laterally in a spine usually sharper and more prominent than in other species of the genus, especially in young or freshly molted individuals.

The lateral spines of most individuals are relatively the longest among species in the genus. Anterolateral teeth may be bilaterally asymmetrical in number. Tips of the teeth may lie in a nearly straight line providing relatively flat anterolateral arcs. All older individuals have a rounded notch between the first two anterolateral teeth. The lower side of each anterolateral margin becomes hairy at an early age.

Openness of the inner orbital fissure is random, bearing no relationship to age or width of carapace. When the fissure is closed, a V-shaped notch usually remains open on the orbital margin.

First gonopods of males are not completely S-shaped and not overlapping in juveniles; in a few males they extend to the level of a suture between thoracic sternites VI and VII. The first gonopods may be unnaturally splayed in preserved specimens. Abdominal segment 6 is often poorly calcified at midlength in males.

Distribution.—West Africa from Baie de Saint-Jean, 19°27′N, 16°22′W, Mauritania, to Baia do Lobito, Angola (Figure 24).

Habitat.—Longhurst (1958) provided an excellent ecological summary of the West African marine benthos primarily in and off the Sierra Leone River, but elsewhere as well. He found that in shelf regions under the influence of tropical shelf water a characteristic fauna was revealed by otter trawls in each sector investigated; the most important species were the swimming crabs *C. gladiator* and *Portunus validus* Herklots which occur in most hauls together with *Penaeus duorarum notialis* Burkenroad, *P. kerathurus* (Forsskål), *Parapenaeus longirostris* (Lucas), *Panulirus rissonii* (Desmarest), and *Sepia officinalis* Linn. Off the Sulima River [=Moa River, Sierra Leone] occurrence of this fauna corresponded with the inshore *Cynoscion* fauna of demersal fish, with the thermocline as its lower limit. In samples, this fauna extended from Senegal to the Bight of Biafra, the genera *Callinectes, Portunus,* and *Panulirus* occurring in a high proportion of hauls from shallowest to 50 m. Irvine (1947), Rossignol (1962), and Crosnier (1964) essentially said the same, that this coastal marine species lives on the bottom from shore to depths of 30 m on sand, sandy mud, or gravel, sometimes with a mixture of shell fragments (Sourie, 1954a) in warm water.

Both Monod (1927) and Rossignol (1957) remarked on the small size and abundance as well as the rapidity and aggressiveness with which *C. gladiator* moves, the latter saying that it often rests three-fourths buried in a predatory position with only antennae and pincers exposed. In addition to trawl hauls, the crab is captured in nets allowed to hang a few feet from the bottom (Irvine, 1947) and at the surface with dip nets under lights at night.

Though found in estuaries to some extent, these accounts imply that *C. gladiator* is much like *C. similis* of the western Atlantic in ecological association and behavior, and less estuarine than *C. latimanus.*

Spawning.—Museum records provide only an outline of spawning that may go on all year. Records of ovigerous females are: December, Angola; January, Guinea, Liberia, and Cameroon; February, Cameroon; March, Sierra Leone, Congo; April, Ghana; May, Senegal, Sierra Leone, and Nigeria; June, São Tomé; October, Congo.

Economic importance.—No direct statements of economic importance are made in literature. Irvine (1947) reported the flesh and eggs edible and of good quality.

Remarks.—Aside from taxonomic accounts and faunal lists, there is less published information on *C. gladiator* than most *Callinectes.* Like others, larger or older specimens often bear one or more barnacles of the genus *Chelonibia* on the carapace. Teeth of fingers on the major chelae are often worn, and the major hands often seem disproportionately large for the size of the animal. One ovigerous female in the BMNH (unregistered)

from Victory Bay, Cameroon, has two major chelae.

The holotype is an immature male somewhat the worse for wear. The left chela is present but dismembered from the body, as are other legs or parts of legs and the abdomen. The left lateral spine is broken about halfway along its length, and only the left first gonopod remains.

Figures provided by Irvine (9 and 13, 1932; 202 and 203, 1947) are difficult to assign to synonymy with confidence, and both Capart (1951) and Monod (1956) had trouble with them. Figures 13 and 202 could represent either *C. gladiator* or *marginatus*, but 9 and 203 are labelled as *C. gladiator*, yet internal carpal spines on the latter indicate a species of *Portunus*. Since the features are sketchy, it is best to accept the author's designation with allowance for error.

The specimen named by Leach (in White, 1847) is an immature female with prominently ridged areas on the carapace and straight lateral spines typical of *C. gladiator*. There is a small mature female in this same collection.

Material.—Total: 80 lots, 412 specimens.

USNM. 18 lots, 95 specimens.

SENEGAL
21384, Dakar, 3 May 1892, 1 ♂, O. F. Cook. 119469, Dakar Harbor, 25-26 July 1964, 2 ♂, 2 ♀, *Geronimo*.

LIBERIA
20670, Mouth of Mesurado, Monrovia, no date, 1 ♀ juv, O. F. Cook. 87395, Farmington River at Snafu Docks, Nov. 1946, 3 ♂, 1 ♀, H. A. Beatty. 97861 and 97862, off St. Paul River mouth, Monrovia, 6 Jan. 1953, 2 ♀ (ov), G. C. Miller. 97863, off St. Paul River mouth, Monrovia, 4 Mar. 1953, 1 ♂, G. C. Miller.

IVORY COAST
120937, 05°02.5′N, 03°49.5′W, 30 May 1964, 2 ♀, *Pillsbury*.

GHANA
14879, Baya River, Elmina, Ashantee, 1889, 1 ♂, W. H. Brown, Jr., (Type).

NIGERIA
120938, Lagos, 9 May 1965, 1 ♂, *Pillsbury* Stn. 226. 123094, Lagos, 23 May 1964, 18 ♂, 22 ♀, 1 juv, *Pillsbury* Stn. 2. 120939, Lagos, 10 May 1965, 4 ♂, 6 ♀, *Pillsbury* Stn. 229. 120940, 04°06′N, 05°58′E to 04°02′N, 06°04′E, 14 May 1965, 9 ♂, 11 ♀, 1 juv, *Pillsbury* Stn. 250. 120941, 04°04′N, 06°18′E, 14 May 1965, 1 ♀, 1 juv, *Pillsbury* Stn. 252.

FERNANDO PÓO
120942, 03°35′N, 08°48′E, 15 May 1965, 1 juv, *Pillsbury* Stn. 258.

ZAIRE
54251, Banana, mouth of Congo River, Aug. 1915, 1 ♂, 1 ♀, H. Lang. 54252, Banana, mouth of Congo River, no date, 1 ♂, H. Lang.

AMNH. 4 lots, 7 specimens.

ZAIRE
3403 and 3470, Banana, Aug. 1915, 3 ♂, 1 ♀, H. Lang and J. Chapin.

ANGOLA
3385 and 3463, Santo Antonio do Zaire, Aug. 1915, 2 ♂, 1 ♀, H. Lang and J. Chapin.

BMNH. 19 lots, 64 specimens.

GAMBIA
1927.1.27.1, Cape St. Mary, 1 ♂, T. R. Hayes, Sir C. H. Armitage. 1952.9.9.19/20, 1 mi N Gunjur on coast, 1 ♂, 1 ♀, M. H. Routh.

SIERRA LEONE
1955.10.7.35, Rokel estuary [NE Freetown], 1 ♀ juv, T. S. Jones. 1957.5.26.76/78, Banana I., 2 ♂, 2 ♀, A. R. Longhurst. 1922.0.13.1/5, Sherbro I., 5 ♂, 5 ♀ (juv), C. H. Allan.

GHANA
1931.5.21.1, Accra, 1 ♂, F. R. Irvine. Two unreg. lots, Accra, 2 ♂, 3 ♀ (1 ov), F. R. Irvine.

NIGERIA
1966.10.17.3/4, 1 ♂, 1 ♀, Ejike. 1938.8.15.47/48, 5 juv, A. G. Taylor.

CAMEROON
1967.11.4.1/2, Ambas Bay [4°N, 9°10′E], Feb. 1966, 2 ♂, T. S. Jones. 1962.2.1.24/27, Victoria Bay, 4 ♂, 1 ♀, J. T. Swarbrick. Unreg., Victoria Bay, 16 ♀ (3 ov), J. T. Swarbrick. Unreg., Cameroon coast, Mar. 1962, 1 ♂, 1 ♀, R. C. Ward.

WEST AFRICA

Unreg., 22, 1♀. Dry coll. vi/9, 1♀, Congo Exped., I. Cranch. Unreg., 1♀, *Lupa smythiana* Leach MS, *Neptunus sanguinolentus* in White Catalogue, 1847, J. Cranch.

MNHNP. 11 lots, 27 specimens.

SENEGAL

Rufisque, 11 and 13 May 1947, 2 ♂, T. Monod. M'bour, 1948, 1 ♀, Dekeyser-Villiers. Off M'bour-N'gaparou, May 1949, 2♀ (ov), *G. Tréca,* Crémoux.

SIERRA LEONE

Gulf of Guinea, 07°20′15″N, 12°39′W, 1956, 1 ♀ (juv), *Calypso* Stn. 11.

IVORY COAST.

Off Abidjan, 05°16′12″N, 04°0′20″W, 1956, 9 juv, *Calypso* Stn. 20.

CAMEROON

Longji (Kribi)?, 30 May 1956, 1 ♂, *Calypso* Stn. 34. Mouth of the Kienke, Kribi, 1 ♀, T. Monod. Souelaba, 1932, 3 ♂ (juv), T. Monod.

SÃO TOMÉ

Gulf of Guinea, 1956, 1 ♀ (ov), *Calypso* Stn. T27. 3 ♂, 3 juv, *Calypso* Stn. T9.

RMNH. 13 lots, 95 specimens.

LIBERIA

1871, Grand Cape Mount, 1881, 1 ♂, 2 ♀, J. Büttikofer and J. A. Sala.

NIGERIA

24186, Gulf of Guinea, 03°45′N, 08°03′E, 03°45′N, 08°02′E, 14 May 1965, 1 ♀, *Pillsbury* Stn. 256. 23520, off Nigeria, 04°03′N, 06°03′E, 04°04′N, 06°04′E, 14 May 1965, 3 ♂, 5 ♀ (1 ov), *Pillsbury* Stn. 251. 20597, Lagos Harbor, 23 May 1964, juv 5 ♂, 14 ♀, *Pillsbury* Stn. 2. 23519, Lagos Harbor, 10 May 1965, 1 ♂, 2 ♀, *Pillsbury* Stn. 228. 15532, Port Harcourt, Niger Delta, May-Aug. 1960, 4 ♂, H. J. G. Beets.

FERNANDO PÓO

24185, 03°45′N, 08°48′E, 15 May 1965, 1 ♂ (juv), *Pillsbury* Stn. 257.

CAMEROON

21572, Kribi, 9 Aug. 1964, 30+ (juv), B. de Wilde-Duyfies. 21149, Kribi, 9 Mar. 1964, 11 ♂, 4 ♀, B. de Wilde-Duyfies. 21178, Doula, 10 Feb. 1964, 1 ♂, B. de Wilde-Duyfies.

GABON

14995, Port Gentil, 1 juv, J. H. Logeman

CONGO

374, 1880, 1 ♀, 2 juv, T. Kamerman.

ANGOLA

1876, Musserra, 1882, 1 ♂, 1 ♀, T. Kamerman.

UNC-IMS. 15 lots, 125 specimens.

TOGO

2717, 06°06′30″N, 01°37′30″E, 16 Oct. 1963, 1 ♀, A. Crosnier.

DAHOMEY

2718, 06°19′N, 02°24′E, 20 July 1964, 1 ♂, 2 ♀, A. Crosnier.

CAMEROON

2719, 03°55′N, 09°00′E, 5 Jan. 1963, 3 ♀ (2 ov), A. Crosnier. 2720, 03°32′N, 09°35′E, 24 Aug. 1963, 5 ♂, 5 ♀, A. Crosnier.

GABON

2721, Baie de Corisco, near Libreville, 3 July 1960, 1 ♂.

CONGO

2722, off Pointe-Noire, Mar. 1962, 4 ♂, 1 ♀ (ov), A. Crosnier. 2723, Beach and Bay at Pointe-Noire, Oct. 1963, 6 ♂, 10 ♀ (5 ov), A. Crosnier. 2724, 3 June 1964, 2 ♂, A. Stauch. 2725, 27 May 1964, juv, 29 ♂ (1 adult), 13 ♀, A. Stauch. 2727, Nov. 1962, 9 ♂, 12 ♀, A. Crosnier. 2728, 26 June 1964, 1 ♂, 1 ♀, A. Stauch. 2729, 27 May 1964, 2 ♂, A. Stauch. 2730, July 1963, 2 ♀, A. Crosnier. 2731, Estuaire de la Songolo, near Pointe-Noire, 1 ♀, A. Stauch.

ANGOLA

2732, off Cabinda, Dec. 1962, 6 ♂, 8 ♀ (1 ov), A. Crosnier.

Supplementary literature records.—Baie de Saint-Jean [19°27′N, 16°22′W], Mauritania; Hann, Gorée, M'bour, and Joal, all S of Dakar, Senegal; Baixos das Galinhas, Ilha de Bissau, Portuguese Guinea; Iles de Los, 1 and 3 mi W and NW Tamara, near Cap Matakong, all near Conakry,

Guinea; Grand Lahou, Ivory Coast (Monod, 1956); Gold Coast shelf (Longhurst, 1958); Fernando Póo (Crosnier, 1964); 7°20′N, 12°39′W, Sierra Leone; lagoon at Abidjan, Ivory Coast; Kribi, Cameroon; Morro Peixe, São Tomé (Forest and Guinot, 1966); Cabinda, Luanda, and Baía do Lobito, Angola (Guinot and Ribeiro, 1962).

CALLINECTES ORNATUS ORDWAY

Figures 6, 18d, 20d, 22d, 25

Callinectes ornatus Ordway, 1863, p. 571 (syntypes: labelled "types," 2 ♀, MCZ 5120, Charleston, South Carolina; 1 ♂, 2 ♀, MCZ 5128, Charleston, South Carolina; ♂ [dry], MCZ 5137, Gonaives, Haiti; ♂, MCZ 5136, Cumaná, Venezuela; those from Tortúgas and Bahamas not found).- Smith, 1869, p. 8.- Rathbun, 1896, p. 356 (part), pl. 15; pl. 24, fig. 3; pl. 25, fig. 2; pl. 26, fig. 2; pl. 27, fig. 2.- 1898, p. 596.- 1901, p. 48.- 1930, p. 114 (part), text-figs. 15b, 16a, 17a, 18b, pl. 50.- 1933, p. 48, fig. 40.- Young, 1900, p. 188 (var. of *C. diacanthus*).- Verrill, 1908a, p. 366, text-figs. 22c, 23b; pl. 17, fig. 1; pl. 21, fig. 3.- Boone, 1927, p. 32.- Contreras, 1930, p. 232 (part), fig. 4.- Chace, 1940, p. 33.- 1956, p. 154.- Chace and Hobbs, 1969, p. 132, fig. 37e.- Balss, 1957, p. 1692 (part).- Holthuis, 1959, p. 200.- Guinot-Dumortier, 1960, p. 514, figs. 13a, b.- Williams, 1965, p. 172 (part).- 1966, p. 84, figs. 1A, B, 4A, B.- Taissoun, 1969, p. 69, fig. 25A-D, photo 9.- 1973, p. 22, figs. 4D, 5A, photo 1.

Callinectes diacanthus.- A. Milne Edwards, 1879, p. 225 (var. of *C. diacanthus*).- Young, 1900, p. 186 (part).

Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part; specimens c, k, n_3, West Indies; d, e, Brazil).

Callinectes acutidens.- Boschi, 1964, p. 45, pl. 2, figs. e, f, g; pl. 12, figs. 1, 2.

?*Callinectes humphreyi* Jones, 1968, p. 187.

Description.—Carapace (Figure 6) with lateral pair of frontal teeth prominent but submesial pair small, often almost completely rudimentary. Metagastric area of adults not deeply sculptured, anterior width about 2.8-2.9 times length, posterior width about 1.75 times length. Anterolateral margins broadly arched, teeth exclusive of outer orbital and lateral spine progressively more acuminate laterad; first five teeth with posterior margins longer than anterior margins, shouldered, distinctly separated by narrow-based, rounded notches; last two teeth with margins approximately equal in length, separating notches broad, next to last tooth distinctly more acuminate than spiniform last one. Lateral spine trending forward. Surface of carapace with granulations most prominent on anterior half and on mesobranchial regions, granulations smaller and more closely crowded on meso-metagastric and cardiac regions, nearly smooth along posterolateral and posterior borders.

Chelipeds with smoothly granulated ridges on chelae, carpus almost smooth dorsally, inferior lateral ridge terminating in a low tooth occasionally followed by an inconspicuous eminence. Major chela usually with strong basal tooth on dactyl and, especially in adult males, lower margin of propodal finger often decurved near base.

Male abdomen and telson reaching beyond suture between thoracic sternites IV and V, usually with distal portions recessed below plane of sternum in retracted position; telson slightly longer than broad with somewhat inflated sides; sixth segment of abdomen relatively narrow, sides slightly constricted, not parallel. Mature female abdomen and telson reaching as far forward as in male, telson as broad as long. First gonopods of male (Figures 18d, 20d) reaching almost to suture between thoracic sternites VI and VII, overlapping each other completely near base but diverging distally and tapering to usually lanceolate membranous tip; armed subterminally with short retrogressive spinules quite visible at low magnification, somewhat more numerous and longer distally than proximally with tendency to arrangement in rows near tip on ventral and mesial margin. Gonopores of females (Figure 22d) irregularly ovate with apex on long axis directed anteromesad; aperture of each irregularly and broadly lunate, sloping from surface on mesial side under rounded crenate anterior border and rounded eminence on posterior border.

Size of carapace in mm.—Largest male: length 60, width at base of lateral spines 105, including lateral spines 130. Two largest females: length 58, width at base of lateral spines 84, including lateral spines 107—length 69, width at base of lateral spines 83, including lateral spines 99. These two females demonstrate variability in mature form that is characteristic of all species in the

genus. Summary of selected measurements is given in Tables 1 and 2.

Color.—Adult males with carapace dull olive to dark brown, usually with a large, ill-defined, roundish spot of orange or orange-red on each side posteriorly; lateral spines and anterolateral teeth maroon, light blue or whitish, white tipped. Eyestalks purple. Chelipeds proximally similar to carapace, spotted with blue or soft purple and with spines paler, joints red; inner surface of palm white, but with a large bright red patch bordered with purple; fingers mostly purple, tipped with red. Walking legs bright blue above, with a band of scarlet at each joint and a patch of paler blue or green on posterior and lower side of each article; dactyls red or violet. Swimming legs similar in color, but with red articular bands wider, a patch of orange or yellow on each article; dactyl with proximal blue band separated from distal scarlet band by an orange band. Abdomen light blue posteriorly. Females similar to males except upper surface of chela more violet; fingers with white or fuschia colored teeth.

Many individuals less brilliantly colored, juveniles often dull or plain olive-yellow to greenish above. Some males more melanistic, exhibiting shades of dark brown and purple with accents of yellow and brownish red. Albinistic (or light hued) forms not uncommon (Verrill, 1908a as condensed in Williams, 1966; Taissoun, 1969).

Variation.—A close relative of *C. danae* and *C. similis* (shape of carapace, metagastric area, and reduced submesial frontal teeth), *C. ornatus* is perhaps most often confused with *C. danae* because of their broad sympatric geographic ranges. *Callinectes ornatus* has the most obsolescent submesial frontal teeth of the three species, they being entirely absent in many individuals but developed somewhat in others. Within a single lot of equal-sized specimens both extremes may be seen (USNM 48401, Cuba; 18227, Jamaica) and keys to identification based on this character alone are of limited usefulness. The lateral pair of frontal teeth may have either rounded or quite sharp tips in the same lot of specimens (USNM 48401). Both types of variation in frontal teeth may be seen anywhere in the geographic range.

The anterolateral teeth are more acuminate, forward pointing, and longer than in *C. similis*. Brazilian and some Guianian juveniles in samples have erect anterolaterals, relatively longer for their width, and more cleanly separated than teeth on those from Florida, whereas adult specimens from Brazil (also North Carolina and some from Bermuda and Jamaica) tend to have narrower sharper anterolateral teeth than those from Venezuela, Curaçao, Cuba, and especially Florida. A line of iridescent patches occurs along the bases of anterolateral teeth in some individuals. One specimen from Trinidad (BMNH) has coalesced third and fourth teeth on the right side.

Major chelae may be broad, even on moderate sized juveniles (Florida).

The abdomen of males usually is recessed, but may be flush with the sternum as in immature male *C. similis* and *C. danae*, but is never as broad as in *C. similis*.

First gonopods of males usually extend forward to the anterior one-fourth of thoracic sternite VII, but may reach beyond the suture between thoracic sternites VI and VII among individuals in the same lot. Usually overlapping at the base, at least one specimen was seen in which no gonopod overlap occurred. The lanceolate tip is not always well developed in juveniles, and the membranous extreme tip tends to be longer in Brazilian (and North Carolinian) material than through most of the range.

Distribution.—Bermuda; North and South Carolina through southern Florida; northwestern Yucatán to Estado de São Paulo, Brazil (Figure 25).

Habitat.—Essentially a tropical species found mainly on sandy or muddy bottom from shore to about 75 m, the young have also been collected on shell and sponge bottoms. Occurrence in bays and river mouths (Holthuis, 1959; Rouse, 1970; in addition to collection data presented here), as well as entrapment in fresh water (Brues, 1927), indicate tolerance of a broad range of salinity (recordings of 0-50 ‰ in temperatures ranging from 18° to 31°C); nevertheless, most collections have come from waters of relatively high salinity. Taissoun (1969) reported occurrence in a temperature of 9°C, but this is perhaps a reference to *C. similis* which occurs in colder water.

Spawning.—The spawning season probably extends year round. Museum collections studied include ovigerous females as follows: January, Puerto Rico; April, Guyana, Estado de Rio de Janeiro, Brazil; May, Estado de São Paulo, Brazil;

July, Estado de Rio de Janeiro, Brazil; August, Trinidad, Guyana, Surinam; September, Venezuela, the Guianas; December, St. Thomas, Estado de Rio de Janeiro, Brazil. Taissoun (1969) reported ovigerous females from the Golfo de Venezuela in January and May. Undated collections are recorded from southern Florida, Margarita Island, Venezuela, and Estado de São Paulo, Brazil.

Remarks.—It is difficult to distinguish some juveniles, immature males, and adult females of *C. ornatus* from *C. danae* and *C. similis*. Helpful distinguishing comparisons are the following: males have a narrower abdomen than *C. danae;* mature females have a smaller abdomen than *C. danae;* identification of small- to moderate-sized juveniles is often a matter of judgment based on shape of anterolateral teeth, length of obsolescent submesial frontal teeth, and width of the metagastric area.

Width of the metagastric area approaches that of *C. similis* in some individuals and is a good separating character from *C. danae* for juveniles in regions where no confusion with *C. similis* can occur. Borders of this area are more prominently defined than in *C. similis,* but become indistinct with age; in that condition they approach the smoothness of young *C. similis. Callinectes ornatus* apparently shows less variation than *C. danae.*

Callinectes humphreyi Jones, 1968, was based on an albinistic immature female from Barbados (carapace length 29, total width 60 mm). Though its status must remain an enigma because the type was lost through accident in 1969 (dried specimen destroyed by a bloodhound pup; Jones, pers. commun.) and no illustration was furnished with the description, it was characterized as, "nearest to *C. ornatus,* from which it may be immediately distinguished by its very different coloring . . . . *C. humphreyi* is pure white, except for a band of intense violet-purple on the inner surface of each cheliped, which fades to light red in dried specimens. *C. humphreyi* is also distinguished by its smaller size, the deeper, more conspicuous sinuses between the anterolateral teeth, the relatively longer intramedial area and the distinctly triangular shape of the abdomen." The form was found to be quite common along the southwestern coast of the island where it was usually seen quite near shore at low tide, the white color camouflaging the animals well on the area's sandy bottom. In view of the obvious similarity to *C. ornatus,* endemic occurrence, and coloration falling within the range recognized by Verrill (1908a), it seems likely that this is a color variant of *C. ornatus.*

Williams (1966), in restricting *C. ornatus,* noted that syntypes from Charleston, S.C. were from a locality representing an apparent extreme northern limit of geographic range. At that time no other specimens were known from the Carolinas, although the species is abundant in southern Florida. Other material from northeastern Florida as well as North Carolina is now available. There is little doubt that these northern records still represent peripheral localities, as do those from southwestern Florida between Charlotte Harbor and Tampa Bay. Records for *C. ornatus* in New Jersey (Chace and Hobbs, 1969; Taissoun, 1969) represent *C. similis,* the Carolinian congener of *C. ornatus.* Collections from Bermuda are large, and it was primarily on the basis of these that Verrill (1908b) postulated drift of larvae in oceanic currents as island colonizers for the genus.

Locality data for specimens 30-6 and 30-8 in MNHNP (M. Fontaines) from "Chili" identified as *Neptunus diacanthus* Latr. (identified as *C. ornatus* by Rathbun, 1896) are in error.

Material.—Total: 351 lots, 1,260+ specimens.

Specimens listed in Rathbun (1930) from USNM and MCZ (listings from New Jersey, North Carolina, South Carolina, Louisiana, and Texas = *C. similis*).

USNM. 161 lots, 646 specimens, including the following not cited above:

BERMUDA

65644, Hungry Bay, Apr. 1928, 1 ♂, E. Deichmann.

UNITED STATES

North Carolina: 77013, Sea Buoy, Beaufort, 10 Oct. 1935, 1 ♂, 1 ♀, J. S. Gutsell.

Florida: 122995, 28°21.5′N, 80°33.5′W, 4 Apr. 1940, 1 ♂, *Pelican* Stn. 207-1. 122987, shoreline, W side Norris Cut, N end Virginia Key, Miami, 23 Aug. 1966, 1 ♀ (juv), col. unknown. 76989, Coral Gables, no date, 1 ♀, 1 juv, J. F. W. Pearson. 76966, Coral Gables, no date, 1 ♀ (parasitized), J. F. W. Pearson. 122994, Biscayne Bay, 5 Sept. 1938, 5 ♂, 5 ♀, USFWS Launch 58. 113459, Pigeon Key, Monroe Co., 7 Aug. 1965, 6 ♂, 4 ♀ (parasitized), R. B. Manning. 122988, beach area and tidal flats SW

end Bahia Honda Key, Monroe Co., 14 June 1964, 2 ♀ (juv), Foster and Kaill. The following from Key West—45805, no date, 1 ♂, H. Hemphill. 71638, 1934, 1 ♀, H. H. Darby. 76992, no date, 6 ♂, 5 ♀, col. unknown. 76988, front of Biol. Stn., 31 Oct. 1922, 7 juv, USBF, S. and F. 76987, no date, 1 ♂, USBF. 76986, front of Biol. Stn., 25 Nov. 1922, 1 ♀ (juv), USBF, F. and S. 76985, Little Salt Pond Key, 7 Nov. 1922, 1 ♂, 1 ♀, (juv), USBF. 76983, 26 Feb. 1919, 1 ♂, 1 ♀ (juv), USBF, H. and S. 76982, no date, 2 ♂, 1 ♀ (juv), USBF. 76981, Marquesas Keys, no date, 4 ♂, 2 ♀, A. S. Pearse. 122997, Marquesas Keys, 11 Aug. 1931, 8 juv, A. S. Pearse. The following from Dry Tortugas—76976, 5 Aug. 1930, 1 ♀ (juv), W. L. Schmitt. 76977, Long Beach, 7 Aug. 1930, 1 ♂, 1 ♀ (juv), W. L. Schmitt. 76978, Long Key, 25 June 1931, 1 ♂, W. L. Schmitt. 76995, from Long Key to Bush Key, 5 Aug. 1930, 1 ♂, 2 ♀ (1 ov), W. L. Schmitt. 77011, Long Key, 25 June 1931, 1 ♂, 1 juv, W. L. Schmitt. 76997, Long Key, Aug. 1930, 3 ♂, 1 ♀, W. L. Schmitt. 77012, Long Key, 24 June 1932, 3 juv, W. L. Schmitt. 76979, Fort Jefferson moat, 26 June 1931, 1 ♂, 1 ♀ (juvs), A. S. Pearse. 71637, Bush Key, 4 Aug. 1934, 1 ♂, 1 ♀, H. H. Darby. 113009, Charlotte Harbor, 30 July 1964, 4 ♀ (juv), from C. H. Saloman, USFWS, Stn. X-9A. 113010, Charlotte Harbor, 27 Jan. 1964, 1 ♂, 2 ♀ (juv), C. H. Saloman, USFWS, Stn. X-9A. 122989, oyster bed, Cape Haze Marine Lab., Sarasota, 21 July 1965, 1 ♂ (juv), R. Cressey. 113007, Tampa Bay, 9 Oct. 1964, 1 ♂ (juv), from C. H. Saloman, USFWS, Stn. B-13. 113008, Tampa Bay, 16 Sept. 1964, 1 ♀ (juv), from C. H. Saloman, USFWS, Stn. B-13.

Unknown locality "South Atlantic and Gulf Coasts of the United States": 2157, no date, 3 ♂, 2 ♀, col. unknown.

BAHAMAS

88653, Bimini, 13 Nov. 1948, 2 ♀ (juv), A. S. Pearse. 88654, Bimini, Nov. 1948, 1 ♀ (juv), A. S. Pearse. 122990, Clifton Bay, Lyford Cay, Nassau, 14 Aug. 1961, 1 ♂, 2 ♀ (juv), W. L. Schmitt. Uncatalogued, Great Inagua Island just N Matthewtown, 20 Jan. 1968, 1 ♂, Gosner. 76994, no date, 1 ♂, Owen Bryant. 122991, British West Indies, no date, 1 ♂, 1 ♀ (juv), R. Robbins.

CUBA

73306, Bahía de la Habana, 11 May 1937, 2 ♂, 5 ♀, W. L. Schmitt. 76481, Siguanea Bay, 12 Apr. 1937, 1 ♂, (juv), Paul Bartsch. 76485 and 76493, Isla de Pinos, opposite Siguanea I., 11 Apr. 1937, 50 juv, Paul Bartsch, R113 and R114. 76492, Isla de Pinos, opposite Siguanea I., 11 Apr. 1937, 2 ♂, Paul Bartsch, R115 and 116.

JAMAICA

122976, 17°53′N, 77°48′W, 18 May 1965, 2 ♂, 1 ♀, *Oregon* Stn. 5396. 73287, Jamaica or Cienfuegos, Cuba, 4 May 1937, 1 ♀, W. L. Schmitt, Stn. 76.

DOMINICAN REPUBLIC

122996, Bahía de Calderas, 1 ♀ (juv), through I. B. de Calventi and S. Jakowska, 10 July 1967.

PUERTO RICO

73286, San Juan, 27 Apr. 1937, 1 ♂, 1 ♀, W. L. Schmitt. 122999, off Fort San Gerónimo, San Juan, 30 Apr. 1937, 1 ♂, W. L. Schmitt.

VIRGIN ISLANDS

St. Thomas: 2457, no date, 1 ♂ (dry), A. H. Riise. St. Croix: 73288, Christiansted, 7 Apr. 1937, 1 ♀ (juv), W. L. Schmitt, Stn. 31. 73289, same, 9 Apr. 1937, 1 ♂, Stn. 34. 76470, Christiansted Harbor, Dec. 1937, 1 ♀, H. A. Beatty, No. 214. Prickly Pear Island: 122981, Vixen Point, Gorda Sound, 15 Apr. 1956, 2 ♂, Nicholson, Schmitt, and Chace, Stn. 111-56, *Freelance*.

BARBUDA

122982, Oyster Pond Landing, lagoon side, 25 Apr. 1959, 6 ♂, 3 ♀ (immat), W. L. Schmitt, et al., Stn. 92-59. 122980, near Oyster Pond Landing, W shore lagoon, 6 Apr. 1956, 4 ♂, 6 ♀ (immat), Schmitt, Chace, Nicholson, and Jackson, Stn. 85-86, *Freelance*. 122978, 6 Apr. 1956, 1 ♂, Stn. 88-56, *Freelance*.

GUADELOUPE

122977, Pointe à Pitre, between Monroux and Rat Is., 30-31 Mar. 1956, 10 (juv), Chace and Nicholson, Stn. 68-56, *Freelance*.

ST. LUCIA

122979, Marigot Lagoon, shore of bay outside, 21 Mar. 1956, 1 ♂, Schmitt, Chace, Nicholson, and crew, Stn. 38-56, *Freelance*.

BARBADOS

76993, 1918, 1 ♀, Barbados-Antigua Exped.

MEXICO

Yucatán: 12992, ocean beach at Progreso, 400 yd W steamship wharf, 30 Mar. 1936, 1 ♂, M. B.

Trautman. 12993, same, 600 yd W steamship wharf, 8 ♂ (6 juv), 1 ♀ (juv), Trautman, Patton, and Costello.

Quintana Roo: 122984, Bahía de la Ascensión, about ⅓ mi W Allen Pt. light, 13 Apr. 1960, 1 ♂, 3 ♀ (juv), Daiber and Rehder, Stn. 66-60, *Blue Goose*. 122983, Bahía de la Ascensión, shore in front Allen Pt. light, 13 Apr. 1960, 1 ♂, 2 ♀ (1 parasitized), 6 juv, Daiber, Stn. 65-60, *Blue Goose*. 122986, Bahía del Espíritu Santo, N shore, 5 Apr. 1960, 2 ♂, 2 ♀ (juv), Bousfield, Stn. 37-60, *Blue Goose*. 122985, Bahía del Espíritu Santo, N shore near Lawrence Pt., 6 Apr. 1960, 1 ♀ (juv), Rehder, Daiber, and Haynes, Stn. 42-60, *Blue Goose*.

BRITISH HONDURAS

76990, Belize, Sergeants Caye, no date, 2 ♀ (juv), P. W. Shufeldt.

VENEZUELA

101824, Estado Falcón, Bahía de Amuay, Península de Paraguaná, May 1957, 1 ♀, F. A. Aldrich. 122965, SE Trinidad and off Orinoco Delta, 09°55′N, 60°53′W, 26 Aug. 1958, 3 ♀ (1 ov, 1 juv), *Oregon* Stn. 2208. 122966, 09°32′N, 60°24′W, 20 Sept. 1958, 4 ♂, 5 ♀ (3 ov), *Oregon* Stn. 2348.

GUYANA

122970, 08°30′N, 58°56′W, 28 Aug. 1958, 1 ♀, *Oregon* Stn. 2228. 122969, 08°20′N, 58°30′W, 29 Aug. 1958, 4 ♀ (2 ov), *Oregon* Stn. 2234. 122975, 06°54′N, 57°47′W, 25 Mar. 1963, 1 ♂, *Oregon* Stn. 4306.

SURINAM

103177, 06°15′N, 55°54′W, 6 June 1957, 1 ♂, *Coquette* Stn. 182. 103178, 06°22′N, 55°03.5′W, 4 June 1957, 37 juv, *Coquette* Stn. 157. 103179, 06°22′N, 55°06′W, 11 May 1957, 1 ♂, *Coquette* Stn. 1. 103180, 06°23′N, 55°05.5′W, 11 May 1957, 1 ♂, 1 ♀ (juv), *Coquette* Stn. 2. 103181, 06°28′N, 54°57.5′W, 11 May 1957, 1 ♂ (juv), *Coquette* Stn. 20. 122968, 06°26′N, 54°20′W, 15 Sept. 1958, 1 ♂, *Oregon* Stn. 2327. 103454, 07°12′N, 57°22′W, 18 Sept. 1958, 1 ♀ (ov), *Oregon* Stn. 2339. 122967, off the Guianas, 1958, 1 ♀ (ov) *Oregon*.

FRENCH GUIANA

122971, 05°56′N, 52°20′W, 11 Sept. 1958, 1 ♀ (ov), *Oregon* Stn. 2307. 122972, off Cayenne, 05°30′N, 52°10′W, 12 Sept. 1958, 1 ♀ (ov), *Oregon* Stn. 2310.

BRAZIL

122973, off N mouth Amazon R., 02°29′N, 48°58′W, 14 Nov. 1957, 2 ♂, (1 juv), *Oregon* Stn. 2058. 122974, off Ceará, 02°23′S, 40°31′W, 12 Mar. 1963, 1 ♀, *Oregon* Stn. 4250. 72313, Villa Bella, São Sebastião, 18 Sept. 1925, 3 carapaces (dry), W. L. Schmitt. 122998, Barro, Santos, 12 Sept. 1925, 5 ♂, 1 ♀, W. L. Schmitt.

AHF. 13 lots, 26 specimens.

UNITED STATES

Florida: Hillsboro Inlet, Sept. 1943, 1 ♂, 2 ♀, (immat), E. R. T. Hillsboro Inlet, 15 May 1945, 1 ♂, 2 ♀, J. S. Garth, No. 8-45. Pompano Beach, Sept. 1944, 1 ♀ (juv), E. R. J. Hawk Channel, Key Largo North, 7 June 1949, 1 ♀ (juv), Stn. LM32-49. Same, 29-31 May 1949, 3 ♂, 3 ♀ (immat), Stn. LM25, LM-27. Key Largo, Florida Bay, 0.8 km SW "My Place" near Hamper Pt., 23 May 1949, 2 parasitized apparent ♀♀, Stn. LM18-49. Hawk Channel, Plantation Key near Tavernier Creek, 26 May 1949, 1 ♂ (juv), Stn. LM21-49. Lower Matecumbe Key, Hawk Channel, 5.3 km SW Indian Key Drawbridge, 23 Sept. 1950, 1 ♀ (juv), Stn. LM-57. Hawk Channel, Grassy Key, E coast 1.6 km S "Seaside Cabins," 24 May 1949, Stn. LM19-49. Margo Island near channel S Big Marco Pass, 14 June 1949, 1 ♂ (juv), Stn. LM39-49.

CURAÇAO

Schottegat, Santa Anna Harbor, 12°07′03″N, 68°55′34″W, 23 Apr. 1939, 2 ♀, *Velero III* Stn. A47-39.

VENEZUELA

Isla Cubagua, 10°48′48″N, 64°13′30″W, 30 Apr. 1939, 2 ♂, 1 frag., *Velero III* Stn. A30-39. Isla Cubagua, 10°49′25″N, 64°16′W, 15 Apr. 1939, 1 ♀ (juv), *Velero III* Stn. A28-39.

AMNH. 26 lots, 73+ specimens.

BERMUDA

11252, 2 Sept. 1932, 1 ♀ (juv), W. Beebe Bermuda Exped. 11223, 1939, 6 ♂, 2 ♀, (juv), W. Beebe Bermuda Exped. 295, no date, 1 ♂, W. M. Rankin. 11220, 1939, 1 ♂, W. Beebe Bermuda Exped. 11250, 1930, 1 ♀ (juv), W. Beebe Bermuda Exped. 11225, 1929, 1 ♂, W. Beebe Bermuda Exped. 11221, 29 Apr. 1937, 1 ♀, W. Beebe Bermuda Exped.

UNITED STATES

Florida: 6684, Indian River, Nov. 1920, 2 ♂ (juv), Prince. 10367, Lake Worth, July and Aug. 1945, 3 ♂ (1 dry), 1 ♀ (juv), W. G. Van Name and A. H. Verrill.

BAHAMAS

11222, North Bimini, June 1939, 1 ♀ (juv), W. Beebe Bermuda Exped. 11291, Bimini, 5 Sept. 1947, 1 ♀, J. C. Armstrong. 11292, Bimini, 1 ♀ (ov), J. C. Armstrong. 11634, Bimini, 14 June 1953, 1 ♀, W. D. Clarke. 11296, Bimini, 21 Oct. 1947, 3 ♂, 2 ♀, J. C. Armstrong. Nassau and Andros Islands, Mar.-Apr. 1930, 1 ♂ (juv), Bacon-Miner Exped. and International Exped. to Andros I. 10368, Andros I., 1926, 1 quart juv and immat, R. A. Miner.

HAITI

1949-1950, 2 ♂, 2 ♀ (1 juv), A. Curtiss. 11219, Bizoton Reef [NW Port au Prince], 4 Mar. 1927, 2 ♂ (1 juv), W. Beebe Exped.

DOMINICAN REPUBLIC

8641, W shore north half of El Cayo [Barahona Harbor], 7 July 1932, 1 ♂, 1 ♀ (juv), J. C. Armstrong. 9395, southern part La Piedra Prieta Reef, Barahona Harbor, 16 July 1932, 1 ♀ (juv), J. C. Armstrong.

PUERTO RICO

2945, Bahía de Guanica, Ensenada, 14 June 1915, 3 juv, R. W. Miner and H. Mueller. 2999, yard at Miramar, Santurce Barrio, San Juan, 14 July 1914, 1 juv, R. W. Miner and L. Estrada.

ANSP. 3 lots, 8 specimens.

UNITED STATES

4897, Lake Worth Inlet, Fla., no date, 1 ♂ (immat), 4 ♀ (immat), H. A. Pilsbry.

BAHAMAS

3489, New Providence Island, no date, 1 ♂, 1 ♀, H. C. Wood, Jr.

HAITI

5422, Port au Prince, 1950, 1 ♂ (dry), A. Curtis.

BMNH. 11 lots, 18 specimens.

UNITED STATES

Florida: 1966.12.5.558/559, coast of Everglades Park, 1 ♂, 1 ♀, Univ. Miami Inst. Mar. Sci. 61.44, south coast of United States, 2 ♂, 3 juv (dry), vi/9, W. Stimpson.

CARIBBEAN SEA

1955.10.6.98/99, Stn. 28 (44), 1 ♂, 1 ♀ (juv), Oxford Univ. Cayman Exped.

ANTIGUA

1967.4.4.136, 1 ♀ (juv), F. H. Mansell, H. M. S. *Dorsetshire*. 1928.12.1.57, 1 ♂, W. R. Forrest.

BARBADOS

1963.5.16.33, 1 ♀, H. M. S. *Frobisher*, 15 Feb. 1933.

TRINIDAD

1962.12.12.2, Mayaro-Point Radix, Stn. 1125, 1 ♂, D. W. Richardson. Unregistered, San Fernanda, 1 ♀, N. Boutakoff.

GUYANA

1958.11.12.27/28, 07°39′N, 57°44′W to 07°47′N, 57°32′W, 23-24 Apr. 1958, 1 ♂, 1 ♀ (ov), Trawler *Cape St. Mary*.

BRAZIL

50.32, 1 ♀ (dry), vi/6.

MCZ. 32 lots, 106 specimens.

BERMUDA

8377, July 1903, 2 juv, O. Bryant. 8459, Sinky Bay, 30 May 1916, 1 ♂, Bermuda Biol. Stn. 8460, Fairyland Bay in eelgrass, 14 Feb. 1916, 1 ♂, W. J. Crozier. 8890, 1 ♂, recd. from E. L. Mark, 19 Oct. 1920. 8891, Tom Woods Bay, 25 Apr. 1916, 1 ♂, 2 ♀ (juv), E. L. Mark. 8892, Sinky Bay, 11 Apr. 1916, 1 ♂ (immat), E. L. Mark. 9203, Richardsons Inlet, S side St. George Island, June 1936, 5 ♂, 6 ♀ (immat), F. A. Chace, Jr. 9256, Vaughns or Whites Bay, St. Davids Island, 18 June 1936, 4 ♂ (juv), F. A. Chace, Jr. 9447, July 1936, 2 juv, L. H. Kleinholtz.

UNITED STATES

South Carolina: 5210, Charleston, no date, 2 ♀ labelled "Types," col. unknown.

Florida: 8749, 1 ♀ (ov), Maynard. 5130, Key West, no date, 1 ♀, C. E. Faxon. 1134, Tortugas, 1 ♀ (juv), Holder, recd. 8 June 1960. 8748, July 1859, 4 ♂, 2 ♀ (juv), Woodbury. 5131, Tortugas, 3 ♂, 1 ♀, Woodbury, recd. from Smithson. Inst., 13 Feb. 1861. 5206, Fort Jefferson, Tortugas, 3 ♂, part of Ordway's material.

BAHAMAS

9481, N entrance Hawksbill Creek, Grand Bahama Island, 8 Apr. 1936. 1 ♂, W. J. Clench. 11673, Alicetown, North Bimini, May 1941, 1 ♀, R. W. Foster and J. Huntington. 9488, Governors Harbor, Eleuthera Island, 2 May 1936, 1 ♂, W. J. Clench. 9426, Simms, Long Island, 7 July 1936, 1 ♂ (juv), Harvard-Bahama Exped.

MNB. 4 lots, 17 specimens.

BRAZIL

Pernambuco: 331, Praia do Pina, Recife, Sept. 1944, 3 ♀ (juv), col. unknown.

Rio de Janeiro: 49, no other data, 1 ♂. 82, Rio Guanabara, no other data, 2 ♂, 9 ♀ (3 juv). Praia do Fundao, Baía de Guanabara, Dec. 1951, 2 ♂, N. Santos.

MNHNP. 9 lots, 16 specimens.

UNITED STATES

Florida: Tortugas, 4 ♂, from MCZ.

FRENCH GUIANA

Stn. 354, 23 m, mud, 12 Aug. 1957, 2 ♂, 1 ♀, juv, J. Durand, ORSTOM II. Stn. 413, 48 m, dead shells-rocks, 24 July 1958, 1 juv, J. Durand, ORSTOM II. Îles du Salut, July 1957, 2 ♂, 1 ♀, J. Durand, ORSTOM II.

Following are a series of dry specimens with poor or questionable locality data that were also determined by M. J. Rathbun in 1896.

Guadeloupe: 1 ♂, 1 ♀, M. Beaupertuis. Chili: 1 ♂, 30-6, 1 ♀, 30-8, M. Fontaines. Côte de Amérique, 1 ♂, 30-19.

RMNH. 60 lots, 200+ specimens.

UNITED STATES

Florida: Bear Cut, N point Key Biscayne, Miami, 15802, 15 Sept. 1960, juv. 15803, 4 Sept. 1960, juv. 15804, 14 Sept. 1960, juv. 15805, 15 Sept. 1960, juv. 18718, 2-9 Sept. 1963, 1 juv. 23385, 6 Dec. 1964, 1 ♀ (parasitized). 24372, 22 Nov. 1964, juv. 23366, 1 Jan. 1965, juv (parasitized). 23415, 9 Jan. 1965, 1 ♂, juv. 23418, Jan. 1965, 1 ♂, juv. 24371, 1 Jan. 1965, juv. 24373, 10 Jan. 1965, juv. 23430, 9 Jan. 1965, juv (parasitized). 23421, 1 Feb. 1965, 1 ♂ and juv (parasitized), all by J. A. Cabrera and L. B. Holthuis. 23271, 16 Jan. 1965, 2 ♀ (parasitized), L. B. Holthuis. 18717, 1-9 Sept. 1963, 2 ♂, 1 juv, L. B. Holthuis. 23377, Pigeon Key, W Marathon, 30 Jan. 1965, 1 ♂, L. B. Holthuis and J. A. Cabrera. 4920, Tortugas, July 1925, juv, H. Boschma. 15632, Marco Beach S of Marco, 12 Sept. 1960, 1 ♀, beached after hurricane Donna, L. B. Holthuis.

BAHAMAS

2853, Nassau, New Providence, 1887, 2 ♂, 1 ♀, A. de Haas. 1870, Bahama Islands, no date, 1 ♂, 1 ♀, Dr. de Haas.

ST. MARTINS

23457, freshwater pond, 3 Oct. 1963, 2 ♀ (juv), P. W. Hummelinck. 14997, Great Bay, 23 June 1955, 2 juv, P. W. Hummelinck. 11870, Oyster Pond, E coast, 22 Feb. 1957, 4 juv, L. B. Holthuis. 11872, coast near Philipsburg, 16-17 Feb. 1957, 1 ♀, 2 juv, L. B. Holthuis. Simsons Bay, washed ashore on beach, 19 Feb. 1957, 1 carapace (dry), L. B. Holthuis. 11873, freshwater pond W Philipsburg, 17 Feb. 1957, 3 ♂, 1 ♀, 1 juv, L. B. Holthuis. 11875, Simsons Bay, 23 Feb. 1957, 20 juv, L. B. Holthuis.

VENEZUELA

10721, Margarita Island?, possibly Caracus Bay, Curaçao, 1955, 2 ♀ (1 ov), P. W. Hummelinck. 1868, coast, no date, 1 ♂ (juv), T. Buitendijk.

ARUBA

2372, Vaardenbaai (?), 1 June 1905, 1 ♂, Prof. Boeke. Pova Beach, NW coast of island, 27 Apr. 1955, 3 ♂ (dry), J. S. Zaneveld and P. W. Hummelinck. 1307, 1883, 1 ♂, K. Martin. 2261, lagoon, 3 July 1905, 1 ♂ (juv), Prof. Boeke. 1867, June 1883, 1 ♀ (juv), A. J. v. Koolwijk. 1869, July 1883, 1 ♂ (juv), Dr. de Haas.

CURAÇAO

St. Kruis Baai, 7 Oct. 1948, 2 juv, P. W. Hummelinck. 23351, NW part Piscadera Baai, 25 Nov. 1963, 5 juv, P. W. Hummelinck. Piscadera Baai, 16 Mar. 1957, 1 carapace (beached, dry), L. B. Holthuis. 23393, S part Piscadera Baai, 15 Oct 1963, 1 ♀, col. unknown. 11874, Piscadera Baai, fish trap, 11-14 Feb. 1957, 1 ♂, 1 ♀, L. B. Holthuis. 3272, Schottegat, 10 Feb. 1939, 5+ ♂, 2 ♀, H. W. C. Cossee. 2234, reefwater (lagoon), 2 m, 26 July 1905, 1 ♂ (juv), Prof. Boeke.

BONAIRE

NE coast of Cay, 1 Sept. 1948, 2 ♂, P. W. Hummelinck.

GUYANA

22510, 06°54′N, 57°47′W, 25 Mar. 1963, 2 ♂, *Oregon* Stn. 4306.

SURINAM

22518, 06°16′N, 55°56′W, 19 Feb. 1963, 2 ♂, 2 ♀ (juv), *Oregon* Stn. 4171. 21154, off coast between mouths of Suriname and Coppename Rivers, 25-27 Aug. 1964, 1 ♀ (ov), juv, *Coquette*. 11869, 10 mi N mouth of Suriname R., 6-9 May 1957, juv and subadult, *Coquette*. 14999, mouth Suriname R. near Resolutie, 22 Dec. 1942, 1 juv, D. C. Geijskes. 14996, near lightship *Suriname Rivier*, 3 May 1957, 1 juv, *Coquette*. 18672, 20 mi E lightship *Suriname Rivier*, 20 Feb. 1963, 1 ♂, *Coquette*. 11871, 20 mi from coast, NNW mouth Marowijne R., 8-12 Apr. 1957, 1 ♂ (juv), *Coquette*.

FRENCH GUIANA

11868, 06°00′N, 53°29′W, 29 May 1957, 2 ♂, juv, *Coquette*. 14998, 05°56′N, 53°17′W, 21 May 1957, 1 juv, *Coquette*.

BRAZIL

São Paulo: 21587, Ribeira Beach, Ubatuba, 18 July 1962, 1 ♂, L. Forneris. 21694, Enseada Palmas, Anchieta I., Ubatuba, 28 Feb. 1962, 1 ♂ (juv), L. Forneris. 21695, Pedra Andorinha, Ubatuba, 22 Jan. 1963, 1 juv, L. Forneris. 17536, Santos, 12 Sept. 1960, 3 juv, L. R. Tommasi. 17537, Santos, 20 Apr. 1961, 1 ♂ (juv), L. R. Tommasi.

SADZ-B. 27 lots, 125 specimens.

UNITED STATES

Florida: 1466, Key West, 1883, 2 subadult carapaces (dry), Jordan.

BRAZIL

Rio de Janeiro: 1728, Atafona, 1964, 2 ♂, 1 ♀, N. Meneses. 1959, Praia do Forma, Cabo Frio, July 1957, 1 ♂ (juv), Luiz Tommazi. 3255, Praia do Forte, Cabo Frio, Jan. 1964, 1 ♀, S. J. Rand, N. Papanen, S. Tocchetreu, and S. Tacla. 2336, Ilha Grande, Dec. 1965, 1 ♀ (ov), *Emilia* Stn. 14. 3084, Ilha Grande, 30 July 1966, 1 ♀ (ov), *Emilia* Stn. c-288. 2335, Ilha Grande, no date, 1 ♀, Stn. 12. 3226, S side Ilha Grande, 43 m, mud, 17.8°C, 26 Apr. 1968, 2 ♀ (1 ov), Hydrographic Stn. 283. 3247, 25 m, dredge, 11 Nov. 1956, 1 ♂, Corvette *Solimoés* Stn. 99/56. 3249, Ilha Grande, Aug. 1960, 2 ♂, *Emilia* Stn. 1. 3261, 3228, Enseada das Estrêlas, Ilha Grande, 18 July 1966, 27 ♂, 5 ♀, 16 juv, G. Melo. 3237, Enseada das Estrêlas, Ilha Grande, 26 Feb. 1966, 22 ♂, 5 ♀, col. unknown. 2339, Enseada das Estrêlas, Ilha Grande, 26 July 1966, 1 ♂, 1 ♀, G. Melo. 3082, Angra dos Reis, Ilha dos Conqueiros, 21 Apr. 1966, 1 ♂, G. Melo.

São Paulo: 3217, Ubatuba, 1905, 1 ♂, E. Garbe. 3259, Ubatuba, 1905, 1 ♀ (juv), E. Garbe. 1745, Ilha Bela, São Sebastião, Mar. 1962, 1 ♂, 1 ♀ (juv), P. E. Vanzolini. 3227, São Sebastião, 1895 [?], 1 ♀ (juv), H. Britski. 348, Ilha São Sebastião, 1915, 8 ♂, 2 ♀ (1 ov), Bicego. 1740, Praia Grande, São Sebastião, Feb. 1962, 2 ♂ (juv), H. Britski. 2109, Santos, 1959, 1 ♂, 1 ♀, Servico Especial Pesca. 1673, Ilha da Moela [near Santos off Guarujá], 18 May 1962, 3 ♂, 2 ♀ (1 ov), C. Jesús. 1671, Baía do Guarujá, 22 May 1962, 1 ♂, 1 ♀, C. Jesús. Praia Grande, São Vincente, 4 Aug. 1954, 1 ♂, 1 ♀, L. Travassas, E. Dente, and Werner. 2064, unknown locality, July 1959, 2 ♂, 2 ♀, *Emilia* (first trip).

YPM. 5 lots, 25+ specimens

BERMUDA

3850, 1901, 1 ♀ (juv), A. E. Verrill and party. 6397, April 1901, 5 ♂, 4 ♀, A. E. Verrill and party. 6398, 1901, 4 ♂, A. E. Verrill and party. 6392, 1901, 1 ♂, Bermuda Biol. Stn. 6394, 1901, several juv, A. E. Verrill and party.

Supplementary literature records.—Southern Florida (Rouse, 1970); Isla de Pinos, Cuba (Boone, 1927).

CALLINECTES DANAE SMITH

Figures 7, 18e, 20e-f, 22e, 24

Lupa dicantha.- Dana, 1852, p. 272, (type: 1 ♂, dry, USNM 2371, Rio de Janeiro, Brazil).- 1855, pl. 16, fig. 7a-c.

Callinectes diacanthus.- Ordway, 1863, p. 575 [10].- A. Milne Edwards, 1879, p. 226 (var. of *C. diacanthus*).- Young, 1900, p. 186 (part).

?*Neptunus diacanthus*.- Heller, 1868, p. 26.- Doflein, 1899, p. 186 (part, the Colombia and Brazil specimens).

Callinectes Danae Smith, 1869, p. 7 (syntypes: 1 ♂, 1 ♀, MCZ 5143; 1 ♂, 1 ♀, YPM 824, Recife [=Pernambuco, Estado de Pernambuco], Brazil, C. F. Hartt). (Type locality restricted by Rathbun, 1930.)

?*Lupa (Neptunus) diacantha*.- von Martens, 1872,

p. 92, (part, the Rio de Janeiro specimens).

Callinectes danae.- Rathbun, 1896, p. 357, pl. 16; pl. 24, fig. 4; pl. 25, fig. 3; pl. 26, fig. 3; pl. 27, fig. 3.- 1898, p. 596.- 1901, p. 48.- 1930, p. 118 (part), text-figs. 15d, 16d, 17b, 18d, pl. 51.- 1933, p. 49.- Verrill, 1908a, p. 370, fig. 22e (not 22d).- Chace, 1940, p. 33.- Chace and Hobbs, 1969, p. 130, fig. 37b.- Holthuis, 1959, p. 201.- Lemos de Castro, 1962, p. 39, pl. 2, fig. 9.- Williams, 1966, p. 86, fig. 2A-D, 4C, D.- Jones, 1968, p. 187.- Taissoun, 1969, p. 75, fig. 28A-D, photo 10.- 1973, p. 33, figs. 4B, 5D, photo 4.

Callinectes.- Kretz and Bücherl, 1940, p. 173, unnumbered col. pl., figs. 1-22.

Description. — Carapace (Figure 7) bearing four frontal teeth, submesial pair no more than half length of lateral pair. Metagastric area of adults with anterior width about 2-2.5 times length, posterior width about 1.5 times length. Anterolateral margins somewhat arched, teeth exclusive of outer orbital and lateral spine varying from often convex sided with subacute tips at orbital end of row to sharper and more spiniform laterally, each with anterior margin shorter than posterior and separated from contiguous ones by narrow-based rounded notches. Surface of carapace rather evenly and smoothly granulate, except granules more widely spaced on epibranchial region and near anterolateral border, most crowded on gastric, mesobranchial, and cardiac regions; nearly smooth along frontoorbital, posterolateral, and posterior borders.

Chelipeds with granulate ridges, upper surface of carpus bearing slightly developed interrupted ridges trending longitudinally with axis of limb, ridges bearing obsolescent granules often better developed in males than in females, inferior lateral ridge terminating in a strong lateral spine or tooth often followed by a strong eminence. Male abdomen and telson reaching beyond suture between thoracic sternites IV and V; telson triangular, longer than broad with somewhat inflated sides; sixth segment of abdomen with sides nearly straight, diverging proximally, poorly calcified proximally except for variably indurated basal portion often connected to distal part by a narrow central column. Mature female abdomen and telson reaching as far forward as in male, sixth segment shorter than fifth, telson triangular with slightly inflated sides. First gonopods of male (Figures 18e, 20e, f) reaching beyond midpoint of thoracic sternite VI, overlapping each other near base, or adjacent, and tapering to narrow membranous tips usually bent ventrolaterally; armed with scattered but mainly dorsal minute spinules and two to four subterminal sternomesial exceedingly slender elongate spinules. Gonopores of females (Figure 22e) broadly and irregularly ovate with apex on long axis directed anteromesad, aperture of each broadly open mesially, narrowing laterally, and sloping from surface on mesial side under curved and rounded superior border and a rounded prominence on posterolateral border.

Size of carapace in mm.—Largest male: length 58, width at base of lateral spines 104, including lateral spines 139. Largest female: length 48, width at base of lateral spines 84, including lateral spines 108. Summary of selected measurements is given in Tables 1 and 2.

Color.—Live males from Cubatão River near Santos, São Paulo, Brazil: Carapace olive, becoming indigo on edges of lateral spines and outer anterolateral teeth in some individuals, more uniformly olive in others; teeth and spines on chelae white tipped; a white patch in deepest part of depression above third walking leg. Cheliped with upper surface of palm, dactyl, part of carpus, and spined edge of merus indigo to purple, and same color in splashes on inside of fingers, distally on merus and laterally on carpus. Flat outer dorsal surface of palm and upper surface of merus reticulate blue and olive (but many crabs predominantly olive on this part). Walking and swimming legs predominantly china blue to azure blue, grading to greenish and olive in darker parts. Lower edge of chelae grading from purple to china blue or azure individually. Chelipeds with inner face of palm, outer face of palm and fingers, lower face of merus, as well as meri of remaining legs and ventral surface of cephalothorax, white.

Described above is a colorful male which should be called the "purple crab" if *C. sapidus* is called a "blue crab." Some individuals are duller and some have a reticulate pinkish-blue cast on the upper surface of chelipeds.

Color notes by Kretz and Bücherl (1940) and Taissoun (1969) emphasized the distal intense purple coloration of legs and a grayish-blue carapace on adult males.

Variation.—Individual variation of first gonopods outlined by Williams (1966) can be elaborated here. The first gonopods of males vary somewhat in length, being either a little longer or shorter than as described above (long in southern, short in northern parts of the range). Males from Rio de Janeiro, Brazil, southward tend to have first gonopods reaching near or beyond the suture between thoracic sternites V and VI, as do some specimens examined from St. Lucia in the Windward Islands, but some south Brazilian specimens have shorter first gonopods. Males from north of Rio de Janeiro, northeastern South America, and the West Indies tend to have first gonopods reaching from near the middle of thoracic sternite VI to the suture between thoracic sternites VI and VII. The ill defined shortening trend is accentuated in Cuban, Honduran, and a single lot of Floridian material, reaching extreme shortness in the Panamanian region of the Caribbean, especially in USNM lot 43931 in which male gonopods extend only to the suture between thoracic sternites VII and VIII. But in these areas, too, there is enough variation that groupings are hard to define.

The lower margin of the major chela is often decurved opposite the molar complex of the propodus and strongly developed proximal tooth of the dactyl.

Distribution.—Bermuda; southern Florida and eastern side of Yucatán Peninsula to Estado de Santa Catarina, Brazil (Figure 24).

Habitat.—*Callinectes danae* is a common species in Brazil where it occurs from muddy estuaries in mangroves and algae covered broken shell bottoms, to beaches and open ocean depths of 75 m. Specific limits of salinity tolerated are not well documented, but ranges indicated are from fresh to full sea water, and perhaps to hypersaline lagoons.

Kretz and Bücherl (1940) gave no specific designation to species of *Callinectes* studied, but they gave (p. 173) a fairly clear description of the first gonopods of *C. danae*, and their figures, especially 2 and 14, indicate this species. *Callinectes danae* is the most abundant member of the genus along beaches from Santos to Rio de Janeiro where they worked.

Park (1969) found *C. danae* only on or adjacent to the ocean side of islands in Biscayne Bay, usually on wave beaten shores. He reported it absent from the Florida Keys.

Spawning.—The spawning season probably extends year round. Museum collections studied include ovigerous females as follows: January, Surinam; February, Rio de Janeiro; March, Puerto Rico, Haiti, Panama; May, Haiti, Estado de São Paulo, Brazil; June, Estado de São Paulo, Brazil; July, Colombia, Rio de Janeiro; August, Estados de Rio de Janeiro and Santa Catarina, Brazil; November, Curaçao, St. Lucia. Undated collections are from Estados de Bahia, Rio de Janeiro, São Paulo, and Santa Catarina, Brazil. Taissoun (1969) reported an abundance of ovigerous females from May to July in the Golfo de Venezuela, implying an even longer spawning season.

Economic importance.—Literature available does not deal with commercial exploitation of this species except that incidental reports of purchase in markets and capture on fishing vessels imply fairly general usage.

Vendors along roads NW of Santos, Estado de São Paulo, Brazil, near mangrove swamps sell the crabs alive, displaying bunches of a dozen or so each suspended on strings to which the crabs cling by the chelae when they are out of water.

Remarks.—Closest structurally to *C. arcuatus*, its Pacific counterpart (shape of carapace, metagastric region, male first gonopods, and frontal teeth), *C. danae* also shows similarity to *C. marginatus*. The metagastric area is much alike in all three species. In *C. marginatus* the well separated anterolateral teeth trend forward, and the portion of carapace anterior to the epibranchial line is coarsely granulate. In both *C. arcuatus* and *C. danae*, although anterior borders of the anterolateral teeth are shorter than posterior borders, the teeth point outward rather than sweep forward. *Callinectes danae* is quite smoothly granulate over most of the carapace; *C. arcuatus* is much the same but shows more sculptured relief. Among males of the three, *C. marginatus* has much the slenderest abdomen for its length. The telson of *C. danae* males is relatively longer than in *C. arcuatus*.

Width of the sixth abdominal segment in adult female *C. danae* is relatively greater than in adult female *C. ornatus*, a character valued by Rathbun (1930) but one that requires practice to assess. Williams (1966) misnumbered the sixth abdominal segment as the fifth in discussing this character.

Specimens of *C. danae* reported from Chile in literature must be regarded as of uncertain origin, either mistakenly identified with this Atlantic species by early naturalists unfamiliar with similar Pacific forms, or carried from the Atlantic to Pacific sides of South America by sea captains or collectors who recorded destination of voyages as country of origin rather than source of collection (Garth, 1957). Locality data for USNM 20270 (1 ♂), and MNHNP 30.3, 30.2, 30.10, 30.11, 3 [?], S31 (dry, 5 ♂, 1 ♀) listed as "Chili," and 30.20 (1 ♂, dry) as "Amerique" [labelled as *Neptunus diacanthus*], col. Fontaines, are erroneous or incomplete. Corrected identifications were also made by Rathbun in 1896.

A carapace and abdomen of an immature male from the Pleistocene of Maryland (Wailes Bluff: Bed 1) reported as *Callinectes ornatus* by Blake (1953) is probably *C. danae*. Shape of the abdomen is nearer to *C. danae* or *C. similis* than *C. ornatus*, and the metagastric area in both proportions and granulation is most like the average condition for modern *C. danae*, next nearest to *C. sapidus*, and not like *C. ornatus*.

Material.—Total: 202 lots, 782+ specimens.

Specimens listed in Rathbun (1930) from USNM (24427, 24428, 24429, 22044, not found; 20115, 22817 = *C. similis;* 60984 = *C. ornatus;* 1 ♂, 1 ♀ 40591 = *C. marginatus*) and MCZ (4278 not found).

USNM. 86 lots, 310+ specimens, including the following not cited above:

UNITED STATES

Florida: 77087, Long Key, Tortugas, 5 Aug. 1930, 1 ♂ juv, W. Bullington. [?] Uncatalogued, Pompano Beach, Sept. 1943, 1 ♂, E. R. Tinkham.

CUBA

123003, Bahía del a Habana, 11 May 1937, 2 ♂, W. L. Schmitt. 99862, Playa Baracoa, 16 Nov. 1954, 1 ♂ juv, K. K. Caldwell et al. 99916, Playa Baracoa, Fisheries Lab., 16 Nov. 1954, 1 ♀, H. H. Hobbs, Jr. 99937, E Xanadú, Hicacos Pen., Matanzas Prov., 24-27 Jan. 1957, 1 ♂, W. L. Schmitt.

JAMAICA

42854, Montego Bay, 20 July 1910, 1 ♂ juv, C. B. Wilson. 46246, Montego Bay, 12 Nov. 1910, 1 ♂, A. E. Andrews. 61364, 4 Feb. 1928, 2 ♀ juv, C. R. Orcutt.

PUERTO RICO

24421, Palo Seco, Bahía de San Juan, 13 Jan. 1899, juv 2 ♂, 1 ♀, *Fish Hawk*. 123004, Bahía de San Juan, 29 Mar. 1937, 1 ♀, W. L. Schmitt. 73280, Boca de Cangrejos, 7 mi E San Juan, 31 Mar. 1937, 1 ♀ (ov), W. L. Schmitt.

VIRGIN ISLANDS

St. Croix: 77101, Rust-op-Twist, on sea coast, no date, 1 ♂, 2 juv, H. A. Beatty. 72833, St. Croix, Salt River, no date, 8 juv, H. A. Beatty.

ST. LUCIA

22044, Port Castries, 29 Nov. 1887, 5 ♂, 6 ♀, *Albatross*.

MEXICO

Quintana Roo: 123002, Bahía del Espíritu Santo, N shore, 5 Apr. 1960, 1 ♂ (parasitized), E. L. Bousfield.

HONDURAS

78099, Utila I., 25 mi off coast, Sept. 1938, 1 ♂, Louis Mouquin.

PANAMA

59283, 1912, 2 ♂, 2 ♀, 4 juv, Meek and Hildebrand. 59344, no date, 1 ♀, Meek and Hildebrand. 77089, Fox Bay, Colón, 23 Feb. 1935, 2 ♂ juv, S. F. Hildebrand. 89575, Galeta Pt., Ft. Randolph, C. Z., 1949, 2 ♀, 1 juv, V. Walters.

COLOMBIA

105034, Golfo del Darién, 7°56.8′N, 76°47′W to 7°56.5′N, 76°47′W, 8 Feb. 1960, 1 ♀ juv, *Atlantis*.

VENEZUELA

Falcón: 101825, Bahía de Amuay, Península de Paraguaná, May 1957, 1 ♂, F. A. Aldrich. Miranda: 89645, Tacarigua de la Laguna, 1 Mar. 1949, 1 ♂, Soc. Cienc. Nat. La Salle, Stn. C-4. Sucre: Gulf of Paria, 10°29′N, 62°30′W, 24 Oct. 1963, 1 ♂, *Oregon* Stn. 4495. Delta Amacuro: 123001, off Orinoco Delta, 09°39′N, 60°49′W, 26-27 Aug. 1958, 1 ♀, *Oregon* Stn. 2211.

BRAZIL

40590, 1875-77, 1 ♀ juv, Hartt. Rio de Janeiro: 77086, São Francisco, 25 Aug. 1925, 1 ♂, 2 ♀ juv, W. L. Schmitt. 77107, Porto da Inhauma, May 1935, 11 ♂, 12 ♀, Doris Cochran. Paraná: 77095, 77096, Paranaguá, 3 Oct. 1925, 4 ♂, 1 ♀ juv, W. L. Schmitt.

AHF. 3 lots, 3 specimens.

CURAÇAO
Schottegat, Santa Anna Harbor, 23 Apr. 1939, 1 ♂, *Velero III* Stn. A47-39.

TRINIDAD
West Manzanilla, 10°30′N, 61°02′W, 18 Apr. 1939, 1 ♀, *Velero III* Stn. A36-39. Port of Spain, 18 Apr. 1939, 1 ♂, *Velero III* Stn. A37-39.

AMNH. 13 lots, 57 specimens.

HAITI
11219, Bizoton Reef, 4 Mar. 1927, 1 ♀ (ov), W. Beebe Exped. 11224, 21 May 1927, 2 ♀ (ov), W. Beebe. 11242, 1927, 1 ♀, W. Beebe. Unreg. 1949-50, 1 ♂, A. Curtiss.

SANTO DOMINGO
9393, NW corner Bahía de Neiba, Bahía de Barahona, 6 July 1933, 23 juv, J. C. Armstrong. 9394, N half of El Cay, Bahía de Barahona, 7 July 1933, 1 ♂, J. C. Armstrong.

PUERTO RICO
2681, Ensenada, 17 June 1915, 1 ♀, R. W. Miner. 2695, Ensenada, June 1915, 2 ♀, Mayer. 2665, San Juan, Palo Seco Pt., 18 July 1914, 7 ♂, 5 ♀, R. W. Miner. 2899, San Juan, 17 July 1914, 1 ♂, R. W. Miner. 2687, San Juan, 1 Aug. 1914, local boys. 2680, Id. S Catano R. mouth Cano de San Fernando, San Juan, 11 July 1914, 1 ♂, 1 ♀, R. W. Miner and J. T. N..

PANAMA
11241, Bahía de Colón, no date, 4 ♂, 5 ♀, *Arcturus* Exped.

ANSP. 2 lots, 3 specimens.

UNITED STATES
3394, America, no date, 1 ♂, 1 ♀, E. Wilson and I. Lea [listed in catalogue as N. America].

CUBA
4697, Cojímar near La Habana, 10 July 1940, 1 ♂, R. A. McLean.

BMNH. 13 lots, 20 specimens.

BARBADOS
72.28, no date, 2 ♂ juv, F. G. Beckford.

WEST INDIES
43.7, no date, 1 ♀ (dry) vi/9.

TRINIDAD
1962.12.12.1, Tapora Point, 1 ♂, D. W. Richardson, Stn. 1123. Unreg., San Fernando, 2 ♂, N. Boutakoff. 1962, Tapora Point, 9 Feb. 1962, 1 ♂ juv, D. W. Richardson, Stn. 1121/3.

BRAZIL
919b, 2 ♂ (dry) vi/6/7, C. Stewart. 919a, 1 ♂ (dry) vi/7, C. Stewart. Pernambuco: 80.37, juv. 1 ♂, 1 ♀, W. Forbes. Bahia: unreg., 1 ♂ (dry) vi/6. Rio de Janeiro: 1952.3.6.12, 1948, 1 ♂, P. Drach. 74.20, 3 ♀ (2 ov), A. Fry. 50.32, Rio de J. market, 2 ♂, juv (dry) vi/6/7, Rothesay.

MCZ. 10 lots, 102 specimens including the following not cited above.

CUBA
10886, Cienfuegos, 29 Mar.-1 Apr. 1939, 3 ♂, 2 ♀, Harvard-Havana *Atlantis* Exped.

COLOMBIA
5135, Cartagena, no date, 1 ♂ juv, A. Schott.

TRINIDAD
9975, Otheite, 9 mi N La Brea, 22 Aug. 1937, 1 ♂, 1 ♀, 2 juv, E. Deichmann. 9958, Caroni Swamp, 8 Aug. 1937, 1 ♂, 3 ♀, E. Deichmann.

BRAZIL
Rio de Janeiro: 5145, no date, 61 specimens. Thayer Exped. 5146, recd. 1 Dec. 1863, 4 ♂, G. N. Davis. São Paulo: 5142, Santos, no date, 4 ♂, 1 ♀ juv, Coutinho, Thayer Exped.

MNB. 7 lots, 44 specimens.

BRAZIL
Pernambuco: 60, no date, 24 ♂, 5 ♀. Rio de Janeiro: 65, Rio-Guanabara, 2 ♂. Unnumbered, Praia do Fundão, Baia de Guanabara, Dec. 1951, 1 ♂, N. Santos. 51, Rio-Guanabara, 5 ♂, 3 ♀. 260, Recreio dos Bandeirantes-Guanabara, 24 May 1953, 1 ♂, N. Santos. São Paulo: 54, Santos, 1 ♀ (ov). Santa Catarina: 53, São Francisco do Sul, no date, 1 ♂, 1 ♀, L. Jualberti.

MNHNP. 3 lots, 6 specimens.

BRITISH HONDURAS
Belize, 1 ♂ (dry), date, col. unknown.

BRAZIL

30-21, 1 ♂ (dry), date, col. unknown. Santa Catarina, 1875, 1 ♂, 1 ♀ (ov), Vignes 1129. 202.64, Desterro [= Florianópolis], 1 ♂ (dry), M. Müller.

ARGENTINA [?]

Suitreé [?], 1922, 3 ♂ (dry), from Museo de Historia, Nat., Buenos Aires. Incomplete data or erroneous localities: 6♂, 1♀ (dry) from "Chile" and "Amerique" by M. Fontaines and col. unknown. (No. 30.3, 30.2, 30.10, 30.11, 30 [?], 30.20, and S31).

RMNH. 21 lots, 49+ specimens.

ST. MARTIN

Great Bay, 7 June 1955, 1♂, P. W. Hummelinck. 10716, freshwater pond, 27 July 1955, 1♀, P. W. Hummelinck. 11850 and 1112, freshwater pond W Philipsburg, 17 Feb. 1957, 2♀, juv, L. B. Holthuis.

MARTINIQUE

3273, Fort de France, 6 Feb. 1939, 1♀, H. W. C. Cossee.

PANAMA

Canal Zone, Bahía de Limón, N Limón Point, 5 July 1966, 6 juv, *Pillsbury* Stn. 322.

COLOMBIA

23518, Golfo de Urabá, 08°0.1′N, 76°50.3′W to 08°1.2′N, 76°47.7′W, 12 July 1966, 3♂, 2♀ (1 ov), 2 juv, *Pillsbury* Stn. 357.

NETHERLANDS ANTILLES

Aruba: 15040, Lagoon NW Savaneta, 21 Mar. 1957, 2 juv, L. B. Holthuis.

Curaçao: St. Kruis Baai, 7 Oct. 1940, 1 carapace, P. W. Hummelinck. 15038, within St. Martha Baai, near St. Nicolaas, 3 Nov. 1957, 1 juv, L. B. Holthuis. 11852, Piscadera Baai, 11 Feb. 1957, 2♂, 1♀, L. B. Holthuis. 15039, Piscadera Baai, mudflat behind mangroves, Caraibisch Mar. Biol. Inst., 24 Jan. 1957, 1♀ juv, L. B. Holthuis. 10717, Caracas Baai, Nov. 1954, 1♀ (ov), J. S. Zaneveld. 11849, Waaigat, Willemstad, 30 Jan. 1957, 3♂, 3♀, L. B. Holthuis. 11851, South shore St. Joris Baai at Choloma, 3 Jan. 1957, 3♂, 1♀, L. B. Holthuis.

TRINIDAD

23368, and unnumbered, Diego Martin River, 1965-66, 2♂, H. O. von Hagen.

SURINAM

11848, near lightship *Suriname Rivier,* 12-13 Jan. 1953, 1♀ (ov), H. W. Lijding.

BRAZIL

Cat. a, no date, 2 ♂ (dry). 375, Bahia, 1909, 5 juv ♂ and ♀, J. A. Bierens de Haan.

ATLANTIC OCEAN

1859, 1♂ juv, R. Conradsen.

SADZ-B. 43 lots, 186+ specimens.

BRAZIL

Bahia: 2098, Ilha de Itaparica, July 1959, 1♂, Tagea Bjornberg. 350, June 1896, 1♂, 1♀, Bicego. 3225, Ilhéus, 1919, 4♂, 1♀, E. Garbe. 1725, Ilha Madre de Deus, 1932, 1♂, Oliviera Pinto. Rio de Janeiro: 401, São João da Barra, 1911, 2♂, E. Garbe. 3239, Atafona, 12 July 1963, 5♂, 6♀, N. Meneses. 3213, Atafona, lagoon, 3♂, 6♀, N. Meneses. 1730, S. J. Barra, 1963, 1♂, N. Meneses. 3232, Macaé, 24 Oct. 1942, 1♂, A. Castro and J. Feio. 370, Rio de Janeiro, 1898, 1♂, Bicego. 3252, Ilha Grande, 17 May 1966, 1♀ juv. 3256, Angra dos Reis, 27 July 1966, juv. 3257, Praia do Baia, Angra dos Reis, 20 May 1966, 1♀, G. Melo. 3258, Praia Grande, Angra dos Reis, 18 May 1966, 1♂, G. Melo. 1734, Angra dos Reis, 1945, 1♂, 1♀, 1 juv, L. T. Filho. 3083, Ilha Grande, 14 May 1966, 1♀, *Emilia.* 3238, Enseada das Estrêlas, Ilha Grande, 26 Feb. 1966, 13♂, 10♀ (2 ov). 3260 and 3229, Enseada das Estrêlas, Ilha Grande, 18 July 1966, 26♂, 24♀ (8 ov), G. Melo. 3248, [off Rio de J.?], 11 Nov. 1956, 1♂, Corvette *Solimoés,* Stn. 99/56.

São Paulo: 891, São Sebastião, 1915, 3♂, 4♀, E. Garbe. 1724, São Sebastião, no date, 2♂, 2♀, P. E. Vanzolini. 1741, Praia Grande, São Sebastião, Feb. 1962, 1♀, H. Britski. 2108, São Sebastião, July 1959, 2♂, H. R. Costa. 1737, 3253, Estrada Caraquatatoba, São Sebastião, no date, 1♂, 2♀, 1 carapace. 3251, Farol da Moela, Aug. 1965, 1♀, Inst. Pesca Santos. 1662, Farol da Moela, Mar. 1964, 4♀ (1 ov), Inst. Pesca Santos. 522, Piassaquera, Jan. 1914, large left merus of chela. 398, Piassaquera, Sept. 1910, 3♂, 3♀. 359, Piassaquera, June 1903, 5♀ (2 ov), Luederwaldt. 1813, Santos, 11 Sept. 1962, 2♂, 6♀, G. Melo. 1732, Santos, no date, 2♀, E. Rabello. 1735, Porto Nôvo, Santos, Nov. 1947, 2♂, L. Damico. 1403, Itanhaen, May 1926, 1♂, R. Spitz. 1407, Itanhaen, May 1927, 1♂, 1♀ (ov), R. Spitz. 1302, Itanhaen, July 1935, 1

♀, R. Spitz. 3236, Praia da Trincheira, Cananéia, 27 June 1964, 6 ♂, Cory and Isauro.

Santa Catarina: 665, Itajá, 1900, 3 ♂, Luederwaldt. 3235, Praia de Itapema, Itapema, July 1965, 1 ♂, Dep. Zool. Exped. 3244, 27°15'S, 48°47'W, 70-75 m, sand-shell, 21 Aug. 1966, 3 ♂, 2 ♀ (1 ov), M. Iwai. Rio Grande do Sul: 3233, Praia de Torres, 5 Oct. 1964, 2 ♂, J. Bertoletti. 3250, Praia na desembocadure, Rio Tramandai, 8 Apr. 1965, 2 ♂ juv, R. P. Leal.

YPM. 1 lot, 2 specimens.

BRAZIL

824, Pernambuco, 1867, 1 ♂, 1 ♀, C. F. Hartt.

Supplementary literature records.–Bermuda (Verrill, 1908a); Florida (Futch, 1965; Park, 1969); Golfo de Venezuela and Estr. de Maracaibo, Venezuela (Taissoun, 1969); Curaçao (Nobili, 1897); Barbados (Jones, 1968); Barra das Jangadas [S Recife], and estuaries, Pernambuco, Brazil (Coêlho, 1966, 1970, 1971); Ilha de São Sebastião and ocean beaches, Estado de São Paulo, Brazil (Luederwaldt, 1929; Lavallard, 1960).

CALLINECTES ARCUATUS ORDWAY

Figures 8, 18f, 20g-h, 22f, 24

Callinectes arcuatus Ordway, 1863, p. 578 [13] (type: ♂, USNM 61833, Cape San Lucas [Baja California]).- A. Milne Edwards, 1879, p. 228 (var. of *C. diacanthus*).- Rathbun, 1896, p. 362, pl. 20; pl. 23, , fig. 1; pl. 24, fig. 8; pl. 25, fig. 7; pl. 26, fig. 7; pl. 27, fig. 7.- 1898, p. 596.- 1910, p. 537, 577, pl. 56.- 1930, p. 121, text-figs. 15h, 16h, 17f, 18g, pl. 52.- Young, 1900, p. 190 (var. of *C. diacanthus*).- Nobili, 1901, p. 31.- Boone, 1929, p. 564, text-fig. 3.- Contreras, 1930, p. 233, text-fig. 5.- Garth, 1948, p. 35.- 1957, p. 36.- 1961b, p. 141.- Garth and Stephenson, 1966, p. 43, pl. 5, fig. A; pl. 8, fig. A; pl. 10, fig. A; pl. 12, fig. D.- Buitendijk, 1950, p. 275.- Bott, 1955, p. 56.

Callinectes pleuriticus Ordway, 1863, p. 578 [14] (syntypes: 2 ♂, 1 ♀, MCZ 4701; ♂, MCZ 987; Panama, A. Agassiz).- A. Milne Edwards, 1879, p. 228 (var. of *C. diacanthus*).- Young, 1900, p. 190 (var. of *C. diacanthus*).

Callinectes sp. Smith, 1871, p. 91.- Lockington, 1876, p. 107 [13].

?*Neptunus diacanthus* Brocchi, 1875, p. 54, pl. 16, fig. 82.- Cano, 1889, p. 90, 99, 100, 102, 211.- Doflein, 1899, pl. 186 (part; the Ecuador specimen).

Callinectes nitidus A. Milne Edwards, 1879, p. 228, explan. pl. 41 (var. of *C. diacanthus*) (syntype: ♂, USNM 20269, Tanesco [= Tahuesco, 14°01'13"N, 91°07'03"W] Guatemala, on the borders of the Esteros).- Young, 1900, p. 190 (var. of *C. diacanthus*).

Callinectes diacanthus.– A. Milne Edwards, 1879, pl. 41 [var. *nitidus*].

Callinectes dubia Kingsley, 1879, p. 156 (type: ♂, MCZ 5178, Gulf of Fonseca, west coast of Nicaragua, J. A. McNeil).- Young, 1900, p. 191.

?*Neptunus (Callinectes) diacanthus* Ortmann, 1894, p. 77 (part; the S. Chile specimen).

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Description.—Inflated carapace (Figure 8) bearing four triangular frontal teeth, submesial pair no more than half length of lateral pair. Metagastric area of adults with anterior width about 2.5 times length, posterior width between 1.3 and 1.5 times length. Anterolateral margins arched, teeth exclusive of outer orbital and lateral spine well separated and varying from convex-sided with subacute tips at orbital end of row to sharper and more spiniform laterally, each with anterior margin shorter than posterior. Surface of carapace with granulation fairly uniform, most crowded on gastric, mesobranchial, and cardiac regions, more scattered near anterolateral margins, and smooth along frontoorbital, posterolateral, and posterior borders. Epibranchial line prominent, interrupted slightly at corner of mesogastric area.

Chelipeds with sharply granulate ridges on propodus, basal portion of dactyl, and exposed surfaces of carpus. Dactyl of major chela with large basal tooth closing against molariform complex at base of propodal finger, lower margin of propodal finger often decurved near base in adults.

Male abdomen and telson reaching beyond suture between thoracic sternites IV and V; telson triangular, longer than broad; sixth segment of abdomen with sides nearly straight distally, diverging proximally, segment poorly calcified proximally except for triangular basal portion connected to distal half by a narrow (sometimes obsolescent) central indurated column. Mature female abdomen and telson reaching as far forward as in

male, last two segments nearly equal in length, telson triangular with slightly inflated sides, apices acute. First gonopods of male (Figures 18f, 20g, h) reaching about to abdominal locking tubercles on fifth sternite, often partially overlapping near base, tapering to narrowly flared tips bent ventrolaterally and opening mesioventrally, armed with scattered minute spinules sternally and laterally and with a subterminal sternomesial row of elongate slender spinules. Gonopores of females (Figure 22f) elliptical with long axis in transverse plane, sinuous aperture of each with rounded margins except mesial side sloping from surface under overhanging anterior and inferior bulbous posterolateral border.

Size of carapace in mm.—Largest male: length 54, width at base of lateral spines 93, including lateral spines 123. Largest female: length 55, width at base of lateral spines 96, including lateral spines 114. Summary of selected measurements is given in Tables 1 and 2. Estévez (1972) judged females to attain sexual maturity at a length of 28-34 mm, but smaller ones are known (see Spawning).

Color.—Male: "Carapace dull olive gray-green. Chelipeds olive green dorsally, whitish ventrally, washed with bluish-violet and chelae tipped with pale yellow-brown. Legs turquoise washed with olive; hairs straw gold; swimming legs olive green with suggestion of turquoise, paddles washed with black; hairs straw; tubercles at leg joints golden orange; eyes straw with brownish streaks; underparts pure white" (Garth, 1961b; Garth and Stephenson, 1966).

Female: Carapace generally blue, central portion blue violet; anterolateral portions deep purplish-vinaceous. Chelipeds with base of merus olive, inner portion of hands blue-violet, remainder purplish but varied, fingers barred with purple, propodal fingers usually white tipped. Remaining legs Italian blue, hairs olive, swimming legs with articulations and margins narrowly violet, paddles sometimes turquoise. Abdomen violet, joints and sternum white (Garth, 1961b).

Variations.—Lateral spines in *C. arcuatus* vary considerably, some being relatively no longer than in *C. exasperatus*. Inner orbital fissures are open in some individuals. Chelipeds often have smooth ridges rather than granulate ones, and the propodal molariform complex of the major chela is often worn. The proximal portion of abdominal segment 6 may be almost completely uncalcified in males.

Variations in *C. arcuatus* are often those associated with proportional growth changes. These are pronounced enough to make identification difficult, especially among juveniles. *Callinectes pleuriticus* and *C. dubia* were based on immature *C. arcuatus*. The mesogastric area grows relatively broader with the maturing carapace. Adult females have a more arched carapace than the immature, and seemingly more females than males have a hairy growth under the anterolateral border. First gonopods of juvenile males are short; those of adult males range in length from short, with tips terminating at level of the suture between thoracic sternites VI and VII, to long, terminating near the suture between thoracic sternites IV and V. The tips of these appendages usually curve ventrolaterally but may curve ventrally, mesially, or asymmetrically, and the slender distal portions occasionally are sinuous rather than straight. Subterminal dorsal spinules may be worn off of first gonopods.

An ovigerous female from Panama (AHF, Stn. 111-33) has seven anterolateral teeth on the left side.

Distribution.—Los Angeles Harbor, Calif., to Mollenda, Peru; Galápagos Islands (Figure 24). The record from southern Peru is an immature male. A record from the Galápagos Islands in April 1941, is a soft mature male, and two other records in February 1964, are an immature male and female.

Habitat.—Garth and Stephenson (1966) summarized habitat as sand or mud bottom, oyster beds, lagoons, estuaries, channels among mangroves, or river mouths. Recorded depth range is shoreline to 27.5 m, with many occurrences limited to shallows less than 1 or 2 m along shore, but Estévez (1972) reported common occurrence in Colombia on sand or sand-mud bottom, preferentially between 10 and 20 m in salinities 22‰ or higher. Estévez found the diet included mainly crustaceans, bivalves, fishes, inorganic remains, gastropods, and cephalopods in order of precedence (330 stomachs examined).

Spawning.—The spawning season extends year round. Museum records include ovigerous females as follows: January, Costa Rica; March, Oaxaca,

Mexico, Panama; April, between San Felipe and mouth of Colorado River, Mexico, Peru; May and June, Sinaloa, Mexico; July, Panama; August, Jalisco, Mexico; September, Guerrero, Mexico; November, Sonora and Jalisco, Mexico; December, Sonora, Mexico. A female from near the mouth of the Colorado River (AHF, Golfo de California, 6-9 April 1947, Stn. H47-53) is the smallest egg bearer seen in this species, the carapace having a length of 23, and width at base of lateral spines 39, or including lateral spines of 52 mm. Month of collection is unknown for an ovigerous female from Anaheim Slough, Calif., in 1928. Estévez (1972) considered ovigerous females rare.

Remarks.—The cognate species *C. arcuatus* and *C. danae* are so similar that differentiation is difficult except on grounds of male first gonopod morphology or geographic distribution. In general, *C. arcuatus* is the more robust species, having a tumid carapace emphasized in the arched anterolateral border and inflated branchial regions. Anterolateral teeth stand up from the surface, as if each is reinforced with an axial rib extending from the borders of the anterolateral area, but almost never are shoulders developed on their margins, whereas in *C. danae* there is less prominent central reinforcement in the teeth but a tendency to development of shoulders. Such differences are inconsistent.

Distribution of *C. arcuatus* along the Pacific side of Baja California parallels, but is more extensive than, that of *C. bellicosus*. In this region, marine climate that is transitional between tropical and dominant temperate extends from Punta Entrada (Bahía Magdalena) to Point Conception north of Santa Barbara Channel (Garth, 1961a). Here temperate and tropical faunas mingle, but tropical elements thin out in the north surviving only in protected areas or in favorable years. Records of *C. arcuatus* along this outer coast are less numerous than in the Golfo de California and southward, but occurrence of an ovigerous female at Anaheim Slough, Calif., indicates enough tolerance of temperate conditions to develop breeding populations, at least in favorable years. *Callinectes arcuatus* shows adaptation to a broader spectrum of marine climates than *C. bellicosus* in its much more extensive distribution from temperate southern California, through the essentially insular oceanic province at the tip of Baja California and tropical eastern Pacific, to temperate fringes of the Humboldt Current along Peru.

Callinectes arcuatus is questionably listed from the Caribbean side of Colombia at Turbo on the Golfo de Urabá in MCZ lot 9666. I agree with the cataloger that this must be an erroneous locality for the collection.

A collection of *C. arcuatus* from Estero de los Algodones, SE of Guaymas, Sonora, Mexico (USNM 15431) contains a large female which has a broken male first gonopod inserted in the left genital opening. The gonopod fragment is 14 mm long, completely inserted, and is that of a male *C. arcuatus*.

Brocchi's (1875) discussion of male gonopods in *Callinectes* is a puzzle because there is no sure way to know which species he studied; neither his descriptions nor figures are accurate enough to allow certainty in forming synonymy. This would be of no real concern were it not for the relationship of his work to that of Milne Edwards (1879). Brocchi studied material obtained from Milne Edwards, and both considered gonopod structure of males to be among the diagnostic characters for species or "varieties" of *Callinectes*. Reasonable assessment of Brocchi's material rests on the geographic source of material then available, his discussion, and its probable influence on Milne Edwards's thinking. The evidence is present in both papers. Summarizing: species with short first gonopods came from the Antilles, coast of America, and Chile; those with long ones came from Cayenne and Guatemala. Chile must be regarded as an erroneous locality for species in this genus (Garth, 1957).

Milne Edwards (1879) described *C. cayennensis* (= *C. bocourti*) with long first gonopods from Cayenne and remarked on likeness of the male gonopods to those of *C. hastatus*. Brocchi (1875) may have worked with *C. bocourti* from Cayenne but more likely with *C. hastatus* (= *C. sapidus*) itself, for he remarked on its broad, strong frontal teeth and designated it as the *hastata* of Ordway (plate 16, Figure 81).

By designation "very long," Brocchi indicated that his illustration of male first gonopods from Guatemalan material (plate 16, Figure 82) must refer to *C. arcuatus*, a species regarded as having nearly straight gonopods (Milne Edwards, 1879).

Species with short male first gonopods from provenances listed by Brocchi (1875) and described in more detail by Milne Edwards (1879) were: Antilles, *C. ornatus* and *larvatus* (= *C.*

marginatus); coast of America, the same species; Chile, species undetermined by either Brocchi or Milne Edwards because of fragmentary information. Brocchi's illustration of a strongly curved gonopod (plate 16, Figure 76) seems closest to *C. marginatus*. Figure 78 depicting a short and straight gonopod seems closest to *C. ornatus* as does the undesignated Figure 79. Figure 77, though clearly called "short," resembles that of *C. bellicosus* in sinuosity. Milne Edwards (1879), making no mention of "long" or "short" gonopods for this species, was impressed with the double curvature, but listed *C. bellicosus* only from Cabo de San Lucas, Baja California. We must regard Figure 77 as possibly an illustration of *C. marginatus* because it seems closest to that species from geographic origins listed.

Following is an outline summary of first gonopod characters as understood by Milne Edwards (1879).

ATLANTIC

hastatus [= *sapidus*]: long, reaching to near end of abdomen; Nantucket to Mobile, perhaps on coast of Brazil.

ornatus: short and straight; Charleston-Cumaná, including Tortugas, Bahamas, also Santa Catarina, Brazil.

larvatus [= *marginatus*]: very short and curved; coast of Florida, Key West, Tortugas, Bahamas, Haiti, Veracruz, Mexico.

tumidus [= *exasperatus*]: long but moderate and distinctly hooked, approaches *hastatus;* Key West, Fla., Haiti.

bocourti: long, to end of abdomen as in *hastatus;* Honduras.

cayennensis [= *bocourti*]: long and reach end of abdomen as in *hastatus;* Guyana.

danae: long and straight; Rio de Janeiro *(diacanthus)*.

PACIFIC

toxotes: very long, end of abdomen; Cabo de San Lucas.

robustus [= *toxotes*]: very long as above; Colombia.

bellicosus: "the verges reach almost the middle of the penultimate article, they are incurved strongly and outward near the extremity, then inward similarly and finally the point is directed externally" [sinuous]. Golfo de California; Cabo de San Lucas.

arcuatus: long and straight, resembles *diacanthus* of Rio de Janeiro; but more slender; Cabo de San Lucas.

pleuriticus [= *arcuatus*]: long and straight; Panama.

nitidus [= *arcuatus*]: slender, straight and long; Guatemala, Tanesco.

In addition, those from Chile resemble the Guatemalan forms.

Material.—Total: 199 lots, 655 specimens.

Specimens listed in Rathbun (1930) from USNM [correction, USNM 62050=62051] and MCZ; Garth and Stephenson (1966) from AHF and USNM.

USNM. 76 lots, 316 specimens, including the following not cited above:

MEXICO

Baja California: 64119, Isla San Lucas, 15 Jan. 1930, 1 ♂ juv, M. Valerio. Sonora: 111769, Golfo de Calif.? no date, 1 ♂, T. H. Bullock, Stn. W53-289.

Nayarit: 123089, Estero de San Blas, 7.5 mi by road NNE San Blas, 14 Feb. 1955, juv 6 ♂, 2 ♀, Miller and Greenbank, M55-18. 123090, slough at N end Laguna de Mexaltitán, 28 Mar. 1955, 1 ♂ juv, Miller and Greenbank, M55-74.

GUATEMALA

20269, Tanesco [= Tahuesco, 14°01′13″N, 91°07′33″W] on the borders of the Esteros, 1 ♂ (dry). 123088, Iztapa, 5 Apr. 1950, 1 ♂.

NICARAGUA

77085, El Realejo, no date, 1 ♂ juv, Kingsley.

COSTA RICA

61034, Puntarenas, Mar. 1927, 1 ♂ (dry), M. Valerio. 76137, San Lucas [= Isla San Lucas], 15 Feb. 1931, 2 juv, M. Valerio. 76685, Golfo Dulce, 2 Feb. 1933, 1 ♀ (dry), M. Valerio.

PANAMA

77090, Balboa, C.Z., 4 Feb. 1937, 1 ♂ juv, 1 ♀, S. F. Hildebrand. 77094, Drydock, Balboa, C.Z., 8 Feb. 1937, 1 ♂, S. F. Hildebrand. 76917, Miraflores Locks, C. Z., no date, 2 juv, S. F. Hildebrand. 77081, Farfán Beach, C. Z., 23 Feb. 1937, 1 ♂ juv, S. F. Hildebrand. 77082, Venado Beach, 26 Feb. 1937, 1 ♂ juv, S. F. Hildebrand. 77083, Puerto Pilón, 2 Mar. 1937, 1 ♀ juv, S. F. Hildebrand. 77093, Taboga I., 8 Feb. 1937, 1 juv, H. C. Clark. 82134, Miraflores Locks (Lower Chamber), 4 juv,

S. F. Hildebrand. 82135, Dry Dock, Balboa, C.Z., 18 Mar. 1937, 1 ♂ juv, S. F. Hildebrand. 82136, Miraflores Locks (Lower Chamber), C.Z., 26 and 29 Mar. 1937, 1 juv, S. F. Hildebrand. 111779, Río Antón, Golfo de Panamá, 2 Apr. 1957, 2 ♂, W. L. Klawe. 119846, Punta Paitilla, 24 Feb. 1964, 1 ♂, R. Dutary. 123091, Bahía Piñas, near mouth of estuary at Santa Dorotea, 07°34.5′N, 78°11.5′W, 9 Sept. 1961, 7 juv, *Argosy* Stn. 10. 123092, Bahía Piñas, shallow end along crescent beach to E end at Santa Dorotea, 9 Sept. 1961, 3 juv, *Argosy* Stn. 9.

COLOMBIA

68552, Tumaco, no date, 2 ♂.

ECUADOR

123093, Esmeraldas, in harbor and fish market, 0°57.5′N, 79°42.5′W, 25 Sept. 1961, 1 ♂, *Argosy* Stn. 41. 70990, Salada, Guayaquil, 1 and 2 Oct. 1926, 1 ♂, W. L. Schmitt. 97899, Manta, Prov. Manabí, 0°56′30″S, 80°44′W, Aug. 1949, 1 ♂ (dry), T. Mena. 97930, supra cit., 1 ♀ (dry).

PERU

76574, Paita, 8 Oct. 1926, 1 ♂, W. L. Schmitt. Uncatalogued, Negritos, Apr. 1941, 1 ♂, 1 ♀, H. E. and D. L. Frizzell (160/433).

GALAPAGOS ISLANDS

111676, Conway Bay, 15 Apr. 1941, 1 ♂, W. L. Schmitt.

AHF. 66 lots, 221 specimens, including the following not cited above:

MEXICO

Sonora: Guaymas, tidal flats N of Motel Tular, 22 June 1966, 2 ♂, 1 ♀, R. Reimer and A. Alvarez, Stn. 2a.

Sinaloa: Topolobampo, 25 June 1966, 1 ♂, 1 ♀, R. Reimer and A. Alvarez, Stn. 4g.

Jalisco: Bahía Chamela, North Lagoon, 17 Nov. 1937, 1 ♂, 3 ♀ (2 ov), *Zaca* No. 37,142.

Guerrero: Acapulco Beach, 26-28 Nov. 1937, 1 ♀, *Zaca*-NYZS 37,277.

EL SALVADOR

Golfo de Fonseca, La Unión, 27 Dec. 1937, 1 ♀, *Zaca* Stn. 199, D-8 to D-16, 5-6 fm.

HONDURAS

Golfo de Fonseca, Cutuco and Potosí Lights 20 Dec. 1937, 4 ♂, 6 ♀, 3 juv, *Zaca* No. 37,666.

NICARAGUA

Corinto, 29 Dec. 1937, 1 juv, *Zaca* Stn. 200, D-7, 3.6 m. Corinto, Castenones Lagoon and mid-harbor, 6 Jan. 1938, 4 ♂, 4 ♀, *Zaca* NYZS 3814. Corinto, 7 Jan. 1938, juv 1 ♂, 1 ♀, *Zaca* 200, D-20 to D-26, 2.7-11.9 m.

COSTA RICA

Port Parker [= Golfo Elena], 13 Jan. 1938, 1 ♂, 3 ♀ (1 ov), 4 juv, *Zaca* No. 3859. Golfo Elena, 22 Jan. 1938, 2 ♂ juv, *Zaca* Stn. 203, D-9, 2.7-7.3 m. Puerto Culebra, 26 Jan. 1938, 8 ♂, 3 ♀, 2 juv, *Zaca* NYZS 38,115. Mata de Limón, 30 July 1964, 2 ♂, J. Mohr. Piedra Blanca [= Bahía Carrillo], 6 Feb. 1938, 2 ♂, 2 ♀, *Zaca* No. 38,195. Golfo de Nicoya, Isla Cedro, 12 Feb. 1938, 1 ♂, *Zaca* NYZS 38,302. Golfo Dulce, Golfito, 5 Mar. 1938, 1 ♂, 1 ♀, 4 juv, *Zaca* No. 38,472. Golfo Dulce, Golfito, 9 Mar. 1938, 1 ♀ juv, *Zaca* 218, NYZS 38,596. Supra cit., juv 1 ♂, 5 ♀, *Zaca* 218, D-4, D-5, D-8, 11 m.

PANAMA

Bella Vista, Panama City, 1944, 5 ♂, 2 juv, *Zaca*. Balboa, C.Z. 1940, 2 ♂, 1 ♀, 5 juv, *Zaca*. Balboa, C.Z., Apr. 1938, 3 ♂, 2 ♀, 8 juv Bahía Honda, 16 Mar. 1938, 3 ♂ juv, *Zaca* No. 38,701. Bahía Honda, 19 Mar. 1938, 1 ♂, *Zaca* NYZS 38,734.

ECUADOR

Puerto Bolívar, Apr. 1944, 1 ♂ juv, *Zaca*.

AMNH. 9 lots, 11 specimens.

MEXICO

Baja California: 5527, San José del Cabo, 21 Mar. 1911, 1 ♂, *Albatross*. Sinaloa: 7228, off Topolobampo, 17 Nov. 1935, 1 ♀, Templeton–Crocker Exped.

PANAMA

5405, 5408, 5419, 5434, Punta Paitilla, 26 Mar. 1926, 2 ♂, 1 ♀, 2 juv, W. G. Van Name. 5406, between Punta Paitilla and Panamá Viejo, 29 Mar. 1926, 1 ♂, W. G. Van Name. 10568, Santelmo Bay [= Ensenada Santelmo], Isla del Rey, Archipiélago de las Perlas, 15 Feb. 1941, 1 ♂, *Askoy* Exped.

PERU

Uncatalogued, Mollendo, 3 Dec. 1934, 1 ♂ juv.

BMNH. 4 lots, 8 specimens.

COSTA RICA
1892.6.7.14, Río Punta Mala, 1 ♂, H. Pittier.

PANAMA
67.77, 2 ♂, J. C. Dow.

COLOMBIA
1925.4.27.8/9, Tumaco, 1 ♂, 1 ♀ juv, R. H. Thomas.

PERU
1890.10.7.103/105, Santa Lucía, 2 ♂, 1 ♀, Stalzman collection, Warsaw Mus.

MCZ. 14 lots, 36 specimens, including the following not cited above:

MEXICO
Baja California: 5181, Cabo de San Lucas, no date, 1 ♂, J. Xantus. Guerrero: 5180, Acapulco, no date, 1 ♂, 1 ♀, *Hassler* Exped.

NICARAGUA
5178, Golfo de Fonseca, May 1869, 1 ♂, J. A. McNiel.

HONDURAS
5179, Golfo de Fonseca, recd. Nov. 1885, 5 juv, J. A. McNiel.

PANAMA
987, 15 Mar. 1869, 1 ♂, A. Agassiz. 4701, 15 Mar. 1860, 2 ♂, 1 ♀, A. Agassiz. 4702, July 1872, 1 ♂, *Hassler* Exped. 4703, recd. 13 Feb. 1861, 2 ♂, J. Rowell. 5175, Mar. 1860, 3 ♂, 2 ♀, A. Agassiz. 5176, recd. 10 June 1862, 2 ♂, 1 ♀, C. F. Davis. 5177, 4 ♂, 3 ♀, *Hassler* Exped. 8376, 12 Mar. 1891, 1 ♀ juv, *Albatross* Exped. 9669, no date, 3 ♂, Maack.

COLOMBIA
9666, Turbo?, no date, 1 ♂, Maack, Darien Exped. [Error?].

MNB. 1 lot, 4 specimens.

PANAMA
Bahía Honda, 10 Mar. 1933, 2 ♂, 2 ♀, *Velero III*, Stn. 111-33.

MNHNP. 1 lot, 6 specimens.

GUATEMALA
445a, 445d, Tanesco [= Tahuesco, 14°01′13″N, 91°07′33″W], 3 ♂, 3 ♀ (1 ov) (dry), Exp. du Mexique.

RMNH. 18 lots, 27 specimens.

MEXICO
Sonora: 7535, Guaymas, 20 May, 1945, 1 ♂, M. Cárdenas. 7529, Guaymas, 25 July 1946, 1 ♀ juv, M. Cárdenas. 7536, Yavaros, Bahía de Sta. Bárbara, 29 Nov. 1944, 1 ♂, 1 ♀ (ov), M. Cárdenas. 7532, coast of, 23 Nov. and 1 Dec. 1944, 1 ♂, 1 ♀ (ov), M. Cárdenas. Canjeme [?], 22 Nov. 1944, 1 ♀ (ov), M. Cárdenas.
Sinaloa: 7528, Ahome, 1 June 1945, 1 ♀, M. Cárdenas. 7537, Topolobampo, 21 June 1945, 1 ♀ (ov), M. Cárdenas. 7531, Macapule [Bahía de Navachiste], 22-23 Apr. 1948, 1 ♂, M. Cárdenas. 7533, Macapule, 7 May 1946, 2 ♀, M. Cárdenas.
Colima: 7534, Manzanillo, 13 Jan. 1943, 1 ♂, 1 ♀, F. Bonet.

EL SALVADOR
9839, W of Bocana Río Lempa at Isla Tasajera, San Vicente, 19 Mar. 1953, 1 ♂, 2 juv, M. Boeseman. 9840, coast at El Cuco, San Miguel, 19 Apr. 1953, 2 juv, M. Boeseman.

PANAMA
23516, Panama Canal, C.Z., 8°59.5′N, 79°30.5′W, Strand, Laagwater, 30 Apr. 1967, 1 ♂, *Pillsbury* Stn. 482. 23517, Golfo de Panamá, 8°14.3′N, 78°25.2′W-8°14.3′N, 78°25.5′W, 7 May 1967, *Pillsbury* Stn. 547.

ECUADOR
1 ♂, Frank, Cat-a.

PERU
23402, Puerto Pizarro, dept. Tumbes, Apr. 1966, 1 ♀ (ov), 1 juv, H. O. van Hagen. 23433, Paracas bight S of Pisco, 13 Apr. 1966, 2 ♂, H. O. van Hagen. 2699, 1 ♂ from Museo de Hist. Nat., Lima.

Supplementary literature records.—Bahía de Santa Elena, Ecuador (Nobili, 1901); a resume of records in Peru (Solar, Blancas, and Mayta, 1970); along Pacific coast of Colombia (Estévez, 1972).

CALLINECTES EXASPERATUS (GERSTAECKER)

Figures 9, 18g, 20i, 22g, 26

Lupea exasperata Gerstaecker, 1856, p. 129 (type: ♂, Berlin Mus. 2104 [dry], Puerto Cabello, Venezuela, Appun).

Callinectes tumidus Ordway, 1863, p. 574 [9] (syntypes: 2 ♂, MCZ 5159, Key West, Fla., J. E. Mills; 1 mature ♀, MCZ 5162, Haiti, A. Hilchenbach).- A. Milne Edwards, 1879, p. 226 (var. of *C. diacanthus*).- Rathbun, 1896, p. 359, pl. 18; pl. 24, fig. 6; pl. 25, fig. 5; pl. 26, fig. 5; pl. 27, fig. 6.- Rankin, 1898, p. 232.- Young, 1900, p. 189 (var. of *C. diacanthus*).

?*Lupa (Neptunus) diacantha*.- von Martens, 1872, p. 92 (part, the Puerto Cabello, Venezuela, specimens).

Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part, specimen n, Haiti).

Callinectes exasperatus.- Rathbun, 1897, p. 150.- 1901, p. 49.- 1930, p. 130, text-figs. 15f, 16f, 17e, 18e, pl. 56.- 1933, p. 49.- Contreras, 1930, p. 236, fig. 7.- Chace, 1940, p. 33.- 1956, p. 154, unnumbered fig.- Chace and Hobbs, 1969, p. 131, fig. 37c.- Taissoun, 1969, p. 81, fig. 31A-D, photo 11.- 1973, p. 37, figs. 4C, 5C, photo 6.

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Description.—Carapace (Figure 9) bearing four well developed frontal teeth, submesial pair narrower and slightly shorter than lateral pair. Metagastric area with posterior width 1.2-1.3 times length, anterior width 2.3-2.5 times length. Anterolateral margins strongly arched with anterolateral teeth exclusive of outer orbital and lateral spine usually but not always curved forward; teeth progressively broader laterally with fifth tooth often largest. Lateral spine stout, usually less than twice length of preceding tooth. Surface of carapace conspicuously granulate with densest concentrations on central eminences, coarsest and most widely spaced granules in front of epibranchial line separated by smooth surfaces. Central sulci on carapace definite but not deep; epibranchial line rather flatly arched, slightly sinuous.

Chelipeds robust, ridges and crests of all articles coarsely granulate; fingers of major chela strong but not markedly gaping.

Male abdomen and telson reaching along posterior quarter of thoracic sternite IV; telson lanceolate with sinuous inflated sides, length 1.5 times basal width; basal portion of fused segments 3-4-5 truncate laterally. Mature female abdomen and telson reaching about same level as in male; telson triangular with inflated sides, length 1.2 times basal width; fifth segment longer than sixth. First gonopods of male (Figures 18g, 20i) reaching slightly beyond suture between thoracic sternites VI and VII, sinuously curved, overlapping in proximal half along midline then diverging distally, twisting on axis near tip and bending abruptly mesad; armed distally with scattered minute spinules, tip slightly broadened and opening posteromesially. Gonopores of female (Figure 22g) broadly and somewhat asymmetrically ovate in outline with orientation of long axis mainly in frontal plane but with apex directed anteromesad; aperture of each laterally elongate and sinuous, sloping from broadest area at surface on mesial side to narrower and deeper portion under rounded overhanging anterior border with prominent central projection and posterior border with elongate posterolateral eminence.

Size of carapace in mm.—Largest male: length 67, width at base of lateral spines 114, including lateral spines 129. Largest female: length 59, width at base of lateral spines 101, including lateral spines 124. Summary of selected measurements is given in Tables 1 and 2.

Color.—Carapace of adult male purplish red, more accented on proto-, meso-, and metagastric areas and at base of lateral spines and anterolateral teeth; branchial region and anterolateral teeth obscure maroon. Dorsal surface of all legs purplish red with intense orange red on articulations; inferior portion of merus, carpus, and fingers of chelipeds intense violet; internal and external portion of chelae as well as entire ventral portion of animal white with tints of soft purple (Taissoun, 1969).

Variation.—There is notable variation in anterolateral tooth pattern; the fifth, sometimes described as largest (Rathbun, 1930) may be exceeded by the fourth, sixth, or a combination of both, or there may be asymmetrical size and tooth number differences.

Distribution.—Bermuda; Veracruz, Mexico; southern Florida to Estado de Santa Catarina, Brazil (Figure 26). Reason for lack of collections from the Guianas and northern Brazil is unknown.

Habitat.—This species lives primarily in shoal marine, estuarine, and perhaps fresh water, espe-

cially in association with mangroves and around river mouths from water's edge to recorded depths of about 7.5 m (Rankin, 1900; Coêlho, 1967b, 1970; Chace and Hobbs, 1969; Taissoun, 1969).

Spawning.—Few dated collections contain ovigerous females: March, Puerto Rico and Guadeloupe; April, Barbuda and Panama; May, Jamaica; June, West Indies; August, Estado de Santa Catarina, Brazil. Other undated collections in museums are from Bermuda, southern Florida, Estados de Pernambuco and São Paulo, Brazil.

Remarks.—*Callinectes exasperatus* has a number of distinctive features. It has the roughest appearing carapace and chelipeds of any species in the genus because the granulations are coarser and sharper than in others. The median epistomial tooth is more widely separated from the front than among the congeners, perhaps a function of the vaulted carapace which contributes to deep-bodied form. Similar to *C. bocourti* in structure of frontal teeth, *C. exasperatus* has less prominent cardiac lobes and sulci bounding the metagastric area. The lateral spines are relatively shorter than among other species of the genus. A blunt anteromesial eminence on the carpus is pronounced. Narrowest width of the male abdomen is in the distal third of the sixth segment, the narrowed portion becoming increasingly distal with age together with progressive crossing of the pleopods.

Dahl (1954) worked at Cañango Beach, Venezuela, at or near the type-locality for *C. exasperatus* and published a photograph of the beach at Puerto Caballo together with a short description of the area, saying that the tidal difference is small and wave exposure very great on the rather steeply sloping beach.

Locality data for specimen 303-7 in MNHNP (M. Fontaines) from "Chili" identified as *Neptunus diacanthus* Latr. (= *C. exasperatus*) is an error.

Material.—Total: 97 lots, 372 specimens.

Specimens listed in Rathbun (1930) from USNM (24463, 24464, 18631 not found) and MCZ.

USNM. 38 lots, 282 specimens, including the following not cited above:

UNITED STATES

Florida: 77125, E of Bush Key, Tortugas, 29 July 1931, 1 ♂, Pearse. 80665, Key West, no date, 1 ♂, U.S. Bur. Fish.

CUBA

77127, Bahía Honda [Pinar del Río, WSW Habana], 1 June 1893, Univ. Iowa.

JAMAICA

123077, Kingston Harbor, 17 May 1965, 1 ♀ (ov), B. B. Collette.

HAITI

71232, Muertos I., Seven Brothers group, Feb. 1929, 1 ♂, Poole and Perrygo.

PUERTO RICO

61563, Cataño [San Juan Harbor], 4 Jan. 1899, 1 ♂, *Fish Hawk*. 73281, Bahía de San Juan, 29 Mar. 1937, 1 ♂, W. L. Schmitt. 123084, Boca de Cangrejos, 7 mi E San Juan, 31 Mar. 1937, 1 ♂, 2 ♀ (1 ov), W. L. Schmitt.

VIRGIN ISLANDS

71639, St. Croix, no date, 1 ♂, H. A. Beatty. 72353, St. Croix, 1935-36, 2 ♂, H. A. Beatty. 76466, St. Croix, no date, 1 ♀, H. A. Beatty.

BARBUDA

123079, west shore of lagoon near Oyster Pond Landing, 6 Apr. 1956, 1 ♀ (ov), Schmitt, Chace, Nicholson, and Jackson, Stn. 85-56, *Freelance*.

GUADELOUPE

123080, between Monroux and Rat Is., Pointe a Pitre, 30-31 Mar. 1956, 3 ♂, 2 ♀ (1 ov), Chace and Nicholson, Stn. 68-56, *Freelance*.

GRENADINES

123078, Tyrrell Bay, Carriacou I., 16 Mar. 1956, 2 ♂, D. V. Nicholson, Stn. 17-56, *Freelance*.

MEXICO

Quintana Roo: 78391, Bahía de la Ascensión, 28 Mar. 1939, 1 ♂, Ralph Elliott. 123082, N end Bahía de la Ascensión, 15 Apr. 1960, 3 ♂, 1 ♀, Daiber and Schmitt. 123083, Bahía de la Ascensión behind Pta. Allen, 16 Apr. 1960, 1 ♂, Daiber and Haynes. 123081, Bahía del Espíritu Santo, near Pta. Lawrence, 6 Apr. 1960, 1 ♀, Rehder, Daiber and Haynes.

VENEZUELA

95713, Gran Roque, Los Roques Is., 7 Sept. 1950, 1 ♂, F. H. Weibezahn.

AHF. 3 lots, 4 specimens.

UNITED STATES
Florida: Key Largo, North Hawk Channel, 29-31 May 1949, 2 ♂, Stn. LM 25, 27. Hawk Channel, Plantation Key, 3 mi S Tavernier Bridge, 25 May 1949, 1 ♂, Stn. LM20-49.

TRINIDAD
Purchased from fisherman near Port of Spain, 17 Apr. 1939, 1 ♀.

AMNH. 4 lots, 4 specimens.

BERMUDA
11223, 1939, 1 ♀ (ov), W. Beebe, Bermuda Exped.

BAHAMAS
2286, Andros, 1908, 1 ♀, B. E. Dahlgren and H. Mueller.

PUERTO RICO
2673, San Juan, entrance of Bahía de Condado, 14 July 1914, 1 ♀, R. W. Miner. 2661, July-Aug. 1914, 1 ♂ (dry), R. W. Miner.

ANSP. 1 lot, 1 specimen.

BRAZIL
3514, no date, 1 ♀ (dry), T. B. Wilson.

BMNH. 7 lots, 12 specimens.

UNITED STATES
Florida: 1938.3.19.22, Dry Tortugas, 1 ♂, Colman and Tandy.

BRITISH HONDURAS
1967.7.1.49/50, Long Cay Island, 23/10/1941, 1 ♂, 1 ♀, I. Sanderson.

CAYMAN ISLANDS
1955.10.6.59, Stn. 33, 1 ♂, Oxford Univ. Exped.

JAMAICA
vi/8, no date, 2 ♂, 2 ♀ (dry), Banks.

BRAZIL
80.37, Pernambuco, no date, 2 ♂, W. Forbes. 61-44, vi/7, Rio de Janeiro, no date, 1 ♂ (dry), U.S. Explor. Exped. 919/C, vi/7, no date, 1 ♂ (dry), C. Stewart Banks.

MCZ. 14 lots, 26 specimens.

UNITED STATES
Florida: 5160, Key West, no date, 1 ♂ (juv), 1 ♀ (ov), J. E. Mills.

BAHAMAS
Bimini: 11671, Alicetown, May 1941, 1 ♂, R. W. Foster and J. Huntington. 11692, Nixons Harbour, May 1941, 1 ♂, R. W. Foster and J. Huntington. 10360, Great Inagua I., Salt pond canal 1½ mi SE Matthew Town, 24 June 1938, 1 ♂, 1 ♀, R. H. McLean and B. Shreve.

CUBA
10889, Bahía de Siguanea, Isla de Pinos, 14 Feb. 1938, 1 ♂, 1 juv, Harvard-Havana Exped.

BRAZIL
5167, Santos, Estado de São Paulo, no date, 1 ♀ (ov), Coutinho, Thayer Exped.

MNB. 6 lots, 9 specimens.

BRAZIL
56, Pernambuco, no date, 1 ♂, 2 ♀ (ov). 58, Rio Guanabara, no date, 1 ♂. 52, Rio Guanabara, no date, 2 ♂. 1380, Baía de Guanabara, 1948, 1 ♂, P. Drach. Estado de Santa Catarina: 59, São Francisco do Sul, 1901 (?), 1 ♀, L. Gralberto. 499, no data, 2 ♀.

MNHNP. 2 lots, 2 specimens.

QUESTIONABLE LOCALITIES
Suitrée(?), 1922, 1 ♂, from Museo de Historia Natural, Buenos Aires. Chili(?), 303-7, no date, 1 ♀ (dry), M. Fontaines.

RMNH. 17 lots, 26 specimens.

UNITED STATES
Florida: 15631, Key Biscayne, Miami, 14 Sept. 1960, 1 ♂, R. B. Manning and L. B. Holthuis.

WEST INDIES
2326, June 1920, 1 ♀ (ov), J. Boeke.

ST. MARTIN
11879, Baie Orient, 23 Feb. 1957, 1 ♂, L. B. Holthuis.

ARUBA
15044, 1882-1883, 2 ♂ (juv), A. J. van Koolwijk.

CURAÇAO

St. Kruis Baai, 7 Oct. 1948, 1 carapace (dry), P. W. Hummelinck. 15056, shore of Piscadera Baai near Raphaël, 13 Nov. 1956, 1 (juv), L. B. Holthuis. 11877, Piscadera Baai, 27-28 Dec. 1956, 1 ♂, 2 ♀, 3 juv, L. B. Holthuis. Schottegat at Pasanggrahan, 22 Aug. 1948, 1 ♀ (dry), P. W. Hummelinck. South shore St. Joris Baai near Choloma, 3 Jan. 1957, 1 ♀ (dry), L. B. Holthuis. 11878, South shore St. Joris Baai near Choloma, 3 Jan. 1957, 1 ♂, 1 ♀, L. B. Holthuis.

BONAIRE

11880, lake on E coast, 10 Mar. 1957, 1 ♂, 1 ♀, L. B. Holthuis. 11876, lake on E coast, 6 Mar. 1957, 1 ♂, L. B. Holthuis. Paloe Lechi, 6 Apr. 1955, 1 carapace (dry), Zaneveld.

TRINIDAD

23413, Cocorite, 25 Aug. 1965, 1 ♂, 1 ♀, H. O. von Hagen.

VENEZUELA

10719, Isla de Margarita, Feb. 1955, 1 ♂, J. S. Zaneveld. 23396, Punta Mangle, Isla de Margarita, 11 Jan. 1964, 1 ♂, P. W. Hummelinck.

BRAZIL

4873, Bahia, 1909, 1 ♂, J. A. Bierens de Haan, Zool. Lab. Utrecht.

SADZ-B. 5 lots, 6 specimens.

BRAZIL

Bahia: 3223, Ilhéus, 1919, 1 ♂, 1 ♀, E. Garbe. 3214, Ilha Madre de Deus, Jan. 1933, 1 ♂. Rio de Janeiro: 3242, Atafona, 12 July 1963, 2 juv, N. Meneses. 3246, Atafona, no date, 1 ♂, N. Meneses. Santa Catarina: 3245, 27°15′S, 48°47′W, near Florianópolis, 21 Aug. 1966, 1 ♀ (ov), M. Iwai.

UNC-IMS. 1 lot, 3 specimens.

PUERTO RICO

2137, Mangrove channels behind Bahía Fosforescente, 2 May 1967, 2 ♂, 1 ♀, D. R. Torres and P. R. Ramos.

Supplementary literature records.—Southern Florida, Futch (1965); Biscayne Bay, Fla. (Park, 1969); Veracruz, Ver., Mexico (Contreras, 1930); Jamaica (White, 1847); Golfo de Venezuela (Taissoun, 1969); Gran Roque, Venezuela (Chace, 1956); Jangadas, south of Recife, and other localities in Pernambuco, Brazil (Coêlho, 1966, 1967b); Texas ? (tentatively identified specimen not available for confirmation, Pounds, 1961).

CALLINECTES BELLICOSUS (STIMPSON)

Figures 10, 18h, 20j-k, 22h, 27

Lupa bellicosa (Sloat, MS) Stimpson, 1859, p. 57 [11] (type locality: Guaymas, Gulf of California, C. P. Stone, types not extant).- ? Lockington, 1876, p. 105 [11].

Callinectes bellicosus Ordway, 1863, p. 577 [12].- Streets and Kingsley, 1878, p. 107.- A. Milne Edwards, 1879, p. 227 (var. of *C. diacanthus*).- Rathbun, 1896, p. 365, pl. 22; pl. 24, fig. 10; pl. 25, fig. 8; pl. 26, fig. 8.- 1898, p. 596.- 1926, p. 75 [Signal Hill Pleistocene].- 1930, p. 112, text-figs. 15k, 16i, 17g, 20, pl. 49.- Holmes, 1900, p. 73.- Young, 1900, p. 190 (var. of *C. diacanthus*).- Schmitt, 1921, p. 236, text-fig. 140.- Meredith, 1939, p. 108 [figure].- Steinbeck and Ricketts, 1941, p. 468, pl. 14, fig. 2.- Buitendijk, 1950, p. 275.- Garth and Stephenson, 1966, p. 47, pl. 5, fig. B; pl. 8, fig. B; pl. 10, fig. B; pl. 12, fig. B.- ? Contreras, 1930, p. 240, text-fig. 11.

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Callinectes ochoterenai Contreras, 1930, p. 229, text-figs. 2, 3A-C (type localities: LaPaz, Baja California, and Punta Arena, Guaymas, Sonora [Mexico]).

Description.—Carapace (Figure 10) with two slender frontal teeth separated by a space often bearing a rudimentary submesial pair of teeth; median epistomial spine below front prominent and slightly exceeding frontal teeth. Metagastric area with lateral sulci fairly deep but anterior and posterior margins obsolescent, posterior width greater than length. Inner orbital fissure usually open. Anterolateral margins broadly arched, teeth exclusive of outer orbital and lateral spine relatively short and concave sided with acuminate tips directed outward more than forward; lateral spines short, about twice length of preceding tooth, longer in juveniles. Surface finely granulate and remarkably smooth except on anterolateral

region where granules are more widely spaced; sulci and lines of granules more prominent on young than on adults.

Chelipeds with prominent and sharply tuberculate or spiniform ridge on outer surface of propodus, other ridges lower and nearly smooth.

Male abdomen and telson reaching a bit beyond suture between thoracic sternites IV and V; telson triangular, longer than broad, sixth segment slightly constricted in proximal half. Mature female abdomen and telson reaching about same level as male, telson with inflated sides longer than wide, segments 5 and 6 almost equal in length. First gonopods of male (Figures 18h, 20j, k) reaching to midlength of thoracic sternite VI with tips slightly inclined mesad toward each other, not overlapping but thrown into sinuous curves, twisting on axis at level of suture between thoracic sternites VI and VII and armed at this level with a crowded lateral band of assorted short, rather blunt, retrogressive spinules becoming less numerous and more slender proximal and distal to this level, longer distally and shorter proximally; a subterminal row of rather prominent well separated exceedingly slender setae on sternomesial aspect. Gonopores of female (Figure 22h) asymmetrically ovate in outline with orientation of long axis mainly in frontal plane but with apex directed anteromesad; aperture of each laterally elongate and sloping from broadest area at surface on mesial side to narrower deeper portion under uniformly rounded borders on remaining sides.

Size of carapace in mm.—Largest male: length 76, width at base of lateral spines 135, including lateral spines 154 (from crab purchased in Mexico City fish market by Edgard Taissoun and Alfredo Vidal after statistical analysis was completed). Largest female: length 89, width at base of lateral spines 160, including lateral spines 178. Summary of selected measurements is given in Tables 1 and 2.

Color.—The only good published color description is that of Garth and Stephenson (1966), "Carapace mottled greenish yellow to brownish green, sometimes with dark spot on center of orbit and dark green areas roughly outlining epibranchial ridge. Arms generally greenish yellow to greenish brown, wrist articulations purple red. Hand with blotch at level of finger articulation, this blue-green in smaller and purple in larger specimens. Similar internal blotch purple throughout. Inner surface hand and fingers centrally white to pale blue, dorsally purple to red-purple, and ventrally blue to purple-blue. Cheliped colors most vivid in largest male." Almost brown above, cream colored below, tubercles and ridges of hand tinged with red (Lockington, 1876).

Specimens purchased at a fish market in Mexico City and preserved in Formalin[2] about 21 June 1972, by Edgard Taissoun and Alfredo Vidal were seen by me on June 23. Colors were: male tannish purple overall; ridges of chelipeds, carpi, and front edge of meri having deepest purplish cast. Posterior areas of carapace grading through brownish cast to areas of beige on posterolateral slopes and swimming paddles. A round beige spot on posterolateral border just anterior to insertion of swimming legs. Upper surfaces of palms with a reticulate pattern of purple lines on beige to off-white background. Inner and outer surfaces of chelipeds and ventral aspect off-white with suggestion of yellow. Superior and inferior edges of fingers purple grading to blue on inner face of fingers, and a reticulate blue stripe along lower inner border of palm. Teeth of chelipeds oyster white at their crowns, but their bases light purple giving impression of a purple "gum" line.

Female similar to male but with a more tan to beige hue on carapace and upper surface of palms. Blue color confined to inner surface of propodal finger only.

Prominent tubercles and tips of spines oyster white in both sexes.

Variation.—Variation in *C. bellicosus,* as in other members of the genus, seems largely a matter of differential growth changes. Openness of the inner orbital fissures has been used as a key character for this species, but large series show the character to vary individually; though usually open, the fissure is often closed. The edge of the frontal area slopes upward from contact with the exposed median epigastric spine to a row or cluster of obsolescent granules which mark the site of obsolescent submesial frontal teeth. In all other species the front overhangs this spine to at least some extent. The species is notable for sharpness of teeth and spines. Anterolaterals pointing forward in the young are directed more outward in mature specimens. These teeth are often almost

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

rectilinear but still sharp tipped. Sub- and outer orbital spines become increasingly acuminate with age. The mesogastric area changes shape with age, the anterior border becoming increasingly sinuous and indistinct. Adjacent portions of the mesobranchial regions remain sharply outlined in old individuals. Some older specimens show "expansion scars" on the carapace as if stresses incurred while molting had stretched the carapace during the hardening process. Such "scars" seem to radiate from centers in the cardiac region.

The chelae sometimes have lower propodal margins slightly decurved in conjunction with development of a strong basal tooth on the opposing dactyl. Except for the sharply granulate outer propodal ridge, usually smooth remaining ridges on the chelipeds are occasionally as roughly granulate as in *C. exasperatus*.

In sternal view, males have a great resemblance to *C. similis* in that the abdomen and sternum are nearly plane and that the anterior curvature of fused segments 3-5 is shallow. Males may show a central proximal column of indurated exoskeleton in the 6th abdominal segment. The first gonopods of mature males may reach beyond the middle of sternite VI to the suture between V and VI.

Distribution.—San Diego, Calif., to Bahía Almejas (southeastern extension of Bahía Magdalena) Baja California; La Paz Harbor around Golfo de California to Topolabampo, Sinaloa, Mexico (Figure 27). The species is apparently absent from the extreme southern tip of Baja California, but was listed as the commonest large crab in the Golfo de California by Steinbeck and Ricketts (1941).

Habitat.—Garth and Stephenson (1966) summarized the little available ecological data noting that the known depth range is 0 to 18 m, usually over sand bottom, and that many crabs had been captured swimming under lights at night. From museum records it is clear that the species frequents estuarine areas. A few specimens from Espíritu Santo, Golfo de California (AHF) are covered with a red clay deposit.

Spawning.—Only one lot taken in September from Scammon Lagoon, Baja Calif., in water 0.6 m deep contained ovigerous females. This is curious in light of the fact that more mature females have been collected than males (Tables 1 and 2), but the record is probably biased by times of collection. Of 94 lots for which collection date is recorded, the monthly frequency is: January 5, February 11, March 43, April 17, May 3, June 2, August 3, September 2, October 1, November 5, and December 2. Either spawners were beyond depths sampled (unlikely) or early spring is not the main spawning period for this species.

Economic importance.—No data are available on uses of this crab other than notes above on its availability in fish markets of Mexico City. Thirteen lots of fragments, mostly parts of fingers, from archeological sites near Municipio Caborca, La Cholla Bay, Sonora, Mexico, are recorded in the USNM as *Callinectes* (probably *C. bellicosus*) indicating pre-Columbian use of the large crabs by peoples of the area.

Remarks.—*Callinectes bellicosus* resembles *C. similis* of the Carolinian province of the Atlantic in that both are restricted in distribution at the northern fringes of the tropical homeland of the genus, but the analogy is a loose one for *C. bellicosus* is the more restricted, essentially endemic to the Golfo de California which is a transitional body of water with Panamanian relationships grading from tropical in the south to temperate (but warm in summer) in the north, and the Pacific coast of the Baja California peninsula whose marine climate is transitional between tropical and dominant temperate from Punta Entrada (Bahía Magdalena) to Point Conception north of Santa Barbara Channel (Garth, 1961a). Temperate and tropical faunas meet and mingle along this outer coast, but tropical forms thin out northward surviving only in protected shallows. Records of *C. bellicosus* are few north of Scammon Lagoon, northern extensions of range being favored by warm periods (Garth, 1961a). The southern tip of the peninsula, from which *C. bellicosus* is absent, is essentially an insular oceanic region distinct from adjacent coastlines and dependent on accidental transport for its marine fauna (Garth, 1961a).

Belonging to the group of species with moderately long first gonopods, *C. bellicosus* has diverged from the remainder of the group in having gonopods with rather straightened sinuosity and possession of prominent sternomesial setae. The form of the body bears some resemblance to *C. similis*, the distributional western Atlantic

analog, in having a smooth and finely granulate carapace, reduced submesial frontal teeth, shallow anterolateral teeth, nearly plane sternum and abdomen in males, and similar length-width proportions in mature males.

A Pleistocene record for *C. bellicosus* (USNM 372804) is represented by the distal two-thirds of a propodal finger from a minor left chela of a large crab from the upper San Pedro formation, Signal Hill, northeast of Long Beach, Calif. (Rathbun, 1926). Size and tooth pattern of this specimen are indistinguishable from the modern form.

Material.—Total: 87 lots, 322 specimens.

Specimens listed in Rathbun (1930) from USNM (4630 not found) and AMNH; Garth and Stephenson (1966) from AHF and USNM.

USNM. 32 lots, 137 specimens, including the following not cited above:

MEXICO

Baja California: 12464, [?] 3 ♂, col. unknown. 63280, S end Bahía Magdalena, 20 Mar. 1911, 4 ♂, *Albatross*. Uncatalogued, Ricason I., Bahía Concepción, 7 Apr. 1911, 3 ♂, *Albatross*. 60006, Bahía Concepción, mouth of Rio Mulegé, 4 Apr. 1911, 1 ♂, *Albatross*. 57909, Bahía de los Angeles, 1921, 1 ♂, Calif. Acad. Sci. Sonora: 80666, Bay at Guaymas, 31 Jan. 1923, 1 ♂, 2 juv, B. F. Yost. 97611, Estero de Agiabampo, no date, 1 ♂ (dry), E. F. Ricketts. 81926, 1 ♂, 2 ♀, 7 juv. 122921, Agiabampo, May 1939, 1 ♀, R. Hermosillo.

AHF. 44 lots, 158 specimens.

AMNH. 4 lots, 18 specimens, including the following not cited above:

MEXICO

Baja California: 5498, Bahía Tórtolo, Punta San Bartolomé, 14 Mar. 1911, 1 ♂, *Albatross*. 5508, Bahía Ballenas, 16 Mar. 1911, 2 ♂, 1 ♀, *Albatross*. 5524, Bahía Magdalena, 20 Mar. 1911, 6 ♂, 2 ♀, *Albatross*. 5504, Bahía Pichilinque, 27 Mar. 1911, 3 ♂, 3 ♀, *Albatross*.

BMNH. 1 lot, 1 specimen.

79.1, off San Francisco, 1 ♂, E. Gerrard, Jr. [Error, or San Francisco I., 24°50′N, 110°35′W, G. de Calif.?].

MCZ. 1 lot, 3 specimens.

MEXICO

Baja California: 4253, Shoal Point, Colorado River, 29 Mar. 1889, 2 ♂, 1 ♀, *Albatross*.

RMNH. 4 lots, 4 specimens.

MEXICO

Baja California: La Paz, 15 Oct. 1945, 1 ♀, M. Cárdenas. Sonora: 7540, Guaymas, 25 Sept. 1945, 1 ♀, M. Cárdenas. Sinaloa: 7538, Ahome, 1 June 1945, 1 ♀, M. Cárdenas. 7539, Topolobampo, 21 Apr. 1945, 1 ♂, M. Cárdenas.

Los Angeles County Museum. 1 lot, 1 specimen.

MEXICO

Baja California: Bahía Santa María, Mar. 28, year unknown, 1 ♀, A. E. Colburn, A748.

Supplementary literature record.—Punta Santa Inés [Baja Calif.] (Crane, 1937).

CALLINECTES TOXOTES ORDWAY

Figures 11, 18i, 20l, 22i, 27

?*Callinectes diacanthus* Stimpson, 1860, p. 220.

Callinectes toxotes Ordway, 1863, p. 576 [11] (syntypes: ♂, USNM 2413: 2 ♂, MCZ 5182; ♂ [dry], MCZ 5183; Cape San Lucas [Baja California], John Xántus, col.).- A. Milne Edwards, 1879, p. 227 (var. of *C. diacanthus*).- Rathbun, 1896, p. 363, pl. 21; pl. 24, fig. 9; pl. 25, fig. 9; pl. 26, fig. 9; pl. 27, fig. 8.- 1910, p. 536, pl. 55.- 1930, p. 127, figs. 15i, 16g, 17i, 18h, pl. 54.- Young, 1900, p. 189 (var. of *C. diacanthus*).- Contreras, 1930, p. 237, fig. 8.- Garth, 1948, p. 35.- 1957, p. 37.- 1961b, p. 142.- Garth and Stephenson, 1966, p. 50, pl. 5, fig. C; pl. 8, fig. C; pl. 10, fig. C; pl. 12, fig. F.- Bott, 1955, p. 56.

Callinectes robustus A. Milne Edwards, 1879, p. 227 (var. of *C. diacanthus*) (type locality: Colombia; type listed by Rathbun, 1930, in MNHNP, not found in 1968, considered lost, 1973, fide J. Forest).- Young, 1900, p. 189 (var. of *C. diacanthus*).

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Description.—Carapace (Figure 11) bearing four large, rounded frontal teeth; submesial pair narrower than, partially coalesced with, and reaching half the length or more of lateral pair.

Metagastric area with length approximately equal to posterior width, anterior width about 2 times length. Anterolateral margins moderately arched, teeth exclusive of outer orbital and lateral spine varying from triangular or inflated triangular at inner end of row through acuminate forward trending intermediate teeth to forward curving spiniform tooth at outer end of row, base of first and last tooth narrowest. Surface of carapace coarsely granulate and uneven, nearly smooth around margins and along regional sulci, more granulate over branchial and gastric areas, most closely crowded granules on cardiac, mesobranchial, and anterior half of mesogastric regions. Epibranchial line prominent and nearly uninterrupted.

Propodus and carpus of chelipeds with sharply and rather coarsely granulated ridges, especially on propodus, rarely worn smooth; dactyl of major chela with basal teeth (often a single strong tooth) closing against cuspate molariform complex on propodus, both chelae with sectorial teeth.

Male abdomen and telson reaching beyond midlength of thoracic sternite IV; telson much longer than broad, triangular with inflated sides; sixth segment of abdomen narrowest in proximal third. Mature female abdomen and telson reaching no more than midlength of thoracic sternite IV; telson elongate triangular with inflated sides, sixth segment longer than fifth. First gonopods of male (Figures 18i, 20l) very long, reaching to or beyond suture between thoracic sternites IV and V; sinuously curved, overlapping proximally, diverging distally, twisting mesioventrally on axis at midlength of thoracic sternite V and recurving to termination near midline; armed distally with lateral band of retrogressive spinules thinning to absence near tip. Gonopores of female (Figure 22i) asymmetrically and narrowly ovate in outline with apex on long axis directed anteromesad; rounded borders with series of wrinkles conforming to contours; aperture of each sloping from surface on mesial side under anterolateral border superior to a rounded eminence on posterior border.

Size of carapace in mm.—Largest male: length 88, width at base of lateral spines 156, including lateral spines 193. Largest female: length 74, width at base of lateral spines 133, including lateral spines 174. Estévez (1972) reported a female with carapace 75 mm long estimated to have a width including lateral spines of 182 mm, and estimated general growth rate per molt to be 15% in length, 24% in width. Summary of selected measurements is given in Tables 1 and 2.

Variation.—This species attains the largest size in the genus, but old individuals apparently do not show teeth or spines worn to an extent comparable with other species. Anterolateral teeth vary individually in degree of laterally progressive upturning in the row. Submesial frontal teeth vary considerably in length as well as acuity, but none are really sharp pointed. Chelae in seemingly old individuals retain basal teeth with well defined molariform structure on the major hand; sectorial tooth development seems more prominent on both right and left chelae than in other species. Females have granules more prominent and closely crowded on the carapace than males. Male first gonopods cross over each other at the tips in some individuals.

Distribution.—Cabo de San Lucas, Baja California, to extreme northern Peru; extraterritorial, Juan Fernández (Figure 27).

Habitat.—Ranging from shore to 27-m depths, *C. toxotes* has been characterized as a mangrove swamp crab (Estévez, 1972). It occurs from freshwater streams to open bays, and a number of collections come from lagoons or river mouths.

Stomachs of 521 specimens contained bivalves, gastropods, inorganic debris, crustaceans, fishes, and polychaetes in order of precedence (Estévez, 1972).

Spawning.—Material available for study includes only three ovigerous females: January, Panama; August, Acapulco, Mexico; a third undated specimen from Cabo San Lucas, Baja California, in MCZ was collected by John Xántus, perhaps with the type material.

Only one-third of the specimens of *C. toxotes* in museum collections are sexually mature, and among these males outnumber females 2:1. The small number of ovigerous females should therefore not cause surprise.

Economic importance.—The species is used as food and sold at the market of Buenaventura, Colombia. Crabs there are brought from Málaga Bay and others, many (mostly immature) being caught by shrimpers along the coast (Mario Estévez, pers. commun.). Collections from Estados de Sinaloa and Nayarit, Mexico; Tumaco, Colombia;

and Guayaquil, Ecuador; are from places where fishing is active or from fish markets.

Remarks.—The type locality lies at the extreme northern end of the distributional range, seemingly so far removed from the remainder of the range that one might question origin of the syntypes. Xántus (Madden, 1949) was an excellent and energetic collector for the Smithsonian Institution who lived and worked at Cabo de San Lucas from 4 Apr. 1859 to 7 Aug. 1861. Collectors then were not so precise about recording locality data as today, and Xántus was no exception. It is known that collections were brought to Xántus from Bahía Magdalena to the north and Revillagigedo Island to the south, etc., and that he visited Mazatlán on the mainland in summer, 1861, returning to Cape San Lucas on 1 Aug. Though no collection date is recorded with the types, MCZ received its specimens from the Smithsonian Institution on 13 Feb. 1861, which would seem to limit origin of the specimens to the tip of Baja California or at least rule out collection on the mainland closer to the rest of the range for the species. Moreover, an ovigerous female bearing a Cabo de San Lucas label (MCZ 5184), received with the mature types, suggests a breeding population and not an accidental occurrence.

Usual habitat of the species suggests that the Juan Fernández collection is extraterritorial. Set of currents between this isolate and the nearest known population in Peru suggest that if a breeding population does exist there, it is introduced. Further collecting both here and in the Cabo de San Lucas area would be useful.

Material.—Total: 30 lots, 120 specimens.

Specimens listed in Rathbun (1930) from USNM and MCZ; Garth and Stephenson (1966) from AHF and USNM.

USNM. 19 lots, 44 specimens, including the following not cited above:

MEXICO
Sinaloa and Nayarit: 61023, 1926, 1 ♂ (dry), C. Stansch, No. 33.

COSTA RICA
112356, Golfo de Nicoya, Jan. 1952, 2 carapaces (dry), S. E. Erdman.

PANAMA
73283, Bahía Honda, 9 Mar. 1933, 1 juv, W. L. Schmitt. 122920, no date, 1 ♂.

COLOMBIA
77045, Buenaventura, 18 Nov. 1934, 1 ♀ juv, R. Mensing.

AHF. 8 lots, 44 specimens, including the following not cited above:

[Nicaragua material Stn. 962-39 = a *Portunus* species].

COSTA RICA
Bahía Carrillo, 6 Feb. 1938, 1 ♂, *Zaca* Stn. 208, NYZS 38,194. Golfito, Golfo Dulce, 6 Mar. 1938, 1 ♂, *Zaca*, NYZS 38,525.

MCZ. 5 lots, 28 specimens, including the following not cited above:

MEXICO
Baja California: 5184, Cabo de San Lucas, no date, 1 ♀ (ov), J. Xántus. (recd. from Smithsonian Inst. 13 Feb. 1861). Guerrero: 5185 and 8755, Acapulco, Aug. 1872, 9 ♂, 15 ♀ (1 ov), *Hassler* Exped.

AMNH. 1 lot, 3 specimens.

COLOMBIA
10587, Tumaco, 19 Apr. 1941, 2 ♂, 1 ♀, *Askoy* Exped.

RMNH. 1 lot, 1 specimen.

Cat. a. South America, 1 ♂ (dry), Latreille.

Supplementary literature records.—Acapulco, Guerrero, Mexico (Contreras, 1930); Acajutla, Barra Ciega, La Libertad, La Unión, El Salvador (Bott, 1955); NW Corinto, Nicaragua (Garth and Stephenson, 1966); Baudó, Juanchaco, Catripe, Togoromá, Málaga, Buenaventura, Guapi, San Juan del Sur, Cabo Manglares, Punta Coco, and Tumaco, Colombia (Estévez, 1972).

CALLINECTES BOCOURTI A. MILNE EDWARDS Siri (Brazil)

Figures 12, 18j, 20m, 22j, 27

Cancer pelagicus.- de Geer, 1778, p. 427, pl. 26, figs. 8-11.

Callinectes bocourti A. Milne Edwards, 1879, p. 226 (syntypes: 2 ♂, MNHNP, Mullins River, 20 miles south Belize, [British] Honduras, M. Bocourt).

Callinectes Cayennensis A. Milne Edwards, 1879, p. 226 (syntypes: 2 ♂, MNHNP [French] Guiana, M. Mélinon).

Lupa diacantha.- Kappler, 1881, p. 143.

?*Neptunus diacanthus*.- Thallwitz, 1892, p. 53.

Callinectes bocourti.- Rathbun, 1896, p. 369, pls. 19; 24, fig. 7; 25, fig. 6; 26, fig. 6; 27, fig. 6 [part].- 1897, p. 151 [part].- 1901, p. 49.- 1930, p. 128, text-figs. 15g, 16e, 17h, 18f, pl. 55.- 1933, p. 49.- 1936, p. 383.- Young, 1900, p. 192.- Bott, 1955, p. 56.- Holthuis, 1959, p. 201, text-fig. 47, pl. 5, fig. 2.- Chace and Hobbs, 1969, p. 127, text-figs. 35, 37a.- Taissoun, 1969, p. 57, figs. 20A-D, photo 7.- 1972, p. 31, figs. 1a-d, 2 [part], 3 [part], 9C, 10C-D; photos 4b, 5-6, (col.), 7.- 1973, p. 24, figs. 4G, 5G, photo 2.

Callinectes diacanthus.- Young, 1900, pls. 2, 3.

Callinectes cayennensis.- Young, 1900, p. 192.

Callinectes danae.- Tesch, 1914, p. 195 (fide, Holthuis, 1959, p. 205).

Description.—Carapace (Figure 12) bearing four triangular frontal teeth with tips reaching a nearly common level, lateral pair obtuse with mesial side having flatter angle than lateral side, submesial pair narrower than laterals. Metagastric area with length and posterior width about equal, anterior width 2 times length. Anterolateral margins moderately arcuate, anterolateral teeth exclusive of outer orbital and lateral spine swept forward, anterior margin of teeth shorter than posterior margin, teeth in lateral half of row always acuminate. Surface of carapace dorsally smooth and glistening around perimeter (when wet) and on epibranchial surfaces; central portion granulate, coarsest granules over mesobranchial and rear half of cardiac areas and lateral half of branchial lobes. Epibranchial line prominent and nearly continuous, sulci on central part of carapace deeply etched.

Chelipeds remarkably smooth except for usual spines and obsolescent granules on ridges; fingers of major chela heavily toothed, lower margin of propodal finger often decurved near base in adults.

Male abdomen and telson long, extending nearly to juncture between thoracic sternites III and IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching as far forward as in male, sixth segment nearly as long as fifth, its distal edge uniformly arched, telson elongate-triangular with inflated sides. First gonopods of male (Figures 18j, 20m) very long, often exceeding telson and crossed near tips; sinuously curved and overlapping in two places proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving gradually to termination near midline; armed distally with a dorsolateral band of large and small retrogressive spinules. Gonopores of female (Figure 22j) asymmetrically ovate in outline with apex on long axis directed anteromesad; aperture of each sloping from surface on mesial side under rounded, sinuous anterolateral border superior to a low rounded eminence on posterior border.

Size of carapace in mm.—Largest male: length 76, width at base of lateral spines 132, including lateral spines 156. Largest female: length 70, width at base of lateral spines 121, including lateral spines 146. Summary of selected measurements is given in Tables 1 and 2. The species characteristically reaches fairly large size.

Color.—Complete color descriptions (Chace and Hobbs, 1969; Taissoun, 1969, 1972) and notes (Rathbun, 1896, 1930; Holthuis, 1959) give a range of color variations. These can be broadly summarized as: Overall cast olive green with prominent reddish markings. Carapace olive, grayish green, greenish chestnut, or forest green with variable purplish to red markings, especially on branchial, hepatic, cardiac, and gastric areas, individuals of large size sometimes being dark chestnut tinted blackish brown on gastric and metagastric areas, with an oblique spot on subbranchial region; anterolateral teeth olive green with brown to red tints and yellowish white tips. Chelipeds red to dark reddish brown above and whitish below with bluish tints, main colors being sharply separated on outer surface of palm; fingers red to reddish brown, a purplish cast on internal articulation of merus with carpus and this member with chela; tubercles, tips of fingers, and spines on articles cream. Remaining legs reddish above with shades of maroon, yellow, and olive green ventrally except distal articles scarlet to red or dark red distally; hairs olive-tan. Underparts of body mainly dirty white to purplish red with suffusion of blue marginally, first abdominal seg-

ment mainly reddish tan. Males tend to be reddish, females greenish.

Variation.—This species greatly resembles both *C. rathbunae* and *C. maracaiboensis* but generally has more obtuse frontal and anterolateral teeth as well as more pronounced smoothness on chelipeds and carapace. Considerable variation attributable to growth and age is evident. The submesial pair of frontal teeth become relatively more slender with age, but seldom extremely acute. Some young have quite lobate frontals, scarcely separated; an extreme case is represented by MCZ lot 5186 from Caruca, Rio Maria [= Rio Caraçaua near Belem?] Brazil, in which an immature female has lobate frontal teeth partially coalesced while more mature males in the lot have fairly sharp submesial frontals. There is great variation in length of lateral spines, the relationship of spine length to that of the last anterolateral tooth as cited by Rathbun (1930) and Taissoun (1972) not holding up as a key character for large series of specimens. Anterolateral teeth vary from obtuse to acuminate, acuteness increasing somewhat with age, and edges of the teeth vary from smooth to granulate with greatest amount of granulation usually on the posterior margin. There is more apparent variation in chelipeds than among other species of the genus. A character accentuated with age, especially among males, is a major cheliped with gaping fingers in which the propodus is decurved along its lower margin. At one extreme is a heavy gaping hand with strong basal tooth on the dactyl, whereas at the other both chelae may be slender and almost symmetrical. Many individuals have a major chela that is halfway along this scale of development; others possess two minor chelae of nearly uniform size—evidence of regeneration.

From Rio de Janeiro south, specimens seen have stronger and more sharply granulate ridges on the chelae than those from other parts of the species' geographic range. Likewise on these southern forms, granules are bold on the posterior slope of the cardiac area and sometimes crowded into suggestion of a transverse ridge at summits of the cardiac and mesobranchial areas. Both developments are reminiscent of similar patterns found in the acutidens form of *C. sapidus*. Frontal teeth, mesogastric area, and first pleopods of these forms seem typical of *C. bocourti*.

More obscure are other variations which have bearing on the separation of *C. bocourti* from *maracaiboensis*. A series of variant specimens from over the geographic range of *C. bocourti* demonstrate these.

Brazil: An ovigerous female from Praia Inglese, São Francisco (USNM 60978) has its sixth abdominal segment relatively narrow for its length with the distolateral edge angular (typical), not rounded as in *C. maracaiboensis*, the anterolateral teeth sharp and not curved forward, and the frontal teeth fairly sharp.

Puerto Rico: A mature female from Hucares (USNM 24460) has an abdomen as above but frontal teeth rather short and lobate, and anterolateral teeth short and not curved forward but with their anterior margin shorter than the posterior one. Another mature female (USNM 24457), from near Palo Seco, has its sixth abdominal segment shaped as in *C. maracaiboensis* (short, broad, rounded distally), short and rounded frontal teeth (mesial pair a bit sharper), and anterolateral teeth curved forward only in the lateral half of the row. A mature male from Cataño (USNM 24455) has anterolateral teeth short and not trending forward, first gonopods distorted in preservation but armed with spinules typical of *C. bocourti* (but a tip as in *maracaiboensis*), and short, lobulate frontal teeth (mutilated).

Trinidad: A mature female (USNM 137731) has the abdomen shaped as in *C. maracaiboensis*, and lobulate frontal and anterolateral teeth quite sharp and decidedly curved forward. Males in this lot have first gonopods typical of *bocourti* and anterolateral teeth moderately curved forward.

Venezuela: A mature female from Tacarigua de la Laguna, Estado Miranda (USNM 89644) has the sixth abdominal segment rounded distally and relatively short for its width, as in *C. maracaiboensis*, the mesial pair of frontal teeth moderately acute, lateral pair broader (both pairs fairly short), and sharply acuminate anterolateral teeth trending forward but not curved.

Costa Rica: A mature female (USNM 113279) has very lobate frontal teeth, erect anterolateral teeth strong and trending forward, and the sixth abdominal segment broken but rather indeterminate in shape (trending toward typical).

British Honduras: A mature female from near Belize (21377) has prominently lobulate frontal teeth, anterolateral teeth trending forward but sharp tipped only in the lateral half of the row, and the sixth abdominal segment halfway between the two extremes for the species (wide and broadly rounded distally).

Taissoun (1972) included some of these specimens in his comparative study. From this welter of conflicting trends, separation of *C. bocourti* from *maracaiboensis* was a weighted decision resting on characters prevalent in the Lago de Maracaibo populations plus environmental separation.

Distribution.—Jamaica and British Honduras to Estado de Santa Catarina, Brazil (Figure 27); extraterritorial occurrences in southern Florida and Mississippi, USA (both mature males).

Habitat.—*Callinectes bocourti* is associated with *C. sapidus* in many estuarine areas, but seems more tolerant of stagnant, polluted situations. Around the mouth of Lago de Maracaibo *C. bocourti* was found in the Golfo de Venezuela, Bahía de El Tablazo, Río Limón, and Estrecho de Maracaibo, but less abundantly in Lago de Maracaibo itself (Taissoun, 1969, 1972). Only adult females were found in the Golfo de Venezuela, but elsewhere both sexes in all stages of growth were common, abounding in Río Limón and mangroves around Puerto Caballo and in Bahía de El Tablazo, large males and juveniles being especially numerous around sewers of San Carlos and Punta de Palmas. Bottoms in this area vary from mud to sand. Griffiths, Cadima, and Rincón (1972) presented a similar account, showing that juveniles recruit to a fishery there in July and November, with mature males tending to remain in low-salinity water whereas females move to saltier water after mating. Coêlho (1967a) reported *C. bocourti* (called the blue crab there) abundant in a lagoon in Pernambuco that varies from 5‰ salinity in the rainy season to 29‰ in the dry season, and from other estuaries in northeastern Brazil (1970).

The broad range of tolerance is emphasized by presence in places such as a pool inside porous old coral rubble on Bonaire (Rathbun, 1936), and dark somewhat stagnant, polluted water at mouths of the Mero, Indian, and Salisbury Rivers on Dominica where sand bars blocked river flow at the time of investigation (Chace and Hobbs, 1969). Here the crabs actively fed on garbage in daytime over a bottom of rock-strewn sand covered with silt. In other streams on Dominica whose mouths were open to flow, only *C. sapidus* was found.

Spawning.—In all of the museum collections studied there are many containing mature females, but only five in which there are ovigerous specimens and only three of these are accurately dated: January, Puerto Rico, Panamá; February, Curaçao; November, São Francisco [Estado de Santa Catarina], Brazil. Taissoun (1969, 1972) found ovigerous females most abundant from March to August in the Golfo de Venezuela, and Griffiths et al. (1972) found them most abundant around the mouth of Lago de Maracaibo in July. These data suggest nearly year-round spawning (Taissoun, 1972) in one part or another of the range, perhaps with seasonal peaks associated with latitude.

Economic importance.—Holthuis (1959) described a fishery for *C. bocourti* in brackish waters of Surinam where it is the only portunid routinely caught, its tolerance of this habitat apparently favoring success there. The crabs are sold alive on the market in Paramaribo. A crab trap fishery around the mouth of Lago de Maracaibo started in 1969 and is increasing rapidly (Griffiths, et al., 1972). Though directed primarily at *C. sapidus,* a considerable number of *C. bocourti* are taken as well. Second half of the year is the season of highest catch per unit effort in a brackish area where males make up 90% of the take.

Remarks.—The collections examined contain an unusually large number of mature females.

The type series of *C. bocourti* in the MNHNP is somewhat confused by labels. No clear designation is given on labels of specimens which, by implication, can be associated with the original description. Two mature male specimens labelled "*Callinectes bocourti* A. M. Edw., Riviere de Mullins (12 m. NNW Stann Creek) au de Belize, Honduras, Coll. Bocourt" represent the types in the opinion of J. Forest. Identification, locality (excepting the parenthetic emendation), sex, and collector agree with Milne Edwards' description. The smaller specimen (size of carapace in mm: length 48, width at base of lateral spines 80, including lateral spines 90) has more granulate gastric, metagastric, cardiac, and branchial areas than the larger (length 60, width at base of lateral spines 102, including lateral spines 120). A small *Chelonibia* is affixed over the left epibranchial line on the anterolateral aspect of the mesobranchial area of the larger specimen. Both specimens lack right chelae, but have slender left minor hands with smooth rounded upper sides on the

propodus, that of the smaller specimen showing obsolescent granules; in both, the merus and carpus are smooth, with a very blunt outer spine on the carpus. The small specimen has a missing right third pereopod. In both, the first gonopods reach slightly beyond the telson.

Two male specimens labelled "*Callinectes cayennensis* A. M. Edw., Cayenne, Coll. Melinon" are possibly the types of *C. cayennensis*. Identification, locality, sex, and collector agree with Milne Edwards's description. Both dark in color, the specimens are obviously *C. bocourti*. The larger has only seven anterolateral teeth on the right side, the first tooth being enlarged. Both specimens have two apparent minor chelae, the larger of each smooth dorsally, and the smaller with obscurely granulate obsolescent ridges.

Finally, a dry male specimen labelled "*Callinectes bocourti* A. M. Edw., TYPE?, Honduras, Belize (Crust. Mexique, p. 226, 1881, Bocourt) A. Milne Edwards 1903" has a badly cracked carapace and bears the word "Belize" written obscurely in ink on the right mesobranchial eminence. The specimen, as shown by carapacic and pleopodal characters, is not *C. bocourti*, but rather *C. danae*, and was undoubtedly mislabelled subsequent to Milne Edwards's death in 1900, according to J. Forest. The broken abdomen exposes the tip of an intact first pleopod with tip turned ventrolaterally at the two-thirds level of sternite VI bearing a subterminal hair on the sternal aspect.

In the ANSP collection is a dry male specimen of *C. bocourti* (No. 2808 labelled *Lupa dicantha*) that is badly shrunken and distorted bearing the label "North America," but no date of collection nor indication of collector. The name and specimen suggest a collection made over a century ago representing a possible third record of the species from somewhere in the United States.

North American records may be explained by drift from the Caribbean, possible routes being suggested by drift bottle returns (Brucks, 1971).

Bott (1955) listed the species from the west rather than the east coast of Middle America by mistake.

Material.—Total: 117 lots, 290+ specimens.

Specimens listed in Rathbun (1930) from USNM (24459 not found) and MCZ, and in Holthuis (1959) from Surinam in RMNH.

USNM. 33 lots, 82 specimens, including the following not cited above:

PUERTO RICO

123085, 73279, Boca de Congrejos, 7 mi E San Juan, 31 Mar. 1937, 2 ♀, W. L. Schmitt. 77104, beach near Ponce, 17 Aug. 1932, 1 ♀, T. J. Barbour.

VIRGIN ISLANDS

St. Croix: 72354, Fairplain str. above bridge, 1935-36, 2 ♂, H. A. Beatty, No. 129. 76963, Altona str. 100 ft from sea, no date, 3 juv, H. A. Beatty, No. 199. 77100, Salt River reefs, no date, 17 juv, H. A. Beatty, No. 157.

BRITISH WEST INDIES

St. Lucia: 123086, Pigeon Island, 22 Mar. 1956, 3 ♂, 1 ♀, *Freelance*, Stn. 46-56.

COSTA RICA

113279, Limón Prov., Tortuguero R. about 2 mi above mouth at Leo's, 28 Apr. 1964, 1 ♀, 1 juv, D. P. Kelso.

COLOMBIA

78382, Puerto Colombia, no date, 1 ♀, Bro. Elias, No. 21.

VENEZUELA

89644, Estado Miranda, Tacarigua de la Laguna, 1 Mar. 1949, 1 ♀, Soc. Ciencias Nat. La Salle, Stn. c-3.

AHF. 1 lot, 1 specimen.

BRITISH WEST INDIES

Trinidad, West Manzanilla, 10°31′20″N, 61°02′37″W, 18 Apr. 1939, 1 ♂, *Velero III* Stn. A36-39.

AMNH. 4 lots, 4 specimens.

PUERTO RICO

2669, San Juan near San Antonio Bridge, 10 July 1914, 1 ♀, R. W. Miner. 5378, Culebra [18°18′N, 65°18′W], 1926, 1 ♂, H. E. Anthony.

BRITISH HONDURAS

Crique Salada [16°35′N, 88°37′W], Apr. 1951, 1 ♀, M. Gordon, Chable, and George.

PANAMA

11241, Harbor at Colón, no date, 1 ♀, *Arcturus* Exped.

ANSP. 3 lots, 9 specimens.

NORTH AMERICA [?]
2808. no date, 1 ♂ (dry).

[DOMINICAN REPUBLIC]
3519, Santo Domingo, no date, 2 ♀ (dry), W. M. Gabb.

PANAMA
1305, 5 ♂, 1 ♀, McNeil Exped.

BMNH. 9 lots, 12 specimens.

BRITISH WEST INDIES
1925.1.28.13, Tobago, 1 ♂, P. L. Guppy. 1938.3.29.18, Tobago, 1 ♂, A. K. Totton.

GUYANA
1960.10.5.15/16, Georgetown, Kitty Jetty, 1 ♂, 1 ♀, R. H. McConnell. 44.82, Georgetown, 1 ♂ (dry), vi/9. 62.93, 2 ♂, Leadbeater. 1949.5.26.1/2, 2 ♀, V. Graham.

SURINAM
1959.3.20.1, Suriname River near Paramaribo, 1 ♂, I. T. Sanderson.

BRAZIL
1923.8.14.1, Marajó I. mouth of Amazon, 1 ♂, Erhardt. 80.37, Pernambuco, 1 ♀, W. Forbes.

MCZ. 9 lots, 22 specimens, including the following not cited above:

PANAMA
5472, Aspinwall [= Colón], no date (recd. 13 Feb. 1861), 1 ♀, J. Rowell.

BRAZIL
5172, 13 Oct. 1873, 1 ♂ juv, C. Linden.

MNB. 2 lots, 3 specimens.

BRAZIL
Pernambuco: 329, Manques de Olinda, 1945, 2 ♂, Berla. Rio de Janeiro: 48, Maricá, no date, 1 ♀.

MNHNP. 2 lots, 4 specimens.

BRITISH HONDURAS
148, Rivière de Mullins au Sud de Belize, no date, 2 ♂, Bocourt.

FRENCH GUIANA
69, Cayenne, no date, 2 ♂, Melinon.

RMNH. 45 lots, 130+ specimens.

BRITISH WEST INDIES
Barbados: 23456, Holetown river pool, 18 Feb. 1964, 1 ♂, P. W. Hummelinck.

NETHERLANDS ANTILLES
Curaçao: 23450, N part Piscadera Baai, 25 Nov. 1963, 1 ♂, P. W. Hummelinck. 8122, Zaquito Lagoon, 1 Feb. 1949, 1 ♂, P. W. Hummelinck. 3270, Schottegat, 10 Feb. 1939, 1 ♀ (ov), H. S. C. Cossee. Schottegat near Pasanggrahan, 22 Aug. 1948, 1 ♀ (dry), P. W. Hummelinck. 11855 and 11858, slough in mangroves, Santa Cruz, 11 Feb. 1957, 2 ♂, 2 ♀, L. B. Holthuis, No. 1099. 11857, Waaigat, Willemstad, 30 Jan. 1957, many ♂♂ and juv, L. B. Holthuis.

Bonaire: Paloe Lechi, Apr. 1955, 1 juv (dry), J. S. Zaneveld. Paloe Lechi, Dralendijk, 5 Mar. 1957, 3 adult carapaces, (dry), L. B. Holthuis, No. 1137. 11856, Paloe Lechi, N Kralendijke, 5 Mar. 1957, ♂♂, ♀♀, and juv, L. B. Holthuis.

VENEZUELA
Estado Miranda: 7613, Laguna de Tacarigua, 1948-49, 2 ♀ (ov), G. Marcuzzi. Estado Sucre: 7615, beach by airfield, Cumaná, Sept. 1948, 1 ♀, G. Marcuzzi.

TRINIDAD
23403, Diego Martin R., 1965-66, 1 ♂, H. A. van Hagen.

SURINAM
21163, coast off mouth of Suriname and Coppename R., 25-27 Aug. 1964, 2 ♀, M. Boeseman. 21573, mouth of Suriname R. at Leonsberg near Paramaribo, 27 Dec. 1963, 1 ♂ juv, P. Leentvaar. 5367, Swamp near Agricultural Experiment Gardens, Paramaribo, 10 June 1941, 1 ♀ juv, D. C. Geijskes. 22495, brackish water at Matappica near Paramaribo, 6 Nov. 1965, ♂♂ and ♀♀, G. F. Mees. 22598, shore at Matappica near Paramaribo, 8-13 Jan. 1966, 1 ♂ and juv, G. F. Mees.

SADZ-B. 9 lots, 23 specimens.

BRAZIL
Maranhão: 876, 1919, 1 ♂, F. E. Sawyer, Smithsonian Inst. Alagoas: Lagoa Jequia Mangebeira Camargo, Nov. 1952, 3 ♂, 3 ♀. Bahia: 1248, Ilhéus, 1919, 2 ♀, E. Garbe. Rio de Janeiro: 1729,

Atafona, no date, 2 ♂, 2 ♀, Meneses. 3241 Atafona, 12 July 1963, 3 juv, N. Meneses. 399, Serra de Macaé, 1912, 2 ♂, E. Garbe. São Paulo: 400, Ubatuba, 1905, 1 ♀, E. Garbe. 403, Piassaquera, 1905, 3 ♂, J. S. Fialho. 352, Iquape, 1901, 1 ♂, R. Krone.

Gulf Coast Research Laboratory. 1 lot, 1 specimen.

UNITED STATES

Mississippi: 172:1062, Biloxi Back Bay, No., 1971, 1 ♂, from commercial fisherman (Perry, 1973).

Supplementary literature records.—Biscayne Bay, Fla. (Provenzano, 1961); St. Croix (Beatty, 1944); Dominica (Chace and Hobbs, 1969); Puerto Cortez, Honduras (Bott, 1955); Lake Maracaibo vicinity, Venezuela (Taissoun, 1969); Forteleza, Ceará, Brazil (Fausto Filho, 1966).

CALLINECTES RATHBUNAE CONTRERAS JAIBA PRIETA (MEXICO)

Figures 13, 19a, 20n, 22k, 27

Callinectes rathbunae Contreras, 1930, p. 238, text-figs. 9, 10 (type localities: Barras de Boca del Río, Buen País and Alvarado, Veracruz, Mexico).-Manrique Colchado, 1965, p. 30, figs. 10-15.-Taissoun, 1972, p. 35, figs. 1i-l, 2 (part), 3 (part), 9A, 10E-F, photos 8-11.

Callinectes rathbuni Pounds, 1961, p. 42, pl. 7, fig. 2d.

Description.—Carapace (Figure 13) bearing four acuminate frontal teeth with tips reaching a nearly common level, submesial teeth narrower and slightly shorter than laterals. Metagastric area with length and posterior width about equal, anterior width 2 times length. Anterolateral margins slightly arcuate, anterolateral teeth exclusive of outerorbital and lateral spine all acuminate with edges variably granulate, anterior margins of teeth a bit shorter than posterior margins, tendency to development of a shoulder on posterior margin of all except last tooth in row. Surface of carapace dorsally smooth and glistening around perimeter (when wet) and on epibranchial surfaces; central portion lightly and evenly granulate, cardiac area smooth anteriorly, granulate posteriorly. Epibranchial line prominent and sulci on central part of carapace deeply etched.

Chelipeds with sharply granulate ridges and usual spines; fingers of major chela heavily toothed but not gaping.

Male abdomen and telson long, extending nearly to juncture between thoracic sternites III and IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching as far forward as in male, sixth segment nearly as long as fifth and with mesiodistal borders oblique, not markedly curved; telson elongate triangular with inflated sides. First gonopods of male (Figures 19a, 20n) reaching nearly to tip of telson beyond suture between sternites III and IV, overlapping in proximal half, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle on thoracic sternite V and recurving gradually to termination near midline; armed distally with a dorsolateral narrow band of large and small sharp retrogressive spinules. Gonopores of female (Figure 22k) ovate in outline with apex on long axis directed anteromesad; aperture of each sloping from surface along long mesial side under rounded, sinuous anterolateral border superior to prominent rounded eminence on posterolateral border.

Size of carapace in mm.—Largest male: length 61, width at base of lateral spines 107, including lateral spines 134. Largest female: length 66, width at base of lateral spines 116, including lateral spines 141. Summary of selected measurements taken from the small sample available is given in Tables 1 and 2. Manrique Colchado (1965) reported a male with length 62, width including lateral spines 144, and a female with length 62, width including lateral spines 150.

Color.—The only published descriptions of color are brief. Pounds's (1961) general account indicated that the colors are "clear shades of green and blue with tints of red, orange, and purple." Manrique Colchado (1965) characterized the carapace as obscure or dark green. Judging by greenish coloration of recently preserved specimens, both descriptions apply. Underparts are white.

Distribution.—Mouth of Rio Grande, Texas-Mexico border to southern Veracruz, Mexico (Figure 27).

Habitat.—Specimens available for study came from estuarine waters of ditches, lagoons, and river mouths, the type of environment reported by Manrique Colchado (1965) as coastal lagoons of varying salinity at depths of 1-3 m.

Spawning.—Although mature females are represented in the small study collection, none are ovigerous.

Remarks.—Apparently an isolate of *C. bocourti* stock confined to the western and southwestern Gulf of Mexico, *C. rathbunae* has various angularities on the body and legs more accentuated than in *C. bocourti*: 1) acute frontal spines contrasted with more rounded or lobate frontal spines (excepting juvenile *C. rathbunae* from Tamaulipas having rounded lobate frontals); 2) all anterolateral teeth acute (or acuminate) rather than anterior portion of series being rounded at tips; and 3) hand of chelae moderately ridged rather than smoothly rounded. First gonopods of mature male *C. rathbunae* are not crossed at the tips and fall a bit short of the telson tip whereas in mature *C. bocourti* they are crossed at the tips and slightly exceed the telson.

Specimens of neither species from Yucatán are available, thus areas of possible intergradation between seemingly close relatives have not been studied.

Material.—Total: 10 lots, 18 specimens.

USNM. 4 lots, 10 specimens.

MEXICO
Tamaulipas: 122925. Río Soto la Marina at Soto la Marina, 21 Jan. 1959, 1 ♀ (juv), R. R. Miller and R. J. Schultz, M59-1.
Veracruz: 122922, Laguna de Alvarado, 27 Apr. 1966, 1 ♂, 2 ♀, S. de la Campa, E. Ramírez and E. Chávez, L. B. 5093. 122923, Laguna de Pueblo Viejo off the corals, 4 Sept. 1964, 1 ♂, 1 ♀, J. A. Macías, L. B. 3333. 122924, Río Tuxpan, taken between Cobos and the Estero Quetumilco, 21 Nov. 1964, 2 ♂, 2 ♀, R. Márquez, L. B. 3632.
A ♂ with carapace 30 mm long collected from Rio Grande by Trevino and sent to USNM for identification by H. Hildebrand, 4 Sept. 1956; identified by F. A. Chace, Jr., and returned to sender.

AHF. 2 lots, 3 specimens.

MEXICO
Veracruz: Boca del Río, seined in shallow water, 9 Aug. 1949, 1 ♂, 1 ♀, B. W. Halstead. Drainage ditch 5 mi W Veracruz, seined in brackish water, 19 Aug. 1949, 1 ♀ (juv), B. W. Halstead.

BMNH. 1 lot, 1 specimen.

MEXICO
65.29, 1 ♀, (dry), vi/7.

RMNH. 1 lot, 2 specimens.

MEXICO
Veracruz: 21814, Laguna de Pueblo Viejo, 25 Apr. 1964, 1 ♂, 1 ♀, F. A. Manrique Colchado.

Instituto Nacional de Investigaciones Biológico Pesqueras, Mexico, D. F. 2 lots, 2 specimens.
Tamaulipas: Laguna del Chairel y río Tamesí, 18 Aug. 1964, 1 ♂, J. A. Macías. Veracruz: Estero Jacome, 18 Dec. 1963, 1 ♀ (juv), S. García.

Supplementary literature record.—Mouth of Rio Grande, Tex. (Pounds, 1961).

CALLINECTES MARACAIBOENSIS TAISSOUN

Figures 14, 19b, 20o, 22l, 27

Callinectes sp., Taissoun, 1969, p. 63, fig. 23, photo 8.
Callinectes maracaiboensis Taissoun, 1962, p. 12, 23, figs. 1e-h, 2 (part), 3 (part), 4, 9B, 10A-B; photos 1-2 (col.), 3, 4m (type: ♂, Museo de Ciencias Naturales, Caracas, Venezuela, Lago de Maracaibo, Venezuela).- 1973, p. 28, figs. 4F, 5E, photo 3.

Description.—Carapace (Figure 14) bearing four triangular frontal teeth with tips meeting a nearly common level, lateral pair moderately acute with mesial side having a flatter angle than lateral side, submesial pair much narrower, acute, sometimes slightly shorter than lateral pair. Metagastric area with length and posterior width about equal, anterior width 2 times length. Anterolateral margins slightly arcuate, teeth exclusive of outer orbital and lateral spine with tips directed outward, tending to be acuminate especially in outer portion of row, posterior margin of teeth usually longer than and more granulate

than anterior margin. Surface of carapace dorsally smooth and glistening around perimeter (when wet) and on epibranchial and posterolateral surfaces; granules scattered on epibranchial surfaces, progressively more crowded on proto-, meso-, and anterior portion of metagastric areas and branchial lobes and on cardiac area (especially posterior slope). Epibranchial line prominent and relatively uninterrupted, sulci on central part of carapace deeply etched.

Chelipeds granulate on ridges, fingers of major chela heavily toothed, lower margin of propodal finger often decurved near base in adults.

Male abdomen and telson long, extending to anterior quarter of thoracic sternite IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching at least as far forward as in male, nearly to juncture between thoracic sternites III and IV, sixth segment as long as fifth and fully rounded at its distolateral corners, telson elongate-triangular with sides slightly inflated. First gonopods of male (Figures 19b, 20o) very long, often extending nearly to tip of telson and crossed near tips; sinuously curved and overlapping in two places proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercles on thoracic sternite V, and recurving gradually to termination near midline; armed distally with a dorsolateral band of large and small retrogressive spinules. Gonopores of female (Figure 22l) asymmetrically ovate in outline with apex on long axis directed anteromesad; aperture of each sloping from surface on mesial side under rounded sinuous anterolateral border superior to rounded lateral and much smaller mesial eminences on posterior border.

Size of carapace in mm.—Largest male available: length 78, width at base of lateral spine 134, including lateral spines 159. Largest female available: length 58, width at base of lateral spines 102, including lateral spines 124. Taissoun (1972) measured large samples made up of individuals whose mean sizes were comparable to the above specimens, males generally being larger than females. Summary of selected measurements for the few specimens available is given in Tables 1 and 2.

The following account is from Taissoun (1972), the only person who has studied the species in detail.

Color.—Adult male: carapace olive green with tints of light brown and blue toward central region, anterolateral region with light chestnut areas. Chelipeds with upper portion light chestnut and olive green with orange tints; distal portions of merus, internal portion of carpus, internal and external sides of fingers intense blue; spines of merus brownish orange distally with tips light chestnut and cream, bases obscure brown; distal tubercles on propodus orange and intense blue. Ambulatory legs cream proximally, blue distally, articulations with tubercles intense orange. Swimming legs intense blue and cream dorsally, terminal article blue, obscure brown and light orange, tubercles orange. Underparts cream and light yellow, except anterior portion and pereopods light blue.

Females: as males but with more intense blue on internal part of chelipeds. Taissoun (1972) included colored illustrations, but the female pictured is more reddish than as described above.

Variation.—Granulation of the carapace varies from nearly smooth to fairly marked, but is not so prominent as in some specimens of *C. bocourti*. Lateral spines of males are occasionally curved forward at the tips, but in females are often relatively longer and straighter. Meral spines on the chelipeds vary in number as usual in the genus (four or five) and all spines become worn in old individuals.

Distribution.—Confined to the Lago de Maracaibo estuarine system, roughly 120 km wide × 215 km long, extending from Bahía del Tablazo emptying into Golfo de Venezuela in north, through Estrecho de Maracaibo southward into Lake proper.

Habitat.—The species occurs on sandy and muddy bottoms, and among roots of mangroves, in brackish to occasionally fresh waters containing much silt and decomposing organic material. Both *C. maracaiboensis* and *bocourti* occur in the Lake and its outlet, apparently most abundantly near the mouth where all developmental stages of both are found, but the majority of these are adult males in salinities ranging from 0.35 to 15.12‰. Surface temperatures in the Lake are fairly uniform, ranging from 27.2° to 32°C, and undergoing a diurnal change of ± 1°C, but below depths of 10 m temperature remains even more uniform. Tem-

perature of surface water in the Golfo de Venezuela is less than in the Lake (28.6°C in October and 25.9°C in February were recorded by Taissoun (1972)).

Spawning.—Adaptation to the Lake environment is shown by spawning habits. Ovigerous *C. maracaiboensis* were occasionally taken in Bahía del Tablazo and Estrecho de Maracaibo from April to August where salinity ranged from 3.15 to 15.13‰. Ovigerous female *C. bocourti* were usually found in the Golfo de Venezuela where salinity varied between 23.9 and 34.6‰, and only occasionally in the fresher Bahía del Tablazo.

Economic importance.—A developing fishery in the Lago de Maracaibo region employing crab traps concentrates chiefly on *C. sapidus*, but includes *C. maracaiboensis* and *C. bocourti*.

Remarks.—Recognition of this new species from a restricted geographic range comes as some surprise in view of the broader distribution of other members of the genus. There is no doubt that *C. bocourti, maracaiboensis,* and *rathbunae* are very closely related, the widely ranging *bocourti* probably being the parent stock from which the isolates in peripheral areas have evolved. *Callinectes maracaiboensis* and *rathbunae* are similar in having somewhat less robust bodies than *bocourti,* smaller, sharper, outwardly directed anterolateral teeth and, in adults, more acuminate frontal teeth. In this regard, Taissoun's (1972:10) outlined median saggital sections of the three species do not seem to represent the average. Shape of abdomen in adult females is another useful character, that of *C. maracaiboensis* being somewhat smaller, having a sixth segment short and evenly rounded on the distal edge, but narrower than in *rathbunae.* Typically mature *C. bocourti* females have a relatively smaller abdomen than either of the others, with the distal edge of the sixth segment being somewhat angular distolaterally rather than broadly rounded.

Taissoun (1972) marshalled evidence for estuarine adaptations in *C. maracaiboensis,* which apparently parallels similar trends in engraulid fishes, the whole process presumably being associated with isolation of the Lake accompanying fall in sea level during the Pleistocene. The habitat of this species suggests interesting comparative experiments on larval development of a form adapted to living in lowered salinity throughout life as contrasted with the other more catadromous species of the genus.

Material.—Total: 4 lots, 16 specimens.

USNM

VENEZUELA

139621, Lago de Maracaibo, 19 July 1970, 1 ♂, 1 ♀ (Paratypes), E. Taissoun. 143392, Lago de Maracaibo, no date, 5 ♂, 1 ♀, E. Taissoun. 143391, Lago de Maracaibo, 23 June 1972, 5 ♂, 1 ♀, E. Taissoun. 143393 Puerto Caballo, Maracaibo, Lago de Maracaibo, 17 June 1968, 1 ♂, 1 ♀, E. Taissoun.

CALLINECTES LATIMANUS RATHBUN

Figures 15, 19c, 20p, 23a, 27

Callinectes bocourti.- Rathbun, 1896, p. 362 (part), fide Rathbun, 1921.- 1897, p. 151 (part), fide Rathbun, 1921.- 1900a, p. 290.- Balss, 1921, p. 58.

Callinectes latimanus Rathbun, 1897, p. 151, text-figs. 6-8 (syntypes: 4 ♂, 3 ♀, BMNH 91.4.1.63/69; 1 ♂, USNM 19877; Lagos, Bight of Benin, Guinea [Nigeria], A. Moloney).- 1900a, p. 291.- 1921, p. 398, text-fig. 4, pl. XV, fig. 2, pl. XXI, pl. XXII, fig. 1.- Odhner, 1923, p. 22.- Monod, 1927, p. 606.- 1956, p. 211, figs. 240- 243.- Irvine, 1947, p. 297, fig. 202 [?].- Vilela, 1949, p. 58.- Capart, 1951, p. 132, fig. 47.- Rossignol, 1957, p. 82.- 1962, p. 116.- Forest and Guinot, 1966, p. 65.

Neptunus marginatus var. *truncata* Aurivillius, 1898, p. 5, pl. 1, figs. 1-4 (type: 1 immature ♀ [not ♂], fide Rathbun, 1921, Cameroon).

Callinectes diacanthus var. *africanus*.- A. Milne Edwards and Bouvier, 1900, p. 71 (not col. pl. 4, fig. 5 = *C. sapidus*).- Lenz, 1910, p. 125 [5].- Gruvel, 1912, p. 3, 6, pl. 2, fig. 1.

Callinectes marginatus.- Odhner, 1923, p. 21.

Callanectes Sp. (?).- Irvine, 1932, p. 14, fig. 13.

Description.—Carapace (Figure 15) bearing four frontal teeth with variably rounded tips, submesial pair shorter than lateral pair. Metagastric area with length approximately equal to posterior width, anterior width about 2 times length. Anterolateral margins moderately

arched, anterolateral teeth exclusive of outer orbital and lateral spine varying from acute with serrate margins to increasingly acuminate and forward curving with nearly smooth margins at lateral end of row. Lateral spine relatively stout. Surface of carapace coarsely granulate, but granules more widely spaced or absent near margins, on epibranchial surfaces, and along regional sulci; most closely crowded granules on mesogastric, cardiac, and mesobranchial areas. Epibranchial line prominent and nearly uninterrupted.

Chelipeds with propodus and carpus moderately ridged, granules on dorsal and lateral ridges becoming smooth with age; chelae of large specimens very strong, major one often very broad with fingers heavily toothed (if not worn), lower margin of propodal finger often decurved near base opposite enlarged basal tooth of dactylus.

Male abdomen and telson reaching beyond midlength of thoracic sternite IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching about midlength of thoracic sternite IV; telson elongate triangular with inflated sides, sixth segment longer than fifth. First gonopods of male (Figures 19c, 20p) very long, usually exceeding telson and crossed near tips; sinuously curved and overlapping proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving to termination near midline; armed distally with dorsolateral band of large and small retrogressive spinules. Gonopores of female (Figure 23a) ovate in outline with apex on long axis directed anteromesad; aperture of each sloping from surface on mesial side under rounded, sinuous anterolateral border superior to a rounded eminence on posterior border.

Size of carapace in mm.—Largest male: length 71, width at base of lateral spines 125, including lateral spines 151. Largest female: length 59, width at base of lateral spines 105, including lateral spines 127. Summary of selected measurements is given in Tables 1 and 2. The species is characteristically large at adult size, Irvine (1947) reporting carapace widths of 8-12 inches (20-30 cm).

Color.—Uniform greenish brown with articulations and internal face of chela and dactyl bluish; ventral aspect yellowish white (Rossignol, 1957). Khaki colored with bluish tinge and bluish legs (Irvine, 1932, 1947); predominantly brown, perhaps where waters are often turbid with silt (Longhurst, 1958). A mottled olive coloration persists at least as long as 20 yr in some preserved specimens.

Variation.—Aptly named for one of their most distinctive features, adults of *C. latimanus* have broad major chelae. Chelae with worn tooth rows and gaping fingers seem disproportionately large in old males, and in their smooth surfaces these may resemble the hands of *C. bocourti* (excellent example, AMNH 3111), but the entire cheliped is shorter and thicker than in that species. There is usually a strongly developed proximal tooth on the dactyl of the major hand and opposite it a strongly decurved propodal finger. The minor chela (normally left) is much slimmer than the major, its two fingers toothed with meshing sectorial triads or variants of this pattern.

Especially in juveniles, the submesial pair of frontal teeth often overhangs and obscures the epistomial tooth, though not so completely as in *C. toxotes*. Adult females have coarse granulations over the whole carapace though not so closely crowded at the edges as in central elevated parts behind the epibranchial line. There are smooth areas between more scattered granules in front of the epibranchial line in both sexes.

First gonopods of males may extend beyond the telson.

Distribution.—Baie de Saint-Jean [19°27′N, 16°22′W], Mauritania, to Cabinda, Angola (Figure 27). (Perhaps farther south in Angola on basis of published accounts such as Gruvel [1912] and Monod [1956], and specimens of uncertain origin [AMNH 5895].)

Habitat.—In a category Longhurst (1958) called "mobile invertebrates," the most important estuarine species in the Sierra Leone River (site studied) appeared to be *C. latimanus* and *Parapenaeopsis atlantica* Balss. Neither of these was completely restricted to the estuary but occurred only sporadically outside it. *Callinectes latimanus* was most abundant in the midestuarine region in many of the otter-trawl hauls, and extended far up creeks to low-salinity water. Sourie (1954b) found *C. latimanus* widely distributed in estuaries of Senegal ranging from fresh water to salt concentrations near saturation, and Gruvel (1912) reported brackish water habitats in

Ghana where the species abounds on muddy bottoms. Crosnier (1964, and pers. data) and a number of others listed the depth range as 0-35 m in warm water.

Callinectes latimanus is preyed upon by *Galeoides decadactylus* Bloch and *Pomadasys jubelini* Cuvier (Longhurst, 1957), and *Callinectes* sp. [probably *latimanus*] by *Dasyatus margarita* Gunther and *Caranx alexandrinus* Cuvier and Valenciennes (Monod, 1927).

Spawning.—In all museum material available to me only four collections that are dated contain ovigerous females: January-February, Ivory Coast; May, Senegal, Nigeria; October, Togo. In the warm West African region it is likely that spawning occurs the year round, but may be concentrated at seasonal peaks.

Economic importance.—There is no literature on strictly commercial aspects of a fishery for this species, but it is important as food in coastal communities. Rathbun (1900a) recounted an early report that the crab was found only in fresh water of rivers, and much sought after for the exceptionally good meat. Monod (1927) listed *C. latimanus* as common in the Cameroons and customarily eaten there. Gruvel (1912) wrote that it is extremely abundant along the coast from Senegal to Angola, and so much so in certain areas such as the Ivory Coast, Dahomey, etc., that the people there brought large basketfulls alive to the markets to be either boiled in water or fried in palm oil. He regarded the crabs as extremely tasty and therefore subjects for a fishery, at least from Senegal to the Cameroons, where they were captured around lagoons and among mangroves in brackish water, generally on mud bottom, by means of small seines, baited traps, or fishing lines. Irvine (1947) listed similar fishing methods and considered the crabs quite edible, while Rossignol (1957, 1962) considered this crab the most abundant in the genus, subject to a regular fishery by native peoples in estuaries and lagoons, and although acceptable, not always so savory as *Portunus validus* Herklots.

Remarks.—The syntype male in the USNM (19877) is a mature specimen with first gonopods extending beyond the telson, a quite sharply granulate carapace with acute anterolateral teeth (especially from the fourth tooth laterad), and a left chela with strong proximal tooth on the dactyl heavier than the right, but it is a poor specimen because both chelipeds are detached from the body and parts of other legs are detached or missing. The series of syntypes in the BMNH (91.4.1.63/69) is in much better condition, consisting of two mature and two immature males, and one mature and two immature females. The largest male is the most perfect specimen, and the first gonopods on it exceed the tip of the telson.

The early confusion of this species with the American *C. bocourti* is easy to understand because each is described comparatively in terms of the other, the relationships being obviously close.

Material.—Total: 39 lots, 116 specimens.

USNM. 9 lots, 16 specimens.

SENEGAL
18735, no date, 1 ♂ juv, from Mus. Nat. Hist., Paris.

LIBERIA
123087, Robertsport, Grand Cape Mount Co., 28 Dec. 1947, 1 ♀, J. T. Baldwin, Jr.

NIGERIA
120943, Lagos, 06°28′N, 03°23′E, 10 May 1965, 1 ♀, *Pillsbury*. Lagos, Guinea [= Nigeria], no date, 1 ♂, A. Molony, (Type).

ANNOBÓN ISLAND
120944, 01°24′S, 05°37′E, 20 May 1965, 2 ♂, 2 juv, *Pillsbury*, Stn. 281.

ZAIRE
54253, 54254, 54310, Banana, mouth of Congo River, July-Aug. 1915, 5 ♂, 2 ♀, H. Lang.

AMNH. 6 lots, 15 specimens.

ZAIRE
3326, no date, 1 ♂, Congo Exped. 3110, 3111, 3112, 3417, Banana, July-Aug. 1915, 7 ♂ (1 dry), 4 ♀ (1 juv), H. Lang and J. Chapin.

ANGOLA [?]
5895, 1925, 2 ♀, Vernay Angola Exped.

BMNH. 6 lots, 17 specimens.

SIERRA LEONE
1916.6.23.1/2, Gbanbama, 1 ♂, 1 ♀, N. W. Thomas. 1922.9.13.6/7, Sherbo I., 2 ♀, C. H. Allan.

GHANA
Accra, no date, 1♂, 1♀, F. R. Irvine.

NIGERIA
91.4.1.63/69, Lagos, Bight of Benin, 4♂, 3♀ (2 juv), A. Moloney, (Types). 1948.4.30.1/2, Lekki Lagoon, 16.2.1947, 2♂, Trewavas.

ANGOLA
1912.4.2.4/5, Chiloango River, Cabinda, July 1911, 2♂, Ansorge.

MNHNP. 5 lots, 7 specimens.

GAMBIA
Basse, Côte de Troire, 1907, 1♂, Bouet.

SENEGAL
No number, 1♂, 1♀ juv, date and col. unknown. Bignona, May 1946, 2♂, P. L. De Keyser and A. Villiers.

GUINEA
Conakry, Guinée, 1♀, Inst. Fr. d'Afrique Noire.

CONGO
1892-94, 1♂ juv, Dybowski.

RMNH. 6 lots, 20 specimens.

LIBERIA
Grand Cape Mount, 1881, 1♂, J. Büttikofer and J. A. Sala. 1864, Fishermans Lake, [35 mi NW Monrovia], among stones, Jan. 1881, juv 2♂, 2♀, J. Büttikofer and J. A. Sala.

GHANA
376, St. George d'Elmina, 1♂, H. S. Pel.

NIGERIA
20614, Lagos harbor, 23 May 1964, 1♀ (ov), *Pillsbury*. 15533, Niger Delta, May-Aug. 1960, 3♂, 3♀, H. J. G. Beets.

CONGO
No number, 1880, (juv) 2♂, 5♀, T. Kamerman.

UNC-IMS. 7 lots, 41 specimens, from A. Crosnier.

TOGO
2733, Lagune D'Anecho, 5♂, 3♀, A. Stauch. 2734, Côtes du Togo, 06°06′30″N, 01°37′30″E, 16 Oct. 1963, 1♀ (ov), A. Crosnier.

CAMEROON
2735, Cotes du Cameroun, 03°34′N, 09°35′E, 23 Aug. 1963, 1♀, A. Crosnier.

CONGO
2736, Lagune de Zambi [03°58′S, 11°17′E], 13 May, 1964, 2♀, A. Stauch. 2737, Lagune de Conkouati [03°58′S, 11°19′E], 14 May 1964, 1♀, 17 juv, A. Stauch. 2738, Plage de Pointe-Noire, no date, 2♂, 2♀. A. Crosnier. 2739, Plage de Pointe-Noire, July 1963, 4♂, 4♀, A. Crosnier.

Supplementary literature records.—Baie de Saint-Jean [19°27′N, 16°22′W], Mauritania; St. Louis, Yof, Sobané [= Sobène?], Bignona, Sédhiou + 3 nearby localities, Ziguinchor, Senegal; Tamara, Ile Poulet, Guinea; Abidjan, Lagune Ébrié, Baie de Cocody, Ivory Coast; near Densu, Gold Coast [= Ghana] (Monod, 1956); Bissau, porto de Biombo, Ilhéu de Âncora, Portuguese Guinea (Vilela, 1949); Sierra Leone River (Longhurst, 1958); Gold Coast (Irvine, 1947); Fernando Póo (Crosnier, 1964); Príncipe I. (Forest and Guinot, 1966); Senaga, Cameroon (Odhner, 1923); Songolo [= Songololo], Loya, Longo, Djeno, Congo (Rossignol, 1957).

CALLINECTES SAPIDUS RATHBUN
Blue Crab

Figures 1, 16, 17, 19d, 21, 23b-c, 26

Portunus hastatus.- Bosc, 1802, p. 212-214,219.- 1830, p. 234.

Lupa hastata.- Say, 1817, p. 65 (not *L. hastata* Desmarest, 1832 = *Cancer hastatus* Linnaeus, 1767).

Portunus diacantha Latreille, 1825, p. 190 (variety) (type localities: North America, Antilles, Brazil, etc.; types not extant; restricted to Philadelphia, Pa., by Holthuis, 1962, p. 232; name suppressed by International Commission of Zoological Nomenclature, Opinion 712 [1964, p. 336]).

?*Lupea dicantha*.- H. Milne Edwards, 1834, p. 451 (part).

Lupa dicantha.- Gould, 1841, p. 324.- de Kay, 1844, p. 10, pl. 3, fig. 3.- Holmes, 1858, p. 9 (fossil).

Callinectes diacanthus.- Stimpson, 1860, p. 220.- Young, 1900, p. 186 (part).

Callinectes hastatus.- Ordway, 1863, p. 568 [3].- A. Milne Edwards, 1879, p. 224 (var. of *C.*

diacanthus).- R. Rathbun, 1884, 1893, p. 775, pl. 267.- Young, 1900, p. 187 (var. of *C. diacanthus*).

?*Neptunus hastatus*.- Brocchi, 1875, p. 55, pl. 16, fig. 81.

Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part: specimens g, Florida; l, Brazil; n, Haiti).

Callinectes sapidus Rathbun, 1896, p. 352, pl. 12; pl. 24, fig. 1; pl. 25, fig. 1; pl. 26, fig. 1; pl. 27, fig. 1 (type locality restricted to "east coast of United States" by Williams, 1965).- 1929, p. 31, fig. 41.- 1930, p. 99, text-figs. 15a, 16c, 17c, 18a, 19, pl. 47.- Bouvier, 1901, p. 16.- Clark, 1906, p. 172, pl. 41, figs. 1-3 (fossil).- Verrill, 1908a, p. 370, text-figs. 22a, 23a, 24, pl. 17, fig. 2.- Hay and Shore, 1918, p. 432, pl. 35, fig. 1.- Chace, 1940, p. 33.- Chace and Hobbs, 1969, p. 133, figs. 36, 37f.- Balss, 1957, p. 1641.- Holthuis, 1961, p. 50, pl. 1, fig. 2, pl. 2, fig. 2.- 1969, p. 34, pl. 1.- Holthuis and Gottlieb, 1955, p. 91, pl. 3, fig. 11.- Pounds, 1961, p. 42, unnumbered col. frontis., unnumbered text-fig. p. 9, text-figs. 1-2, pl. 7, figs. 1, 2a.- Futch, 1965, p. 2, figs. 1, 2, 3, 4, 5c.- Williams, 1965, p. 168, fig. 151.- Christiansen, 1969, p. 72, fig. 29.- Taissoun, 1969, p. 37, photos 3-6, figs. 11A-D.- 1973, p. 34, figs. 4E, 5F, photo 5.

Callinectes sapidus acutidens Rathbun, 1896, p. 354, pl. 13; pl. 24, fig. 2 (type: ♂, MCZ 4696, Santa Cruz [Estado de Bahia] Brazil, Thayer Exped.).-1901, p. 47.- 1930, p. 111, text-fig. 15 c, pl. 48.- 1933, p. 48.- Young, 1900, p. 191.- Contreras, 1930, p. 228, fig. 1.- Pretzmann, 1966, p. 305, 2 pls.- Bulgurkov, 1968, fig. 1.

Callinectes africanus.- A. Milne Edwards and Bouvier, 1900, pl. 4, fig. 5 (not p. 71, var. of *C. diacanthus* = *C. marginatus*).

Description.—Carapace (Figures 16, 17) bearing two broad either obtuse or acuminate, triangular frontal teeth with mesial slopes (incorporating a pair of rudimentary submesial teeth) longer than lateral slopes. Metagastric area with posterior width approximately 1.2 times length, anterior width about 2 times length. Anterolateral margins slightly arched; anterolateral teeth exclusive of outer orbital and lateral spine obtuse to acuminate and directed outward more than forward. Much of surface smooth, with scattered granules, but granules concentrated locally on mesobranchial, posterior slope of cardiac, and anterior portion of mesogastric area; a tendency to crowding of granules into transverse ridge at summit of cardiac and mesobranchial area in some individuals. Sculpturing of surface varying individually from low to raised relief. Lateral spines varying from rather stout, blunt, and forward trending to slender, elongate, and slightly backward trending. Epibranchial line nearly straight over branchial region, otherwise sinuously curved.

Propodus and carpus of chelipeds with moderate finely granulate ridges, width of chelae similar, propodal finger of major hand occasionally with lower margin decurved proximally.

Male abdomen and telson reaching about midlength of thoracic sternite IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching about midlength of thoracic sternite IV; telson with inflated sides almost equilaterally triangular, fifth and sixth abdominal segments equal in length. First gonopods of male (Figures 19d, 21) very long, reaching beyond suture between thoracic sternites IV and V but not exceeding telson; sinuously curved and overlapping proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving to termination near midline; armed distally with row of large and small retrogressive spinules following ventral and lateral borders with twist of axis; tip membranous, flared portion suggesting an elongate quadrilateral in outline. Gonopores of female (Figure 23b, c) paraboloid in outline with apex on long axis directed anteromesad, aperture of each sloping from surface on mesial side under irregularly rounded and linearly wrinkled anterior border superior to bulbous posterolateral border.

Size of carapace in mm.—Largest male: length 91, width at base of lateral spines 168, including lateral spines 209. Largest female: length 75, width at base of lateral spines 143, including lateral spines 204. Mature size of females varies considerably, the smallest examined having a carapace length of 21, width at base of lateral spines 41, including lateral spines 55. Summary of selected measurements is given in Tables 1 and 2.

Pretzmann (1966) discussed a large immature female with acute spines: length 65, width 132.5. The largest immature female I have seen, also with fairly acute spines, reached a carapace

length of 60, width at base of lateral spines 109, including lateral spines 135. Some others in material studied approached this size. All such specimens seen by me are from the Gulf of Mexico and may represent parasitized individuals in which the maturation process has been altered.

Color.—Grayish, bluish, or brownish green of varying shades and tints dorsally on carapace and chelipeds; spines may have reddish tints, tubercles at articulations of legs orange, and legs varyingly blue and white with traces of red or brownish green. Males with propodi of chelae blue on inner and outer surfaces, fingers blue on inner and white on outer surfaces and tipped with red. Mature females with orange fingers on chelae tipped with purple. Underparts off-white with tints of yellow and pink. Futch (1965) and Taissoun (1969) gave a good description of color; De Kay (1844), Milne Edwards and Bouvier (1900; plate IV, Figure 5), Churchill (1919), and Pounds (1961) published colored illustrations of the species, and still others are scattered in popular literature.

Color variations other than those associated with sexual dimorphism and molt cycle are known. Albinos or partial albinos are in museum collections and have been reported both in systematic literature and elsewhere (Gowanloch, 1952; Sims and Joyce, 1966). Haefner (1961) reported an adult male lacking dorsal green coloration and bright blue and scarlet markings on the legs. Instead, the upper surface of the carapace was "robins egg blue" and the appendages were paler than usual, but the abdomen and underparts had normal color. A similar blue specimen was reported elsewhere (Maryland Tidewater News, 1950). Haefner also pictured a bilateral gray and brown colored specimen from the collection of L. Eugene Cronin. Hopkins (1962, 1963) discussed biochemistry of the sexual color dimorphism.

Variation.—There are morphological variations in this species having far greater systematic interest than size and color. Study of many specimens from throughout the range of the species bears out the conclusion of Chace and Hobbs (1969) that extreme variants "are so different from each other that they could easily be interpreted as distinct species," but there is "no point of demarcation"—morphological, geographic, bathymetric—between the "typical" rather blunt-spined form predominating along the east coast of the United States and the acute-spined form named *C. sapidus acutidens* by Rathbun predominating from Florida southward.

Rathbun (1896) characterized the "acutidens" form (paraphrasing) as being wider than the "typical" with all prominences more strongly marked, areolations separated by deeper depressions, granules more raised, gastric ridges stronger and more sinuous, a transverse granulate ridge on each cardiac lobe, frontal teeth narrower and more acute and bearing two small intervening teeth, anterolateral teeth broad at base and narrowing abruptly to long acuminate tips with margins granulate, lateral spines longer than in "typical" specimens of equal size, and ridges of chelipeds quite prominent and strongly granulate. Figures 16 and 17 show two extremes, the first a mature young male of typical form, and the second a mature male of "acutidens" form.

I thought for a time that a species distributed through approximately 85° of latitude from North Temperate through Tropic to South Temperate Zones might reflect responses to temperature in spination or other characters, "typical" structure being prevalent in the temperate zones and sharp spination in the tropics, the differences thereby justifying nomenclatural recognition. There is weak but inconsistent evidence for this pattern. Though "acutidens" individuals are uncommon outside the tropics, intermediates occur everywhere to some degree, and some "typical" individuals occur in the tropics. Genetic pooling or environmental response reflected in morphology seems poorly structured.

For example: Occasional specimens found as far north as Woods Hole, Mass., (USNM 4946, 40723, 43178) are nearly as sharp spined as some Caribbean material. Churchill (1919, plates 53-54) pictured individuals from Chesapeake Bay that approach the "acutidens" form. In the collection of the USNM is a huge male from Wye River, Md., (92452) that has acuminate anterolateral and suborbital teeth, though not so attenuated as in Florida material; two carapaces from Virginia (76184) have such acute spines that Rathbun identified them as the "acutidens" form; and a huge lot (60601) from Hatteras, N.C., composed of mainly "typical" blunt-spined individuals characteristic of eastern United States shows variation in frontal teeth from no submesial frontals to rudimentary evidence for their presence. In Maryland, few specimens examined show easily identifiable submesial teeth on the inner

slopes of the prominent frontal teeth, but in material from Louisiana there is a tendency to development of the submesial frontals, and the anterolateral teeth are generally more acute than in Chesapeake Bay material. Specimens from Veracruz, Mexico, in the AHF collection show rather blunt frontal but acuminate anterolateral teeth and rather prominent regions on the carapace. Most specimens from southern Florida to southern Brazil approach the "acutidens" form, but throughout this vast region there is much variation.

The sharpest- and longest-spined forms with most prominent development of rudimentary submesial frontal teeth occur in the western Caribbean Sea along the Guatemala-Panama coast. These individuals also have regions on the carapace more deeply and sharply sculptured than in the "typical" form, sharp granulation on both carapace and chelipeds, and cardiac and to some extent mesobranchial regions exhibiting a crowding of granules at the apex leading to formation of slight transverse ridges, but with the anterior slopes of these regions lacking granules. While some specimens from Puerto Rico approach those from the western Caribbean in ornamentation, there is a mixture of "typical" features in many individuals, as elsewhere in the Antilles. Perhaps the best illustration of mingling features is illustrated by three lots of specimens in the RMNH. In 23404 from Trinidad are two males. Both have crowding of granules into a transverse ridge on the cardiac lobes with largest granules behind and fewer on the anterior slope, and a faint tendency to ridging of granules on the mesobranchial regions. The smaller specimen has the more deeply sculptured carapace, but rather blunt frontal, outer orbital, and suborbital teeth, and rather short, acute anterolateral teeth except for the last two which are acuminate. The larger specimen has a rather smooth carapace, but acuminate, long, and outwardly turned outer orbital and suborbital teeth, rather acute frontals with rudimentary submesial teeth, and quite acuminate anterolateral teeth throughout the length of the row. Another male from Trinidad (17738) has a transverse row of crowded granules on each cardiac lobe with the anterior slope relatively smooth, and mesobranchial regions with crowded granules but no ridging. The frontal teeth are neither especially sharp nor sinuous mesially, and the anterolateral, outer orbital, and suborbital teeth, like many "typical" specimens, are acuminate but not markedly so. Two females from Curacao (11881) seem to be nearly "typical" in all respects. One of them has granules crowded into a poorly defined transverse ridge on each cardiac lobe; however, there are granules on the anterior slopes of these lobes. In sum, each of these specimens shows different combinations of the "sapidus"-"sapidus acutidens" complex.

The paratype male "acutidens" from Rio de Janeiro (USNM 19083) is not as acute spined as Panamanian material and the outer orbitals are rather blunt by "acutidens" standards.

In rather scanty material available from southern Brazil and Uruguay, though the "acutidens" form predominates, teeth are not so sharp as in Panama and the ridging of granules on the carapace is suppressed to give a smoothed effect reminiscent of that in North American specimens.

The first gonopods of males, one of the most reliable characters for separating species of *Callinectes*, offer no help in separating "typical" and "acutidens" forms of *sapidus*. This pair of appendages shows individual variation on a basic structural theme (Figure 21) having more correlation with age than with general body facies or geographic region. It is apparent that movable retrogressive spinules in the main row of spinules increase in length with age, and that there is no set arrangement except a tendency to an irregular grouping of slender subterminal spinules more erect than the proximal ones. The flared membranous tip has an irregular quadrilateral or elliptical shape.

Abdominal segments of mature females vary in shape, some (such as USNM 126789, Dominica) having the distal edge of the sixth segment broadened at its distal corners to an almost rectilinear form, whereas in most this segment tapers toward the telson.

Gonopores of the females vary in width of aperture and ornamentation of margins. The variations shown in Figure 23b, c represent some extremes, but there is no association of pattern with geography, the only constant being the elongate opening characteristic of species in which gonopods of males are long.

Distribution.—Occasionally Nova Scotia, Maine, and northern Massachusetts to northern Argentina, including Bermuda and the Antilles; Øresund, Denmark; the Netherlands and adjacent North Sea; southwest France (found twice); Golfo di Genova; northern Adriatic; Aegean, western

Black, and eastern Mediterranean Sea (Figure 26).

The extreme southern record by Ringuelet (1963) is substantiated by the figure in his paper. Records north of Cape Cod occur only during favorable warm periods (Scattergood, 1960).

Holthuis and Gottlieb (1955, 1958), Holthuis (1961, 1969), and Christiansen (1969) summarized the introduction of *C. sapidus* into Europe, and Bulgurkov (1968) extended the known range, recording an adult female taken in the western part of Varna Bay in October 1967. From these accounts it is clear that introduction in the Mediterranean and adjacent waters is an active one involving a breeding population, whereas the others seem to be temporary occurrences, but all are judged to have come from transport of small specimens in the ballast tanks of ships (op. cit., and Wolff, 1954a, 1954b). Banoub (1963) published one of the most complete accounts, noting that presence in Egypt does not seem to have been recorded before 1940. When *C. sapidus* was first noticed in Lake Manzilah, Egypt, it was confused with *Portunus pelagicus* (Linnaeus), itself an immigrant to the area from the Indian Ocean via the Suez Canal, and this confusion has persisted in literature on both species. Banoub thought that *C. sapidus* may have migrated from Greece around the eastern Mediterranean to flourish in the brackish lakes of Egypt, reproducing the life pattern it exhibits in the Western Hemisphere.

Habitat.—The blue crab is a coastal creature occurring on a variety of bottoms in fresh, estuarine, and shallow ocean from the water's edge to approximately 90 m (Franks et al., 1972), but mainly in the shallows to depths of 35 m. Biology of the species is better known than that of any other in the genus. Hatching in mouths of estuaries and shallow ocean, development of larvae progresses in the ocean (development studied both in nature and the laboratory), followed by migration of megalopae and young crabs back into estuaries to mature into adults (summarized in Williams, 1965, 1971; Tagatz, 1968; Taissoun, 1969; and literature compilation, Tagatz and Hall, 1971). It is probable that all species in the genus carry out their life histories on this model.

Tolerant of extremes, the species has been found from fresh water to hypersaline lagoons such as Laguna Madre de Tamaulipas, Mexico, where collections have been made in salinities ranging from 44 to 48‰ and unproductive portions of the lagoon range up to 117‰ (Hildebrand, 1957), in temperatures ranging from 3° to 35°C, and in tertiary sewage treatment ponds in which mean daily O_2 tension dropped as low as 0.08 mg/liter in summer (Smith, 1971). In Lebanon it has been collected in winter in 39‰ salinity water at 17.5°C where there is no good place for estuarine development because streams are small, seasonal, and exceedingly foul in dry weather (George and Athanassiou, 1965). In Marion Co., Fla., large males have been taken from salt springs in the St. Johns River over 180 miles from the sea.

Often considered a scavenger, which it certainly is, the normal diet includes a variety of materials including fishes, benthic invertebrates, and plant material (Darnell, 1959; Tagatz, 1968). Odum and Heald (1972) confirmed this assessment, finding mainly an abundance of small mussels in stomach contents of individuals in a marsh in SW Florida.

Spawning.—Most spawning occurs in spring and early summer, warm months helping to assure survival of larvae. Females with egg masses have been found in North Carolina from mid-March to late November. Northward the season is somewhat shorter and to the south (United States) it is longer (Williams, 1965). Early spring spawners may cast a second batch of eggs in late summer contributing to a lengthened spawning season or a secondary late summer peak. The number of eggs per spawning has been estimated at 700,000 to more than 2 million (Williams, 1965). Ovigerous females in museum collections are rare, but suggest that at least some eggs are spawned almost the year round in tropical waters. Taissoun (1969) showed this to be true in the Golfo de Venezuela where ovigerous females are most abundant between April and September, reaching a sample maximum of 75% in July and August. Also, in the northern part of Bahía del Tablazo, Venezuela, ovigerous females occur during all of the year except between August and November, reaching a sample maximum of 95% in May. Absence of ovigerous females there in late summer and fall occurs because heavy rainfall and increasing river flow freshen the area, driving females downstream to areas of higher salinity; consequent increases of ovigerous females occur in the Golfo de Venezuela during August and September.

Economic importance.—Though all species of *Callinectes* are consumed as human food, there is

no doubt that *C. sapidus* is the most valuable in commercial fisheries, providing a highly acceptable, nutritious product worth several million dollars annually in the United States alone. Traditionally, the seat of this fishery in the United States has been Chesapeake Bay where records on the fishery have been kept for about a century. Pearson (1948), summarizing annual catch for this area from 1880 to 1942, showed the annual catch to have increased from 9.5 million pounds in 1890 to a peak of 68.7 million pounds in 1930. Catch, however, fluctuated before and after 1930, declining to 35.8 million by 1942 during World War II. Van Engel (1962) provided a history of the types of gear used in this fishery, an evolution from hand-dip trotline to the baited crab pot (trap) and dredge. Adoption of the baited pot and its spread to the Carolinas and elsewhere during the late 1950's, along with other methods of capture including incidental harvest of crabs from shrimp trawls, greatly expanded the catch. By 1967 (latest available annual summary) the U.S. fishery landed nearly 150 million pounds of hard and soft crabs worth 10 million dollars (Lyles, 1969).

The species is harvested throughout its range either as an object of commercial enterprise or for home use. Taissoun (1969, and pers. commun.) reported a growing industry in Venezuela. Banoub (1963) reported growth of an Egyptian fishery in lakes (poor flavor) and sea (good flavor), but remarked on losses from damage to nets and on the myriads of crabs having no local commercial value because the Egyptians consider the meat unpalatable (Fishing News International, 1965). A developing fishery in Northern Greece (Kinzelbach, 1965) declined because of overfishing (Boschma, 1972).

Fossil record.—I have reviewed the fossil material treated by Rathbun (1919a, b, 1935) and more recent acquisitions in collections of the USNM and U.S. Geological Survey (USGS) and concluded that only two specimens can be positively identified as *C. sapidus*. Eighteen lots of specimens are probably *Callinectes*, and some of these are possibly *C. sapidus*, but most of the remains are too fragmentary for positive identification. The entire record ranges from lower Miocene of Florida to Pleistocene of Maryland and New Jersey, material identifiable to species probably being limited exclusively to the Pleistocene.

Published records of Pleistocene occurrence include *Lupa dicantha* (= *C. sapidus*) from sandy beds in Wadmalaw Sound, S.C. (Holmes, 1858), a two-thirds grown specimen of *C. hastatus* (= *sapidus*) in a concretion from excavation for a Hudson River Tunnel on the New Jersey side (Whitfield, 1891), a male *C. sapidus* from near the mouth of Choptank River at Cook Point, Dorchester Co., Md., and fragmentary remains from Wailes Bluff near Cornfield Harbor, and Federalsburg, Md., as well as Heislerville, N.J. (Clark, 1906), all cited by Rathbun (1935).

USGS 25272. (= Locality of Tulane University Department of Geology, Field No. 546). Eight-foot (+) vertical exposure 0.52 mi (0.84 km) due E Florida hwy. 84 (30°29′55″N, 85°11′32″W) along N bank of prominent sharp bend in Ten Mile Creek, Calhoun Co., Fla. Material collected "in situ" from the lower 3 ft (0.9 m) of section. Chipola Formation; late Lower Miocene. Paul E. Drez, summer, 1972, on loan from Warren C. Blow, Paleontology and Stratigraphy Branch, USGS. (A) A well-preserved right palm and one-third of propodal finger, facets bearing resemblance to *C. declivis* on external face, but hand broad and flat dorsally as in females of modern *Callinectes*, molar complex absent. (B) One disarticulated right dactyl with broken tip having moderate-sized, worn, proximal tooth. (C) One rather large, straight, right propodal finger with sectorial teeth.

USGS 25273. Fifteen foot (4.6m) vertical exposure along S bank Mattiponi River, just below White Oak Lodge at White Oak Landing (about 2.5 mi [4 km] E King William Courthouse) King William Co., Va. Material collected "in situ" between 1 and 2.5 ft (30-76 cm) above beach level in a blue gray, highly burrowed, sparsely fossiliferous, silty sand (devoid of mollusks) which overlies a highly fossiliferous shell bed consisting of abundant *Turritella*. "Virginia" St. Marys Formation; Middle Miocene. Lauck W. Ward, 1961, on loan from Warren C. Blow, Paleontology and Stratigraphy Branch, USGS. An immature female *Callinectes* with triangular abdomen (length about 23 mm from posterior edge of exposed segment 3 to tip of telson) and broad sternites, few remnants of carapace not coarsely granulate.

USGS 25274. White Oak Landing, about 2.5 mi (4 km) E King William Courthouse, along S bank Mattiponi River, King William Co., Va. Material collected as "float" along 400 ft (120 m) (+) beach between tributary just below landing proper and

next tributary upstream. The material, though "float," apparently washed out of the lower bed of the "Virginia" St. Marys Formation, which outcrops along this beach. Lauck W. Ward, 1961, on loan from Warren C. Blow, Paleontology and Stratigraphy Branch, USGS. Three immature specimens of *Callinectes*. Two females with broad sternites and triangular abdomen exposed; (A) a half-grown individual with fragmented abdomen distorted (abdomen length about 29 mm from posterior edge of exposed segment 3 to estimated tip of telson); (B) a much smaller individual with incomplete abdomen (abdomen length about 12 mm from posterior edge of exposed segment 3 to estimated tip of telson; (C) cephalothorax of an immature individual about 45 mm wide, with broad sternal plates as well as areolations of carapace suggesting *C. sapidus*, frontal and anterolateral teeth missing, abdomen unexposed, shape of telson suggesting a female.

USGS 25275. "Road fill" NW side of Virginia hwy. 360, along both sides of Manquin Creek, King William Co., Va. Material is "spoil" thought to be derived from nearby road cut(s) during construction of addition to hwy. 360. Age unknown, probably Yorktown Formation; Late Miocene. Lauck W. Ward, 1961, on loan from Warren C. Blow, Paleontology and Stratigraphy Branch, USGS. Large, complete right palm (dorsal length about 30 mm), propodal finger, and mold of dactyl broken out of a concretion; palm heavily ridged, facets between ridges reticulated as in *C. reticulatus* (internal mold of hand), but remnants of exoskeleton externally smooth except for granules on ridges; portion of finger remaining resembling *Callinectes* with proximal enlarged tooth on dactyl and molar apparatus on propodal finger. The palm is compressed in preservation, but appears as broad in restoration as a modern *Callinectes*.

USGS 3859. Pleistocene (Miocene?), "tonged up in the Rappahannock River near the Chesapeake Bay by an oysterman" and sent to the Smithsonian Institution in 1902 by W. McD. Lee. Flattened partially crushed central portion of an adult male *C. sapidus*, including part of carapace with regions exposed and sternum with abdomen missing. The dark color of the specimen only suggests similarity to other Pleistocene (Miocene?) material from the area of origin, for exact horizon is unknown.

USNM 371729, Pleistocene, Broadwater, Va., R. Phillips. A large adult male fragment consisting of a deformed carapace (length 67, width at base of lateral spines 127 mm) along with a right cheliped lacking fingers. The chela is disarticulated. Shape of abdomen, carapace, and carpus of cheliped with no internal spine indicate *C. sapidus*.

Seven lots from the Pleistocene, Wailes Bluff, St. Marys Co., Md., treated in part by Rathbun (1935) and Blake (1953), are similar to Modern *C. sapidus* but lack definitive characters.

USNM 145356. Talbot Formation, Bd. 1 (of Mansfield), 1937, S. F. Blake. Immature male with carapace and sternum exposed.

USNM 146701. Frank Burns, 1886, Stn. No. 2032. Portion of left minor dactyl and right propodal finger.

USNM 371726. Talbot Formation, L. W. Stephenson, W. C. Mansfield, and W. P. Popenoe, 26 June 1925, (10902). Portion of left propodal finger and hand, and nearly intact right propodal finger.

USNM 371727. Talbot Formation, W. C. Mansfield, 8-12 June 1920 (8932). Fragments of a left chela (propodus), tips of two fingers, and fragments of a minor chela.

Uncatalogued lot. (Bd. 1), R. J. Taylor, 15 June 1941. Mostly fragments of four right propodal fingers, six left propodal fingers, and one complete right dactyl.

Uncatalogued lot. (Bd. 1), R. J. Taylor, 15 June 1941. Three immature female and one immature male fragmentary sterna.

Uncatalogued lot. Pamlico Formation, W. E. Salter. Two dactyls from right and left chelae.

Five lots from Pleistocene, Cape May and Atlantic Counties, N.J., similar to modern *C. sapidus*.

USNM 371930. Cape May Formation, Stone Harbor, H. G. Richards. A short section of finger.

USNM 371933, Cape May Formation, Two Mile Beach, H. G. Richards. A short, stocky propodal finger with well developed molar complex.

USNM 371934. Cape May Formation, Two Mile Beach, H. G. Richards. Five central portions of right propodal fingers of half- to full-grown individuals, three central portions of left propodal fingers of comparable size, two proximal portions of probable left dactyls of large crabs, and three other pieces possibly broken from above.

USNM 371936. Cape May Formation, Two Mile Beach, H. G. Richards. Tooth row and tooth sockets on finger, probably a dactyl.

Uncatalogued lot. Brigantine I., Atlantic Co., H. B. Roberts, May 1953. A large, somewhat crushed right chela with proximal half of fingers.

Remarks.—Resolution of the taxonomic confusion surrounding the correct name for *C. sapidus* by Holthuis (1962) greatly simplifies both discussion of the species' systematic history and variability over its range. From Latreille's (1825) description, it is apparent that the original material from Philadelphia (possibly not the actual site of collection) indeed represented the "typical" form from eastern North America. Holthuis' selection of a lectotype from this material and Williams' (1965) restriction of the type locality to "east coast of the United States" support the facts as well as they can be known today. Search of the collection at ANSP revealed no specimens of *C. sapidus* that date from the time of Latreille, and it is almost certain that specimens on which he based his description are lost. There is no need now to designate a new type specimen, indeed selection of a neotype would not be in keeping with the spirit of the International Code (Art. 75), for no complex zoological problem now depends upon a specimen for its solution in this case.

The earliest "scientific" treatment of the species (Bosc, 1802) was more a natural history account than a description, the name *Portunus hastatus* being taken from a description paraphrased from J. C. Fabricius (1798) that applied to the European species originally described as *Cancer hastatus* by Linnaeus (1767).

I consider the whole *C. sapidus* complex to be a single species which has diverged into ill defined populations in certain portions of its range. The "acutidens" form predominates over most of the latitudinal range, but there are variations. Among these are "typical" features that reach their most pronounced expression in the population along the east coast of the United States. Taxonomic thinking of biologists has been clouded by the fact that the form originally described was the North American variant which became the standard against which all comparisons were made.

Callinectes sapidus is the member of the genus which has most successfully invaded the Temperate Zone, and in this respect it may be that speciation into forms associated with temperature regimes is progressing, but the process is not yet complete enough that morphological separation is distinct.

Material.—Total: 460 lots, 1,500+ specimens. Specimens listed in Rathbun (1930) from USNM (45656 and 26092 not found), MCZ, and BMNH.

USNM. 284 lots, 1,060+ specimens, including the following not cited above plus 7 lots and 13 specimens from undetermined localities and 2 lots of fingers from Indian mounds.

UNITED STATES

Massachusetts: 122952, Deadneck, Cotuit, Barnstable Co., 1 July 1949, 1 ♂, 3 ♀ (juv), H. E. Winn.

New York: 63260, Sing Sing [Ossing], no date, 1 ♂, 1 ♀, A. K. Fisher.

New Jersey: 63177, 63178, 63181, off New England Creek, 19 Oct. 1929, 2 ♂, 1 ♀ (juv), H. G. Richards. 63179, 1 mi off Dennis Creek, 13 Aug. 1929, 3 juv, H. G. Richards. 77006, 77041, Dennis Cove, 13 and 25 Aug. 1929, 61 juv, H. G. Richards. 77007, 77040, Barnegat Bay, Lavalette, 15 Aug. 1931, 2 ♂, 3 ♀, 4 juv, H. G. Richards.

Delaware: 77037, Delaware Bay near Woodland Beach, no date, 1 ♂ (juv), Coltam and Saylor. 63180, Mispillion River, 10 July 1929, 1 ♂ (juv), H. G. Richards. 77039, Mispillion Cove, 26 Aug. 1931, 3 ♂ (juv), H. G. Richards.

Maryland: 92452, Wye River, 16 Aug. 1951, 1 ♂, M. Sandoz. 113230, Sullivan Cove, Severn River, 31 Aug. 1966, 1 ♂, deformed chela, B. Truett. 77036, Lake Ovington, near Bay Ridge, 19 July 1936, 3 ♂, 2 ♀ (juv), C. R. Aschemeir. 76996, mouth Patuxent River, Solomons I., 16 July 1934, 2 ♀ (juv), P. Bartsch. 77033, Coster, about 3 mi N Solomons I., no date, 1 ♂, deformed chela, B. Coster. 67646, Coster, no date, 1 ♀, albino, W. Everett. 76148, Point Lookout, 9 Sept. 1932, 1 ♀ (juv), E. Bowles. 77004, Ridge, St. Marys Co., 26 Apr. 1930, 1 ♂ (juv), W. H. Ball. 76129, Blakistone I., 9 Sept. 1932, 1 ♀ (juv), E. Bowles. 66326, Herring Creek (Lower Potomac), 31 July 1929, 5 ♀ (juv), B. A. Bean. 66328, 77000, Riverside, 21 Nov. 1912, 2 ♂, 3 juv, U.S. Bur. Fish. 66614, Cobb I., Rock Point, Potomac River opposite Colonial Beach, 14 Aug. 1931, 1 ♂, E. D. Reid, W. L. Brown, and W. Pike. 75448, Analostan I., Potomac River at Georgetown, D.C., 11 Sept. 1930, 2 ♂, W. Reynold. 81473, 81474, Crisfield, 7 Oct. 1941, 41 juv, W. L. Schmitt. 95733, off Smiths I., 20 Aug. 1953, 1 ♂, partial albino, J. M. Ingley.

Virginia: 61146, Tangier, Dec. 1927, 1 deformed chela, J. Parks. 76998, Smiths I., 5 July 1935, 4 juv, W. H. Ball. 77034, Smiths I., Northampton

Co., 6 July 1935, 1 ♂, Lombino. 63320, Cape Charles, no date, 1 ♂, 1 ♀ (juv), H. G. Richards. 112857, Chesapeake Bay (believed to be in southwest middle grounds area), 15 Oct. 1964, 1 ♂, H. A. Martin. 67739, Elizabeth River, Portsmouth, 16 June 1933, 1 ♂, deformed chela, W. L. Hughes. 81483, Craney Island Lab., Norfolk, no date, 1 ♀ (juv), F. F. Ferguson. 81485, U.S. Public Health Serv., Craney I., Norfolk, Aug. 1940, 1 ♀, F. F. Ferguson. 76184, Virginia Beach, 4 July 1932, 2 carapaces (dry), G. E. Brandt.

North Carolina: 107137, Currituck Sound, 15 Nov. 1960, 1 ♂ (juv), J. A. Kerwin. 122964, Currituck Sound, no date, 1 ♂ (juv), J. R. Davis. 60601, Hatteras, May 1927, 67 ♂, 23 ♀, A. J. Poole and R. Kellogg. 107477, approx. ½ mi S Silver Lake Inlet and Ocracoke Village, 6 Aug. 1958, 2 ♀, col. unknown. 62462, Gallant Point, Beaufort Harbor, 13 Sept. 1928, 3 ♀ (juv), Schmitt and Shoemaker. 76999, Beaufort, no date, 1 ♂, col. unknown. 77002, Newport R. above "narrows," Beaufort, 3 Apr. 1931, 1 ♂ (juv), S. F. Hildebrand. 77003, Beaufort, 29 Sept. 1929, 1 ♂ (juv), Hobbs and Maloney.

South Carolina: 17191, South or North Carolina, no date, 1 ♀, *Fish Hawk* Stn. 6850.

Florida: 99892, Sewall Point, Martin Co., 27 Feb. 1955, 1 ♂ (juv), D. K. Caldwell, et al. 122944, Deep Lake, Miami, 5 Apr. 1952, 2 ♂, H. Field and Y. Lazor. 122949, Little Duck Key on S side of Rt. 1, Dade Co., 21 Dec. 1962, 1 juv, E. Kotkas and R. Chandler. 122950, Beach area and tidal flats on S ridge of Bahia Honda Key, Monroe Co., 3 Aug. 1965, 1 juv, N. R. Foster and D. G. Smith. 71606, S side of County Road, Key West, 13 Nov. 1922, 1 juv, Stephenson. 77038, Marquesas Keys, 11 Aug. 1931, 7 juv, A. S. Pearse. 77031, between Long and Bush Key, Tortugas, 26 July 1931, 1 ♀, A. S. Pearse. 77030, Tortugas, 25 June 1931, 1 ♂, W. L. Schmitt. 122958, Charlotte Harbor, 13 Sept. 1939, 1 ♀ (juv), USFWS Launch 58, hauls 1, 2, 3. 122953, Sarasota near Cape Haze Marine Lab., 26 Jan. 1966, 1 ♀, 4 juv, R. F. Cressey and R. H. Brown. 122954, Sarasota, near Cape Haze Marine Lab., 27 Jan. 1966, 2 juv, R. F. Cressey and R. Brown. 71654, Sarasota Bay, summer 1930, 4 juv, W. W. Wallis. 122943, Homasassa Springs, 30 Mar. 1946, 1 ♂, Herald and Strickland. 122929, Hernando Co., Gulf of Mexico, Gulf Beach and March outlet to Gulf at Pine I., 8 mi NW Weekiwachee Springs, 7 Apr. 1955, 2 ♂, 3 ♀ (juv), R. D. Suttkus and Sylvia A. Earle. 77566, Cedar Key, 25 Jan. 1938, 1 ♂, 15 juv, C. R. Aschmeier. 98085, Choctawatchee Bay, no date, 1 deformed chela, col. unknown. 122951, Florosa, Okaloosa Co., 3 Dec. 1941, 4 ♂ (juv), W. F. Blair. 66753, Florida, no date, 1 ♂, 1 ♀, Ross Allen.

Alabama: 81480, Big Lake, Gulf State Park, 14 Oct. 1939, 1 ♂, col. unknown.

Mississippi: 85543, Mississippi Sound, east end, 1 Sept. 1947, 1 ♂, J. W. Ward, et al. 122947, inside Petit Bois I., Mississippi Sound, 20 Apr. 1967, 1 ♂, 2 ♀, *George M. Bowers* Stn. 4, 5.5 m. 122938, Simmons Bayou trib. to Davis Bay, 2 mi SE Ocean Springs, 2 Aug. 1957, 1 ♂ (juv), R. D. Suttkus. 90299, S side of Cat I., Mississippi Sound, 9 Aug. 1949, 1 ♀ (juv), col. unknown. 2028, Washington [Adams Co.], no date, 1 ♂, Wailes. 77035, coast, May 1937, 1 ♀, J. S. Dolley.

Louisiana: 69676, Ycloskey [Bernard Parish], 10 June 1934, 2 ♀, J. N. Gowanloch. The following from Point aux Herbes, Lake Pontchartrain, 122940, 15 July 1955, 4 ♂, 18 ♀ (juv), R. R. Lubritz. 122939, 22 June 1955, 83 juv, R. R. Lubritz. 122927, 4 June 1955, 80+ juv, R. D. Suttkus. 122926, 4 June 1955, 1 ♂, 1 ♀ (soft), R. D. Suttkus. 122928, W Pearl River immediately above, N of Mill Bayou, St. Tammany Parish, 11 Aug. 1955, 1 ♀, M V *Lyman* Stn. 136. 122934, 1¼ mi up West Pearl River from mouth, St. Tammany Parish, 11 Aug. 1955, 1 ♀, M V *Lyman* Stn. 138. 122933, Lake Pontchartrain, Salt Bayou, 9 June 1955, 10 juv, R. D. Suttkus. 122935, 2.5 mi NW Salt Bayou on Pearl River, St. Tammany Parish, 11 Aug. 1955, 1 ♀, M V *Lyman* Stn. 143. 122936, ¼ mi SE West Pearl River Bridge, Lake Pontchartrain, St. Tammany Parish, 11 Aug. 1955, 1 ♂, M V *Lyman* Stn. 144. 122930, Lake Pontchartrain, first point W Liberty Bayou, 9 June 1955, 2 juv, M V *Lyman* Stn. 18. 122931, St. Joe Channel [Lake Pontchartrain], 21 June 1954, 2 parasitized, Patursan and Peterson. 97992, Lake Pontchartrain just S mouth of Tanipahoa River, 17 Oct. 1953, 11 ♂, 2 ♀, R. M. Carnell. 96990, Lake Pontchartrain, no date, 1 ♀ parasitized, col. unknown. 96322, Rigolets, Lake Pontchartrain, 29 Oct. 1953, 1 ♀ deformed carapace, L. Eddy. 122932, Rigolets at Lake Borgne, 7 June 1955, 1 ♀ (juv), R. D. Suttkus. 122960, Lake Pontchartrain at mouth of Tchefuncta River, St. Tammany Parish, 1 Apr. 1948, 2 ♀, R. M. and M. K. Bailey. 122945, Lake Pontchartrain, Aug. 1962, 1 ♂, J. Q. Burch. 64145, off Breton I., Nov. 1930, 1 ♂, S. Springer. 122963, 3-6 mi ESE of SW Pass, 16 Feb. 1934, 1 ♂, T. C. D., M. J. L., and W. W. A. 122959, [S of Plaquemines Parish] 29°01′N, 89°33′W, 8 July 1938, 1 ♀, *Pelican* Stn. 77-2. 105317, Barataria Bay, Jefferson

Parish, 27 Feb. 1960, 1 ♂, 4 ♀ (parasitized), E. H. Behre. 122937, Grand Isle, 3 Feb. 1957, 1 ♂, 1 ♀, R. D. Suttkus. 122961, [off Caillou Bay] 28°39.5′N, 91°04.5′W, 11 July 1938, 1 ♀, *Pelican* Stn. 81-2. 122962, on 9-fathom line between Ship to Trinity Shoal Buoy, 28°39.5′N, 91°04.5′W, 11 July 1938, 3 ♀, *Pelican* Stn. 81-2. 122956, 28°51.5′N, 91°33′W to 28°56.5′N, 91°50′W, 11 July 1938, 2 ♂, 2 ♀, *Pelican* Stn. 82-1 to 82-5. 5509, Louisiana, 1883, 2 ♂, 1 ♀, R. W. Shufeldt.

Texas: 78397, Galveston Bay, Galveston Co., 16 Apr. 1939, 3 ♀, C. E. Burt. 122957, Galveston, 4 May 1941, 1 ♂, 3 ♀ (2 juv), J. L. Baughman. 122955, Galveston south of ferry landing, 27 Aug. 1965, 1 ♀ (juv), J. McCain. 122948, south end, west side new Galveston-Houston causeway, Galveston, 24 Aug. 1965, 1 juv, J. C. McCain. 122946, 17 mi S, 7 mi E Alvin, Brazoria Co., 28 July 1952, 1 ♂, S. Alvin. 122942, Freeport, 12 May 1940, 1 ♀ (ov), J. L. Baughman. 122941, Alligator Head, Matagorda Bay, no date, 13 juv of ♀ form parasitized (dry), J. D. Mitchell. 81479, Aransas Pass, 8 July 1941, 1 ♂, 2 ♀ (soft and 2 parasitized), J. L. Baughman. 99243, Laguna Madre, 15 mi N of Port Isabel, 24 Jan. 1956, 2 juv, col. unknown. 71663, Texas, no date, 1 ♂, C. T. Reed. 81475, Texas, no date, 1 ♂ (juv), col. unknown.

JAMAICA

120626, Fresh River headwaters, N end of Caymanas Plantation, St. Catherine Parish, 7 Apr. 1959, 1 ♂, Hart, G. Thomas, R. Bengry, Thornton.

PUERTO RICO

80667, no date, 1 ♀ (recently ov, bearing jar label "nov. var?"), S. T. Danforth. 77044, Río Canovanillas, Canovanas [18°23′N, 65°55′W], 16 Feb. 1934, 2 ♂, S. F. Hildebrand.

VIRGIN ISLANDS

The following from St. Croix: 71524, Fairplain, no date, 1 ♂, 1 ♀ (juv), H. A. Beatty. 71794, Fairplain Stream, Dec. 1934, 1 ♀ (juv), H. A. Beatty. 72337, Fairplain Stream, 1935-36, 1 juv (soft), H. A. Beatty. 72356, Fairplain stream below bridge, 1935-36, 2 ♂, H. A. Beatty. 77032, on sea coast, Rust-op-Twist, no date, 1 ♀, H. A. Beatty.

GUATEMALA

123096, Atlantic at Punta Marrabique, N of Puerto Barrios, 1 May 1947, 1 ♂, R. R. Miller. 123097, Lago de Izabal, 26 Apr. 1947, 1 ♂, Miller et al.

COSTA RICA

113278, Tortuguero, May 1964, 1 ♂, 1 ♀, D. P. Kelso.

PANAMA

77043, Gatun Locks, C.Z., 21 Feb. 1935, 12 juv, S. F. Hildebrand.

VENEZUELA

The following from Golfo de Venezuela: 123099, 11°46′N, 71°16′W, 6 Oct. 1965, 1 ♀, *Oregon* Stn. 5670. 123095, 11°33′N, 71°31′W, 6 Oct. 1965, 1 ♀ *Oregon* Stn. 5672. 123100, 11°27′N, 71°39′W, 6 Oct. 1965, 4 ♀, *Oregon* Stn. 5673. 80649, Lago de Los Pájaros, 1 km above Lago de Maracaibo, 30 Apr. 1942, 2 ♂, L. P. Schultz. 80650, Lago de Maracaibo, 20 Feb. 1942, 2 ♀ (juv), L. P. Schultz. 80651, Lago de Maracaibo, 7-9 Apr. 1942, 2 ♂, L. P. Schultz. 80652, Cãno de Sagua, 25 km N Sinamaica, 12 Mar. 1942, 3 ♀, L. P. Schultz.

BRAZIL

Rio de Janeiro: 77042, Recreio dos Bandeirantes, 9-16 Feb. 1935, 1 chela, D. M. Cochran. Santa Catarina: 123098, Nov. 1965, 1 ♀ (juv), Jones-Lowe.

URUGUAY

99848, Roca Arroya de Balizas [= Valizes?], Jan.-Feb. 1953, 2 ♀, R. Vaz-Ferreira.

AHF. 6 lots, 10 specimens.

UNITED STATES

Florida: Pompano Beach, Sept. 1943, 1 ♀, E. R. T. Marco I., Collier Co., 10 Mar. 1946, 1 ♀ (juv), *Velero* A87-46. Santa Rosa Sound at Camp Navarre, 12 May 1949, 2 ♂, Stn. LM4-49.

Louisiana: Lake Borgne, 27 Aug. 1954, 1 ♀, R. Darnell.

MEXICO

Veracruz: Drainage ditch 5 mi W Veracruz, 19 Aug. 1949, 1 ♀ (juv), B. W. Halstead. Boca del Río, 9 Aug. 1949, 1 ♂, 3 ♀, B. W. Halstead.

AMNH. 19 lots, 26 specimens, including 4 lots with no data.

UNITED STATES

Massachusetts: 1002, Chappaquiddick I., Martha's Vineyard, 28 July 1909, 1 ♂ (dry), R. W. Miner.

New York: 221, New York Harbor, no date, 1 ♂, 1 ♀, L. P. Gratacap. 6267, Mastic, Long Island, Aug. 1930, 1 ♂, J. T. Nichols. 9856, Hudson River opposite Spuyten Duyvil, Sept. 1945, 1 deformed chela, J. Dvorak. 9778, Sheepshead Bay, N.Y. City, 1944, 1 ♂, H. Savalli. 6316, Freeport, Long Island, 5 Oct. 1930, 1 ♀, F. Limekiller. 6258, Inner Harbor, Cold Spring, Long Island, 26 July 1930, 1 ♂, C. H. Curran. 983, Fort Schuyler, N.Y. City, no date, 1 ♂, and extra chelae, E. Forshan.

New Jersey: 6491, Newark Bay, foot 27 St., Bayonne, 28 Aug. 1931, 1 ♂ (deformed chela), K. Wangler. 6653, Barnegat Bay, no date, deformed right chela (dry), col. unknown.

Florida: Lake Worth, July-Aug. 1945, 1 ♀, W. G. Van Name and A. H. Verrill. 10249, Destin, 29 July 1948, 6 juv, L. A. Burry.

BAHAMAS

Nassau and Andros I., Mar.-Apr. 1930, 1 ♀, Bacon-Miner Exped. and International Exped. to Andros.

CUBA

1024, 1913, 1 juv, J. T. Nichols.

PUERTO RICO

2787, Tallaboa [18°00′N, 66°43′W], 29 July 1914, 1 ♂ (juv), R. W. Miner.

ANSP. 26 lots, 41 specimens.

UNITED STATES

North America: 35, [Delaware Bay], no date, 1 ♀ (dry) Blanding.

New Jersey: 2798, along coast, no date, 2 ♀ (dry), W. M. Wood. 2933, Ventnor, Aug. 1928, 1 deformed chela (dry), R. D. Benson, Jr. 3659, Great Egg Harbor, no date, 1 ♂ (dry), S. Ashmead. 3604, Point Breeze, Delaware River, no date, carapace, F. L. LeCompte. Delaware River, 30 July 1951, 2 ♂, 1 ♀, J. Bates.

Maryland: Potomac River at Popes Creek, Charles Co., Aug. 1966, 3 ♂, 1 ♀ (juv), S. L. H. Fuller. Potomac River ¼ mi above Lower Cedar Pt., WNW Morgantown, Charles Co., Aug. 1966, 3 ♀ (juv), S. L. H. Fuller. 3492, Chesapeake Bay, no date, 1 ♂ (dry), from U.S. Explor. Exped.

Virginia: York River, 31 May 1956, 1 ♀, F. A. Aldrich. York River, 2 June 1956, 3 ♀ (1 ov), F. A. Aldrich. York River, 21 Sept. 1956, 1 ♂, 1 ♀, F. A. Aldrich. James River, 17 June 1957, 1 ♂, F. A. Aldrich.

North Carolina: 4873, Fort Macon, 2 ♀, Yarrow.

Florida: 3481, Key West, no date, 1 ♀ (juv), S. Ashmead. 3569, Manatee River, no date, 1 ♂ (dry), S. Ashmead.

Texas: Houston-Galveston Ship Canal, July 1954, 1 ♂, 1 ♀ (juv), F. A. Aldrich. Cow Bayou, trib. of Sabine River, Orange Co., 11 Aug. 1962, 1 ♂, C. W. Hart, Jr. Sabine River, Orange Co., 9 Aug. 1962, 2 ♂, C. W. Hart, Jr. Sabine River, N of Sabine I., Orange Co., 13 Aug. 1962, 2 ♂, C. W. Hart, Jr.

CUBA

4697, Cojímar near La Habana, 10 July 1940, 2 ♀, R. A. McLean.

DOMINICAN REPUBLIC

3519, no date, 1 ♂ (dry), W. M. Gabb. 2957, no date, 1 ♀ (dry), W. M. Gabb.

PUERTO RICO

3179, off Guánica Harbor, no date, 1 ♂ (dry), Fowler.

PANAMA

1305, no date, 1 ♀ (juv), McNeil Exped.

BRAZIL

3514, no date, 3 ♂ (dry), T. B. Wilson.

BMNH. 15 lots, 28 specimens.

UNITED STATES

Connecticut: 98.5.7.312, Long Island Sound, 1 ♂, 1 ♀, Norman. 80.26, New Haven, 1 ♀, Norman.

New Jersey: 98.5.7.317/18, 3 ♂, 1 ♀ (juv) Verrill and Smith. Unreg., Cape May, 1 ♂ (dry) vi/9, J. K. Townsend. Unreg., 1 ♀ (juv, dry) vi/6.

Maryland: 1964.9.7.13, Chesapeake Biological Lab. Pier, Solomons, 1 ♂ (juv), F. J. Schwartz and A. C. Edwards. 1964.9.7.14/16, Patuxent River at Evans pier, Solomons, 1 ♂, 1 ♀ (juv), A. C. Edwards and F. J. Schwartz.

Florida: 1966.12.5.555/557, coast of Everglades Park, 3 juv, U. Miami, Inst. Mar. Sci. 1966.12.5.667, 1 ♂, Univ. Miami, Inst. Mar. Sci. 1966.12.5.666, 1 ♂, Univ. Miami, Inst. Mar. Sci. 1966.12.5.668/671, 4 juv, Univ. Miami, Inst. Mar. Sci.

TOBAGO

1925.1.28.11/12, 1 ♂, 1 ♀, P. L. Guppy.

TRINIDAD

1940.7.8.15, 1 ♂, A. K. Totton.

BRAZIL
Unreg. 1 ♀ (juv, dry) vi/6, col. unknown.

MCZ. 42 lots, 159 specimens.

BERMUDA
5122, no date, 1 ♀ (juv), Bickmore.

UNITED STATES
Massachusetts: 322, Cohasset, 1922, 1 ♀, J. A. Murphy. 5110, Naushon I., Buzzards Bay, 1873, 2 ♀, W. Faxon. 333, Pocasset, 1919, 1 ♀, J. A. Cushman.

Connecticut: 5563, New London, no date, 2 ♂, 3 ♀, G. G. Hammond, Aug. 1876. 8510, New London, no date, 3 ♂, 10 ♀, G. G. Hammond, 1876.

New York: 332, Fishers I., 1874, 1 ♀ (ov), Hyatt and Rathbun. 5471, 1 ♂, 2 ♀, L. Agassiz, 1859.

New Jersey: 5112, Somers Point [N shore across from Ocean City], no date, 3 ♂, 3 ♀, W. Stimpson, recd. Oct. 1864. 5212, Somers Point, no date, 50 juv, W. Stimpson, recd. Dec. 1864.

Maryland: 5117, Baltimore, 1860, 2 ♂, A. Hyatt.

North Carolina: 11351, 2 mi SE Roanoke I., 19 Dec. 1940, 1 ♂, R. Foster. 11353, 5 mi SW Nags Head, near Roanoke I., Dec. 1940, 1 ♂ (juv), R. Foster. 5113, Beaufort, no date, 3 ♂, 3 ♀ (juv), A. S. Bickmore.

South Carolina: 5116, Waccamaw, no date, 1 ♀, L. Agassiz. The following from Charleston: 5114, no date, 2 ♂, 2 ♀, L. Agassiz (part of Ordway's material). 5202, no date, 2 ♂, 12 ♀, col. unknown. 8751, no date, 1 ♂, 1 ♀, T. Lyman.

Georgia: 5201, May 1859, 1 ♂, T. S. Allanson.

Florida: 5205, June 1859, 1 ♀, G. Wurdemann. 8752, no date, 6 ♂, col. unknown. 11936, Key West, May 1940, 2 juv, J. R. Miller. 5118, Tortugas, 2 ♂, Jacques, from Peabody Acad. Sci. Nov. 1885. 5203, Fort Jefferson, Tortugas Is., no date, 2 ♂, col. unknown. 10163, Sanibel I., Mar. 1938, 3 ♂, 3 ♀, F. A. Chace, Jr. 5119, Charlotte Harbor, 1 ♂, L. Gibbes, recd. 13 Feb. 1861. 8334, Lemon Bay and Gulf, Englewood, Sarasota Co., Jan.-Apr. 1935, 2 ♂, 2 ♀, 3 juv, D. J. Zinn.

Alabama: 5204, Mobile, no date, 1 ♂, 1 ♀, 2 juv, L. Agassiz.

Mississippi: 11942, Ship I. off Biloxi, June 1941, 1 juv, J. R. Miller.

Louisiana: 12046, Bayou La Fourche near Shriever, June 1941, 1 ♂, J. R. Miller.

Texas: 5120, no date, 1 ♂, G. Wurdemann. 5121, Galveston, 1871, 1 ♀, Boll.

CUBA
5123, La Habana, no date, 1 ♂, S. Garman. 10887, Cienfuegos [22°09′N, 80°27′W], 19 Feb. 1938, 1 ♀, Harvard-Havana Exped.

HAITI
5213, Jérémie. Apr. 1865, 1 ♂, 1 ♀, D. F. Weinland.

MEXICO
Yucatán: 8623, Progreso, 1904, 1 ♂, L. J. Cole.

BRAZIL
The following from Rio de Janeiro: 5126, no date, 1 ♂, Thayer Exped., recd. 1865. 5127, no date, 1 ♂, Thayer Exped. Estado de Rio Grande do Sul: 4699, Rio Grande, June 1861, 1 ♂, Harrington.

MNB. 1 lot, 1 specimen.

BRAZIL
Santa Catarina: 57, Ponta do Farol, São Francisco do Sul, 1 ♀, recd. July 1901.

MNHNP. 1 lot, 1 specimen, plus 3 specimens in old dry collection.

FRANCE
Rochefort, 1900, 1 ♂, from M. Vieuille.

RMNH. 49 lots, 109+ specimens.

UNITED STATES
East coast of N America, Sept. 1836, 1 ♂, 1 ♀, G. Troost.

Connecticut: 401, New Haven, no date, from Smithsonian Inst.

New York: 13790, Shinnecock Bay, Long Island, Oct. 1955, 4 juv, A. Perlmutter.

New Jersey: 15253, Creek at Stone Harbor, Cape May Co., 8 May 1960, 2 ♀, juv, J. L. Scheltema.

Delaware: 11407, 11408, Delaware Bay, juv, date and col. unknown. 11344, Delaware Bay about 1 mi off Lewes, Sussex Co., 27 Apr. 1957, 1 ♀, L. B. Holthuis.

Maryland: 14616, Mouth of Potomac River, Point Lookout, St. Marys Co., 20 Mar. 1960, 2 ♀, J. L. Scheltema. 9827-9832, Chesapeake Bay, series of juv from 6 localities, date and col. unknown. 9833, mouth of harbor at Snowhill Landing, Snowhill, Worcester Co., 30 Sept. 1952, 1 ♂, juv, L. B. Holthuis. 9836, northern portion of Chincoteague

Bay, N of Snowhill, Worcester Co., 29 Sept. 1952, 1 ♂, 1 ♀, L. B. Holthuis. 9837, Johns Creek at mouth of St. Leonards Creek in cove of Patuxent River, W of Lusby, Calvert Co., 16 May 1953, 1 ♀, L. B. Holthuis.

Virginia: 9838, Harborton, Accomack Co., 28 Sept. 1952, 1 ♀, L. B. Holthuis.

Florida: The following from Biscayne Bay—21351, off Rickenbacker Causeway, 1 Feb. 1965, 1 ♀, J. A. Cabrera and L. B. Holthuis. 23432, near Mathesan Hammock S of Miami, 3 Jan. 1965, 1 ♂, juv, L. B. Holthuis. 21346, S of Rickenbacker Causeway, Miami, 4 Feb. 1965, 1 ♀ (ov), L. B. Holthuis. The following from Bear Cut near Marine Lab., Virginia Key—24258, 1 Sept. 1965, 1 juv, J. A. Cabrera and L. B. Holthuis. 24259, 22 Dec. 1964, 1 juv, L. B. Holthuis. 18710, 2-9 Sept. 1963, 1 ♀, L. B. Holthuis. 15635, Marco Beach S of Marco, washed ashore by hurricane Donna, 12 Sept. 1960, 1 ♀, L. B. Holthuis. 15634, mangroves near Marco Beach S of Marco, 12 Sept. 1960, 1 ♀ (juv), L. B. Holthuis.

PUERTO RICO

23465, Rio Guánica, 15 Sept. 1963, 1 ♂, 1 ♀, P. W. Hummelinck.

TRINIDAD

23404, mouth of Diego Martin River [5 mi NNW Port of Spain], 1965-66, 2 ♂, H. O. von Hagen. 17738, Matura, NE coast of island, 19 June 1961, 1 ♂, I. Kristensen.

CURAÇAO

11881, Waaigat, Willemstad, 30 Jan. 1957, 2 ♀, L. B. Holthuis.

NETHERLANDS

23434, Friesland, washed ashore, 7 May 1967, 2 ♂, 1 ♀, T. P. Broerse. 24754, southern North Sea 25 mi NW Ijmuiden [14 mi WNW Amsterdam], 19 Jan. 1968, 1 ♀, Rijks. Inst. Visserij Onderzoek. Beach at Dishoek between Flissingen and Zoutelande, Zeeland, 20 Jan. 1967, a large right swimming leg (dry), G. R. Heerebout. Washed ashore at Vlissingen in cooked condition, Aug. 1950, carapace of adult ♀ (dry), A. C. Visser.

GREECE

Delta area of Axiós and Gallikós near Pírgos, Thessaloníki, 15 June 1964, part of ♀ carapace and abdomen, from shallow water in *Salicornia* fields, from fisherman, W. J. Wolff and M. Loosjes. 18689, fishmarket in Thessaloníki, from Gulf of Thessaloníki, 14 Mar. 1963, 1 ♀, R. Kinzelbach. Beach at Strimonikós Kólpos (= Gulf of Orfani) near Aspróvalta, about 15 km W Tsgezi (= Iraklítsa), 10 Mar. 1963, 2 rather worn carapaces (dry), R. Kinzelbach. 13082, Aegean Sea near harbor of Pórto Lágo, 29 June 1959, 2 ♀, C. Swennen.

TURKEY

21148, on S coast near Silifke (Seleucia), 19 Aug. 1964, 1 ♀, Turkey Excursion, 1964 from Hamburg Mus. 13137, E coast of Akyatan Lagoon 45 km S Adana, 18 May 1959, 4 ♂, 2 ♀.

ISRAEL

The following from Naaman River S of Acre: 18829, mouth of River, 2 Feb. 1955, 1 ♂ (juv), A. Perlmutter. 13795, near Acre, 13 Oct. 1955, 2 juv, A. Perlmutter. 13794, same, 17 Aug. 1955, 1 ♀, E. Gottlieb. 17840, between railroad bridge and mouth, 30 Apr. 1962, 2 ♂, 3 ♀, L. B. Holthuis. Mouth of river, 30 April 1962, carapace and chelae of 2 or more individuals (dry), L. B. Holthuis. 18832, Lagoon on Kishon River, N of Haifa, 31 Jan. 1955, 1 ♀, Sea Fish Res. Stn., Haifa. 10722, Mouth of Tiphlis River near Tantura, about halfway between Cesarea and Atlit, 26 Oct. 1955, 1 ♂ encrusted with *Chelonibia patula* (Ranzani), A. Perlmutter. 13793, Mouth of Hefzibah [Hadera?] River near Hadera, 21 Nov. 1951, 1 ♀ (juv), E. Gottlieb. 13792, Hefzibah, 21 Nov. 1951, 1 ♀ (juv), E. Gottlieb. 13791, Alexander River near mouth [S Hadera], 20 Dec. 1955, 1 ♀ (juv), E. Gottlieb.

SADZ-B. 7 lots, 27 specimens.

BRAZIL

Rio de Janeiro: 3240, Atafona, 12 July 1963, 10 ♂, 8 ♀, N. Meneses. 1721, Atafona, 1964, 1 ♂, N. Meneses. 950, S. João da Barra, Nov. 1911, 1 ♀, E. Garbe.

São Paulo: 1814, Santos, 11 Sept. 1962, 1 ♀, G. Melo. 1727, Guarujá, Jan. 1920, 1 ♀, Hempel.

Santa Catarina: 664, Itajaí, Dec. 1914, Luederwaldt.

Rio Grande do Sul: 3234, Praia de Torres, 5 Oct. 1964, 1 ♂, 2 ♀ (1 ov), J. Bertoletti.

UNC-IMS. 8 lots, 34+ specimens.

UNITED STATES

Delaware: 1853, Near Port Mahon, 1 July 1954, 2 ♀, H. J. Porter.

North Carolina: 2246, West Bay near Cedar I., Pamlico Sound, Carteret Co., 21 July 1969, 2 ♀ (ov), includes smallest mature ♀ on record, from fisherman. 821, Neuse River near New Bern, Craven Co., 24 July 1957, 1 ♂ (juv), Tagatz and Dudley. 738, Neuse River at Smith Farm, near North Harlowe, Craven Co., 1 Oct. 1957, 3 ♂, 1 ♀, juv, Judy and Dudley. 739, Neuse River at North Harlowe, 26 July 1957, 3 ♀ (juv), Tagatz and Dudley. 820, Pivers Island near Beaufort, Carteret Co., 27 May 1957, 1 ♂, 4 ♀ (juv), Talbot and Fischler. 913, off Beaufort Inlet, 26 Nov. 1959, 4 ♀ (3 ov), covered with *Chelonibia,* H. J. Porter.

PUERTO RICO

2136, Fresh water canal, 5 km S Lajas, 10 Feb. 1967, 3 ♂, 1 ♀ juv.

YPM. 1 lot, 1 specimen.

BRAZIL

6399, Rio Grande, 7 June 1860, 1 ♂ bearing *Chelonibia,* G. Harrington.

Supplementary literature records.—Nova Scotia (Piers, 1923); Maine and Nova Scotia (Scattergood, 1960); Bermuda (Verrill, 1908a, b); Laguna Madre de Tamaulipas, Mexico (Hildebrand, 1957); Alvarado, Veracruz, Mexico (Contreras, 1930); Dominica (Chace and Hobbs, 1969); Lago de Maracaibo and Golfo de Venezuela (Taissoun, 1969); Quenquén, Buenos Aires, Argentina [?] (Boschi, 1964); Elbe estuary, Germany (Kühl, 1965); Netherlands and North Sea localities (Holthuis, 1969); mouth of Gironde, France (Amanieu and Dantec, 1961); Gulf of Spezia and Genoa Harbor, Italy (Tortonese, 1965); northern Adriatic lagoons, Italy (Holthuis, 1961 [review]); Greece and parts of eastern Mediterranean (Serbetis, 1959); Beirut, Lebanon (George and Athanassiou, 1965); Buḥayrat Idkū and Buḥayrat Manzilah, Egypt (Banoub, 1963).

QUESTIONABLE SPECIES

Rathbun (1907) described *Callinectes alexandri* from Papeete, Tahiti, and Suva, Fiji Islands, on basis of two juveniles, and later (1911) noted a small mature male from Cragados, Carajos [Shoals, Mascarene Islands, Indian Ocean]. Stephenson and Campbell (1959) synonymized this confusing form with *Portunus pelagicus* (Linn.), commenting on its close similarity to members of *Callinectes* and temporarily questioning the validity of *Callinectes.* Later Stephenson et al. (1968) accepted the generic status quo. Stephenson (1968) confirmed his recognition of *Callinectes* and, after examination of Rathbun's specimens of *C. alexandri,* reidentified the Tahiti and Fiji material as *P. sanguinolentus* (Herbst) and the Indian Ocean specimen as *P. pelagicus.* The history of these bleached specimens emphasizes the difficulty in identifying some juvenile portunid material.

Chen (1933) described *Callinectes platei* on basis of a small male (length 14, width 29 mm), and *C. alcocki* on basis of a small ovigerous female (length 10.5, width including lateral spines 16 mm) from Tuticorin [Madras, India]. There is no sure way to identify these forms because specimens from the Plate collection are apparently no longer in existence. From the descriptions and figures, the two species possibly represent male and female of the same form, a small portunid with internal carpal spine. This alone is enough to remove them from *Callinectes.* Moreover, no known *Callinectes* is ovigerous at the tiny size of this female.

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ELECTROPHORETIC COMPARISON OF FIVE SPECIES OF PANDALID SHRIMP FROM THE NORTHEASTERN PACIFIC OCEAN

ALLYN G. JOHNSON, FRED M. UTTER, AND HAROLD O. HODGINS[1]

ABSTRACT

Pandalid shrimp from off Alaska, Washington, and Oregon were investigated using starch-gel electrophoresis. Each species was found to be polymorphic for phosphoglucomutase, and the general protein patterns separated them into two groups—one consisting only of *Pandalus hypsinotus* and the other containing *P. borealis, P. goniurus, P. jordani*, and *Pandalopsis dispar*.

A key based on biochemical characters was developed which could separate the five pandalid species investigated.

The increase of commercial fishing for shrimp along the Pacific coast of North America in recent years has stimulated interest in the biology and identification of species and population units. Ronholt (1963) reported on the distribution and relative abundance of five species of pandalid shrimp from the northeastern Pacific Ocean. Butler (1965) presented a comprehensive report on the growth, reproduction, and distribution of pandalid shrimp in British Columbia waters, demonstrating the importance of inlets and bays to this group of crustaceans. Several reports on sampling techniques, diel vertical migration, and population movements have occurred which emphasize the need for additional information on the biology of pandalid shrimp for optimal utilization of this resource (Barr and McBride, 1967; Barr, 1970, 1971; Gotshall, 1972).

One of the more promising techniques for the detection of population units is the biochemical genetic approach, utilizing starch-gel electrophoretic separation of proteins coupled with histochemical staining procedures (Hunter and Markert, 1957). This method has been widely used and successfully applied to fisheries problems (reviewed by de Ligny, 1969, 1972).

This paper reports our application of starch-gel electrophoresis to separation of species and populations of five species of shrimp which occur along the coast of the northeastern Pacific ocean.

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MATERIALS AND METHODS

Five species of adult pandalid shrimp from two genera were investigated; *Pandalopsis dispar, Pandalus borealis, P. goniurus, P. hypsinotus*, and *P. jordani*. All samples except those of *P. jordani* and one collection of *P. hypsinotus* were obtained from Marmot and Kazakof Bays of Kodiak Island, Alaska, during May 1972, and identified by personnel of the National Marine Fisheries Service at Kodiak, Alaska. These samples were shipped frozen to our laboratory where they were kept at −15°C until tested. Two collections of *P. jordani* were obtained off Coos Bay and Astoria, Oreg., in 1971 and identified by personnel of the Fish Commission of Oregon, shipped to us frozen and kept at −15°C until tested. Additional samples of *P. jordani* and *P. hypsinotus* were obtained during December 1972 from Bellingham Bay, Wash.

Extracts of muscle tissue were prepared by mixing equal volumes of tissue and 2% phenoxyethanol in distilled water into uniform pastes with glass rods. The starch-gel electrophoretic procedure followed the methods reported by Johnson, Utter, and Hodgins (1972). The buffer system used was described by Ridgway, Sherburne, and Lewis (1970). After electrophoresis the gels were sliced into four horizontal slices and stained for phosphoglucomutase (PGM), lactate dehydrogenase (LDH), tetrazolium oxidase (TO), peptidase (Johnson et al., 1972), malate dehydrogenase NAD and NADP (MDH), glyceraldehyde-3-phosphate dehydrogenase (GAPDH; Shaw

and Prasad, 1970), naphthyl acetate and propionate esterases (modified after Utter, Stormont, and Hodgins, 1970), and general protein (Johnson et al., 1972).

RESULTS AND DISCUSSION

Bands of identical electrophoretic mobility for a given enzyme system were observed in all species for the following systems: MDH (NADP), one anodal band; MDH (NAD), one anodal band; peptidase (valyl-leucine), three anodal bands; TO, one anodal band; and GAPDH, three anodal bands.

Esterase patterns varied among species; however, the patterns were weak and not completely repeatable. Gasser and Rowlands (1972) noted similar problems in interpreting esterase patterns from human serum and related the differences to nongenetic causes. We have, therefore, excluded them from further consideration in this study. Esterases have been found useful in studies of other invertebrates and may indeed be of use in studies of pandalid shrimp if reliable methods can be developed for stabilizing expression of patterns (Manwell and Baker, 1970; Barlow and Ridgway, 1971).

Lactate dehydrogenase was expressed as one anodal band—with a broad, faint-staining area anodal to it—in each species. The bands of *P. jordani, P. borealis,* and *P. goniurus* had an identical mobility slightly more anodal than the bands of *P. hypsinotus* and *Pandalopsis dispar.*

The general protein patterns observed are shown in Figure 1. *Pandalus hypsinotus* had bands C, E, F, and G; *P. jordani* and *P. borealis,* bands A, B, D, and G; and *P. goniurus* and *Pandalopsis dispar*, bands A, B, and G. The B band, although qualitatively invariable, varied considerably in intensity in all species expressing it. A greater degree of difference in the protein pattern was observed between *Pandalus hypsinotus* (processing three unique bands) and the other four species than was observed among these four species.

Phosphoglucomutase (PGM) was polymorphic in all five species. Two-banded phenotypes (Figure 2) were observed in some individuals of all species, presumably reflecting heterozygous individuals, and the pattern suggests that the active PGM enzyme in shrimp is a monomer (Shaw, 1964). This agrees with reports of PGM polymorphisms found in vertebrates (see Johnson, Utter, and Hodgins, 1971). A diagrammatical representation of the allelic forms found within the five species (Figure 3) shows the six allelic bands that were observed and designated (in decreasing anodal mobility) A, B, C, D, E, and F. The distribution of these alleles, as indicated in Figure 3, was *P. hypsinotus*, A, B, E, and F; *P. goniurus*, A and B; *P. borealis*, C, E, and F; *P. jordani*, B, C, and E; and *Pandalopsis dispar*, C, D, and E. The phenotypic distributions of PGM in the five species of shrimp along with gene frequencies, Hardy-Weinberg calculations and collections data are presented in Tables 1 and 2. With the exception of *Pandalus hypsinotus*, the phenotypic distributions of PGM of the collections of shrimp species did not deviate significantly

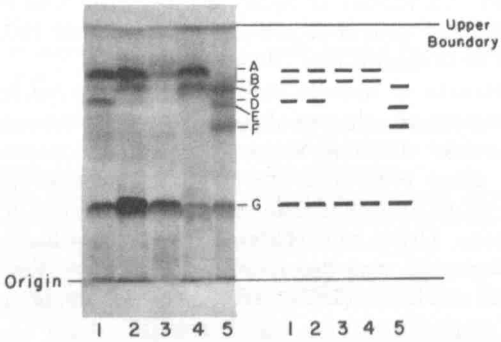

FIGURE 1.—Electrophoretic patterns on starch gel of muscle protein of five species of shrimp from the northeastern Pacific Ocean. Numbers below the patterns indicate the following species: 1. *Pandalus jordani*, 2. *P. borealis*, 3. *P. goniurus*, 4. *Pandalopsis dispar*, and 5. *Pandalus hypsinotus*.

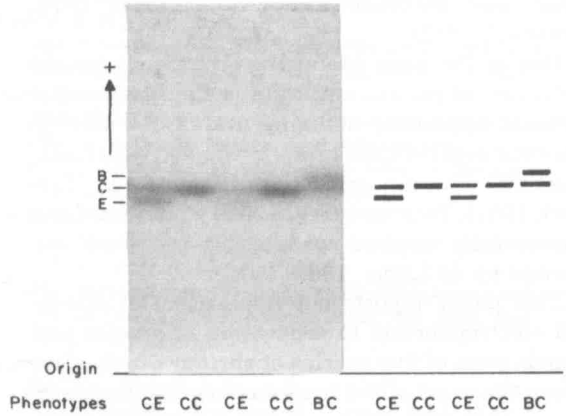

FIGURE 2.—Phosphoglucomutase phenotypes of *Pandalus jordani* in starch gels suggesting monomeric configuration of this enzyme.

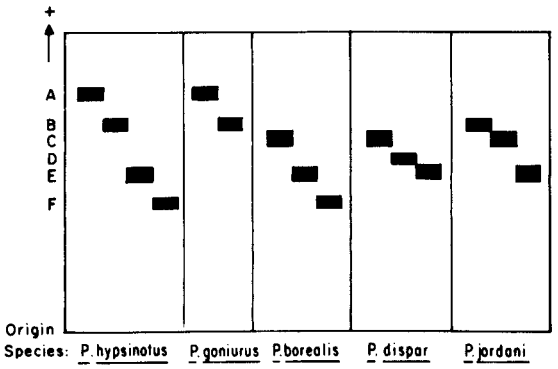

FIGURE 3.—Diagrammatical representation of the alleles of phosphoglucomutase in five species of pandalid shrimps as shown by the technique of starch-gel electrophoresis.

from expected Hardy-Weinberg values, and the gene frequencies of intraspecific samples were similar over the geographic range samples for *P. jordani*.

The collections of *P. hypsinotus* from Alaska showed highly significant deviation from Hardy-Weinberg expectations. Variation from expected Hardy-Weinberg proportions has also been observed for PGM variants of Pacific ocean perch, *Sebastes alutus* (Johnson et al., 1971) and related to depth of capture. Gene frequencies were similar for shallow- and deepwater collections; however, deepwater collections deviated significantly from expected Hardy-Weinberg frequencies. Further sampling stratified by depth (or other measurable variables) may reveal similar relationships for PGM variants of *P. hypsinotus*.

Inspection of the allele frequencies of the Alaskan and Washington collections of *P. hypsinotus* showed marked differences, especially with the A and E alleles (Table 1). These differences indicate that PGM variation may be useful in population identification of *P. hypsinotus*. Bullini and Coluzzi (1972) have presented evidence for selection of PGM alleles over a broad geographic range in mosquitoes *Aedes aegypti* and *A. mariae*. Additional sampling of *P. hypsinotus* may reveal a similar phenomenon as that found in the mosquito species.

The general protein, LDH, and PGM patterns observed in the five species were used to produce a key by which the species can be separated (Figure 4). This type of key should prove useful in application to shrimp identification problems.

CONCLUSION

The general protein patterns separated the species examined into two groups, one consisting only of *P. hypsinotus* and the other containing the remaining species of *Pandalus* and *Pandalopsis dispar*.

All five species of shrimp studied were polymorphic for PGM, with *Pandalus hypsinotus* possessing the greatest number of alleles (four

TABLE 1.—Phosphoglucomutase phenotypes of *Pandalus hypsinotus* taken off Alaska and Washington, 1971-72.[1]

Location	Sample size	Phenotypes of PGM									
		AA	AB	AE	AF	BB	BE	BF	EE	EF	FF
Alaska: Marmot Bay and Kazakof Bay	89	1 (1.8)	15 (9.0)	4 (8.5)	4 (4.1)	11 (11.5)	20 (21.5)	7 (10.3)	9 (10.2)	18 (9.8)	0 (2.3)
Washington: Bellingham Bay	80	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.9)	15 (14.6)	0 (0.1)	55 (55.5)	8 (8.9)	1 (0.0)

Location	Allelic frequencies				Test Data		
	A	B	E	F	df	χ^2	P
Alaska: Marmot Bay and Kazakof Bay	0.140	0.360	0.337	0.163	6	17.23	[2]$0.01 > P > 0.001$
Washington: Bellingham Bay	0.000	0.106	0.831	0.063	—	—	—
Contingency test comparing allelic composition of Alaska and Washington samples					3	89.64	$P < 0.001$

[1]In parentheses are the expected values of a Hardy-Weinberg distribution.
[2]Chi-square test of Hardy-Weinberg distribution.

TABLE 2.—Phosphoglucomutase gene frequencies of four species of pandalid shrimp taken off Alaska, Oregon, and Washington; 1971-72.

Species and location	Sample size	Gene frequencies						Test data[1]		
		A	B	C	D	E	F	df	χ^2	P
Pandalus goniurus										
Alaska:										
Marmot Bay and Kazakof Bay	94	0.016	0.984	—[2]	—	—	—	1	2.34	$0.2>P>0.1$
Pandalus jordani										
Oregon:										
Coos Bay	150	—	0.010	0.980	—	0.010	—	3	0.00	$P>0.99$
Astoria	151	—	0.003	0.990	—	0.007	—	3	0.02	$P>0.99$
Washington:										
Bellingham Bay	79	—	0.000	1.000	—	0.000	—	3	0.00	$P>0.99$
Pandalus borealis										
Alaska:										
Marmot Bay and Kazakof Bay	418	—	—	0.059	—	0.934	0.007	3	7.60	$0.1>P>0.05$
Pandalopsis dispar										
Alaska:										
Marmot Bay	269	—	—	0.011	0.981	0.008	—	3	0.00	$P>0.99$

[1]Chi-square test of Hardy-Weinberg distribution.
[2]Indicates not observed in this species.

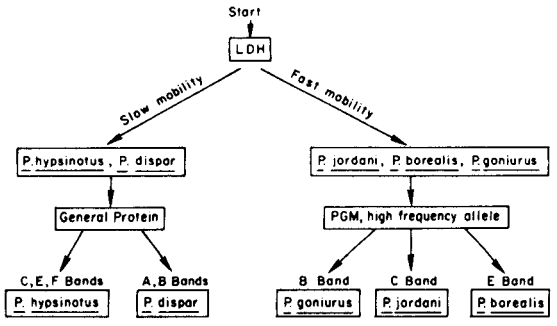

FIGURE 4.—Key to five species of pandalid shrimp based on three biochemical characters.

alleles). This polymorphism may prove useful for separation of breeding groups and as genetic markers in shrimp culturing experiments.

All five species could be identified based on a biochemical key that was developed.

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DISTRIBUTION AND RELATIVE ABUNDANCE OF LARVAE OF KING CRAB, *PARALITHODES CAMTSCHATICA*, IN THE SOUTHEASTERN BERING SEA, 1969-70

EVAN B. HAYNES[1]

ABSTRACT

During the spring and summer of 1969 and 1970, larvae of the king crab, *Paralithodes camtschatica*, were abundant in plankton samples from the southeastern Bering Sea. Abundance was highest near shore and generally lowest in the central and western parts of the study area. As the season progressed, the center of abundance moved northeastward along the Alaska Peninsula toward the head of Bristol Bay. This change in distribution was apparently related to water current patterns.

This report is based on collections of larvae of king crab, *Paralithodes camtschatica*, made by the Auke Bay Fisheries Laboratory, National Marine Fisheries Service, Auke Bay, Alaska, in the spring and summer of 1969 and 1970 in the southeastern Bering Sea. The larvae were collected during studies of migrating salmon and exploratory fishing for shellfish. In this report, I describe the distribution and relative abundance of the king crab larvae in the southeastern Bering Sea in 1969 and 1970 and relate seasonal changes in the distribution of the larvae to current patterns.

The only reports on distribution and abundance of king crab larvae in the study area are those by Takeuchi (1962, 1968) and Rodin.[2] Takeuchi sampled with various types of plankton nets from Japanese crab processing ships off the Black Hills-Port Moller area in 1957, 1958, and 1960. He found more king crab larvae off Port Moller than the Black Hills area, but because his sampling was restricted in area, he could not determine where the larvae had been released or where they dispersed. Rodin's study encompassed a greater area than Takeuchi's but was of shorter duration (less than 1 mo as compared with an average of nearly 2 mo). Rodin speculated, however, that king crab larvae were released primarily in the Port Moller area.

My study provided further evidence that a major area of release of king crab larvae occurs in the Black Hills-Port Moller area and the larvae generally disperse northeastward along the Alaska Peninsula toward the head of Bristol Bay.

MATERIALS AND METHODS

A total of 249 plankton tows were made in the southeastern Bering Sea from May to September 1969, and 237 were made from March to September 1970. Ten-minute oblique hauls were taken from the bottom to the surface during daylight with paired bongo nets (Posgay, Marak, and Hennemuth, 1968), each with a mouth area of 0.03 m^2 and nylon netting of 0.333-mm mesh. Tows were made at a speed of about 3 knots without regard to tide stage. The plankton samples were preserved in 5% Formalin[3] and seawater immediately after they were collected.

Although flowmeters were inside each sampler to determine the amount of water strained, mechanical difficulties prevented an accurate measure for most tows. However, the data have been converted to numbers of larvae under 10 m^2 of sea surface, as an index sufficiently precise to determine the general distribution and relative abundance of the larvae. Because the correlation between the two nets fished simultaneously was high (r = 0.979) and it is desirable to use whole numbers, I summed the catch of the two nets in

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[2]Rodin, V. E. 1966. Soviet investigation in 1965 to determine the status of king crab (*Paralithodes camtschatica* (Tilesius)) stocks in southeastern Bering Sea. Unpubl. manuscr., 12 p. Auke Bay Fisheries Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, AK 99821.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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each tow rather than use the average in my analysis. The terms "positive tow" and "negative tow" are used to describe plankton tows that contained king crab larvae and those that did not. The station locations and developmental stages of king crab larvae captured for the positive tows are given in Table 1; the locations of both positive and negative tows are indicated in the charts showing distribution of larvae (Figures 1 to 7). Charts showing distribution and abundance of larvae were made by plotting the number of larvae under 10 m² of sea surface at each station and then drawing isopleths. Identification of the larval stages was based on descriptions given by Marukawa (1933), Sato and Tanaka (1949), and Kurata (1964).

TABLE 1.—Station location and number and stage of development of king crab larvae captured for each positive tow collected in the southeastern Bering Sea, 1969 and 1970.

				Larval stage					
		Station location		Zoea					
Date	Depth (m)	Lat. N	Long. W	I	II	III	IV	Glaucothoe	Total
1969									
May									
18	55	55°00′	165°00′	39	32	5	—	—	76
19	45	58°00′	163°22′	1	—	1	—	—	2
20	75	56°20′	162°12′	10	—	—	—	—	10
26	116	55°20′	165°45′	—	1	7	—	—	8
26	107	55°40′	165°10′	—	4	10	7	—	21
27	116	55°40′	165°47′	—	—	6	4	—	10
29	44	57°40′	163°22′	—	1	—	—	—	1
June									
3	45	56°20′	161°00′	5	18	8	4	—	35
3	63	57°00′	160°57′	4	13	6	—	—	23
3	63	57°00′	159°43′	49	60	1	—	—	110
3	47	57°40′	159°38′	5	1	1	—	—	7
4	57	57°40′	160°53′	8	1	—	—	—	9
4	47	58°00′	160°51′	4	2	—	—	—	6
4	40	58°00′	162°07′	1	—	—	—	—	1
5	75	56°20′	162°12′	—	2	2	—	—	4
17	19	56°03′	160°58′	—	—	—	2	—	2
18	63	57°00′	160°57′	—	—	—	2	—	2
19	63	57°00′	159°43′	2	23	20	6	—	51
19	47	57°40′	159°38′	2	9	—	—	—	11
19	57	57°40′	160°53′	2	3	1	—	—	6
19	47	58°00′	160°51′	—	3	5	—	—	8
20	46	57°40′	162°08′	1	2	—	—	—	3
20	60	57°00′	162°10′	—	—	1	1	—	2
24	66	56°40′	160°59′	—	1	—	4	—	5
24	68	56°30′	160°59′	—	—	2	1	—	3
24	45	56°20′	161°00′	—	—	1	6	—	7
26	68	56°30′	160°59′	—	—	3	7	—	10
27	29	56°54′	159°08′	—	—	—	1	—	1
27	36	57°00′	159°07′	—	—	—	1	—	1
27	45	57°09′	159°05′	—	—	2	3	—	5
27	51	57°20′	159°04′	—	2	9	5	—	16
28	51	57°29′	159°03′	—	5	42	7	—	54
28	44	57°40′	159°01′	—	—	11	—	—	11
28	35	57°49′	159°00′	—	1	8	1	—	10
28	37	57°55′	158°59′	—	—	5	1	—	6
29	43	58°00′	158°58′	—	—	4	1	—	5
July									
1	45	58°10′	160°50′	—	—	—	1	—	1
1	47	58°00′	160°51′	—	—	3	2	—	5
2	63	57°00′	160°57′	—	—	—	4	—	4
4	25	57°31′	158°54′	—	—	—	1	—	1
4	29	57°41′	158°17′	—	—	—	—	1	1
4	35	57°47′	158°23′	—	—	—	1	—	1
7	22	58°33′	159°31′	—	—	—	—	1	1
7	23	58°29′	159°32′	—	—	—	—	3	3
7	28	58°14′	159°30′	—	—	—	1	—	1
8	35	57°55′	158°33′	—	—	—	4	—	4
8	36	57°44′	158°20′	—	—	—	6	—	6
9	51	57°20′	159°04′	—	—	1	4	—	5
9	45	56°20′	161°00′	—	—	—	—	1	1
13	63	57°00′	159°43′	—	—	—	4	—	4
14	47	57°40′	159°38′	—	—	2	29	—	31
14	57	57°40′	160°53′	—	—	—	1	—	1
1970									
March									
29	111	55°08′	165°12′	1	—	—	—	—	1

TABLE 1.—Continued.

Date	Depth (m)	Station location Lat. N	Station location Long. W	Larval stage: Zoea I	Zoea II	Zoea III	Zoea IV	Glaucothoe	Total
1970—Continued									
May									
9	60	55°00′	164°35′	399	20	2	—	—	421
13	73	56°40′	163°23′	1	—	—	—	—	1
13	75	56°20′	162°48′	1	3	—	—	—	4
14	47	55°40′	162°50′	16	9	—	—	—	25
14	76	56°00′	162°14′	26	2	—	—	—	28
14	75	56°20′	162°12′	2	—	—	—	—	2
15	65	56°40′	162°11′	1	—	—	—	—	1
15	65	57°00′	161°34′	1	—	—	—	—	1
16	65	57°20′	161°32′	2	—	—	—	—	2
16	55	57°20′	160°56′	1	—	—	—	—	1
16	58	57°20′	160°18′	11	2	—	—	—	13
16	63	57°00′	159°43′	1	—	—	—	—	1
17	35	56°40′	159°45′	9	1	—	—	—	10
17	58	56°40′	160°22′	9	—	—	—	—	9
17	58	57°00′	160°20′	12	1	—	—	—	13
17	63	57°00′	160°57′	7	—	—	—	—	7
18	66	56°40′	160°59′	14	2	—	—	—	16
18	86	56°40′	161°35′	20	1	—	—	—	21
18	61	56°20′	161°37′	40	10	2	—	—	52
19	45	56°20′	161°00′	163	106	—	—	—	269
19	25	56°20′	160°25′	5	3	—	—	—	8
22	73	56°10′	162°14′	11	4	—	—	—	15
22	52	56°06′	161°53′	4	1	—	—	—	5
22	70	56°26′	161°59′	16	7	—	—	—	23
23	71	56°40′	161°22′	3	1	—	—	—	4
23	60	56°26′	161°33′	35	17	—	—	—	52
24	22	57°07′	160°52′	1	—	—	—	—	1
24	47	56°19′	161°04′	9	2	—	—	—	11
24	70	56°31′	161°17′	36	22	—	—	—	58
24	83	56°43′	161°30′	3	1	—	—	—	4
24	64	56°55′	161°42′	6	2	—	—	—	8
24	51	57°07′	161°55′	4	—	—	—	—	4
25	36	58°02′	161°33′	1	—	—	—	—	1
25	22	58°13′	160°08′	1	—	—	—	—	1
26	45	57°41′	159°50′	2	1	—	—	—	3
26	45	57°29′	159°37′	3	1	—	—	—	4
26	51	57°17′	159°25′	2	1	—	—	—	3
26	47	57°06′	159°12′	5	12	—	—	—	17
26	21	56°54′	159°00′	—	2	—	—	—	2
28	89	55°52′	163°17′	1	—	—	—	—	1
28	59	55°39′	163°04′	1	—	—	—	—	1
29	111	55°33′	165°36′	—	1	1	—	—	2
29	111	55°21′	165°24′	—	12	4	—	—	16
29	111	55°08′	165°12′	—	2	1	—	—	3
29	91	54°56′	164°59′	—	13	1	—	—	14
29	43	54°43′	164°47′	2	5	2	—	—	9
June									
8	111	55°08′	165°12′	1	36	36	1	—	74
15	48	56°19′	161°00′	1	7	15	5	—	28
21	49	56°22′	161°00′	—	4	3	—	—	7
21	42	56°17′	161°00′	—	4	2	4	—	10
25	27	56°09′	161°00′	—	—	5	11	—	16
25	21	56°07′	160°52′	—	—	2	8	—	10
26	47	56°19′	161°04′	—	1	—	1	—	2
26	70	56°31′	161°17′	—	2	—	—	—	2
26	83	56°43′	161°30′	—	—	2	—	—	2
26	64	56°55′	161°42′	—	2	1	—	—	3
26	51	57°07′	161°55′	1	—	—	—	—	1
27	47	57°06′	159°12′	—	—	15	18	—	33
27	51	57°17′	159°25′	—	2	38	16	—	56
27	45	57°29′	159°37′	—	3	23	7	—	33
27	45	57°41′	159°50′	—	4	34	4	—	42
27	42	57°54′	159°42′	—	—	15	9	—	24
27	22	57°59′	157°55′	—	—	—	1	—	1
27	33	58°04′	158°25′	—	—	—	1	—	1
28	22	58°13′	160°08′	—	—	—	2	—	2
28	41	58°38′	162°16′	—	—	—	1	—	1
29	40	58°22′	163°24′	—	1	—	—	—	1
30	59	55°39′	163°04′	—	—	1	1	—	2
30	28	55°27′	162°52′	—	—	—	1	—	1
July									
1	111	55°33′	165°36′	—	—	—	—	1	1

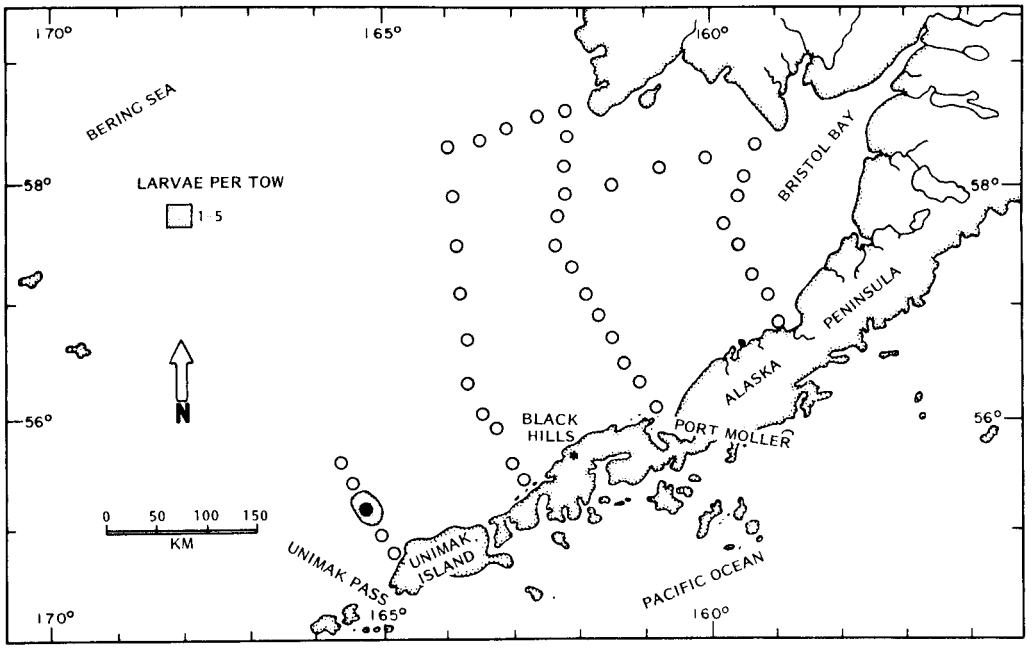

FIGURE 1.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 29 March-30 April 1969 and 1970. Solid circle indicates larvae were present at station.

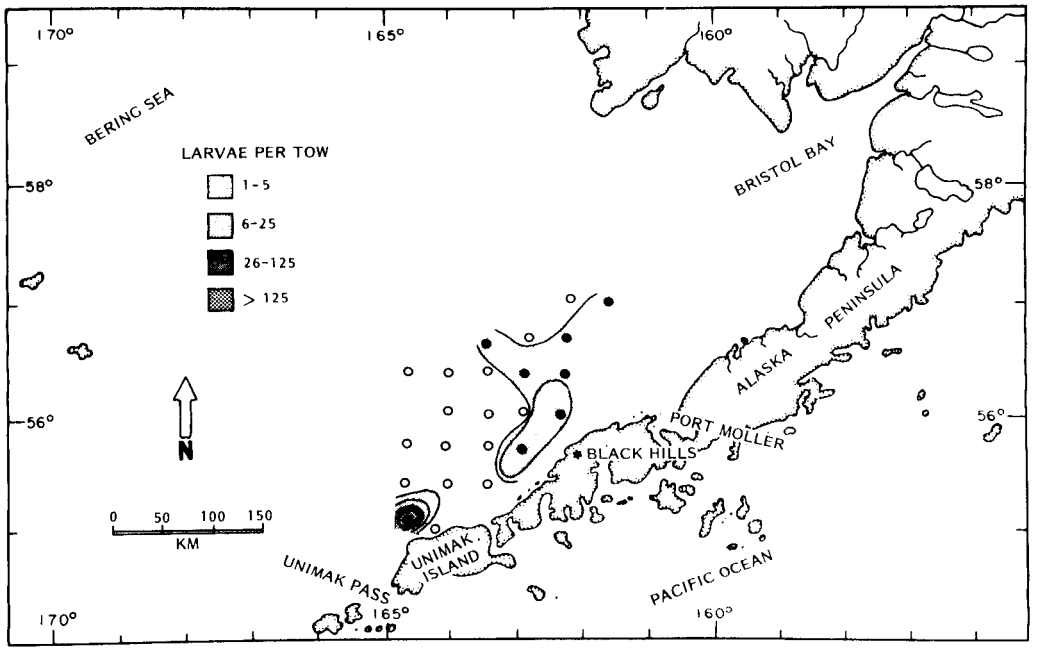

FIGURE 2.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 1-15 May 1969 and 1970. Solid circles indicate larvae were present at station.

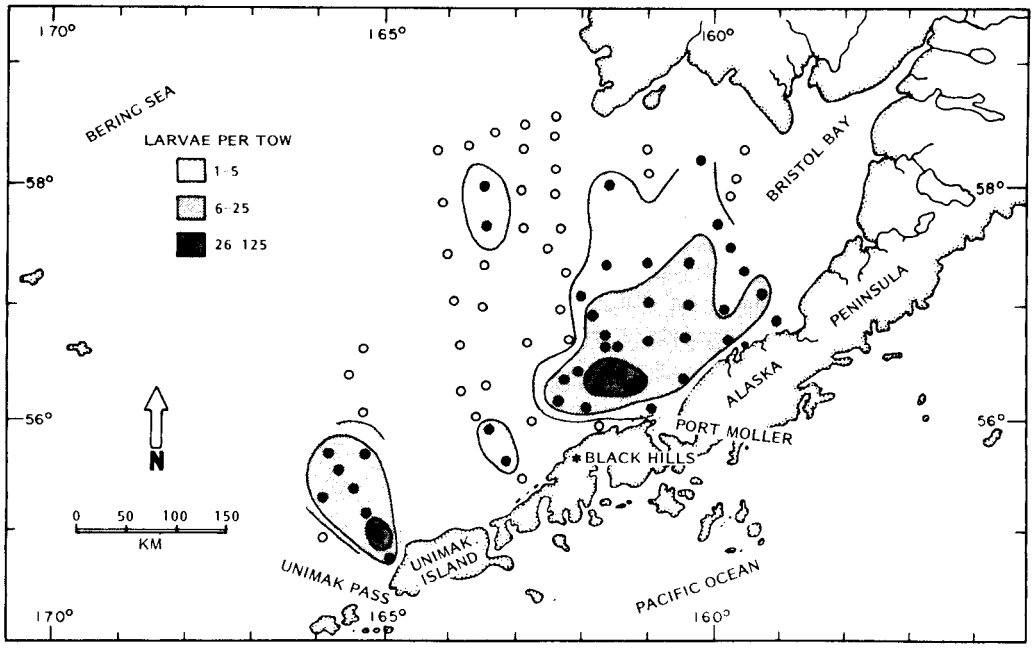

FIGURE 3.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 16-31 May 1969 and 1970. Solid circles indicate larvae were present at station.

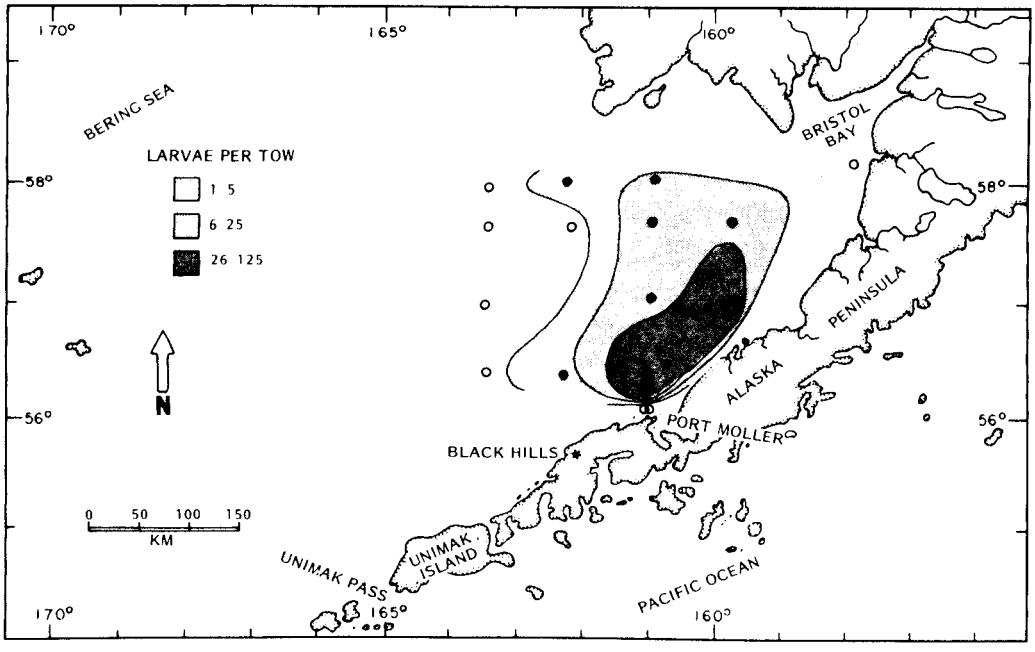

FIGURE 4.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 1-15 June 1969 and 1970. Solid circles indicate larvae were present at station.

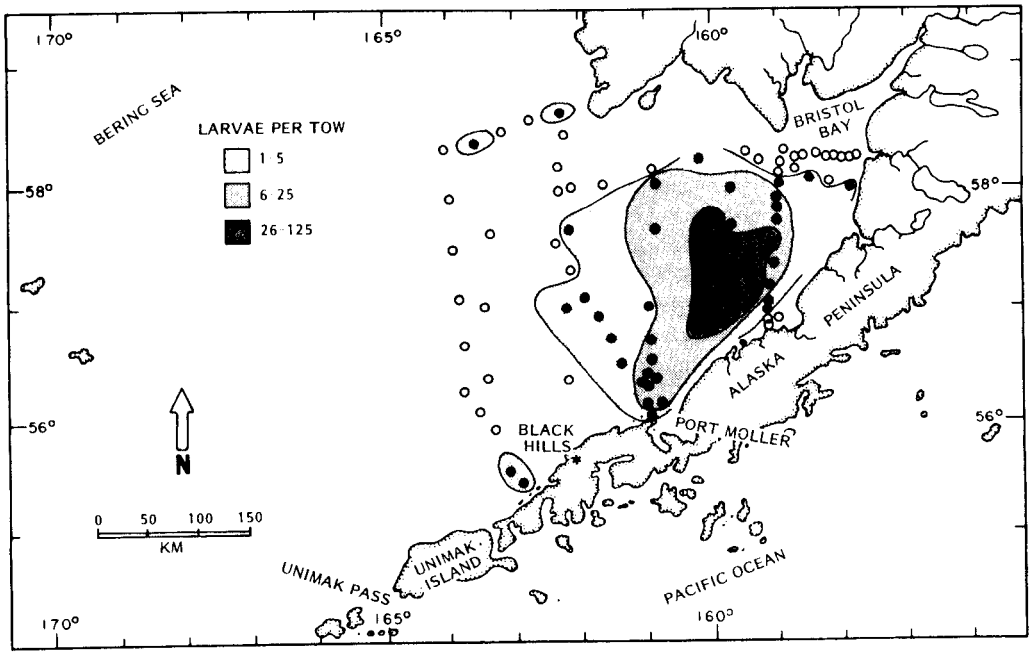

FIGURE 5.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 16-30 June 1969 and 1970. Solid circles indicate larvae were present at station.

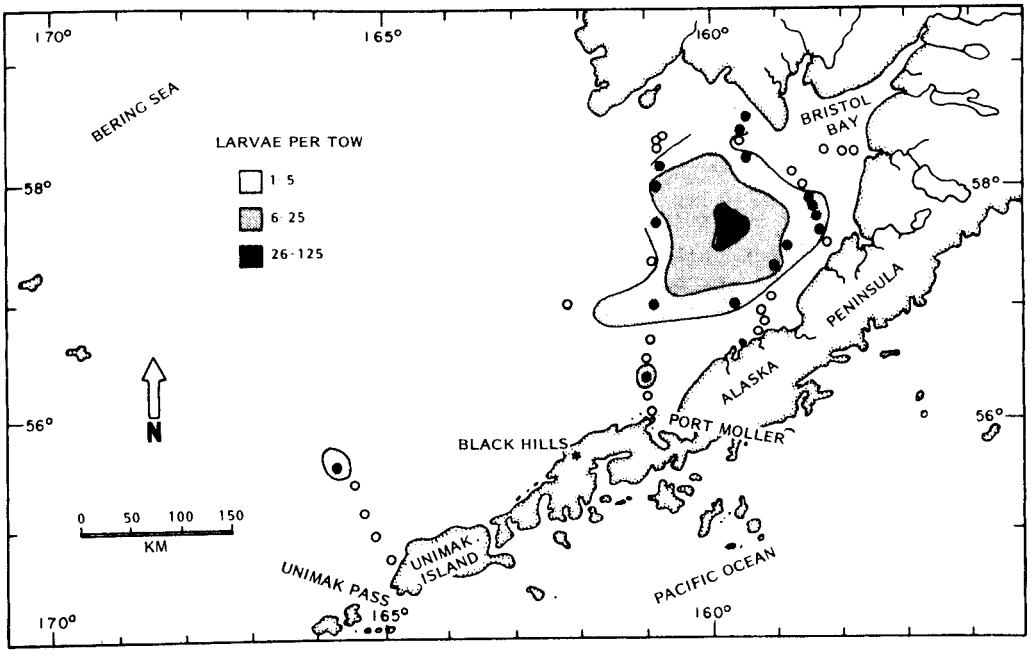

FIGURE 6.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 1-15 July 1969 and 1970. Solid circles indicate larvae were present at station.

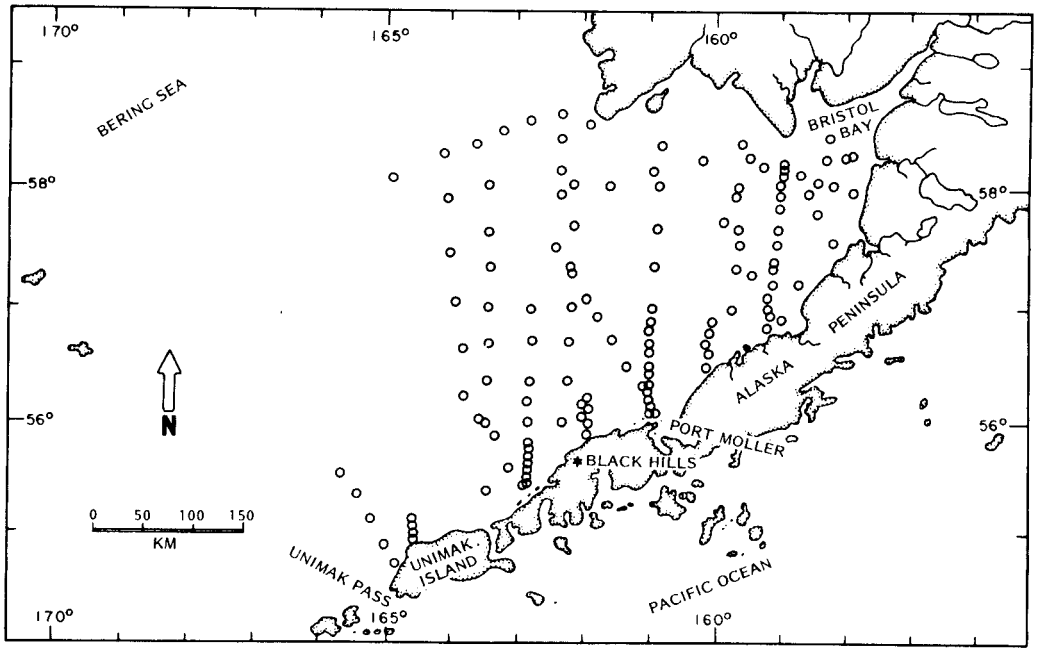

FIGURE 7.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 16 July-21 September 1969 and 1970.

DISTRIBUTION AND RELATIVE ABUNDANCE

Although sampling locations and dates were different each year, I determined that I could combine the data for both years for consideration of distribution and abundance. For each semimonthly period, I tabulated the degree squares (the areas bordered by 1° of latitude and longitude) that were sampled in both years. This resulted in 14 degree squares, 7 each for the latter half of May and June. For each of the two semimonthly periods, the median catch per tow was computed and the degree squares were ranked "good" or "poor" on the basis of whether their catch per tow was greater or lesser than the median. In this manner it was possible to compare degree squares without considering the actual abundance of larvae. The degree square data indicated that in every instance except one the same degree squares for each year were consistently good or poor.

I assumed therefore that the distributions were not random and that the data for the two sampling years could be combined for analyzing larval distribution.

The combined data on distribution of larvae in 1969 and 1970 are presented by time periods (usually semimonthly) between 29 March and 21 September (Figures 1 to 7). Most of the larvae were in the southern and eastern portions of the study area and within these areas were most abundant close to shore. The largest catches (more than 1,000 larvae under 10 m² of sea surface) were made near Unimak Pass and Port Moller; the smallest (usually fewer than 10 larvae under 10 m² of sea surface) were generally made in the more central and western parts of the area.

The distribution and abundance of larvae in the Black Hills-Port Moller area increased gradually toward the head of Bristol Bay. During the first half of May (Figure 2), larvae were found off the Black Hills area; 2 wk later (Figure 3), these larvae apparently had been carried northeastward along the coast and became mixed with larvae released off the Port Moller area. As the season continued, the center of abundance shifted farther toward the head of the bay (Figures 4 and 5). This trend continued until mid-July (Figure 6), when no more larvae were taken (Figure 7).

The seasonal progression of occurrence of larvae off Unimak Island is less clear. A small concentration of larvae was found in this area in early May (Figure 2); 2 wk later they were most abundant to

the northwest toward the open sea (Figure 3). Too few samples were taken in the Unimak Island area after May to determine the extent of the drift of larvae.

The four zoeal stages that king crab larvae pass through before molting to the glaucothoe (settling) stage were all represented in my samples (Table 1). The percentage of larvae in each zoeal stage is shown by semimonthly intervals in Figure 8. A comparison of this figure with Figures 1 to 7 shows that the progression of larval stages corresponded closely with the seasonal progression of larval distribution. For instance, the abundant larvae found early in the season off Unimak Island and Port Moller were mostly stage I. As the areas of greatest abundance moved toward the head of the bay, the percentage of later larval stages in the samples increased, and by July most of the larvae were stage IV (Figure 8).

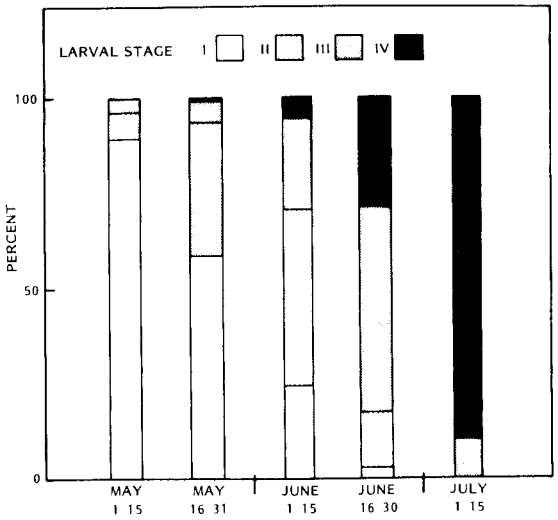

FIGURE 8.—Percentages of four zoeal stages of king crab larvae sampled at stations in the southeastern Bering Sea, 1969 and 1970. Data for 1969 and 1970 combined by semimonthly periods (see Figures 3 to 7).

LARVAL RELEASE AREAS

Areas of relatively high abundance of stage I larvae are generally assumed to be the areas where the larvae were released by the female. This proved to be true in the present study: stage I larvae were abundant near Unimak Island and the Black Hills-Port Moller area where female king crabs with empty egg cases were also abundant (Figure 9). (The egg cases remain attached to the pleopods of the female for some time after the larvae have been released.) The

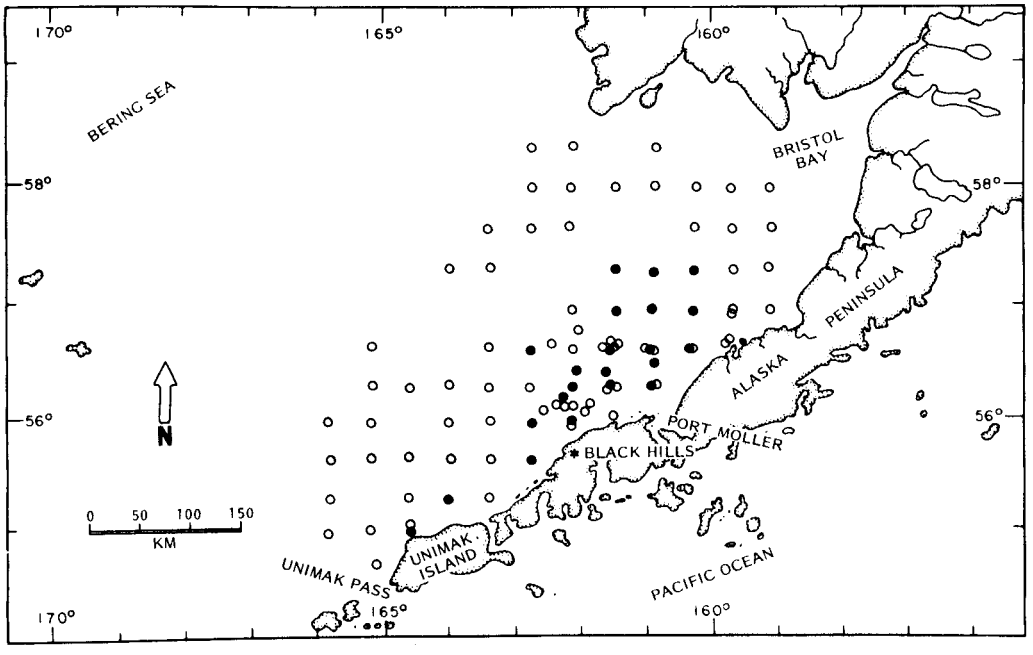

FIGURE 9.—Trawling stations (circles) in the southeastern Bering Sea where female king crabs were taken in May 1969 and 1970. Stations with crabs with empty egg cases are designated by solid circles.

distribution of egg-bearing king crabs with empty egg cases shown in Figure 9 was determined from trawling in May 1969 and 1970 (data combined). Weber (1967) also reported that in Bristol Bay, king crabs usually release their larvae in May.

RELATION BETWEEN DISTRIBUTION OF LARVAE AND CURRENT PATTERNS

My observations of the dispersal of stage I larvae from the release areas generally agree with the known patterns of water currents in the study area. Hebard (1959) found that in the southeastern Bering Sea water moved counterclockwise toward Bristol Bay along the Alaska Peninsula and away from Bristol Bay in the more northern parts of the southeastern Bering Sea. Under these conditions larvae released in the Black Hills-Port Moller area would be carried northeastward along the Alaska Peninsula toward the head of Bristol Bay. The seasonal shift of larvae shown in Figures 1 to 7 corresponds closely with this pattern of water movement.

Because of differences in water currents, the direction of seasonal shift of larvae is different in the Unimak Island area than it is to the east. Oceanographic studies in this area, summarized by Dodimead, Favorite, and Hirano (1963), show that water from the Gulf of Alaska flows northward through the interisland passages of the Aleutian Islands in the southeastern Bering Sea. Such a flow pattern through Unimak Pass is consistent with the apparent northward movement of king crab larvae from the Unimak Island area (Figure 3).

On the basis of his findings on water currents in the southeastern Bering Sea, Hebard (1959) postulated that recruitment of king crab larvae into the Bering Sea may occur through the island passages of the Aleutian Islands, especially Unimak Pass. If this is so, then the possibility exists that the stock of king crabs in Bristol Bay is derived to some extent from larvae released south of the Alaska Peninsula. Unfortunately, plankton was not collected south of Unimak Pass during the present study, and the question of recruitment of king crab larvae into Bristol Bay from areas south of the Alaska Peninsula must await a more detailed investigation.

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OCCURRENCE OF SILVER HAKE, *MERLUCCIUS BILINEARIS*, EGGS AND LARVAE ALONG THE MIDDLE ATLANTIC CONTINENTAL SHELF DURING 1966

MICHAEL P. FAHAY[1]

ABSTRACT

During an ichthyoplankton survey over the continental shelf between Martha's Vineyard, Mass. and Cape Lookout, N.C., from December 1965 to December 1966, 3,241 eggs and 11,032 larvae of the silver hake, *Merluccius bilinearis*, were collected. Eggs were collected from May until November, with a peak in June. Most of the eggs (77%) were collected south of Martha's Vineyard, Mass. The southernmost occurrence of eggs was off North Carolina in November. Larvae were collected from May until December, with a peak in September. Larvae were most abundant on the shelf between Hudson Canyon and Martha's Vineyard. The evidence suggests that most of the eggs and larvae collected on the survey had been spawned near the northeastern edge of the survey area and drifted southwesterly. There is also evidence of a size-related, diel, vertical migration by the postlarvae.

In December 1965, the Sandy Hook Marine Laboratory began a 1-yr ichthyoplankton survey of the continental shelf between Martha's Vineyard, Mass. and Cape Lookout, N.C. The survey was designed to delimit the spawning times and locations of marine game fishes, define dispersal patterns of larvae, and form the first phase in a study to determine what species depend on an estuarine environment during some phase of their early life history. We placed emphasis on no one species and began the survey with no preconceived notions on either the geographical extent or the seasonality of spawning of any species. This report on the eggs and larvae of silver hake, *Merluccius bilinearis* (Mitchill), represents one of a series resulting from that survey.

The silver hake is an important sport and commercial species widely distributed over the continental shelf of eastern North America from the Gulf of St. Lawrence (McKenzie and Scott, 1956) southward to South Carolina, with centers of abundance between Nova Scotia and New York (Bigelow and Schroeder, 1953). Silver hake are found in both shoal and deep water within a wide temperature range, usually over bottoms of sand or sand-silt mixtures (Fritz, 1965). When winter cooling occurs on the shelf, silver hake migrate to warmer waters on the continental edge and slope.

Silver hake in the western North Atlantic consist of two morphologically separable and nonmingling populations (Conover, Fritz, and Vieira, 1961) roughly separated by the 41°30′N meridian (Nichy, 1969). Hence, the Gulf of Maine and northern edge of Georges Bank contain one population, while the southern slopes of Georges Bank and continental shelf south and west of Cape Cod contain the other. This report concerns the eggs and larvae produced by the latter population.

Spawning in the Gulf of Maine extends from June to October, with a peak in July and August (Bigelow and Schroeder, 1953). Kuntz and Radcliffe (1917) described the embryological and larval development of silver hake and suggested that "the spawning period for this species is a protracted one and not all the eggs mature at one time." Sauskan and Serebryakov (1968), in a study of the gonads of silver hake from Georges Bank and the Nova Scotian shelf, showed: 1) larger females mature and spawn earlier than smaller ones; 2) vitellogenesis is asynchronous, and individual fish spawn in three portions within a season; 3) the initial spawning of an individual female accounts for half the total seasonal production of oocytes.

Silver hake eggs and larvae have been collected from Halifax, Nova Scotia to Cape May, N.J. (Bigelow and Schroeder, 1953). Eggs and larvae

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have been reported in local plankton collections as follows: off Nova Scotia (Dannevig, 1919); over Georges Bank (Marak and Colton, 1961); in Block Island Sound (Merriman and Sclar, 1952). Sauskan and Serebryakov (1968) discussed the distribution of silver hake eggs and larvae but limited their sampling and discussion to areas east of our 1966 sampling area.

MATERIALS AND METHODS

We conducted eight cruises aboard the RV *Dolphin* from December 1965 to December 1966. On each cruise, we sampled 92 stations arranged on 14 transects between Martha's Vineyard, Mass. and Cape Lookout, N.C. (Figure 1). The station arrangement allowed us to sample from nearshore to the 183-m (100-fathom) contour along each transect. We scheduled cruises to occur at 6-wk intervals, and the average cruise occupied 17 days. We sampled four transects from Martha's Vineyard to New Jersey on a supplemental cruise in September 1966. Dates and sampling sequences and locations of collecting stations listed to the nearest 0.8 km (0.5 nautical mile) are contained in Clark et al. (1969).

We used loran, radar and, where possible, visible ranges to position the *Dolphin* on station. Routine work on station involved the use of a bathythermograph to obtain temperature profiles, a stem thermometer to measure surface temperatures, and a Beckman[2] RS-5 portable salinometer to obtain salinities and temperatures from the surface to the maximum plankton sampling depth. In water deeper than the length of the salinometer cable, we used Frautschy water bottles and measured the salinities of these samples with a hydrometer kit. Temperature and salinity profiles resulting from the survey are found in Clark et al. (1969).

We chose the Gulf V high-speed plankton sampler (Arnold, 1959) to overcome many of the problems inherent in sampling ichthyoplankton. It samples at 5 knots, thus allowing capture of organisms capable of avoiding slower nets. Its large mouth opening provides large quantities of eggs and larvae per tow and, hence, samples with high reliability for comparative purposes. Flow-through characterisitcs of the net prevent extensive damage to larvae. Finally, the Gulf V is ruggedly built and requires a minimum of shipboard maintenance. Our sampler (Figure 2) consists of a conical net of 0.33-mm (0.013-inch) Monel wire with 12 meshes/cm (30 meshes/inch) and an

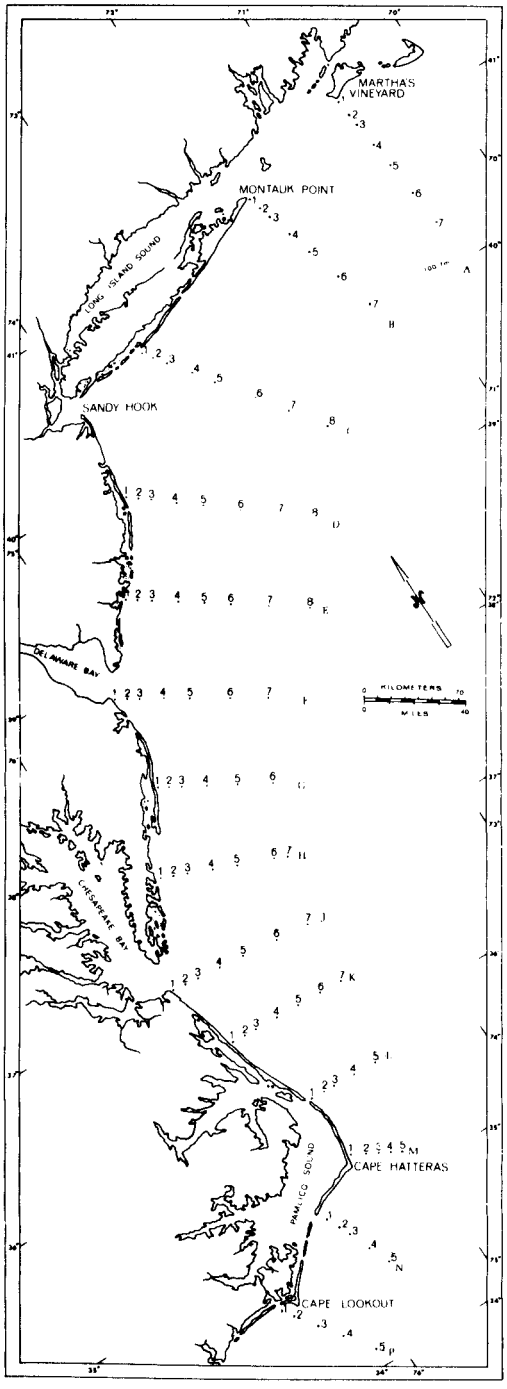

FIGURE 1.—RV *Dolphin* survey, December 1965 to December 1966. Location of transects and collecting stations.

[2]Reference to trade names does not imply endoresement by the National Marine Fisheries Service, NOAA.

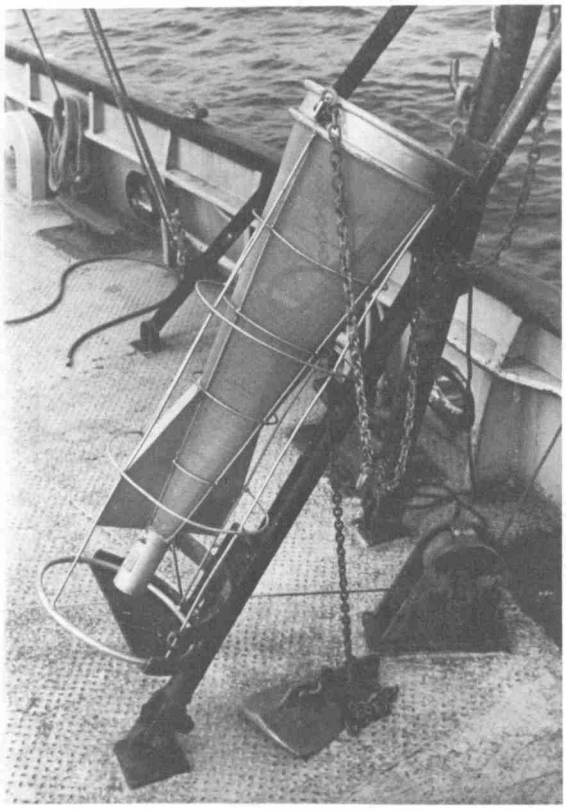

FIGURE 2.—Gulf V high-speed plankton sampler with depressor.

aperture size of 0.52 mm (0.02 inch). Other dimensions are as described by Arnold (1959).

Our method of towing two samplers consecutively was described in detail in Clark et al. (1969), Richards and Kendall (1973), and Smith (1973). Figure 3 illustrates schematically our towing methods over various depths of water. As illustrated in Figure 3, the step-oblique method sometimes resulted in unequal sampling intensity at certain depths under a unit of surface area. Therefore, to diagram the horizontal distribution on maps, I combined the catch of the two nets and adjusted them as shown in Table 1.

The catches of the two nets presented separately provide added useful information. This is especially true in view of 1) observed differences in numbers and length-frequencies between the catches of the two nets, and 2) the presence of a thermocline within the stratum sampled by the deep net. In Appendix Table 1, I tabulated the catch of the deep net as observed. However, the deep net was not equipped with a closing device and was subject to contamination in the upper 15 m during setting out and hauling back procedures. Therefore, for study of vertical distribution, I adjusted the deep net catch after assuming that it sampled the upper zone for 3 min.

Tows are labeled "D" (day), "N" (night), or "C" (crepuscular, i.e. within 1 h of sunrise or sunset) in Appendix Table 1.

After each tow, we washed the samplers down, removed the cups, and preserved the samples in buffered 5% Formalin. The samples were returned to the laboratory where all ichthyoplankton was removed and larvae divided into family groups. Gadids and merlucciids were then identified to species. Eggs were initially grouped according to their diameters. Early silver hake eggs are indistinguishable from the eggs of many other species of marine fishes. Common characteristics include: outside diameter of about 1.0 mm, presence of a single oil globule, narrow perivitelline space, and 4:1 ratio of egg diameter to oil globule diameter. Consequently, specific identifications were limited to eggs in advanced stages of development. I based identifications of late stage *M. bilinearis* eggs on published descriptions (Kuntz and Radcliffe, 1917; Sauskan and Serebryakov, 1968) and on my own rearing experiments with artifically fertilized eggs. The purpose of my experiment was to determine whether pigment was present on the yolk. It was terminated before hatching occurred. Prolarval offshore hake, *M. albidus*, were identified following the descriptions by Marak (1967) and removed from the *M. bilinearis*

TABLE 1.—Method used to combine the catches of shallow and deep samplers.

Shallow net		Deep net		
Number of steps	Minutes per step	Number of steps	Minutes per step	Total station catch formula
2	15	0	0	⅓ shallow
3	10	0	0	½ shallow
6	5	0	0	Total shallow
6	5	2	15	Total shallow + ⅓ deep
6	5	3	10	Total shallow + ½ deep
6	5	6	5	Total shallow + total deep

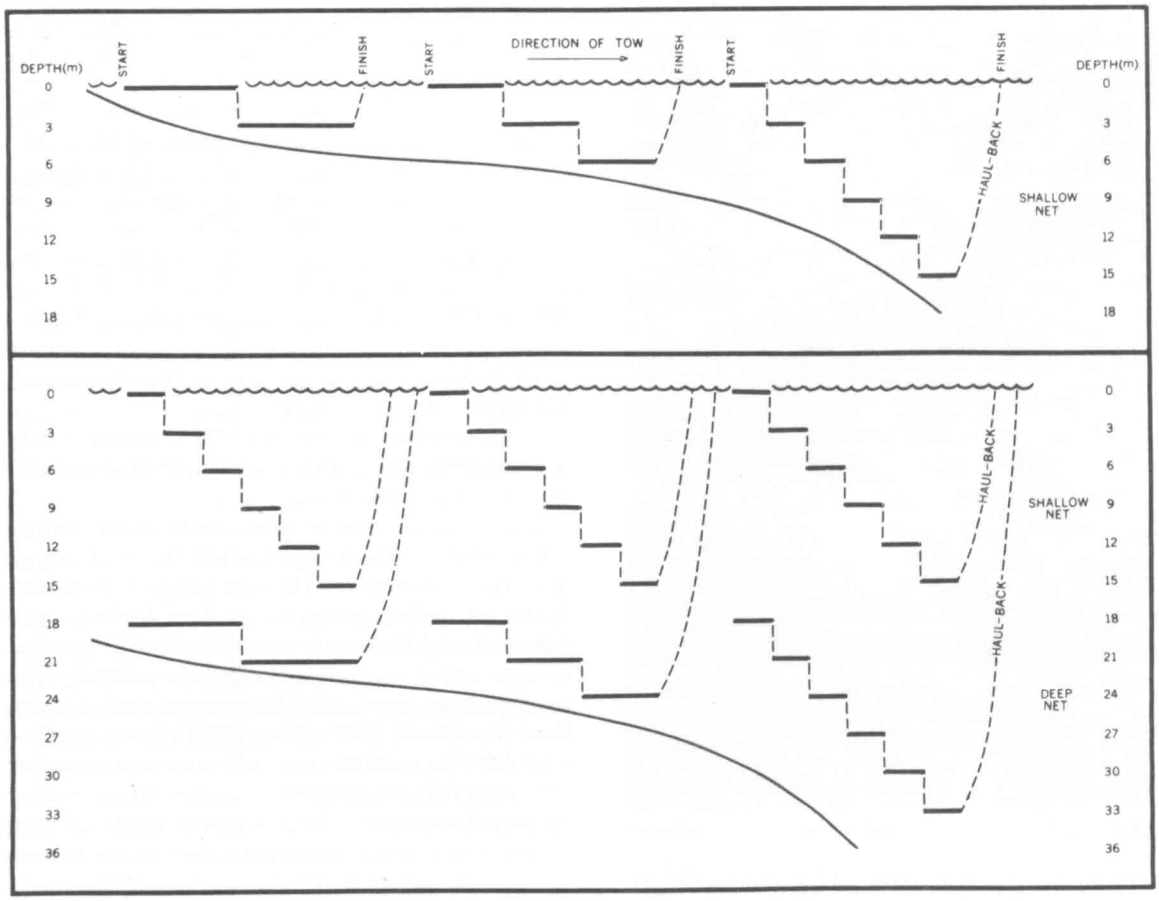

FIGURE 3.—Six sampling methods for ½-h plankton tows over different water depths.

collection. I also removed several postlarvae recognized as *Merluccius* sp. but which I presume are *M. albidus*, the postlarvae of which are undescribed.

We measured all specimens, except mutilated ones, from the tip of the snout to the tip of the notochord or urostyle with an ocular micrometer or point-to-point dial calipers. Measurements are expressed as millimeters notochord length (mm NL) and recorded to the nearest 0.1 mm. Because preservation resulted in shrinkage of specimens, the recorded size of some larvae is smaller than the reported hatching length of 2.8 mm (Kuntz and Radcliffe, 1917).

RESULTS

Egg and larval distributions are shown in Appendix Table 1 and Figures 4 through 8. A map is not shown for the one egg and one larva caught off the Virginia coast on May 20 and 22, respectively.

Distribution of Eggs

Eggs identified as silver hake for this report are in stages III and IV of development, when the embryo encompasses at least 75% of the yolk and the tail tip is separated from the yolk surface. Fine pigment is present on the part of the yolk surface lying under the snout of the embryo. This is not shown by Kuntz and Radcliffe (1917).

We collected 3,241 silver hake eggs from May through November 1966, with a peak in June. The temporal distribution of eggs changed geographically. Spawning began earlier in the northeastern end of our survey area and progressively later to the south. Table 2 demonstrates this trend for four transect groups. According to Sauskan and Serebryakov (1968), about half the total seasonal

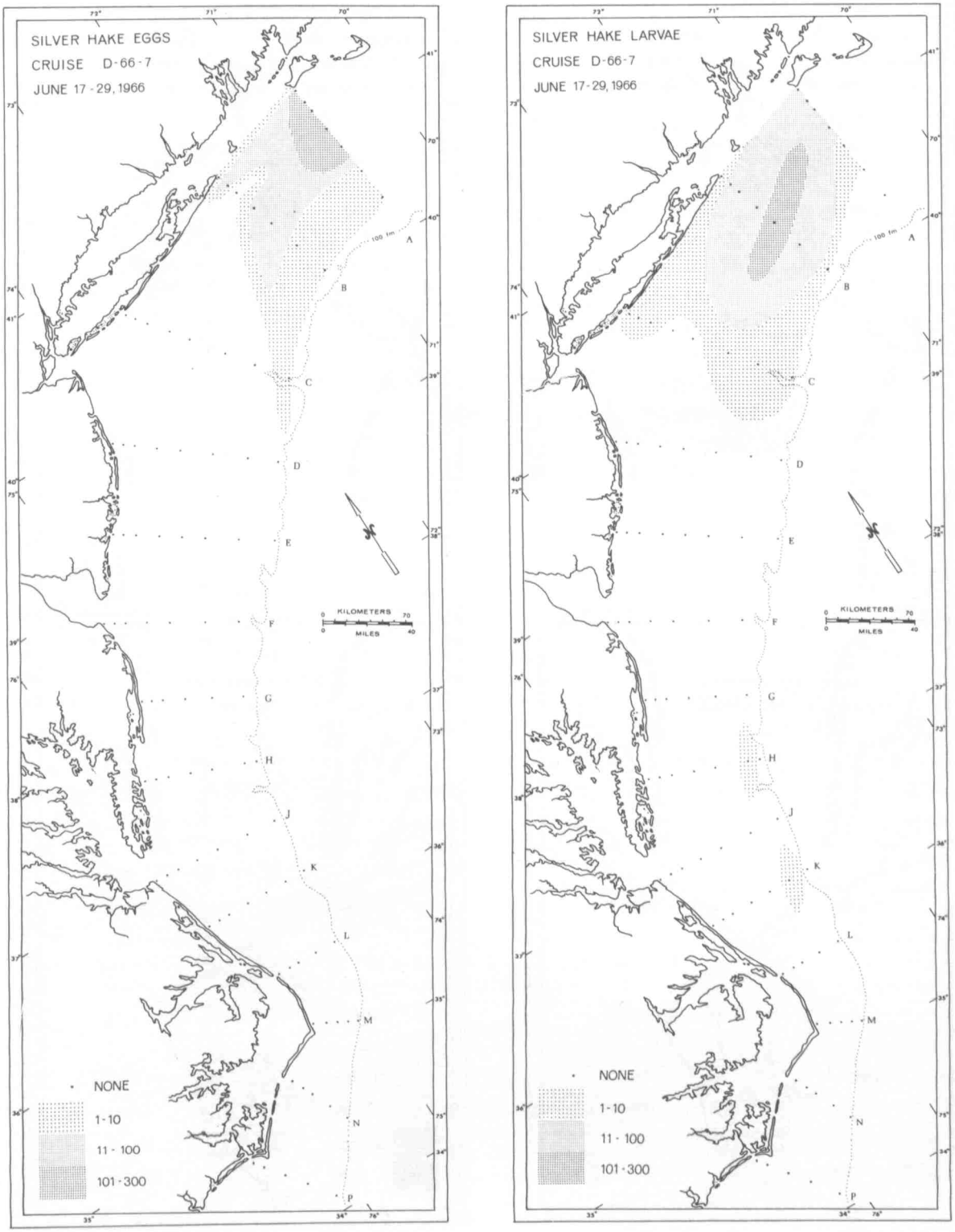

FIGURE 4.—Occurrence of silver hake eggs and larvae, June 1966.

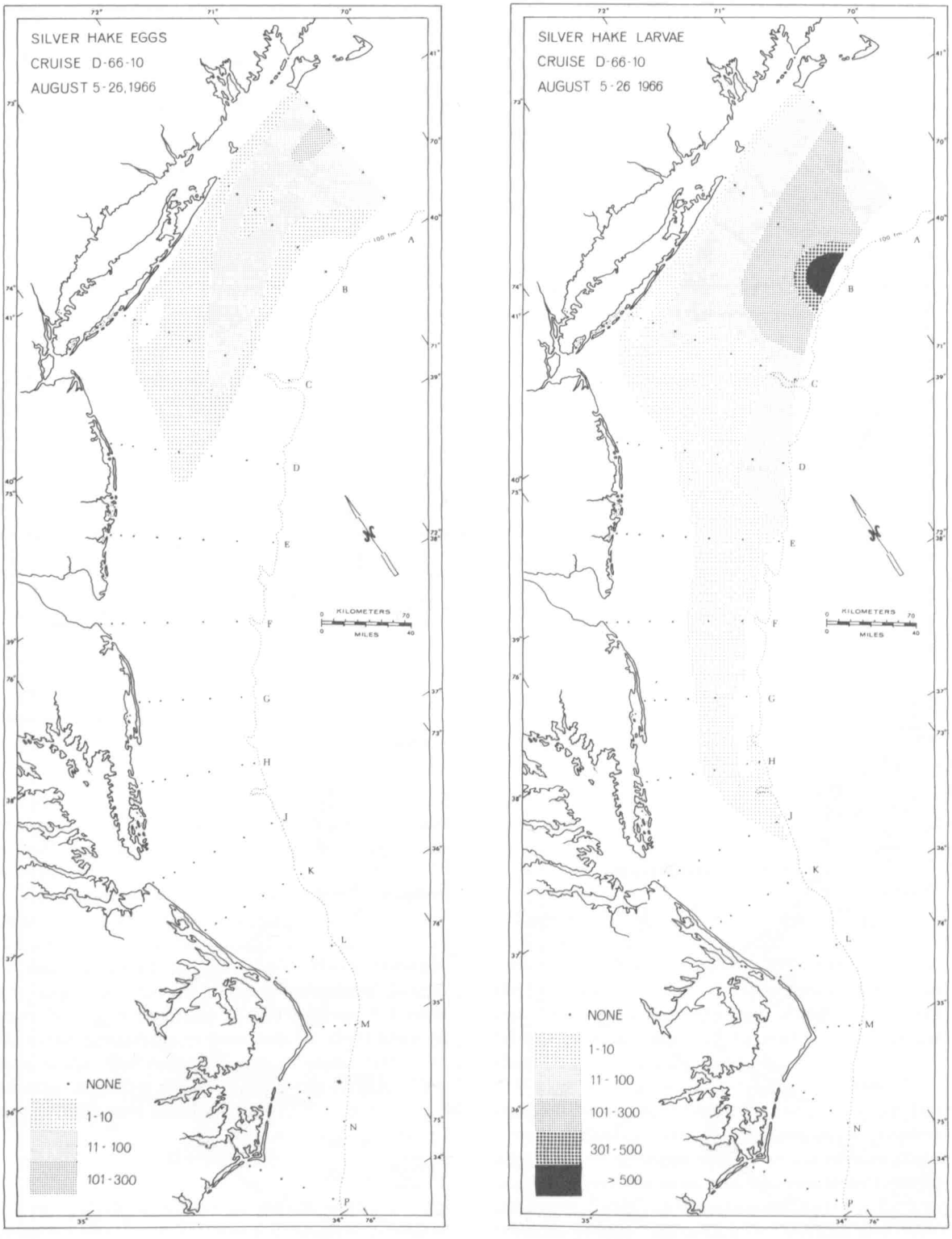

FIGURE 5.—Occurrence of silver hake eggs and larvae, August 1966.

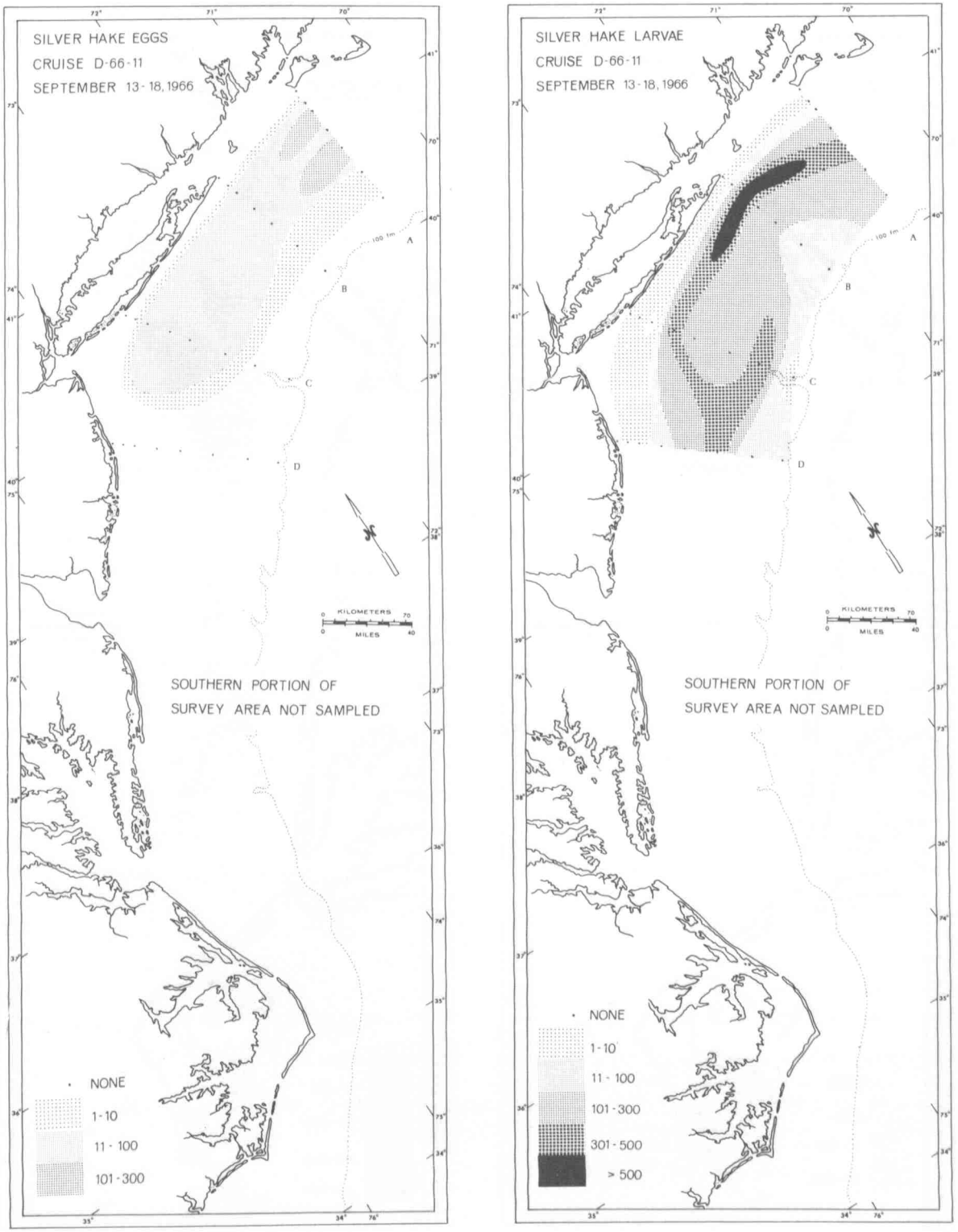

FIGURE 6.—Occurrence of silver hake eggs and larvae, September 1966.

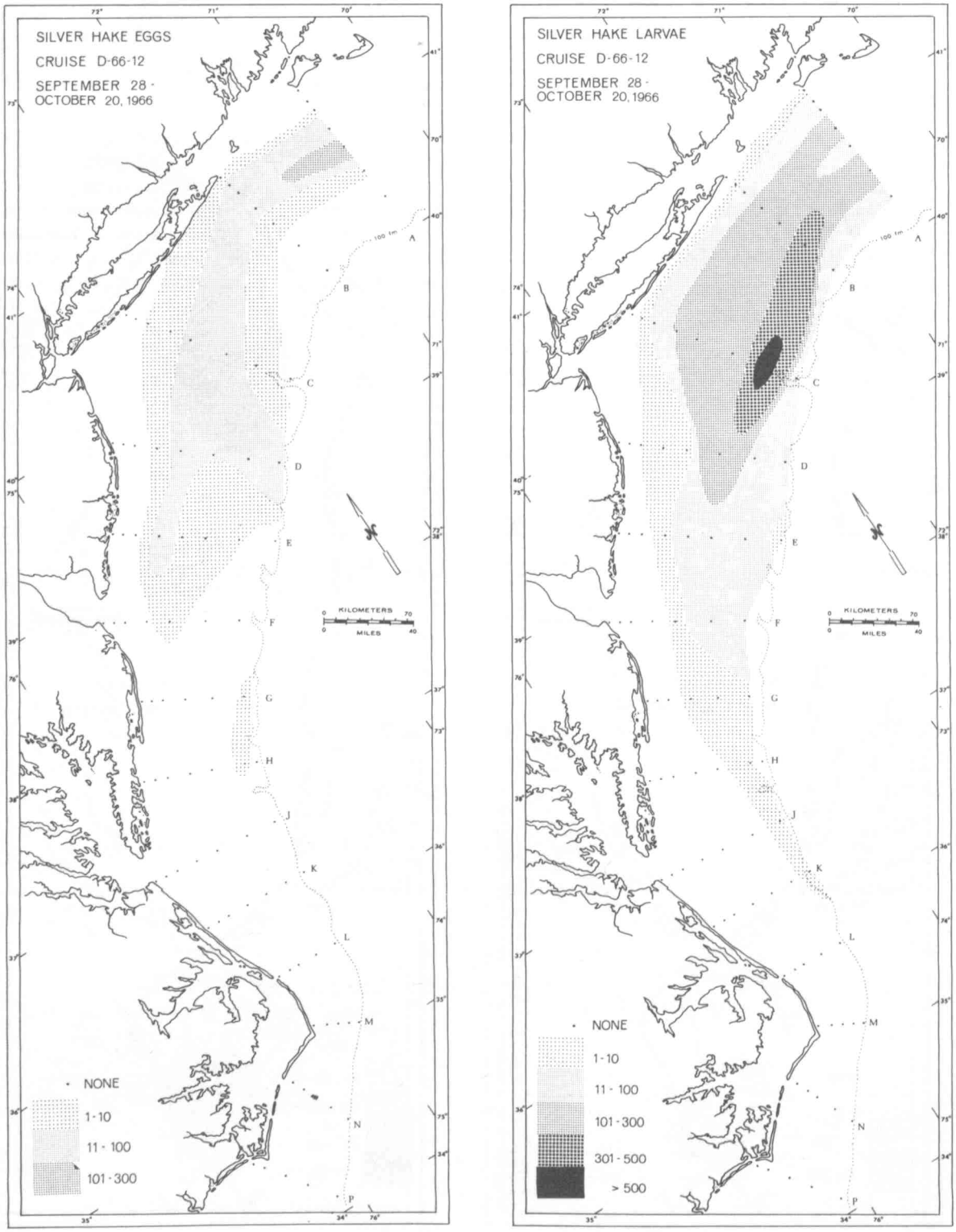

FIGURE 7.—Occurrence of silver hake eggs and larvae, September-October 1966.

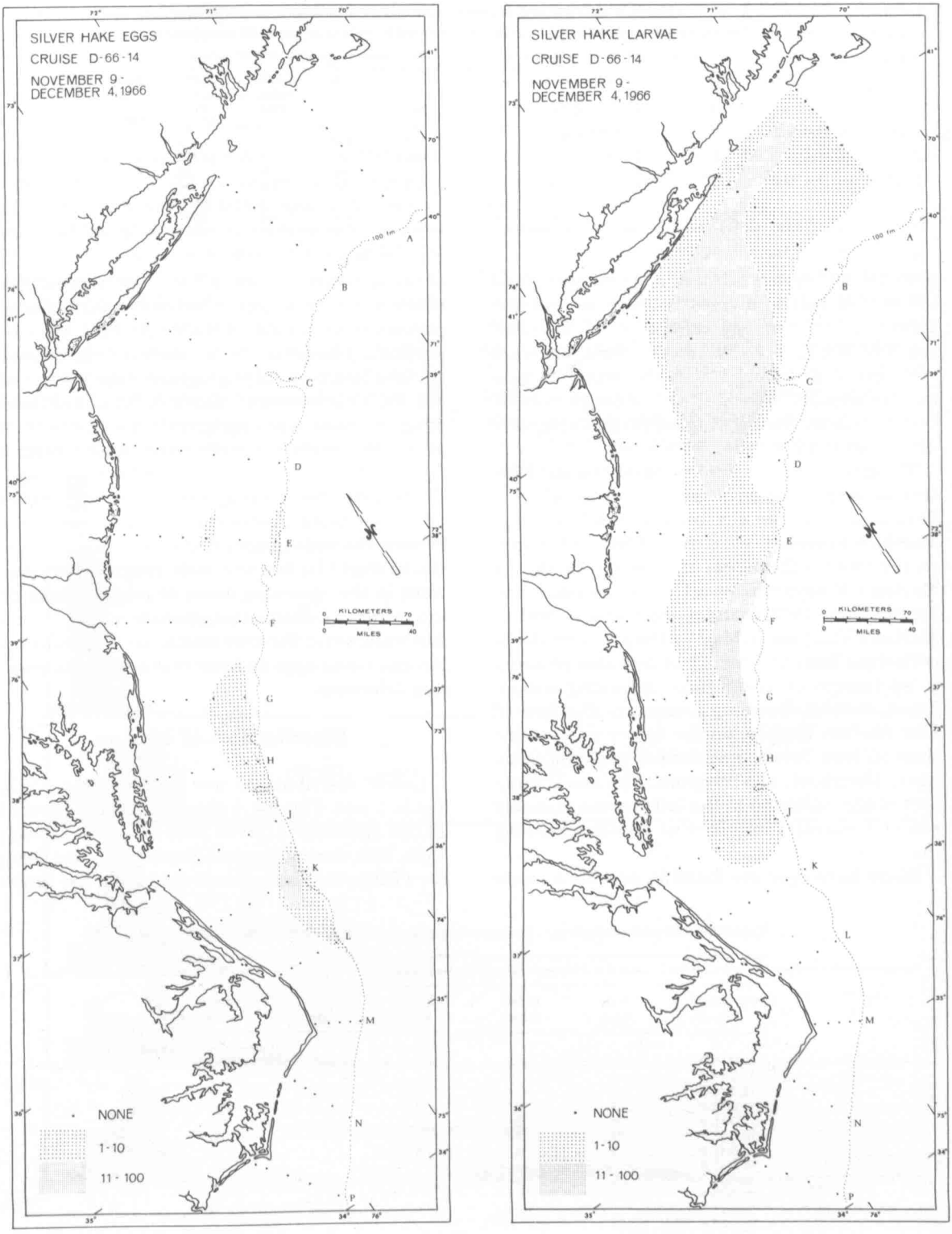

FIGURE 8.—Occurrence of silver hake eggs and larvae, November-December 1966.

TABLE 2.—Monthly distributions of silver hake eggs arranged by transect-groups. Monthly peak abundance for each group indicated by bold type. ns = not sampled.

Transect groups	Numbers of eggs collected						
	May	June	Aug.	Sept.	Oct.	Nov.-Dec.	Total
AB	0	**1,362**	415	617	454	0	2,848
C	0	5	26	**108**	48	0	187
DEF	0	0	6	0	**141**	9	156
GHJKL	1	1	0	ns	3	**45**	50
Total	1	1,368	447	725	646	54	3,241

production of eggs is released in a first batch, and the second half is divided between second and third batches. Our egg collections on the shelf south of Montauk Point and Martha's Vineyard (transects A and B in Table 2) are consistent with their conclusion. We collected 1,362 eggs in June, the remainder during August (415), September (617), and October (454).

The silver hake eggs collected during our 1966 cruises originated principally over Nantucket Shoals and on the continental shelf south of Martha's Vineyard. We collected 88% of the eggs on the two northernmost transects, 77% on the Martha's Vineyard transect alone. Sauskan and Serebryakov (1968) found concentrations south of Martha's Vineyard in May, on the southern slopes of Georges Bank in June. Thus, this area probably is an important silver hake spawning center. Small, distinct spawning groups are also located near Hudson Canyon, on the deeper parts of the shelf off New Jersey, and further south off Delaware, Maryland, and Virginia. The small numbers of eggs collected in the latter areas probably reflect the small numbers of adults occurring there.

Silver hake eggs are found in as wide a range of temperatures as the adults. The relation between numbers of eggs collected and surface temperatures is shown in Table 3. This may be misleading however, for we observed egg concentrations in a particular geographic area (south of Martha's Vineyard and Montauk Point) and these concentrations were apparently independent of prevailing surface temperatures which ranged from 13.5° to 21.7°C. It is not known how near the bottom silver hake spawn, nor in what range of temperatures. Assuming they spawn near the bottom, the wide temperature range of egg occurrences might be due to a wide range of temperatures in the spawning areas or might simply be the result of extreme temperature ranges in surface waters over the spawning areas, in which case the ascending eggs demonstrate a wide temperature tolerance.

Distribution of Larvae

Larval distributions are shown in Appendix Table 1 and Figures 4 through 8. We collected 11,032 silver hake larvae from May to December 1966, 91% during August, September, and October (Table 4). We captured no postlarvae larger

TABLE 3.—Abundance of silver hake eggs relative to observed surface temperatures.

Surface temperature (°C)	Number of tows which collected:				Total number of tows
	1-10 eggs	11-100 eggs	101-200 eggs	200+ eggs	
10.0-10.9	1				1
11.0-11.9	1				1
13.0-13.9	5			1	6
14.0-14.9	16	6	3	3	28
15.0-15.9	14	6	1		21
16.0-16.9	13	2			15
17.0-17.9	9	3	3		15
18.0-18.9	3	4	1		8
19.0-19.9	4	4			8
20.0-20.9	6	5			11
21.0-21.9	7	2			9
22.0-22.9	1				1
Total tows	80	32	8	4	124

TABLE 4.—Numbers of silver hake larvae collected during six cruises in 1966.

May	June	Aug.	Sept.	Oct.	Nov.-Dec.	Total
2	585	2,989	3,875	3,175	406	11,032

than 18.0 mm NL until the August cruise (Figure 9). Since the spawning season probably began in early June, and since 18.0 mm approximates the size at which silver hake postlarvae begin to live near the bottom, the length of pelagic life is apparently about 2 mo.

Within our 1966 sampling area, larvae were most densely concentrated between Nantucket Shoals and Hudson Canyon. Progressing southward, we found larvae increasingly restricted to the offshore part of the shelf. Distribution varied according to the size of larvae. Generally, we found smaller larvae inshore and near the surface, and larger larvae offshore and deeper. Smaller larvae were also more numerous in the northeastern part of the survey area than the southwestern. Tables 5 through 7 illustrate this trend for the August, September, and October cruises. These differences in distribution by size are partly a result of a southwesterly drift during growth, partly a preference by larger larvae for deeper water.

Silver hake larvae in 1966 were distributed in areas where surface temperatures ranged from 8.6° to 25.8°C. Since silver hake larvae are not necessarily surface-dwelling animals, the mean observed temperatures within the depths sampled by the two Gulf V nets may be more significant. Table 8 shows the number of tows containing larvae (arranged by volume of catch) relative to these temperatures. The total number of tows, regardless of the presence of silver hake, is in-

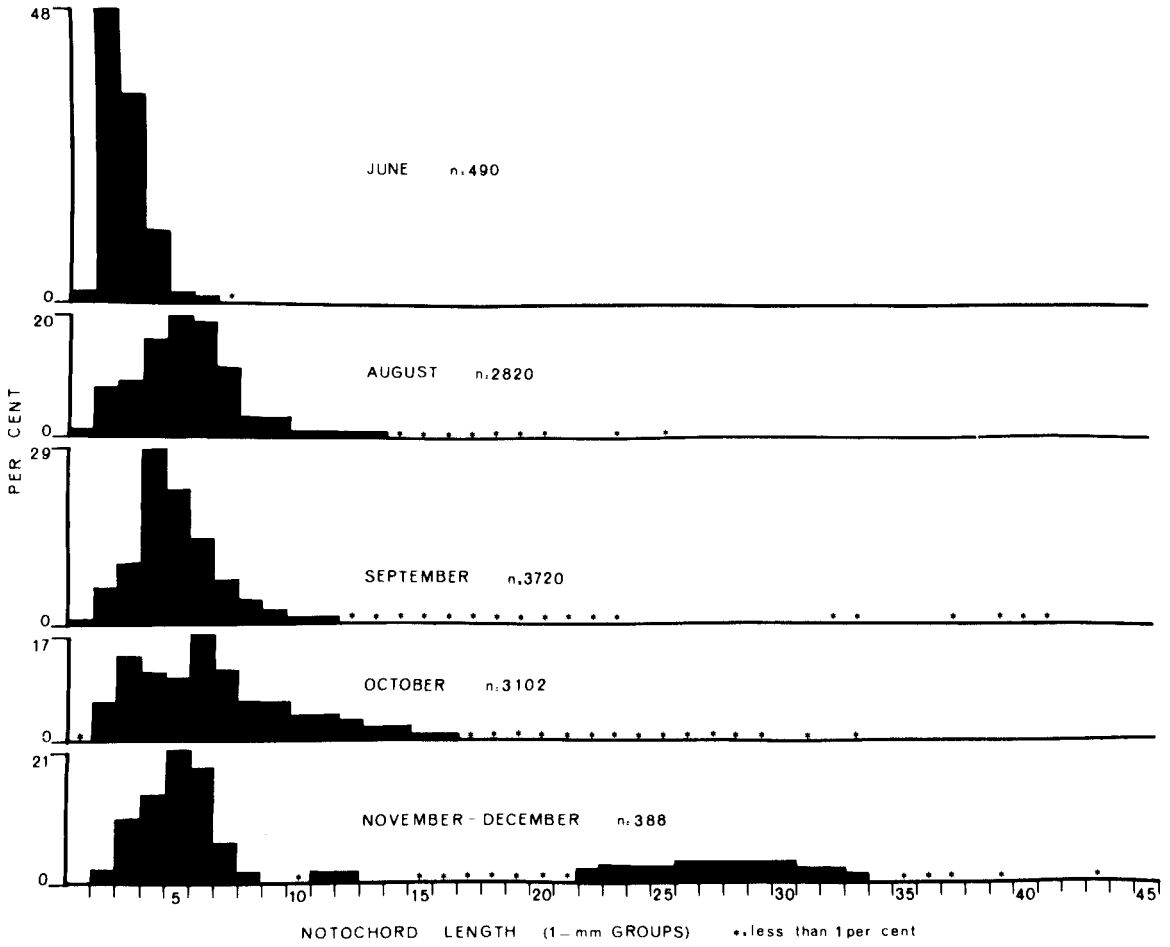

FIGURE 9.—Length-frequency distributions of silver hake larvae during five cruises, 1966.

TABLE 5.—Mean lengths (mm NL) of silver hake larvae collected during *Dolphin* cruise D-66-10 (August 1966), arranged by transect, net 1 (0-15 m) or net 2 (18-33 m), and station.

Transect	Net	Station 1	2	3	4	5	6	7	8	Mean length	*N*
A	1	3.2	2.8	4.0	3.1	5.0	4.0	3.6		3.8	598
	2			5.8	5.1	5.3	5.8	4.2		5.6	658
B	1	2.6	3.8	2.0	3.9	4.1	5.4	6.6		5.4	413
	2		3.6	3.3	5.5	6.2	6.8	8.5		7.8	1,037
C	1	2.1		3.2	3.6		3.2		4.9	3.5	54
	2				4.7	3.5		5.3	5.4	5.3	98
D	1					3.8	5.8	6.0	3.6	5.6	33
	2					3.2		12.2	10.2	10.3	71
E	1						5.3	3.3		4.0	3
	2						6.0	5.5		5.7	8
F	1						6.0	7.5		7.3	8
	2						7.0			7.0	2
G	1					3.6				3.6	1
	2										
H	1					14.8				14.8	1
	2					14.5		15.1		15.0	3
J	1										
	2							5.7		5.7	1
Mean length		3.0	3.2	4.2	3.6	5.1	5.6	7.9	7.4	6.1	
N		18	67	82	357	472	853	987	153		2,989

TABLE 6.—Mean lengths (mm NL) of silver hake larvae collected during *Dolphin* cruise D-66-11 (September, 1966), arranged by transect, net 1 (0-15 m) or net 2 (18-33 m), and station.

Transect	Net	Station 1	2	3	4	5	6	7	8	Mean length	*N*
A	1		3.0	3.6	4.2	4.5	5.8	5.0		4.7	478
	2		3.0	3.9	3.8	4.8	5.9	5.2		4.9	529
B	1	2.7	2.8	4.2	3.5	5.6	7.0	11.6		4.8	79
	2			5.6	4.9	4.1	6.6	12.0		5.7	921
C	1	3.0	2.7		4.4	3.0		12.3	8.2	7.2	29
	2				4.2	6.9	5.6	8.5	9.7	6.4	1,011
D	1		3.6	2.8	3.4	3.8	6.0	8.8		4.5	62
	2				2.8	4.9	5.5	7.0	9.1	5.8	620
Mean length		2.8	2.9	5.4	4.3	5.0	5.7	7.9	9.1	5.6	
N		14	22	615	730	799	840	650	59		3,729

cluded in the table to demonstrate the possibility that the temperature relationship is simply an artifact created by our cruise schedule. The probability of collecting these temperature-tolerant larvae at any temperature increases as sampling at that temperature increases.

Our maximum sampling depth was below the thermocline on all stations where we captured larval silver hake. Larvae apparently were more concentrated near the thermocline than near the surface during the summer months. Table 9 compares the percentage of the total catch contributed by the deep net (which sampled near the thermocline) during each cruise with observed surface temperatures and indicates that during August and September, when surface temperatures were highest, silver hake larvae were distributed more deeply where temperatures were lower.

Our cruise schedule and sampling sequence resulted in many consecutive stations being sampled during the same light regime. Thus, opportunities for comparing the diel differences in the captures of silver hake larvae are limited.

TABLE 7.—Mean lengths (mm NL) of silver hake larvae collected during *Dolphin* cruise D-66-12 (October, 1966), arranged by transect, net 1 (0-15 m) or net 2 (18-33 m), and station.

Transect	Net	Station 1	2	3	4	5	6	7	8	Mean length	*N*
A	1	3.4	4.2	4.7	3.5	3.1	5.5	9.9		3.8	143
	2		4.1	4.9	3.5	3.0	4.7	13.5		4.7	554
B	1		2.8	3.3	5.8	9.6	10.2	11.2		9.7	77
	2		5.5	4.4	6.4	7.5	10.8	9.6		8.7	699
C	1		8.7	7.1	5.8	5.0	7.6	13.5	19.8	8.3	157
	2			5.6	6.7	6.0	7.8	9.9	12.8	8.6	825
D	1	2.7		7.1		6.2	6.2	4.2	2.9	5.6	172
	2				15.0	6.1	6.9	5.6	4.5	6.3	212
E	1				2.8	6.4	6.6	8.0	3.5	6.4	67
	2					5.1	8.5	10.0	3.0	8.7	87
F	1					5.6	6.5	4.7		6.3	70
	2					3.7	7.0	6.3		6.4	27
G	1				5.4					5.4	1
	2					4.6	7.4			5.5	3
H	1										
	2						15.0			15.0	1
J	1										
	2							22.5		22.5	1
K	1							11.0		11.0	1
	2										
Mean length		3.2	4.5	5.1	4.8	6.2	7.7	9.6	4.8	7.3	
N		3	53	84	560	536	1,001	816	44		3,097

TABLE 8.—Abundance of silver hake larvae relative to mean temperature within the sampling depths of individual Gulf V nets.

Temperature (°C) within samplers' depth range	Number of tows which collected: 1-10 larvae	11-100 larvae	101-300 larvae	301-500 larvae	500+ larvae	Number of tows: Containing silver hake	Total
6.0-6.9	5	2				7	9
7.0-7.9	3					3	12
8.0-8.9	4	2		1		7	18
9.0-9.9	17	2				19	34
10.0-10.9	9	8	2			19	32
11.0-11.9	5	5				10	17
12.0-12.9	4	6	3	2		15	22
13.0-13.9	14	7	3	1		25	48
14.0-14.9	22	14	8		2	46	75
15.0-15.9	8	8	2	1		19	38
16.0-16.9	12	6	1			19	36
17.0-17.9	12	5	2			19	44
18.0-18.9	4	6				10	33
19.0-19.9	1	5	4			10	39
20.0-20.9	8	3	1			12	23
21.0-21.9	6	1	1			8	25
22.0-22.9	6					6	29
23.0-23.9	1					1	14
24.0-24.9	1					1	20
25.0-25.9						0	11
26.0-26.9						0	6
Total tows	142	80	27	5	2	256	

Although day and night tows were equally productive (Table 10), differences exist when larval size is considered. Most of the smallest larvae were taken during the day, while most larger larvae and postlarvae were taken from dusk to dawn (Figure 10).

There are several possible explanations for the higher incidence of larger larvae and postlarvae

TABLE 9.—Contribution of deep net to total catch of larvae on stations where both nets were used, compared to weighted mean surface temperature.

Cruise	Month	Percent caught in deep net	Weighted mean surface temperature (°C)	Total number caught in both nets
D-66- 5	May	0	14.4	1
D-66- 7	June	34	14.5	408
D-66-10	Aug.	62	20.6	2,940
D-66-11	Sept.	82	19.9	3,836
D-66-12	Oct.	78	15.5	3,164
D-66-14	Nov.-Dec.	52	11.7	398

TABLE 10.—Diel differences in captures of silver hake larvae, cruises D-66-7 (June) through D-66-14 (November-December).

Light regime	Number of tows		Number of larvae	Weighted mean length (mm NL)	Average catch	
	Total	Containing silver hake			Total tows	Tows containing silver hake
Dawn	62	21	810	5.4	13.1	38.6
Day	265	112	4,741	5.3	17.9	42.3
Dusk	48	18	1,255	5.7	26.1	69.7
Night	240	104	4,226	7.8	17.6	40.6

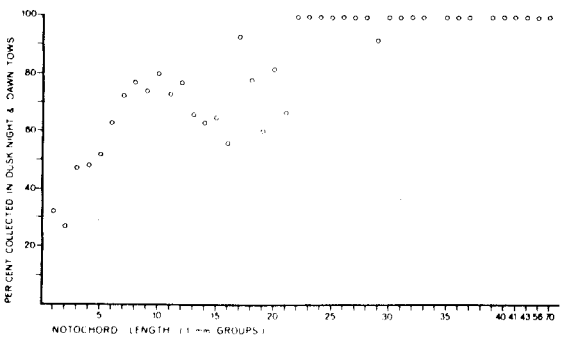

FIGURE 10.—Percentage of silver hake larvae collected in non-day tows per 1-mm size groups.

in night tows, the most generally accepted being that larvae avoid the approaching sampler during daylight in response to visual warning. The difference cannot be attributed to vibration of the towing cable or inefficient filtration by the sampler because these factors are equal during all light regimes. Undersampling of larger larvae of other species during daylight has been well documented (Silliman, 1943; Bridger, 1956; Ahlstrom, 1959; Colton, 1965). These authors, however, noted diel differences resulting from tows made at 1 knot. Miller, Colton, and Marak (1963) towed a high-speed plankton sampler at 7 knots and found no significant differences in the day and night catches of haddock larvae and pelagic juveniles. Ryland (1963) concluded that a towing speed of 5 knots (257.4 cm/s) was sufficient to prevent net avoidance by plaice larvae up to 20.0 mm whose maximum "darting velocity" he found to be 20 cm/s. If, by towing at 5 knots, we were able to overcome net avoidance by larger larvae, then the presence of larger larvae in night tows only must reflect some form of diel activity or vertical migration. Kelly and Barker (1961) found a significant difference in depth distribution with growth of young redfish, the larger juveniles occurring in deeper layers. A similar difference plus a diel change in depth distribution is observed with silver hake when the light regime, capture depth (net 1 vs. net 2), and mean larval length are combined (Figure 11). The largest larvae were captured in the deep net during the night, the smallest larvae in the shallow net during the day. In both nets, night tows contained larger larvae than day tows, and in both light regimes the deep net contained larger larvae than the shallow net. Evidently, with growth, silver hake larvae seek deeper water, perhaps in response to increasing negative phototropism, perhaps simply approximating the adult habitat.

During the summer of 1970, we made two cruises to investigate the size at which silver hake larvae first occur on or near bottom. On 12 stations northeast and southwest of Hudson Canyon, we made reciprocal tows with Gulf V samplers and an otter trawl (39-foot headrope) fitted with a ¼-inch mesh cover bag and separate cod end. Length frequencies of the Gulf V catches, compared with those of the otter trawl (Figure 12), indicate that silver hake first become available to bottom

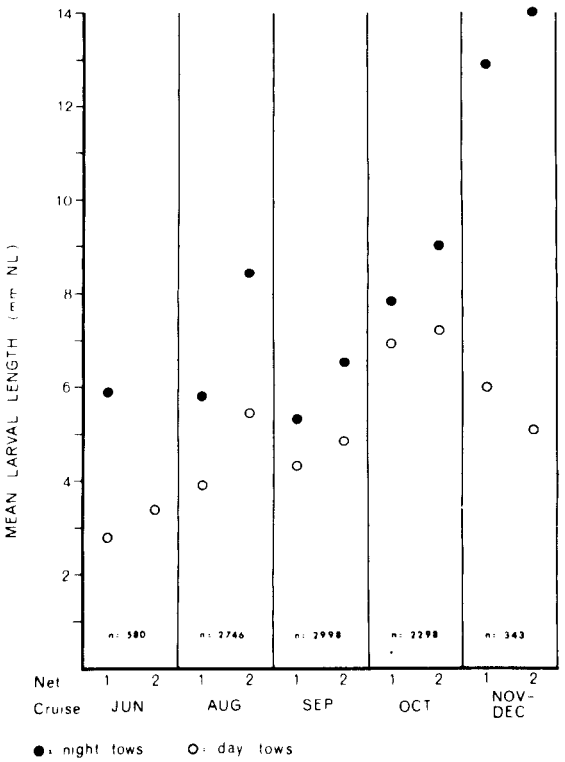

FIGURE 11.—Comparisons of silver hake mean larval size, light condition, and depth of capture. Net 1 sampled to a maximum of 15 m; net 2 to a maximum of 33 m.

sampling gear at about 17.0 to 20.0 mm NL. This figure is somewhat smaller than that indicated by Nichy (1969), whose smallest specimens taken by otter trawl were about 50 mm.

During 1966, all postlarvae larger than 21.0 mm NL (except one) were captured at night, and most of those were taken in the deep net, which sampled above, within, and below the thermocline, if one was present. Postlarvae larger than 21.0 mm NL were taken in the shallow net only when the thermocline was weak or nonexistent. All this suggests that silver hake postlarvae seek the bottom at about 17.0 to 20.0 mm NL and migrate vertically at night, ascending at least to the thermocline depth or, in the absence of a thermocline, to levels nearer the surface.

DISCUSSION

The area encompassing the southern slope of Georges Bank, Great South Channel, Nantucket Shoals, and the shelf south of Martha's Vineyard is evidently an important spawning center for silver hake. Unfortunately, neither the *Dolphin* survey nor the Soviet surveys (Sauskan and Serebryakov, 1968) sampled this area extensively enough to determine all the possible drift patterns of eggs and larvae. The 70°40′W meridian approximates the eastern limit of the *Dolphin* survey and the western limit of the sampling reported by Sauskan and Serebryakov.

Within this wide area, eggs should be expected to drift in several different directions, depending on the location of spawning and on long-term prevailing winds. One component of the westerly current on the shelf south of Martha's Vineyard and Nantucket Island originates on the southern slope of Georges Bank where it forms the southern part of a rotational eddy (Bigelow, 1927; Klimenkov and Pakhorukov, 1963; Bumpus and Chase, 1965; Bumpus and Lauzier, 1965; Harrison et al., 1967). Eggs spawned on Georges Bank may 1) drift with the eddy, develop, and recruit back to Georges Bank, or 2) drift west and south of Martha's Vineyard where we consistently found concentrations. Walford (1938) described similar patterns for haddock larvae spawned on Georges Bank. A third possibility may result in the loss of the brood. Colton (1959) reported that silver hake larvae spawned on Georges Bank were killed when a southerly drift carried them off the bank and into warm slope water (the rate of warming exceeding the larvae's rate of acclimation). Presumably, in addition to the perils of warming waters, silver hake larvae carried off Georges Bank into the slope water or Gulf Stream would be carried to the east and, unable to find suitable depths in which to begin the demersal stage, would perish.

Eggs spawned south of Martha's Vineyard drift west but probably not far before hatching, for the incubation period is only 48 h (Kuntz and Radcliffe, 1917). Unfortunately, these authors did not cite the temperature at which incubation or hatching occurred. If we assume (as did Sauskan and Serebryakov, 1968) that Kuntz and Radcliffe incubated their eggs at a maximum temperature of 20°C, then the maximum incubation period in degree-hours would be 960 ($48 \times 20 = 960$). We encountered the heaviest concentrations of eggs on the Martha's Vineyard transect when surface temperatures ranged from 13° to 22°C. Even at the minimum temperature of 13°C, incubation would occupy no more than 73.8 h ($960/13 = 73.8$). Currents between Georges Bank and Delaware

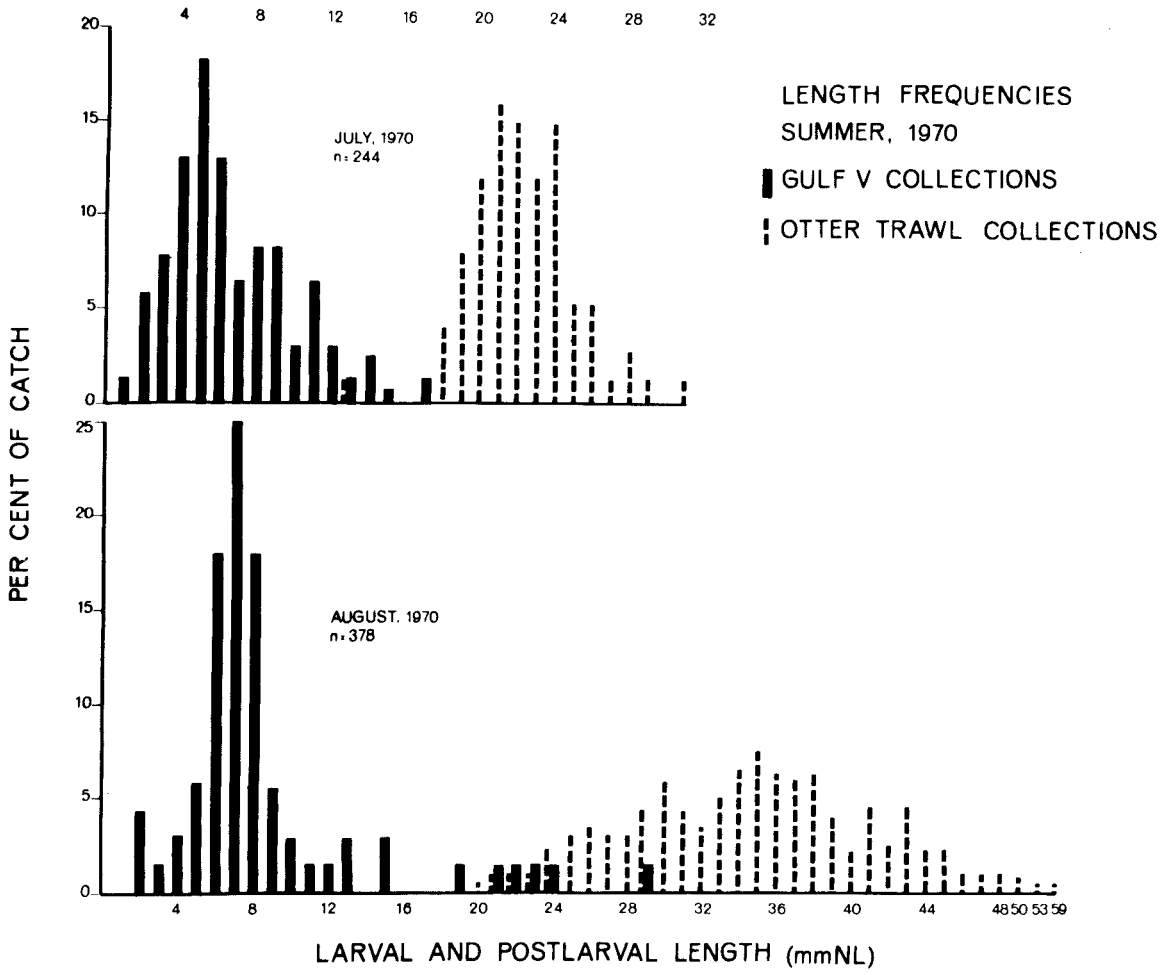

FIGURE 12.—Comparison of length frequencies of silver hake larvae and post-larvae captured in Gulf V plankton samplers near surface and otter trawl on bottom during summer cruises, 1970.

Bay flow west to southwest at average speeds of 0.93 km/h over the shelf between Nantucket Shoals and New Jersey (U.S. Navy Hydrographic Office, 1965) to 1.04 km/h over the southeast slope of Georges Bank (Sauskan and Serebryakov, 1968). Thus, the maximum distance an egg would drift from spawning to hatching is 76.8 km ($1.04 \times 73.8 = 76.8$) in the area of greatest egg abundance which we observed. This is substantiated by the fact that the center of abundance of the prolarvae is only slightly further to the southwest than that of the eggs. Also contributing to the short drift of eggs and prolarvae is the sluggish, meandering nature of currents on the shelf south of New England. During the summer of 1971, while studying vertical distribution of silver hake larvae on the shelf south of Montauk Point, we deployed a free-drifting staff buoy and sampled around it for 48 h. The course of the buoy (Figure 13) demonstrates the capriciousness of surface currents in the area, while indicating a net westerly drift.

I consider the silver hake eggs and larvae which we collected to be 1) representatives of a small brood spawned on the deeper portions of the shelf between Hudson Canyon and Cape Hatteras; 2) representatives of a brood spawned over Nantucket Shoals and the shelf south of New England; 3) survivors of a brood spawned over Georges Bank or Great South Channel.

It is during the pelagic period of development that eggs or larvae, unable to control their own movements, are most susceptible to prevailing currents, surface winds, and changing hydro-

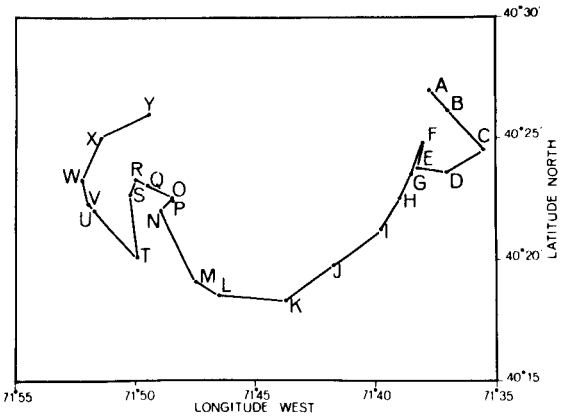

FIGURE 13.—Position of free-drifting staff buoy at 2-h intervals on the continental shelf south of Montauk Point, N.Y.

graphic conditions. The results of the *Dolphin* survey indicate several things about sampling fishes during this phase in their development. 1) One cannot hope to fully understand the early life history of any one species of fish on exploratory surveys. Such facts as gross seasonality and geographic limits of spawning might be revealed but a complete evaluation of a species' early life history can only follow a series of frequent cruises where all efforts are focused on one or a very few species. 2) Known or suspected zoogeographic barriers should be included well within the limits of a survey area, not made to coincide with the edge. 3) Sampling between the surface and levels immediately below the thermocline is inadequate when dealing with pelagic young of groundfish. A more complete and accurate picture of developing silver hake could have been drawn if the entire water column, surface to bottom, had been sampled on all stations. 4) The diel activity and vertical distribution of a postlarval fish may be directly related to the behavior of invertebrate food organisms. An analysis of the invertebrate plankton collected with the ichthyoplankton should be considered as an integral part of a survey. 5) Unless discrete-level tows are made with opening-closing nets, an exact temperature-catch relationship cannot be determined, except in vertically isothermal conditions.

I found no evidence that silver hake depend on or utilize estuaries during their early life history. Their occasional presence in estuarine areas must be considered accidental.

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APPENDIX TABLE 1.—Silver hake: station data, number of eggs, and number and length range of larvae collected during 1966.

Cruise and station	Net	Date	Start time	Depth of water (m)	Maximum tow depth (m)	Light regime[1]	Total number of eggs	Larvae: Total number captured	Larvae: Number measured	Larvae: Notochord length: Mean (mm)	Larvae: Notochord length: Range (mm)
D-66-5			EDST								
B-1	1	13 V 66	2233	24-20	6	N	—	1	1	71.20	71.2
H-5	2	20 V 66	0527	24-40	24	C	1	—	—	—	—
K-5	1	22 V 66	0533	33-35	15	C	—	1	1	2.50	2.5
D-66-7			EDST								
A-1	1	17 VI 66	0927	11-27	6	D	206	81	54	2.40	1.7-2.8
A-2	1	17 VI 66	1037	29-37	15	D	242	75	55	2.28	1.8-3.2
A-3	1	17 VI 66	1137	29-48	15	D	117	49	35	2.21	1.8-2.6
A-3	2	17 VI 66	1137	29-48	24	D	209	3	3	2.10	1.9-2.3
A-4	1	17 VI 66	1322	51-53	15	D	107	3	3	3.33	3.2-3.6
A-4	2	17 VI 66	1322	51-53	33	D	158	16	15	2.43	2.0-3.1
A-5	1	17 VI 66	1703	62-62	15	D	123	4	3	2.70	2.2-3.1
A-5	2	17 VI 66	1703	62-62	33	D	79	1	1	2.80	2.8
A-6	1	17 VI 66	1919	73-75	15	C	1	—	—	—	—
A-7	1	17 VI 66	2343	117-102	15	N	1	—	—	—	—
B-1	1	18 VI 66	1732	24-24	15	D	4	3	3	2.77	2.5-3.3
B-2	1	18 VI 66	1622	46-42	15	D	16	18	16	2.61	2.0-5.3
B-2	2	18 VI 66	1622	46-42	24	D	3	—	—	—	—
B-3	1	18 VI 66	1525	53-51	15	D	—	15	15	2.95	2.1-4.4
B-3	2	18 VI 66	1525	53-51	33	D	—	4	4	2.55	2.4-2.8
B-4	1	18 VI 66	1402	62-64	15	D	20	15	14	3.34	2.8-4.1
B-4	2	18 VI 66	1402	62-64	33	D	7	6	3	3.63	2.7-5.0
B-5	1	18 VI 66	1036	77-75	15	D	1	120	116	3.33	2.4-5.7
B-5	2	18 VI 66	1036	77-75	33	D	64	62	56	3.33	2.4-4.7
B-6	1	18 VI 66	0833	86-86	15	D	—	24	24	3.93	2.7-4.6
B-6	2	18 VI 66	0833	86-86	33	D	3	60	60	3.65	2.9-4.4
B-7	1	18 VI 66	0412	88-99	15	C	—	1	1	3.10	3.1
B-7	2	18 VI 66	0412	88-99	33	C	1	—	—	—	—
C-1	1	19 VI 66	0628	20-29	15	D	—	8	2	3.60	2.7-4.5
C-2	2	19 VI 66	0733	31-31	27	D	—	1	1	2.90	2.9
C-3	1	19 VI 66	0827	35-37	15	D	—	2	2	4.15	4.1-4.2
C-6	1	19 VI 66	1531	58-58	15	D	—	1	1	5.20	5.2
C-6	2	19 VI 66	1531	58-58	33	D	—	5	5	5.74	5.1-6.3
C-7	1	19 VI 66	2043	79-77	15	C	—	4	3	6.30	5.8-6.9
C-8	1	19 VI 66	2310	112-320	15	N	4	2	2	4.90	4.7-5.1
C-8	2	19 VI 66	2310	112-320	33	N	1	—	—	—	—
H-6	1	27 VI 66	0654	79-97	15	D	—	1	1	6.30	6.3
H-7	2	27 VI 66	0758	102-214	33	D	1	—	—	—	—
K-6	1	25 VI 66	2205	42-49	15	N	—	1	1	7.80	7.8
D-66-10			EDST								
A-1	1	5 VIII 66	0502	9-22	6	C	1	14	13	3.15	2.2-5.6
A-2	1	5 VIII 66	0607	26-33	15	C	47	31	29	2.82	1.6-5.1
A-3	1	5 VIII 66	0701	33-35	15	D	73	41	34	4.02	2.2-6.2
A-3	2	5 VIII 66	0701	33-35	24	D	18	20	20	5.78	2.2-8.6
A-4	1	5 VIII 66	0840	49-55	15	D	119	217	193	3.14	1.6-5.7
A-4	2	5 VIII 66	0840	49-55	33	D	4	54	49	5.11	2.4-6.9
A-5	1	5 VIII 66	1219	58-57	15	D	6	144	141	5.03	2.7-8.1
A-5	2	5 VIII 66	1219	58-57	33	D	8	120	116	5.26	2.1-8.6
A-6	1	5 VIII 66	1441	68-71	15	D	71	144	131	4.00	2.2-6.6
A-6	2	5 VIII 66	1441	68-71	33	D	—	424	401	5.79	2.0-9.2
A-7	1	5 VIII 66	1741	102-113	15	D	5	7	5	3.58	2.3-4.3
A-7	2	5 VIII 66	1741	102-113	33	D	10	40	36	4.18	2.2-10.1
B-1	1	6 VIII 66	1349	24-16	15	D	—	2	1	2.60	2.6
B-2	1	6 VIII 66	1149	38-29	15	D	9	7	7	3.83	2.5-4.7
B-2	2	6 VIII 66	1149	38-29	21	D	1	29	22	3.58	2.1-7.1
B-3	1	6 VIII 66	1101	46-42	15	D	22	2	2	2.05	1.9-2.2
B-3	2	6 VIII 66	1101	46-42	33	D	2	10	10	3.34	2.1-6.5
B-4	1	6 VIII 66	0720	60-58	15	D	4	29	25	3.90	1.7-6.4
B-4	2	6 VIII 66	0720	60-58	33	D	—	15	15	5.53	2.9-9.2
B-5	1	6 VIII 66	0544	73-73	15	C	12	112	88	4.07	2.0-5.7
B-5	2	6 VIII 66	0544	73-73	33	C	2	85	65	6.22	2.2-13.0
B-6	1	6 VIII 66	0133	87-82	15	N	1	98	96	5.37	2.6-15.1
B-6	2	6 VIII 66	0133	87-82	33	N	—	172	149	6.81	3.0-16.7
B-7	1	5 VIII 66	2340	91-99	15	N	—	163	162	6.58	3.2-15.3
B-7	2	5 VIII 66	2340	91-99	33	N	—	726	701	8.53	3.5-25.9
C-1	1	7 VIII 66	0043	18-20	6	N	—	2	2	2.10	1.8-2.4
C-2	1	7 VIII 66	0137	27-29	15	N	1	—	—	—	—
C-3	1	7 VIII 66	0239	31-33	15	N	—	9	9	3.19	2.6-5.5
C-4	1	7 VIII 66	0413	40-40	15	N	4	41	39	3.66	1.7-6.3
C-4	2	7 VIII 66	0413	40-40	33	N	—	1	1	4.70	4.7
C-5	1	7 VIII 66	0745	48-48	15	D	2	—	—	—	—
C-5	2	7 VIII 66	0745	48-48	33	D	—	3	3	3.50	2.8-4.8

APPENDIX TABLE 1.—Continued.

Cruise and station	Net	Date	Start time	Depth of water (m)	Maximum tow depth (m)	Light regime[1]	Total number of eggs	Larvae: Total number captured	Larvae: Number measured	Larvae: Notochord length: Mean (mm)	Larvae: Notochord length: Range (mm)
D-66-10—Continued			EDST								
C-6	1	7 VIII 66	1005	55-55	15	D	19	1	1	3.20	3.2
C-7	2	7 VIII 66	1406	70-60	33	D	—	7	6	5.30	4.5-6.0
C-8	1	7 VIII 66	1630	108-210	15	D	—	1	1	4.90	4.9
C-8	2	7 VIII 66	1630	108-210	33	D	—	87	73	5.39	3.3-7.3
D-5	1	8 VIII 66	0615	40-33	15	D	6	4	4	3.75	2.4-7.1
D-5	2	8 VIII 66	0615	40-33	24	D	—	1	1	3.20	3.2
D-6	1	8 VIII 66	0422	48-54	15	N	—	7	6	5.77	4.5-6.5
D-7	1	8 VIII 66	0018	77-75	15	N	—	21	20	5.95	4.5-13.5
D-7	2	8 VIII 66	0018	77-75	33	N	—	6	6	12.25	6.4-17.6
D-8	1	7 VIII 66	2221	110-126	15	N	—	1	1	3.60	3.6
D-8	2	7 VIII 66	2221	110-126	33	N	—	64	61	10.21	6.0-19.9
E-6	1	9 VIII 66	1306	44-42	15	D	—	1	1	5.30	5.3
E-6	2	9 VIII 66	1306	44-42	33	D	—	3	3	5.97	5.8-6.2
E-7	1	9 VIII 66	1505	64-64	15	D	—	2	2	3.30	2.9-3.7
E-7	2	9 VIII 66	1505	64-64	33	D	—	5	5	5.54	4.2-7.2
F-6	1	9 VIII 66	2306	55-53	15	N	—	1	1	6.00	6.0
F-6	2	9 VIII 66	2306	55-53	33	N	—	2	2	7.05	6.9-7.2
F-7	1	9 VIII 66	2118	77-71	15	N	—	7	7	7.50	5.5-10.1
G-5	1	21 VIII 66	1355	51-48	15	D	—	1	1	3.60	3.6
H-5	1	22 VIII 66	0239	37-44	15	N	—	1	1	14.80	14.8
H-5	2	22 VIII 66	0239	37-44	24	N	—	1	1	14.50	14.5
H-7	2	21 VIII 66	2130	95-163	33	N	—	2	2	15.10	15.0-15.2
J-7	2	23 VIII 66	0717	86-119	33	C	—	1	1	5.70	5.7
D-66-11			EDST								
A-2	1	13 IX 66	1133	29-31	15	D	15	2	2	2.95	2.6-3.3
A-2	2	13 IX 66	1133	29-31	24	D	7	9	7	3.03	2.6-3.7
A-3	1	13 IX 66	1243	38-42	15	D	190	13	12	3.65	2.5-4.8
A-3	2	13 IX 66	1243	38-42	24	D	23	9	8	3.86	2.8-4.6
A-4	1	13 IX 66	1415	46-53	15	D	7	136	131	4.17	2.2-6.2
A-4	2	13 IX 66	1415	46-53	33	D	22	91	86	3.78	2.3-6.5
A-5	1	13 IX 66	1816	60-60	15	C	112	197	187	4.49	1.8-6.7
A-5	2	13 IX 66	1816	60-60	33	C	116	201	198	4.77	1.8-7.5
A-6	1	13 IX 66	2030	68-68	15	N	—	86	83	5.82	2.7-11.9
A-6	2	13 IX 66	2030	68-68	33	N	9	131	123	5.86	4.1-11.5
A-7	1	14 IX 66	0104	113-112	12	N	—	81	63	5.00	3.7-20.0
A-7	2	14 IX 66	0104	113-112	30	N	—	113	107	5.24	2.9-21.0
B-1	1	14 IX 66	2304	26-26	6	N	—	13	10	2.70	2.4-3.2
B-2	1	14 IX 66	0025	33-35	15	N	—	13	9	2.76	2.4-3.1
B-3	1	17 IX 66	0033	49-51	15	N	36	38	32	4.18	2.3-9.4
B-3	2	17 IX 66	0033	49-51	33	N	19	567	558	5.60	2.4-17.3
B-4	1	14 IX 66	1743	60-66	15	C	9	12	12	3.50	2.3-5.8
B-4	2	14 IX 66	1743	60-66	33	C	3	178	178	4.86	2.4-13.0
B-5	1	14 IX 66	1359	73-71	15	D	22	2	2	5.60	4.8-6.4
B-5	2	14 IX 66	1359	73-71	33	D	23	103	96	4.14	2.0-11.0
B-6	1	14 IX 66	1004	80-84	15	D	4	12	4	7.05	4.9-8.8
B-6	2	14 IX 66	1004	80-84	33	D	—	39	38	6.57	5.1-7.8
B-7	1	14 IX 66	0457	95-93	15	C	—	10	10	11.65	6.7-40.0
B-7	2	14 IX 66	0457	95-93	33	C	—	53	51	12.05	6.5-41.1
C-1	1	17 IX 66	0850	18-16	9	D	—	4	4	3.05	2.7-3.7
C-2	1	17 IX 66	0758	29-26	15	D	—	5	3	2.73	2.6-2.8
C-3	1	17 IX 66	0707	38-29	15	C	56	—	—	—	—
C-4	1	17 IX 66	1640	40-42	15	D	8	1	1	4.40	4.4
C-4	2	17 IX 66	1640	40-42	33	D	4	312	300	4.20	2.3-10.3
C-5	1	17 IX 66	1835	49-47	15	C	16	8	7	3.04	2.5-4.5
C-5	2	17 IX 66	1835	49-47	33	C	1	157	157	6.92	2.8-11.9
C-6	2	17 IX 66	2033	57-57	33	N	23	208	207	5.61	2.1-19.5
C-7	1	17 IX 66	2247	71-77	15	N	—	13	12	12.32	3.1-22.5
C-7	2	17 IX 66	2247	71-77	33	N	—	351	345	8.49	3.1-32.8
C-8	1	18 IX 66	0049	110-519	15	N	—	2	2	8.25	7.9-8.6
C-8	2	18 IX 66	0049	110-519	33	N	—	2	2	9.70	9.4-10.0
D-2	1	18 IX 66	1421	22-20	6	D	—	1	1	3.60	3.6
D-3	1	18 IX 66	1326	20-26	15	D	—	6	5	2.80	2.2-4.0
D-4	1	18 IX 66	1159	33-27	15	D	—	12	11	3.39	2.6-4.2
D-4	2	18 IX 66	1159	33-27	24	D	—	11	11	2.78	2.2-4.2
D-5	1	18 IX 66	1043	35-35	15	D	—	25	22	3.82	2.6-5.9
D-5	2	18 IX 66	1043	35-35	33	D	—	136	130	4.93	2.6-11.2
D-6	1	18 IX 66	0843	55-53	15	D	—	22	22	5.99	4.1-8.8
D-6	2	18 IX 66	0843	55-53	33	D	—	372	363	5.48	3.1-12.2
D-7	1	18 IX 66	0624	73-70	15	C	—	1	1	8.80	8.8
D-7	2	18 IX 66	0624	73-70	33	C	—	61	61	6.96	3.5-10.2
D-8	2	18 IX 66	0424	121-115	33	N	—	56	55	9.14	6.5-12.7

APPENDIX TABLE 1.—Continued.

Cruise and station	Net	Date	Start time	Depth of water (m)	Maximum tow depth (m)	Light regime[1]	Total number of eggs	Larvae: Total number captured	Larvae: Number measured	Larvae: Notochord length: Mean (mm)	Larvae: Notochord length: Range (mm)
D-66-12			EDST								
A-1	1	15 X 66	0402	24-9	6	N	—	3	2	3.40	3.1-3.7
A-2	1	15 X 66	0309	31-29	15	N	—	16	15	4.21	3.2-5.8
A-2	2	15 X 66	0309	31-29	24	N	—	31	30	4.06	2.8-5.3
A-3	1	15 X 66	0209	42-37	15	N	—	8	8	4.72	2.8-6.7
A-3	2	15 X 66	0209	42-37	33	N	1	37	33	4.94	2.6-26.5
A-4	1	15 X 66	0715	48-51	15	C	31	105	102	3.47	2.3-6.9
A-4	2	15 X 66	0715	48-51	33	C	63	216	207	3.47	2.3-5.7
A-5	1	15 X 66	0843	58-60	15	D	12	6	6	3.07	2.7-3.7
A-5	2	15 X 66	0843	58-60	33	D	275	73	67	2.98	2.0-4.6
A-6	1	15 X 66	1032	68-71	15	D	1	8	8	5.51	3.1-11.5
A-6	2	15 X 66	1032	68-71	33	D	2	191	177	4.69	1.8-12.8
A-7	1	15 X 66	1226	108-115	15	D	—	2	2	9.90	3.0-16.8
A-7	2	15 X 66	1226	108-115	33	D	—	40	40	13.54	3.7-21.5
B-1	1	14 X 66	1930	7-18	6	N	2	—	—	—	—
B-2	1	14 X 66	2037	33-37	15	N	6	1	1	2.80	2.8
B-2	2	14 X 66	2037	33-37	24	N	14	4	4	5.47	3.2-6.8
B-3	1	14 X 66	2134	42-48	15	N	10	1	1	3.30	3.3
B-3	2	14 X 66	2134	42-48	33	N	19	19	19	4.39	2.2-8.8
B-4	1	14 X 66	1406	62-58	15	D	6	6	6	5.75	4.2-6.8
B-4	2	14 X 66	1406	62-58	33	D	9	145	142	6.36	2.5-18.5
B-5	1	14 X 66	1238	71-71	15	D	2	24	23	9.59	4.1-14.1
B-5	2	14 X 66	1238	71-71	33	D	1	204	200	7.51	2.7-13.8
B-6	1	14 X 66	0850	82-80	15	D	—	31	31	10.20	4.3-16.5
B-6	2	14 X 66	0850	82-80	33	D	—	276	276	10.81	2.2-21.0
B-7	1	14 X 66	0710	91-90	15	C	—	15	15	11.16	6.3-15.7
B-7	2	14 X 66	0710	91-90	33	C	—	59	58	9.63	3.5-15.0
C-2	1	13 X 66	1012	22-27	15	D	—	3	3	8.73	4.2-15.2
C-3	1	13 X 66	1105	31-31	15	D	1	5	5	7.14	3.5-13.2
C-3	2	13 X 66	1105	31-31	24	D	2	15	15	5.65	4.4-7.2
C-4	1	13 X 66	1233	37-40	15	D	—	38	38	5.77	2.6-9.2
C-4	2	13 X 66	1233	37-40	33	D	2	65	62	6.74	2.6-13.0
C-5	1	13 X 66	1555	48-46	15	D	11	34	33	4.98	2.6-7.3
C-5	2	13 X 66	1555	48-46	33	D	7	161	161	5.99	2.6-11.7
C-6	1	13 X 66	1814	55-55	15	C	1	34	34	7.64	3.1-12.2
C-6	2	13 X 66	1814	55-55	33	C	17	100	99	7.84	2.2-16.3
C-7	1	13 X 66	2147	77-70	15	N	4	45	43	13.54	3.9-29.2
C-7	2	13 X 66	2147	77-70	33	N	3	490	487	9.90	2.3-33.8
C-8	1	13 X 66	2359	198-787	15	N	—	1	1	19.80	19.8
C-8	2	13 X 66	2359	198-787	33	N	—	1	1	12.80	12.8
D-1	1	6 X 66	0224	16-20	6	N	—	1	1	2.70	2.7
D-3	1	6 X 66	0408	26-22	15	N	—	3	3	7.13	6.9-7.4
D-4	2	13 X 66	0036	31-22	24	N	2	1	1	15.00	15.0
D-5	1	12 X 66	2304	35-37	15	N	1	1	1	6.20	6.2
D-5	2	12 X 66	2304	35-37	24	N	30	4	4	6.07	4.6-8.3
D-6	1	12 X 66	1901	55-53	15	C	8	125	121	6.18	2.5-18.3
D-6	2	12 X 66	1901	55-53	33	C	3	134	130	6.94	1.6-17.7
D-7	1	12 X 66	1702	70-75	15	C	5	46	45	4.18	3.0-6.7
D-7	2	12 X 66	1702	70-75	33	C	7	42	42	5.58	3.4-8.3
D-8	1	12 X 66	1313	99-121	15	D	36	1	1	2.90	2.9
D-8	2	12 X 66	1313	99-121	33	D	9	39	35	4.50	2.8-6.7
E-4	1	11 X 66	2134	29-29	15	N	33	1	1	2.80	2.8
E-5	1	11 X 66	2310	35-35	15	N	1	21	21	6.37	2.9-20.2
E-5	2	11 X 66	2310	35-35	24	N	1	15	15	5.10	2.7-7.6
E-6	1	12 X 66	0250	44-42	15	N	3	35	34	6.64	3.1-25.0
E-6	2	12 X 66	0250	44-42	33	N	—	18	18	8.49	4.5-23.4
E-7	1	12 X 66	0452	64-66	15	N	1	7	7	7.99	4.7-14.1
E-7	2	12 X 66	0452	64-66	33	N	—	52	52	10.04	2.8-31.4
E-8	1	12 X 66	0903	157-121	15	D	—	4	4	3.52	2.8-4.4
E-8	2	12 X 66	0903	157-121	33	D	—	2	2	3.00	2.8-3.2
F-5	1	4 X 66	2251	37-33	15	N	—	2	2	5.60	4.2-7.0
F-5	2	4 X 66	2251	37-33	24	N	1	1	1	3.70	3.7
F-6	1	4 X 66	2053	53-55	15	N	—	63	62	6.54	2.9-23.3
F-6	2	4 X 66	2053	53-55	33	N	—	10	9	7.03	3.7-13.8
F-7	1	4 X 66	1652	104-79	15	D	—	6	6	4.68	3.0-7.0
F-7	2	4 X 66	1652	104-79	33	D	—	21	17	6.33	3.0-9.3
G-4	1	4 X 66	0727	29-33	15	C	—	1	1	5.40	5.4
G-5	2	4 X 66	0916	49-53	33	D	—	2	2	4.65	3.5-5.8
G-6	2	4 X 66	1309	95-75	33	D	1	1	1	7.40	7.4
H-6	1	3 X 66	0711	88-66	15	C	2	—	—	—	—
H-6	2	3 X 66	0711	88-66	33	C	—	1	1	15.00	15.0
J-7	2	3 X 66	0055	79-91	33	N	—	1	1	22.50	22.5
K-7	1	30 IX 66	1950	823-914	15	N	—	1	1	11.00	11.0

APPENDIX TABLE 1.—Continued.

Cruise and station	Net	Date	Start time	Depth of water (m)	Maximum tow depth (m)	Light regime[1]	Total number of eggs	Larvae: Total number captured	Larvae: Number measured	Larvae: Notochord length: Mean (mm)	Larvae: Notochord length: Range (mm)
D-66-14			EST								
A-1	1	4 XII 66	1956	26-9	3	N	—	2	1	6.50	6.5
A-2	1	4 XII 66	1857	33-29	15	N	—	2	2	5.60	5.4-5.8
A-3	1	4 XII 66	1750	44-33	15	N	—	2	2	5.95	5.9-6.0
A-3	2	4 XII 66	1750	44-33	24	N	—	1	1	3.10	3.1
A-4	1	4 XII 66	1618	53-51	15	C	—	5	5	5.44	4.9-5.7
A-4	2	4 XII 66	1618	53-51	33	C	—	6	6	5.00	4.2-6.4
A-5	2	4 XII 66	1449	58-58	33	D	—	3	3	4.93	4.1-5.5
A-6	1	4 XII 66	1255	73-68	15	D	—	3	3	6.30	6.0-6.6
A-6	2	4 XII 66	1255	73-68	33	D	—	2	2	3.60	2.8-4.4
B-1	1	3 XII 66	1937	18-22	6	N	—	1	1	6.10	6.1
B-2	1	3 XII 66	2056	31-42	15	N	—	1	1	3.60	3.6
B-2	2	3 XII 66	2056	31-42	24	N	—	2	2	5.60	3.0-8.2
B-3	1	3 XII 66	2210	44-51	15	N	—	19	18	5.55	3.2-7.2
B-3	2	3 XII 66	2210	44-51	33	N	—	25	25	5.93	4.2-7.6
B-4	1	3 XII 66	2351	62-71	15	N	—	4	4	4.10	2.9-6.5
B-4	2	3 XII 66	2351	62-71	33	N	—	5	5	8.70	4.5-23.2
B-5	1	4 XII 66	0113	73-73	15	N	—	2	2	8.80	5.7-11.9
B-6	1	4 XII 66	0310	84-84	15	N	—	1	1	8.50	8.5
B-6	2	4 XII 66	0310	84-84	33	N	—	1	1	6.50	6.5
C-3	2	3 XII 66	1047	33-37	24	D	—	1	1	5.10	5.1
C-4	1	3 XII 66	0412	42-40	15	N	—	5	5	15.56	4.1-56.9
C-4	2	3 XII 66	0412	42-40	33	N	—	8	8	4.99	3.6-7.4
C-5	1	2 XII 66	2302	49-47	15	N	—	25	25	5.67	3.5-7.4
C-5	2	2 XII 66	2302	49-47	33	N	—	22	22	5.74	3.5-8.4
C-6	1	2 XII 66	2022	57-57	15	N	—	19	19	7.29	3.1-33.9
C-6	2	2 XII 66	2022	57-57	33	N	—	21	21	5.06	3.1-7.7
C-7	1	2 XII 66	1727	77-70	15	N	—	17	15	7.13	3.2-12.8
C-7	2	2 XII 66	1727	77-70	33	N	—	7	7	11.56	4.4-43.1
D-6	1	2 XII 66	0652	51-53	15	C	—	18	17	4.78	3.1-6.9
D-6	2	2 XII 66	0652	51-53	33	C	—	18	17	5.07	2.7-6.5
D-7	1	2 XII 66	0920	73-79	15	D	—	1	1	6.20	6.2
D-7	2	2 XII 66	0920	73-79	33	D	—	1	1	6.10	6.1
E-6	1	10 XI 66	0722	42-40	15	C	1	1	1	3.60	3.6
E-6	2	10 XI 66	0722	42-40	33	C	—	4	4	3.82	3.5-4.2
E-7	1	10 XI 66	1200	68-62	15	D	—	1	1	29.60	29.6
E-7	2	10 XI 66	1200	68-62	33	D	—	2	2	5.05	4.0-6.1
E-8	1	19 XI 66	0201	110-95	15	N	8	1	1	23.80	23.8
E-8	2	19 XI 66	0201	110-95	33	N	—	1	1	6.00	6.0
F-5	1	11 XI 66	0126	37-38	15	N	—	1	1	3.80	3.8
F-6	1	10 XI 66	2303	51-51	15	N	—	4	4	15.90	8.5-24.2
F-6	2	10 XI 66	2303	51-51	33	N	—	4	4	8.22	6.0-12.9
F-7	1	18 XI 66	2203	68-70	15	N	—	36	36	29.49	20.4-36.5
F-7	2	18 XI 66	2203	68-70	33	N	—	61	61	28.63	16.7-39.3
G-5	1	11 XI 66	2234	51-46	15	N	1	4	4	12.75	3.8-22.6
G-5	2	11 XI 66	2234	51-46	33	N	—	1	1	7.30	7.3
G-6	1	12 XI 66	0050	79-97	15	N	8	6	6	15.17	5.7-24.6
G-6	2	12 XI 66	0050	79-97	33	N	2	9	9	6.99	2.5-17.9
H-5	1	12 XI 66	0754	40-44	15	D	—	2	2	6.80	6.6-7.0
H-5	2	12 XI 66	0754	40-44	33	D	—	1	1	7.10	7.1
H-6	1	12 XI 66	0609	84-82	15	C	1	—	—	—	—
H-6	2	12 XI 66	0609	84-82	33	C	3	3	3	4.73	3.9-5.2
H-7	1	12 XI 66	0503	97-172	15	N	5	—	—	—	—
H-7	2	12 XI 66	0503	97-172	33	N	5	4	4	5.60	2.4-10.4
J-5	1	14 XI 66	1727	26-27	15	C	—	1	1	6.70	6.7
J-6	1	14 XI 66	1935	35-35	15	N	—	1	1	7.60	7.6
J-6	2	14 XI 66	1935	35-35	24	N	—	2	2	8.20	7.6-8.8
J-7	2	14 XI 66	2329	90-71	33	N	—	3	3	4.83	3.2-6.3
K-1	1	18 XI 66	0842	13-16	6	D	—	1	1	3.10	3.1
K-6	1	17 XI 66	2236	53-40	15	N	13	—	—	—	—
K-6	2	17 XI 66	2236	53-40	33	N	4	—	—	—	—
K-7	2	17 XI 66	2127	483-311	33	N	2	—	—	—	—
L-5	2	17 XI 66	1545	88-622	33	C	1	1	1	4.30	4.3
M-4	1	16 XI 66	2339	58-24	6	N	—	1	1	2.90	2.9

[1]Light regime: D = day tow; N = night tow; C = crepuscular tow (when any part of a tow occurred within 1 h of sunrise or sunset).

DISTRIBUTION, VARIATION, AND SUPPLEMENTAL DESCRIPTION OF THE OPOSSUM SHRIMP, *NEOMYSIS AMERICANA* (CRUSTACEA: MYSIDACEA)

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ABSTRACT

Neomysis americana ranges from the Gulf of St. Lawrence to northeastern Florida in estuaries and nearshore ocean and to depths of 100 m on Georges Bank. Samples studied from localities between Nova Scotia and Georgia show no consistent geographic variation. Specific characters are illustrated and discussed.

Neomysis americana (S. I. Smith, 1873) is the most common mysid in shallow marine waters of eastern North America. In his monograph, W. M. Tattersall (1951) gave the range as "from the Gulf of St. Lawrence to the coast of Virginia in shallow water." Since then its known distribution has been extended south to North Carolina (Wigley and Burns, 1971) and recently to South Carolina and Georgia (Sikora, Heard, and Dahlberg, 1972; Williams, 1972). Further details of its distribution are given below.

Published and unpublished distributional data available to us before the present study was undertaken suggested the possible existence of two isolated populations of *Neomysis*: 1) a population north of Cape Henry, Va., mostly in coastal waters but also occurring in large numbers on Georges Bank; 2) a population confined mainly to sounds and estuaries from North Carolina to Georgia. We suspected that there might be taxonomic differences between these or other populations, a likelihood that had occurred independently to other investigators (Bousfield, in litt.; Heard, in litt.). *Neomysis americana* develops two or more generations per year, at least in the United States (Hopkins, 1965), small summer animals and large winter animals. The latter from North Carolina estuaries showed apparent differences that we felt merited further investigation. We decided to determine variation and geographic distribution more precisely in *N. americana*.

The study is a complement to current ecological investigations in coastal environments. *Neomysis americana* is probably an omnivore like its near relative *N. integer* (Mauchline, 1971) or *Mysis relicta* (Lasenby and Langford, 1973), consuming organic detritus, smaller crustaceans, and diatoms and fitting the trophic role attributed to other mysids preyed upon by fishes in Florida estuaries (Odum and Heald, 1972) and Japan (Ii, 1964). It is known to be a significant element in the diet of fishes such as flounder, shad, mackerel, and anchovy (Hopkins, 1965), *Paralichthys dentatus* and *P. lethostigma* (Powell, in litt.), and the hakes, *Urophycis regius* and *U. floridanus* (Sikora et al., 1972) as well as other fishes (Taylor, in litt.).

MATERIALS AND METHODS

Our materials for study were both reliable literature records and museum specimens. Canadian occurrences have been reported by Bousfield (1955, 1956a, b, 1958, 1962), O. S. Tattersall (1955a), Bousfield and Leim (1960), Préfontaine and Brunel (1962), and Brunel (1970). Records from the United States included those of Whiteley (1948), Hulbert (1957), Herman (1963), and Wigley and Burns (1971) in addition to others cited previously. Southern range limits and offshore distribution were partly established by examination of plankton samples taken in waters between Cape Hatteras, N.C., and Jupiter Inlet, Fla., during cruises 4, 5, 7, 8, 9 of MV *Theodore N. Gill* (October 1953-December 1954), concentrating on nearshore samples where the species was expected to occur (station data in Anderson, Moore, and Gordy, 1961a, b). Specimens studied

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for variation were from collections in the National Museum of Natural History (USNM), including new collections acknowledged below.

Measurements and counts used in assessing variation were: 1) carapace length from rear edge of orbit to posterolateral margin, 2) length and width of antennal scale (ventral view), 3) lengths of inner and outer uropods, 4) number of spines in ventral comblike row on inner uropod near distomesial margin of statocyst vesicle, 5) length of this row of spines, 6) number of spines per 0.01 mm in this row, 7) number of spines on margin of telson, and 8) relative widths of cornea and eyestalk. External morphology of representative specimens from over the range was studied and compared.

Specimens measured for comparisons were mature adults (mainly females) from the following collections: USNM 89736, St. Andrews, near Atlantic Biological Station, N.B.; USNM 82658 and 82651, Woods Hole, Mass., received 2 January 1907, Vinal N. Edwards, collector; USNM 78734, Amityville, Long Island, N.Y., 6 August 1938, H. K. Townes, collector; USNM 143770, York River below West Point, Va., 14 January, 1964, W. A. Van Engel, collector; USNM 143771, Garbacon Shoal, 6 May 1964, W. C. Noe, collector, and USNM 143772, Wilkinson Point, 17 June 1964, Frank Holland, collector, Neuse River, N.C.; USNM 143773, Wassau Sound, Ga., 29 August 1972, and USNM 143774, mouth of St. Catherines Sound, Ga., 30 January 1970, Richard W. Heard, Jr., collector. All specimens were large winter animals except the samples of summer animals from Amityville, N.Y., and Wassau Sound, Ga.

RESULTS AND DISCUSSION

Morphological Analysis

Proportional and meristic characters were evaluated for variation in different parts of the range. Mean carapace length in millimeters (rear edge of orbit to posterolateral margin) for the samples analyzed were: (Figure 1) New York, 2.95; (Figures 1, 2) New Brunswick, 3.03; Massachusetts, 3.25; Virginia, 3.51; North Carolina, 3.03; Georgia, St. Catherines Sound, 3.91 - Wassau Sound, 2.09; (Figure 3) New Brunswick, 3.01; North Carolina, 2.74; Georgia, as above. There is no detectable difference in size between males and females of assumed comparable age.

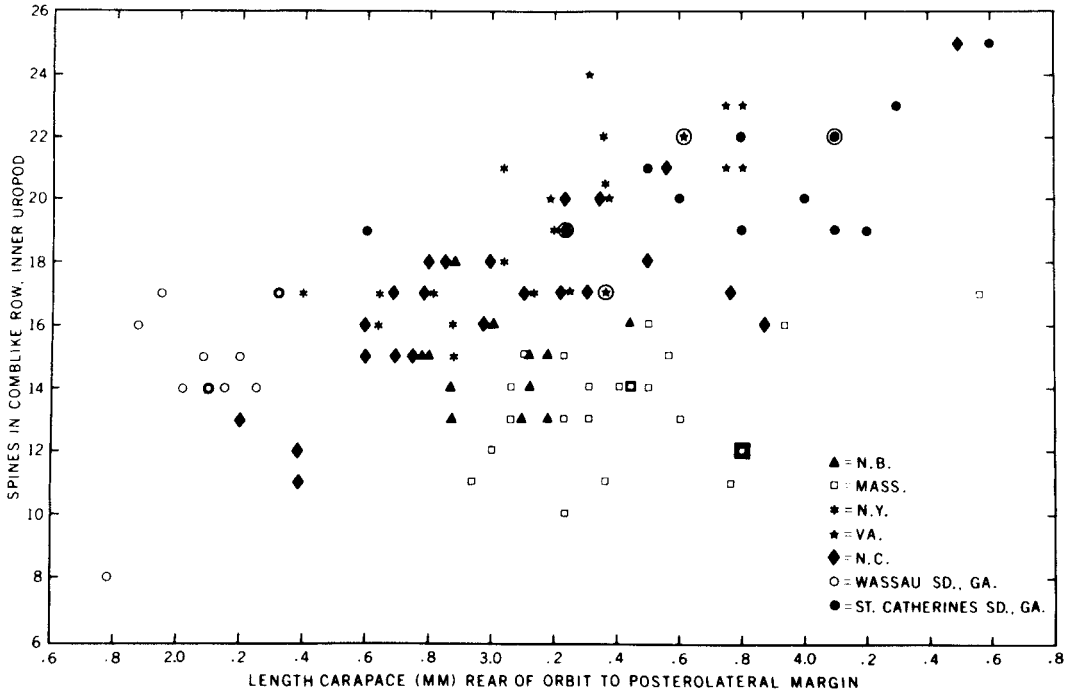

FIGURE 1.—Relation between number of spines in comblike row on inner uropod and length of carapace from rear edge of orbit to posterolateral margin in seven populations of *Neomysis americana*. Framed points = replicates.

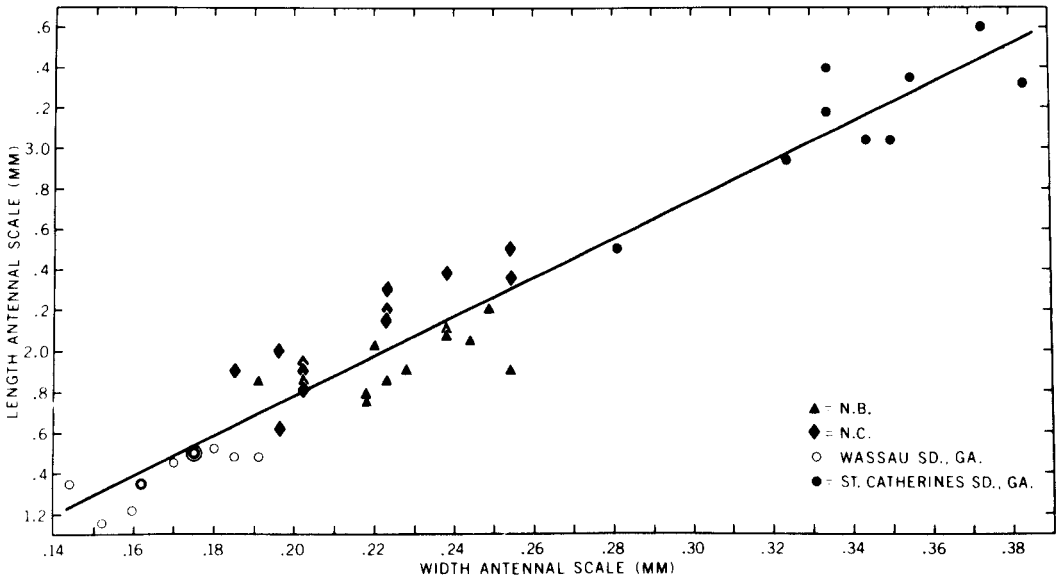

FIGURE 2.—Relation between length and width of antennal scale in four populations of *Neomysis americana*. Framed points = replicates

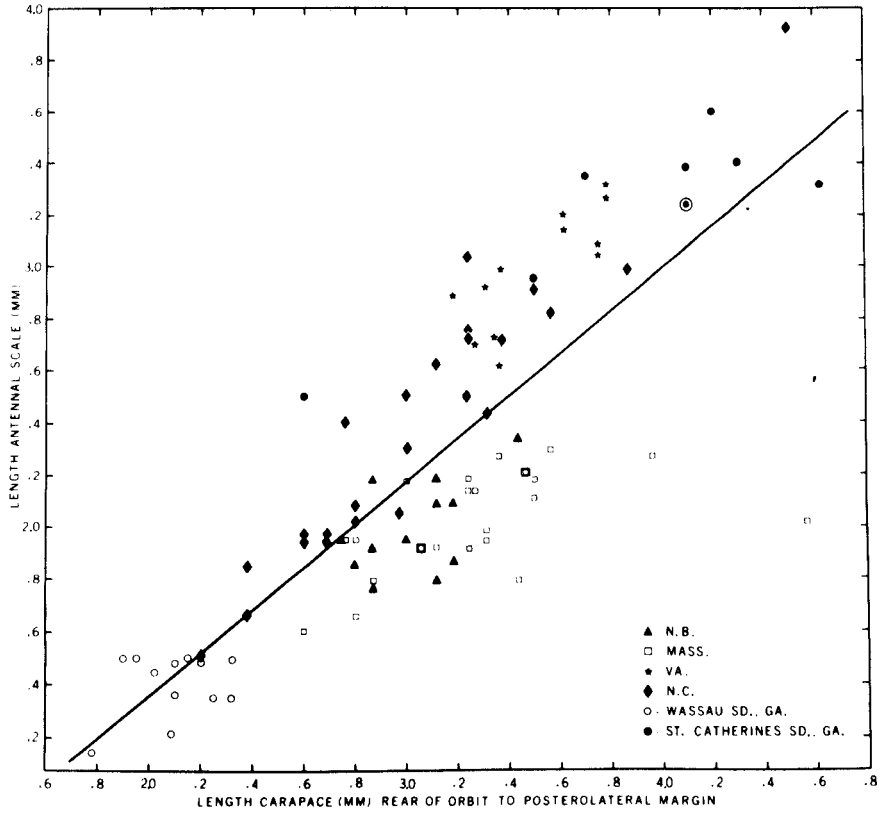

FIGURE 3.—Relation between length of antennal scale and length of carapace from rear edge of orbit to posterolateral margin in six populations of *Neomysis americana*. Framed points = replicates.

The number of spines in the ventral comblike row on the inner uropod first suggested that northern populations might have fewer spines than those in the south. This proves not to be true; rather, the number of spines is apparently a function of body size (Figure 1). A regression analysis shows that the relationship is nonlinear ($Y = 3.39X + 6.08$, $r = 0.579$, $z = 0.661$, $P>0.05$), falling short of statistical significance. Inspection of the scatter of points indicates that number of spines more or less levels off at upper size limits, but distribution is fairly broad at all sizes.

Two other relationships do yield statistically significant correlations but show no geographic association. Length of the antennal scale is correlated with its width (Figure 2) ($Y = 9.726X - 0.177$, $r = 0.967$, $z = 2.043$, $P<0.05$) and with carapace length (Figure 3) ($Y = 0.813X - 0.264$, $r = 0.822$, $z = 1.162$, $P<0.05$).

Other plots analyzed but not discussed in detail here show similar relationships which further substantiate the facts given above: length of comblike row of spines on inner uropod plotted against length of carapace; length of comblike row of spines on inner uropod plotted against longest spine in row; length of inner uropod plotted against length of carapace; number of spines per 0.01 mm in comblike row of spines on inner uropod plotted against length of carapace. Size of cornea, shape of rostrum, shape of antennal scale, spination of telson, and relative lengths of uropods on specimens from throughout the range were compared. No constant differences were noted that would define geographic races.

Supplemental Description

Despite its abundance, *Neomysis americana* has not been described and illustrated fully. The reason for this omission is obvious: of the 16 known species of *Neomysis*, it is the only one that occurs in the western North Atlantic and is not likely to be confused with any other mysid within its range. Three mysid genera are similar to *Neomysis: Acanthomysis, Paracanthomysis*, and *Proneomysis*. The last two are confined to the North Pacific, and the only Atlantic representative of the 13 known species of *Acanthomysis*, *A. longicornis* (Milne Edwards), is limited to European waters.

However, the lack of an adequate description of *N. americana* gave Ii (1964) some difficulty before he decided not to identify a *Neomysis* from Korea as *N. americana* but to describe it as a new species, *N. orientalis*. To obviate problems such as this, we offer Figures 4A-K and 5A-J and comments on some characters for which adequate illustrations are not available.

The rostrum (Figure 4A) is broadly rounded as in *N. intermedia* and *N. japonica*. The eyes are as described by W. M. Tattersall (1951), with a broad cornea occupying half the eyestalk. Medially, just before the eyestalk narrows, it is produced into a low protuberance armed with short setae. W. M. Tattersall described the telson (Figure 4K) as having about 40 spines on each lateral margin; the number of spines depends on the body size and ranges from about 20 to 40. The peduncle of antenna 1 is shown in Figure 4B, C, D, the latter showing the male lobe. W. M. Tattersall's (1951) Figure 77A shows the antennal scale without a suture, which would be unique for the genus. Our specimens have a distinct suture (Figure 4D) setting off a short distal segment. As in other species of *Neomysis* the labrum is produced anteriorly into a spiniform process (Figure 4E, F), and the terminal segment of the mandibular palp (Figure 4G) is relatively slender.

According to W. M. Tattersall (1951) the "tarsus" of pereopods 2-7 is 8-9 segmented. We find that the number of segments increases with body size (Figure 5A, C) as in *N. patagona* (O. S. Tattersall, 1955b; Holmquist, 1957). The proximal suture may be incomplete, not present medially; in such pereopods an additional tarsal segment would be counted when viewed laterally. Our counts are in lateral view and include both partly fused proximal segments. Small juveniles have 6 segments; small adults from Pamlico Sound, N.C., 7 segments; large adults from Woods Hole, Mass., 8 segments; and large adults from the York River, Va., 9 segments. The number appears to be rather constant among the pereopods of an individual, but may differ by 1 segment in one or two of the pereopods.

The genus *Neomysis* is unique in having median fingerlike papillae on the last two or three pereonal sterna of gravid females (W. M. Tattersall, 1932). W. M. Tattersall (1951) found these papillae on the last two sternae of *N. americana*, and we show them in Figure 4J. Their function is unknown. Other characters of *Neomysis* are the presence of a bailing lobe on the posterior margin of the oostegite of pereopod 6 (Figure 5E) and a rudimentary oostegite on pereopod 5 (Figure 5D).

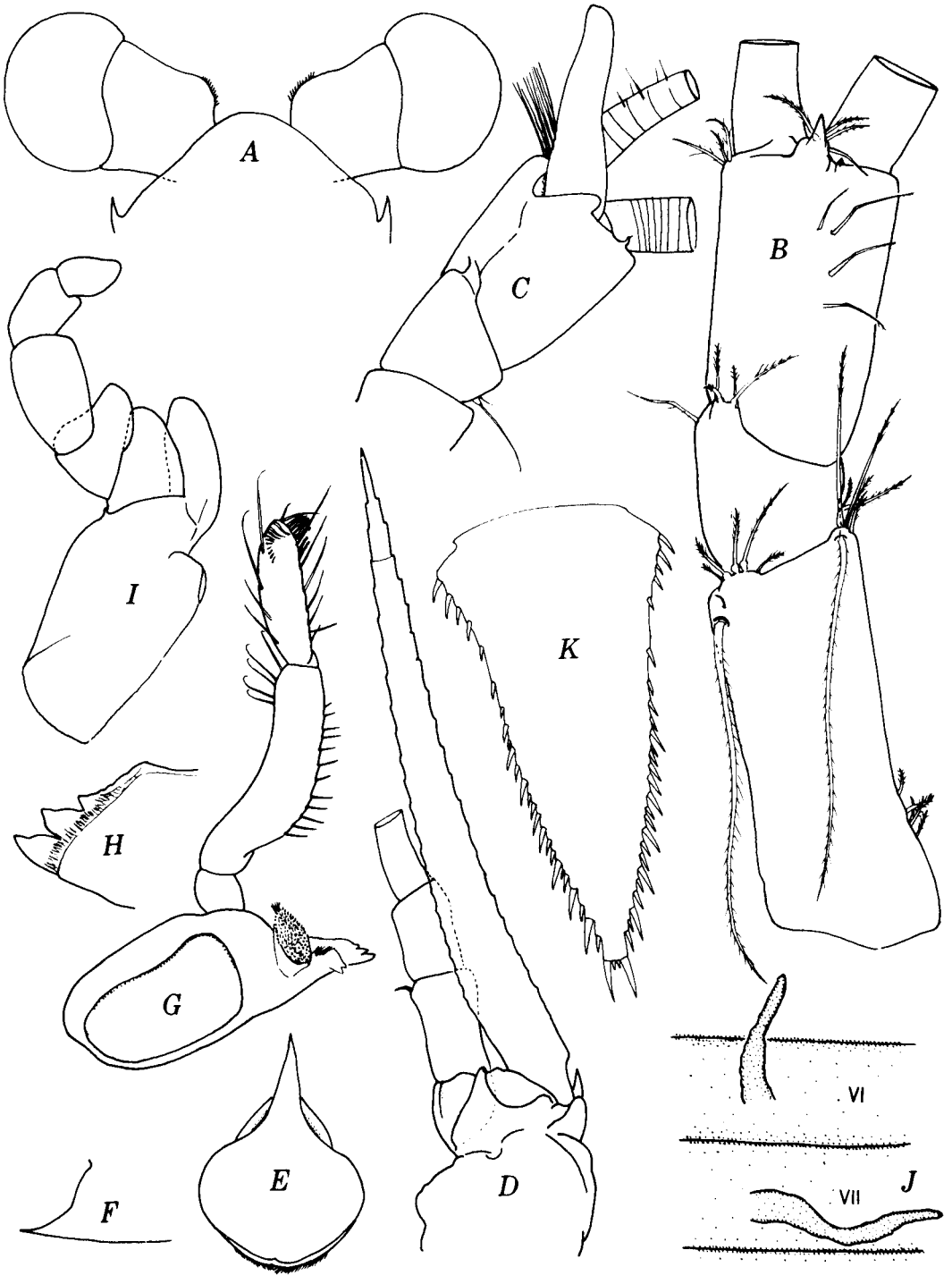

FIGURE 4.—*Neomysis americana*. A, Rostrum and eyes, dorsal (♀, New Brunswick). B, Right antenna 1 peduncle, dorsal, (♀, New Brunswick). C, Antenna 1 peduncle, ventral, (♂, York River, Va.). D, Antenna 2, ventral (♂, Adams Creek, N.C.). E, Labrum, ventral (♀, Pamlico Sound, N.C.). F, Same, lateral. G, Left mandible (♀, New Brunswick). H, Incisor of same. I, Right maxilliped, posterior, setae omitted (♂, York River). J, Sternal processes of pereonites VI and VII. K, Telson, dorsal (♂, Adams Creek).

FIGURE 5.—*Neomysis americana*. A, Endopod of pereopod 6 (♀, New Brunswick). B, Apex of same. C, Endopod of pereopod 7 (♀, New Brunswick). D, Oostegite of pereopod 5. E, Oostegite of pereopod 6 (arrow points to bailing lobe). F, Pleopod 4, ♂. G, Apex of same. H, Uropod, ventral (♀, Pamlico Sound, N.C.). I, Spine row of inner uropod (♂, Nova Scotia). J, Same, (♂, Adams Creek, N.C.).

Distribution

Neomysis americana inhabits estuaries and nearshore ocean from mesohaline reaches of the St. Lawrence River near St. Joachim on the north shore and Montmagny on the south, downstream around the Gaspé Peninsula, and from southern Newfoundland southward through the maritime provinces of Canada, along the United States to St. Augustine, Fla. Collections south of St. Augustine yielded no specimens, but the species may range as far southward as Cape Canaveral.

Prominent in estuaries, *N. americana* is also found at sea. Whiteley (1948) recorded it on Georges Bank inside the 100-m margin but most abundantly in water 75 m deep or less. Wigley and Burns (1971) showed essentially this pattern in their distribution summary. It was partly the distribution shown by these samples produced with the aid of grab samplers and dredges at a great number of stations to depths beyond 100 m between Nova Scotia and southern Florida that suggested an oceanic population north of Cape Henry, Va., separated from a southern estuarine one. None of their southern samples contained *N. americana*.

Neomysis americana was found in only four samples (total of 10 specimens) from the *Theodore N. Gill* material. These were: Cruise 4, 5 October-4 November 1953, Station 56 off Myrtle Beach, S.C. (2) - Cruise 9, 3 November-12 December 1954, Station 22 off St. Augustine, Fla. (1); Station 23 off mouth of St. Johns River, Fla. (6); Station 56 (1). All these stations were in water 10 m deep or less.

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NOTES

THE MEAN ANNUAL CYCLE OF COASTAL UPWELLING OFF WESTERN NORTH AMERICA AS OBSERVED FROM SURFACE MEASUREMENTS

One of the world's major upwelling regions lies off the west coast of the United States and northern Mexico. This paper summarizes marine surface observations to describe the normal yearly cycle of intensity of upwelling for the major portion of the northeastern Pacific coastal upwelling region.

Sverdrup (1938) applied Ekman's (1905) theory to account for a coastal upwelling situation observed off southern California. He proposed a mechanism by which water is transported offshore in the surface Ekman layer due to the stress of the wind on the sea surface and is replaced by water upwelled from depth. Wooster and Reid (1963) presented evidence that this is, indeed, the dominant mechanism acting in regions of slow, diffuse eastern boundary currents wherein lie the major coastal upwelling areas of the world, including that of the northeastern Pacific.

Our approach is to define the mean annual cycle of offshore Ekman transport along the west coast of the United States and the immediately adjacent regions of Canada and Mexico and to correlate this with features indicative of upwelling which appear in the long-term mean monthly distributions of sea surface temperature.

Marine surface weather observations for this study were obtained from a version of the National Climatic Center's tape deck of marine surface observations (Tape Data Family-11) in use at the U.S. Navy Fleet Numerical Weather Central. The observations in this file come primarily from merchant and naval ships and sometimes contain various errors in position, measurement, or processing. Consequently, the sea surface temperature data were subjected to an editing process which consisted of two filters. First, a gross error check was performed to eliminate nontemperatures. Second, the data were checked by comparison with a running mean of 10 reports. When a report of sea surface temperature differed from the running mean by greater than 9°C, the report was rejected. Wind speeds of greater than 100 m/s were rejected. "Variable" winds (no direction reported, low reported speed) were treated as calms.

The Ekman transport was calculated by the following procedure. The stress vector was computed from each wind observation according to the classical square law:

$$\vec{\tau} = \rho_a \, C_D \, |\vec{v}|\vec{v} \, ,$$

where $\vec{\tau}$ is the stress of the wind on the sea surface, ρ_a is the density of air (0.00122 g/cm^3), C_D is an empirical drag coefficient (0.0013), $\vec{v}$ is the observed wind velocity vector, and $|\vec{v}|$ is the observed wind speed The resultant Ekman wind stress transport, $\vec{M}$, was computed according to,

$$\vec{M} = \frac{1}{f} \vec{\tau} \times \vec{k}$$

where $\vec{\tau}$ is the wind stress vector, f is the Coriolis parameter, and $\vec{k}$ is a unit vector directed vertically upward.

Figure 1 displays composite monthly values of these data for the 20-yr period, 1948-67. The plot on the left displays time series isograms of offshore component of Ekman transport while the central plot shows similar isograms of sea surface temperature. The coordinates are north-south distance on the ordinate and time by month on the abscissa. Each plot represents about 75,000 individual observations made within the 1° squares shown in the coastline plot to the right. The number of reports per 1° square per month was in the range 22 (in January off Vancouver Island) to 1,884 (in October off Los Angeles).

The sea surface temperature plot reveals a normal north-south gradation of temperature and a seasonal warming-cooling cycle with minima from February to April and maxima in August and September. The effects of upwelling are seen as distortions of this general pattern.[1]

In the northern portion, Cape Blanco to Vancouver Island, offshore Ekman transport is weak and occurs from about May through

[1]The fine scale details of the temperature distribution are masked by the 1° square spatial averages. For a detailed treatment of the mean temperature cycle in the southern portion of the region the reader is referred to Lynn (1967).

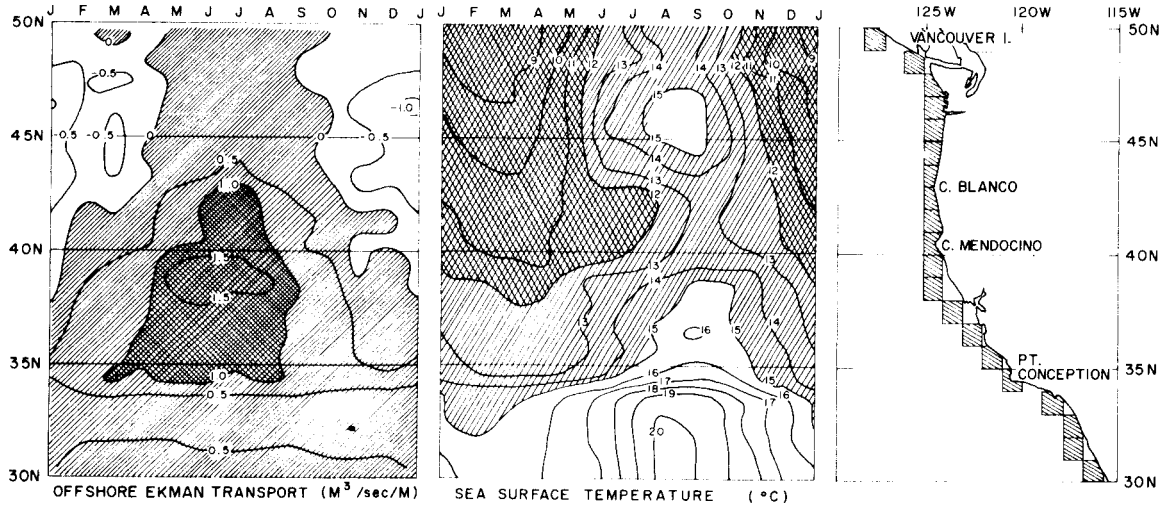

FIGURE 1.—Time series isograms of long-term composite monthly offshore Ekman transports (m^3/s per meter of coastline) and sea surface temperature (degrees Celsius) for the 20-yr (1948-67) period within the indicated 1° coastal squares.

September. The weakness of the transport is reflected by the presence of substantial seasonal warming. The region defined by temperatures greater than 15°C, located off Washington-Oregon during late summer, probably reflects the warming of the low-salinity Columbia River plume water which spreads over a large area of ocean surface. Some of the apparent warming may be due also to the concavity of the coastline in this area which could cause a greater proportion of the observations to be taken farther offshore, both because the 1° squares extend farther off the coast and because the coastwide shipping tracks may be displaced offshore.

South of Cape Blanco an abrupt increase of summer offshore Ekman transport is indicated, particularly during June and July. This is associated with a suppression of seasonal warming during early summer. Consequently, the period of maximum sea surface temperature is delayed until September when offshore transport has relaxed considerably.

South of Cape Mendocino Ekman transport is directed offshore for virtually the entire year and reaches its greatest value for the whole coast at about lat. 39°N during May through August. This maximum corresponds to an extreme suppression of seasonal warming indicated by nearly horizontal isotherms in the figure.

South of Point Conception, the offshore Ekman transport, although remaining generally positive throughout the year, is small and an abrupt southward increase in temperature, particularly during the summer, is apparent. Due to the tendency for a cyclonic eddy to form in the Southern California Bight (Reid, Roden, and Wyllie, 1958), warm advection not directly related to upwelling may be an important factor in this increase.

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THE RESIDUAL LIPIDS OF FISH PROTEIN CONCENTRATES

Previous papers (Medwadowski, Van der Veen, and Olcott, 1967, 1968; Medwadowski et al., 1971), presented data on the residual lipids in fish protein concentrates (FPCs) from red hake, *Urophycis chuss*; Gulf menhaden, *Brevoortia patronus*; pout, *Macrozoarces americanus*; and alewife, *Alosa pseudoharengus*; and some preliminary data on the effects of storage on the lipids. After 6 mo at 37° or 50°C, there were decreases in the contents of highly unsaturated fatty acids (C20:5 for alewife and C20:5 and C22:6 for pout and Gulf menhaden), and an appreciable decrease in the amount of lipid extractable from a menhaden FPC that originally contained 0.56% lipid, but no change in the amount extractable from FPCs that originally contained 0.11% (pout) or 0.06% (alewife) lipids.

In this paper we present data on the composition of lipids extracted from additional samples of FPCs (from Pacific hake, *Merluccius productus*; northern anchovy, *Engraulis mordax*; Atlantic menhaden, *Brevoortia tyrannus*; and Atlantic herring, *Clupea harengus harengus*) and also on the effects of storage, at several temperatures and humidities, on the composition of the residual lipids in a hake FPC preparation.

Materials and Methods

The FPCs had been prepared at National Marine Fisheries Service laboratories by countercurrent extraction of ground fish with hot isopropyl alcohol, followed by solvent removal and milling (Knobl et al., 1971).

Samples of a hake FPC were stored at the College Park Fishery Products Technology Laboratory at 21.1°, 32.3°, and 43.3°C and at 50% and 90% relative humidities for each temperature for periods of 1, 3, 6, and 12 mo (Green, 1972). The control was held at −29°C and ambient freezer humidity. The samples were shipped in plastic bags, cooled with dry ice (except for the zero time control sample which was shipped at ambient temperature), and stored at −18°C pending analyses.

Two procedures for determining moisture content (volatile matter) of the hake FPC samples were compared: 30-45 h at 110°-115°C, and 1 h at 130°C (Association of Official Analytical Chemists method, Horwitz, 1970:211). In the latter case, the drying was interrupted after 30 min; the caked meal was broken with a stirring rod; and the meal adhering to the rod was brushed back into the glass-stoppered weighing bottle in which the sample was being dried and weighed. Results from the two methods were in close agreement. The shorter method with the modification of the intermittent stirring was used thereafter.

The lipids were extracted (Soxhlet) in duplicate or triplicate with chloroform-methanol (2:1) from 200-g portions of the FPCs in large prewashed thimbles and analyzed as described by Medwadowski et al. (1971) with the following modifications in some cases. Purification was accomplished with a 2 × 22 cm Sephadex[1] column chromatography (Siakotas and Rouser, 1965; Rouser, Kritchevsky, and Yamamoto, 1967) and flow was by gravity. The saponification-methylation procedure used for determination of fatty acids was that described by Metcalfe, Schmitz, and Pelka (1966). The amounts of lipid were determined by drying aliquots of their solutions on a warm hot plate in preweighed disposable aluminum pans (Rouser et al., 1967).

Results and Discussion

Yields and fatty acid composition of the lipids extracted from seven separate runs—three from Pacific hake, two from northern anchovy, and one each from Atlantic herring and Atlantic menhaden—are shown in Table 1.

The two anchovy FPCs had somewhat similar fatty acid compositions; the main differences were in the amounts of C16:0 and C20:5. Herring FPC contained relatively larger percentages of C20:1 and C22:1. The Pacific hake FPCs, samples 8, 9, and 10, were similar in fatty acid composition but contained relatively more C18:1 than the FPCs from the other fish. The lipids of samples 8, 9, and 10, in general, resembled those of a red hake FPC, P-5 (reported previously by Medwadowski et al., 1967), and those of fresh red hake (Medwadowski et al., 1967, 1968). The Pacific hake FPCs, samples 8, 9, 10, and 78-103 (Table 3), contained higher percentages of C20:5 and C22:6 than red hake FPC P-5 and fresh red hake. Possibly less oxidation had occurred during processing, or the fish from which the FPCs were made had been subsisting on different foodstuffs.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—A comparison of lipids extracted from several fish protein concentrates.

FPC	Volatile matter (%)	Lipid[2] (%)	Fatty acid composition[1](%)															
			14:0	15:0	16:0	16:1	17:0	iso 18:0	18:0	18:1	18:2	18:4	20:0	20:1	20:5	22:1	22:5	22:6
Anchovy	—	0.08	8.0	1.0	26.2	7.4	1.3	0.2	7.0	13.9	2.3	1.2	0.7	1.9	9.5	2.4	0.5	13.0
Anchovy (B0308)	2.17	0.28	8.2	1.2	16.7	10.6	1.4	0.6	5.8	18.1	1.8	tr	2.0	0.9	15.4	tr	0.8	14.7
Hake - 8	4.12	0.12	4.1	0.4	17.0	10.2	—	—	4.4	29.2	1.1	—	—	3.3	15.4	—	0.4	11.3
Hake - 9	3.95	0.28	4.4	0.4	18.2	9.6	—	—	5.7	28.2	1.2	—	—	3.9	14.4	—	0.8	10.0
Hake - 10	3.77	0.21	3.3	0.3	21.1	8.5	—	—	4.2	31.5	1.0	—	—	2.7	14.2	—	0.5	10.5
Menhaden (B0204)	2.89	0.30	9.6	1.1	17.9	14.3	2.3	2.4	7.7	16.8	1.8	—	1.8	1.6	12.5	—	1.7	5.5
Herring	—	0.17	5.8	0.6	15.9	4.6	—	0.1	3.4	12.2	1.9	0.2	—	13.2	5.7	24.3	—	8.8

[1]Number of carbon atoms: number of double bonds. Additional fatty acids, tentatively identified but present in amounts of 1% or less, were: 12:0, anteiso 15:0, iso 16:0, 16:2, 18:3, 19:0, iso 20:0, 20:2, 20:3, 21:0, 22:2, 22:3, 22:4, 24:1.
[2]Dry basis

The percentages of volatile matter in the Pacific hake (78-103) samples stored at different temperatures and humidities are shown in Table 2. The moisture content of the different samples was relatively constant during several month's storage in plastic bags at −18°C. The increase in volatile matter after equilibrium had presumably been reached, in the samples stored at 90% relative humidity might indicate gradual changes in the affinity of the FPC samples for water or, possibly, the formation of volatile components other than water.

Gas chromatographic analyses of the methyl esters of the fatty acids from the Pacific hake FPC show that it was relatively stable under most of the storage conditions described (Table 3). Shono and Toyomizu (1972) suggested that the rate of decrease of C22:6 acid could be used as an indication of oxidative deterioration in fish products. There were no apparent decreases in C22:6 acid content at 50% relative humidity. However, at 90% relative humidity, there were very significant decreases of C22:6 acid content of from 8.9 to 26.1% in the temperature range of 21° to 43°C. Thus water activity had more effect than temperature on the stability of this FPC preparation.

Each hake FPC extract described in this paper was separated by silicic acid chromatography into three separate fractions, as previously described (Medwadowski et al., 1971). There were little or no significant changes in the amounts recoverable from each fraction (not shown), and they were not analyzed further.

In general, these observations confirm the relative stability of FPC during storage, even under adverse conditions of temperature and humidity.

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TABLE 2.—Changes in the volatile matter of Pacific hake FPC (78-103) with storage at different temperatures and humidities.

Storage time (month)	Average volatile matter (%)						
	Storage conditions[1]:						
	Control	21-50	21-90	32-50	32-90	43-50	43-90
0	5.2						
1	5.4	7.6	10.5	7.8	12.8	7.9	12.5
3	5.2	7.8	10.7	8.1	13.1	8.0	12.4
6	5.3	8.1	11.5	8.7	14.2	7.9	13.4
12	5.8	7.9	12.2	8.3	14.8	7.7	15.4

[1]Hyphens separate degrees Celsius and percent relative humidity.

TABLE 3.—Effect of storage on the lipid composition of Pacific hake FPC (78-103).[1]

Storage conditions[2] T (°C)	RH (%)	Storage time (month)	Total lipid[3] (%)	Percentages of the major fatty acids[4] 14:0	16:0	16:1	18:0	18:1	20:1	20:4	20:5	22:5	22:6	Reduction of C22:6 (%)
		0	0.09	1.3	15.8	3.1	7.5	25.3	3.3	2.9	9.9	1.9	29.1	
		1	0.09	1.4	15.6	3.1	7.4	25.3	3.3	2.8	10.1	1.9	29.2	
-20	AF	3	0.10	1.5	15.9	3.2	7.0	24.9	3.1	2.8	10.2	2.0	29.4	
		6	0.10	2.3	15.1	5.0	6.0	22.8	2.2	2.5	15.1	1.4	27.5	5.5
		12	0.12	2.2	15.4	4.8	6.4	23.7	2.2	2.8	13.7	1.4	27.5	5.5
		1	0.10	1.4	15.6	3.1	7.3	25.4	3.0	2.9	10.3	2.1	28.9	
		3	0.11	1.4	15.6	3.4	8.4	22.8	2.8	3.0	11.1	1.8	29.8	
21	50	6	0.10	1.8	13.7	4.3	7.8	23.2	2.7	3.1	12.9	1.8	28.6	1.7
		12	0.12	2.1	16.2	4.9	6.8	24.2	2.2	2.8	12.9	1.1	26.9	7.6
		1	0.11	1.4	15.4	3.0	7.5	25.1	3.1	2.9	10.2	2.0	29.2	
		3	0.12	1.3	15.2	3.2	9.0	23.7	3.6	2.9	10.2	1.8	29.3	
21	90	6	0.10	1.9	16.8	4.7	7.2	24.1	2.3	2.8	12.3	1.5	26.5	8.9
		12	0.12	2.3	16.1	5.2	6.4	24.1	2.0	3.0	12.9	1.5	26.5	8.9
		1	0.10	1.4	15.9	2.9	7.5	25.3	3.3	2.8	10.6	2.0	28.4	
		3	0.10	1.5	15.4	3.3	8.0	23.5	3.2	2.8	10.6	2.0	29.8	
32	50	6	0.11	1.9	15.2	4.9	8.5	25.1	2.4	2.8	11.5	1.6	26.0	10.7
		12	0.10	2.2	16.7	5.4	5.6	24.4	1.4	2.7	13.9	1.0	26.6	8.6
		1	0.11	1.4	15.5	3.2	7.5	24.3	2.9	2.9	10.1	2.1	30.0	
		3	0.12	1.5	16.3	3.6	8.0	23.5	3.0	3.0	10.5	1.9	28.8	
32	90	6	0.12	1.6	16.4	4.2	8.1	25.3	2.6	2.6	11.2	1.2	26.8	7.9
		12	0.12	2.1	17.6	5.0	7.0	25.8	2.2	2.5	11.4	1.1	25.3	13.1
		1	0.10	1.5	15.2	3.0	8.4	24.7	3.2	3.0	9.6	2.0	29.4	
		3	0.12	1.4	16.5	3.1	8.4	25.2	3.4	2.8	9.3	1.8	28.1	3.4
43	50	6	0.10	1.8	16.6	4.5	7.9	25.6	2.3	2.6	11.5	1.1	26.0	10.7
		12	0.12	2.2	15.6	4.9	6.9	24.4	2.1	2.7	12.9	1.2	27.0	7.2
		1	0.10	1.3	15.5	3.1	8.5	25.9	3.6	3.0	9.0	1.8	28.2	3.1
		3	0.12	1.5	17.0	3.4	8.6	24.9	3.2	2.9	9.1	1.8	27.6	5.2
43	90	6	0.12	2.4	16.7	4.9	7.7	25.3	2.3	2.7	11.3	1.3	25.5	12.4
		12	0.13	3.1	18.8	5.8	7.9	27.9	2.3	2.4	9.7	0.7	21.5	26.1

[1]Values are averages from duplicate or triplicate samples.
[2]T—Temperature, RH—Relative humidity, AF—Ambient freezer humidity.
[3]Based on dry weight of FPC.
[4]Number of carbon atom:number of double bonds. The weight percentages were calculated on the basis of the 10 major acids (shown) constituting 100%.

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LENGTH-WEIGHT RELATIONS FOR FIVE EASTERN TROPICAL ATLANTIC SCOMBRIDS

This paper presents an analysis of fork lengths and body weights of five species of scombrids measured from landings at several ports on the west coast of Africa during 1967 and 1968: yellowfin tuna, *Thunnus albacares*; skipjack tuna, *Katsuwonus pelamis*; bigeye tuna, *T. obesus*; little tunny, *Euthynnus alletteratus*; and frigate mackerel, *Auxis* sp. Sampling of landings took place between 26 September 1967 and 22 May 1968 at the ports of Dakar, Senegal; Freetown, Sierra Leone; Abidjan, Ivory Coast; Tema, Ghana; and Benguela, Angola. Samples were also taken from fish stored at a cannery in Mocamedes, Angola. Fish were captured by bait (pole-and-line) boats, purse seiners, and combinations of both. Only whole fish were used for this study, landed in fresh, iced, frozen, and indeterminate conditions. Fork lengths were usually measured to the nearest centimeter. Weight was usually measured to the nearest 0.1 kg. All nonmetric data were converted to centimeters and kilograms.

The allometric length-weight equation is used to describe the relation between length and weight:

$$W = aL^b e \qquad (1)$$

where W = weight in kilograms
L = length in centimeters
a and b = estimated parameters.
e = error term

Results

Estimates of a and b were made for each sample. A wide range in values of a and b occurred for the same species and, in some cases, for the identical sample category (category is defined as port, gear, and method of preservation of fish), that was at first alarming. However, examination of plots of the estimated curves revealed only minor differences among samples at sizes included in the samples. It was also noted that estimates of a are closely related to estimates of b (Figure 1), again indicating the fish at the same length weighed approximately the same.

Analyses of covariance were used to test the statistical significance of differences among length-weight relations within a sample category. F-tests for the significance of differences of the estimates of both parameters a and b[1] were made instead of F-tests for each parameter as is usually done, because I believe that the close relation between estimates of a and b demonstrates that no additional useful information would be obtained by making the separate tests. F-values for differences among samples within a category were almost always significant for all species with more than one sample. As mentioned previously, plots of the fitted lines showed only minor differences between samples for sizes found in both samples.

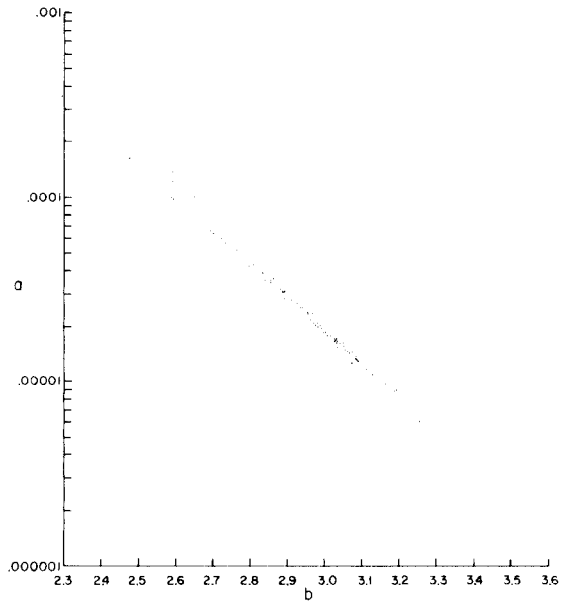

FIGURE 1.—Relation between estimates of a and b of the allometric length-weight relation from samples of Atlantic yellowfin tuna.

Analyses of covariance were also used to test whether differences among sample categories were present. Nested models were used because the significant differences among lines within sample categories indicated that samples rather than individual fish should be used to estimate the error term of the model. Only data for yellowfin and skipjack tunas were examined because there were insufficient data for the other species. Table 1 presents the analysis of covariance of differences among all sample categories for yellowfin tuna. The F-value for difference among sample categories is statistically significant at the

[1] H_0; $a_i = a_j$ and $b_i = b_j$ where a_i = value of a from ith sample, b_i = value of b from ith sample and $i \neq j$.

TABLE 1.—Analysis of covariance of length-weight relation of yellowfin tuna.

Source	Degrees of freedom	Sum of squares	Mean square	F-value
Categories	24	1.321851	0.0550771	3.4115*
Samples within categories	128	2.066484	0.0161444	6.7748*
Residual	3,485	8.304751	0.0023830	
Total	3,637	11.693086		

*Significant at 1% level.

TABLE 2.—Analysis of covariance of length-weight relation of skipjack tuna.

Source	Degrees of freedom	Sum of squares	Mean square	F-value
Categories	20	2.560355	0.128018	5.0189*
Sample within categories	84	2.142605	0.0255072	7.3030*
Residuals	2,448	8.550099	0.0034927	
Total	2,552	13.253059		

*Significant at 1% level.

1% level. The F-value for difference among samples within a category is greater than that among categories. Table 2 presents results for skipjack tuna. Again the F-value is statistically significant at the 1% level, and the F-value among samples within categories is greater than that among categories. The reasons for the differences are not known. Although there was considerable overlap of sizes of fish encountered among the samples, size composition of the samples did differ and may have contributed to the differences in the length-weight relations because Equation (1) may not perfectly describe the length-weight relation for fish of all sizes. Figure 2 illustrates the variability found in the length-weight relations of yellowfin tuna. The variability among the relations increases with size as Equation (1) assumes.

Statistics of length-weight relations from combined samples for each species are presented in Table 3.

Discussion

Length-weight relations for yellowfin tuna from the Pacific (Chatwin, 1959), from the Atlantic (Poinsard, 1969), and from the present study are illustrated in Figure 3. There is reasonably close agreement among the three curves at small sizes. The Pacific yellowfin tuna appear to be heavier at larger sizes than fish from the Atlantic, but Chatwin did not include fish larger than 115 cm in his work. Two relations are used in Poinsard's work. A relation between fork length and predorsal length and one between predorsal length and weight. Poinsard tried several functions to explain the relations. In the case of fork length and predorsal length he chose the following function:

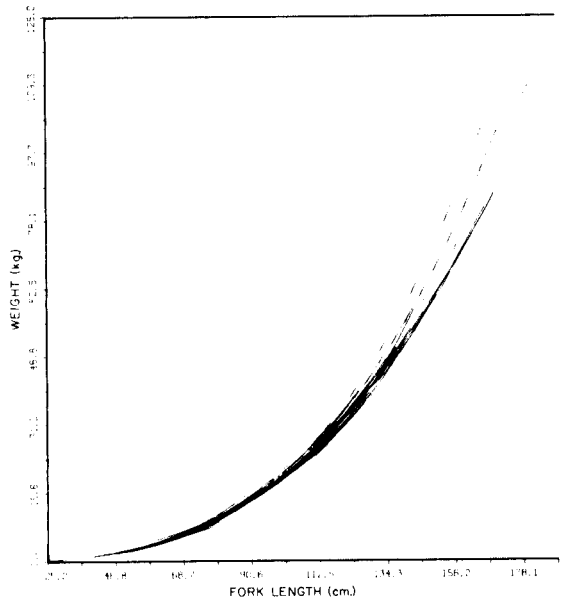

FIGURE 2.—Estimated length-weight relations for all sample categories of Atlantic yellowfin tuna.

$$LD_1 = -16.58774 + 4.66294\sqrt{L} \qquad (2)$$

where LD_1 = predorsal length

He based his choice on the fact that Equation (2) resulted in the highest value of r (correlation coefficient) of the several functions he tried. The value of r when Equation (2) was used was 0.99402, but when a power relation similar to Equation (1) was used the value of r (0.99386) is only slightly less. Figure 3 is based on the square root relation between fork length and predorsal length as recommended by Poinsard. It is very difficult, however, to interpret differences between r values when different dependent variables are used: predorsal length in one case, log (predorsal length) in the other. Equation (2) seems a poor choice because it implies that $LD_1 \leq 0$ when $L \leq 12.65$. The estimated weights using Poinsard's logarithmic relation are illustrated in Figure 4—the two curves are very similar for all lengths. This similarity indicates that the results of Poinsard and of this study are accurate estimates of the average length-weight relationship of eastern tropical Atlantic yellowfin tuna.

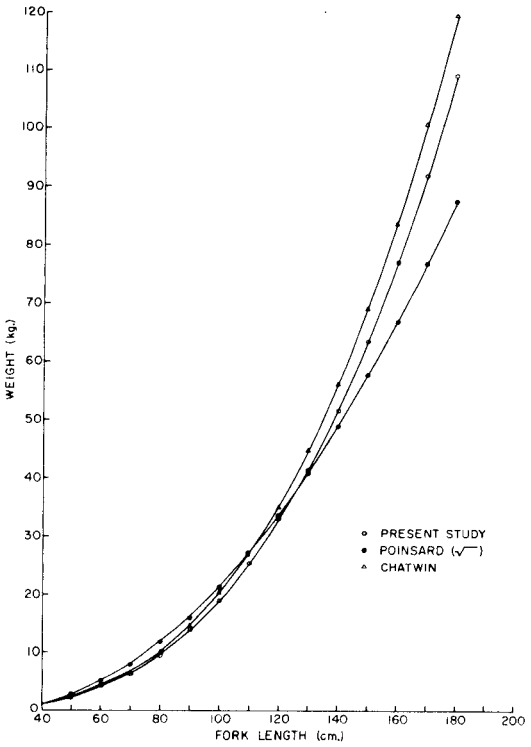

FIGURE 3.—Estimated length-weight relations for yellowfin tuna (Chatwin, 1959; Poinsard, 1969). Poinsard's relation based on square root relation between predorsal and fork length. Chatwin's study did not include fish longer than 115 cm.

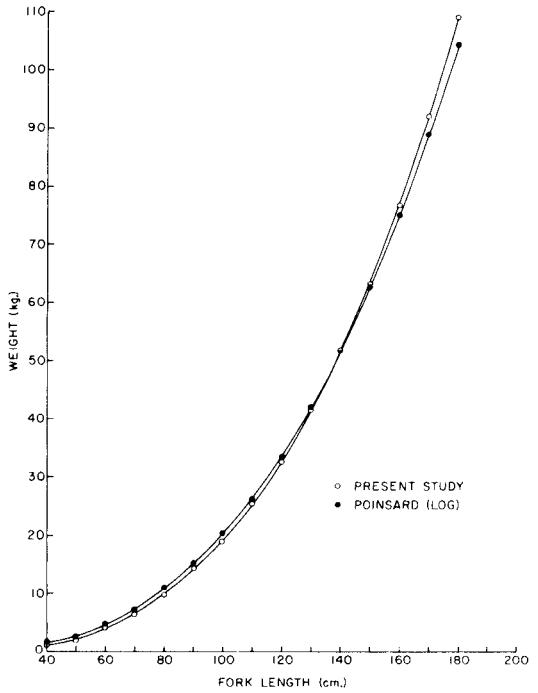

FIGURE 4.—Estimated length-weight relations for yellowfin tuna (Poinsard, 1969). Poinsard's relation based on logarithmic relation between predorsal and fork length.

Since it is desirable to utilize the function which was estimated directly from either predorsal or fork length data, the results of Poinsard should be used when predorsal lengths are measured and the results of the present study should be used when fork lengths are measured.

Beardsley[2] (pers. commun.) allowed me to examine length and weight measurements of more than 2,000 yellowfin tuna captured in the western Atlantic. These data are very similar to the data used in the present study.

Beardsley and Richards (1970) estimated the parameters of Equation (1) for skipjack tuna and little tunny captured off the coast of Florida. Their estimate of the equation for skipjack tuna is

$$W = 0.00007927L^{3.22750}$$

and for little tunny is

$$W = 0.0000181L^{3.02838}$$

[2]Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.

These results are quite similar to the results of the present study. The range in fork length of skipjack tuna in their study was 38-78 cm and for little tunny 34-87 cm. Since these size ranges exceed the ranges encountered in this study their results should be used. Chatwin (1959) obtained similar results for skipjack tuna from the Pacific, and Batts (1972) for skipjack tuna from the western Atlantic.

The number of frigate mackerel used in this study is too small to produce very meaningful results. The results are presented here only to make them available to other workers.

Several authors including Pienaar and Thomson (1969) have questioned the validity of assumptions made about the error term in Equation (1). Also, the logarithmic transformation results in weight being slightly underestimated even if Equation (1) is correct. Results of simulations by Fox (1973)[3] indicate that b is unbiased and an unbiased estimate of a is given by

$$a' = a \exp\left(\tfrac{1}{2}\,(s^2{}_{W \cdot L})\right) \qquad (3)$$

[3]Fox, W. W., Jr. 1973. Some simple biologically useful functions and multiplicative error regression models. Unpubl. manuscr. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92037.

TABLE 3.—Statistics of length-weight relations for all data used in study.

Species	Number of fish	a	[1]b	Mean square error	Minimum fork length (cm)	Maximum fork length (cm)
Yellowfin tuna	3,689	0.000021804	2.96989	0.003265	40	170
Skipjack tuna	2,554	0.000005611	3.31497	0.005193	36	64
Bigeye tuna	190	0.000012494	3.12082	0.003405	41	132
Little tunny	753	0.000012000	3.08340	0.006935	41	57
Auxis sp.	50	0.000000280	4.13514	0.030871	30	45

[1]All estimates are significantly different than 0 at the 1% level.

where a' = unbiased estimate of a
$(s^2{}_{W \cdot L})$ = mean square error about the regression line.

The mean square errors for this study are low (Table 3). Thus the bias should be negligible. The results of this study were examined by comparing average weights of yellowfin used in the study against predicted weights. Differences were negligible as expected.

The significant differences found among samples and categories indicate that the variance of estimated numbers of fish caught, estimated from length frequency samples, could be reduced by a sophisticated sampling scheme which is stratified by category if not sample. Obviously it would be simpler to weigh fish from each sample rather than measure lengths, if one desired to stratify by sample. Logistics rule out this possibility. A formal cost-benefit analysis of the effort required to develop an adequate sampling scheme stratified by category probably would rule out this scheme. The significant differences among samples do point out the desirability of obtaining large numbers of samples rather than large sample sizes in further study of length-weight relations.

Acknowledgments

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ELECTRICAL THRESHOLD RESPONSE OF SOME GULF OF MEXICO FISHES

Threshold voltage is the minimum electrical potential to which an animal responds (Vibert, 1967). Usually threshold measurements are inexpensive and easy to obtain, and they provide guidelines for designing electrical fishing systems. Bary (1956) and Kessler (1965) showed that threshold voltage varied according to water temperature, size of animal, and width of the pulse. Earlier workers clearly demonstrated that threshold voltages are affected by the position of the animal in the electrical field. Klima (1968) documented experimentally the mathematical relationship between the angle of the animal in the

electrical field and its threshold voltage. These authors have defined the basic physical and biological factors which affect the response of selected marine animals to electricity.

To understand more clearly the basic characteristics of electrical fields which control marine fishes, threshold response of selected Gulf of Mexico species was investigated. I determined the minimum threshold voltage (in a field with other specific characteristics) for Atlantic croaker, *Micropogon undulatus*; spot, *Leiostomus xanthurus*; longspine porgy, *Stenotomus caprinus*; chub mackerel, *Scomber japonicus*; and scaled sardine, *Harengula pensacolae*. I further attempted to determine the minimal effective pulse width by estimating the threshold voltage at selected pulse widths.

Procedure

Spot, Atlantic croaker, and longspine porgy were trawled in Mississippi Sound; minimizing injury to fish was accomplished by towing for only 10 min. Chub mackerel and scaled sardines were caught by night-lighting off the Mississippi Coast (Wickham, 1970). The experimental animals were held in shipboard tanks of circulating seawater while being transported to the Laboratory. Only fish acclimated for more than 3 days and in good physical condition were used. Threshold voltages were determined for 140 individuals. Each specimen was subjected to only one test and discarded.

Studies were conducted in a 72 × 45 × 45 cm, 190-liter plexiglass aquarium at temperatures between 15° and 17.5°C; salinities ranged from 19.6 to 26.4‰.

An electrical system providing a uniform electrical field was used. It had a capacitor-discharge stimulation pulse that could be monitored from the center of the aquarium. Pulse shapes which exhibit a rapid rise in amplitude and slow rate of decay, such as capacitor-discharge pulses, are the most effective for controlling fish (Taylor, Cole, and Sigler, 1956; Vibert, 1967; Klima, 1972).

A pulse generator was used for the stimulation pulses. Pulses were applied to two monel electrodes mounted at opposite ends of the aquarium. Pulse characteristics were measured with a pair of pickup probes. These were constructed from two 3-mm diameter bronze rods 10 cm apart and insulated so that only the bottom 10 mm of each rod was exposed. Pulse characteristics were displayed on an oscilloscope as a graph of voltage against time.

Threshold voltages were determined with the fish held immobile parallel to the electric field in a plastic mesh tube in the center of the aquarium facing either the positive or negative electrode. Voltage was slowly increased until the fish responded by fluttering of the body. This value was then recorded from the oscilloscope and assumed to be the threshold voltage.

Results and Discussion

Kessler (1965) found that variations in pulse width alter the threshold voltage for shrimp. Pulse widths longer than 150 μs are satisfactory for stimulating shrimp, whereas below that width the power required for stimulation would be significantly greater. Longspine porgies stimulated with less than 100 μs pulse widths required at least four times more voltage to respond than fish stimulated with a wider pulse (Table 1). At narrow pulse widths threshold voltage was high; at the longer widths it was low, forming an inverse relationship.

Scaled sardine required higher voltages to elicit a response at narrower pulse widths than at wider pulse widths. At 45 μs it took almost 1.9 V/10 cm to elicit a minimum response, but at 100 μs it took only 1.3 V/10 cm, and at 250 and 1,000 μs it took only 1.0 and 0.9 V across 10 cm. A comparison of threshold voltages of scaled sardines at different pulse widths shows a significant difference between the threshold values at pulse widths tested (Table 1). Student's t-test was used in making these comparisons:

$$(t = 6.316,\ t_{0.975\,(18)} = 2.101)\ \text{45 and 100 } \mu\text{s},$$

$$(t = 3.815,\ t_{0.975\,(18)} = 2.101)\ \text{100 and 250 } \mu\text{s},$$

$$(t = 5.000,\ t_{0.975\,(18)} = 2.101)\ \text{250 and 1,000 } \mu\text{s}.$$

Although there was a difference in the minimum voltage within the 250 μs to 1.0 ms range, as shown by the reactions of scaled sardine, the difference in actual voltage was minimal. For scaled sardine the most efficient pulse width in terms of electrical power would be not less than 250 μs. Generally, threshold voltages at pulse

TABLE 1.—A summay of threshold voltages.

Species	Average V/10 cm	Variance	Pulse width (ms)	Electrode which fish faces	Sample size	Range fish length (mm)
Atlantic croaker	0.39	0.006	2.500	+	10	130-150
Atlantic croaker	0.30	0.001	2.500	–	10	120-150
Spot	0.38	0.048	2.300	+	10	102-132
Chub mackerel	0.31	0.005	2.300	+	15	175-189
Longspine porgy	2.90	0.004	0.045	+	10	90-106
Longspine porgy	1.82	0.004	0.100	+	10	91-106
Longspine porgy	0.35	0.001	0.250	+	10	93-111
Longspine porgy	0.35	0.001	2.500	+	10	92-110
Scaled sardines	1.89	0.331	0.045	+	10	85-98
Scaled sardines	1.00	0.010	0.045	–	5	78-93
Scaled sardines	1.29	0.056	0.100	+	10	80-101
Scaled sardines	0.83	0.003	0.100	–	5	84-91
Scaled sardines	1.00	0.020	0.250	+	10	79-94
Scaled sardines	0.80	0.300	0.250	–	5	88-98
Scaled sardines	0.90	0.020	1.000	+	10	80-99

widths greater than 2,000 μs were similar between species.

Atlantic croaker were used to test the hypothesis that fish require more voltage to show a threshold reaction when facing the positive electrode. Analysis of the average threshold voltages of croakers facing the positive and negative electrode by Student's t-test shows a significant difference between the values

$$(t = 3.60 \text{ and } t_{0.975\,(18)} = 2.101).$$

Scaled sardines showed a similar response (Table 1). These results confirm those of Bary (1956) where he showed that mullet required more voltage to respond when facing the anode than the cathode.

The cost of producing a useful electrical field in seawater is dependent upon the power required to elicit specific responses in the desired species. Pulse width obviously is a major factor which affects the power requirements along with voltage and pulse rate (Klima, 1972). Narrow pulse widths require proportionately less power than wider ones. Engineering design criteria for pulse generators are usually based on the minimum pulse width electronically possible. These results, however, indicate that pulse width should not be less than 250 μs and probably should range between 250 and 1,000 μs.

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OCCURRENCE OF A RATFISH IN THE COLUMBIA RIVER ESTUARY

A ratfish, *Hydrolagus colliei* (Lay and Bennett), was captured in the Columbia River estuary, near the Oregon shore, on 24 August 1972. Commercial fishermen Howard and Mark Simonsen captured the specimen near buoy 21, approximately 8 km upstream from the mouth of the river. They were fishing for salmon in 8 m of water with a dacron gillnet of 8 ⅝-inch mesh and an effective fishing depth of between 10 and 12 m. The fish was caught at 2030 h during an incoming tide; the actual depth, temperature, and salinity at place of capture are unknown. At the time of capture, however, our monitoring station, 3.2 km farther upstream, indicated a water temperature of 13.4°C and a salinity of 5‰ at a depth of 10 m. The salinity was increasing and reached 31‰ 5 h later. The ratfish was an adult male, 445 mm in length, weighing 460 gm (Figure 1). There are no known methods of determining the ages of chimaeroids, including the ratfish (Simmons and Laurie, 1972). The specimen was preserved and is now part of the collection at the facility of the Northwest Fisheries Center, National Marine Fisheries Service, at Hammond, Oreg. Although ratfish are distributed along the coast of western North America from southeastern Alaska to Baja California, including the upper Gulf of California (Hart, 1973), this is the first record of one appearing in the Columbia River estuary. In fact, no chimaeroid has been recorded from any estuarine water (Carl L. Hubbs, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92037, pers. commun).

"*Hydrolagus colliei* is the only species of chimaera reported from the west coast of the United States, and, unlike other species in the family, it generally inhabits relatively shallow water." (Halstead, 1970). According to Hart (1973), ratfish are common visitors to shallow Canadian waters but are most abundant at 92 to 275 m in inside waters and at 183 to 366 m in outside waters. He also reports that they are "in deeper water toward the south (as in northern California)". The occurrence in the deeper water toward the south is real and significant, but they may not occur in deeper waters off northern California because that is an area of extremely cold ocean temperatures (Carl L. Hubbs, pers. commun.). Day and Pearcy (1968) captured ratfish off the Oregon coast at depths between 40 and 200 m. Ratfish are weak swimmers, mostly noctural in behavior, but have been seen swimming at the surface in southeastern Alaska and British Columbia waters (Goode and Bean, 1895).

Maximum spawning activity is in late summer and early fall (Sathyaneson, 1966). On 26 June 1957, a large concentration of ratfish became

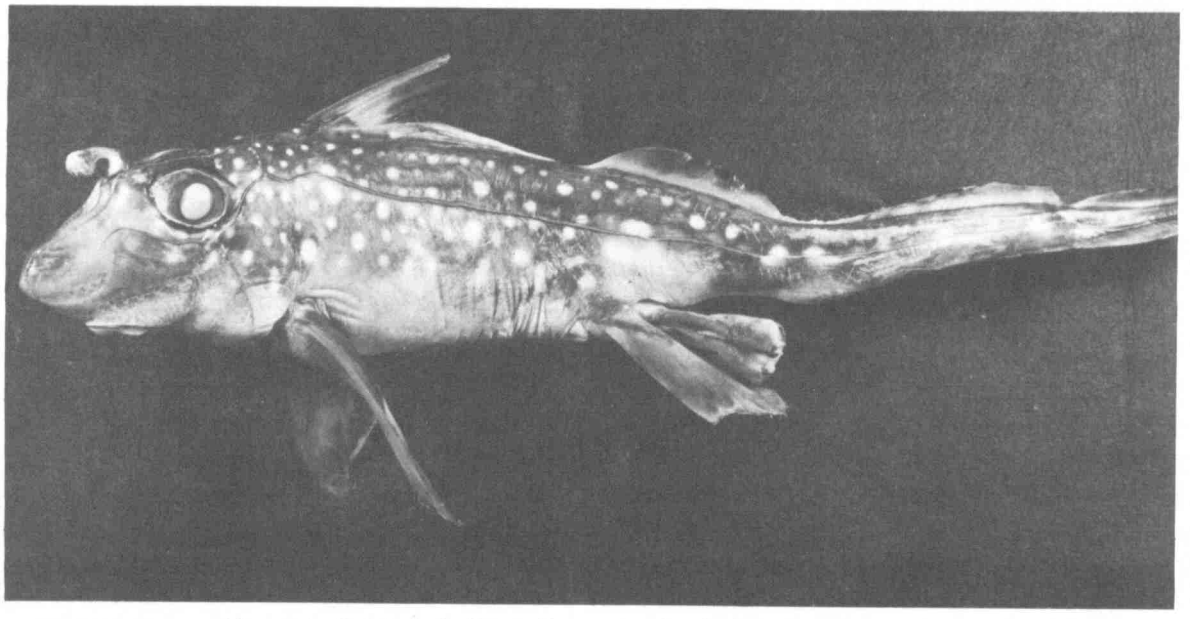

FIGURE 1.—Ratfish, *Hydrolagus colliei*, captured in the Columbia River estuary.

trapped in the tide pools of Cape Arago, Oreg. It was suspected they were spawning near shore (Jopson, 1958).

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UNUSUAL OCCURRENCE OF AN EASTERN BANDED KILLIFISH IN THE LOWER COLUMBIA RIVER

The recorded geographic range for the eastern banded killifish, *Fundulus diaphanus diaphanus*, is in the waters of the Atlantic coastal states from South Carolina north to Newfoundland. They occur in lakes, quiet rivers, and Atlantic coast estuaries (Hubbs and Lagler, 1958).

On 19 August 1971, an eastern banded killifish was collected by the National Marine Fisheries Service on the Oregon side of the Columbia River about 75 km upstream from Astoria. The fish, shown in Figure 1, was taken in shallow water with a 100-m long beach seine. River temperature

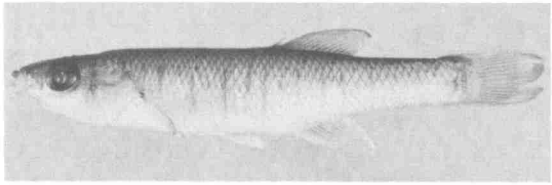

FIGURE 1.—Eastern banded killifish, *Fundulus diaphanus diaphanus*, captured in the lower Columbia River.

on the date of capture was 19°C. The specimen was 59 mm in standard length, and coloration was similar to that described by Trautman (1957) for the species, olivaceous on the dorsal surface with a light yellow ventral surface. This specimen also possessed an iridescent blue-green stripe horizontally along each side, which faded rapidly after capture. It is now in the collection of the National Marine Fisheries Service Biological Field Station at Hammond, Oreg. Additional specimens have not been taken in the area, and the authors conclude that the presence of the fish was probably due to an unauthorized release.

The authors wish to thank Carl E. Bond, Oregon State University, Corvallis, Oreg. and Carl L. Hubbs, University of California, La Jolla, Calif. for verifying the identification of the killifish and their review of the manuscript.

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IN MEMORIAM: ROBERT LOUIS DRYFOOS, 1939-1974

A modest and understanding man, an unselfish and loving husband, an affectionate father, a devoted son and grandson, and a dedicated and accomplished scientist, this is a rich life of accomplishment, Robert Louis Dryfoos.

He was always willing to lend a hand to his many friends and colleagues, always dependable in responsibilities, and solid in his accomplishments. He could achieve, whether it meant leading a local centennial parade high up on a Rotarian float as an old New England sea captain, or elucidating the complexities of the migrations of a million fish from Cape Cod to the Gulf of Mexico. His quiet nature belied his status as a respected fisheries expert and research administrator. As an authority on the dynamics of fish populations he made significant contributions to a better understanding of the complex fisheries in the northeast Pacific, the Atlantic coast, and in his most recent work, the fishery resources of the entire United States.

He had a natural curiosity that led him to the ocean at an early age. As a young boy in San Francisco he was never far from the sea, the fresh wet-smell of the surf, the screeching gulls, and the small fishing boats plying their catches under the Golden Gate. His curiosity and his willingness and ability to help others was to be satisfied in a decade of productive fisheries research. Not esoteric problem solving for problem sake, but rather a dedication to learn about the sea and unravel its vagaries of protein production. He collected, sifted, and synthesized previously unknown bits of information, pieced them together meticulously, systematically, and with keen intelligence and patience he would tell us more about how to develop and maintain our fragile fisheries. He teamed with other young and dedicated men, in Seattle, in Beaufort, at Charleston, Woods Hole, La Jolla, Narragansett, and in Washington. He was intent on learning how to better define and manage the wild populations in their tempest environment. And this was a pressing national need, not headline stuff, but the necessary and critical steps to be taken for the fisheries, that all too often are abused, overexploited, and in some cases damaged beyond repair. He chose this direction. He worked. He sweated. He persevered, and he accomplished.

His earliest work was done as a young college undergraduate with the International Halibut Commission in Seattle. He spent months at a time in the north Pacific, rubbing shoulders with halibut fishermen on the banks. They ran their trawls from Seattle up to Sitka in the Aleutians and into the Bering Sea. Bob's affinity to help and make a significant contribution was evident in his interest in going to sea with all the discomforts of tossing ship, hip boots deep in gurry, fish filled checkers, and cold night watches. He learned first hand about fishermen, their problems, the declining stocks, and pondered on how best to rebuild their catches. This early work began a decade of scientific output. While an undergraduate at the University of Washington in 1960 he published his first paper on new range extensions of fish in the north Pacific. His next contribution was made during his graduate

studies, while working part-time and summers for the College of Fisheries at the University. He and his professor reported on their discovery of the egg maturation, embryo development, and birth rates of the ocean perch of the northeast Pacific.

It was at the University of Washington, as an undergraduate that he caught the eye of his senior colleagues as a "comer." They saw in Bob, that all-too-rare combination of an individual with the ability to detect a problem, the desire to get the job done, and the mental prowess to have it done correctly. He was one of the few selected as a Bureau of Commercial Fisheries Fellow, and worked under this fellowship grant from 1962 to 1964, earning his doctorate in fisheries in 1965 from the University of Washington. His doctoral thesis is an important contribution on the life history and ecology of populations of smelt in Lake Washington. This study of the smelt and associated limnetic species in Lake Washington also has provided a data base for future examinations of changes in the fauna. The study was conducted at a peak of eutrophication in Lake Washington. Public concern, aroused in 1956, culminated in the creation of the Municipality of Metropolitan Seattle (Metro) in 1958 which was charged to develop an effective sewage-disposal system for the entire area. The Metro Program, at a total cost of about $121 million, began diverting sewage from the lake in 1963 and was completed in 1968. In 1968 experts described Lake Washington as a classic case history study of eutrophication and recovery. Changes in the lake's fish populations since this study of the smelt have been marked and are the subject of more recent studies at the College of Fisheries, University of Washington.

The young scientist then moved from Seattle to Beaufort, N. C., to take up the challenge of Government efforts to assist in the revitalization of an ailing menhaden industry. Under his supervision, an ambitious and successful program was undertaken to solve the mystery of menhaden migrations. His team tagged an unprecedented number of fish, some one million, from Long Island to Florida. They proved conclusively that menhaden move north in spring and summer and south in fall. Vital information on fishing mortality and natural mortality was obtained for this resource. His menhaden work for the 7 yr from 1965 to 1971 laid the foundation for what is to become the model program for State-Federal partnership in managing our domestic fisheries. During early 1974 in Washington, an historic meeting took place where his former colleagues presented the first comprehensive plan for managing this valuable but overexploited resource, worth some $50 million a year to the economy. This plan could not have been prepared without the inspired and dedicated work of Bob Dryfoos.

With his menhaden work completed, Bob moved on to greater responsibility at Narragansett, R. I. He was instrumental in developing the first comprehensive national program for assessing the important living resources of our coastal and continental shelf waters. The new initiative is called MARMAP for the Marine Resources Monitoring, Assessment, and Prediction Program. In his April 1972 budget message to Congress, the President cited this program as one of the more significant contributions to our civilian oceanographic effort. MARMAP was another "first" for Bob Dryfoos. He helped shape the concept, and mold the national fiber. Like other new initiatives it was subjected to criticism and doubt. But Bob believed in the concept, and with his colleagues he persevered. Nationally coordinated assessments of fishery resources are now being made from the Gulf of Maine to the Caribbean, the Florida Keys to the Bay of Campeche, from Baja California to the east Bering Sea and in the oceanic waters of the tropical Atlantic and Pacific. The results of his MARMAP efforts are just now bearing fruit, and will continue to yield more important results in the latter half of this decade, in the 1980's and beyond.

Bob will be missed by his many friends and colleagues. His accomplishments were considerable. A fine heritage for his dedicated wife Carol, son Ricky, daughter Janet, and his parents. He always found time in a busy schedule for civic activities, Rotary, the kids' skating, Cub Scouts, swimming, and clamming, and all those wonderful pursuits that bring enrichment to a family and their friends, and their community. He leaves behind many wonderful memories. We are all richer from our association with him.

His outstanding record remains with us, and from his contributions we will move on, we will keep building, for a better and rational and more enlightened tomorrow.

KENNETH SHERMAN

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ERRATA

Fishery Bulletin, Vol. 72, No. 1

WAHLE, ROY J., ROBERT R. VREELAND, AND ROBERT H. LANDER, "Bioeconomic contribution of Columbia River hatchery coho salmon, 1965 and 1966 broods, to the Pacific salmon fisheries," p. 139-169.

The captions of the Appendix Tables on pages 162-165 are correct, but the tabular entries below were transposed:

1) Tabular material on page 165 should have appeared on page 162;
2) Tabular material on page 162 should have appeared on page 163;
3) Tabular material on page 163 should have appeared on page 165.

Fishery Bulletin, Vol. 72, No. 2

APRIETO, VIRGINIA L., "Early development of five carangid fishes of the Gulf of Mexico and the south Atlantic coast of the United States," p. 415-443.

1) Page 419, left column, lines 13 and 14 should read: hemal spine of the first caudal vertebra. In adults, these spines are only slightly differentiated from

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In the **text**, *Fishery Bulletin* style, for the most part, follows that of the *Style Manual for Biological Journals*. Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada*, Third Edition, 1970. The *Merriam-Webster Third New International Dictionary* is used as the authority for correct spelling and word division.

Text footnotes should be typed separately from the text.

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Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations. (Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

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A LINK BETWEEN SCIENCE AND MANAGEMENT IN FISHERIES

D. H. CUSHING[1]

ABSTRACT

In this paper a link is traced between science and management in that good conservation results from good science and that failure in management may be the result of scientific failure; but management failure is of course not the exclusive province of scientists. The argument is developed from a historical study of practice by fisheries scientists in the International Commissions.

The central problem of fisheries biology is to estimate the catch that can be safely taken from a stock. In Europe the problem was formulated by Petersen (1894) and Garstang (1900), who realized that if catches were too great they might subsequently decrease because the stock had been reduced too much. In the first decade of the present century exploratory voyages were made in the North Sea under the auspices of the International Council for the Exploration of the Sea (ICES). The high variability of the catches "precluded the possibility of any reliable combination of the trawling records" (Garstang, 1904). At the same time, Petersen said that overfishing was not the essential question and that the ICES should study the transplantation of small plaice as a method of conserving the weight of catch. Small plaice were caught in large numbers close to the continental coasts and, in summertime, the discards exceeded the retained catch by a factor of six. Petersen, Garstang, and Kyle (1907) subsequently wrote that "the plaice can be returned alive to the sea, where they . . . grow so much in size and value that the same fishermen who caught them in the first instance have a good chance of recapturing them when they have a greatly increased value." During their adult lives some demersal fish, such as plaice, grow by an order of magnitude or so, and if fished heavily the mean weight of the stock is reduced because the little fish do not have the chance to grow. The problem of growth overfishing as stated by Petersen is to conserve this loss of catch in weight.

The scientific judgment that catches were too variable led to a second judgment that management was impossible. The name of the "overfishing" committee in ICES was changed to that "investigating the biology of the Pleuronectidae and other trawl-caught fish." The solution recommended for the small plaice problem was to transplant them from the continental coasts to feeding grounds on or around the Dogger Bank. The ICES did not discuss the problem of overfishing again until after the first world war.

Management depends on the quality of scientific advice. Good science should lead to good management and failure in management is often due to scientific failure, although failure in management might be due to other causes. It has not been established yet whether the plaice stocks in the southern North Sea needed international management before the first world war, but the lack of management was not based on such a judgment; it was because the scientists could not assess the variability of catches, which was not surprising at that time because statistical techniques were not very well developed. This paper traces similar links between science and management in the subsequent history of fisheries science; the historical information is taken from a study of the development of the fisheries commissions in Cushing (1972).

THE DESCRIPTIVE MODEL

During the thirties, changes in populations were accounted for in the theory of balance; for example, a decrement in stock is compensated by an increment in recruitment per unit stock, and as fishing mortality increases a relative increase in recruitment is to be expected. Thompson and Bell (1934) and Graham (1935) stated explicitly that recruitment would not be reduced in magnitude by fishing at the stock levels normally exploited; they both worked on flatfish and their conclusion was well fitted to flatfish biology, if not to clupeids

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or gadoids. Both plaice and halibut grow by more than an order of magnitude during their adult lives. Cushing (1972) distinguished growth overfishing from recruitment overfishing. In the first the stock loses weight by too much fishing, as Petersen suggested, but recruitment is not affected. In the second, recruitment is affected; it is noticeable in the pelagic stocks at a lower rate of exploitation than in the demersal stocks because the pelagic fishes have less capacity for stabilization, being less fecund.

Populations were well described by the logistic curve, which expressed the theory of balance in stating that any change in the carrying capacity of the environment was compensated by a change in the net rate of increase of the stock. From the changes in biomass in time, average estimates of the two parameters (net rate of increase and carrying capacity) can be obtained. Such models are called descriptive because the parameters are not estimated independently but are derived from the changes in biomass. In fish populations the contributions of growth and recruitment are compounded in the application of the logistic curve, whereas it would be desirable to distinguish them. Both Thompson and Bell (1934) and Graham (1935) concluded from the application of the logistic curve that age determination was no longer necessary. Had this conclusion been applied quite firmly the distinction between the effects of growth and recruitment in fish populations would have become impossible.

Graham's (1935) major explicit achievement was the application of the logistic curve to fish populations. Another achievement, an implicit one, was to encourage the application of the methods of operational research arising from the second world war to fish population dynamics by Beverton and Holt (1957), which led to the solution of the problem of growth overfishing. The logistic curve was developed more fully by Schaefer (1954, 1957). He derived a catchability coefficient from the relation of stock density to fishing effort and used it to obtain catch, which he then related to effort in the form of a parabola. Over a long time period, enough annual observations give an estimate of maximum sustainable yield. The advantage of this method is that the result can be expressed simply and convincingly. The disadvantages are 1) that at least a patient decade of data collection is needed to establish the position of the maximum, given a sufficient spread of fishing effort and 2) that upward or downward trends in recruitment would be distinguished with difficulty.

THE ANALYTIC MODEL

The first analytic model was Russell's (1931) in which the changes in stock were separated into components of growth, recruitment, and mortality. Beverton and Holt (1957) devised a series of models, including the well-known yield per recruit one and the less well-known self-regenerating yield curve, in which they incorporated their stock and recruitment relationships. The catch, or yield, was expressed as a function of fishing mortality and of the age at first capture. The most important point about the yield per recruit model is that the maximum yield is obtained from information on growth and fishing mortality, independently of the catches. There is no need to wait for a long time to establish the curve, and management decisions can be taken quickly, other considerations being equal.

The yield per recruit model was the theoretical solution to the problem of growth overfishing, and the practical solution was to increase the age at first capture with increased mesh size in the trawls. For management it is a clear solution and it is likely that the present agreement on management in the North Atlantic originated in its simplicity. There were lengthy discussions on the science and on the technology, but there are now agreed minimum landed sizes and minimum mesh sizes for a number of species throughout the North Atlantic. It must be said, however, that conservation by mesh regulation is least conservation because it is adapted to the smaller and numerous species like the haddock in the North Sea; larger species (for example, cod or turbot) are not necessarily conserved there as well as they might be.

In the yield per recruit model it is assumed that recruitment does not decline under the pressure of fishing. The argument presented by Beverton and Holt was that recruitment is so variable that the downward trend at low stock would be very difficult to detect. In management there was an unforeseen consequence: that fishing could continue until recruitment was seen to fail. Then, because of the same high variability of recruitment, fishing would continue until it was too late. However, with care, the yield per recruit model can be used when the stock and recruitment relationship is unknown; for example, if fishing is reduced, the yield per recruit will not decline and

may even rise if recruitment rises with reduced fishing.

It is likely that if fishing mortality is restrained to the maximum of the yield per recruit curves of most demersal fishes, recruitment would not be very much impaired. However, the curve for the herring is asymptotic and it was tacitly believed that the herring could be fished very hard merely because of the shape of the yield per recruit curve. Another consequence was that the maximum for the cod in the Barents Sea was overshot because in international terms a high catch was needed at the cost of a decreased catch per effort. The recruitment to the Barents Sea stock was severely reduced.

The collapse of herring fisheries throughout the northeast Atlantic and the failure of recruitment to the Arcto-Norwegian cod stock have been attributed to failure in the Commissions. These Commissions, however, are only as good as their scientific advice, and the two great failures are attributable to the unstated concept that fishing could continue until recruitment was seen to fail. Then failure had to be attributed either to natural causes or to fishing, and stocks collapsed while the scientists disputed the two possibilities. If recruitment overfishing had been recognized as a problem, perhaps collapse might have been avoided. The solution to the problem of growth overfishing inadvertently generated the problem of recruitment overfishing.

STOCK AND RECRUITMENT

The dependence of recruitment on parent stock was formulated by Ricker (1954, 1958), but the variability of recruitment is very high and the curve can only be fitted when decades of annual data have been collected. Any decision on how much fishing should be allowed is perhaps delayed for statistical reasons and management cannot proceed. On the other hand, if recruitment were considered to be independent of parent stock, management could start to take decisions more quickly. With hindsight, the assumption made by Thompson and Bell (1934) and Graham (1935) can be justified because their work formed the scientific basis of all international conservation in the North Atlantic and North Pacific. However, the danger of such a procedure is that any decline in recruitment tends to be attributed to natural causes rather than to fishing, and this step has sometimes been taken without evidence.

It is in the nature of the stock and recruitment problem that there should be confusion about attributing decline in recruitment to natural or to man-made causes. However, Cushing and Harris (1973) have devised a method of fitting the Ricker curve which sets confidence limits to the position of the curve itself; the standard deviation of residuals sets limits to the variation of recruitment. Then if stock is near that value which generates maximum recruitment per unit stock, any recruitment that falls below the standard deviation of the residuals has failed through natural causes. If stock is low, such a distinction cannot be made (because any recruitment below the standard deviation of the residuals is zero) and failure is attributed to natural or to man-made causes without evidence either way; however, a prudent manager might prefer to assume that recruitment declined under the pressure of fishing and to take appropriate action in the hope that the stock would recover, as recently happened with the British Columbia herring stock.

The stocks that have failed because of this dilemma are the California sardine, the Japanese sardine, and the northeast Atlantic herring; the Arcto-Norwegian cod stock might fail for the same reason. The failures of the first three were attributed to environmental factors on evidence that is only circumstantial; more recent evidence suggests that failure might have been due to fishing. To pursue the argument further is sterile. The scientific failure was the inability to make clear the distinction between natural and man-made causes. The failure in management was to delay action until the distinction could be made, whereas a prudent manager should have feared the effect of fishing upon recruitment.

In the stock and recruitment problem, long data series are needed before any management decision can be taken. When the development of a fishery proceeded slowly, this may not have mattered because the maximum yield was attained by gentle increments. Today, however, stocks are exploited rapidly, and there is the possibility that recruitment will be diminished before the data are available to describe the maximum sustained yield. What is needed is an analytic model of the stock and recruitment relationship on the lines of that of the yield per recruit one, on the basis of which decisions on management can be made quickly without the laborious acquisition of long series of data.

There are two large fisheries in the Pacific, on the Peruvian anchoveta and on the Alaska pollack. Recently the anchoveta recruitment failed, possibly due to fishing and possibly due to El Niño and perhaps due to both; because there is only about one decade of observations, the cause of failure will probably remain unknown, although it must always be admitted that the fishing mortality is high. In the Bering Sea there is a rising fishery on the Alaska pollack that also had been in existence for less than a decade. The potential managers of this fishery might like to have available now a yield curve before the data are available to describe the stock and recruitment curve. The source of scientific failure here is the inability to generate an analytic stock and recruitment model.

SCIENCE AND MANAGEMENT IN THE COMMISSIONS

When a fish stock fails the question arises whether the failure should be attributed to the Commission charged with its management or to the scientists. There is a distinction between the North Atlantic Commissions and those in the North Pacific. In the North Atlantic the two institutions (International Commission for the Northwest Atlantic Fisheries and Northeast Atlantic Fisheries Commission) are responsible for all stocks exploited in the area, whereas in the eastern North Pacific only those of interest to North American fishermen are conserved. Consequently the Commissions in the North Atlantic cannot disclaim responsibility for any failures that occur in their area, whereas the North Pacific Commissions may be able to do so.

In the North Atlantic, decline of the main demersal stocks has with one exception been prevented. The best conservation has not yet been achieved, but with the use of catch quotas and international enforcement there is considerable hope that conservation will ultimately be very effective. The scientific basis for this was the initial use of the yield per recruit model and in recent years the successful application of first, cohort analysis (Gulland, 1967), and secondly, the Clayden model (Clayden, 1972). On the other hand, the collapse of herring stocks in the northeast Atlantic was due entirely to the scientific failure to understand the nature of the stock and recruitment problem. Both success and failure in the Commissions can be linked to success or failure in the science.

In the North Pacific there are large areas of unregulated fishery, which the North Pacific Commission has not taken under its aegis. The cause of the increase in the maximum sustainable yield of the yellowfin tuna in the area of the Inter-American Tropical Tuna Commission is unknown, although a number of possible reasons have been cited. Halibut are caught by trawl by nations outside the control of the International Pacific Halibut Commission. The question of the offshore exploitation of the Pacific salmon stocks remains unresolved because the boundary between the North American and Asian stocks is not precise and the degree of mixture in the exploited area has not been established.

It remains true, of course, that the stock density of the halibut recovered from 1930 to 1960 by the action of the Halibut Commission, that the offshore exploitation of the North American salmon was prevented by the abstention principle, and that the yellowfin tuna stock is well exploited. Some of the failures in the North Pacific, like those in the North Atlantic, are rooted in scientific deficiencies (apart from the North Pacific failure to consider stocks that are outside the aegis of the Commissions).

The International Whaling Commission failed to conserve the stock of blue whales. The problem was solved in principle for the fin whale by Ruud (International Whaling Commission, 1956) but the solution was rejected by Schlijper (International Whaling Commission, 1957) who said that the age determination was faulty. The Committee of Four evaded this by expressing the results in the form of a Schaefer curve (International Whaling Commission, 1964); Schlijper never saw that age determination was used in the estimation of (recruitment less mortality) which played a considerable part in the solution. Part of the failure to conserve the stock was the delay in reaching an agreed scientific solution.

In contrast to the Whaling Commission, the North Pacific Fur Seal Commission has been well served by its scientists. A form of stock and recruitment relation has been established and the surplus stock is taken each year at somewhere near the best point for exploitation, and some progress has been made towards establishing the nature of the density-dependent control in the population. The Fur Seal Commission is the oldest of the international commissions and its records go back a long way, into the early 19th century.

From this very brief account of the role of

fisheries science in the Commissions there is one general conclusion, that when the science is successful the Commissions can work well but when the scientific evidence is confused the Commissions may fail. Of course, failure may occur for other reasons; for example, a proposal in the ICES to close the small plaice grounds in 1923 was rejected by the British fishing industry in 1926.

THE NATURE OF FISHERIES SCIENCE

The organization of knowledge into science is based on the establishment of laws that interlock. Each law subsumes much information and the network of laws comprises the body of the science. Advance in science is made by the addition to or the rearrangement of the network. Any scientific conclusion is judged in relation to the general framework, and it is tested in the premises and extensions of the argument in the network. It is sometimes said that the end of a scientific procedure is to establish a correlation; without denying the use of correlation, the most important point is to establish whether the correlation is likely and how it fits into the general scientific framework.

In a highly developed science such judgments are made frequently, but in a more primitive one like fisheries biology the necessary network has not yet been established. For example, all our information on stocks depends on catches, with the various biases in availability included; independent methods of estimating stock are being developed but they are not yet reliable. In a highly developed science, a number of methods independently yield the same result; fisheries biologists are pleased to estimate fishing mortality but very rarely is more than one method used. Natural mortality is estimated as the difference between total mortality and fishing mortality, and there is very little independent evidence of its magnitude. The information needed is accumulating quite quickly but the science remains a little weak.

Because biological material is highly variable, any biologist needs a working knowledge of statistics. Without denigrating this very real need, the science needs more than statistics, more information, more hypotheses, and more insight. It has sometimes been stated that fish stocks could be assessed by the study of ecosystems rather than by the study of single populations. This is rubbish; it is my view that not enough is known of any one population primarily because we have examined adult animals to the exclusion of the juveniles. I do not mean that we know nothing of fish larvae or 0-group fish, but that we know too little of their growth rates and death rates. With more knowledge of this sort, the problems of the regulation of numbers and of competition might be solved and we might at the same time learn something of how an ecosystem itself is regulated.

It has been said that fisheries science is fully developed and that its techniques are quite reliable. Much is known about the Pacific salmon but it is only a small fraction of what is needed. It has been said that stock and recruitment is the last problem in fish population dynamics. It is the study of the regulation of numbers, of competition between species, and of the variability of recruitment. In other words, it is the central problem of population dynamics. There is a sense in which fisheries biologists have passed through a long apprenticeship before they have embarked on the real problem that concerns them.

CONCLUSION

The international management of fisheries has developed slowly since it started during the second and third decades of the present century. There are many reasons for this, economic, social, and political; indeed the agreement achieved between nations is considerable when one considers all the difficulties involved. One of the reasons for this slow development, but not the only one, is that where the science has failed, so has management. Conversely, where the science has been successful, management can proceed with confidence, other things being equal. One would expect a link to exist between science and management, as it does in other fields.

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DEVELOPMENT AND DISTRIBUTION OF LARVAE AND JUVENILES OF *SEBASTOLOBUS* (PISCES; FAMILY SCORPAENIDAE)

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ABSTRACT

The North Pacific scorpaenid genus *Sebastolobus* is composed of three deepwater coastal species of potential commercial importance. They are oviparous and produce bilobed gelatinous egg sacs that float to the surface waters where hatching and larval development occur. Transformation into pelagic juveniles occurs at about 20 mm length. The pelagic stage of *S. alascanus* is relatively short-lived, as they transform into benthic juveniles at 22 to 27 mm length. In the deep-living *S. altivelis* the juveniles remain pelagic for well over a year and grow as large as 56 mm.

Larvae of the two species mentioned are collected regularly on plankton surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and pelagic and benthic juveniles are common constituents of mid-water and bottom trawls taken in the CalCOFI region. In this paper specimens from these sources are used to describe the larval and juvenile stages of the two species and to show the striking morphological changes which occur during development. Also presented are data on geographic distribution and patterns of seasonal abundance of larvae. Larvae of *Sebastolobus* smaller than 10.0 mm could not be distinguished to species.

Knowledge of the life history of the scorpionfish genus *Sebastolobus* is scanty. Pearcy (1962) described the floating egg masses, the developing embryos, and the newly hatched larvae of *Sebastolobus*. The larvae of *Sebastolobus* occur in the plankton collections of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and can be differentiated from those of *Sebastes* on the basis of the spination of the parietal ridge (Ahlstrom, 1961). Information on the distribution and abundance of *Sebastolobus* larvae in CalCOFI has hitherto not appeared in the literature, nor has a description of the larval stages. It is the purpose of this paper to fill that void and also to describe the distinctive juvenile stages of *S. altivelis* and *S. alascanus*, which are common constituents of mid-water trawl catches in the eastern North Pacific.

The three known species of *Sebastolobus* inhabit the coastal waters of the North Pacific. *Sebastolobus altivelis* ranges from the southern tip of Baja California to the Aleutian Islands while *S. alascanus* is found from northern Baja California to the Bering Sea and the Commander Islands off the Asiatic mainland. The Asian species, *S. macrochir*, ranges from the coast of Japan northward to the Bering Sea south of Cape Navarin and into the Sea of Okhotsk (Barsukov, 1964). At present the commercial catch of *Sebastolobus* is small, however, data of Best (1964) and Alverson, Pruter, and Ronholt (1964) suggest that these fishes may constitute a substantial resource in the deep coastal waters of the northeast Pacific.

The taxonomic characters of the adult members of this genus have been reviewed by a number of investigators (Starks, 1898; Hubbs, 1926; Matsubara, 1943; Phillips, 1957; Barsukov, 1964; Miller and Lea, 1972). *Sebastolobus* is distinguished from other scorpaenid genera by the unusual pectoral fins, each of which is separated by a notch into dorsal and ventral lobes, by possessing more vertebrae (28 to 31) and dorsal spines (15 to 17), a complete set of circumorbital bones, an uppermost pectoral radial which is free from the scapula, and by a suborbital stay with a broad posterior end anchored firmly onto the preopercular bone. The two North American species may be separated on the basis of the shape and number of rays in the spinous dorsal fin. In *S. altivelis* the third spine is the longest while in *S. alascanus* the fourth or fifth spine is the longest. The former species usually has 15 (rarely 16) spinous dorsal rays while the latter has 16 or 17 (rarely 15) rays. Also, *S. altivelis* usually has 29 (rarely 28) vertebrae and *S. alascanus* has 30 (rarely 31). The Asian species, *S.*

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macrochir, is deeper bodied than the North American species and has a relatively narrower caudal peduncle. Counts of its spinous dorsal rays and vertebrae are close to those of *S. altivelis*.

Hubbs (1926), Barsukov (1964), and Miller and Lea (1972) have given information on the bathymetric ranges of the adults. In summary, *S. altivelis* occurs typically at 550 to 1,300 m with known depth extremes of 200 to 1,550 m. Everywhere along its latitudinal range *S. altivelis* is deeper living than *S. alascanus*, although there is some overlap and the two species are occasionally taken in the same trawls. *Sebastolobus alascanus* commonly occurs at 180 to 440 m, with known depth extremes of 18 to 1,524 m. *Sebastolobus macrochir* occurs commonly at 400 to 640 m.

MATERIALS AND METHODS

Larvae of *Sebastolobus* from 2 yr (1960, 1966) of CalCOFI survey cruises were identified and counted. From these a developmental series that encompassed the entire larval period was established. Larvae of this series were measured with the ocular micrometer of a stereoscopic microscope, according to the methods of Moser (1967, 1972), to produce the tables of morphometrics (Tables 1-3) needed for comparison of body proportions of *S. altivelis* and *S. alascanus*. This series also provided the specimens needed to describe the general morphology and melanophore pattern of the larvae. Measurements of four pelagic juveniles of *S. macrochir* are given in Table 4. An abbreviated series of *S. altivelis* and *S. alascanus* was selected, cleared with a graded series of KOH-glycerin solutions and stained with Alizarin Red-S to produce tables of meristics (Tables 5, 6).

The pelagic juvenile stages of the two species were obtained from the mid-water trawl collections of the Los Angeles County Museum of Natural History (LACM), the Scripps Institution of Oceanography (SIO), and the Southwest Fisheries Center. Demersal juveniles were obtained from otter trawl collections of LACM and SIO. As for larvae, series of juveniles were established for analysis of morphometrics (Tables 2-4), pigment pattern, and meristic characters (Tables 5, 6). In this paper the term "body length" refers to the distance from the snout to the tip of the notochord in larvae which have not yet formed the caudal fin. After dorsad flexion of the tip of the notochord and completion of caudal fin formation "body length" refers to standard length (distance from snout to posterior edge of hypural plate).

TABLE 1.—Measurements (mm) of *Sebastolobus* spp. larvae. Specimens between dashed lines are undergoing notochord flexion.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
3.0	1.3	0.50	0.08	0.20	0.60	0.3	0.14			
3.5	1.4	0.80	0.18	0.25	0.52	0.23	0.20			
3.8	1.6	1.0	0.22	0.27	0.68	0.40	0.38			
4.2	1.8	1.2	0.25	0.30	0.86	0.45	0.40			
4.7	1.9	1.2	0.31	0.30	0.80	0.46	-			
5.0	2.0	1.4	0.35	0.33	0.90	0.65	0.50			
5.2	2.1	1.4	0.43	0.40	1.0	0.62	0.55			
5.5	2.3	1.6	0.42	0.35	1.1	0.65	0.58			
5.7	2.3	1.7	0.56	0.40	1.2	0.95	0.85			
5.8	2.4	1.7	0.51	0.39	1.2	1.0	0.78			
5.9	2.6	1.8	0.62	0.47	1.6	1.0	0.75			
6.0	2.7	1.8	0.55	0.51	1.8	1.3	0.85	0.22	2.3	3.4
6.2	2.7	1.9	0.70	0.48	1.6	1.4	0.90	0.20	-	-
6.4	2.7	1.8	0.60	0.45	1.5	1.2	0.85	0.13	-	-
6.7	3.1	1.9	0.82	0.55	1.8	1.4	1.0	0.15	3.9	3.9
6.8	2.8	2.0	0.82	0.52	1.8	1.4	1.1	0.17	-	3.2
6.9	3.3	2.2	0.80	0.58	2.0	1.5	1.2	0.25	2.7	4.1
7.1	3.5	2.5	0.82	0.71	2.4	1.8	1.2	0.80	2.5	4.2
7.3	3.8	2.5	0.95	0.76	2.4	1.8	1.4	0.85	2.7	4.4
7.7	4.2	2.7	1.1	0.75	2.8	2.1	1.5	0.85	2.9	4.5
7.8	4.3	3.1	1.1	0.82	2.6	2.1	1.4	1.2	3.2	4.8
8.3	4.4	3.1	1.1	0.79	2.6	2.0	1.4	1.0	3.1	4.9
8.6	4.8	3.2	1.2	0.92	3.1	2.4	1.7	1.4	3.5	5.3
8.9	5.2	3.3	1.2	1.0	3.1	2.5	1.7	1.4	3.8	5.4
9.2	5.2	3.5	1.2	1.0	3.2	2.7	1.5	1.5	3.8	5.6
9.6	5.4	3.5	1.2	1.1	3.7	2.8	1.8	1.7	4.1	5.8

TABLE 2.—Measurements (mm) of *Sebastolobus altivelis*. Specimens below dashed line have completed transformation into pelagic juvenile stage.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
10.1	6.2	3.8	1.2	1.2	3.8	2.8	1.8	1.7	4.2	6.4
10.5	6.5	4.2	-	1.2	3.9	3.0	1.9	1.8	4.4	6.7
11.2	6.9	4.5	1.3	1.4	4.2	3.5	2.1	2.4	5.2	7.3
12.7	7.3	4.6	1.3	1.5	4.7	3.8	2.0	2.5	5.4	7.9
13.4	8.0	5.0	1.5	1.6	4.8	3.7	2.0	2.5	5.4	8.3
14.4	8.8	6.2	1.7	2.1	5.7	5.0	2.7	3.1	6.0	9.6
15.2	10.1	6.1	1.8	1.9	6.3	5.2	2.8	2.9	6.7	10.6
15.4	9.8	6.0	1.7	2.2	6.4	4.7	2.8	2.9	6.9	10.1
15.4	9.9	6.5	1.9	2.2	6.3	5.8	2.9	3.8	6.8	11.0
15.7	10.3	6.8	2.1	2.1	6.9	5.8	2.9	3.8	6.7	10.8
16.0	10.3	6.2	1.8	2.0	7.1	5.4	3.1	3.3	7.0	10.6
16.3	10.3	7.2	2.1	2.2	6.6	6.2	3.0	4.0	6.8	11.2
16.6	10.8	7.4	1.8	2.4	6.6	6.4	3.0	3.4	7.6	11.8
16.7	11.2	6.7	1.9	2.2	7.5	5.8	3.2	3.3	7.1	11.3
17.6	11.5	7.6	2.0	2.5	7.2	6.8	3.2	4.2	7.1	12.2
17.6	11.7	7.0	1.9	2.4	7.3	5.9	3.1	3.8	7.7	12.0
18.2	12.0	7.7	2.1	2.6	7.3	6.3	3.1	4.2	7.8	12.7
18.4	12.5	7.1	2.0	2.5	8.3	6.2	3.6	4.2	7.5	12.8
19.3	13.2	7.9	2.1	2.5	8.5	6.7	3.8	3.8	8.3	13.4
19.4	13.0	8.5	2.3	2.5	8.7	7.6	3.8	4.7	8.4	14.0
20.7	13.8	8.5	2.6	2.3	8.4	7.6	3.7	4.8	8.6	14.7
21.3	14.9	9.2	2.8	2.8	9.0	8.1	3.8	4.8	9.5	15.2
22.6	15.9	9.6	2.5	3.1	9.2	8.8	4.2	5.6	9.5	16.7
23.4	16.6	9.8	2.5	2.7	10.1	9.0	4.4	5.6	9.5	17.4
24.5	17.7	10.8	2.9	3.4	11.0	10.0	4.5	5.8	10.1	18.1
25.8	18.6	10.6	2.9	2.9	11.3	9.3	4.4	5.9	10.1	18.9
26.8	17.7	10.6	2.8	3.8	10.6	11.0	4.8	6.5	10.1	18.8
27.7	20.3	11.5	2.9	3.6	12.2	11.0	5.4	7.1	11.7	22.0
28.3	20.3	12.0	3.2	3.7	12.2	11.5	5.0	7.1	11.5	21.8
29.4	20.4	12.3	3.3	3.8	11.5	11.5	5.2	7.2	12.3	21.1
30.5	21.1	13.0	3.8	3.6	11.7	11.7	5.4	7.6	12.3	23.0
31.4	21.1	12.3	3.2	3.5	13.7	12.2	5.8	7.5	12.3	22.9
32.4	21.1	12.5	3.5	3.6	13.0	12.8	5.8	8.3	12.5	22.2
33.6	23.1	14.0	4.2	4.2	13.5	11.7	5.8	7.5	12.8	25.1
34.6	23.5	13.4	3.8	3.8	14.2	13.5	6.0	8.2	13.7	25.5
36.5	25.0	15.2	4.2	4.8	15.5	14.7	6.7	9.2	14.9	27.5
37.5	25.8	15.0	4.2	4.6	15.9	14.4	6.7	8.3	14.7	27.6
38.5	25.6	15.2	4.0	4.8	16.0	15.7	6.6	9.8	15.2	27.5
39.5	27.9	16.2	5.0	4.8	16.0	15.0	6.7	8.9	16.0	29.9
40.4	27.1	16.4	5.0	4.8	15.2	15.0	6.8	10.8	16.0	30.0
41.6	27.9	16.4	4.3	5.8	15.9	15.2	7.1	10.1	16.2	29.6
42.3	28.1	16.9	4.6	5.2	17.4	15.2	7.2	10.0	15.9	29.4
43.5	30.1	16.9	5.2	5.4	16.0	14.7	6.7	9.5	17.4	32.4
44.4	30.0	17.9	-	4.8	16.4	16.4	7.1	9.5	17.2	32.2
45.1	29.5	18.2	4.8	5.4	17.6	16.0	7.8	10.1	17.2	32.0
46.2	30.7	17.9	5.0	4.9	17.7	17.1	8.1	11.5	17.1	33.5
47.1	30.2	18.1	5.0	5.6	17.1	15.2	7.0	10.3	17.7	33.0
48.5	32.0	18.6	5.4	5.8	18.6	16.9	7.8	10.5	17.7	34.7
49.5	32.2	19.8	5.0	5.8	18.6	18.1	8.3	11.8	16.4	36.2
51.3	37.0	20.6	6.7	5.8	18.8	17.4	8.0	11.3	18.9	40.0
53.5	35.7	20.6	6.2	7.5	18.6	16.9	8.2	11.0	18.7	37.8
56.0	37.6	21.4	5.8	7.7	19.2	19.8	8.3	12.3	20.3	40.6
*42.0	26.8	16.6	4.6	5.6	12.0	12.7	6.0	9.3	16.4	29.0
*47.4	29.6	17.7	4.7	6.9	13.9	13.5	6.8	10.1	18.1	31.7
*48.1	31.4	19.1	5.2	7.3	14.4	15.2	7.0	11.5	17.9	33.5
*50.3	33.0	19.2	5.4	7.3	14.0	13.8	7.1	11.8	18.8	35.3
*51.0	33.0	19.5	4.7	7.2	15.0	16.2	7.5	11.2	18.7	35.2
*53.0	33.4	20.5	5.4	8.6	14.6	15.5	7.0	12.1	19.9	37.7
*54.0	35.4	19.7	5.9	7.3	15.5	17.7	7.8	12.6	20.6	38.4
*56.0	35.2	21.1	5.6	7.7	15.5	16.4	7.4	12.6	20.8	38.1
*57.5	37.2	21.4	5.6	8.0	15.3	16.7	8.1	12.5	21.1	40.3
*58.6	37.9	22.6	6.0	8.7	16.5	16.9	8.2	12.7	21.6	40.6
*60.0	38.0	22.0	6.0	8.4	16.2	15.1	8.1	12.8	21.5	41.6

*Benthic juvenile.

TABLE 3.—Measurements (mm) of larvae and juveniles of *Sebastolobus alascanus*.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout anal fin
10.3	6.2	4.2	1.5	1.2	4.0	3.2	1.6	1.9	4.3	6.8
11.2	7.4	5.0	1.8	1.3	4.1	3.2	1.7	2.1	5.0	7.7
11.7	7.2	5.0	-	1.3	3.9	3.1	1.8	2.1	5.1	7.7
12.5	7.7	4.7	1.7	1.5	4.5	3.6	1.8	2.4	5.4	8.3
13.2	7.3	5.0	1.6	1.8	4.6	3.9	1.9	2.7	5.8	8.2
14.0	8.1	5.7	1.8	2.1	4.9	4.1	1.9	2.5	6.2	8.8
14.4	8.4	5.6	1.4	1.8	5.2	4.2	2.1	2.6	5.7	9.1
15.2	9.2	6.2	1.8	2.0	5.2	4.4	2.1	2.9	6.3	10.0
16.0	9.3	6.2	2.0	2.0	5.2	4.8	2.2	2.9	7.1	10.0
16.4	9.8	6.7	1.8	2.5	5.7	4.7	2.3	3.2	7.1	10.5
16.9	10.0	6.8	1.9	2.3	5.9	4.8	2.4	3.1	7.3	10.8
17.6	10.6	6.7	2.1	2.2	6.1	4.9	2.3	3.5	7.1	11.3
18.6	12.7	-	-	2.8	6.8	5.4	2.8	3.8	8.5	13.2
19.8	12.0	7.7	2.0	2.8	7.1	5.9	2.9	4.0	8.3	13.0
20.0	12.0	8.1	2.2	2.9	7.1	6.4	2.8	4.2	8.4	13.0
20.3	12.8	8.2	1.8	3.1	7.2	6.2	7.8	4.0	8.1	13.5
21.0	13.5	8.6	1.9	3.1	7.5	6.5	3.0	4.6	8.1	14.4
21.4	12.8	8.3	2.4	2.9	7.1	6.2	2.8	3.8	8.6	14.4
21.9	12.8	8.5	2.1	3.1	7.1	6.2	2.8	4.2	8.8	14.9
22.3	14.2	9.6	-	2.8	7.9	6.5	3.2	4.4	9.1	15.4
22.9	14.4	9.8	2.6	3.2	7.5	6.7	3.1	4.6	9.3	15.5
23.2	14.7	9.5	2.5	2.9	7.9	7.2	3.0	5.0	9.6	16.0
23.4	14.9	9.0	2.2	3.3	8.0	7.1	3.2	5.0	9.3	16.4
24.0	14.4	9.8	2.2	3.2	8.0	6.8	3.3	5.0	9.8	15.9
24.3	15.5	10.0	2.8	3.2	8.6	7.3	3.3	5.0	9.8	16.9
25.1	15.9	10.0	3.0	3.3	8.4	7.0	3.4	5.0	10.1	17.2
25.5	16.0	10.1	2.8	3.5	8.8	8.2	3.7	5.5	10.1	17.6
26.4	17.9	10.6	3.2	3.5	9.0	8.0	3.7	5.7	11.3	19.1
27.2	17.9	11.2	3.0	-	8.3	8.1	3.3	5.4	10.8	19.3
*22.5	13.0	8.7	2.1	3.2	7.2	6.3	2.9	4.6	9.6	14.7
*25.3	16.9	10.3	3.5	3.2	8.1	6.8	3.3	5.0	11.2	18.9
*37.8	22.0	12.7	2.9	5.0	10.1	9.6	4.2	8.2	13.5	24.3
*39.0	24.0	14.1	4.0	5.1	9.9	9.8	4.0	8.8	15.0	26.7
*40.8	25.1	14.8	3.8	5.3	10.0	9.7	3.8	8.8	15.3	27.3
*42.3	27.7	15.4	4.3	5.8	10.1	10.0	4.2	9.0	16.3	29.6
*43.6	26.3	15.4	4.1	5.8	9.5	10.6	4.4	9.4	16.1	29.5
*44.7	26.2	15.9	4.3	5.8	11.2	10.5	4.8	8.1	16.9	29.7
*46.2	28.1	16.2	4.4	6.4	10.8	10.8	4.7	9.9	16.7	31.2
*48.8	29.1	16.8	4.7	6.5	11.4	11.4	4.7	10.5	18.0	32.9
*50.3	29.4	17.4	4.8	7.0	12.4	12.2	5.0	10.6	18.0	33.0
*51.0	30.6	17.5	5.0	6.8	11.8	11.5	5.2	10.5	17.5	33.6
*59.2	36.6	20.6	5.4	8.4	13.0	13.5	5.6	12.1	20.8	40.0
*60.0	36.8	21.6	5.7	9.0	14.3	14.3	5.9	13.0	21.5	39.7

* Benthic juvenile.

TABLE 4.—Measurements (mm) of pelagic juveniles of *Sebastolobus macrochir*.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
21.0	14.5	9.2	2.5	3.1	9.1	9.2	3.8	5.4	10.0	15.0
25.5	17.9	10.8	3.0	4.5	11.2	11.2	4.7	7.1	11.3	18.2
27.2	18.6	11.8	3.8	4.3	12.5	11.0	4.8	7.7	12.2	19.1
29.8	19.2	13.2	3.0	5.0	13.2	13.2	5.7	8.5	13.5	20.8

TABLE 5.—Meristics from cleared and stained larvae and juveniles of *Sebastolobus* spp. (above dashed line) and *Sebastolobus altivelis* (below dashed line).

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper limb	Lower limb			Left	Right	
6.2	-	-	-	-	5	5	-	-	-	-	-	-	-	-	-	-	-
6.8	-	-	-	-	3	3	14	2	-	-	-	3	-	-	-	-	-
7.0	8	7	-	-	5	5	14	12	-	-	-	2	-	-	-	-	-
7.7	8	7	4	4	7	7	23	24	2	1	3	9	III-5	XV-9	I-5	I-5	28
8.1	8	7	-	2	7	7	23	23	-	-	3	9	III-3	XV-9	I-5	I-5	28
8.3	8	7	3	4	7	7	23	23	2	1	2	8	III-5	XV-9	I-5	I-5	27
8.8	8	7	4	5	7	7	23	24	2	2	3	10	III-5	XV-9	I-5	I-5	29
9.3	8	7	3	4	7	7	24	24	2	1	3	10	III-5	XV-9	I-5	I-5	29
10.1	8	7	6	8	7	7	23	23	1	2	5	12	III-5	XV-9	I-5	I-5	29
10.6	7	7	6	7	7	7	23	23	1	2	5	13	III-6	XV-10	I-5	I-5	29
11.2	8	7	6	7	7	7	23	23	1	2	5	13	III-5	XV-9	I-5	I-5	28
11.5	8	7	7	7	7	7	23	23	1	2	5	13	III-5	XV-9	I-5	I-5	29
12.0	8	7	6	7	7	7	23	23	2	2	5	13	III-5	XV-8	I-5	I-5	28
13.0	8	7	6	7	7	7	23	24	2	2	6	13	III-5	XV-10	I-5	I-5	29
13.7	8	7	6	7	7	7	23	23	2	2	5	13	III-5	XV-9	I-5	I-5	29
14.4	8	7	7	7	7	7	23	24	2	2	6	14	III-5	XV-9	I-5	I-5	29
15.0	8	7	7	7	7	7	23	23	2	2	6	13	III-5	XV-9	I-5	I-5	29
16.6	8	7	7	7	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
17.6	8	7	8	7	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
18.1	8	7	7	7	7	7	24	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
19.4	8	7	7	7	7	7	22	22	2	2	6	14	III-5	XV-9	I-5	I-5	29
20.6	8	7	8	8	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
25.8	8	7	8	9	7	7	24	23	2	2	6	15	III-5	XV-9	I-5	I-5	29
30.5	8	7	6	7	7	7	24	24	2	2	7	15	III-5	XVI-9	I-5	I-5	29
40.4	8	7	7	7	7	7	23	23	2	2	7	15	III-5	XV-9	I-5	I-5	29
50.0	8	7	7	7	7	7	23	23	2	2	7	14	III-5	XV-8	I-5	I-5	29

TABLE 6.—Meristics from cleared and stained larvae and juveniles of *Sebastolobus alascanus*.

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper limb	Lower limb			Left	Right	
7.5	8	7	3	4	7	7	21	21	2	2	3	9	III-5	XVI-8	I-5	I-5	30
11.0	8	7	3	5	7	7	22	22	1	2	4	9	III-5	XVI-9	I-5	I-5	30
11.7	8	7	6	6	7	7	22	22	2	2	4	10	III-5	XVI-8	I-5	I-5	30
12.5	8	7	7	8	7	7	21	21	2	2	5	12	III-5	XVI-10	I-5	I-5	30
13.2	8	7	8	7	7	7	21	22	2	2	5	12	III-5	XVI-9	I-5	I-5	30
14.4	8	7	9	9	7	7	22	22	2	2	5	13	III-5	XVI-9	I-5	I-5	30
15.2	8	7	8	8	7	7	22	22	2	2	5	12	III-5	XVI-9	I-5	I-5	30
16.4	8	7	9	9	7	7	21	21	2	2	7	13	III-5	XVII-9	I-5	I-5	30
17.6	8	7	9	9	7	7	21	21	2	2	6	13	III-5	XVI-9	I-5	I-5	30
18.6	8	7	9	9	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
19.8	8	7	8	8	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
20.3	8	7	9	8	7	7	22	22	2	2	5	13	III-5	XVI-9	I-5	I-5	31
21.4	8	7	8	8	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
22.3	8	7	8	8	7	7	22	22	2	2	6	12	III-5	XVI-9	I-5	I-5	30
24.3	8	7	9	8	7	7	21	21	2	2	7	14	III-4	XVI-9	I-5	I-5	30
25.5	8	7	9	9	7	7	22	22	2	2	6	14	III-5	XV-10	I-5	I-5	30
26.4	8	7	9	9	7	7	21	21	2	2	7	12	III-5	XV-9	I-5	I-5	30
27.2	8	7	10	10			21	21	2	2	7	13	III-5	XVI-10	I-5	I-5	30

DESCRIPTION OF DEVELOPMENT

Distinguishing Features

Early *Sebastolobus* larvae (up to 6 mm) can be distinguished from those of all other genera of eastern Pacific Scorpaenidae on the basis of pigmentation. *Sebastolobus* larvae of this size range are unique in having two large melanistic blotches about midway along the tail, one at the dorsal midline and one at the ventral midline (Figure 1A, B). These are sometimes expanded to form a solid band on the tail. Early larvae of all other eastern Pacific scorpaenid genera have a series of melanophores along the ventral midline of the tail, and in some species of *Sebastes* an opposing row is present at the dorsal midline. The large tail blotches of *Sebastolobus* disappear in larvae between 5.0 and 6.5 mm. Soon after the loss of these large tail blotches in *Sebastolobus* the larvae develop prominent crestlike parietal ridges that terminate in double spines, the posterior (nuchal) spine being longer and more prominent than the anterior (parietal) spine (Figure 1F). Of the other eastern Pacific scorpaenid genera, only the larvae of *Scorpaenodes* have parietal ridges and spines like *Sebastolobus*. If two spines are present on the parietal ridges of other genera, the anterior spine is always longer and more prominent than the posterior. *Sebastolobus* larvae may be distinguished from those of *Scorpaenodes* on the basis of a melanistic shield, which covers the dorsolateral surface of the gut in the former and is absent in the latter. Larvae of *Sebastolobus* smaller than 10.0 mm could not be distinguished to species. Larvae larger than this can be identified to species by a combination of characters. The pectoral fins of *S. altivelis* larvae are relatively longer and are wider at the base than in *S. alascanus*. Also, larvae of *S. altivelis* are deeper bodied than those of *S. alascanus*. Details of the structural and pigmentary characters that differentiate the larvae and juveniles of the two species are given below.

General Morphology

Sebastolobus larvae hatch and are freed from their transparent gelatinous egg masses at about 2.6 mm (Pearcy, 1962). The smallest larvae in our plankton collections are about 3.0 mm long and still have the elliptical yolk sac with a posteriorly positioned oil droplet (Figure 1A). When the larvae reach approximately 3.5 mm, the yolk sac has been resorbed and the jaws and feeding apparatus are well formed (Figure 1B). Flexion of the notochord begins in larvae about 6.0 mm long and is completed in larvae about 7.5 mm (Figure 1E, F). Larvae larger than 10.0 mm and pelagic and benthic juveniles can be identified to species on the basis of characters mentioned above (Figures 2-7). In both species, transformation into the pelagic juvenile stage is initiated within the size range of 14.0 to 20.0 mm. All specimens larger than 20.0 mm have some juvenile pigmentation. The largest pelagic juvenile of *S. alascanus* encountered was 27.2 mm, whereas the smallest benthic juvenile was 22.5 mm. In contrast, in the protracted pelagic juvenile stage of *S. altivelis*, individuals may attain 56.0 mm in length. The smallest benthic juvenile of this species in the collection was 42.0 mm. Pelagic juveniles of *S. macrochir* are similar in shape and pigmentation to those of *S. altivelis*. Although the largest pelagic specimen available was only 30 mm long, it is probable that pelagic juveniles of *S. macrochir* grow larger than this and have a protracted mid-water life as in *S. altivelis*.

Relative body depth (maximum body depth/standard length) changes markedly during development and is an important taxonomic character in the pelagic juveniles (Figure 8). It is 15% at the beginning of the larval period, almost doubles by the onset of notochord flexion, and averages 28% during flexion. It increases further to 35% in larvae 7.5 to 10.0 mm. Relative body depth remains at about this percentage in larvae and pelagic juveniles of *S. alascanus* but decreases sharply to an average of 25% (range of 22 to 32%) in benthic juveniles. Late-stage larvae and pelagic juveniles of *S. altivelis* are much more robust and deeper bodied, averaging 41% (range of 36 to 45%) in the 10- to 40-mm size range. Pelagic juveniles 40 to 50 mm long begin to show a decrease in body depth (mean 38%; range of 36 to 41%), 50- to 55-mm specimens show a further decrease (mean 35%; range of 34 to 37%) and the decrease is precipitous in benthic juveniles (mean 28%; range of 27 to 30%). Body depth in 21- to 30-mm pelagic juveniles of *S. macrochir* averaged 37.5% of the body length (range of 34 to 42%).

The gut has an unusual shape in early larvae up to about 5.5 mm. The narrow, dorsally positioned esophagus runs posteriad from the head for some distance before entering the principal mass of the gut. The effect of this is to produce a space between

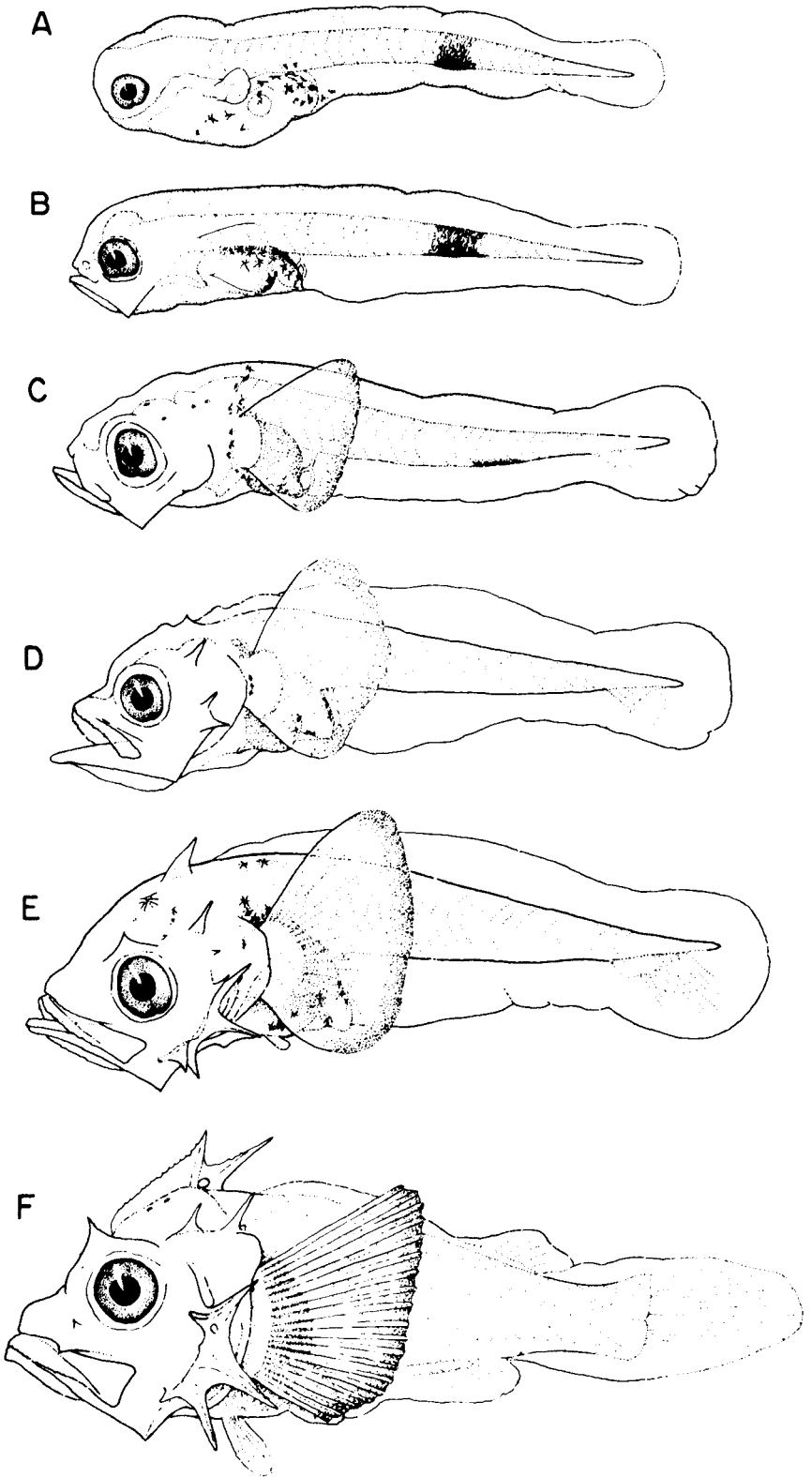

FIGURE 1.—Larvae of *Sebastolobus* spp. from CalCOFI plankton samples. A. 3.0 mm; B. 3.5 mm; C. 5.2 mm; D. 5.7 mm; E. 6.2 mm; F. 7.7 mm.

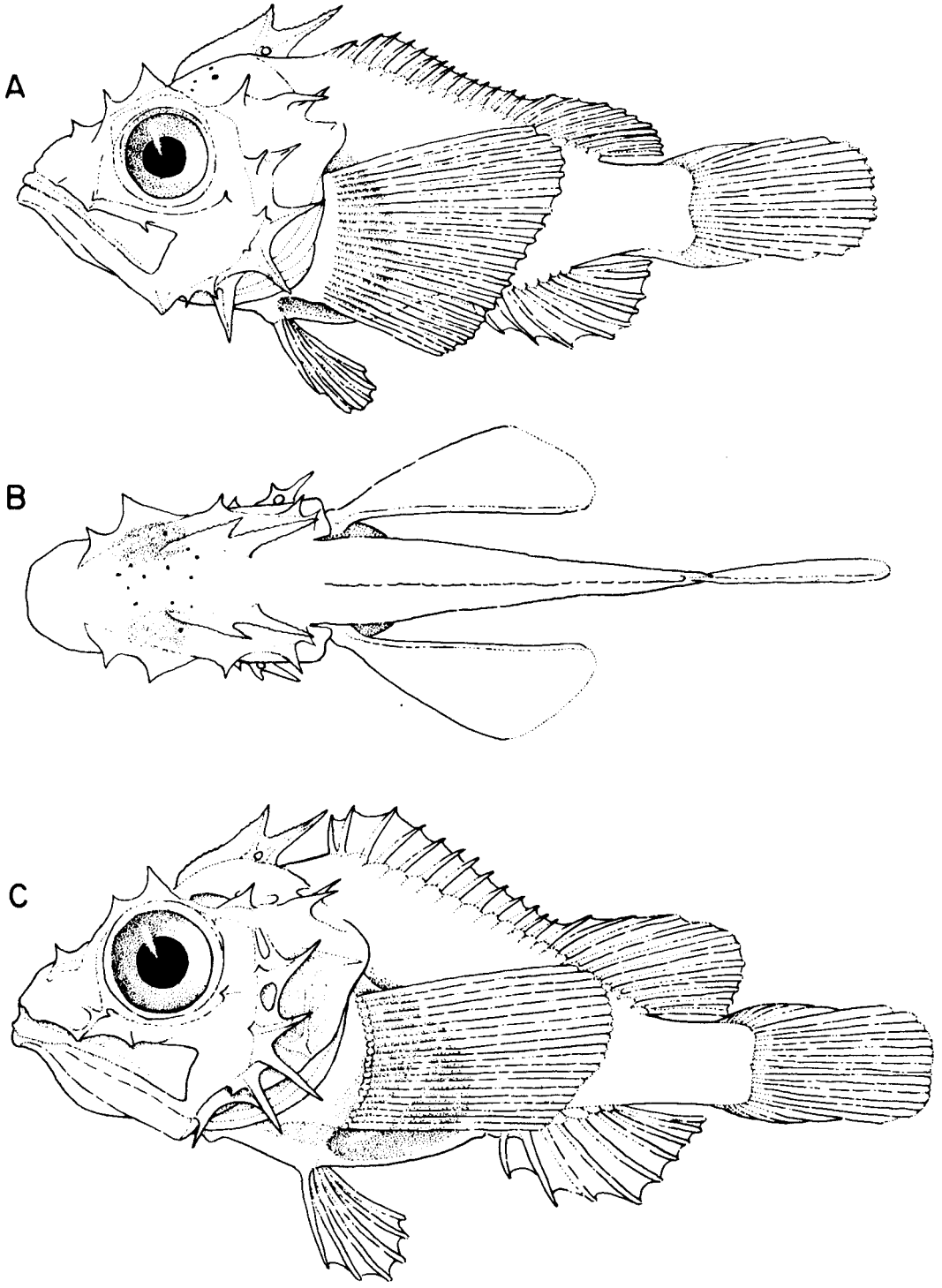

FIGURE 2.—Larvae of *Sebastolobus altivelis* from CalCOFI plankton samples. A. 11.2 mm; B. 11.2 mm, dorsal view; C. 15.4 mm.

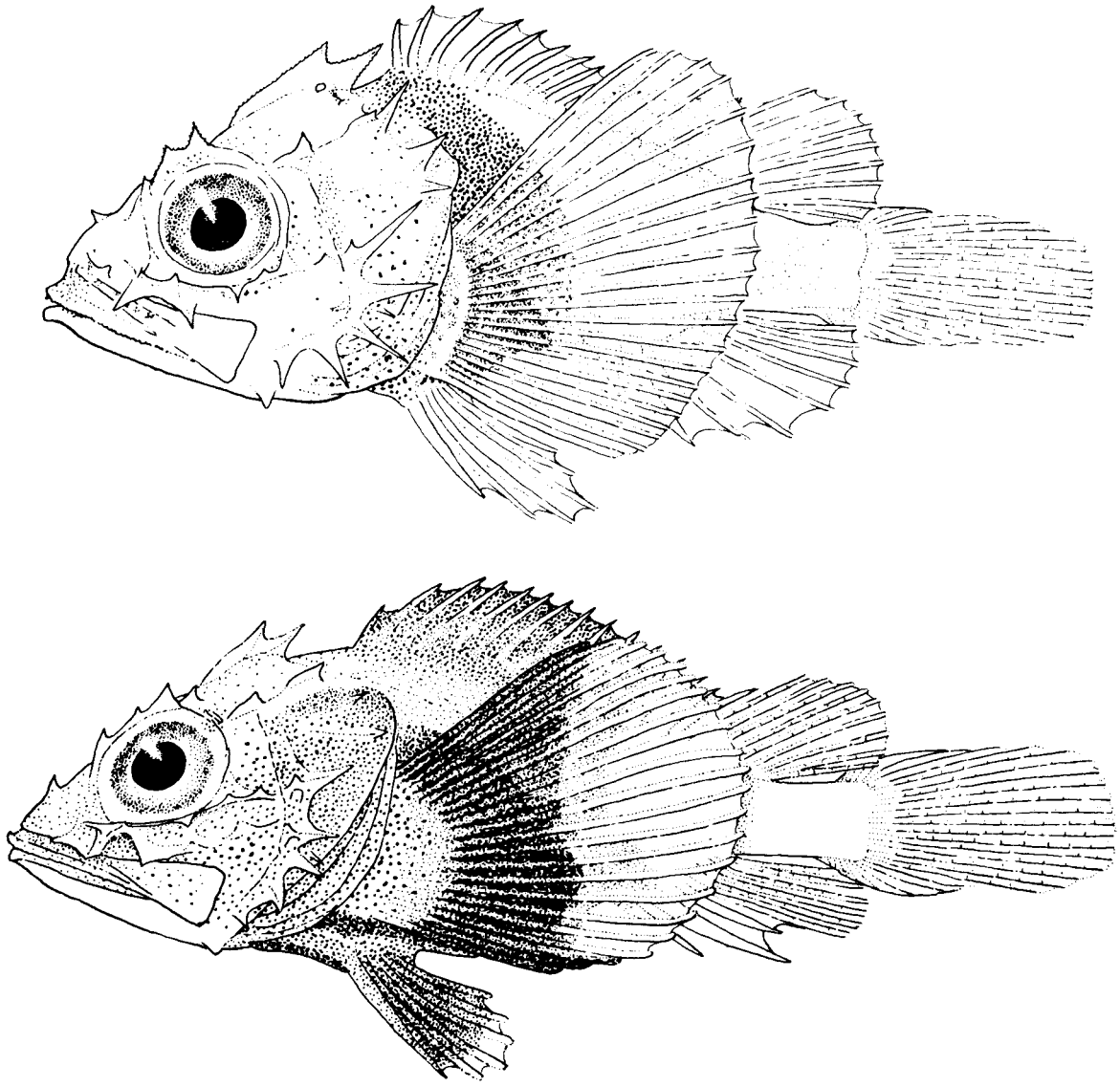

FIGURE 3.—Developmental stages of *Sebastolobus altivelis* from mid-water trawl samples. Above, 16.3-mm transforming specimen. Below, 26.8-mm pelagic juvenile.

the head and the gut (Figure 1B). The space gradually diminishes as the gut enlarges and is absent in larvae larger than 6.0 mm. Relative gut length increases markedly during development. Snout-anus distance averages 41% of the body length up to the stage of notochord flexion, 46% during flexion, and 56% in post-flexion larvae up to 10 mm in length. In larvae and transforming specimens of 10- to 20-mm *S. altivelis* there is an increase to a mean of 64% and in 20- to 56-mm pelagic juveniles there is a further increase to a mean of 68%. In early benthic juveniles snout-anus length averages 64% of body length. The gut is slightly shorter in *S. alascanus;* snout-anus length averages 61% of body length for the larvae and for the pelagic and early benthic juveniles.

The head is moderate in size in early larval stages but enlarges markedly with development. Head length increases from 23% of body length at hatching to an average of 31% during notochord flexion and is 37% in 7.5- to 10.0-mm larvae. Relative head length in larvae and pelagic juveniles of *S. altivelis* in the 10.0- to 40.0-mm size range averages 41%. A slight decrease to a mean of 39%

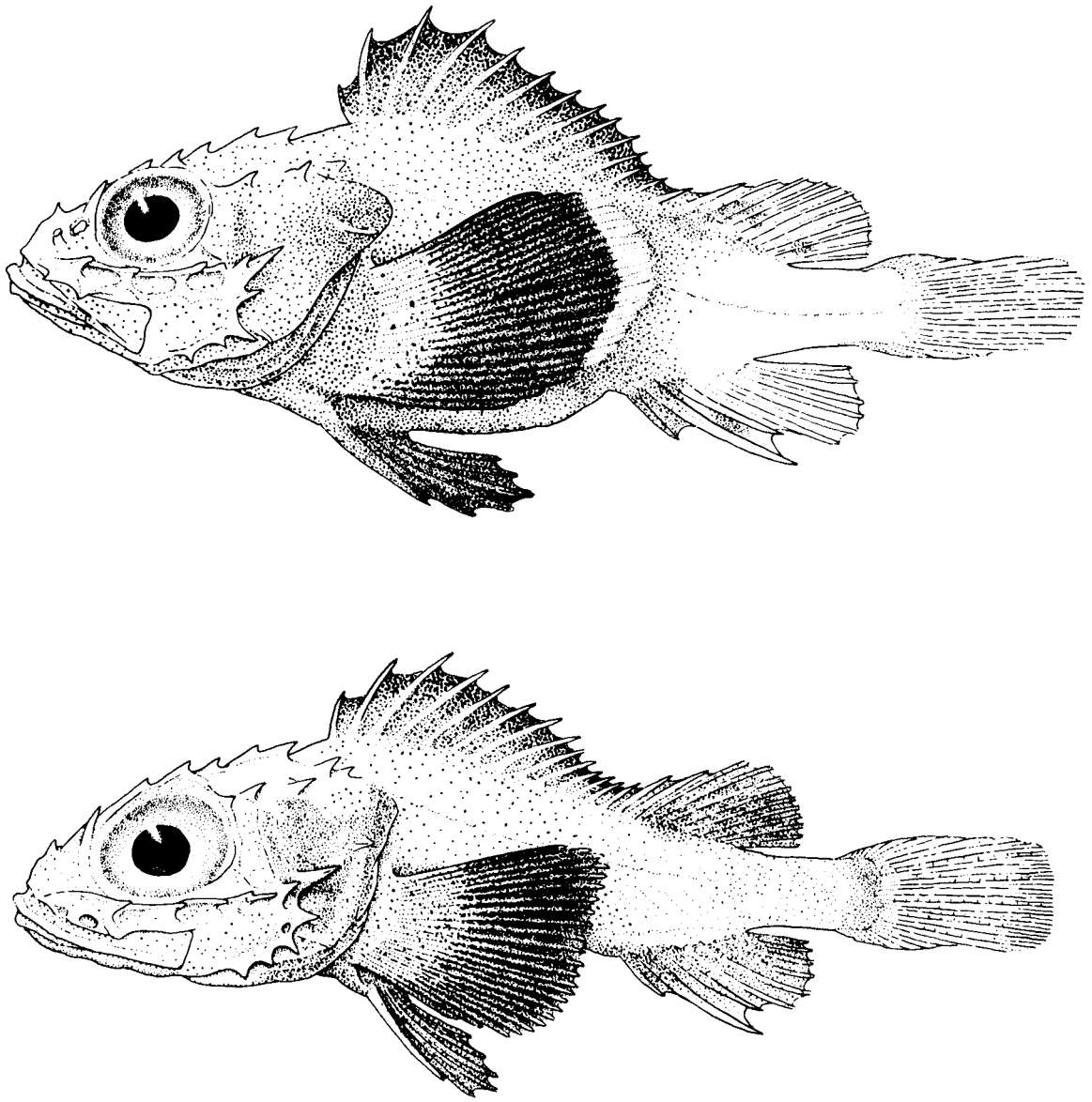

FIGURE 4.—Developmental stages of *Sebastolobus altivelis*. Above, 53.5-mm late pelagic juvenile from mid-water trawl. Below, 53.0-mm benthic juvenile from bottom trawl.

occurs in 40.0- to 56.0-mm specimens and early benthic juveniles average 38%. Virtually the same changes in relative head size occur in *S. alascanus*.

The eyes of early-stage *Sebastolobus* larvae are relatively smaller than in *Sebastes* larvae of comparable size. Eye diameter averages 26% of the head length for larvae up to the beginning of notochord flexion, 27% during flexion, and 28% in post-flexion larvae up to 10.0 mm in length. *Sebastes* larvae average 33 to 35% during comparable stages. Eye diameter in larvae and pelagic juveniles of *S. altivelis* 10.0- to 56.0-mm range) averages 31% of the head length, while in those of *S. alascanus*, eye diameter is slightly larger (mean 33%). In early benthic juveniles of both species, relative eye diameter increases sharply to a mean of 38% of head length. The snout is relatively short in pre-flexion larvae of *Sebastolobus* where snout length averages 27% of head length.

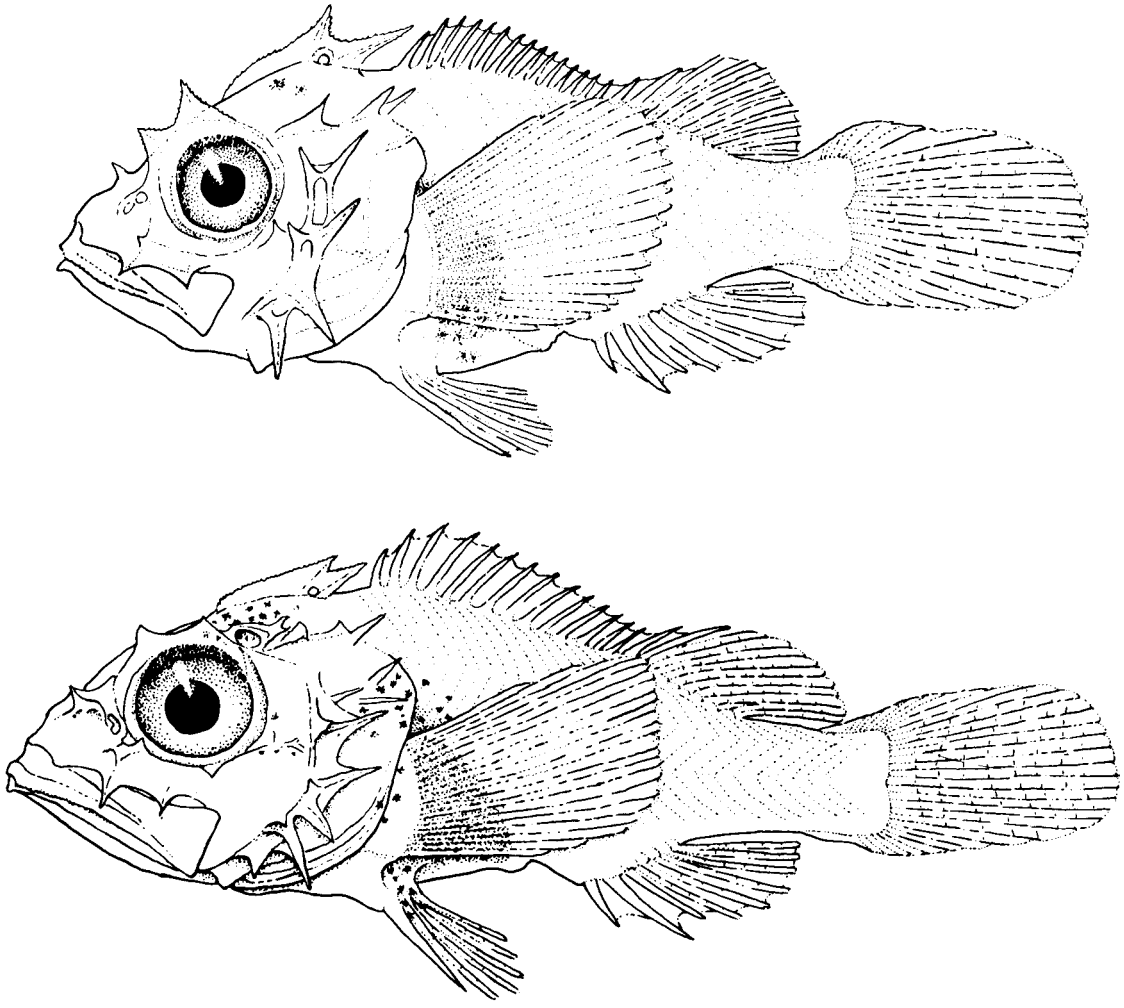

FIGURE 5.—Developmental stages of *Sebastolobus alascanus*. Above, 10.3-mm larva from mid-water trawl. Below, 16.0-mm transforming specimen from mid-water trawl.

This increases to an average 36% in 6.0- to 10.0-mm larvae. Later stages of *S. altivelis* average 28%. *Sebastolobus alascanus* in the 10.0- to 20.0-mm range average 31%, but this is reduced to 27% in the remaining stages.

Fin Development

The pectoral fins of *Sebastolobus* are undifferentiated buds in newly hatched larvae, however, when the larvae reach a length of 3.0 mm the base and blade portions of each fin are beginning to differentiate. From this stage until the initiation of notochord flexion at 6.0 mm the rayed portion of the fin enlarges rapidly to form the large fan-shaped structure characteristic of *Sebastolobus*. At this stage the fin length is about 17% of the body length. This increases to an average of 22% during notochord flexion and 27% in post-flexion larvae up to 10 mm length.

In specimens larger than 10 mm the relative length of the pectoral fin differs considerably between *S. altivelis* and *S. alascanus* (Figure 9). In specimens of *S. altivelis* in the 10- to 20-mm size range, the pectoral fin length averages 34% of the body length (range of 29 to 39%). The pectorals reach their maximum relative length in 20- to 40-mm pelagic juveniles where they average 39% of the body length (range of 35 to 41%). In pelagic juveniles 40 to 50 mm long the average is 35% (range of 32 to 37%), and the fins are still shorter in early benthic juveniles 42 to 60 mm long where they average 29% of the body length (range of 25

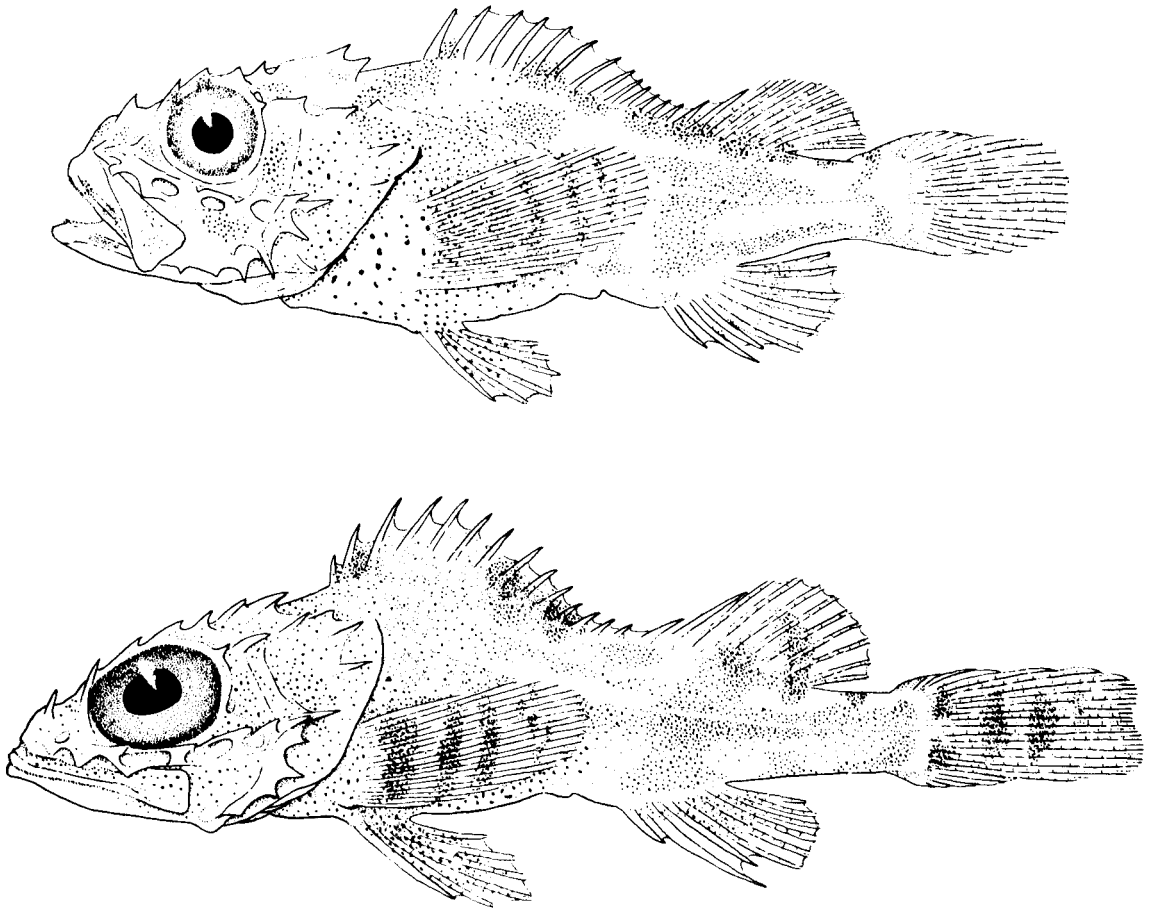

FIGURE 6.—Juveniles of *Sebastolobus alascanus*. Above, 25.3-mm newly transformed benthic juvenile from bottom trawl. Below, 50.3-mm benthic juvenile from bottom trawl.

to 33%). The pectoral fins of *S. alascanus* are considerably shorter than those of *S. altivelis* at comparative sizes. In specimens 10 to 20 mm long fin length averages 29% of body length (range of 26 to 31%). In 10- to 27-mm pelagic specimens pectoral fin length averages 29% of the body length (range of 26 to 32%). In early benthic juveniles 22 to 60 mm long, fin length is reduced to an average of 24% (range of 23 to 28%). The pectoral fin in pelagic juveniles of *S. macrochir* is even longer than in *S. altivelis*. In 21- to 30-mm specimens fin length averaged 43% of the body length (range of 40 to 44%).

The depth of the pectoral fin base is a particularly useful character in distinguishing the larvae of *Sebastolobus* from those of *Sebastes* and is also useful in separating the two species of *Sebastolobus* (Figure 10). In larvae of *Sebastes* examined (e.g., *S. paucispinis*) the depth of the fin base is about 9 or 10% of the body length through notochord flexion; thereafter it gradually diminishes, relative to body length, to about 5 or 6% in the smallest pelagic juveniles. In *Sebastolobus* there is an opposite trend of relative increase from an average of 11% (range of 10 to 15%) in pre-flexion larvae, to 18% (range of 15 to 20%) in subsequent stages of *S. altivelis* up to about 40 mm in length. In larger pelagic juveniles of *S. altivelis* the depth of the pectoral fin base begins to decrease in relation to body length. In 40- to 50-mm specimens the average is 16.5% (range of 15 to 18%) and in 50- to 56-mm pelagic juveniles it is 15% (range of 15 to 16%). It is further reduced to 14% (range of 13 to 15%) in 42- to 60-mm benthic juveniles. The pectoral fin base in *S. alascanus* is significantly shallower

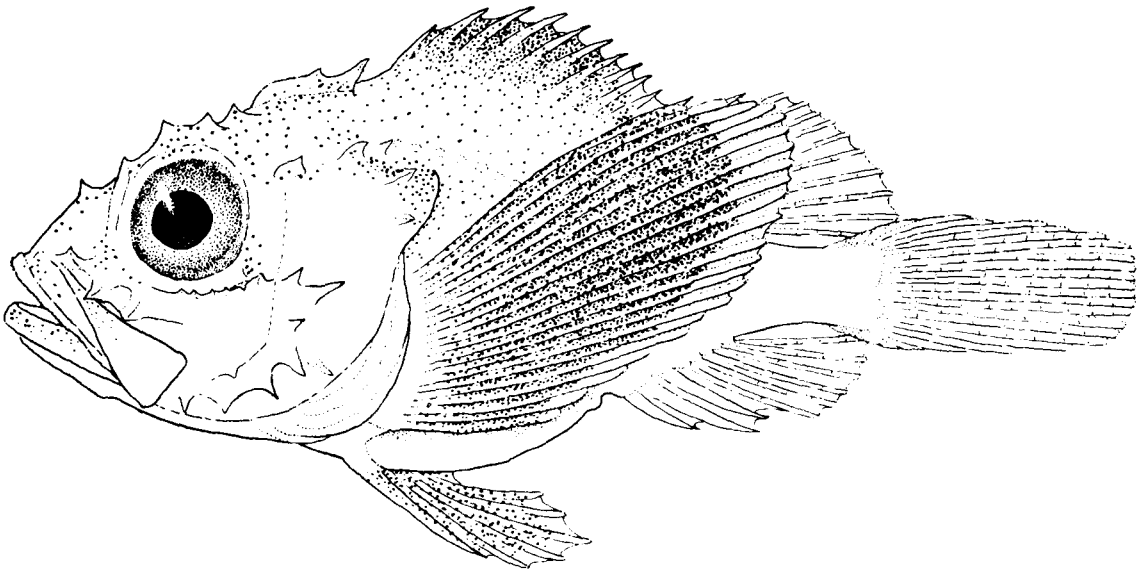

FIGURE 7.—Pelagic juvenile of *Sebastolobus macrochir* from off Kamchatka (27.2 mm).

than in *S. altivelis*. In *S. alascanus* larvae and pelagic juveniles 10 to 30 mm long the fin depth averages 14% of the body length (range of 12 to 16%). In 22- to 60-mm benthic juveniles this is reduced to an average of 10% (range of 9 to 11%).

Ossification of the pectoral fin rays begins in 6.0-mm larvae of *Sebastolobus* (Table 5). The full complements of pectoral rays, 23 to 24 for *S. altivelis* and 21 to 22 for *S. alascanus*, are present in 7-mm larvae (Tables 5, 6).

The pelvic fin buds appear in larvae of about 6.0 mm and elongate to about 12% of the body length by the completion of notochord flexion. Fin length increases to about 17 to 18% of the body length in post-flexion larvae up to 10 mm in length. In *S. altivelis* this increases further to about 24% in pelagic juveniles 20 mm long, and averages 24% (range of 21 to 27%) for the remainder of the pelagic phase. There is a slight decrease to 22% (range of 21 to 24%) in benthic juveniles up to 60 mm long. The pelvic fin is slightly shorter in *S. alascanus* averaging 19% (range of 18 to 20%) in 10- to 20-mm specimens, and 21% (range of 18 to 33%) in larger pelagic juveniles and in benthic juveniles up to 60 mm long. The full complements of one spinous ray and five soft rays are beginning to ossify in 7-mm larvae of *S. altivelis* and *S. alascanus*.

The hypural thickening of the caudal fin first appears in larvae about 3.5 mm long. The hypurals begin to ossify in 7-mm larvae of both species and the full complements of two superior and two inferior elements are ossified in 12-mm larvae of both species. The full complements of eight superior and seven inferior principal caudal rays are beginning to ossify in 7-mm larvae of *Sebastolobus*. The procurrent caudal rays also begin to ossify in 7-mm larvae. The full complements of 6

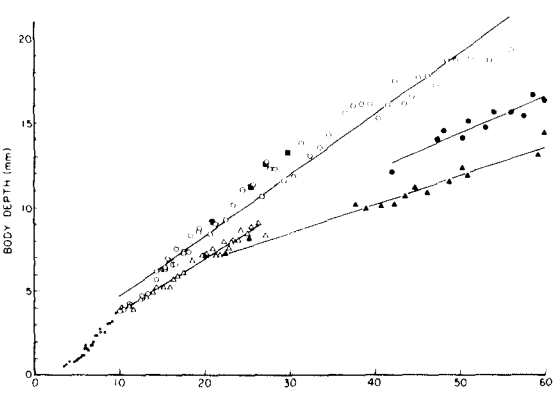

FIGURE 8.—Relationship of body depth to body length in developmental stages of *Sebastolobus*. Small dots = larvae less than 10 mm not identifiable to species. Large open circles = larvae and pelagic juveniles of *S. altivelis*. Large dots = benthic specimens of *S. altivelis*. Open triangles = larvae and pelagic juveniles of *S. alascanus*. Solid triangles = benthic specimens of *S. alascanus*. Solid squares = pelagic specimens of *S. macrochir*. Lines fitted by method of least squares. No regression line drawn for *S. macrochir*.

to 9 superior and 7 to 9 inferior procurrent rays are present in 10-mm larvae of *S. altivelis* and the full complements of 8 to 10 superior and inferior elements are present in 12- to 13-mm larvae of *S. alascanus*.

The dorsal and anal fins begin to develop in 6-mm larvae of *Sebastolobus* and the full complements of rays are ossifying in 7-mm larvae of both species. In *S. altivelis* the usual number of spinous dorsal rays is 15 and in *S. alascanus* the usual number is 16. Both species have 8 to 10 soft dorsal rays with a usual number of 9.

Pigmentation

The melanophore pattern of embryos and yolk-sac larvae of *Sebastolobus* has been described by Pearcy (1962). At the beginning of the larval stage (3.5 mm) the melanophore pattern is distinctive. Large median melanistic blotches oppose each other about midway back on the tail (Figure 1A, B). In some specimens, the blotches are expanded to form a band. Also, melanophores cover the dorsolateral surfaces of the posterior region of the gut. The melanistic tail blotches are transitory; they are lost in some larvae as small as 4.2 mm and one or both are absent in most larvae between 5.0 and 6.0 mm in length. The dorsal spot was absent in all larvae larger than 6.0 mm and the ventral spot was absent in all larger than 6.4 mm. In contrast, the gut pigment is augmented throughout the larval period, extending forward to the axillary region and internally anterior to the cleithrum in larvae about 5.0 mm long. When the larvae reach 6.0 mm the pigment extends onto the ventral surface of the gut and dorsally as deeply embedded pigment at the nape. With continued development the melanophores form a solid sheath on the peritoneum surrounding the gut.

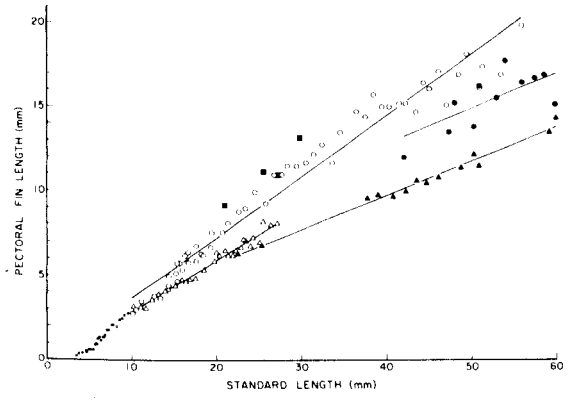

FIGURE 9.—Relationship of pectoral fin length to body length in *Sebastolobus*. Symbols as in Figure 8.

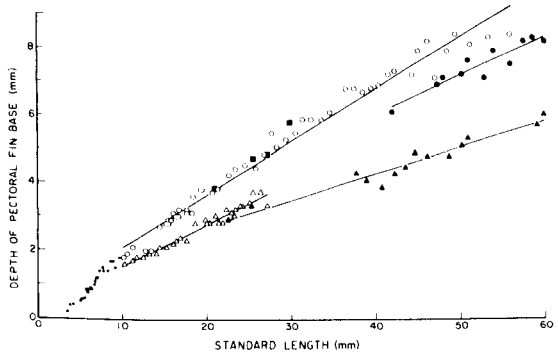

FIGURE 10.—Relationship of depth of pectoral fin base to body length in *Sebastolobus*. Symbols as in Figure 8.

Melanophores appear at the posterior margin of each pectoral fin in some larvae as small as 4.0 mm. About half the larvae examined between 4.0 and 5.0 mm have this posterior margin of fine melanophores and the pigment is present in all larvae in the 5.0- to 11.0-mm range. The melanophores are then lost, and almost all larvae larger than 11.0 mm have pigmentless fins.

Melanophores appear on the posterior lobes of the brain in 5.2- to 7.0-mm larvae and are present in all larvae larger than this. They also appear above the anterior lobes of the brain in larvae between 7.0 and 9.0 mm in length and in most larvae larger than 9.0 mm.

Juvenile pigmentation begins to appear in some specimens of *S. altivelis* of the 14- to 20-mm size range. On the head, patches of melanophores appear on the opercle, cheek, snout, and jaws. In most specimens larger than 22 mm, the patches are confluent, and the head is generally dusky with darker areas at the opercle and along the upper jaw.

A patch of melanophores appears superficially over each side of the gut in specimens as small as 14 mm. These patches expand to form a solid melanistic sheath in some specimens of the 14- to 20-mm size range. The posterior margin of the sheath is an arc running from the vent to the nape and stands out sharply against the pigmentless region of the trunk posterior to the sheath. With continued development the pigment sheath expands posteriad and is a striking feature of the pelagic juveniles. In the 20- to 30-mm size range the sheath extends posteriad to a vertical from the

first or second anal fin spines. In the 30- to 40-mm size range the sheath extends posteriad to the 2nd or 3rd anal spine in most specimens and to the soft dorsal fin in some. In most pelagic juveniles of the 40- to 50-mm size range the dusky sheath extends back to the soft dorsal and it does so in all specimens of the 50- to 60-mm size range. When the juveniles become benthic, the dusky sheath extends posteriad to the caudal fin.

The fins become deeply and characteristically pigmented in juveniles of *S. altivelis*. The anterior portion of the spinous dorsal fin becomes melanistic in specimens as small as 18 mm. In juveniles of the 20- to 25-mm size range the anterior one-half to two-thirds of the fin is melanistic. In the 25- to 30-mm range three-fourths or more of the fin is black. In pelagic juveniles larger than this the pigment has spread onto the soft dorsal fin, and covers both the soft dorsal and soft anal fins in benthic juveniles.

The bases of the pectoral fins begin to be covered with melanophores in specimens as small as 14 mm. In specimens as small as 18 mm the melanophores extend onto the basal region of the rays. With further growth this black basal zone enlarges posteriad and becomes a highly characteristic feature of the pelagic juveniles. The posterior margin of this zone contrasts sharply with the distal clear region of the fin. In juveniles of the 19- to 25-mm size range the width of the black basal zone averaged 20% of the fin length. Enlargement of this zone is shown by the average relative widths for successive size ranges (25 to 30 mm, 38%; 30 to 35 mm, 46%; 35 to 40 mm, 54%; 40 to 45 mm, 65%; 45 to 50 mm, 72%; 50 to 55 mm, 76%). Towards the end of the pelagic juvenile stage a pale translucent layer covers the basal region of the pectoral fin and thus gives the black zone the appearance of a band. The huge pectoral fins, each with their broad black band, are distinctive features of the pelagic juveniles of *S. altivelis*. When the juveniles become benthic the black zone extends to the tips of the fins. Like the pectoral fins, the pelvic fins also develop a black-pigment zone that enlarges with development. In 20- to 25-mm juveniles the basal one-quarter to three-quarters of each fin may be black, although in the majority of specimens the basal one-half is black. In the 25- to 30-mm range most specimens have three-fourths or more of the fin black and in juveniles larger than 30 mm either the fin is entirely black or the extreme tips of the rays are pigmentless.

Juvenile pigment begins to appear in *S. alascanus* in the 14- to 20-mm size range. The first head pigment to appear is a melanistic blotch on the posterior region of the opercle. This gradually spreads anteriorly onto the cheek and in late-stage pelagic juveniles the entire head is speckled with melanophores. A blotch begins to form over each side of the gut in larvae as small as 15 mm. These enlarge dorsad onto the spinous dorsal fin and posteriad as an irregular mottled sheath that contrasts markedly with the solidly pigmented sheath of *S. altivelis* juveniles. In the largest pelagic juveniles the mottling on the dorsal fin and trunk extends posteriad to a vertical from the vent. When the juveniles become benthic the mottling spreads onto the remainder of the body and median fins. Melanophores appear on the bases of the pectoral fins in specimens of the 14- to 20-mm size range. A faint band of melanophores appears on the rays in some specimens of this size range but never becomes highly developed and covers only the basal one-third of the fin in the largest pelagic juveniles. Likewise a faint band of pigment develops on each pelvic fin in specimens as small as 16 mm and only covers the basal half of the fin in the largest pelagic juveniles. When the juveniles become benthic the pectoral fins develop a pattern of four narrow irregular bands.

DISTRIBUTION

The genus *Sebastolobus* has an exceptionally wide latitudinal distribution in the eastern Pacific. *Sebastolobus altivelis* ranges from the Aleutian Islands southward to Cape San Lucas, Baja California, and *S. alascanus* inhabits waters from the Bering Sea to northern Baja California (Barsukov, 1964; Miller and Lea, 1972). The extensive north-south range of *Sebastolobus* is probably related to habitat depth rather than eurythermy. They are deep-living species throughout their latitudinal range and, as such, experience little change in habitat temperature towards the southern end of their range. Alverson et al. (1964) reported that significant catches of *Sebastolobus* are taken at depths shallower than 150 fathoms in the trawl fishery from Oregon to southeastern Alaska, but that the percentage contribution of *Sebastolobus* increased with depth. At the maximum depth range sampled, 500 to 600 fathoms, *Sebastolobus* accounted for about 70% of the total fish catch. Southward of Oregon the shoaler elements of the *Sebastolobus* populations are gradually eliminated and, off

southern California, adults of even the shallower-living species, *S. alascanus*, are generally restricted to waters deeper than 150 fathoms.

Curtailment of spawning or mortality of fertilized eggs off southern California is evident from the distribution of *Sebastolobus* larvae in the CalCOFI sampling area (Figures 11, 12). In 1966, there were no occurrences south of line 97, which runs seaward from the Mexican border, and in 1969 *Sebastolobus* occurred on only two stations below this line. It is apparent that the CalCOFI sampling pattern did not encompass the offshore limits of larval distribution and that larvae occur well seaward of the 200 to 250 mile coastal zone sampled during these years.

The seasonal abundance of *Sebastolobus* larvae for 1966 and 1969 is shown in Table 7. In 1966 larvae were taken from April to October in central and southern California. Numbers of larvae and occurrences were highest in April and diminished in subsequent months. No larvae were taken south of southern California in 1966. In 1969, larvae appeared earlier in the year, from January to December off central California, from January to October off southern California, and from June to September off northern Baja California. Again, numbers of larvae and occurrences peaked in April off central and southern California. Data for the two species are lumped together in Table 7. Of the larvae identifiable to species, those over 10 mm, 6% were *S. alascanus* in 1966 and 12% were *S. alascanus* in 1969. Thus, the data in Table 7 pertain largely to *S. altivelis*.

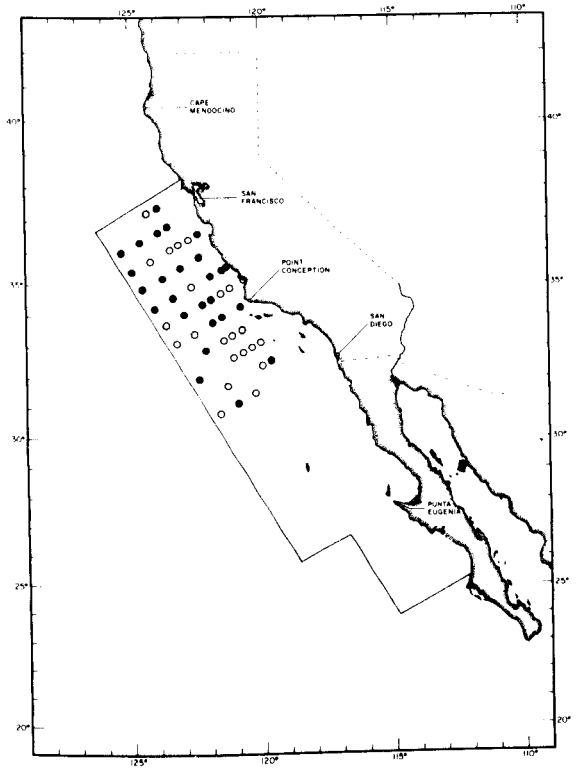

FIGURE 11.—Stations at which larvae of *Sebastolobus* were collected during CalCOFI survey of 1966. Dots indicate stations where numbers of *Sebastolobus* larvae exceeded mean number (7.2) for all positive stations. Area of frequent occupancy is outlined (see Ahlstrom, 1961, for complete grid).

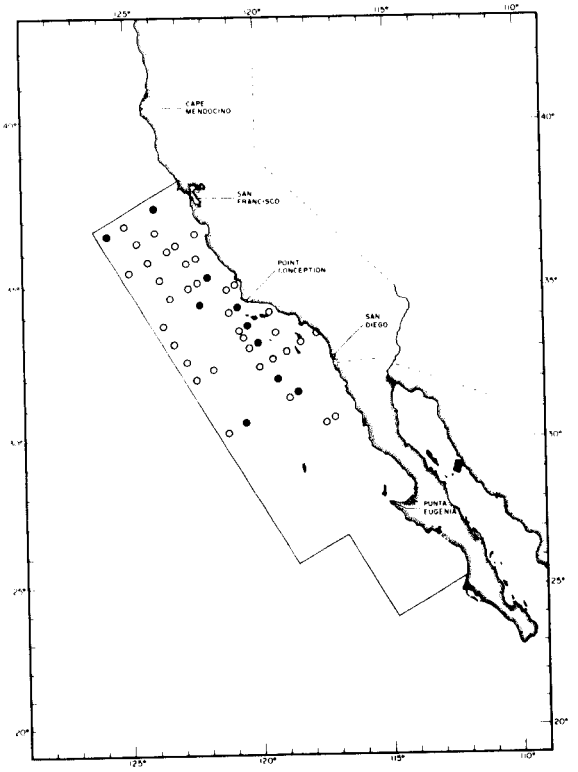

FIGURE 12.—Stations at which larvae of *Sebastolobus* were collected during CalCOFI survey of 1969. Symbols as in Figure 11.

Although *Sebastolobus* larvae are taken in plankton tows over a large proportion of the year, the spawning season is relatively short. Table 8 shows the seasonal change in the size of *Sebastolobus* larvae. The mean size increases steadily throughout the year and small, recently spawned larvae, less than 5 mm, do not occur after June in 1966 and May in 1969. This indicates a spawning season of 4 or 5 mo.

Information on the growth rate of the pelagic juveniles of both species of *Sebastolobus* was obtained by examining mid-water trawl samples

TABLE 7.—Standard numbers and occurrences of *Sebastolobus* larvae taken during 2 yr of the California Cooperative Oceanic Fisheries Investigations. Dashes indicate region not occupied.

	Year	Month																							
		Jan.		Feb.		Apr.		May		Jun.		Jul.		Aug.		Sep.		Oct.		Nov.		Dec.	
		No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.
Central California CalCOFI Lines 60-77	1966	-	-	0	0	227	19	0	0	89	14	67	10	0	0	0	0	13	3	-	-	-	-
	1969	3	1	12	4	81	10	10	2	0	0	17	5	38	9	0	0	14	4	-	-	3	1
Southern California CalCOFI Lines 80-93	1966	-	-	-	-	58	10	34	7	3	1	10	3	37	4	39	8	17	3	-	-	-	-
	1969	3	1	3	1	-	-	3	1	0	0	19	6	13	4	-	-	3	1	-	-	-	-
Northern Baja California CalCOFI Lines 97-107	1966	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	1969	-	-	-	-	-	-	0	0	10	2	13	3	0	0	6	2	-	-	-	-	-	-

from the Los Angeles County Museum, Scripps Institution of Oceanography, and the Southwest Fisheries Center. A total of 260 samples from the years 1950 to 1969 were examined. Most of the samples were taken in the deepwater basins off southern California, but two samples of *S. alascanus* were taken as far north as Crescent City, Calif., and one sample of *S. altivelis* was from the vicinity of Guadalupe Island, Baja California.

The composite monthly size frequencies of mid-water trawl specimens of *S. altivelis* are shown in Figure 13. Two major size classes are present from May through September. One class is formed by larvae and transforming specimens, less than 20 mm in length, from the January-May spawning season. The other class is formed

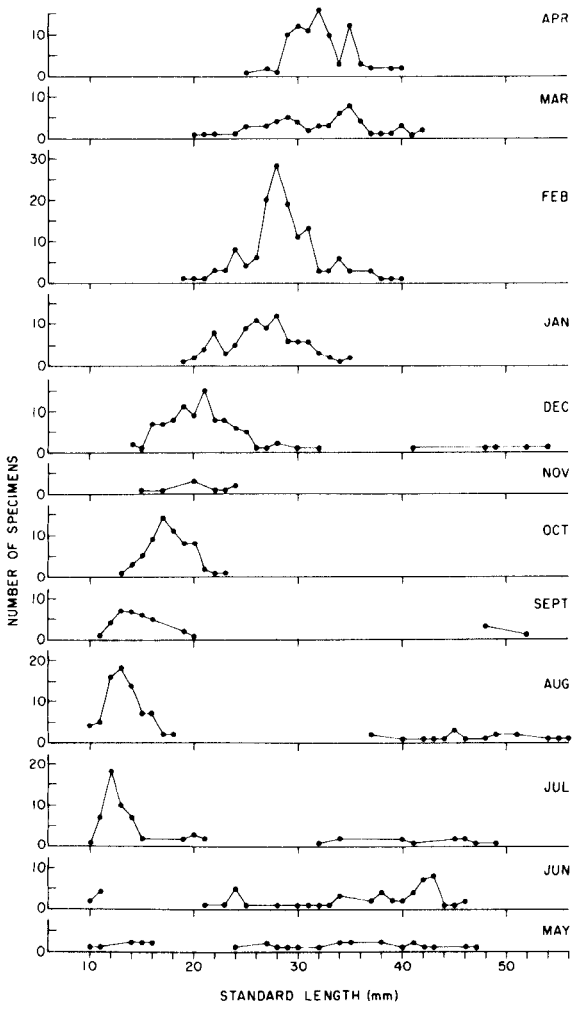

FIGURE 13.—Composite monthly size frequencies for larvae and pelagic juveniles of *Sebastolobus altivelis* from mid-water trawls.

TABLE 8.—Mean lengths with standard deviations in mm (A) and size ranges in mm (B) of *Sebastolobus* larvae taken during 2 yr of the California Cooperative Oceanic Fisheries Investigations.

Year	Month									
	Jan.		Feb.		Apr.		May		Jun.	
	A	B	A	B	A	B	A	B	A	B
1966	-	-	-	-	4.3 ± 1.07	2.2 - 6.9	6.2 ± 1.16	4.2 - 7.8	7.4 ± 1.17	5.1 - 10.0
1969	3.1 ± 0.65	2.8 - 3.4	3.0 ± 0.47	2.8 - 3.4	3.6 ± 0.76	2.6 - 4.7	4.2 ± 0.98	3.1 - 5.2	8.6 ± 0.68	8.1 - 8.9

Year	Month									
	Jul.		Aug.		Sep.		Oct.		Dec.	
	A	B	A	B	A	B	A	B	A	B
1966	8.7 ± 1.15	6.2 - 11.2	11.6 ± 1.42	9.2 - 15.2	14.0 ± 1.57	9.2 - 17.7	16.4 ± 1.37	14.4 - 19.3	-	-
1969	10.8 ± 1.15	8.9 - 13.2	11.8 ± 1.58	9.2 - 18.2	17.0 ± 1.10	16.2 - 17.9	16.3 ± 1.43	15.2 - 18.6	15.0	15.0

by large pelagic juveniles from the previous year's spawning season. A single size class of transforming specimens is present in October and November, however, the absence of the large pelagic juveniles is probably due to inadequate sampling, since they are present in December. From January through April a single class of pelagic juveniles is present. In summary, the early life history of *S. altivelis* is as follows: larvae are produced in a 4- or 5-mo spawning season that peaks in April. Transformation into pelagic juveniles begins as early as July and by the end of December most have completed transformation. The prolonged pelagic juvenile stage lasts until the following summer when the juveniles begin to settle to the bottom. This process probably extends over a 6- to 8-mo period with some juveniles remaining pelagic until December. The total period spent in the pelagic environment from spawning to settling is about 20 mo. The means of the composite monthly length frequencies are plotted in Figure 14 to give an estimation of growth of this species.

The composite monthly length frequencies for mid-water trawl-caught specimens of *S. alascanus* are shown in Figure 15. In contrast to *S. altivelis*, only a single size class is present each month. From July to December a single class of larval and transitional specimens less than 20 mm long is present. Some pelagic juveniles are present in December and by January most of the specimens have completed transformation. Successive samples from February to May contain only pelagic juveniles. In summary, the planktonic and early pelagic life history of *S. alascanus* is similar to that of *S. altivelis*. A probable 4- or 5-mo spawning period that peaks in April gives rise to larvae that appear in mid-water trawl samples in summer. Transformation into the pelagic juveniles begins as early as August and most have completed transformation by the end of December. A class of pelagic juveniles is present from December through May, however, the size ranges for these months overlap the range at which *S. alascanus* juveniles begin to settle to the bottom, and it is

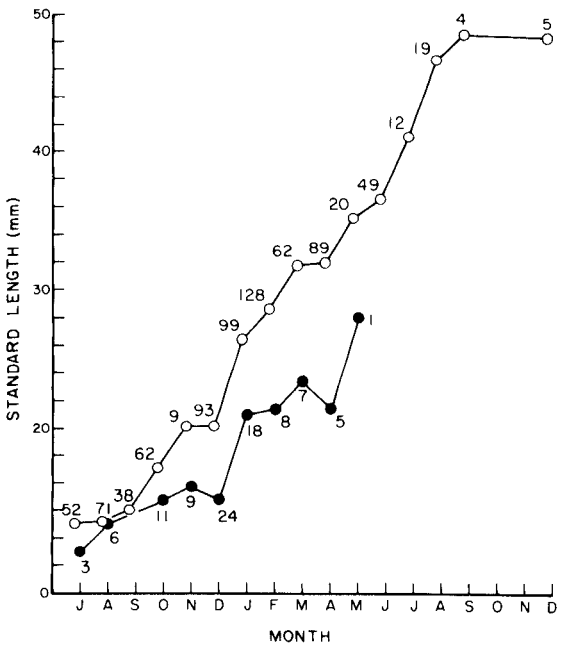

FIGURE 14.—Means of composite monthly size frequencies of larvae and pelagic juveniles of *Sebastolobus altivelis* and *S. alascanus* from mid-water trawls.

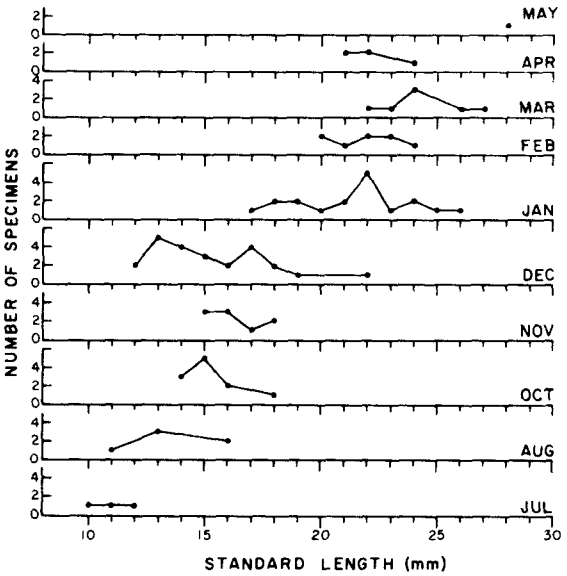

FIGURE 15.—Composite monthly size frequencies for larvae and pelagic juveniles of *Sebastolobus alascanus* from mid-water trawls.

probable that settling begins as early as January. Most have become benthic by May or June. The pelagic juvenile stage in this species is short-lived compared with *S. altivelis* and the total period spent in the pelagic environment from spawning to settling is about 14 or 15 mo. The means of the composite monthly frequencies are plotted in Figure 14.

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SWIMMING ENERGETICS OF THE LARVAL ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

A modification of Gray and Hancock's theoretical method for studying propulsion of spermatozoa was used to estimate the energy expenditure of swimming anchovy, *Engraulis mordax*, larvae. Wave parameters obtained from photographs of feeding anchovy larvae were incorporated into a time dependent sinusoidal body displacement function which is used in the iterated energy integrals of the model. The integrals were numerically evaluated by 2-dimensional 16-point Gaussian-Legendre quadrature. The results for the mean larval length of 1.4 cm was 144.8 ergs/swimming excursion or 4.91×10^{-3} cal/h using known excursion rates. O_2 consumption measurement of similar size larvae indicate a 2.19×10^{-2} cal/h requirement. Extension to other larval sizes can be made using this model with certain qualifications. The relationships of swimming energetics to larval fish behavior are discussed. Current theories of large amplitude intermittent swimming are also discussed in light of the high swimming efficiencies encountered in this study.

The theoretical evaluation of swimming fish energetics by hydrodynamic analysis has been an extensively treated subject in recent years. Most of these treatments however have concentrated on calculation of thrust and thrust efficiencies with the exception of Lighthill (1970, 1971) who gave direct estimates for the mean swimming work rate and has drawn attention to the importance of the accelerative, virtual mass contributions in estimates of mean swimming work rate. Most expositions, however, deal with situations where inertial effects predominate with all subsequent derivations being consistent with that assumption (Taylor, 1952a). The low Reynolds number range of swimming energetics primarily of spermatozoa, has also been extensively treated (Taylor, 1951, 1952b; Gray and Hancock, 1955; Carlson, 1959; Holwill and Miles, 1971). All these treatments disregard inertial and accelerative effects in comparison with viscous effects in their treatment. Also, both viscous and inertial treatments calculate or estimate the mean swimming work rate after steady motion has been established.

The problem attacked in this paper is a synthesis and extension of the two classes of treatments discussed above, specifically to determine the energy expended per excursion by the 1-cm larval anchovy, *Engraulis mordax*. The term excursion as used here requires some elaboration. Larval anchovies have a peculiar swimming behavior because they do not continuously propagate caudally directed waves. In the adult form this behavior is noticeable by observing the tail, i.e., it does not beat continuously even though the fish appears to maintain constant forward motion. In the larval stages, however, this behavior results in an obvious discontinuous motion. The result is a series of bursts of motion from rest to rest which hereafter I refer to as excursions.

The estimation of excursion energetics by a theoretical model rather than indirect metabolic estimators during excursions is demanded because of the small size of the organisms considered, their discontinuous motion, and the investigator's inability to determine which fraction of the total energy consumption is due to swimming alone.

The parameters used in the model to calculate the excursion energy are taken from photographs of a larval anchovy of a specified size executing excursions in search of prey organisms. Since the search for prey constitutes a large proportion of the larva's activity, following Kerr (1971) we can write the total metabolism of the larva as,

$$T_T = T_F + T_C + T_S$$

where T_T = total metabolism
T_F = cost of search for prey

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T_S = standard metabolism
T_C = internal cost of food utilization.

The growth efficiency and subsequent relations derived from T_T are important in estimating fish yields in relation to standing food resources and other factors important to fisheries management. It is this larger view which gives relevance to the rather involved procedure of simply calculating one part of the value of T_T, namely T_F.

THEORY

The derivation of the excursion energy estimate is based on Gray and Hancock's (1955) development for spermatozoa. Instead of a cylinder with an inert head attached, the anchovy larva is regarded here as a ribbon or plate of specified width attached to an inert head (Figure 1). The assumption that the body is a ribbon is justified only if the ratio of the width to thickness (W/t) is $\gg 1$. In the larvae examined in this study this ratio averaged 2.5. While this ratio is not $\gg 1$ I have assumed that it is to simplify the problem. However, the error introduced is, I believe, minimal.

From Figure 1 the following relation is noted and will be used in the following derivations:

$$V_N = V_y \cos\theta - V_x \sin\theta \qquad (1)$$

$$V_T = V_y \sin\theta + V_x \cos\theta \qquad (2)$$

where V_N = normal velocity of an element of body
V_T = tangential component
V_y = y-component
V_x = x-component.

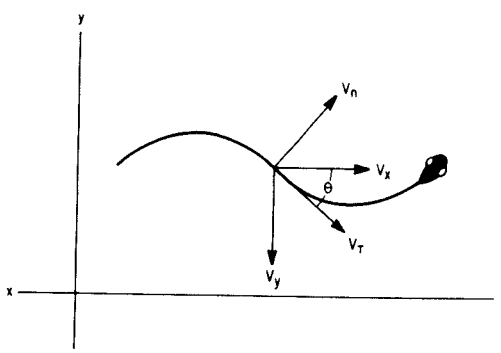

FIGURE 1.—Diagram illustrating the relationship of the velocity components of an element of body when moving transversely in the X-direction.

With the body approximated as an inextensible ribbon we find the use of the normal drag coefficient, C_N, and the tangential drag coefficient, C_T, convenient in addition to an appropriate sagittal contour function $h(s)$ where s denotes distance along the spine of the fish (see Figure 4).

The expression for the velocities V_N and V_T is first expressed in terms of the function which represents the propagated wave along the body $y(x,t)$, and V_x. By noting,

$$V_y = \frac{dy}{dt} \text{ and } \tan\theta = \frac{dy}{dx}$$

we can rewrite Equations (1) and (2) as,

$$\frac{V_N}{\cos\theta} = \frac{dy}{dt} - V_x \frac{dy}{dx} \text{ and } \frac{V_T}{\cos\theta} = \frac{dy}{dt}\frac{dy}{dx} + V_x.$$

$$\text{Given } \cos\theta = \frac{1}{[1+\tan^2\theta]^{1/2}} = \frac{1}{\left[1+\left(\frac{dy}{dx}\right)^2\right]^{1/2}}$$

$$\text{we get } V_N = \left[\frac{dy}{dx} - V_x\frac{dy}{dx}\right]\left[1+\left(\frac{dy}{dx}\right)^2\right]^{-1/2} \qquad (1')$$

$$V_T = \left[\frac{dy}{dt}\frac{dy}{dx} + V_x\right]\left[1+\left(\frac{dy}{dx}\right)^2\right]^{-1/2} \qquad (2')$$

Now we may proceed to write the contributions to the total work of excursion made by the head, body viscous reactive terms, and accelerative body virtual mass.

The element of work performed in moving the inert head is given by,

$$dW_H = 1/2\,\rho\, C_H\, A\, V_x^3\, dt + (m+M)\frac{dV_x}{dt} V_x\, dt$$

(Vlymen, 1970)

where dW_H = element of work performed by the head
C_H = drag coefficient of the head
A = cross-sectional area
m = virtual mass of head
M = mass of head
ρ = density of seawater.

Thus, given the time of excursion as t_E we get,

$$W_H = 1/2\int_0^{t_E} (\rho\, C_H A\, V_x^3 + 2(m + M)\frac{dV_x}{dt} V_x)dt\,. \qquad (3)$$

The element of work performed by the body contributed by viscous-reactive forces can be approximated using experimental values for the normal and tangential drag coefficient of a smooth plate. The choices made are

$$C_N = \frac{k_N}{Re} = \frac{20.37}{Re} \quad \text{(Hoerner, 1965)} \qquad (4)$$

$$\text{and } C_T = \frac{k_T}{\sqrt{Re}} = \frac{1.328}{\sqrt{Re}} \quad \text{(Schlicting, 1960)} \qquad (5)$$

where Re is the appropriate Reynolds number respectively. Although these are primarily low Reynolds number approximations they are within 10% at $Re = 30$. Thus F_N, the normal force on a plate of frontal area A is given by

$$F_N = 1/2\,\rho\, C_N V_N^2\, A.$$

Since for any position along the fish body

$$Re = \frac{2V_N h(s)}{\nu}$$

ν the kinematic viscosity, we get using C_N from Equation (4) the normal force dF_N on an element of body ribbon as,

$$dF_N = \frac{\rho k_N \nu}{4V_N h(s)} V_N^2\, 2h(s)\, ds = \frac{\rho}{2} k_N \nu V_N\, ds.$$

In a similar manner F_T, the tangential force on a plate of total wetted surface area A, is

$$F_T = 1/2\,\rho\, C_T V_T^2\, A.$$

Since the formula for C_T above uses $Re = \frac{V_T l}{\nu}$ where l is distance measured along the body, we get the tangential force dF_T on an element of body ribbon as

$$dF_T = \frac{2\rho k_T \sqrt{\nu}}{\sqrt{V_T s}} V_T^2\, h(s)\, ds = 2\rho k_T \sqrt{\nu}\, V_T^{3/2} \frac{h(s)}{\sqrt{s}}\, ds. \qquad (7)$$

Multiplying each element of force above by the element of distance in the direction of that force and summing yields,

$$dW_B^{V.R.} = \frac{\rho}{2} k_N \nu V_N^2\, dsdt + 2\rho k_T \sqrt{\frac{\nu}{s}} V_T^{5/2}\, h(s)\, dsdt$$

where $dW_B^{V.R.}$ is the element of viscous reactive work performed by an element of body ribbon. Using the Equations (1′) and (2′) for V_N and V_T and integrating over the excursion time t_E and projected body length excluding the head we get,

$$W_B^{V.R.} = \frac{\rho}{2}\int_0^{t_E}\int_{l_H}^{l} \left[\frac{k_N \nu \left[\frac{dy}{dt} - V_x \frac{dy}{dx}\right]^2}{\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{1/2}}\right] dsdt + \rho\int_0^{t_E}\int_{l_H}^{l} \frac{2k_T\sqrt{\nu}\left[\frac{dy}{dt}\frac{dy}{dx} + V_x\right]^{5/2} h(s)}{\sqrt{s}\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{3/4}}\, dsdt\,.$$

where l_H is the x-projected length of the inert head. Eliminating ds by the relation,

$$ds = \left[1 + \left(\frac{dy}{dx}\right)^2\right]^{1/2} dx$$

yields finally,

$$W_B^{V.R.} = \frac{\rho}{2}\int_0^{t_E}\int_{l_H}^{l} \left[\frac{k_N \nu \left[\frac{dy}{dt} - V_x \frac{dy}{dx}\right]^2}{\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{1/2}}\right] dxdt + \rho\int_0^{t_E}\int_{l_H}^{l} \frac{2k_T\sqrt{\nu}\left[\frac{dy}{dt}\frac{dy}{dx} + V_x\right]^{5/2} h(s)}{\sqrt{s}\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{3/4}}\, dxdt\,.$$

As will be noted s is present in the second of the

integrals above; however, later in the discussion s and $h(s)$ will be converted to appropriate functions of x and t so that the integrations may be performed.

The accelerative or virtual mass element of work can be calculated using the fact that the virtual mass of a flat plate accelerating parallel to its normal vector is equal to the mass of the fluid enclosed in a circumscribing cylinder having the plate chord as diameter (Fung, 1969). Hence from Figure 2 the virtual mass is given by

$$dM = \rho \pi h^2(s)\, ds$$

and the magnitude of the acceleration by

$$a \sin \theta_1 = a \sin(\theta - \theta_2)$$

where $a = |\tilde{a}|$.

Now $\theta = \tan^{-1} \frac{dy}{dx}$ and $\theta_2 = \tan^{-1} \frac{V'y}{V'x}$

where $V'y = \frac{dVy}{dt}$ and $V'x = \frac{dVx}{dt}$, giving

$$a \sin(\theta - \theta_2) = a \sin\left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x}\right)$$

Since $|\tilde{a}| = \left(V'^2_y + V'^2_x\right)^{1/2}$, we get

$$a \sin(\theta - \theta_2) = \left(V'^2_y + V'^2_x\right)^{1/2} \cdot \sin\left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x}\right)$$

Thus the magnitude of force $F_{V.M.}$ on an element of body ribbon due to induced mass dM is

$$|F_{V.M.}| = a dM = \rho \pi h^2(s)(V'^2_y + V'^2_x)^{1/2} \cdot \sin(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x}).$$

Since the element of work is given by

$$dW = |F_{V.M.}| \cdot |dx| \cdot \cos(F_{V.M.} \,|\, dx)$$

where

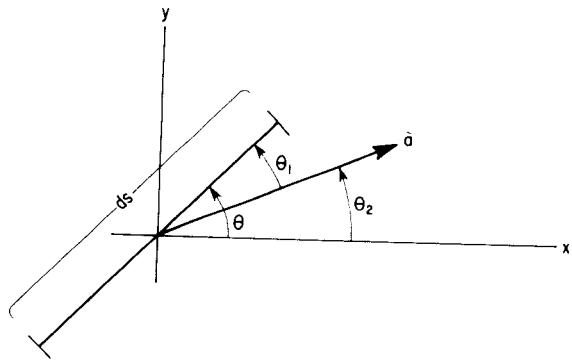

FIGURE 2.—Diagram illustrating body element undergoing acceleration $\tilde{a}$ and relationships of orientation of element to vector $\tilde{a}$ in terms of the angles θ, θ_1, θ_2.

$$|dx| = (V_y^2 + V_x^2)^{1/2}\, dt$$

and

$$\cos(F_{V.M.} \,|\, dx) = \cos(\tan^{-1} \frac{V'y}{V'x} - \tan^{-1} \frac{Vy}{Vx}),$$

we get finally

$$dW = \rho \pi h^2(s)(V_y^2 + V_x^2)^{1/2} \quad (V'^2_y + V'^2_x)^{1/2} \cdot \sin\left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x}\right) \cdot \cos\left(\tan^{-1} \frac{V'y}{V'x} - \tan^{-1} \frac{Vy}{Vx}\right) ds dt.$$

Using the identities for $\cos(a - b)$, $\sin(a - b)$, and ds gives finally,

$$dW^A_{B_I} = \frac{\rho \pi h^2(s)\left[\frac{dy}{dx} V'x - V'y\right]\left[V'x\ Vx + \frac{dy}{dt}\frac{d^2y}{dt^2}\right] dx dt}{\left[V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right]^{1/2}}$$

where $dW^A_{B_I}$ is part I of the element of work performed by the acceleration of the surrounding fluid.

In addition to $dW^A_{B_I}$ above we also want the work done in accelerating the body itself. Calling $\rho_B(s)$ the linear mass density of the body we get, using Figure 2,

$$dW^A_{B\,II} = \rho_B(s)\left(V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right)^{1/2} \cdot \left(V^2_x + V^2_y\right)^{1/2} \cdot \cos\left(\tan^{-1}\frac{V'y}{V'x} - \tan^{-1}\frac{Vy}{Vx}\right) dsdt$$

where $\left(V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right)^{1/2} = |a|$,

$$\left(V^2_x + V^2_y\right)^{1/2} dt = |dx|,$$

$$\rho_B(s)\, ds = dm.$$

When the above terms are expanded we get, taking account of ds,

$$dW^A_{B\,II} = \rho_B(s)\left(Vx\, V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right)\left(1 + \left(\frac{dy}{dx}\right)^2\right)^{1/2} dxdt.$$

Integrating $dW^A_{B\,I} + dW^A_{B\,II}$ from 0 to t_E in t and l_H to l in x we get the accelerative body work,

$$W^A_B = \int_0^{t_E}\int_{l_H}^{l} \rho_B(s)\left(Vx\, V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right)\left(1 + \left(\frac{dy}{dx}\right)^2\right)^{1/2} dsdt \qquad (8)$$

$$+ \rho\int_0^{t_E}\int_{l_H}^{l} \pi h^2(s)\frac{\left[\frac{dy}{dx}V'x - V'y\right]\left[Vx\, V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right]}{\left[V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right]^{1/2}} dxdt.$$

The total work estimated per excursion is then given by the sum of W^A_B, $W^{V.R.}_B$, and W_H.

METHODS

Motion picture photographs (16 mm, 128 fps) of swimming and feeding anchovy larvae were used to ascertain the various parameters in the proposed body displacement function $y(x, t) = A(t) \sin \frac{2\pi}{\lambda(t)}\left(x + \frac{dx_w}{dt} t\right)$ where $A(t)$ is the wave amplitude of the propagated wave, $\lambda(t)$ the wavelength and $x_w(t)$ the wave position as functions of time. Because of the intermittent character of the motion, variance with x was not considered as important an independent variable as t in the various functions comprising $y(x, t)$. The above displacement function is a general time dependent analogue of the function chosen in Holwill and Miles (1971).

The motion pictures used were obtained from John Hunter of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, and the techniques used in obtaining them are described fully (Hunter, 1972). The particular sequences used were of fish larvae varying in length from 1.2 to 1.7 cm standard length. All sequences were analyzed starting with the larvae at rest through the sine-wave execution and subsequent forward movement to rest again. The x-axis was considered to be parallel to the direction of forward motion as monitored by a point midway between the eyes of the fish. This point was also used to monitor forward progression.

The sequences were projected with a 16-mm Kodak[2] analyst projector on an elevated stand, through a right-angle mirror onto a table enclosed with a darkened viewing hood. At the beginning of an excursion the contour of the body was outlined with a fine-point pen on heavy-duty, low-absorbance paper. Once the outline was traced, the next frame was advanced (each frame representing 1/128 of a second) until the larva came to rest again. The mean excursion time of the larvae examined was 12.9 frames. The contour sequences thus obtained were taken to be representative of the feeding-searching behavior and were used in elucidating the wave-form parameters. In addition to the wave-contour parameters, the midpoint between the eyes was monitored for use in determining Vx and $V'x$.

When the above contours and position points were obtained along with the proper magnification factors derived from knowledge of the lengths of the fish in a particular film, relevant parameter values from the tracings were

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

directly measured using a set of dial calipers read to 0.01 cm.

Many of the initial sequences of an excursion when viewed with respect to the x-axis as defined above showed the appearance of a wave along the proximal portion of the fish while the rest of the body coincided closely to the x-axis. This indicated strong x-dependence of the amplitude in the initial portion of the excursion. However, after three frames an almost symmetrical amplitude wave was observed. Thus the amplitude in the first several frames was taken as the maximum length of the wave above the x-axis (Figure 3).

The wave length was taken as that length between two successive crossings of the x-axis by the displacement wave form. During the later part of the excursions no crossings from positive to negative were observed and at this point the wavelength was taken as twice the value from one tangent of the body on the line of motion to the other (Figure 3).

The position of the midpoint between the eyes after each frame was monitored to yield $x(t)$. Each successive movement of that reference point was recorded in the manner outlined above and the distance moved during each frame noted.

The projected length $x_p(t)$ was taken as the length between the two points representing the projection of the tail and snout tip position on the x-axis and was used in a manner to be described later.

The wave position $x_w(t)$ was taken as the projected length of the body from the point where $A(t)$ is measured to the snout tip (Figure 3).

The points representing the functions described above at each unit of time, i.e., one frame, were collected for 18 excursions which were randomly selected from the larval anchovy feeding films. The functions were then nondimensionalized by division by body length and plotted. The geometric form of the resulting function was then used as a guide in selecting an appropriate descriptive function. The parameters of these functional forms were then fitted by computer in the least squares sense using a nonlinear steepest descent approach (Conway, Glass, Wilcox, 1970). The graphical representation of the proposed body displacement function with the internal functions fitted in this manner was found to coincide very closely with the actual body displacements seen in the films.

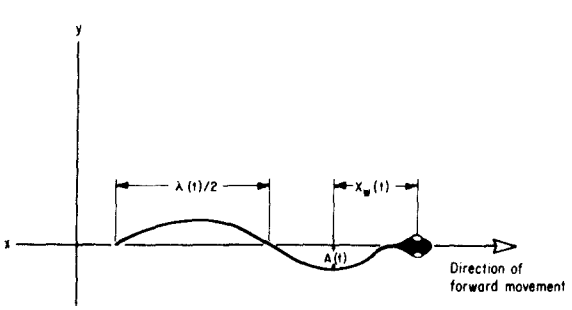

FIGURE 3.—Diagram illustrating the identification of $(t)/2$, $X_w(t)$ and $A(t)$ from photographic records (see text).

In the derivations for total excursion work, W_T, the integral for tangential viscous reactive work contains s, the distance along the fish body, explicitly. The function satisfying $F(x, t) = s$ is extremely complicated for the complete wave-form displacement function using all the fitted internal functions and is almost impossible to calculate explicitly. The alternative used here is to extrapolate back from the measured $x_p(t)$ to yield $s\ (x, t)$.

We know the function $F(x, t) = s$ satisfies

$$F(x_p, t) = L$$

where L is the length of the fish body. Since the maximum amplitude ever encountered in this study was around $0.2\ L$ and the mean integration distance never greater than $\pi/2$, we can calculate, for purposes of comparison, the differences between the true length of a pure sine wave of amplitude A and its projected length.

The unperturbed or no sine-wave form for a $\pi/2$ interval of integration yields simply $\pi/2$. The sine-wave projected length is, for $y = A \sin\theta$,

$$s = \int_0^{\pi/2} \sqrt{1 + A^2 \cos^2\theta}\, d\theta$$

$$= \sqrt{1 + A^2}\ E\left(\pi/2, \frac{A}{\sqrt{1 + A^2}}\right)$$

where $E(\Phi, k)$ is the elliptic integral of the second kind (in this case a complete elliptic integral of the second kind). Taking $\lambda \approx 2.0$ cm we get using $A = 0.2L$.

$$s = \sqrt{1 + 0.16}\ E(\pi/2, 0.37) = 1.625.$$

The difference between this and $\pi/2$ is about 4%. Thus, we expect the projected length and real body length to differ only slightly. With this confidence we make the following additional assumptions:

$$F(\lambda x_p, t) = \lambda L. \qquad \lambda \leq 1$$

This assumption based on the error calculation above postulates a linear relation between projected length and real length. Now $x_p/L = x_p(t)$ and is obtained from excursion analyses. We can rewrite this as

$$\frac{x_p}{x_p(t)} = L$$

$$\frac{\lambda x_p}{x_p(t)} = \lambda L \qquad \lambda \leq 1$$

$$\frac{x}{x_p(t)} = s \qquad x \leq x_p$$

Thus we chose to identify

$$F(x, t) = x/x_p(t) = s(x, t).$$

The determination of the contour $h(s)$ was made using biologically accurate drawings of a 1.84-cm anchovy larva. The term $h(s)$ was established for the body distal to a vertical line tangent to the gill plate as shown in Figure 4.

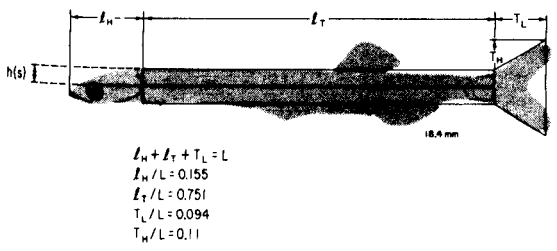

FIGURE 4.—Lateral cross section of 1.84-cm anchovy larvae displaying relationship of idealized contour function $h(s)$ (see text) to appropriate nondimensionalized morphometric parameters.

From that point to the beginning of the tail $h(s)$ was taken as a constant and the relation $h(s) = 0.038\,L$ was found to hold. The dorsal and anal fin contributions were neglected because the plate approximation already constitutes an upper bound estimate for W_T. Thus, the neglect of these fins quantitatively yields a more realistic estimate of W_T. Using the notation of Figure 4 we have,

$$h(s) = 0 \text{ for } s \leq l_H$$

$$h(s) = 0.038\,L \text{ for } l_H < s \leq (l_H + l_T)$$

$$h(s) = 0.038\,L + \frac{(T_H - 0.038\,L)}{T_L}[s - (l_H + l_T)]$$

$$\text{for } (l_H + l_T) < s \leq L$$

or using values in Figure 4 the last relation may be written

$$h(s) = 0.038L + 0.766\,(s - 0.906L).$$

The cross-sectional area A_H which appears in the work integral for the head was determined by randomly selecting Formalin-preserved anchovy larvae from 0.5 to 1.5 cm in length and affixing them, via the Formalin surface tension on their bodies, upright on the side of a small inverted beaker. The largest cross section of the head was then viewed directly with a Nikon optical comparator and an outline traced from the lighted viewing screen. Lengths of the bodies were also measured with dial calipers at the time the tracings were made. Subsequently the tracing areas were measured with a planimeter and corrected to the true value. A least squares analysis of the results yielded the relation $A_H = 0.00423L^{1.23}$ where L is in centimeters and A_H is in square centimeters. The graph is plotted along with the data in Figure 5.

The representation for $\rho(s)$, the linear density of the body, was regarded as constant for any given length and calculated from data in Lasker, et al., (1970). Assuming 90% water, the wet weight of 0.5- to 1.6-cm larvae is then given by $0.00319L^{2.3237} = \rho(s)$ where L is in centimeters and $\rho(s)$ is in grams per centimeter.

The density of the seawater was taken for $T = 17°C$ and was 1.02454. This value was obtained from tables published by the U.S. Navy Hydrographic Office (1956).

In my formulation I assume that the head is propelled through the water as an inert object attached to an undulating body. We want to know the virtual mass and drag coefficient of the inert head for use in the W_H integral. Since the shape of the anchovy larva's head is

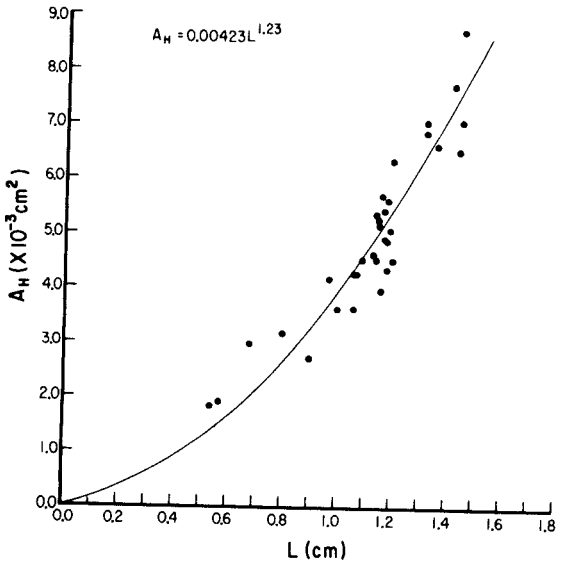

FIGURE 5.—Cross sectional area of larval anchovy head, A_H, as a function of length L.

roughly ellipsoidal or a bluff body, I decided to modify, with due consideration for the geometric differences, the drag relationship observed for a copepod (*Labidocera trispinosa*), which is a naturally occurring bluff body of similar shape, to represent the relevant characteristics of the anchovy larvae head.

If the copepod is taken as an equivalent ellipsoid, we get, from data in Vlymen (1970),

$$\overline{\left(\frac{a_c}{b_c}\right)} = 2.9$$

where a_c is the major axis length and b_c is the semimajor axis length of the copepod *L. trispinosa* and is given respectively by $a_c = \frac{L_c}{2}$ (one-half the metasome length) and $b_c = \left(\frac{A_H}{\pi}\right)^{1/2}$.

For the anchovies studied $\frac{l_H}{L} = 0.155$ (Figure 4) and for $\bar{L} = 1.4$ cm and $A_H = 0.007$ cm^2, $l_H = 0.217$ cm yielding $\overline{\left(\frac{a_a}{b_a}\right)} = 2.3$.

For high Reynolds numbers ($\sim 10^4 - 10^5$) and rotationally symmetrical bluff bodies of various l/d ratios, where l is the bluff body length and d is diameter, we have

$$\frac{C_D \cdot}{C_f} = 3\left(\frac{l}{d}\right) + 4.5\left(\frac{d}{l}\right)^{1/2} + 21\left(\frac{d}{l}\right)^2$$

(Hoerner, 1965)

where C_f is the frictional drag coefficient based on wetted surface area and C_D. is the drag coefficient based on frontal area. We can use this relation to approximate $\frac{C_D \cdot (l/d = 2.9)}{C_D \cdot (l/d = 2.3)}$ assuming $C_f(l/d = 2.9) \cong C_f(l/d = 2.3)$, and use the above ratio to modify the measured drag relation already obtained for the copepod. Substituting $l/d = 2.9$ and $l/d = 2.3$ into the relation for C_D/C_f we get on dividing

$$\frac{C_D \cdot (l/d = 2.9)}{C_D \cdot (l/d = 2.3)} = 1.00.$$

At lower Reynolds numbers we expect the geometric differences to cause a greater discrepancy between C_D ($l/d = 2.9$) and C_D ($l/d = 2.3$). In particular C_D ($l/d = 2.9$) > C_D ($l/d = 2.3$). However, since in my experiments Re was from 0- to 100, the region where we expect the C_D (Re) curve to flatten out to a fairly constant value we take C_D (Re) for the copepod as a first approximation to the C_D (Re) for the anchovy head. That function is C_D (Re) = $85.2/Re^{.80}$, Vlymen (1970). The virtual mass, m, occurring in the integrals for W_H is then calculated by considering the head as if it were an equivalent ellipsoid. Using $(a_a/b_a) = 2.3$ we can calculate

m as $m = k_1 \rho V_D$ where $k_1 = \frac{\gamma}{(2-\gamma)}$

$$\gamma = 2\left(\frac{1-\epsilon^2}{\epsilon^3}\right)\left[1/2 \log\left(\frac{1+\epsilon}{1-\epsilon}\right) - \epsilon\right]$$

$$\epsilon = \left(1 - \frac{b_a^2}{a_a^2}\right)^{1/2}$$

$$V_D = 4/3\pi a_a b_a^2 \text{ Vlymen (1970).}$$

For a 1.4-cm larva m has a value of 1.80×10^{-4} g and assuming the head density is the same as seawater we get $M = 7.9 \times 10^{-4}$ g. Thus W_H may be rewritten as

$$W_H = 1/2 \int_0^{t_E} 85.2\left(\frac{\nu}{L}\right)^{.80} V_x^{2.2} A_H \, dt$$

$$+ \int_0^{t_E} (9.7 \times 10^{-4} \frac{dV_x}{dt} V_x \, dt$$

where ν is the kinematic viscosity of seawater 0.0119 cm^2–s^{-1} (U.S. Navy Hydrographic Office, 1956).

A computer program by Stroud (1971) using 16-point Gauss-Legendre integration, and the above outlined integration scheme was used to compute the integrals comprising W_T. The program was translated into Algol and executed on a Burroughs 6700 at the University of California, San Diego Computer Center. Accuracy of the program was checked by evaluation of the iterated integrals

$$\int_0^w e^{-y^2}\,dy \int_0^y e^{x^2}\,dx \text{ for various } w \text{ and}$$

$$\int_0^1 \int^{\sqrt{1-x^2}} \sqrt{1-x^2-y^2}\,dy\,dx = \frac{\pi}{6}.$$

The results showed the integration scheme to be accurate to the eighth decimal place in the former integral when compared with tables in Rosser (1948) and accurate to the fourth decimal place in the latter integral using standard tables. Details of the mathematical scheme are found in the appendix.

In the integrations of W_T a relative convergence was computed by first doing the integration over the whole interval, that is,

$$I_0 = \int_0^t \int_{f(t)}^{g(t)} F(x, t)\,dxdt.$$

Then the value corresponding to one subdivision is computed, namely,

$$I_1 = \int_0^{t/2} \int_{f(t)}^{g(t)} F(x, t)\,dxdt + \int_{t/2}^{t} \int_{f(t)}^{g(t)} F(x, t)\,dxdt.$$

The relative convergence is then computed as

$$C = \frac{I_1 - I_0}{I_1}.$$

If this value is less than 0.05, the value I_2 is taken as the value of the integral. If it is greater, the intervals comprising I_2 are further subdivided and the process continued until convergence is reached. Thus, if I_n, corresponding to 2^n subdivisions, and I_{n+1}, corresponding to 2_{n+1} subdivisions, are of such values that

$$\frac{I_{n+1} - I_n}{I_{n+2}} < 0.05,$$

then I_0 is assigned the value I_{n+1}.

The convergence is set higher than one might expect because computation of the complex integrals of the type used in this study is manifested by slow and oscillatory relative convergences necessitating a great deal of computer time. However, when the convergence criteria was set at 0.05 in the integrations performed, convergences were better than the critical value. The effect of the higher convergence criteria is thus seen as being an economic and computational convenience.

RESULTS

The plotted values of the nondimensional amplitude, $A(t)/L$, wave position, $X_w(t)/L$, and projected length, $X_p(t)/L$, along with the descriptive functions fitted by the methods discussed are shown in Figures 6 and 7. The points comprising the curves of each represent the mean value of the particular parameter in question at successive units of time where one time unit is $^1/_{128}$ s.

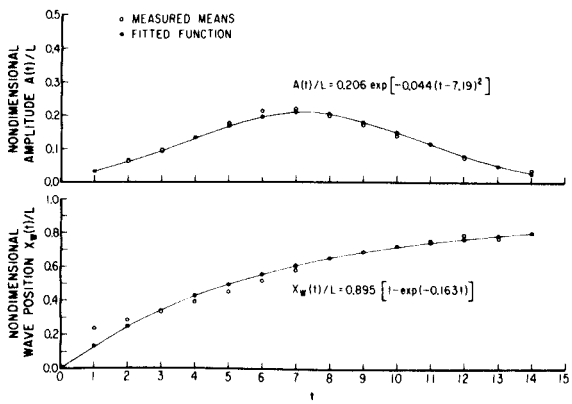

FIGURE 6.—Nondimensional amplitude, $A(t)/L$ and wave position, $X_w(t)/L$, of body displacement function as functions of time, t, in motion frame units. The graphs display the fitted curves (line) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles).

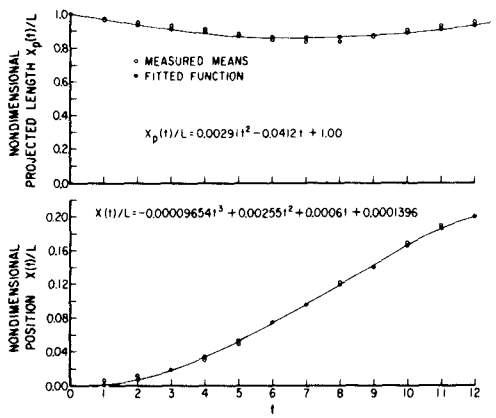

FIGURE 7.—Nondimensional position, $X(t)/L$, and projected body length, $X_p(t)/L$, as functions of time, t, in motion frame units. The graphs display the fitted curves (lines) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles).

The curve for $\lambda(t)/L$, deserves some discussion. Since the amplitude of the propagated wave was known to be zero at $t = 0$, both $\lambda = \infty$ or $\lambda = 0$ would be descriptive of the initial straight-line configuration. However, $\lambda = 0$ implies an infinite number of oscillations varying like sin t/λ with neither the function nor the first derivative existing as $\lambda \rightarrow 0$. Since at the end points of an excursion a slightly perturbed wave form was observed, i.e., a finite wavelength, the nondimensional wavelength of the $t = 0$ excursion wave form was adjusted to be equal to the last. A perfect relation

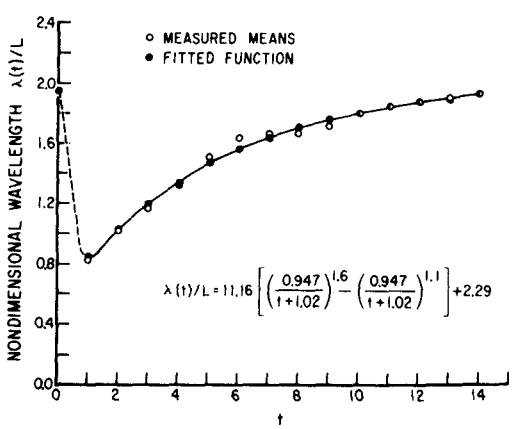

FIGURE 8.—Nondimensional wavelength, $\lambda(t)/L$, as a function of time, t, in motion frame units. The graph displays the fitted function (line) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles). The dotted portion of the fitted curve is discussed in the text.

would have $\lambda = \infty$ at both end points. This, I believe, does not drastically affect the results since the only modulatory component at the end points is the amplitude which is zero at these points. This accounts for the Lennard-Jones type of function which was chosen as a functional representation of $\lambda(t)/L$ and is shown in Figure 8 along with the function itself. The values at other than the end points together with the fact that $A(t) = 0$ at these points is sufficiently descriptive of the contour wavelength to vitiate any physical inconsistencies or mathematical problems that may arise from the end point modification of $\lambda(t)/L$ discussed.

The integrals representing the work per excursion namely $W_B^{V.R.}$, W_B^A, W_H were subdivided further into smaller iterated integrals and, using the mean excursion time of 12.9 frame time units (~0.10s) integrated by the method already outlined. The values obtained were taken to represent the work/excursion of an anchovy larvae of length equal to the mean of the animals used in the study or 1.4 cm.

The values of the work are divided into five categories as follows: 1) head energy representing the value of the integral in Equation (3), 2) normal energy representing the value of the 1st integral of $W_B^{V.R.}$, 3) tangential energy representing 2nd integral of $W_B^{V.R.}$, 4) body inertial energy representing the 1st integral of W_B^A, and 5) inertial energy representing the 2nd integral of W_B^A. The value of these five integrals in ergs/excursion and their fraction of the total excursion energy is given in Table 1. It is observed from the table that accelerative terms such as body inertial and inertial energies account for more than three-fourths of all the energy used in swimming. It is worthwhile noting that although this is an expected outcome of the peculiar behavior of the anchovy larvae, it is possibly true that neglect of such terms in many analyses of fish energetics is cause for errors. Attention to these matters has been given thorough theoretical discussion in Lighthill (1970, 1971). The analysis in this paper,

TABLE 1.—Excursion energy components in ergs for the 1.4-cm anchovy larva.

Item	Energy/ excursion	Percent of total
Normal energy	11.5	7.9
Tangential energy	0.35	0.2
Inertial energy	33.6	23.2
Body inertial energy	99.2	68.5
Head energy	0.15	0.2
Total energy	144.8	

however, depends on incorporating what actually occurs into an easily manipulated theoretical energy construct.

Although the point of this study is to evaluate the swimming energetics in an indirect but nonmanometric manner, it is nevertheless interesting to compare the calculated energy using the theoretical model with values obtained using O_2 consumption measurements obtained with anchovy larvae. Such experiments in limited numbers have been performed by Lasker (pers. commun.) using more than one larva per experiment and with the animals confined to small volume containers. No knowledge of activity levels was possible during these experiments and the values obtained reflect total O_2 uptake per experimental period averaged for the number of larvae per container. Lasker believes, however, that activity levels during such experiments are below natural levels because of the inhibiting effects of the container surfaces and crowding. The value obtained from such experiments was 4.36 ± 1.05 μl O_2/mg dry wt/h. Assuming an RQ of 0.70 we get 1 μl O_2 = 0.005 cal $\pm$ 0.00035 (Lasker, 1962). Thus, the caloric equivalent of the anchovy larval respiratory rate is between 0.0153 cal/mg dry wt/h and 0.0289 cal/mg dry wt/h with a mean value of 0.0218 cal/mg/h (n = 23). A comparison between the theoretically determined energy value and the mean O_2 uptake value given above requires a simultaneous knowledge of swimming activity expressed as an excursion frequency. Such information is not available and it is precisely our inability to make simultaneous observations of O_2 consumption and activity of fish larvae that necessitates the type of study undertaken in this paper. Excursion rates observed during 5-min feeding-searching periods have been measured (Hunter, 1972) using large containers. For the periods observed the excursion rate appropriate to a 1.4-cm larvae was found to be 1.57 ± 0.03 excursions/s with the mean time devoted to intermittent swimming being 82.6% $\pm$ 1.2%. This value is probably a maximum for activity since satiation would probably lead to a decrease in excursions as would the lack of observable food particles. Since available O_2 measurements were not collected during feeding, some modification of the above activity value has to be made to compensate for the inhibition of the container and the absence of food before these values can be used for comparison.

The O_2 consumption measurements of anchovy larvae were performed in small 70-ml containers in light and darkness. The only relative activity measurements that have been performed for similar situations were on 28-day-old herring larvae ca. 1 cm in length in a variety of light conditions by Blaxter (1973). Although herring are continuous swimmers, unlike anchovy larvae, the use of relative activities was deemed an appropriate way of estimating the activity variation of a similar sized nonfeeding organism in the following manner. For herring larvae at 10 different light levels the mean percent difference between maximum and mimimum activity levels was found by Blaxter (1973) to be 78.6%, maximum activity being defined as mean activity plus two standard errors and minimum activity as mean activity minus two standard errors. Although this change is large, it probably reflects behavioral modulation more than effects of the container since in Blaxter's experiment the container (a long tube) contained approximately 1,500 ml of seawater. Thus, regarding the O_2 consumption experiments on the anchovy as representing the minimum activity levels of that organism in the same relationship of active to inactive as found from Blaxter (1973), we can, using known maximum excursion rates during feeding from Hunter (1972), calculate the minimum excursion rate or activity corresponding to our O_2 measurements and hence the energy consumption for swimming based on that excursion rate. This analysis assumes the geometric swimming behavior during feeding and nonfeeding is the same, an assumption confirmed by observation.

Using the mean O_2 consumption value 0.0218 cal/mg dry wt/h and the dry weight of a 1.4-cm larva from Lasker et al. (1970) we get an expenditure of 22.6×10^{-3} cal/h. Taking 1.57 excursions/s as the mean maximum activity value, decreased by 78.6% to convert to minimum activity levels, and multiplied by the theoretically determined energy per excursion of the 1.4-cm larva of 144.8 ergs/excursion, we get 4.91×10^{-3} cal/h. This value yields an estimate of metabolic swimming efficiency of 24.6% for the 1.4-cm larval anchovy assuming a poikilothermic basal metabolic rate of 0.05 μl O_2/mg wet wt/h. This efficiency is quite high when compared to values obtained for larger fish where efficiencies in the range of 8 to 15% (Webb, 1971) are observed. However, such experiments are usually done on large fish constrained by relatively small tanks, swimming continuously, and using a caudal propeller mode of propulsion. Thus any comparison of the above results

with the wide-range Reynolds number motions and large amplitude wave forms encountered in this study must be done cautiously and with appropriate consideration of hydrodynamical dissimilarities. However, using the most obvious behavioral differences between the two types of studies, a higher overall efficiency might be suspected based on the viewpoint of Lighthill (1971) that the large amplitude tail motions exhibited by some fishes be interpreted as a means of producing reactive thrusts which balance the enhanced viscous drag produced upon the commencement of lateral movements. Lighthill thus implies that large amplitude movements interspersed with periods of gliding are more efficient than continuous small amplitude oscillations as a mode of propulsion. This appears to be confirmed in the results of this study where the behavior is of this type and the efficiency apparently high. It should be stressed that a range of efficiencies can exist due to the intrinsic variability in O_2 consumption values and associated activity measurements and the fact that synchronous determinations of both have not yet been performed. The purpose of the swimming efficiency calculation and the associated comparison curves with O_2 values (Figure 9) is to demonstrate the relationship the theoretical values determined here have to the available physiological parameters obtained with simple experimental designs. If excursion energies could be obtained by simpler means, one could circumvent the involved procedures presented in this paper.

It is interesting to note that the Pacific sardine, *Sardinops caerulea,* whose ecological niche was primarily taken over by the anchovy, *Engraulis mordax,* in the California Current (Murphy, 1966) does not exhibit, in the larval stages, the same swimming behavior as the anchovy, i.e., swimming bursts followed by glides. Instead it swims by constant, small amplitude oscillating movements of the body. In light of the results here and theoretical work by Lighthill it is possible that the propulsive efficiencies in the larval stages of the sardine and anchovy are slightly different, the sardine being less efficient. Thus a small behavioral-propulsive difference between the anchovy and the sardine might have permitted the anchovy to compete more favorably when there was a decline in sardine population.

The evaluation of propulsive energetics as outlined in this study is directed at only one size of the anchovy larva because the method

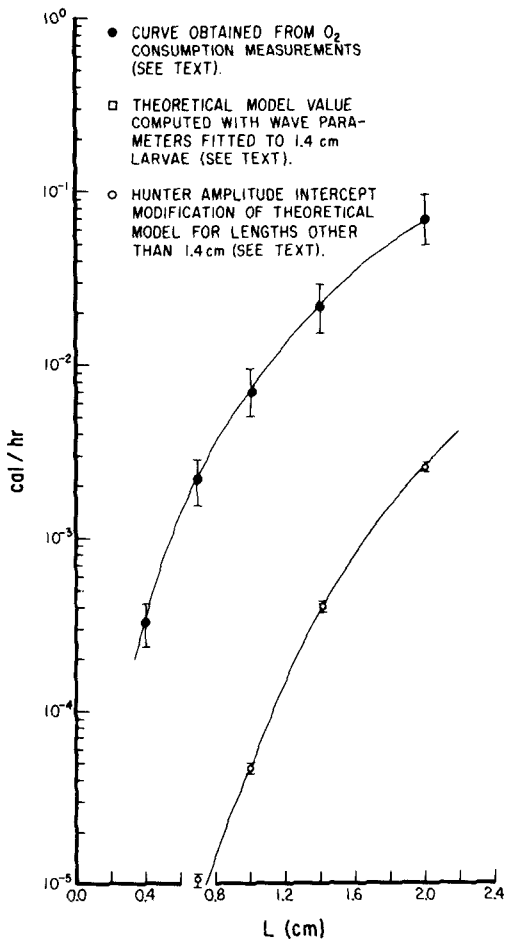

FIGURE 9.—Energy consumption of swimming based on theoretical model (open circles and open square) and total energy consumption based on O_2 utilization (closed circles) as a function of length. Vertical lines on both curves span one standard error of the data.

requires detailed knowledge of the various wave-form parameters as functions of time for each length of the organism studied. Valid results cannot be obtained for other sizes by a mere alteration of the length of the organism in the wave-parameter functions. By the method outlined here, the only way to properly evaluate propulsive energetic costs for different lengths would be to repeat the course of wave-parameter determination completely. However, with such limitations in mind it is interesting to compare results obtained when modification of the existing wave-parameter functions is made using extensions of known length-dependent wave-parameter quantities which have been measured for larval anchovies. The

only such wave parameter available for modification and incorporation into the energy formulation is the wave amplitude.

Hunter (1972) measured the relationship between tail-beat amplitude and larval length for intermittent swimming and found the relationship,

$$A = 0.112 + 0.170L$$

where L and A are in centimeters. Since minimal amplitude dependence on length exists because of the exaggerated whiplike motion of the tail, Hunter's amplitude value is greater than my value for the maximum wave amplitude of 1.4-cm larvae. This is because amplitudes used in this study are measured as the wave crest progresses caudally at each successive time unit, whereas at the tail, wave progression ceases along the body and may even become retrograde due to the whiplike motion. The important point is the intercept at zero length where both measurements must be consistent, i.e., equal. Thus, admitting equality of the interception point at $L = 0$ and adjusting the first order coefficient in Hunter's equation to yield the correct value for maximum amplitudes at L = 1.4 cm we get,

$$A_{max} = 0.112 + 0.094\ L$$

This value was substituted for $A_{max} = 0.026\ L$ in the amplitude function $A(t) = 0.206\ L \exp[-0.044\ (t - 7.19)^2]$ and its first two derivatives used in the L = 1.4 cm formulation. The work integrals were then recomputed at the three new points L = 0.4 cm, L = 0.7 cm, and L = 2.0 cm. Because the A_{max} values coincided at L = 1.4 for both treatments this value was not used again in the integration procedure. The values obtained are shown in Table 2. Least squares regression of the data assuming the functional form $E = aL^b$ where E is energy/excursion in ergs and L length in centimeters yielded $E = 27.5\ L^{4.48}$. The energy/excursion calculated for the four additional lengths was then converted to hourly energy rates using the excursion frequencies cited earlier. The results obtained were plotted with scales of calories per hour vs. length in centimeters. For comparison, another curve of the form $\frac{dO_2}{dt} = f(L)$ was computed and plotted along with the curve formed using the additional model points above (Figure 9). The line shown connecting these points is fitted by eye. The comparison curve was based on the respiration value of 0.0218 cal/mg dry wt/h and the following relationship between dry weight in milligrams and length in millimeters, $\log W = 3.3237 \log L - 3.8205$ (Lasker et al., 1971). This comparison curve is isomorphic to the length-weight curve with no allowance being made for specific respiration changes with increasing weight. Therefore the curve is to be regarded as the best approximation to the total O_2 consumption rate for swimming larval anchovies. It provides only a means of judging the physiological reliability of the energy summation method employed here. However, because the changes in specific respiration as a function of weight would not change this comparison curve appreciably, it can probably be regarded as sufficiently reliable. With this understanding some comparison of these curves can be made.

TABLE 2.—Excursion energies for five larval anchovy lengths using Hunter's modified intercept amplitude function (see text for complete discussion) for extension to larval lengths other than 1.4 cm.

Length (cm)	Energy/ excursion (ergs)
2.0	881.4
1.4	144.8
1.0	16.3
0.70	3.6
0.40	0.76

From laboratory observation of larvae it seems apparent that nondimensional amplitude and wavelength do not remain constant but decrease in absolute value as length is increased. That is, functions descriptive of these nondimensional parameters do not remain descriptive of animals of all lengths. That is exactly what is observed as we deviate from the original L = 1.4 cm point where the nondimensional wave parameters are fitted. Even with modification of A_{max} used to compute the original curve this effect is still observable. Part of the deviation is, however, due to the behavior of the larvae as age increases. Very small larvae float 90% of the time with occasional bursts of intensive activity (Hunter, 1972) which, as I pointed out earlier, is quite inefficient. As the larvae get older, however, intermittent, more efficient swimming becomes the dominant mode of locomotion. This trend is partially reflected in these two curves. As the larvae get older and

larger the intermittent swimming rate decreases and the nondimensional amplitude and wave functions decrease also. This accounts for the large locomotion energy computed for larvae greater than 1.4-cm in length. It is interesting to note how behavioral factors, when unavoidably neglected in extending this curve, become evident when compared with reasonable estimates for total energy consumption.

In view of the behavioral-mathematical factors influencing the shape of the theoretical curve in the directions observed here and the physiologic reasonableness of the metabolic swimming efficiencies obtained when exact wave parameters descriptive of the L = 1.4-cm larva are used, it is reasonable to conclude that the energies calculated from the model are the best estimates of the swimming energetic requirement per excursion of the larval anchovy, excursion being regarded as a discrete, reproducible behavioral entity, currently available.

Therefore, the major results of this study are 1) the demonstration that modifications of existing methods of computing energy of translation yield information on behavior when consideration is given to differences in behavior, shape, and flow scale, 2) that a good correlation exists in terms of metabolic swimming efficiency obtained between direct O_2 measurements and the model, 3) a confirmation of the high efficiency of large amplitude, intermittent swimming behavior, and 4) quantitative estimates of swimming energy requirements derived from this model may be used for other larval anchovy research.

Theoretical studies such as random walk analyses and correlations with feeding behavior and migration which are being studied currently could incorporate these data to provide a comprehensive and quantitative picture of larval anchovy energetics and behavior.

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APPENDIX

The integration of the iterated integrals was accomplished via a two-dimensional extension of the standard Gauss-Legendre guadrature. The one-dimensional fixed limit integration formula was used by Holwell and Miles (1971) for similar classes of functions with good results. The type of integrals requiring evaluation were of the general form

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt$$

a, b, fixed.

Defining

$$G(t) = \int_{f(t)}^{g(t)} F(x, t)\, dx,$$

we get

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt = \int_a^b G(t)dt.$$

By n-point Gauss-Legendre quadrature Abramovitz and Stegun (1966) this is given approximately by,

$$\int_a^b G(t)dt \cong \frac{b-a}{2} \sum_{i=1}^{n} w_i\, G(\xi_i)$$

where $\xi_i = \frac{b-a}{2}\, y_i + \frac{b+a}{2}$

y_i = ith zero of $P_n(x)$, the n-order Legendre polynomial and

$$w_i = 2\Big/\left(1 - y_i^2\right)\left[P'_n(\xi_i)\right]^2 .$$

Using Gauss-Legendre quadrature on $G(\xi_i)$ yields,

$$\int_a^b G(t)dt \cong \frac{b-a}{2} \sum_{i=1}^{n} w_i \int_{f(\xi_i)}^{g(\xi_i)} F(x, \xi_i)\, dx$$

$$\cong \frac{b-a}{2} \sum_{i=1}^{n} w_i \frac{g(\xi_i) - f(\xi_i)}{2} \sum_{j=1}^{n} w_j^* F(\eta_j, \xi_i),$$

where $\eta_j = \frac{g(\xi_i) - f(\xi_i)}{2}\, y_j + \frac{g(\xi_i) + f(\xi_i)}{2}$

$w_j^* = 2/(1 - y_j)\left[P'_n(\eta_j)\right]^2$ and

y_j = jth root of $P_n(x)$.

We have finally the result,

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt \cong \frac{b-a}{2} \sum_{i=1}^{n} \sum_{j=1}^{n} w_i\, w_j^* \frac{g(\xi_i) - f(\xi_i)}{2} F(\eta_j, \xi_i),$$

where the above definitions hold.

ANALYSIS OF MIGRATIONS AND MORTALITY OF BLUEFIN TUNA, *THUNNUS THYNNUS*, TAGGED IN THE NORTHWESTERN ATLANTIC OCEAN[1,2]

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ABSTRACT

An analysis is presented on the release and return data from bluefin tuna, *Thunnus thynnus*, tagged in the northwest Atlantic Ocean from 1954 to 1970. There was an apparent northward movement of fish from the New Jersey area as the fishing seasons progressed. Tag returns from bluefin released in the Long Island and southern New England areas tended to be to the north at first and then to the south. Mean distances between release and return tended to be greater for fish released in the New Jersey area than for the other two areas. Estimates of mortality rates for tagged bluefin were made using the Chapman-Robson method and then adjusted for Type-I and Type-II tag shedding and Type-I tagging mortality. The average estimate of instantaneous fishing mortality is 0.57 and other losses (natural, tagging, and emigration) is 0.68 on an annual basis. The estimate of other losses is considerably higher than the natural mortality that would be expected for bluefin. Evidence is presented suggesting that the rate of emigration may be quite high. The average single season exploitation rate of tagged bluefin was estimated to be 0.33. It was noted that since bluefin may be both immigrating to and emigrating from the fishery the estimate of exploitation may not be representative of the entire population. Even though validity of available effort data is questionable, regression estimates of mortality and survival rates were made using catch per effort data. These estimates of survival are lower than those obtained using the Chapman-Robson method.

The data which form the basis for this report were assembled by the first author. This study is based upon releases of tagged bluefin tuna, *Thunnus thynnus*, that were made by a variety of organizations and individuals under the coordination of the Woods Hole Oceanographic Institution Cooperative Game Fish Tagging Program at various locations along the middle Atlantic bight of North America from July 1954 to August 1970 and returns of these tags to the end of 1970. Additional returns are expected in the future from more recent releases.

MIGRATIONS

Because of the variety of methods, locations, and dates of release, we needed to assemble the data by relatively homogeneous release groups. The criterion for constructing a release group for analysis of migrations was to develop homogeneous time-location strata of releases from which a minimum of 20 tags were recovered. This procedure allowed us to work with homogeneous groups, but eliminated roughly 10% of the recovered tags from our analysis. Table 1 summarizes these release groups and Figure 1 shows their localities. We can see from Table 1 that during the study period the tagging operations tended to shift from the New Jersey coast, to the New York coast, to the southern New England coast, and that releases in July tended to be south of those made in August or September.

Tagging data have been used to show some of the longer migrations of the bluefin tuna (Food and Agriculture Organization, 1972). We examined the shorter term recoveries from an analytic point of view. In order to do this, we made use of a method developed by Rothschild (Bayliff and Rothschild, in press). Using this method each release group was stratified into intervals of time at liberty. Release vectors (latitude and longitude) for each release group were used to compute an average or common release vector. Each recapture vector for the group was then standardized to the common release vector. The standardized vectors were then used to find 1) the average recapture vector and 2) the determinant of the recapture

[1]This paper is dedicated to the memory of Gerald J. Paulik. He was a good friend and colleague and made important contributions to the theory of tagging.

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TABLE 1.—Release groups used for analysis of migrations of tagged bluefin tuna.

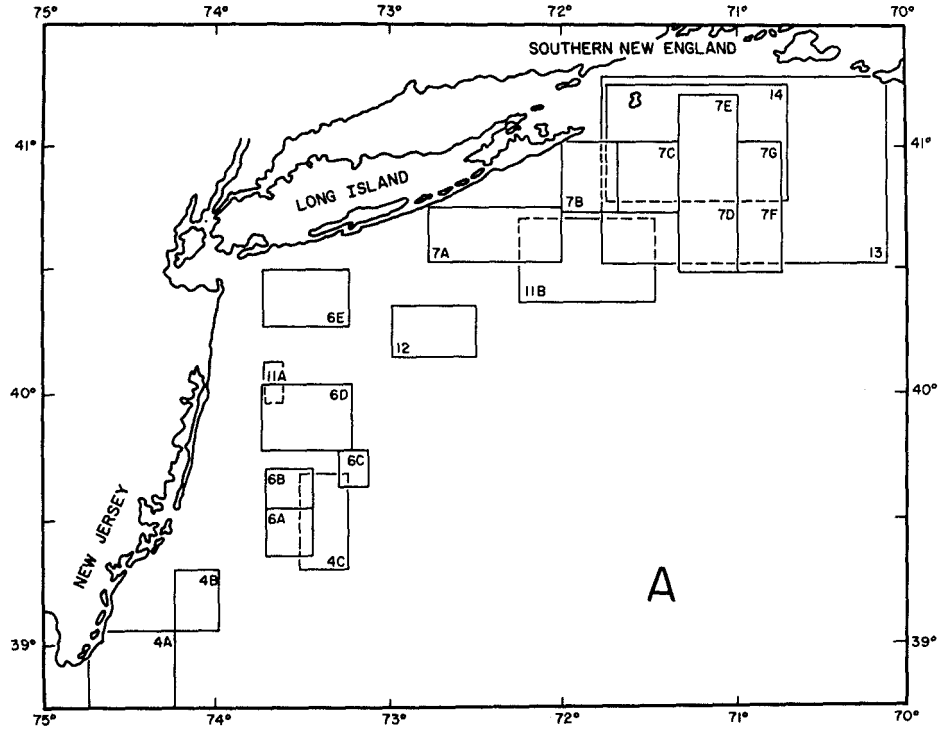
	General location of release					
	New Jersey Coast		Long Island Coast		Southern New England	
Release date	Group No.	No. of returns	Group No.	No. of returns	Group No.	No. of returns
July 1964	2A	33				
	2B	32				
	2C	27				
Aug. 1964			3	33		
July 1965	4A	36				
	4B	86				
	4C	38				
Aug. 1965	5A	22	5B	47	5C	24
July 1966	6A	114				
	6B	127				
	6C	45				
	6D	85	6E	62		
Aug. 1966			7A	20	7C	85
			7B	81	7D	36
					7E	55
					7F	203
					7G	177
Sept.-Oct. 1966			8	23		
July 1967	9A	23				
	9B	94				
Sept. 1967			10	27		
July 1968	11A	21	11B	39		
July 1969			12	24		
Aug. 1969					13	40
Sept. 1969					14	22
July 1970					15	17
Aug. 1970					16	25
1954-63					17	24

variance-covariance matrix. The determinant of the recapture variance-covariance matrix is proposed by Bayliff and Rothschild as an index of the dispersal of the fish. When the distance of the recoveries from one another is large, the determinant is large.

It should be noted that the vectors computed by this method are not on a per-unit-effort basis so that "migration patterns" reflect not only the apparent movement of the fish, but also the distribution of fishing effort. In order to more fully understand the nature of short-term movements, it will be necessary to study in some detail the complex problem of the distribution of bluefin tuna in the northwest Atlantic. Preliminary to more detailed analysis of these statistics, we surveyed some of the main features of the data, of which some are tabulated in Table 2.

First we considered the direction of movement. Figure 2 contains a synthesis of these data and shows the direction of movement by tagging location and time at liberty. It is implicit that we treated each symbol as reflecting the behavior of a sample of fish from the same statistical population. The main features of Figure 2 are that fish tagged off New Jersey in July tended to move in an eastward direction and both north and south during the first 2 wk at liberty, but then movement became strongly directed to the northeast. Fish released in the Long Island area initially tended to move toward the north, but after the first 30 days, their movement appeared to have been concentrated to the west and south. The same conclusion may be obtained from the southern New England releases.

An examination of the mean distance (Figure 2) shows fish released off New Jersey tended to be recovered at a slightly greater distance to the north than the south. The fish moved approximately 7 or 8 miles per day. By the second 15-day period, the fish moved about 60-100 miles to the northeast. The pattern for Long Island releases, based on only a few observations, shows that movement distance of these fish during 1-15 days was approximately the same as that for the New Jersey releases. The short-term recoveries of southern New England tagged fish reflect even less average distances than New Jersey short-term releases suggesting that either the fish off southern New England moved less than off New



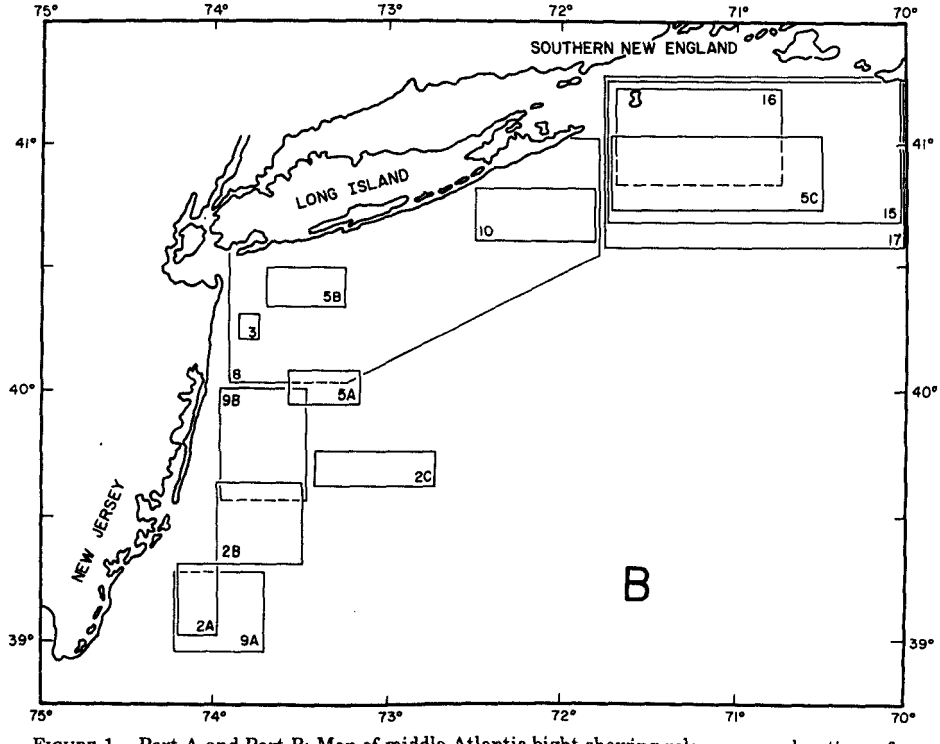


FIGURE 1.—Part A and Part B: Map of middle Atlantic bight showing release group locations of tagged bluefin tuna.

TABLE 2.—Summary of statistics on movements of tagged bluefin tuna. All distance measures are nautical miles.

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x 10^4)	Mean distance	No. of fish	Release month	General release location
2A	1-15	26.5	34.1	2.3	50.5	13	July	N.J.[3]
	16-30	74.2	74.9	26.0	114.0	9	1964	
	31-60					1		
	61-180					0		
2B	1-15	−9.2	11.4	2.9	31.8	18	July	N.J.
	16-30	25.1	58.5	1.4	89.7	7	1964	
	31-60					2		
	61-180					0		
2C	1-15	−7.2	−15.0	1.3	29.6	14	July	N.J.
	16-30					1	1964	
	31-60					1		
	61-180					0		
3	1-15	8.0	12.2	0.3	32.6	12	Aug.	L.I.[4]
	16-30					1	1965	
	31-60					0		
	61-180					0		
4A	1-15	12.0	18.3	3.8	33.6	18	July	N.J.
	16-30	83.6	52.8	11.7	102.0	8	1965	
	31-60					1		
	61-180					1		
4B	1-15	20.9	7.4	8.7	46.4	39		N.J.
	16-30	70.8	21.2	0.2	74.6	28		
	31-60					3		
	61-180					0		
4C	1-15	25.3	−16.6	13.4	47.9	17	July	N.J.
	16-30	62.3	3.1	1.1	64.8	13	1965	
	31-60					0		
	61-180					0		
5A	1-15	25.8	−15.4	19.4	48.5	9	Aug.	N.J.
	16-30	53.5	5.4	17.2	60.4	12	1965	
	31-60					0		
	61-180					0		
5B	1-15	24.8	−17.9	9.5	47.2	8	Aug.	L.I.
	16-30	44.8	−1.8	36.0	54.9	5	1965	
	31-60					0		
	61-180					0		
5C	1-15					0	Aug.	S.N.E.[5]
	16-30					0	1965	
	31-60					0		
	61-180					0		
6A	1-15					2	July	N.J.
	16-30					3	1966	
	31-60	59.1	25.9	18.7	86.4	11		
	61-180	57.0	−11.1	0.01	58.6	23		
6B	1-15					4	July	N.J.
	16-30	52.8	39.6	0.2	76.7	5	1966	
	31-60	62.2	70.0	90.9	112.0	20		
	61-180					4		
6C	1-15					0	July	N.J.
	16-30					2	1966	
	31-60					1		
	61-180	39.9	−23.7	0.002	46.7	9		
6D	1-15	−5.5	5.6	62.3	41.1	10	July	N.J.
	16-30	4.0	3.3	1.7	20.7	6	1966	
	31-60	30.6	15.6	51.9	64.7	9		
	61-180	30.0	−13.2	0.006	33.1	14		

See footnotes at end of table.

TABLE 2.—Continued.

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x10[4])	Mean distance	No. of fish	Release month	General release location
6E	1-15	-28.2	3.0	1.8	35.9	14	July 1966	L.I.
	16-30	5.0	58.1	36.0	82.4	6		
	31-60					3		
	61-180	-3.8	-3.6	1.2	16.8	10		
7A	1-15					1	Aug. 1966	L.I.
	16-30					2		
	31-60					1		
	61-180					0		
7B	1-15	0.6	22.1	0.8	26.8	11	Aug. 1966	L.I.
	16-30	-11.4	-15.5	8.8	52.4	7		
	31-60					1		
	61-180					0		
7C	1-15	-2.0	6.0	1.3	17.9	9	Aug. 1966	S.N.E.
	16-30	-3.6	6.0	1.0	28.9	8		
	31-60					1		
	61-180					0		
7D	1-15	13.2	2.5	6.2	28.2	10	Aug. 1966	S.N.E.
	16-30	7.2	-14.9	12.0	46.5	8		
	31-60					1		
	61-180					0		
7E	1-15	-17.3	2.6	8.8	29.3	15	Aug. 1966	S.N.E.
	16-30	-8.8	-21.7	30.3	50.3	5		
	31-60					1		
	61-180					0		
7F	1-15	7.5	-20.0	4.5	36.0	39	Aug. 1966	S.N.E.
	16-30	7.5	-17.4	3.3	28.9	65		
	31-60	1.3	-26.2	15.6	48.0	14		
	61-180					1		
7G	1-15	-3.8	-19.1	3.0	32.2	37	Aug. 1966	S.N.E.
	16-30	-0.7	-15.9	3.1	29.9	50		
	31-60	-4.6	-24.6	12.8	48.0	14		
	61-180					1		
8	1-15					1	Sept.-Oct. 1966	L.I.
	16-30					0		
	31-60					0		
	61-180					0		
9A	1-15					2	July 1967	N.J.
	16-30	87.7	12.7	0.003	69.1	9		
	31-60	86.8	26.8	9.4	76.6	8		
	61-180					0		
9B	1-15	-18.4	-7.1	1.0	27.4	14	July 1967	N.J.
	16-30	13.1	-3.6	1.7	24.0	12		
	31-60	27.0	7.1	13.5	39.3	47		
	61-180					2		
10	1-15					0	Sept. 1967	L.I.
	16-30					0		
	31-60					2		
	61-180					0		
11A	1-15					0	July 1968	N.J.
	16-30					2		
	31-60					0		
	61-180		-4.0	0.008	22.8	9		
11B	1-15	5.8	22.4	4.2	32.8	13	July 1968	L.I.
	16-30	10.4	35.8	0.3	39.9	11		
	31-60					1		
	61-180					4		
12	1-15					4	July 1969	L.I.
	16-30					0		
	31-60					4		
	61-180					0		

See footnotes at end of table.

TABLE 2.—Continued

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x 10^4)	Mean distance	No. of fish	Release month	General release location
13	1-15					1	Aug.	S.N.E.
	16-30					1	1969	
	31-60					1		
	61-180					0		
14	1-15					0	Sept.	S.N.E.
	16-30					0	1969	
	31-60					0		
	61-180					0		
15	1-15					3	July	S.N.E.
	16-30	−1.7	−20.6	3.5	28.1	9	1970	
	31-60	−24.4	−6.8	0.5	28.2	5		
	61-180					0		
16	1-15	−13.1	−14.7	2.0	28.3	9	Aug.	S.N.E.
	16-30	−33.0	−11.6	69.6	67.7	7	1970	
	31-60					3		
	61-180					1		
17	1-15					0	1954-63	S.N.E.
	16-30					3		
	31-60	−.2	−10.4	222.9	57.1	5		
	61-180					0		

[1]Positive values signify northward movement. Negative values signify southward movement.
[2]Positive values signify eastward movement. Negative values signify westward movement.
[3]New Jersey.
[4]Long Island.
[5]Southern New England.

Jersey or that the intensity of the southern New England fishery was greater than that off New Jersey. While the latter may be true, there may be alternative interpretations and additional analysis is required. It is also suggested that analysis be undertaken for tags returned after the season of release.

MORTALITY ESTIMATION

The number of recoveries per year from releases by year, months within years, and various groupings of years, months, and release locations were employed to estimate the survival rates for young bluefin in the middle Atlantic bight of North America. The first analyses were run using only the data employed to form the basic groups as defined in the migration analysis, thus eliminating some releases which were substantially different with respect to their location and/or time of release than for most of the fish tagged. Although this reduced the numbers of returns used, it probably did not greatly affect the estimates of mortality rates.

Method of Release

In all years since 1961, with the exception of 1963, tuna were captured for tagging by both sport and commercial gear (purse seine). In Table 3 the

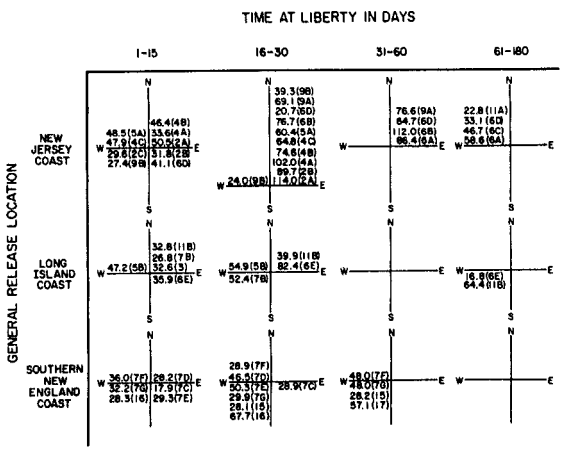


FIGURE 2.—Summary of mean distance and direction of migration of tagged bluefin tuna stratified by time at liberty and by general area of release. Distances are in nautical miles. Release group numbers are given in parentheses.

proportions of tagged fish returned were compared for the two methods of original capture. Five of the nine chi-square tests of the hypotheses of homogeneity indicate highly significant differences in the return percentages between the types of gear used to capture the tuna for tagging. When only the 5 yr with significantly different return rates for the types of gear, i.e., 1965, 1966, 1968, 1969, and 1970 are considered, higher return percentages were obtained for sport tagged fish in 4 of

TABLE 3.—Chi-square tests of equality of return probabilities between sport and commercial gear releases of tagged bluefin tuna in the northwestern Atlantic Ocean. Each test has 1 degree of freedom.

	Sport			Commercial			
Year	Release	Return	Return rate (%)	Release	Return	Return rate (%)	Chi-square value
1961	129	7	5.4	21	0	0	1.20
1962	52	4	7.7	25	0	0	2.03
1964	10	3	30.0	455	128	28.1	0.02
1965	43	17	39.5	1,629	244	15.0	19.18**
1966	187	84	44.9	3,772	1,094	29.0	21.60**
1967	14	3	21.4	614	183	29.8	0.46
1968	41	11	26.8	219	104	47.5	5.98*
1969	244	91	37.3	92	15	16.3	13.63**
1970	425	162	38.1	32	6	18.8	4.80*

**Significant at the 0.01 level.
*Significant at the 0.05 level.

the 5 yr. The data cannot be pooled over years to increase the numbers in individual cells in the chi-square tables since the recovery percentages and numbers tagged vary so greatly from year-to-year.

However, the Mantel-Haenszel test can be used to examine the data in toto (Snedecor and Cochran, 1967:255-256). The calculations resulted in a value of 8.89, which is highly significant. As is discussed in a later section, we think that most of the difference between return rates of sport and commercial tagged fish is caused by immediate tagging mortality. Immediate tagging mortality does not affect estimates of instantaneous total mortality. Therefore, we decided to use as much of the available data as possible and combined the data for estimates of mortality rates. Immediate tagging mortality does affect estimates of rates of exploitation and the components of mortality. Adjustments were made in an attempt to remove the effects of immediate tagging mortality and tag shedding.

Total Mortality Estimates – Chapman and Robson Method

Following the notation of Bayliff and Mobrand (1972), the number of tags remaining on bluefin at time t (years) is given by

$$N_t = N_0 \pi \rho e^{-Zt} \qquad (1)$$

where N_t = Number of tags remaining on bluefin at time t
N_0 = number of released tags
π = portion of bluefin which remain alive after Type-I, immediate, tagging mortality takes place
ρ = portion of tags which are retained after Type-I shedding takes place
Z = instantaneous total losses on an annual basis.

$$Z = F + X$$

where F = instantaneous fishing mortality on an annual basis
X = instantaneous other losses on an annual basis.

$$X = M + G + L + E$$

where M = instantaneous natural mortality on an annual basis
G = instantaneous Type-II tagging mortality on an annual basis
L = instantaneous Type-II tag shedding on an annual basis
E = instantaneous emigration from fishing grounds on an annual basis.

The number of tags returned during a year is given by

$$n_t = \frac{FcN_t}{Z}(1 - e^{-Z}) \qquad (2)$$

where n_t = number of tags returned between t and $t + 1$
c = portion of recovered tags that are returned.

Many assumptions are implicit in the above model. An exponential model is assumed to be

correct. It is assumed that all instantaneous shedding, mortality, and emigration rates are constant—within years and among years. Since fishing was concentrated during the summer season, the assumption of constant fishing mortality is not valid. Also fishing effort probably varied over the years of the study. Available measures of fishing effort are thought to be inaccurate but were used in the last part of the analysis. The validity of the assumption of constant rate of emigration is not known, but tag returns suggest that transatlantic migrations are sporadic. This suggests that the assumption of constant emigration is not valid. While we recognize that some of our assumptions probably are invalid, it is our judgment that the effect of the violations on our results is not serious.

For the first part of the analysis we assumed that c, π, and ρ equal one. In the first analysis minimum variance unbiased estimates of the total annual survival rates were computed by the method developed by Chapman and Robson (1960) for the recovery data by year pooled in a variety of different ways over release categories. Confidence intervals were computed for s, the fraction surviving per year, and Z, the associated instantaneous mortality rate. A chi-square test was used to determine if the number of recaptures in the first recovery period is compatible with the survival pattern exhibited by the rest of the data, i.e., if the hypothesis of constant F and X is true. This test was applied sequentially, i.e., the second year was defined as the first recapture category and the test repeated until either all recapture years were eliminated or a survival rate was obtained from some subset of the data. For all releases the tagging year was taken as the first recapture category at the start of the analysis. The results of the survival rate computations are shown in Table 4 for the following data groupings:

1) Over all years
2) Over three adjacent release years
3) Individual years
4) July releases for three adjacent release years
5) Individual months within years
6) Release groups as defined in Table 1.

An obvious feature of this analysis is that in many of the recapture series, the numbers recovered the first year or two were higher than expected from the entire recapture series. This result is somewhat surprising because it might be expected that the number recaptured the first year would be underrepresented because of less exposure to the fishery. Three possible factors that could have caused the higher than expected recaptures in the first year or two after release are:

1) Tagged fish were released into an area where fishing activity was concentrated.
2) The proportion of the population migrating into the fishing area decreased as the fish became older; thus the availability of the tagged fish in the fishing area may have fallen off rapidly enough in later years to have caused a disproportionate number of recaptures in the first and second years after release.
3) The method of estimation assumes constant fishing mortality rates and other loss rates; variability in recovery effort could have caused the number of recaptures per year to deviate from a simple exponential decline with time.

Several aspects of the data emerge from Table 4. The estimates of survival rates are low but highly erratic; restricting the releases to finer time-location grids did not improve the stability of the estimates as might be expected. Since no time trend in survival is evident, pooling over years is a useful device to average out some of the fluctuations in the data. In one sense this is a substitute for use of recapture effort statistics and working with the number of recoveries per unit of recovery effort. The recaptures per year were combined over years using various weighting factors to develop adjusted numbers recaptured per year. None of these weighting schemes offered an improvement in the use of the simple unweighted average percent recapture per year at liberty for the years 1964-68. The proportion surviving per year as estimated from the simple average of the percentages was 0.188. This value is well within the confidence interval of the s-value of 0.231 estimated from the actual numbers pooled over all years. For the latter estimate, however, we did not use the recoveries made during the first 2 yr at liberty.

Inclusion of the first two recapture periods in the Chapman-Robson analysis, particularly for the last set of release groups which are fairly homogeneous, had the general effect of reducing the survival estimates. The numbers of recaptures

TABLE 4.—Survival rate estimates for various release group categories of tagged bluefin tuna.

Type of group[1]	Group	Recapture years used in s and Z computation	s(95% confidence interval)	Z(95% confidence interval)
1	All	[2](1, 2), 3, 4, 5	0.231 (.16, .30)	1.44 (1.14, 1.75)
	1963-65	-	Not constant (NC)	
	1964-66	[2](1, 2), 3, 4, 5	.174 (.09, .26)	1.70 (1.23, 2.16)
[1]2	1965-67	(1)[1], 2, 3, 4, 5	.118 (.10, .14)	2.13 (1.93, 2.32)
	1966-68	[2](1, 2), 3, 4, 5	.254 (.14, .37)	1.32 (0.88, 1.77)
	1967-69	[2](1), 2, 3, 4	.103 (.04, .17)	2.19 (1.60, 2.79)
	1968-70	-	NC	
3	1964	-	NC	
	1965	1, 2, 3, 4	.343 (.29, .39)	1.07 (.93, 1.21)
	1966	[2](1, 2), 3, 4, 5	.233 (.14, .32)	1.42 (1.03, 1.81)
	1967	(1)[1], 2, 3, 4	.323 (.24, .41)	1.11 (0.86, 1.37)
	1968	1, 2, 3	.243 (.17, .31)	1.39 (1.11, 1.68)
	1969		NC	
	July 1963-65	1, 2, 3	.146 (.10, .19)	1.90 (1.61, 2.19)
	July 1964-66	[2](1, 2), 3, 4, 5	.400 (.20, .60)	0.87 (0.39, 1.34)
4	July 1965-67	[2](1, 2), 3, 4, 5	.355 (.18, .53)	0.99 (0.51, 1.46)
	July 1966-68	[2](1, 2), 3, 4, 5	.367 (.19, .55)	0.96 (0.49, 1.42)
	July 1967-69	1, 2, 3, 4	.246 (.19, .30)	1.39 (1.17, 1.61)
	July 1968-70	-	NC	
	July 1964	1, 2	.128 (.06, .19)	2.00 (1.50, 2.49)
	Aug. 1964	-	NC	
	July 1965	1, 2, 3	.160 (.11, .21)	1.81 (1.48, 2.13)
	Aug. 1965	-	NC	
[3]5	July 1966	[2](1, 2), 3, 4, 5	.407 (.21, .60)	0.85 (0.40, 1.30)
	Aug. 1966	[2](1, 2), 3, 4, 5	.085 (.05, .12)	2.43 (2.08, 2.79)
	July 1967	1, 2, 3, 4	.244 (.18, .31)	1.39 (1.13, 1.66)
	Aug. 1967	-	NC	
	July 1968	1, 2, 3	.201 (.13, .27)	1.57 (1.23, 1.92)
	July 1969	-	NC	
	Aug. 1969	-	NC	
	G1	1, 2, 3, 4	.582 (.45, .72)	0.53 (0.31, 0.75)
	G2A	1, 2	.189 (.06, .32)	1.57 (0.90, 2.24)
	G2B	1, 2	.065 (.00, .15)	2.45 (1.10, 3.79)
	G2C	1, 2	.160 (.01, .31)	1.68 (0.78, 2.58)
	3	-	NC	
	4A	1, 2, 3	.190 (.07, .31)	1.57 (0.95, 2.20)
	4B	1, 2, 3	.165 (.09, .24)	1.75 (1.30, 2.21)
	4C	1, 2	.083 (.00, .18)	2.27 (1.18, 3.36)
	5A	-	NC	
	5B	-	NC	
	5C	-	NC	
	6A	-	NC	
	6B	-	NC	
	6C	-	NC	
	6D	-	NC	
6	6E	-	NC	
	7A	-	NC	
	7B	[2](1, 2), 3, 4, 5	.375 (.01, .74)	0.88 (0.04, 1.71)
	7C	[2](1), 2, 3, 4	.083 (.01, .16)	2.34 (1.49, 3.19)
	7D	-	NC	
	7E	-	NC	
	7F	-	NC	
	7G	-	NC	
	8	[2](1), 2, 3, 4	.125 (.00, .26)	1.88 (0.83, 2.94)
	9A	1, 2	.154 (.01, .30)	1.72 (0.82, 2.62)
	9B	1, 2, 3, 4	.205 (.13, .28)	1.55 (1.19, 1.92)
	10	-	NC	
	11A	1, 2, 3	.357 (.17, .54)	0.98 (0.48, 1.47)
	11B	1, 2, 3	.240 (.12, .36)	1.37 (0.87, 1.87)
	12	-	NC	
	13	-	NC	
	14	-	NC	

[1]Includes tags assigned by cruise number.
[2]Recapture years eliminated by chi-square test of full recruitment to tagged population are shown in parentheses.
[3]July results include tags assigned by cruise number.

dropped off so rapidly, however, after the first two recapture periods that little reliability can actually be placed on estimates using only data from the tail end of the time series.

This first examination of the recaptures by time at liberty was followed by a revised analysis of the July releases each year and all releases each year for 1964 through 1968. An attempt to include all tags in the analysis was made by assigning tags without recorded release dates to most likely release dates by means of the accompanying information, e.g., by cruise number. For the most part this revision produced minor changes in the estimates of total survival rates. Raw exploitation rates were estimated from the total number of recaptures per release using all data whether or not any information was available on date of recapture.

Estimates of Fishing and Other Losses

We used the following equations to estimate rates of exploitation, fishing, and other losses:

$$\hat{u}_T = R/N_0$$

where $\hat{u}_T$ = estimate of total exploitation of tagged bluefin tuna over n years

R = number of tag returns.

$$\hat{u}_1 = \hat{u}_T / {}_i \sum_0^n \hat{s}^i$$

where $\hat{s}$ = survival rate estimated from revised data by the Chapman-Robson method

$\hat{u}_1$ = estimate of single season exploitation of tagged bluefin tuna.

$$\hat{F} = \hat{u} \ (-\ln \hat{s})/(1 - \hat{s})$$

$$\hat{X} = \ln(\hat{s}) - \hat{F}$$

These estimates for July releases are shown in Part A of Table 5, and in Part B of the same table, estimates of the same set of parameters for all releases are given with the exception of the single season exploitation rates. We believe that distributing the releases during the entire fishing season, rather than restricting them to the first part of the season, July, makes it impossible to estimate a single season exploitation rate. It will be noted that the actual observed exploitation rates are high, especially in view of the fact that no corrections were made for either immediate tagging mortality, tag shedding, or nonreporting. The total recapture percentages range from 16% to 48%.

Lenarz et al. (1973) estimated that the rate of immediate tag shedding $(1 - \rho)$ for Atlantic bluefin tuna is 0.027 and that the instantaneous rate of tag shedding (L) is 0.310. Their estimates were used to correct our estimates of exploitation and mortality rates for shedding as follows:

TABLE 5.—Estimates of total survival, rate of exploitation, fishing mortality rate and total other loss rate of tagged bluefin tuna for July releases and for all releases by year of release.

Item	1964	1965	1966	1967	1968
Part A. July releases only:					
(N) Numbers released	397	951	2,047	448	226
(R) Numbers recovered	96	169	461	131	108
$\hat{s}$	0.128	0.160	0.407	0.244	0.201
$\hat{u}_1$	0.211	0.150	0.143	0.224	0.385
$\hat{u}_T$	0.242	0.178	0.225	0.292	0.478
$\hat{F}$	0.497	0.327	0.217	0.418	0.773
$\hat{X}$	1.558	1.506	0.697	0.999	0.838
$(\hat{F} + \hat{X})$	2.056	1.833	0.899	1.411	1.604
Part B. All releases by year:					
(N) Numbers released	465	1,672	3,959	628	260
(R) Numbers recovered	132	262	1,177	187	116
$\hat{s}$	0.196	0.343	0.233	0.323	0.243
$\hat{u}_T$	0.284	0.157	0.297	0.298	0.446
$\hat{F}$	0.463	0.168	0.433	0.337	0.631
$\hat{X}$	1.167	0.902	1.024	0.793	0.784
$(\hat{F} + \hat{X})$	1.630	1.070	1.457	1.130	1.415

$$(\hat{F} + \hat{X})^* = \hat{F} + \hat{X} - L$$

where $(\hat{F} + \hat{X})^*$ = estimate of total instantaneous apparent mortality corrected for tag shedding rate,

$$\hat{s}^* = e^{-(\hat{F} + \hat{X})^*}$$

where $\hat{s}^*$ = estimate of annual survival corrected for shedding rate,

$$\hat{u}_T^* = \hat{u}_T / \hat{\rho}$$

where $\hat{u}_T^*$ = estimate of total exploitation of tagged bluefin tuna corrected for immediate tag shedding,

$$\hat{u}_1^* = \hat{u}_1 / \hat{\rho}$$

where $\hat{u}_1^*$ = estimate of seasonal exploitation corrected for immediate tag shedding,

$$\hat{F}^* = \hat{u}_1^* \ (-\ln s)/(1 - \hat{s})$$

where $\hat{F}^*$ = estimate of F corrected for immediate tag shedding,

$$\hat{X}^* = -\ln(\hat{s}^*) - \hat{F}^*$$

where $\hat{X}^*$ = estimate of X corrected for immediate tag shedding,

$$\hat{u}_1^{**} = \frac{\hat{F}^*}{\hat{F}^* + \hat{X}^*} \ (1 - \hat{s}^*)$$

where $\hat{u}_1^{**}$ = estimate of single season exploitation of tagged and untagged bluefin corrected for all tag shedding, and

$$\hat{u}_T^{**} = \hat{u}_1^{**} \sum_{i=0}^{n} (\hat{s}^*)^i$$

where $\hat{u}_T^{**}$ = estimate of total exploitation of tagged and untagged bluefin corrected for all tag shedding.

The estimates are shown in Table 6. Estimates of $\hat{X}^*$ (other losses) range from 0.366 to 1.234 (average = 0.792). The estimates of $\hat{X}^*$ are considerably higher than expected values of M (natural mortality) for bluefin. Bluefin are very long-lived fish and values of M of 0.1 to 0.2, if M is constant, would seem reasonable. Thus, there may be significant amounts of Type-I (immediate) and Type-II (long-term) tagging mortality, nonreporting, and/or apparent mortality caused by emigration.

TABLE 6.—Estimates of rates of exploitation and mortality of bluefin tuna corrected for tag shedding.

Item	1964	1965	1966	1967	1968
$(\hat{F} + \hat{X})^*$	1.746	1.523	0.589	1.101	1.294
$\hat{s}^*$	0.174	0.218	0.555	0.333	0.274
$\hat{u}_T^*$	0.249	0.183	0.231	0.300	0.491
$\hat{u}_1$	0.217	0.154	0.147	0.230	0.396
$\hat{F}^*$	0.512	0.336	0.223	0.429	0.795
$\hat{X}^*$	1.234	1.187	0.366	0.671	0.499
$\hat{u}_1^{**}$	0.242	0.172	0.168	0.260	0.446
$\hat{u}_T^{**}$	0.284	0.218	0.342	0.388	0.611

It seems plausible that some Type-I tagging mortality exists. In an earlier section it was noted that, more returns were obtained from sport gear releases than from commercial gear releases. Statistically significant, more returns were obtained from sport releases than commercial releases in 1965, 1966, 1969, and 1970. A possible cause of the difference in return rates could be that sport tagged bluefin are of different ages than commercially tagged bluefin. Bluefin of different ages could suffer different rates of tagging mortality and shedding, and could behave differently. Data have not been compiled in a fashion that allows examination of the age at release by the two gear types. We recommend that it be and assume for the present that age-dependent effects are negligible. The differences in return rates could also be caused by Type-I tagging mortality. Experienced taggers report that sport-gear-caught bluefin appear to be in better condition than those caught by commercial gear. Also, commercial gear tends to capture entire schools of bluefin while sport gear captures one bluefin at a time. Thus, bluefin released from sport gear tend to be released into the immediate area of a school of bluefin while bluefin released from commercial gear are not. There may be an advantage for bluefin to be in a school. Bayliff (1973) found that return rates of purse-seine-caught yellowfin tuna tagged immediately after a set is made can be more than two times higher than yellowfin tagged at a later time (Table 7). This evidence suggests that Type-I tagging mortality is very important

TABLE 7.—Releases, returns, and percentages of return of yellowfin tuna for IATTC[1] Cruise 1055, by time between commencement of tagging and release of fish (from Bayliff, 1973).

Time (min)	Number released	Number returned	% returned
0-10	1,920	277	14.4
10-20	1,972	195	9.9
20-30	1,563	86	5.5
30-40	1,145	47	4.1
40-50	934	44	4.7
>50	975	23	2.4
Total	8,509	672	7.9

[1]Inter-American Tropical Tuna Commission.

for purse-seine-caught yellowfin tuna. Bayliff[6] (pers. commun.) believes that bluefin tuna are more hardy than yellowfin tuna and thus expects that Type-I tagging mortality is lower for bluefin than for yellowfin.

Assuming that sport releases suffered insignificant amounts of Type-I tagging mortality and using the Mantel-Haenszel weighting procedure, the 1964-68 average Type-I tagging mortality for commercial tagged fish was 21%. During this period, 96% of the releases were commercial tagged fish. The average Type-I tagging mortality for all releases during 1964-68 was 20%.

The rates of exploitation and mortality were corrected for Type-I tagging mortality as follows:

$$\hat{u}_T^{***} = \hat{u}_T^{**}/\pi$$

where $\hat{u}_T^{***}$ = estimate of total exploitation corrected for shedding and Type-I tagging mortality,

$$\hat{u}_1^{***} = \hat{u}_1^{**}/\pi$$

where $\hat{u}_1^{***}$ = estimate of seasonal exploitation corrected for shedding and Type-I tagging mortality,

$$\hat{F}^{**} = \hat{u}_1^{***}\,(-\ln \hat{s}^*)/(1 - \hat{s}^*)$$

where $\hat{F}^{**}$ = estimate of F corrected for shedding and Type-I tagging mortality, and

$$\hat{X}^{**} = -\ln(\hat{s}^*) - \hat{F}^{**}$$

where $\hat{X}^{**}$ = estimate of X corrected for shedding and Type-I tagging mortality.

The estimates are shown in Table 8. The values of $\hat{X}^{**}$ range from 0.300 to 1.109 (average = 0.678) and are still higher than the expected rate of natural mortality for bluefin. The large difference between values for 1964-65 and the values for 1966-68 is worth noting. Food and Agriculture Organization (1972) reports that a relatively large number of bluefin tuna tagged in the northwest Atlantic in 1965 were recovered in the Bay of Biscay during the following year. This suggests that a large-scale transatlantic migration occurred between the 1965 and 1966 fishing seasons. Thus migration from the fishery is a plausible explanation for a portion of $\hat{X}^{**}$.

TABLE 8.—Estimates of rates of exploitation and mortality for northwest Atlantic bluefin tuna. The rates have been corrected for tag shedding and a hypothetical value of Type-I tagging mortality.

	1964	1965	1966	1967	1968	Average
u_T^{***}	0.355	0.272	0.428	0.485	0.764	[1]0.456
u_1^{***}	0.302	0.215	0.210	0.325	0.558	[1]0.327
F^{**}	0.639	0.419	0.278	0.536	0.995	0.573
X^{**}	1.110	1.104	0.311	0.564	0.300	0.678

[1]Calculated from averages of F^{**} and X^{**}.

Total Mortality Estimates – Regression Method

We next used available effort data for examining the effect of changes in effort on our estimates of mortality. The effort data were obtained from inquiries and logbooks of purse seiners that participated in the commercial fishery for bluefin in the northwestern Atlantic. The data have not been standardized by vessel class. We question the validity of the data as a measure of fishing effort, i.e., proportional to F, because a varying portion of the fleet relied heavily on airplane scouting. Conversion of the data to a standard unit of effort is worth a study in itself and we recommend that such a study be carried out.

In another attempt to estimate total mortality the natural logarithm of the number of returns per unit effort (Table 9), taking the number of boat-days recorded per season as a legitimate measure of effort, was regressed on time as measured to the center of each year following the release. An exact

[6]Bayliff, W. H. Inter-Am. Trop. Tuna Comm., P. O. Box 271, La Jolla, CA 92037.

TABLE 9.—Returns of tagged bluefin tuna per boat-day by years at liberty.

Year	0	1	2	3	4
Part A. July releases only:					
1964	0.0902	0.0344			
1965	0.3538	0.0968	0.0374		
1966	0.9839	1.3957	0.1059	0.0526	0.0111
1967	0.5080	0.3647	0.0421	0.0037	
1968	1.0235	0.1579	0.0222		
Part B. All releases:					
1964	0.1100	0.0786			
1965	0.4029	0.3280	0.1925	0.0718	
1966	2.8495	3.1016	0.6235	0.0842	0.0222
1967	0.5241	0.7059	0.1684	0.0481	
1968	1.0353	0.2000	0.0333		

analytical formulation of this mortality model has two independent variates—cumulative time and cumulative effort. Not only are these two variables so highly correlated that it is virtually impossible to obtain useful estimates of the two regression coefficients, but also there are too few data points available for multiple regression analysis. The regression coefficient of the simple cumulative time regression is a crude measure of the total mortality rate. The fitted regression lines are shown in Figure 3 for July releases and in Figure 4 for all releases for each year. The values of the coefficients are given in Table 10.

With the exception of 1966, when the returns per boat-day increased during the year following release (and the data were eliminated from the regression), the logarithms of the recaptures per unit effort decrease in a linear fashion and it is clear the regressions provide reasonable fits to the data points. Seven of the eight estimated survival rates shown in Table 10 are lower than their counterparts in Table 5. Both of these analyses provide at best only crude approximations of the true survival rates; however, they do show fair general agreement. The catch-per-effort estimates indicate the loss rates are tending to increase with time.

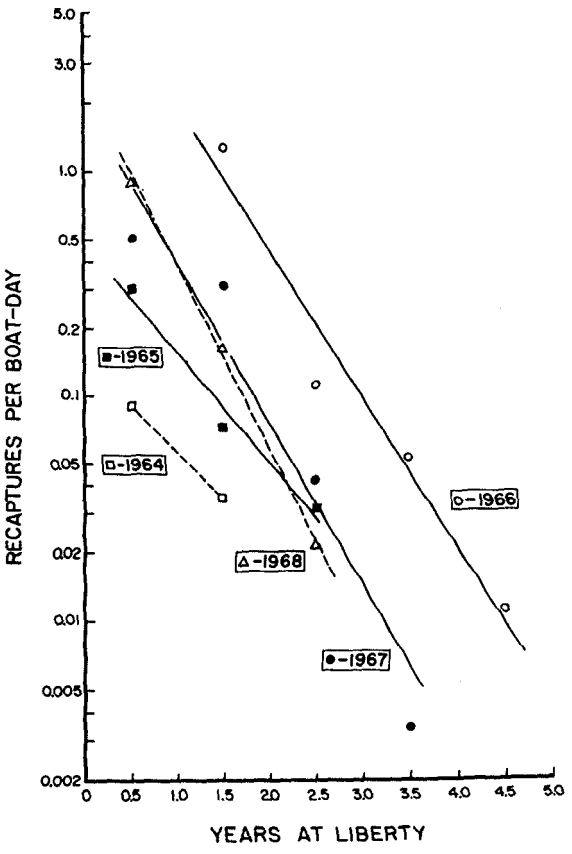


FIGURE 3.—Regression of recaptures per boat-day vs. time at liberty for July releases of tagged bluefin tuna.

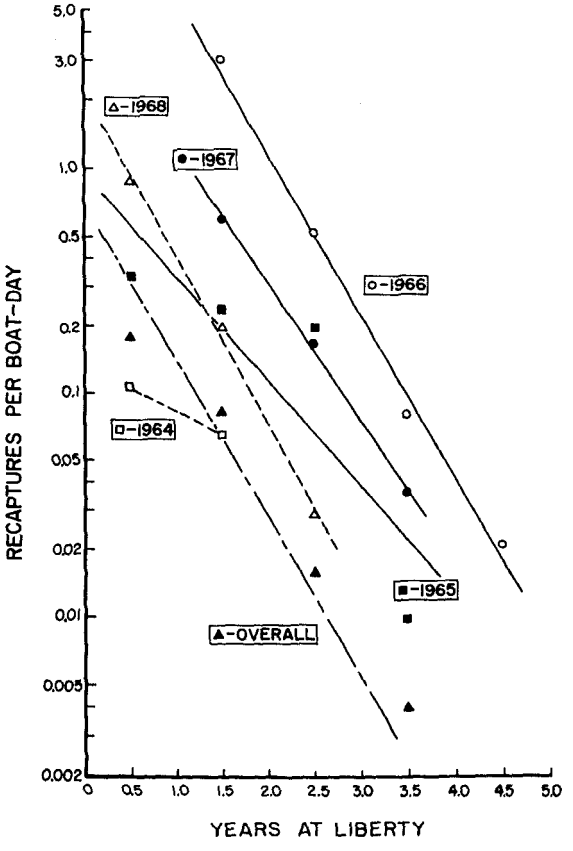


FIGURE 4.—Regression of recaptures per boat-day vs. time for all releases, by year, of tagged bluefin tuna.

TABLE 10.—Estimates of total survival rates of tagged bluefin tuna from regression analysis of return per unit-of-effort data.

	July releases only		All releases	
Year	Z	s	Z	s
1965	1.12	0.33	1.08	0.34
1966[1]	1.51	0.22	1.68	0.19
1967	1.70	0.18	1.41	0.24
1968	1.87	0.15	1.73	0.18
Average[2]	1.55	[3]0.21	1.48	[3]0.23

[1]Recaptures in release year not included in 1966 regression analysis.
[2]Regression estimates using average unweighted percentage returns for 1964-68 are: $Z = 1.67$ and $s = 0.19$. This estimate happens to be exactly the same as the estimate of $Z = 1.67$ = (average time at liberty) ^{1} where average time at liberty is 0.60 yr.
[3]Survival rate computed from average Z-value.

DISCUSSION

Exactly what these "survivals" are measuring is of prime interest. They are properly thought of as the results of disappearance rates which are composed of mortalities (F, M, and G), tag shedding, and changing migratory patterns with age. Apparently few of the older fish entered the surface fishery in the western north Atlantic during the period of the study and the decreasing proportion of the population that entered the fishery is a primary factor lowering the apparent survival. In 1966 when the fish tagged were significantly younger than in the other years—having an average age of 1.4 yr as opposed to average ages of at least a year older in other tagging years—the greatest return of tags occurred during the year after release. For these younger bluefin, a higher proportion returned to the fishing area the year after they were released than for the older tagged fish.

The exploitation rate on the tagged fish was exceedingly high when they were in the fishery. The high fishing mortality rates in Table 8 may underestimate the true rates for tagged bluefin; most of the various sources of error that may bias these estimates act to decrease the estimate of the fishing rate relative to its true value. However, it is known that bluefin available to the northwest Atlantic fisheries are not a closed population. Tagging studies have revealed transatlantic migrations to and from the fishery. Migration could also occur from the middle Atlantic. Thus it must still be determined whether the high exploitation rate applied to the population or just to the portion of the population that entered the fishery. Ricker (1958:35) describes the effects of tagging fish that are more vulnerable to fishing than other members of the population. "Again, if fish of certain sizes are more vulnerable than others, a Peterson tagging experiment is apt to overemphasize the vulnerable ones both in respect to tags put out and recaptures made; hence the estimate of rate of exploitation is too high and the population estimate is too low." Future analysis stratifying the data by age at release would help to answer some questions that arise because of the migratory behavior of bluefin. We suggest cohort analysis in the fashion of Bayliff (1971) as a productive method of analysis.

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The tagging results were made possible by the thousands of anglers, captains, and mates who have tagged, and released many of their catches, the commercial tuna fishermen who have cooperated with the tagging program, and the clubs, committees and individuals who have encouraged tagging. We regret that space does not permit individual acknowledgments here; the major participants are listed in the informal progress reports which are issued periodically by the Woods Hole Oceanographic Institution. The press and the broadcasting media have also done much to encourage tagging and the return of tags.

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FEEDING RELATIONSHIPS OF TELEOSTEAN FISHES ON CORAL REEFS IN KONA, HAWAII

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ABSTRACT

Feeding relationships of teleostean fishes on coral reefs at Kona, Hawaii, were studied during 1969 and 1970.

Fishes that have a generalized feeding mechanism, including those carnivores whose morphologies place them close to the main line of teleostean evolution, are predominantly nocturnal or crepuscular. These include holocentrids, scorpaenids, serranids, apogonids, priacanthids, and lutjanids. The major prey of the nocturnal species are small, motile crustaceans, which are most available to the direct attacks of generalized predators when they leave their shelters after dark. The major prey of the crepuscular species are smaller fishes, whose defenses against direct attacks of generalized predators are less effective during twilight. Feeding by generalized predators during the day depends largely on being within striking distance of prey that make a defensive mistake, a position best attained by those predators that ambush their prey from a concealed position, or by those that stalk.

Ambushing and stalking tactics have produced some highly specialized forms that, during the day, prey mostly on smaller fishes. Diurnal ambushers include the highly cryptic synodontids, scorpaenids, and bothids; diurnal stalkers include aulostomids, fistulariids, belonids, and sphyraenids—all of them long, attenuated fishes.

Some predators—most notably the muraenid eels—are specialized to hunt deep in reef crevices, and here they capture some of the many small animals that shelter themselves in those crevices, day and night, when resting, injured, or distressed. Mullids use their sensory barbels to detect small animals that have sheltered themselves amid the superficial covering on the reef, or in the surrounding sand; at least some mullids further use their barbels to drive these prey into the open.

Most of the fishes on Kona reefs are among the more highly evolved teleosts, having reached, or passed, the percoid level of structural development. The adaptability of the feeding apparatus in these more advanced groups has given rise to a wide variety of specialized species, including both carnivores and herbivores, that have diverged from one another mostly on the basis of differing food habits. These fishes, most of which are diurnal, include the chaetodontids, pomacentrids, labrids, scarids, blenniids, acanthurids, and *Zanclus*, among the perciforms; and the balistids, monacanthids, ostraciontids, tetraodontids, canthigasterids, and the nocturnal diodontids, among the tetraodontiforms. With their specialized feeding structures and techniques, these fishes consume organisms like sponges, coelenterates, large mollusks, tunicates, and tiny or cryptic crustacea that are protected by behavioral or anatomical features from fishes not appropriately specialized.

Many important ecological relations among marine fishes are understood only by considering in broad overview during both day and night the different forms living together under natural conditions. With this in mind, I undertook a broad study of reef fishes at Kona, Hawaii, between June 1969 and August 1970. A segment of this study dealing with the twilight situation was published earlier (Hobson, 1972). The present report describes the situations that prevail throughout day and night. The work is centered on direct observations of activity in the fishes, as was my earlier study of predatory behavior of shore fishes in the Gulf of California (Hobson, 1968a), but here with greater emphasis on detailed analysis of food habits.

Several other workers adopted broad overviews in considering fishes of various areas. Limbaugh (1955) studied fishes in California kelp beds during the day, whereas Starck and Davis (1966) described the habits of fishes in the Florida Keys at night; both of these studies present extensive direct observations of activity, but little data on food habits. On the other hand, Hiatt and Strasburg (1960), as well as Randall (1967), and Quast (1968), treated extensively the food habits of fishes collected during daylight in the Marshall Islands, the West Indies, and southern California, respectively, but offered relatively few direct observations of activity. Suyehiro (1942) comprehensively treated the feeding morphology of fishes in Japan

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and included data on food habits; however, he included little information on activity. The 1970 United States Tektite II program provided many scientists with the opportunity to make direct observations on a Virgin Island reef, and reports concerning the fishes have been published in one volume (Collette and Earle, 1972). Many other reports of limited scope are scattered through the literature, most of them being fragmented data on food habits; nevertheless, accounts of activity based on direct observations are sparse, especially of nocturnal activity.

The great variety of feeding mechanisms for which teleostean fishes are so well known occur among coral-reef fishes far more so than among the fishes of any other habitat. I take advantage of this circumstance in the discussion that concludes the present report and consider the feeding relationships among fishes on Kona reefs in the context of teleostean evolution.

METHODS

Direct Observations

I observed activity of the fishes during 632 h underwater at all periods of day and night using scuba and by snorkeling. Except when collecting specimens, I tried not to influence the fishes or their environment, hoping that events were taking a natural course. Fishes considered in this report are those that can be seen by an underwater observer at some time during day or night. Although this includes by far most of the reef fishes, some abundant species are not included because they remain secreted in the reef at all hours.

Food Habits

The gut contents of 1,547 fish specimens of 102 species were analyzed. With a few isolated exceptions, noted below, all the specimens were collected with spears. I find spearing the most effective way to collect fishes for study of food habits. Using this method, specimens were collected in specific locations at the times of day and night that best define diurnal-nocturnal activity patterns. Because I speared all the specimens myself, I know what each individual was doing when captured, and this knowledge significantly influenced analysis of the data. Even the response of the various fishes to being stalked and speared (or missed) provided certain behavioral insights.

Food habits change over the life of at least most fishes, usually along with recognizable changes in behavior and morphology. Unless otherwise indicated, specimens selected for this study showed behavior and morphology judged typical of adults.

The collections were spread over time and space, so that possible effects of transient localized, perhaps atypical, situations were reduced. Generally, only a single individual of any one species was collected during a single period of observations; thus, for a given species, most individuals each represent a separate collecting station. For these reasons, I judge the data from the food habit analysis to accurately represent the situation existing on Kona reefs over the 15 mo of this study.

The collections were spaced throughout day and night, so that relative digestion of gut contents supplements direct observations of activity in determining specific feeding times. All specimens were sealed in individual plastic bags immediately after being speared, most while still underwater. Gut contents of specimens collected while snorkeling were preserved immediately by injecting a concentrated formaldehyde solution directly into the gut cavity, whereas gut contents of fishes taken by scuba were preserved as soon as possible after emerging from the water. I was unable to see a difference in the digestion undergone by material collected in each of these two ways, suggesting that digestion is sharply curtailed by the death of the fish. Where practical, identifications of items in the guts were carried far enough to establish such general prey characteristics as habitat and mode of life.

Quantifying Food Habits

For those species represented by enough numbers in the analysis of gut contents, I state: 1) the number of fish of that species containing each food item, and 2) the mean percent of that item in the *diet volume,* which is the total volume of gut contents in all specimens of that species. This second figure was calculated from estimates of the percent each item taken by the species contributed to the gut contents of each individual fish (0 to 100%). The food items are listed in order of a *ranking index,* which is computed by multiplying the ratio of fish containing the item to the number of fish sampled, by the mean percent that item represented of the diet volume. Thus, for example, for *Holocentrus sammara* (Table 10), the number one prey, xanthid crabs, has a ranking index of

$12/17 \times 52.5 = 37.05$. The data are tabulated when there are more than a few items in the gut contents of a given species.

In species with a well-defined stomach, usually only stomach contents were analyzed, as materials in the intestines generally were too far digested for satisfactory analysis. On the other hand, some fishes that do not have a well-defined stomach have much material in their intestine that is suitable for study, and so was included in the analysis. Thus data sometimes are specified as being from stomach contents, but at other times the more general term gut contents is used.

Transect Counts

To characterize the fishes inhabiting each of the various inshore habitats described below, 100-m transect lines were established in locations judged typical of each habitat. Twenty-two counts of fishes within 5 m of transect lines at 17 sites representing five habitat categories (see below) were made between September 1969 and May 1970; at least 1 mo passed between counts in any one habitat.

Quantifying Relative Abundance

In the Tables below that present data from the transect counts, the relative abundance of the different species is represented by a relative abundance index. This is the percentage that species represented of all fishes (individuals) counted along all transect lines in that habitat.

Assessing Nocturnal Colorations

A number of species possess distinctive day and night differences in coloration. Earlier (Hobson, 1968b), I discussed the problem of distinguishing true nocturnal hues from those elicited as a response to the diving light—a frequent source of error in literature reports of nocturnal color patterns. No color pattern that becomes intensified under the diving light is considered here to be a nocturnal pattern; the vast majority described herein were in fact almost immediately lost when the fish was illuminated.

Study Area

The study area extends 7.7 km along the southwestern shore of the Island of Hawaii, from Keawekaheka Point just north of Kealakekua Bay, to Alahaka Bay, south of Honaunau (Figure 1). This is part of what is known as the Kona coast. Except for short stretches of sand and cobble beaches at Napoopoo and Keei, the shoreline is a rough basalt face that drops abruptly into the sea from 2 to 3 m above the water's surface (Figure 2), to a similar depth below. From the base of this face the sea floor slopes down to water depths of about 20 to 30 m, about 50 to 600 m from shore, then falls away sharply to much greater depths. Thus, along this coast water less than 20 m deep is limited to a relatively narrow shelf, the outer rim of which provided a convenient natural boundary to the study area (Figure 1).

Environmental conditions in Kona are remarkably constant, which greatly aided this study. Surface water temperatures ranged from 29°C in the fall to 22°C in the spring, but I noted no marked seasonal variations among the fishes either in their activity or species composition. Conditions

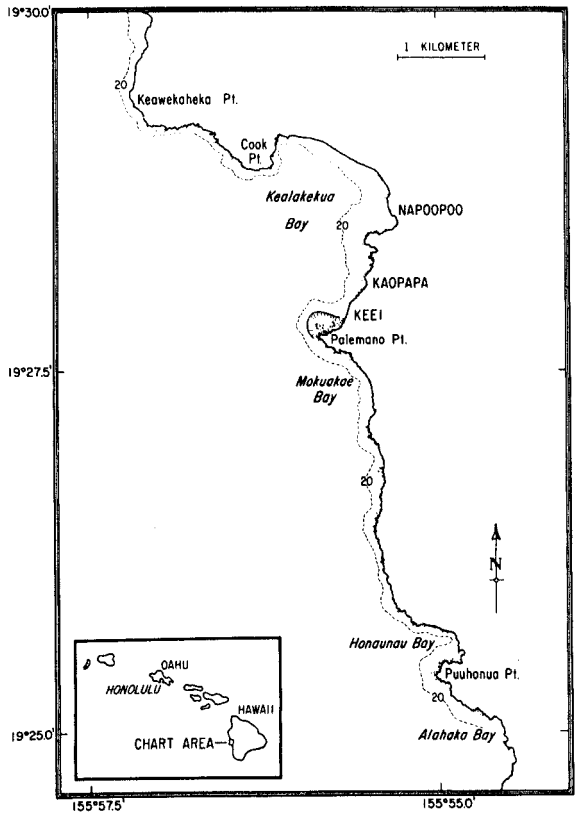


FIGURE 1.—The study area along the Kona coast, Island of Hawaii. Adapted from C. & G.S. chart 4123. Depth contour in meters.

are especially moderate on the Kona coast, in part because towering volcanoes shelter the area from the trade winds.

THE INSHORE HABITATS AND THEIR CHARACTERISTIC FISHES

The study area in Kona encompasses a variety of submarine habitats, each with a distinctive assemblage of fishes. For convenience, these habitats are here grouped subjectively into five categories: 1) coral-rich habitat, 2) boulder habitat, 3) shallow reef-flat habitat, 4) reef-face habitat, and 5) outer drop-off habitat. Along with the following habitat descriptions, there are listed the 10 fish species most often seen in each habitat, as observed in the transect counts.

Coral-Rich Habitat

In many places where there is shelter from the long Pacific swells, the sea floor in water between 2 and 12 m deep is richly overgrown with corals (Figure 3). The predominant coral is *Porites pukoensis,* which grows in a variety of massive formations. Examples occur in Honaunau Bay, in the lee of Palemano Point, and in the sheltered waters on the north side of Kealakekua Bay (Figure 1). Overall in the parts of the study area that are richly overgrown with corals, *P. pukoensis* variably shares dominance with another form, *P. compressus,* that grows as fingerlike branches 10 to 20 mm in diameter. *Porites compressus* is dominant where there is increased exposure to the prevailing swell, but where there is still some protection from a lee shore or increased water depth. Thus, in the middle of both Kealakekua Bay and Honaunau Bay, as well as in much of the study area where the water is more than about 15 m deep, broad fields of fingerlike *P. compressus* dominate the scene. In extreme situations, habitats dominated by either one of these coral forms are as distinct from one another in their characteristic faunas as any two habitat types characterized here. I group the two coral habitats together because in most of the coral-rich areas where observations were made during this study

FIGURE 2.—The shoreline at Cook Point, Kealakekua Bay (looking southeast), which is typical of the shoreline throughout most of the study area.

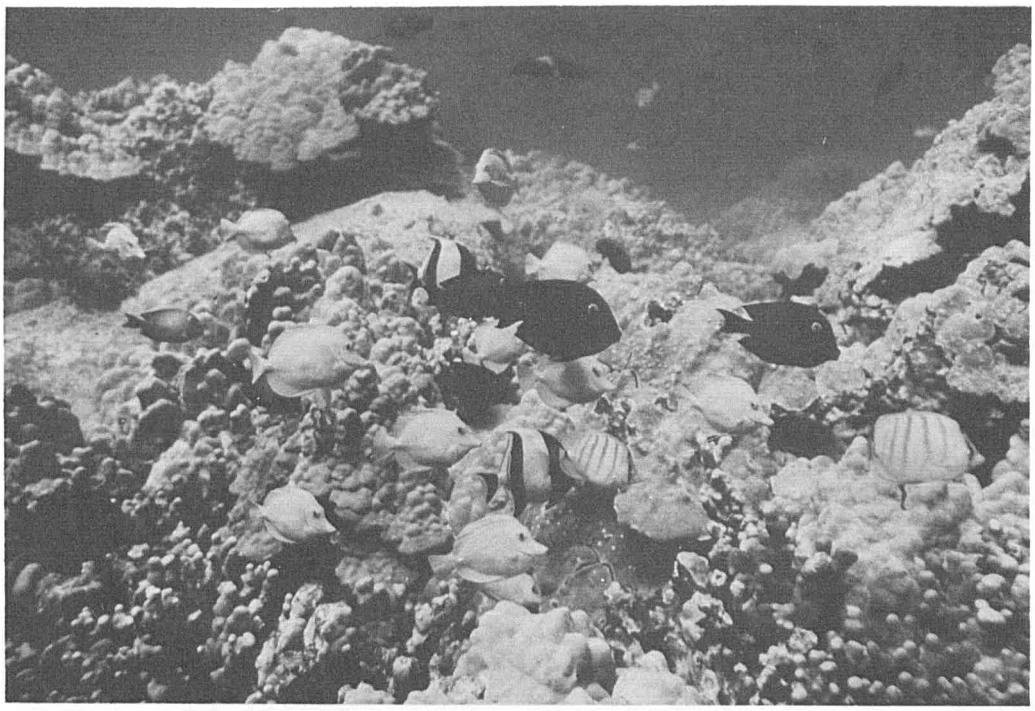


FIGURE 3.—Coral-rich habitat. Fishes shown include: *Chaetodon multicinctus, Ctenochaetus strigosus, Zebrasoma flavescens, Acanthurus nigrofuscus,* and *Zanclus canescens.*

the two forms of *Porites* share dominance. Nevertheless, the fishes listed in Table 1,[2] which are characteristic of those seen in the coral-rich habitat by day, were observed where *P. pukoensis* was the more dominant coral. Table 2[3] lists fishes characteristic of those seen in this same habitat at night. Because of difficulties inherent in making transect counts after dark, data in Table 2 are only rough approximations; they are presented primarily to illustrate the differing situation after dark, and to emphasize that the other counts reflect a situation characteristic of daytime only.

[2]Table 1 is based on data from five transects at four coral-rich sites—two at Honaunau, and two at Kaopapa in Kealakekua Bay (see Figure 1). Total number of species observed on these five transects: 82; mean number of individuals of all species for a single transect: 522.

[3]Table 2 is based on data from three nocturnal transects (one on a dark night, two on moonlit nights) at three coral-rich sites—two at Honaunau, one at Kaopapa in Kealakekua Bay (see Figure 1), all three of which were also used in daytime counts (Table 1). Counts were made by switching on a light briefly about every 10 m as we swam along the line. Listing of a species does not necessarily imply activity; as becomes clear in the species accounts, below, some of these fishes are inactive on or near the reef at night. Total number of species observed on these three transects: 36; mean number of individuals of all species for a single transect: 165.

Boulder Habitat

From shore to depths of about 15 m throughout that part of the study area lying off exposed shorelines, the sea floor is strewn with basalt boulders. Often these boulders are dotted with various algae and corals—mostly encrusting varieties—but because these forms are small, the

TABLE 1.—The 10 fish species most frequently seen along transect lines in the coral-rich habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 5$
1	*Ctenochaetus strigosus*	15.45	5
2	*Chromis leucurus*[1]	12.30	5
3	*Zebrasoma flavescens*	10.58	5
4	*Pomaentrus jenkinsi*	6.71	5
5	*Thalassoma duperrey*	5.71	5
6	*Chaetodon multicinctus*	4.41	5
7	*Acanthurus nigrofuscus*	4.37	5
8	*Acanthurus nigroris*	3.64	3
9	*Plectroglyphidodon johnstonianus*	3.07	5
10	*Centropyge potteri*	2.49	2

[1]In making transect counts I followed Gosline and Brock (1960) in recognizing *Chromis leucurus* to include two color forms. Further study may show that two (or more) species are included here (see species account for *C. leucurus* in this report).

FIGURE 4.—Boulder habitat. Fishes shown include: *Aphareus furcatus, Monotaxis grandoculis* (showing barred color pattern), *Acanthurus leucopareius,* and *Zebrasoma flavescens.*

TABLE 2.—The 10 fish species most frequently seen along transect lines in the coral-rich habitat at night.

Rank	Species	Relative abundance index	No. times in top 5 of individual transects $n = 3$
1	*Myripristis kuntee*	23.61	3
2	*Apogon menesemus*	14.52	3
3	*Myripristis murdjan*	12.33	2
4	*Apogon snyderi*	11.90	3
5	*Zebrasoma flavescens*	6.85	2
6	*Chaetodon multicinctus*	4.03	0
7	*Acanthurus sandvicensis*	2.40	1
8	*Acanthurus nigroris*	2.22	0
9	*Holocentrus lacteoguttatus*	1.21	0
10	*Chaetodon ornatissimus*	1.21	0

TABLE 3.—The 10 fish species most frequently seen along transect lines in the boulder habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 4$
1	*Acanthurus nigrofuscus*	13.74	4
2	*Ctenochaetus strigosus*	10.77	4
3	*Zebrasoma flavescens*	9.61	4
4	*Acanthurus achilles*	8.00	4
5	*Thalassoma duperrey*	6.44	4
6	*Pomacentrus jenkinsi*	5.25	4
7	*Acanthurus nigroris*	4.88	3
8	*Acanthurus leucopareius*	4.73	4
9	*Abudefduf sindonis*	3.64	4
10	*Chromis vanderbilti*	2.35	3

general appearance is one of bare rocks (Figure 4). Especially in the shallower regions, but decreasing with greater depths, this habitat is regularly swept by a strong surge. At depths varying with the relative proximity of a lee shore or protecting reef, but usually at about 12 to 17 m, the boulder habitat in many locations grades into the fields of fingerlike *Porites compressus,* one of the coral-rich habitats described above. Fishes listed in Table 3 [4] are characteristic of those seen in the boulder habitat during the day.

Shallow Reef-Flat Habitat

Shallow surge-swept reefs, the remains of ancient lava flows, extend offshore in several locations (Figure 5). Here, a solid pavement of exposed basalt, containing many cracks and crevices, supports a distinctive array of marine organisms. The predominant benthic life form is the coral

[4]Table 3 is based on data from four transects at four boulder sites—one at Cook Point, one at Mokuakae Bay, and two at Alahaka Bay (see Figure 1). Total number of species observed on these four transects: 77; mean number of individuals of all species for a single transect: 672.

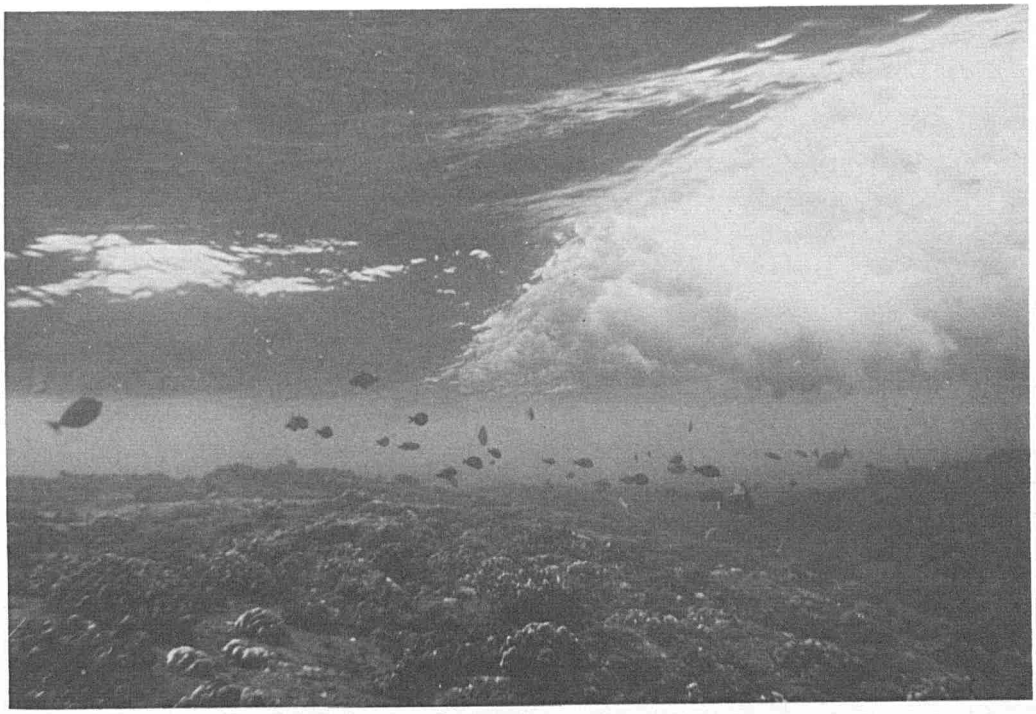


FIGURE 5.—Shallow reef-flat habitat. Most of the fishes shown are acanthurids, and include *Naso lituratus* and *N. unicornis*.

Pocillopora meandrina, growing as isolated heads 10 to 50 cm wide. The outstanding characteristics of this habitat, which generally has a maximum water depth of only about 3 to 4 m, are extreme water movement and wave shock. The fishes listed in Table 4 [5] are characteristic of those seen on shallow reef flats during the day.

[5]Table 4 is based on data from three transects at three shallow reef-flat sites at Palemano Point (see Figure 1). Note: one of the transect counts was aborted after 60 m when the surge became too strong to continue. Total number of species observed on these three transects: 54; mean number of individuals of all species for a single transect: 578.

TABLE 4.—The 10 fish species most frequently seen along transect lines in the shallow reef-flat habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 3$
1	*Acanthurus nigrofuscus*	20.23	3
2	*Thalassoma duperrey*	17.41	3
3	*Abudefduf imparipennis*	15.12	3
4	*Chromis vanderbilti*	10.33	3
5	*Thalassoma fuscus*	4.78	3
6	*Stethojulis balteata*	2.88	3
7	*Gomphosus varius*	2.78	3
8	*Naso literatus*	2.02	1
9	*Zebrasoma flavescens*	1.79	1
10	*Pomacentrus jenkinsi*	1.67	1

Reef-Face Habitat

At the offshore edge of the shallow reef flats, and at many locations along the shore, a sheer basalt face falls precipitously to water depths of 10 to 15 m (Figure 6). This situation produces a wide range of conditions within a limited area. In its upper regions the surge and wave shock are that of the reef-top habitat, but these rapidly abate with increasing depth. Conditions adjacent to the base of the reef face are essentially those of the boulder habitat, with fragmented pieces of the reef lying about as large boulders. The predominant forms of benthic life, dotting the rock surfaces, are *Pocillopora meandrina* (in the shallower regions), and smaller encrusting corals and algae. Many planktivorous fishes are concentrated in the water column adjacent to the reef face. Understandably, there is a greater variety of fishes in this habitat than in the other habitats characterized here. Fishes listed in Table 5 [6] are characteristic of those seen along the reef face during the day.

[6]Table 5 is based on data from three transects at two reef-face sites at Palemano Point (see Figure 1). Total number of species observed on these three transects: 89; mean number of individuals of all species for a single transect: 937.

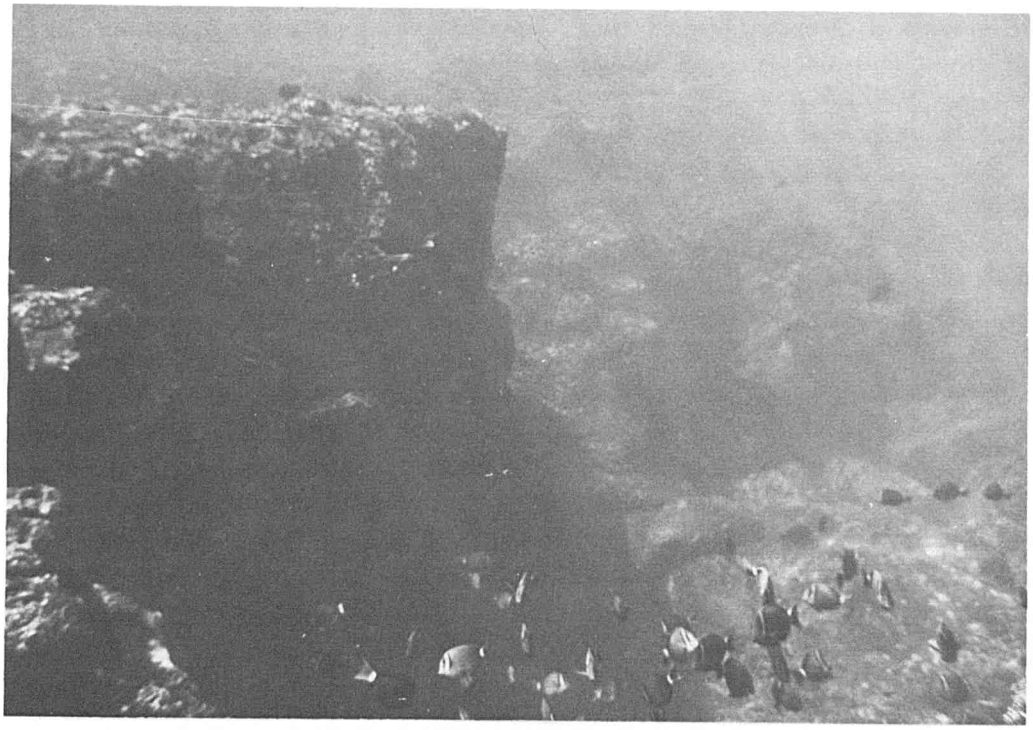


FIGURE 6.—Reef-face habitat. Most of the fishes shown swimming at the base of the reef are *Acanthurus leucopareius*. The reef face shown here drops 8 to 10 m.

TABLE 5.—The 10 fish species most frequently seen along transect lines in the reef-face habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 3$
1	*Chromis vanderbilti*	11.74	3
2	*Ctenochaetus strigosus*	9.54	3
3	*Zebrasoma flavescens*	9.11	3
4	*Acanthurus leucopareius*	7.18	3
5	*Acanthurus nigrofuscus*	6.17	3
6	*Thalassoma duperrey*	4.41	3
7	*Pomacentrus jenkinsi*	3.95	3
8	*Abudefduf abdominalis*	3.56	3
9	*Acanthurus achilles*	3.56	3
10	*Melichthys niger*	3.38	3

Outer Drop-Off Habitat

At the rim of the outer drop-off, 50 to 600 m from shore, where the sea floor falls abruptly from about 25 m to much greater depths, the sea floor generally is overgrown with the fingerlike form of *Porites compressus*, interspersed with massive heads of *P. pukoensis*, bare basalt boulders, and sand patches (Figure 7). The most striking characteristic of this habitat, aside from the spectacular way the sea floor falls away, is the large number of planktivorous fishes that abound in the water column. Obviously conditions for feeding on plankton are especially well developed here. The fishes listed in Table 6 [7] are characteristic of those seen on the rim of the outer drop-off during the day.

[7]Table 6 is based on data from four transects at four outer drop-off sites—two at Palemano Point and two at Puuhonua Point (see Figure 1). Total number of species observed on these four transects: 78; mean number of individuals of all species for a single transect: 478.

TABLE 6.—The 10 fish species most frequently seen along transect lines in the outer drop-off habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 4$
1	*Naso hexacanthus*	11.39	4
2	*Chromis leucurus*[1]	11.19	4
3	*Xanthichthys ringens*	10.50	4
4	*Thalassoma duperrey*	6.64	4
5	*Zebrasoma flavescens*	4.76	3
6	*Ctenochaetus strigosus*	3.87	2
7	*Chaetodon multicinctus*	3.76	3
8	*Centropyge potteri*	3.45	3
9	*Chromis verater*	3.24	2
10	*Pseudocheilinus evanidus*	2.40	2

[1]In making transect counts I followed Gosline and Brock (1960) in recognizing *Chromis leucurus* to include two color forms. Further study may show that two (or more) species are included here (see species account for *C. leucurus* in this report).

FIGURE 7.—Outer drop-off habitat. Most of the fishes shown in the water column are *Acanthurus thompsoni*.

Fishes Observed on Transect Lines

All fishes observed on transect lines in the five Kona habitats are listed in Table 7, where the value given for each species in each habitat is the relative abundance index, as defined in the methods. Transect data for each habitat category (number of transects, total number of species observed, and mean number of individuals on a single transect) are given in footnotes 2 to 7.

SPECIES ACCOUNTS

Family	*Page*
Muraenidae: moray eels	926
Congridae: conger eels	929
Synodontidae: lizardfishes	929
Brotulidae: brotulas	930
Atherinidae: silversides	931
Holocentridae: squirrelfishes	932
Aulostomidae: trumpetfishes	942
Fistulariidae: cornetfishes	944
Scorpaenidae: scorpionfishes	944
Serranidae: sea basses	947
Kuhliidae: aholeholes	948
Priacanthidae: bigeyes	948
Apogonidae: cardinalfishes	950
Carangidae: jacks	954
Lutjanidae: snappers	955
Sparidae: porgies	956
Mullidae: goatfishes	957
Kyphosidae: sea chubs	964
Chaetodontidae: angelfishes and butterflyfishes	964
Pomacentridae: damselfishes	978
Cirrhitidae: hawkfishes	986
Labridae: wrasses	989
Scaridae: parrotfishes	995
Blenniidae: combtooth blennies	998
Acanthuridae: surgeonfishes	1000
Zanclidae: moorish idol	1003
Bothidae: left-hand flounders	1005
Balistidae: triggerfishes	1005
Monacanthidae: filefishes	1009
Ostraciontidae: boxfishes	1011
Tetraodontidae: balloonfishes	1012
Canthigasteridae: sharp-backed puffers	1013
Diodontidae: spiny puffers	1015

This study treats only teleostean fishes, as these were almost the only kind observed on Kona reefs during this study. Elasmobranchs occurred infrequently and seemed to have little impact on the reef situation. No marine animals are more prominent than sharks in Hawaiian lore (e.g. Hobson and Chave, 1972), yet compared with most other tropical Pacific Islands, relatively few sharks are seen in Hawaiian nearshore waters today.

TABLE 7.—Relative abundance of fish species observed along transect lines in each of the Kona reef habitats.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
Superorder Elopomorpha:						
Order Anguilliformes:						
Family Muraenidae:						
Gymnothorax meleagris	—	—	0.04	0.06	—	—
Superorder Protacanthopterygii:						
Order Myctophiformes:						
Family Synodontidae:						
Synodus variegatus	0.04	—	—	—	—	—
Superorder Acanthopterygii:						
Order Beryciformes:						
Family Holocentridae:						
Holocentrus sammara	0.04	0.60	0.04	—	—	0.05
H. tiere	—	0.81	—	—	—	—
H. xantherythrus	—	0.60	—	—	—	—
H. diadema	—	1.01	—	—	—	0.05
H. lacteoguttatum	—	1.21	—	—	—	—
Holotrachys lima	—	0.81	—	—	—	—
Myripristis kuntee	0.23	23.61	0.19	—	0.43	0.26
M. murdjan	0.08	12.33	—	—	0.25	0.31
M. sp. (uncertain: either *M. murdjan* or *M. amaenus*)	—	5.24	—	—	—	—
Order Gasterosteiformes:						
Family Aulostomidae:						
Aulostomus chinensis	0.12	0.40	—	—	0.36	—
Family Fistulariidae:						
Fistularia petimba	—	—	—	0.12	—	—
Order Scorpaeniformes:						
Family Scorpaenidae:						
Taenianotus triacanthus	0.04	—	—	—	—	—
Scorpaena coniorta	—	0.20	—	—	—	—
Scorpaenopsis cacopsis	—	—	—	—	0.07	0.05
Order Perciformes:						
Family Serranidae:						
Cephalapholis argus	—	—	—	—	0.04	—
Family Priacanthidae:						
Priacanthus cruentatus	—	0.20	—	—	—	—
Family Apogonidae:						
Apogon menesemus	—	14.52	—	—	—	—
A. snyderi	—	11.90	—	—	—	—
Family Malacanthidae:						
Malacanthus hoedtii	—	—	—	—	—	0.16
Family Carangidae:						
Caranx melampygus	—	—	0.04	—	0.11	—
Family Lutjanidae:						
Aphareus furcatus	0.15	—	0.11	—	0.21	—
Family Sparidae:						
Monotaxis grandoculis	0.12	—	0.04	—	1.25	0.05
Family Mullidae:						
Mulloidichthys auriflamma	—	—	—	—	0.93	—
M. samoensis	0.12	—	—	—	0.14	—
Parupeneus multifasciatus	0.58	0.20	0.45	0.23	0.82	1.41
P. bifasciatus	0.12	—	0.07	—	0.71	0.05
P. chrysérydros	0.27	—	0.15	—	0.25	—
P. porphyreus	0.08	—	—	—	—	—
P. pleurostigma	0.04	—	—	—	—	0.05
Family Kyphosidae:						
Kyphosus cinerascens	—	—	0.22	—	0.11	—
Family Chaetodontidae:						
Holacanthus arcuatus	—	—	—	—	0.11	0.10
Centropyge potteri	2.49	—	—	—	1.00	3.45
C. fisheri	—	—	—	—	—	0.16
Forcipiger flavissimus	0.96	—	1.01	0.35	0.78	1.41
F. longirostris	0.50	0.40	—	0.12	0.07	0.31
Hemitaurichthys thompsoni	—	0.40	—	—	—	0.73
H. zoster	—	—	0.26	—	—	2.09
Chaetodon corallicola	—	—	—	—	—	1.05
C. miliaris	—	—	—	—	—	1.05
C. quadrimaculatus	0.69	—	0.89	1.44	0.53	0.10
C. unimaculatus	—	—	0.22	1.21	—	—
C. multicinctus	4.41	4.03	1.08	0.58	0.82	3.76
C. ornatissimus	1.80	1.21	0.68	0.29	0.25	0.31
C. auriga	—	—	—	—	0.04	0.05
C. fremblii	0.08	0.20	0.30	0.12	0.32	0.05
C. lunula	0.69	1.21	0.15	0.40	2.03	0.58
C. lineolatus	—	0.20	0.11	—	0.11	—

TABLE 7.—Continued.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
C. reticulatus	—	—	—	0.12	—	—
C. trifasciatus	0.04	—	—	0.12	—	—
Family Pomacentridae:						
Plectroglyphidodon johnstonianus	3.07	0.20	0.07	1.04	0.25	1.25
Pomacentrus jenkinsi	6.71	—	5.25	1.67	3.95	0.68
Abudefduf sindonis	—	—	3.64	—	—	—
A. sordidus	—	—	0.22	—	0.39	—
A. impariпennis	—	—	0.22	15.12	—	—
A. abdominalis	0.35	0.20	—	—	3.56	—
Dascyllus albisella	0.19	1.21	0.07	—	—	2.30
Chromis vanderbilti	0.15	—	2.35	10.33	11.74	0.84
C. leucurus	12.30	—	—	—	0.82	11.19
C. verater	0.96	0.80	0.11	—	0.14	3.24
C. ovalis	0.11	0.40	—	—	—	—
Family Cirrhitidae:						
Paracirrhites arcatus	0.69	—	0.74	0.86	0.89	0.99
P. forsteri	0.23	—	—	0.12	0.11	—
Cirrhitops fasciatus	0.12	—	0.34	0.17	0.82	0.47
Cirrhitus pinnulatus	0.04	—	—	0.52	0.18	0.05
Family Labridae:						
Bodianus bilunulatus	—	—	—	—	—	0.05
Cheilinus rhodochrous	1.57	—	0.15	—	0.57	1.41
Pseudocheilinius octotaenia	1.30	—	0.07	—	0.82	1.93
P. tetrataenia	0.31	—	0.04	0.23	0.07	0.42
P. evanidus	0.04	—	—	—	—	2.40
Labroides phthirophagus	0.31	—	—	—	—	0.05
Thalassoma duperrey	5.71	—	6.44	17.41	4.41	6.64
T. fuscus	—	—	1.97	4.78	—	—
T. ballieui	0.04	—	0.15	0.17	0.21	0.05
T. lutescens	0.08	—	—	—	—	—
T. quinquevittata	—	—	—	0.23	—	—
Halichoeres ornatissimus	1.15	—	1.67	0.58	0.53	1.15
Stethojulis balteata	2.15	—	1.56	2.88	1.35	0.68
Anampses cuvier	0.08	—	0.34	0.06	0.07	0.05
Coris gaimard	0.81	—	0.26	0.35	0.71	1.31
C. flavovittata	—	—	—	—	0.04	—
C. venusta	—	—	—	—	0.11	—
Macropharyngodon geoffroy	0.15	—	0.07	0.52	0.21	0.73
Gomphosus varius	1.00	—	1.53	2.78	0.60	0.78
Cirrhilabrus jordani	—	—	—	—	—	0.16
Pseudojuloides cerasinus	—	—	—	—	—	0.05
Hemipteronotus taeniourus	—	—	—	—	—	0.16
Family Scaridae:						
Scarus sordidus	1.73	—	0.82	1.04	1.81	1.93
S. taeniurus	0.19	—	0.63	0.98	0.43	—
S. dubius	0.46	—	0.52	—	0.50	0.16
S. perspicillatus	0.35	0.20	1.53	—	0.28	0.10
S. rubroviolaceus	0.35	0.20	0.04	0.29	0.50	0.10
Calotomus spinidens	0.50	—	0.04	0.12	0.11	0.26
Unidentified juveniles	—	—	—	—	0.89	—
Family Blenniidae:						
Exallias brevis	0.15	—	0.11	0.06	0.11	0.05
Cirripectus obscurus	—	—	0.15	—	—	—
C. variolosus	0.31	—	0.04	—	0.07	—
Plagiotremus goslinei	—	—	0.19	0.98	0.04	—
P. ewaensis	—	—	—	—	0.04	—
Family Acanthuridae:						
Acanthurus achilles	0.69	1.41	8.00	0.35	3.56	0.10
A. dussumieri	0.35	—	0.74	—	0.28	—
A. glaucopareius	0.04	—	0.19	—	0.07	—
A. guttatus	—	—	1.64	—	—	—
A. leucopareius	0.69	1.01	4.73	0.40	7.18	—
A. nigrofuscus	4.37	0.40	13.74	20.23	6.17	1.62
A. nigroris	3.64	2.22	4.88	1.38	1.60	1.57
A. olivaceus	0.19	—	0.11	—	0.07	0.31
A. sandvicensis	0.12	2.40	1.64	0.12	0.71	—
A. thompsoni	—	—	—	—	—	1.88
A. xanthopterus	—	—	—	—	0.43	—
Ctenochaetus strigosus	15.45	—	10.77	—	9.54	3.87
C. hawaiiensis	0.58	—	0.82	—	0.75	0.05
Zebrasoma flavescens	10.58	6.85	9.61	1.79	9.11	4.76
Z. veliferum	0.15	—	0.22	—	—	—
Naso brevirostris	—	—	—	—	—	0.10
N. hexacanthus	—	—	—	—	1.28	11.39
N. lituratus	1.46	1.21	0.74	2.02	1.07	1.20
N. unicornis	0.35	—	0.60	1.50	0.25	0.05

TABLE 7.—Continued.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
Family Zanclidae:						
Zanclus canescens	0.38	—	1.38	1.21	0.82	1.10
Order Tetraodontiformes:						
Family Balistidae:						
Melichthys niger	1.00	—	0.82	0.12	3.38	—
M. vidua	0.04	—	—	—	—	0.15
Xanthichthys ringens	—	—	0.04	—	0.39	10.50
Rhinecanthus rectangulus	—	—	0.19	1.33	—	—
Sufflamen bursa	0.73	—	0.37	—	1.57	1.57
Balistid sp.	—	—	—	—	0.04	—
Family Monacanthidae:						
Cantherines dumerili	0.15	—	—	0.12	0.11	—
C. sandwichiensis	0.15	—	0.40	0.64	0.32	0.16
Pervagor spilosoma	0.35	—	—	—	0.04	0.10
P. melanocephalus	0.42	—	0.19	—	—	0.10
Alutera scripta	—	—	—	—	0.04	—
Family Ostraciontidae:						
Ostracion meleagris	0.19	—	0.86	0.12	0.18	—
Family Tetraodontidae:						
Arothron hispidus	—	—	—	—	0.04	—
A. meleagris	—	—	0.04	0.06	—	—
Family Canthigasteridae:						
Canthigaster amboinensis	0.12	—	0.22	0.17	0.11	—
C. jactator	0.46	—	0.04	—	0.78	0.05
C. coronatus	—	—	—	—	0.04	0.10

The observations for each species are grouped by order and family in phylogenetic sequence, as listed by Greenwood et al. (1966). Species names generally are those used by Gosline and Brock (1960), except where more recent taxonomic studies indicate change. All sizes given are standard length. For most species, the number of specimens collected is followed by, in parenthesis, their mean size and the range in their sizes. All species accounts consider individuals showing morphology and behavior of adults.

ORDER ANGUILLIFORMES

Family Muraenidae: moray eels

Most Hawaiian eels belong to this family, which comprises the moray eels, or *puhi,* as Hawaiians call them (Gosline and Brock, 1960). Morays are denizens of crevices in the reefs, and because most remain secreted under cover, their great abundance cannot be appreciated by a casual observer. Nevertheless, the morays include more species (32 reported) on Hawaiian reefs than any other family of fishes, except perhaps the wrasse family Labridae (Gosline and Brock, 1960). Most Hawaiian morays do not grow to more than about 60 cm long, although a few may attain a length of about 2 m (Gosline and Brock, 1960). Most of them remain secreted in reef crevices, but the five species considered below are examples of those that are often exposed on the reef top.

Gymnothorax meleagris (Shaw and Nodder) —spotted moray, *puhi 'oni'o*

This medium-sized eel characteristically protrudes its head from crevices during the day (Figure 8), and thus is the moray most often in view on the reef; however, I seldom saw it after dark. Of the nine specimens collected, the stomachs of five were empty, although three of these contained unidentified fragments at the posterior end of their intestines. Of the four with prey in their stomachs, one (455 mm) taken during midmorning contained a fresh damselfish, *Abudefduf imparipennis* (40 mm) that appeared to have been recently captured. Two others with full stomachs were collected during late afternoon: one (321 mm) contained a moderately digested xanthid crab, whereas the other (121 mm) contained a well-digested fish. On the other hand, the fourth specimen (361 mm) contained a moderately digested xanthid crab that appeared to have been in the eel's stomach at least several hours when it was collected during morning twilight.

CONCLUSION.—*Gymnothorax meleagris* captures small fishes and crustaceans by day and probably also at night.

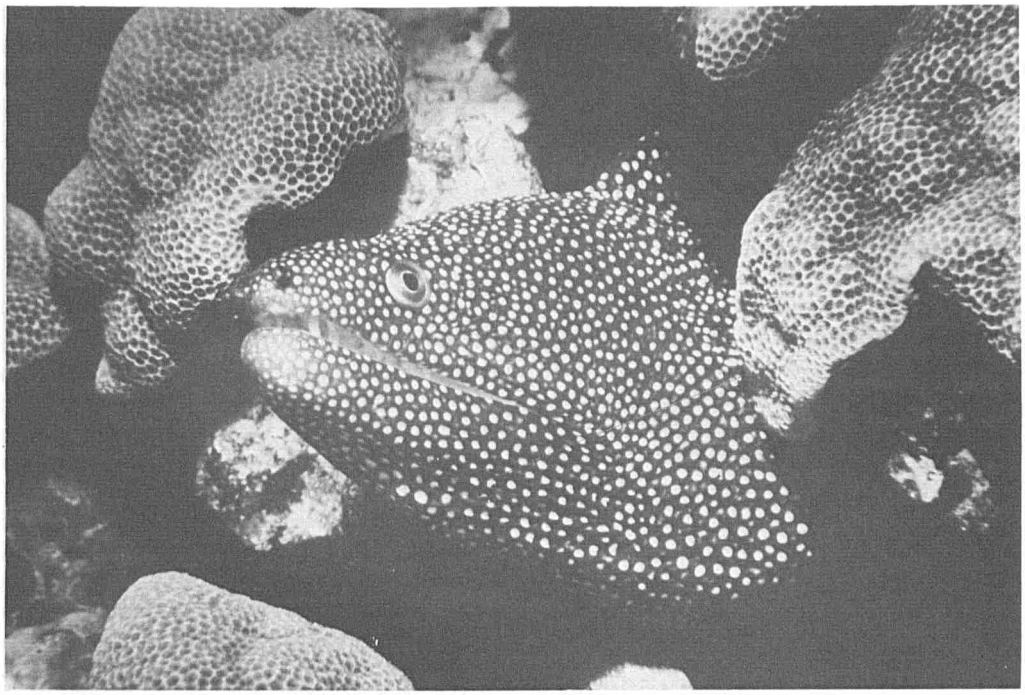


FIGURE 8.—*Gymnothorax meleagris,* a moray eel, showing daytime attitude.

Gymnothorax eurostus (Abbott)

This small species, which attains a maximum length of about 60 cm, is probably the most numerous moray in Hawaii (Gosline and Brock, 1960). However, it is a secretive species, only occasionally visible on the reef. Although the four individuals collected (360: 294-432 mm) were speared as they protruded their heads from holes in the reef during the day, this habit is not characteristic of *G. eurostus,* as it is of *G. meleagris,* above. Two of those collected had empty stomachs, but the other two, both taken during midday, contained relatively fresh prey—a caridean shrimp in one, a xanthid crab in the other.

CONCLUSION.—*Gymnothorax eurostus* captures crustaceans during the day. The nighttime situation remains uncertain.

Gymnothorax flavimarginata (Rüppell)—*puhi paka*

This eel, which attains a length of about 120 cm (Gosline and Brock, 1960), is the most numerous of the larger muraenids in Kona. Being so abundant, as well as large, this heavy-bodied eel probably represents the greatest threat among morays to humans. It is the species that most often appears when a fish has been speared during daylight. The regularity and promptness of these appearances make it clear that *G. flavimarginata* is especially sensitive to fish that are injured, or perhaps otherwise under stress. In this respect it is similar to *G. castaneus* in the Gulf of California (Hobson, 1968a). Usually when a reef fish is injured, or seriously threatened, it takes cover in a reef crevice. Usually such individuals are to some extent incapacitated, and thus vulnerable to predators equipped to seek them out. Probably *G. flavimarginata* is adapted to this task. Other large morays on the reef show the same behavior, but to a lesser degree. Most encounters with *G. flavimarginata* were by day; although its behavior would seem equally adaptive to nocturnal conditions, it was only occasionally observed after dark.

CONCLUSION.—*Gymnothorax flavimarginata* is especially sensitive to stimuli emanating from a fish in distress, and appears adapted to seeking out such individuals when they have sought shelter in reef crevices.

Gymnothorax petelli (Bleeker)—broad-banded moray

The broad-banded moray generally is out of sight within the reef during daylight, but often active in exposed locations after dark (Figure 9). A second species, *G. undulatus,* similarly forays away from cover at night, but during this study was seen less often than *G. petelli.* Although no specimens were examined, one *G. petelli* seen on the reef at night was grasping between its jaws a pufferfish, *Canthigaster jactator.* Additional evidence of nocturnal habits in *G. petelli* was given by Chave and Randall (1971), who described it pursuing crabs over underwater sand patches at night.

CONCLUSION.—*Gymnothorax petelli* is a nocturnal predator.

Echidna zebra (Shaw)—zebra moray

The zebra moray has a blunter snout than the species of *Gymnothorax* treated above, but its dentition is even more distinctive. Morays of the genus *Gymnothorax* have fanglike teeth that are suited to grasping prey, but the zebra moray, like other species of the genus *Echidna,* has blunt, pebblelike teeth that are suited to crushing prey. Gut contents are consistent with this observation: all four specimens (750: 485-835 mm) taken at various times of the day contained the crushed remains of relatively large crabs—considerably larger than crabs found in comparably sized individuals of *Gymnothorax.* The zebra moray is a sluggish animal, even for a moray, and is generally secretive. Usually all one sees of this animal, day or night, is a motionless segment of its body, visible at a narrow opening in the reef.

CONCLUSION.—*Echidna zebra* captures crustaceans within reef crevices, taking larger individuals of the more heavily armored prey than do species of *Gymnothorax.*

General Remarks on Moray Eels

Morays have been widely considered, collectively, as nocturnal animals (e.g. Winn and Bardach, 1959; Starck and Davis, 1966; Randall,

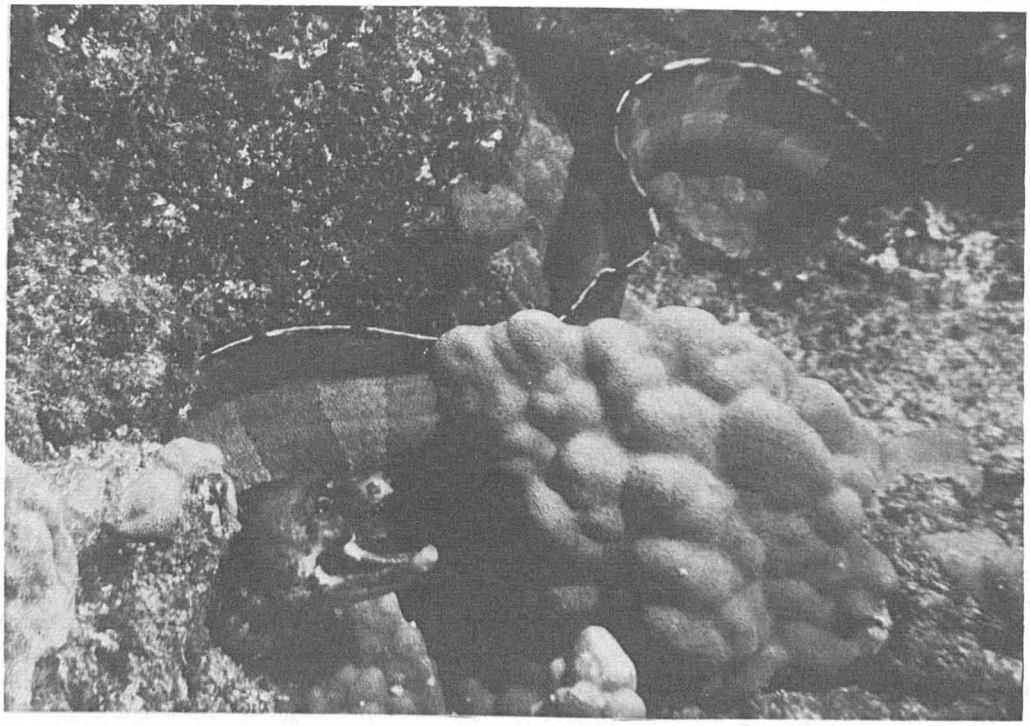


FIGURE 9.—*Gymnothorax petelli,* a moray eel, on the reef top at night.

1967; Collette and Talbot, 1972). Hiatt and Strasburg (1960) attributed the high incidence of empty stomachs in morays from the Marshall Islands during daylight to nocturnal habits; however, I concur with Gosline and Brock (1960), who attributed the empty stomachs of Hawaiian morays during the day to infrequent feeding, rather than necessarily to nocturnal feeding. Certainly some morays seem to be primarily nocturnal—*Gymnothorax petelli* and *G. undulatus*, described above, are examples. But others described here, such as *G. meleagris, G. eurostus,* and *G. flavimarginata,* feed regularly in daylight. That some morays are primarily diurnal was illustrated by Chave and Randall (1971), who described a diurnally active, nocturnally inactive pattern for *G. pictus* in the central Pacific. Conclusions on relative activity between day and night for moray eels remain tenuous if based solely on how often, and at what time, the species is seen in exposed positions. Moray eels are adapted to activity within reef crevices, and one would expect at least most of them to best capture their prey there; indeed, most species rarely expose themselves, day or night.

Family Congridae: conger eels

Conger marginatus Valenciennes—white eel, *puhi uha*

The white eel, which may exceed a length of 1 m (Gosline and Brock, 1960), is relatively numerous in Kona. It moves about in the open on the reef after dark and rests in reef crevices during daylight. In the Marshall Islands, Hiatt and Strasburg (1960) reported similar behavior in *C. noordzieki,* which preys on both fishes and invertebrates.

CONCLUSION.—*Conger marginatus* is active in exposed locations on the reef after dark.

Order Myctophiformes

Family Synodontidae: lizardfishes

Saurida gracilis (Quoy and Gaimard)–*'ulae nihoa*

Attaining lengths of over 300 mm, this is the largest of those lizardfishes that are numerous on the reef. During both day and night it rests motionless and fully exposed on sand patches, rock, or coral. Despite these exposed positions, it is difficult to detect, so closely does its coloration match the surroundings. Six specimens (223: 165-315 mm) were examined. The guts were empty in five—four speared at night, between 2300 h and dawn, and one taken during midday. The sixth specimen (165 mm), taken 1 h before midnight, contained the well-digested anterior half of a trumpetfish, *Aulostomus chinensis* (about 90 mm when intact). Because digestion was far advanced, this prey may have been ingested during the previous day or evening twilight. These limited data suggest that attacks are infrequent, or perhaps that feeding habits are diurnal or crepuscular. Hiatt and Strasburg (1960) reported strictly piscivorous habits for this species in the Marshall Islands, and described daylight attacks in which it darted upward from a resting spot on the sea floor.

CONCLUSION.—*Saurida gracilis* attacks small fishes in daylight.

Synodus variegatus (Lacépède)—*'ulae 'ula*

This is the most numerous synodontid on Kona reefs. During both day and night it rests on the sea floor (Figure 10), as does *Saurida gracilis,* above. Although usually in exposed positions, it is difficult to detect because its coloration closely matches the background. Frequently it becomes even more inconspicuous by burying in the sand, leaving only its eyes and the tip of its snout exposed.

Once, during early afternoon, an individual of this species shot up from the coral and captured a small wrasse, *Thalassoma lutescens,* that I was stalking. The wrasse was watching me when the lizardfish struck, and the attacker may have sensed this distraction in its prey. I speared the predator immediately after the attack, and found it to be 166 mm long (it lost the wrasse when speared and is included below among those with an empty gut). Two other noteworthy incidents occurred at night: On both occasions I was hunting specimens among the coral, and my spear, projecting into my path, was faintly illuminated by my companion's diving light. Suddenly, an individual of this species darted up and struck the silver barb on the otherwise grey spear. Although the nearby diving light created here an unnatural nocturnal situation, these two fish obviously were alert for prey at these times.

Twelve specimens (142: 94-158 mm) were collected during day and night from exposed posi-

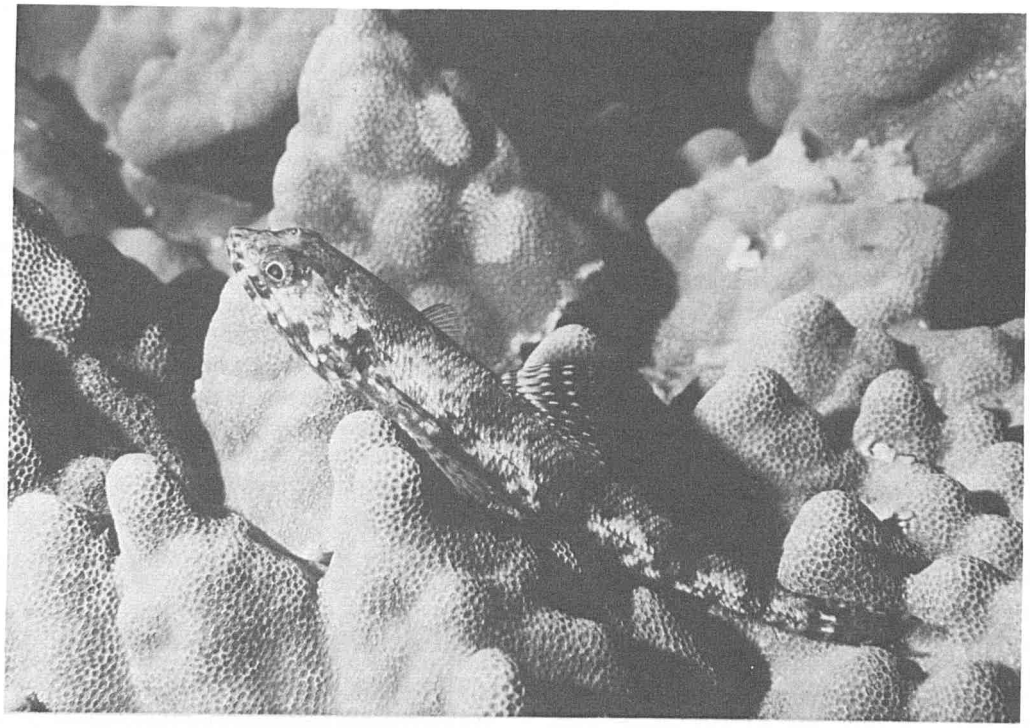


FIGURE 10.—*Synodus variegatus,* a lizardfish, poised to strike at prey in the water overhead.

tions on the sea floor. Of nine speared during afternoons, six had empty guts, but two contained fish fragments, and one contained three fish—two digested beyond recognition, and one relatively fresh *Plagiotremus goslinei* (32 mm). Of two collected during morning twilight, one was empty, while the other contained an extensively digested fish (25 mm). Finally, one collected at night, 5 h after sunset, contained fish fragments.

CONCLUSION.—*Synodus variegatus* attacks small fishes during the day and probably also at night.

General Remarks on Lizardfishes

Similar behavior is widely reported for the synodontids of tropical seas. In the Florida Keys, Starck and Davis (1966) reported that *Synodus synodus* and *Trachinocephalus myops* lie partially buried in the sand and erupt to capture prey swimming overhead during the day. Similarly, Randall (1967) noted that lizardfishes in the West Indies, including *S. synodus, S. intermedius,* and *S. foetens,* may rest on rocks, sand, or mud, where they sometimes partially bury themselves. Hartline et al. (1972) observed on several occasions during the day *Synodus* sp. in the Virgin Islands attacking the damselfish *Chromis cyaneus* from resting positions on the substratum. Similar observations were also reported by Smith and Tyler (1972). Although fishes seem to be the major prey of synodontids, Randall (1967) found some shrimps and squids in the predominantly piscivorous diet of lizardfishes in the West Indies. Suyehiro (1942) also reported shrimps and squid secondary prey to fishes in the diet of *Saurida undosquamis* in Japan. Probably any free-swimming animal of appropriate size becomes prey if it passes close above a waiting lizardfish when conditions are suitable for attack. The jaws of lizardfishes are profusely rimmed with sharp, inwardly depressible canine teeth, like those of many morays, and this type of dentition is especially well suited to grasping small fishes.

ORDER GADIFORMES

Family Brotulidae: brotulas

Brotula multibarbata Temminck and Schlegel—*puhi palahoana*

This fish is not in view during daylight, except to one who enters some of the darker caves. Although diurnally secretive, it swims into the open

on the reef after dark, but even then is mostly exposed only during transit from one crevice to another.

Seven individuals (169: 73-250 mm) were speared during day and night. Two collected about 2 h before daybreak as they swam close among rocks were both full of prey, including fresh material. Of three others collected in dark caves during midmorning, one was empty and the other two contained only well-digested fragments. Finally, two individuals collected within 1 h after nightfall as they swam in exposed locations among rocks were both empty—apparently having not yet captured prey on their nocturnal foray. The four individuals containing identifiable prey had fed on the items listed in Table 8.

CONCLUSION.—*Brotula multibarbata* is a nocturnal predator that feeds mostly on crustaceans and fishes.

General Remarks on Brotulas

Hiatt and Strasburg (1960) concluded that *Dinematichthys ilucoeteoides* in the Marshall Islands is very secretive because they never saw a live one, but did not suggest that it might be nocturnal. They believed that by concealing itself in crevices this brotulid is able to dash out and capture small fishes and crustaceans that unsuspectingly venture close to its hiding place. Starck and Davis (1966) recognized nocturnal habits in an Atlantic species, *Petrotyx sanguineus,* which is unseen in daylight, but swims close among reef ledges at night.

Order Atheriniformes

Family Atherinidae: silversides

Pranesus insularum (Jordan and Evermann)—*'iao*

This silverside is not numerous in Kona, but in daylight small schools of relatively inactive individuals occur at various places along the rocky shore, right at the water's edge. At nightfall these schools disperse, and the members move away from shore, over the reef. They swim high in the water column, just under the water surface, and some of them range out at least as far as the offshore drop-off.

Using a hard net, 13 individuals (47: 39-70 mm) were collected during both dark nights and moonlit nights—9 between 4 and 6 h after sunset and 4 during the 2 h before first morning light. Although the gut of 1 was empty, the other 12 were full, including fresh material, as listed in Table 9.

CONCLUSION.—*Pranesus insularum* is a nocturnal planktivore that takes mostly crustaceans and foraminiferans.

TABLE 8.—Food of *Brotula multibarbata.*

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	1	25.0	6.25
2	Fish	1	16.3	4.08
3	Decapod shrimps	1	6.3	1.58
4	Mysids	1	5.0	1.25
5	Crab megalops	1	0.3	0.08
Also, crustacean fragments		2	37.5	18.75
	Unidentified fragments	3	9.6	7.20

TABLE 9.—Food of *Pranesus insularum.*

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Mysids	5	14.2	5.92
2	Decapod shrimp larvae	5	6.7	2.79
3	Foraminiferans	4	6.3	2.10
4	Calanoid copepods	2	4.2	0.70
5	Larvaceans	1	2.1	0.18
6	Crab zoea	1	1.7	0.14
7	Spider	1	0.4	0.03
Also, crustacean fragments		12	40.8	40.80
	Unidentified fragments	7	23.6	13.79

General Remarks on Silversides

It is widely recognized that silversides prey largely on zooplankton. Hiatt and Strasburg (1960) found mostly zooplankton in three species in the Marshall Islands, as did Randall (1967) in two species from the West Indies. Each report listed shrimp larvae and copepods among the major food items, but neither mentioned nocturnal habits. At Majuro Atoll, Marshall Islands, *Pranesus pinguis* is inactive in schools along lagoon beaches during the day, and then migrates offshore into the lagoon at nightfall, where it disperses and feeds on zooplankton in the surface waters (Hobson and Chess, 1973). The closely related *P. insularum* does not move so far from shore at night in Kona, presumably because its feeding grounds are over the nearshore reefs.

ORDER BERYCIFORMES

Family Holocentridae: squirrelfishes

The squirrelfishes compose one of the more prominent groups of fishes on Hawaiian reefs. The species fall into two major categories: those in one group include members of the genus *Holocentrus,* which are known by the generic Hawaiian name *ala 'ihi,* and one species of the genus *Holotrachys*; those in the second group include species of the genus *Myripristis,* which are known by the generic Hawaiian name *'u'u,* or perhaps more often today by the Japanese equivalent *menpachi.*

Holocentrus sammara (Forskål)

This solitary fish is numerous in coral-rich surroundings at depths between 4 and 20 m. It is a relatively large species—up to 300 mm long (Gosline and Brock, 1960)—and characteristically hovers in visible locations at the openings of reef caves during the day. During evening twilight it moves away from its daytime shelter-sites and throughout the night ranges over the nearby areas of the reef, staying close to the sea floor. During morning twilight it gradually moves closer to cover and by sunrise has resumed its daytime mode of behavior. After dark the coloration of this fish differs from its coloration in daylight (Figure 11a and b).

Twenty-one specimens (162: 128-202 mm) were collected during day and night for food-habit study. All 13 that were speared as they swam in exposed positions on the reef during the last hours of darkness, before daybreak, and during morning twilight contained prey in varying stages of digestion. In comparison, of seven speared as they hovered close among coral shelter during the afternoon, four were empty, two contained only well-digested fragments, and one contained an apparently recently ingested crab. Finally, one that was speared in the open 4 h after nightfall was full of prey, most of it fresh. Items in the 17 specimens containing identifiable material are listed in Table 10.

CONCLUSION.—*Holocentrus sammara* is a nocturnal predator that feeds mostly on benthic crustaceans, especially xanthid crabs and caridean shrimps, but some feed diurnally.

Holocentrus spinifera (Forskål)

This is the largest squirrelfish on Kona reefs, and of those considered in this report it is also the least numerous. A solitary species during both day and night, it is secretive within reef crevices in daylight, but ranges out and forages close to the reef after dark. In daylight, the body of this fish is a plain rosy-red, and its dorsal fin is yellow; in darkness, however, a small but prominent white spot appears on each side of its body, just behind its dorsal fin. Because this large fish is not numerous, I came to recognize certain individuals and found that after nocturnal forays on the reef each tended to return each morning to its particular shelter spot.

Six specimens (213: 68-350 mm) were speared during day and night for study of food habits. The one that was taken during midday contained a large caridean shrimp, *Saron marmoratus* (about 40 mm), that was extensively damaged by digestion and could have been taken during the previous night. A second, taken as it emerged from cover at nightfall, was the only one taken with an empty gut. Of the other four, all of which contained relatively fresh prey, three were collected as they swam in the open at night, more than 3 h after sunset, and the fourth was collected under a ledge during morning twilight.

All five specimens containing food had fed on crustaceans exclusively. Three had taken caridean shrimps (mean percent of diet volume: 34; ranking index: 20.4), three had taken xanthid crabs (mean percent of diet volume: 31; ranking index: 18.6), and one had taken a scyllarid lobster (mean percent of diet volume: 11; ranking index:

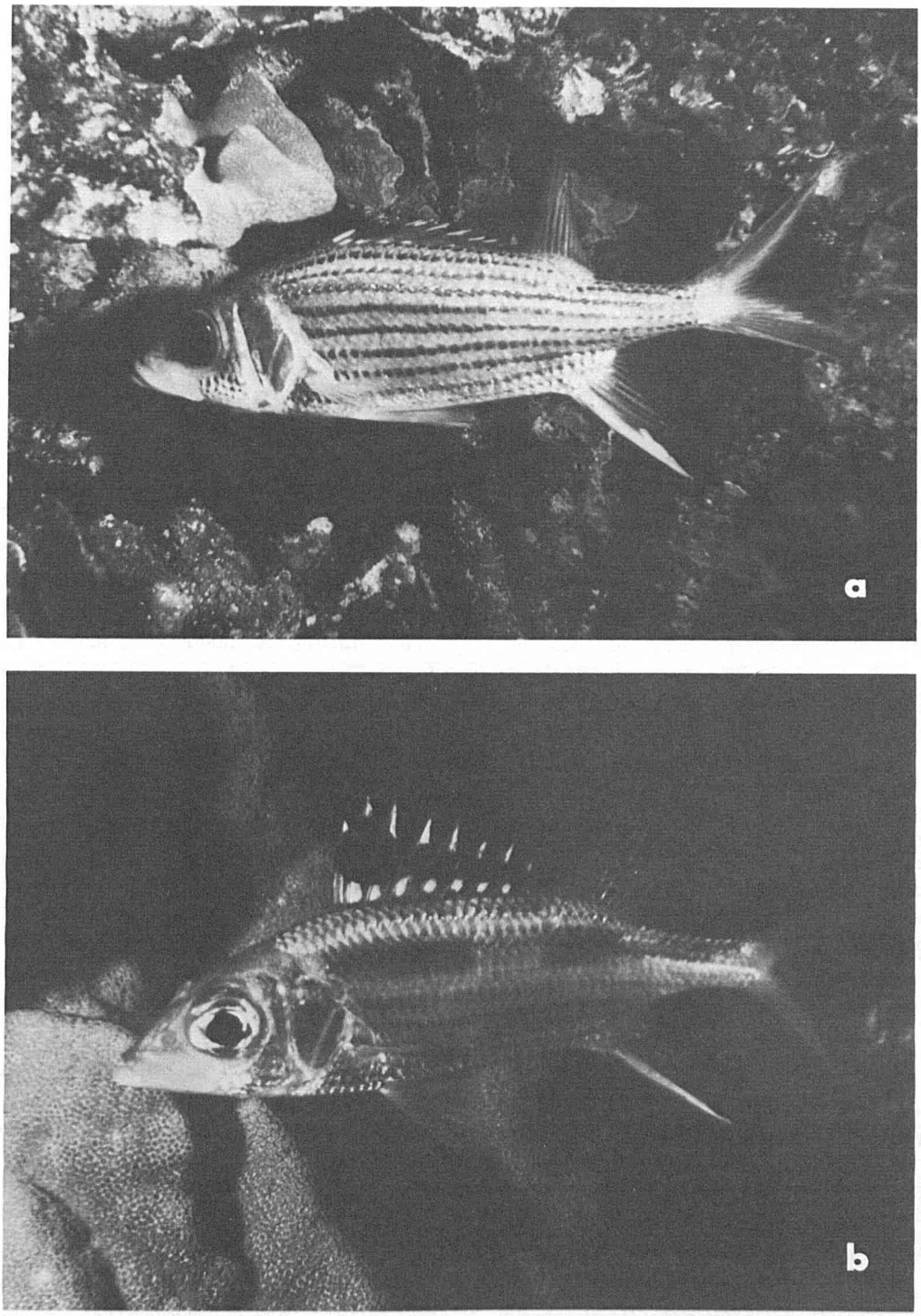


FIGURE 11.—*Holocentrus sammara*, a squirrelfish: a, showing its diurnal coloration under a ledge during the day; b, showing nocturnal coloration as it swims close to the reef at night.

TABLE 10.—Food of *Holocentrus sammara*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	52.5	37.08
2	Caridean shrimps	4	12.2	2.88
3	Portunid crabs	2	7.8	0.92
4	Fish	2	7.8	0.92
5	Penaeid shrimps	1	5.9	0.35
Also, crustacean fragments		4	13.8	3.25

2.2). Three contained unidentified crustacean fragments (mean percent of diet volume: 24; ranking index: 14.4).

CONCLUSION.—*Holocentrus spinifera* is a nocturnal predator that feeds mostly on benthic crustaceans, especially caridean shrimps and xanthid crabs.

Holocentrus tiere Cuvier

This relatively numerous holocentrid is mostly secreted in reef caves during the day, but after dark swims in exposed locations at depths below 5 m, especially along reef ledges. It emerges from cover after last evening light and regains shelter before, or at, first morning light. Like *H. sammara* and *H. spinifera,* above, *H. tiere* has distinctive diurnal and nocturnal color patterns (Figure 12a and b).

Fifteen specimens (141: 67-160 mm) were speared as they swam in the open at night, or just after they had returned to shelter at daybreak: 11 of these had food in their stomachs; 3 taken within 4 h after sunset were empty—apparently their nocturnal hunt had not yet been successful; 1 taken under a ledge during morning twilight also had an empty gut, indicating that it had passed the night without feeding. Items in the 11 specimens containing identifiable material are listed in Table 11.

CONCLUSION.—*Holocentrus tiere* is a nocturnal predator that feeds mostly on benthic crustaceans, especially xanthid crabs and caridean shrimps.

Holocentrus xantherythrus Jordan and Evermann

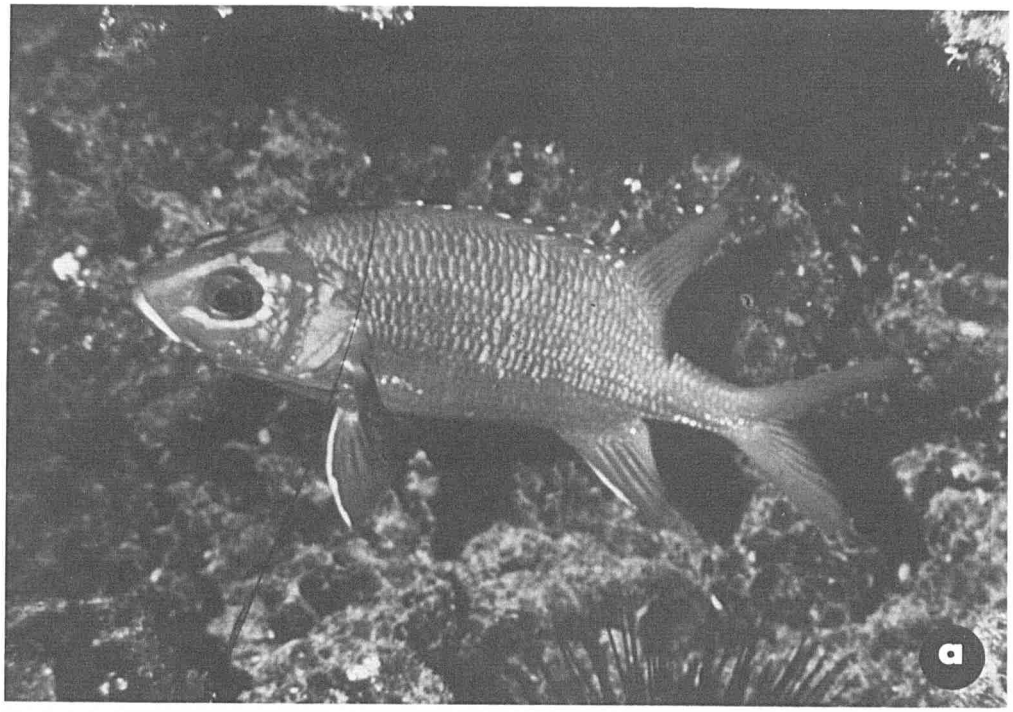
During the day this relatively small holocentrid aggregates in crevices and under overhangs of basalt reefs (Figure 13) in water deeper than 6 m, but especially below 20 m. After dark it ranges out from this shelter and into the surrounding areas, where solitary individuals are active close to rock, coral, or pockets of sand. By first morning light it has returned to its daytime retreats. At night this fish has prominent white vertical markings on its body like those illustrated for *H. tiere* (Figure 12b).

Of the 29 individuals (106: 88-123 mm) speared at different times of day and night, the stomachs of all 15 that were active in exposed locations on the reef during the 2 h immediately before daybreak, or were under reef shelter within an hour of sunrise, contained prey in varying stages of digestion, whereas the stomachs of all 11 taken from reef crevices during afternoons were empty. The remaining three were taken within 2 h after last light, shortly after they had begun their nightly foraging, and although one was empty, the other two contained fresh prey. Items in the 17 specimens that contained identifiable material are listed in Table 12.

CONCLUSION.—*Holocentrus xantherythrus* is a nocturnal predator that feeds mostly on benthic crustaceans, although some free-swimming crustaceans are also taken close to the bottom.

Holocentrus diadema Lacépède

After dark, many individuals of this relatively small squirrelfish swim close to the sea floor where coral growth is rich at depths below 3 to 4 m. *Holocentrus diadema* is secretive by day, generally remaining out of sight within the many narrow interstices of its coral-rich habitat, but is occasionally glimpsed in the shadows at the base of coral heads. Generally, it does not leave its daytime shelter until after last evening light, and returns to cover before or at first morning light. At night this fish, like *H. xantherythrus,* above, has prominent white vertical markings on its body that are similar to those on the nocturnally active *H. tiere* (Figure 12b).



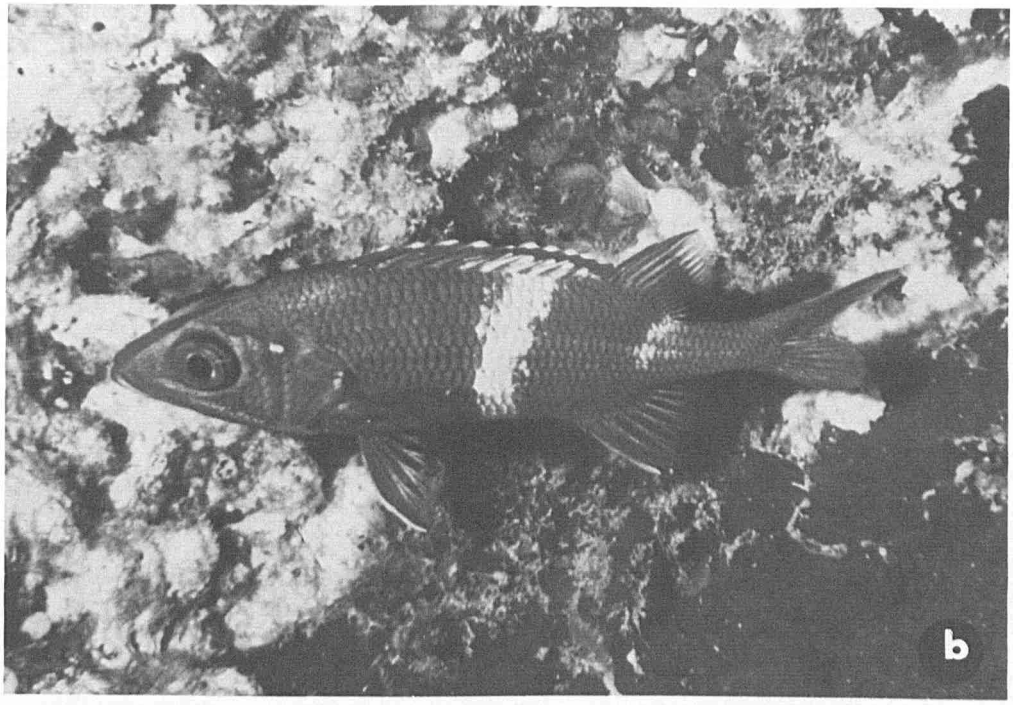


FIGURE 12.—*Holocentrus tiere*, a squirrelfish: a, showing diurnal coloration under a ledge during the day; b, showing nocturnal coloration as it swims close to the reef at night.

TABLE 11.—Food of *Holocentrus tiere*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	8	38.7	28.15
2	Caridean shrimps	5	24.7	11.23
3	Crab megalops	5	4.8	2.18
4	Fish	1	1.8	0.16
5	Polychaetes	1	0.2	0.02
6	Sipunculid introverts	1	0.1	<0.01
Also, crustacean fragments		8	29.7	21.60

TABLE 12.—Food of *Holocentrus xantherythrus*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	42.3	29.86
2	Crab megalops	11	14.8	9.58
3	Caridean shrimps	7	15.1	6.22
4	Prosobranch gastropods	4	2.3	0.54
5	Stomatopods	2	1.9	0.22
6	Opisthobranch gastropods	1	0.9	0.05
7	Sipunculid introverts	1	0.8	0.05
8	Pelecypods	1	0.6	0.04
9	Euphausiids	1	0.3	0.02
10	Oxyrhynchid crabs	1	0.3	0.02
11	Tanaids	2	0.2	0.02
12	Flabelliferan isopods	1	0.1	0.01
13	Mysids	1	0.1	0.01
Also, crustacean fragments		10	20.3	11.94

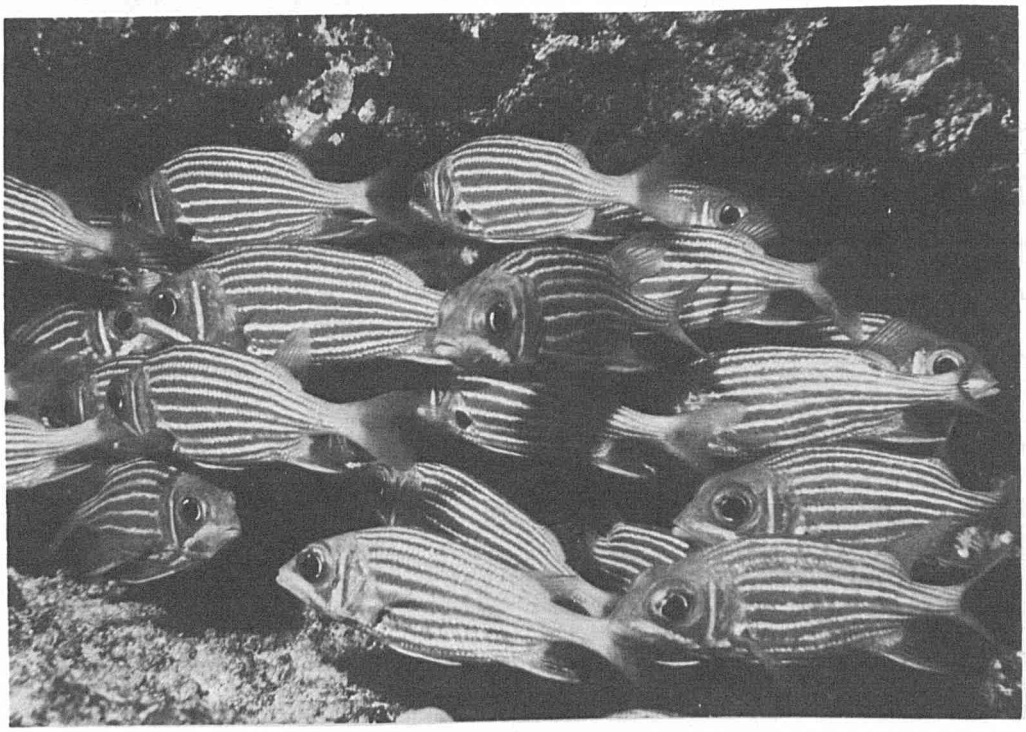


FIGURE 13.—*Holocentrus xantherythrus*, a squirrelfish, aggregated under a ledge during the day.

TABLE 13.—Food of *Holocentrus diadema*.

Rank	Items	No. fish with this item (n = 26)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	17	26.7	17.46
2	Ophiuroids	12	12.0	5.54
3	Crab megalops	11	12.4	5.25
4	Caridean shrimps	11	9.7	4.10
5	Prosobranch gastropods	13	6.2	3.10
6	Polychaetes	6	6.1	1.41
7	Gammaridean amphipods	5	1.7	0.33
8	Penaeid shrimps	2	2.3	0.18
9	Isopods	3	1.4	0.16
10	Chitons	1	1.7	0.07
11	Mysids	2	0.8	0.06
12	Portunid crabs	1	0.8	0.03
13	Holothurians	1	0.6	0.02
14	Oxyrhynchid crabs	1	0.4	0.02
15	Tanaids	1	0.4	0.02
16	Calanoid copepods	1	0.4	0.02
17	Pelecypods	1	0.4	0.02
18	Opisthobranch gastropods	1	0.2	0.01
19	Echinoids	1	0.2	0.01
20	Harpacticoid copepods	1	0.1	<0.01
21	Limpets	1	0.1	<0.01
Also, crustacean fragments		15	11.3	6.63
	Unidentified fragments	4	3.9	0.60

Twenty-eight specimens (109: 85-127 mm) were speared as they swam in exposed locations on the reef at various times during the night. Only two had empty stomachs: in one of these, taken shortly after nightfall, the entire gut was empty, which indicated it had not as yet hunted successfully that night; the other, taken with an empty stomach just before daybreak, had a full intestine, suggesting that it had fed early but not late during the night. The other 26 specimens all contained food in varying stages of digestion, most of it identifiable, as listed in Table 13.

CONCLUSION.—*Holocentrus diadema* is a nocturnal predator that feeds mostly on benthic crustaceans, although it also takes free-swimming forms close to the bottom.

Holocentrus lacteoguttatum Cuvier

This small squirrelfish is similar to *H. xantherythrus* and *H. diadema,* but frequents shallower water than the other two, being most numerous during the day in rocky crevices along surge-swept shores, often where the water is only 1 to 4 m deep. It aggregates in these crevices, and after nightfall ranges out over coral, rock, or pockets of sand on the surrounding reef. Gosline and Brock (1960) also noted the shallowwater habits of this species, but in at least some situations it occurs in depths below 30 m (Gosline, 1965). These habitat distinctions are clearest in daylight, when the three species have retired to their shelters. The differences are less clear at night, when their activity ranges overlap. *Holocentrus lacteoguttatum* does not seem to have prominent nocturnal color features, as do certain other species of *Holocentrus,* treated above; however, several individuals after having been speared at night showed faint traces of essentially the same white markings characteristic of nocturnally active individuals of *H. xantherythrus, H. diadema,* and *H. tiere* (see Figure 12b).

Twenty-one specimens (88: 52-104 mm) were collected at various times of day and night. All but 1 of 13 active individuals that were speared in the open at night (more than 4 h after sunset and before they had returned to shelter at daybreak) had food in their stomachs; the lone exception, collected 4 h after sunset, had a completely empty gut, indicating it had not yet hunted successfully that night. In comparison, only one of five collected from aggregations under shelter during midmorning had material in its stomach, and this was extensively digested (all had full intestines, however). Finally, all three that were collected from aggregations under shelter during late afternoon had completely empty guts, except for a few well-digested fragments posteriorly. Items in the 13 specimens containing identifiable material are listed in Table 14.

TABLE 14.—Food of *Holocentrus lacteoguttatum*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	13	36.3	36.30
2	Crab megalops	9	8.0	5.54
3	Gammaridean amphipods	8	5.1	3.14
4	Tanaids	6	3.7	1.71
5	Polychaetes	4	4.9	1.51
6	Caridean shrimps	3	1.9	0.44
7	Harpacticoid copepods	3	0.8	0.19
8	Echinoids	3	0.8	0.19
9	Sipunculid introverts	1	1.8	0.14
10	Prosobranch gastropods	1	1.0	0.08
11	Oxyrhynchid crabs	1	0.3	0.02
12	Calanoid copepods	1	0.3	0.02
13	Limpets	1	0.2	0.02
14	Ophiuroids	1	0.1	0.01
Also, crustacean fragments		13	28.1	28.10
	Unidentified fragments	4	6.7	2.06

CONCLUSION.—*Holocentrus lacteoguttatum* is a nocturnal predator that feeds primarily on benthic crustaceans, although some free-swimming forms close to the bottom are also taken.

Holotrachys lima (Valenciennes)

This fish is secreted far back in reef crevices during daylight. After dark, however, solitary individuals are widespread in exposed positions, swimming even closer to the reef than do the species of *Holocentrus*, discussed above. Unlike the others, which often swim over sand patches, this species stays over rock or coral. It did not display distinctive day or night color features, being at all times a solid rose-red.

Twenty specimens (91: 70-113 mm) were collected during day and night. Thirteen were active in exposed positions on the reef at night when speared, and the stomachs of eight contained prey, much of it fresh. Of the five taken after dark with empty stomachs, the entire gut was empty in three collected before midnight, indicating they had not yet hunted successfully that night; however, the gut was also empty in one speared just before dawn, indicating it had passed the entire night without feeding; the fifth individual with an empty stomach also was collected just before dawn, but its intestine was full, indicating that it probably had fed earlier during the night. Six of seven specimens collected from deep crevices during late morning had empty stomachs, and the extensively damaged material in the seventh individual probably had been ingested during the previous night. (Rotenone was used to collect this species during the day, a departure from the standard collecting method that was necessary because this secretive fish is only rarely seen in daylight.) Items in the 10 specimens containing identifiable material are listed in Table 15.

CONCLUSION.—*Holotrachys lima* is a nocturnal predator that feeds mostly on benthic crustaceans, although some free-swimming forms close to the bottom also are taken.

Myripristis kuntee Cuvier

This is the smallest of the three species of *Myripristis* that are numerous on the nearshore Kona reefs. It remains secreted in small crevices

TABLE 15.—Food of *Holotrachys lima*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Caridean shrimps	6	31.5	18.90
2	Xanthid crabs	5	33.0	16.50
3	Crab megalops	2	7.0	1.40
4	Fish	1	3.5	0.35
5	Gammaridean amphipods	1	0.5	0.05
Also, crustacean fragments		5	24.5	12.25

and coral interstices during the day, but emerges and aggregates in the lower levels of the water column, above the reef, about 30 min after sunset. After remaining active during the night, it returns to its daytime shelter on the reef about 30 min before sunrise (Hobson, 1972, as *M. multiradiatus*). When this fish is under cover during the day its body is solid red, but when active in the water column after dark, its lower sides are silvery, affording countershading like that described for nocturnally active *M. leiognathus* in the Gulf of California (Hobson, 1968a). This nocturnal pattern was illustrated earlier (Hobson, 1972: Figure 6).

Thirty-nine specimens (120: 74-145 mm) were speared at different times of the day and night. All 20 that were collected either over the reef at night (later than 4 h after sunset), or from shelter sites within an hour of sunrise, had their guts full of food. In contrast, 13 of 14 collected from shelter sites during the afternoon and evening twilight had empty guts (3 had a few fragments posteriorly in their intestines), and the 14th had in its stomach only well-digested fragments. Of the remaining five, collected above the reef early during the night (within 1 h after last light), four had their guts completely empty, indicating they had not as yet hunted successfully at that early hour, but the fifth was full of fresh calanoid copepods of a species that was exceptionally numerous around our diving lights for about 45 min shortly after last light on that particular evening. Items in the 22 individuals that contained identifiable material are listed in Table 16.

CONCLUSION.—*Myripristis kuntee* is a nocturnal planktivore that takes mostly crab megalops and other crustacea.

Myripristis murdjan (Forskål)

This holocentrid is numerous in Kona, where during the day it aggregates in reef crevices and under coral overhangs, especially where there is shelter from prevailing seas (Figure 14). The twilight activity of this species has been described (Hobson, 1972, as *M. berndti*). About 30 min after sunset it emerges from its daytime shelter and aggregates in the water column above the reef, generally rising to levels higher than those attained by *M. kuntee* (see above). Immediately, there is a general movement offshore. It remains uncertain how far it swims offshore —perhaps it does not go much beyond the drop-off into deep water, which is a major feeding ground for diurnal planktivores (Hobson, 1972). The offshore move is obscured by the circumstance that at any given time during the night many individuals of this species are swimming over the inshore reefs. Nevertheless, there are consistently fewer of them over inshore reefs on dark nights than on moonlit nights. Gosline (1965) also noted offshore migrations at night by species of *Myripristis* in Hawaii. About 40 min before sunrise this species begins to assemble above its diurnal shelter, and within 10 min all have taken cover for the coming day. This species shows essentially the same day-night difference in color patterns as *M. kuntee*, above.

Of 25 individuals (169: 139-270 mm) speared at different times of day and night, all 16 that were taken above the reef at night (later than 4 h after

TABLE 16.—Food of *Myripristis kuntee*.

Rank	Items	No. fish with this item (n = 22)	Mean percent of diet volume	Ranking index
1	Crab megalops	19	25.2	21.76
2	Decapod shrimps	9	11.8	4.83
3	Calanoid copepods	9	8.0	3.27
4	Mysids	7	9.3	2.96
5	Polychaetes	4	4.8	0.87
6	Fish	3	4.6	0.63
7	Stomatopods	4	2.8	0.51
8	Gammaridean amphipods	7	0.9	0.29
9	Gnathiid isopod larvae	2	1.8	0.16
10	Ostracods	2	0.1	0.01
11	Tanaids	1	0.1	0.01
12	Invertebrate eggs	1	0.1	0.01
Also, crustacean fragments		14	27.8	17.69
	Unidentified fragments	3	2.7	0.37

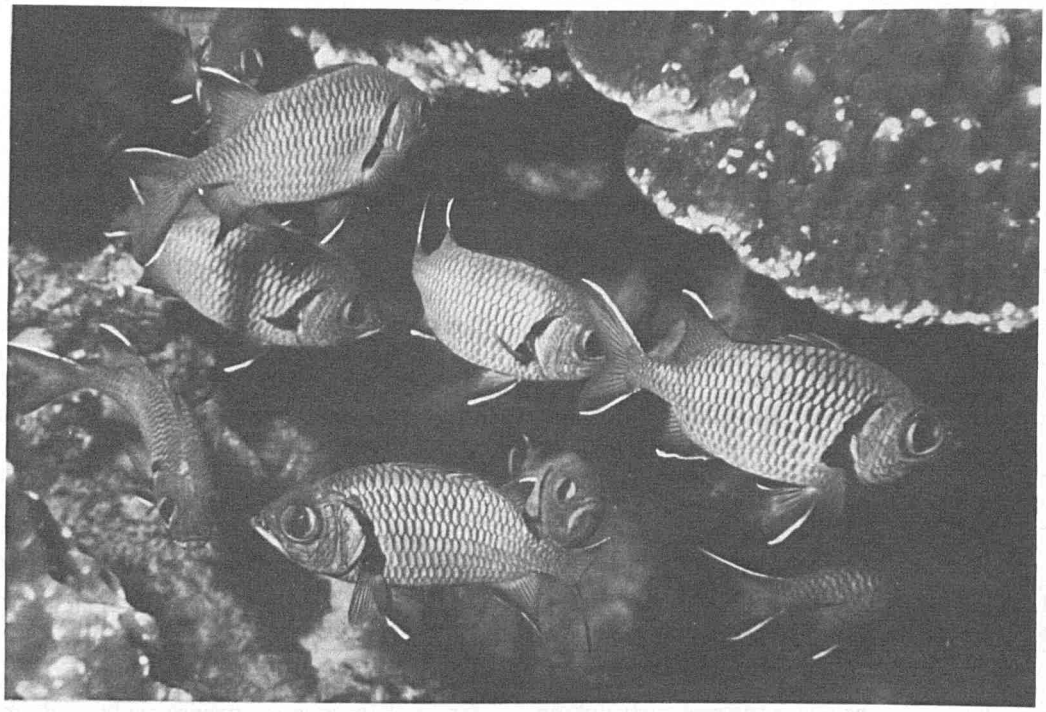


FIGURE 14.—*Myripristis murdjan*, a squirrelfish, aggregated under a coral ledge during the day.

sunset) contained food, whereas 8 of 9 that were collected from shelter sites during the afternoon were empty (the ninth specimen, collected during late afternoon, had only well-digested fragments in its stomach). Items in the 17 individuals containing identifiable material are listed in Table 17.

Hiatt and Strasburg (1960) found shrimp fragments in *M. murdjan* (reported as *M. berndti*) in the Marshall Islands, and suspected nocturnal habits, as did Randall (1955) for this species in the Gilbert Islands.

CONCLUSION.—*Myripristis murdjan* is a nocturnal planktivore that takes mostly crab megalops and other crustaceans.

Myripristis amaenus (Castelnau)

This squirrelfish, which congregates during the day in large caves cut into reefs exposed to an open-sea swell, is very similar to the preceding, *M. murdjan*, but is less numerous in most Kona habitats. Its behavior during twilight was described earlier (Hobson, 1972, as *M. argyromas*).

TABLE 17.—Food of *Myripristis murdjan*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Crab megalops	16	53.5	50.35
2	Decapod shrimps	3	8.1	1.43
3	Mysids	3	6.5	1.15
4	Fish	2	2.0	0.24
5	Polychaetes	2	1.5	0.18
6	Stomatopods	2	0.9	0.11
7	Euphausiids	1	1.2	0.07
8	Cephalopods	1	1.2	0.07
9	Gammaridean amphipods	1	0.5	0.03
10	Prosobranch gastropods	1	0.3	0.02
11	Calanoid copepods	1	0.1	<0.01
12	Ostracods	1	0.1	<0.01
Also, crustacean fragments		8	14.5	6.82
	Unidentified fragments	4	9.6	2.26

Myripristis amaenus, like its congeners, emerges from its daytime retreats about 30 min after sunset, and at least many individuals move offshore, especially when there is no moonlight. *Myripristis amaenus* shows essentially the same day-night distinction in coloration that is described above for its congeners.

Of 19 individuals (176: 116-210 mm) speared at different times of day and night, all 14 collected above the reef at night (later than 4 h after sunset), or from shelter sites within 2 h after the species had returned to cover in the morning, contained food, whereas all 5 collected from shelter sites during late afternoon were empty. Items in the 14 individuals containing identifiable prey are listed in Table 18.

CONCLUSION.—*Myripristis amaenus* is a nocturnal planktivore that takes mostly crab megalops and other crustaceans.

General Remarks on Squirrelfishes

Squirrelfishes are known throughout tropical seas to hunt prey after dark. For example, they have been thus described in the Marshall Islands (Hiatt and Strasburg, 1960), the Gulf of California (Hobson, 1965, 1968a), and the West Indies (Randall, 1967). Similar behavior has been noted in the Florida Keys by Starck and Davis (1966), who noted there were no distinctive nocturnal color features in tropical Atlantic holocentrids, such as are reported for all but two of the Hawaiian species above.

The two major categories noted above in the introduction to the squirrelfishes each represents a generally different mode of predation. All feed primarily on crustaceans, but whereas species of *Holocentrus* and *Holotrachys lima* capture their prey close to the sea floor, species of *Myripristis* hunt prey up in the water column.

BOTTOM FEEDERS.—The seven holocentrids in this category feed mostly on benthic forms, but also take some prey that are free-swimming at the base of the water column. Xanthid crabs comprised the major prey item for all species except the largest, *Holocentrus spinifera,* which contained a slightly larger volume of caridean shrimps. Xanthid crabs are ubiquitous benthic animals in all Kona inshore habitats, and are widely active in exposed positions after dark.

Of the seven bottom-feeding squirrelfishes, only three similar species, *Holocentrus diadema, H. lacteoguttatum,* and *H. xantherythrus,* hunt significantly over sand in addition to feeding on hard reef substrata; however, even these three do not range away from cover during this activity, which is limited to sand pockets on the reef and only the fringes of more extensive sandy areas. Nevertheless, it is probably because of this habit that these three have more varied diets than do the others. Hiatt and Strasburg (1960) reported that some of the holocentrids in the Marshall Islands forage on sandy bottoms, citing sand-dwelling gastropods as being prominent prey of *H. diadema* in that area.

The other four bottom feeders, *Holocentrus sammara, H. spinifera, H. tiere,* and *Holotrachys lima,* restrict their activity largely to hard substrata on the reef, and prey more heavily on caridean shrimps—especially on snapping shrimps. Some of the larger individuals of *Holocentrus sammara* and *H. spinifera* capture the caridean *Saron marmoratus*; although individuals of this shrimp exceeding a length of 30 mm are numerous

TABLE 18.—Food of *Myripristis amaenus.*

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Crab megalops	14	75.1	75.10
2	Decapod shrimps	4	9.3	2.66
3	Fish	3	2.9	0.62
4	Cephalopods	1	1.4	0.10
5	Mysids	4	0.3	0.09
6	Prosobranch gastropods	2	0.4	0.06
7	Polychaetes	1	0.4	0.03
8	Gammaridean amphipods	1	0.2	0.01
9	Calanoid copepods	1	0.1	<0.01
10	Stomatopods	1	0.1	<0.01
11	Isopods	1	0.1	<0.01
Also, crustacean fragments		8	9.7	5.54

in exposed positions on the reef after dark, most are too large to serve as prey for all but the biggest squirrelfishes.

WATER-COLUMN FEEDERS.—These are the species of *Myripristis,* all of which are primarily planktivores. This habit is reflected in their sharply upturned mouths, a feature well known as adaptive to feeding on plankton (e.g. Rosenblatt, 1967). Based on the food-habit data, crab megalops are the major prey of all three species reported here.

Earlier (Hobson, 1965, 1968a), I reported that *M. leiognathus* in the Gulf of California feeds in the water column after dark on planktonic crustaceans, including crab larvae. Similarly, Randall (1967) reported that *M. jacobus* in the tropical Atlantic feeds at night primarily on planktonic organisms, especially crustacean larvae, and Collette and Talbot (1972) noted that this species feeds at least 3 m above the reef. Probably similar habits are universal in species of *Myripristis.*

Order Gasterosteiformes

Family Aulostomidae: trumpetfishes

Aulostomus chinensis (Linnaeus)—*nunu*

This distinctive, solitary fish (Figure 15) is numerous on Kona reefs, where it attains the length of at least 700 mm. It exhibits three basic color forms: plain reddish brown, brown with light striping and other marks, and plain yellow. Several trumpetfish recognized as individuals were seen repeatedly in the same areas throughout the study, and none changed coloration during this time. The habitat of this species is in water deeper than about 5 m close to coral or irregular rocky substrata that offer many ledges and crevices.

I observed no difference in the behavior of this fish between day and night. At all hours it moves slowly, close to cover, propelling its long, cylindrical, rod-straight body mainly by undulating its soft dorsal and anal fins, which are set far back near the tail. The trumpetfish is a stalking predator, and on a few scattered occasions I saw it

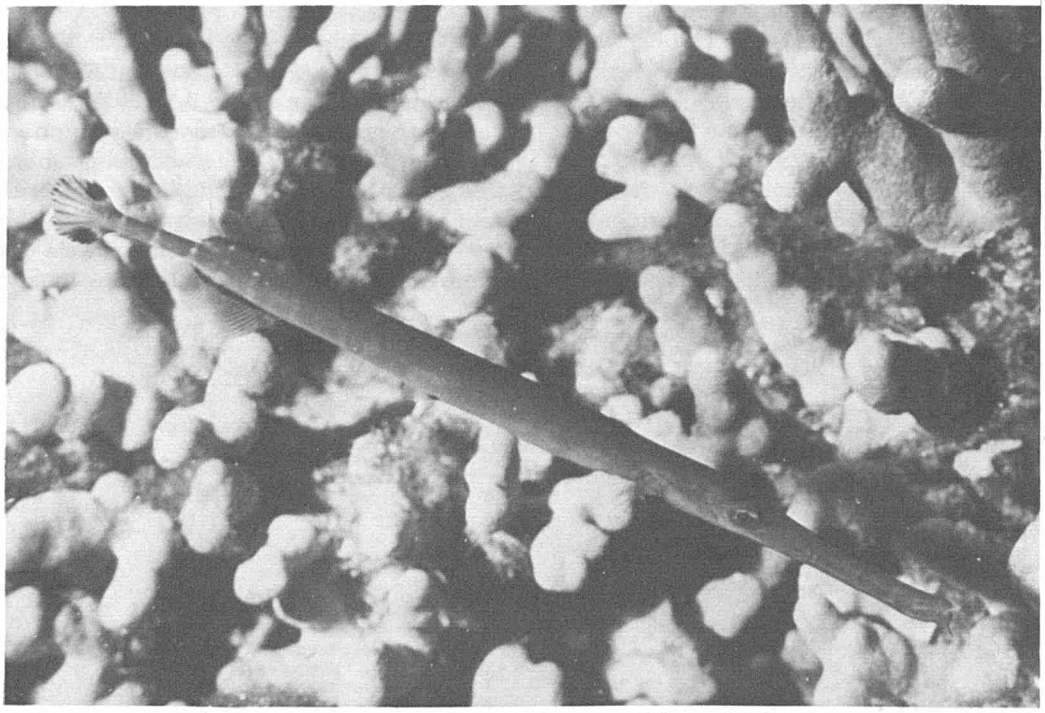


FIGURE 15.—*Aulostomus chinensis,* the trumpetfish, a stalking predator.

capture prey during daylight. After gaining a position close to its quarry, the attack is consummated with a short dart forward, the victim being literally sucked in with a sudden expansion of its tubular snout. Hiatt and Strasburg (1960) did not observe feeding, but speculated that this species in the Marshall Islands probes with its long snout in shallow holes and interstices of the reef and captures prey there by rapidly dilating its mouth. They found a small atherinid fish in the gut on one specimen. Sometimes trumpetfish accompany schools of grazing surgeonfishes—usually mixed groups of *Acanthurus sandvicensis* and *A. nigroris,* which frequently move across the reef. At these times, small organisms probably are driven out from algal cover by the grazing herbivores and become available as prey to the trumpetfish. Occasionally, the trumpetfish swims close beside large herbivores, especially parrotfishes, apparently using these large fishes as shields behind which to get close to prey not threatened by the herbivore.

Although 52 individuals (410: 220-621 mm) were speared at different times of day and night, no pattern was evident in the condition of the gut contents from specimens taken at these different times. Of 27 that contained food in their stomachs, 18 had captured fishes (mean percent of diet volume: 63; ranking index: 42), and 11 had taken caridean shrimps (mean percent of diet volume: 37; ranking index: 15.07).

It probably is significant that, with only two exceptions, those sampled had preyed on either fishes or shrimps—not both. The data cannot relate this selectivity to day or night activity or to size of predator. The 16 individuals that had preyed exclusively on fishes were within exactly the same size range (241-528 mm) as the 9 individuals that had preyed exclusively on shrimps. Furthermore, the mean sizes of the two groups differed only slightly—401 mm for the fish eaters, 396 mm for the shrimp eaters. The two individuals that had taken both fishes and shrimps were 241 and 337 mm long.

Aulostomus chinensis takes relatively large prey: the 15 fish items (representing among others *Apogon snyderi, Acanthurus nigrofuscus, Canthigaster* sp., and a labrid) that could be measured accurately had a mean standard length of 58 mm (range 25-88 mm) whereas the 11 shrimps that could be measured accurately had a mean total length of 55 mm (range 13-110 mm). Ten of the 11 shrimps were *Saron marmoratus,* the only shrimp this large that was numerous in exposed locations on the reef. Although this shrimp occupies exposed positions only at night, I have no evidence that it is taken by *Aulostomus chinensis* in greater numbers after dark.

Because the trumpetfish has an especially long, attenuated body, and because it takes relatively large prey, individuals that have recently ingested a meal often can be recognized by their distended bellies. Such individuals were occasionally seen during all periods of day and night, but most often during, or shortly after, twilight. Consistent with this, all three specimens that contained fresh prey (little or no damage by digestion) were collected during late twilight: in two of these instances (one in the morning, one in the evening) the prey were fishes; in the other instance (evening), the prey was a shrimp, *S. marmoratus.* Beyond this, the gut contents were of little help in establishing a pattern to feeding times; nor did the incidence of individuals with empty stomachs indicate a pattern, for they were collected during all periods of day and night.

CONCLUSION.—*Aulostomus chinensis* stalks prey, mostly fishes and caridean shrimps, most successfully during twilight, but also during the day and perhaps also at night.

General Remarks on Trumpetfishes

The activity of *Aulostomus chinensis* in Kona seems to be typical of the genus in other seas. Randall (1967) reported only fishes and caridean shrimps in 79 *A. maculatus* from the West Indies, and also remarked on the large size of these prey, as well as the way this trumpetfish sucks them into its mouth by expanding its tubular snout. Randall often observed *A. maculatus* hovering vertically in the water over small fishes and several times darting down on them (I did not see *A. chinensis* feed this way). Collette and Talbot (1972) judged *A. maculatus* in the Virgin Islands to be primarily crepuscular. They were uncertain about its nocturnal activity, but judged one they saw in a gorgonian at 2330 h to be quiescent. Eibl-Eibesfeldt (1955) described the way trumpetfish in the Indian Ocean use other fishes as cover behind which to approach small prey, and this was also reported by Collette and Talbot (1972) from the Virgin Islands.

Family Fistulariidae: cornetfishes

Fistularia petimba Lacépède

The cornetfish (see Hobson, 1968a: Figure 9) looks much like the trumpetfish, but grows considerably larger, many being over 1 m long. It is a pale-green fish with light-blue markings, and under certain circumstances instantaneously displays a series of broad bands along its body. Earlier I (Hobson, 1968a) reported that this species in the Gulf of California displays these bands when poised to strike prey. In Kona, the bands appear in similar circumstances and also in situations that suggest the fish might feel threatened, as when it is approached underwater by a human—especially a human carrying a diving light at night. *Fistularia petimba* frequently swims in loosely spaced groups of several individuals, generally in exposed shallowwater locations over the reef top.

Occasionally, *F. petimba* was seen in Kona stalking its prey during daylight, as observed in the Gulf of California (Hobson, 1968a). It does not move suddenly until within a few centimeters of its prey. When positioned for attack, it often draws its midsection into a modified "s" (as viewed from above), then darts forward for the capture. *Fistularia petimba* is more agile than *A. chinensis,* and undulating body movements not seen in the latter are regularly used to provide greater thrust in attacks and accelerated swimming. In the Gulf of California, I saw *F. petimba* use other fish as shields behind which to approach prey, as described above for *A. chinensis,* but did not see this in Kona. The behavior of *F. petima* was not seen to differ between day and night.

The 10 specimens (673: 363-1,069 mm), although collected during both day and night, were too few to provide much evidence on feeding times; however, of the 2 with empty guts, 1 was collected during late afternoon, and the other just before first morning light, indicating that these 2 had not fed during the preceding day and night, respectively. Only two specimens contained fresh prey, and both were collected shortly after twilight —one after evening twilight, the other after morning twilight. Though limited, these data suggest crepuscular feeding. Although prey in the other six specimens were in stages of digestion not inconsistent with predominantly crepuscular feeding, they clearly showed that prey are also taken at other times. All eight individuals with material in their stomachs had fed on fishes exclusively; only two prey could be identified to species, one a 70-mm cardinalfish, *Apogon snyderi,* the other a 52-mm damselfish, *Abudefduf imparipennis*. Both of these prey could have been captured close to reef crevices during the day.

Thus, *F. petimba* in Kona, as in the Gulf of California (Hobson, 1968a), was found to prey only on fishes. Hiatt and Strasburg (1960) also reported this species in the Marshall Islands to be exclusively piscivorous. My data suggest that *F. petimba* takes somewhat smaller prey than does *A. chinensis* of comparable length, as might be expected in view of the deeper body and snout of the latter. The mean length of the seven *F. petimba* containing measurable prey was 593 mm (range: 363-795 mm). The 11 measurable prey in these individuals had a mean length of 32 mm (range: 8-70). Comparable data for *A. chinensis* are given above.

CONCLUSION.—*Fistularia petimba* stalks fishes most successfully during twilight, but also during the day and perhaps at night.

General Remarks on Cornetfishes

The exclusively piscivorous habits of *Fistularia petimba* are paralleled by the similar diet of *F. tabacaria* in the tropical Atlantic (Randall, 1967). Suyehiro (1942) claimed that *F. petimba* feeds on tiny floating organisms by using its snout like a pipette, but I join Hiatt and Strasburg (1960) and Randall (1967) in contesting this opinion of the size of its prey. Starck and Davis (1966) found *F. tabacaria* to be more numerous on Florida reefs at night than during the day, but did not speculate that this reflected differences in feeding behavior.

ORDER SCORPAENIFORMES

Family Scorpaenidae: scorpionfishes

Pterois sphex Jordan and Evermann — lionfish, *nohu pinao*

The lionfish is a sluggish, solitary species that usually rests motionless on the reef, yet draws attention by its spectacular appearance (Figure 16). Perhaps because its fin spines carry a potent toxin, this fish makes little effort to evade a human collector. It is not numerous in Kona, and

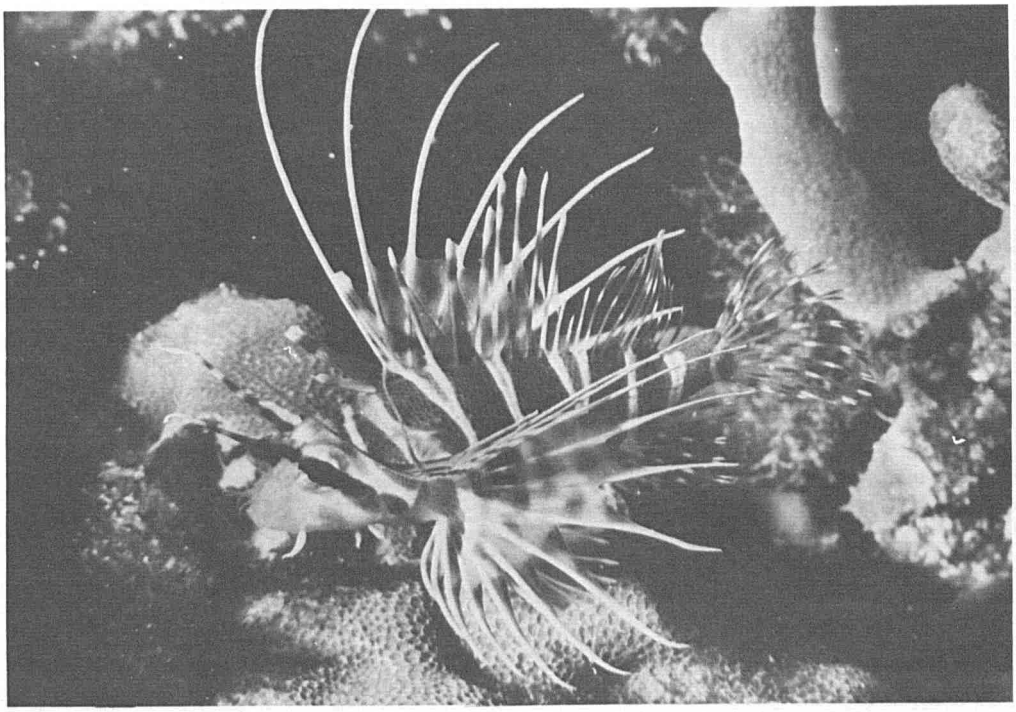


FIGURE 16.—*Pterois sphex*, a lionfish, swimming close to the reef at night.

occurs in visible locations on the reef most often after dark—though never far from shelter.

Fourteen specimens (83: 58-121 mm) were speared during day and night. Of nine that were collected during the afternoon or evening twilight, the guts in six were empty, and three had only well-digested crustacean fragments in their stomachs. On the other hand, all five specimens collected at night (more than 2 h after sunset) contained relatively fresh prey in their stomachs.

All eight specimens that contained food had fed on crustaceans exclusively. Caridean shrimps, which occurred in six, were the major food item (mean percent of diet volume: 56.3; ranking index: 42.19). Other food items were: xanthid crabs in three (mean percent of diet volume: 13.8; ranking index: 5.16) and pagurid crabs in one (mean percent of diet volume: 0.6; ranking index: 0.08). Five individuals contained unidentified crustacean fragments (mean percent of diet volume: 29.4; ranking index: 18.36).

CONCLUSION.—*Pterois sphex* is a nocturnal predator that takes benthic crustaceans, especially caridean shrimps.

Scorpaena coniorta **(Jenkins)**

Although this small species is the most numerous scorpaenid on Kona reefs, the casual observer will encounter it only at night. During the day individuals more than about 50 mm long are deep in reef crevices, whereas many smaller individuals are motionless among the branches of the coral *Pocillopora meandrina* (Figure 17). After nightfall, many of these fish occur in exposed positions: the larger individuals are spread widely across the reef, resting immobile on rock or coral, whereas the smaller ones are perched motionless on the sea floor close by the same coral heads that shelter them during the day. However, at any given time of night some of these fish are among the coral branches, just as in daylight.

Thirty-four specimens (46: 36-67 mm) were collected during various times of day and night. Of 12 that were taken during afternoon or early evening, most from among coral branches, only 1 had food in its gut (3 had a few fragments posteriorly in their intestine). The one containing food, taken from a coral head, had in its stomach a crab that, based on damage by digestion, probably had been

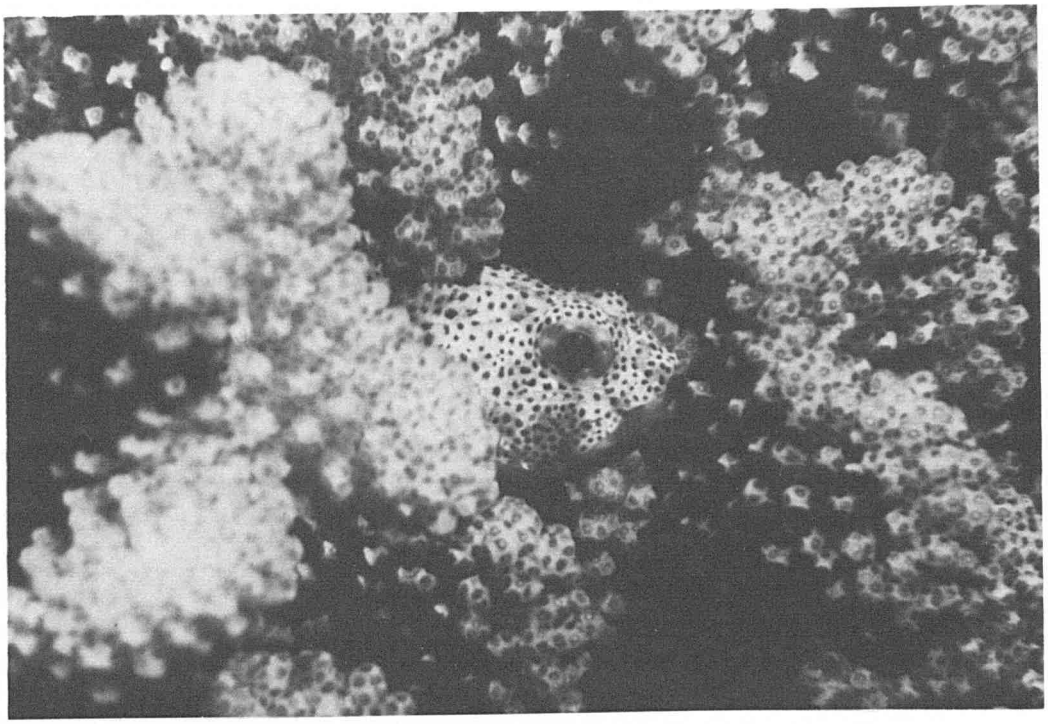


FIGURE 17.—*Scorpaena coniorta*, a scorpionfish, nestled among coral branches during the day.

captured during the day. In comparison, 14 of 22 individuals collected at night, between 3 h after sunset and first morning light, had food in their stomachs. Brachyuran crabs, almost all of them xanthids, occurred in 7 of the 15 individuals that contained identifiable items (mean percent of diet volume: 39; ranking index: 18.2). Caridean shrimps occurred in six (mean percent of diet volume: 28.3; ranking index: 11.33), and fishes in one (mean percent of diet volume: 6.7; ranking index: 0.45). Unidentified crustacean fragments occurred in six (mean percent of diet volume: 26; ranking index: 10.4). Many of the xanthids and carideans found in specimens less than 50 mm long are forms that cooccur with these fish among the coral branches.

CONCLUSION.—*Scorpaena coniorta* is a nocturnal predator that takes benthic crustaceans, mostly xanthid crabs and caridean shrimps. Some prey are also captured during the day.

Scorpaenopsis cacopsis Jenkins—*nohu 'omakaha*

This species, the largest Hawaiian scorpaenid, grows to over 50 cm long (Gosline and Brock, 1960). I observed no overt difference in its behavior between day and night as it was seen resting immobile on the reef at all hours, often fully exposed. Despite its large size and frequent disdain for cover, this fish remains virtually unseen, owing to body hues and texture that render it much like the reef on which it rests. It was not seen feeding, but its morphology and behavior suggest that it lunges forward to attack prey that have strayed within range, and sucks them in with a sudden expansion of its cavernous mouth.

Of the five specimens (256: 73-375 mm) examined, three had prey in their stomachs: one, taken within 1 h after sunrise, contained a fresh fish, *Pomacentrus jenkinsi* (104 mm); a second taken at night, 4 h after sunset, contained a relatively fresh octopus; and the third, taken late in the afternoon, contained fish fragments. The other two, both empty, were collected during morning twilight.

CONCLUSION.—*Scorpaenopsis cacopsis* attacks fishes and motile invertebrates during the day. Its nocturnal activity remains uncertain.

General Remarks on Scorpionfishes

Scorpionfishes on tropical reefs are widely described as predators that rest on the bottom, and

because they resemble their surroundings they remain unseen by small prey that swim within striking range (Longley and Hildebrand, 1941; Hiatt and Strasburg, 1960; Starck and Davis, 1966; Randall, 1967). This behavior is descriptive of some scorpaenids, but probably is overdrawn as a generalization encompassing the entire family. Such a tactic is adaptive to daylight, and is used by *Scorpaenopsis cacopsis* in Hawaii (the one fish identified as prey of this predator, a damselfish, is strictly a diurnal species that is not active over the reef at night). Significantly, the fishes that have been reported by other investigators as prey of scorpaenids on tropical reefs similarly imply diurnal predations: blennies (Longley and Hildebrand, 1941); a wrasse and a parrotfish (Hiatt and Strasburg, 1960); and an angelfish, a surgeonfish, a sardine, a sea horse, and a conger eel (Randall, 1967). With perhaps the lone exception of the conger eel, these are fishes that swim close to the reef during daylight, and at that time would be vulnerable to the ambushing tactic of scorpaenids; however, they would not be readily available after dark when most of them rest under cover on the reef or, in the case of the sardine, swim away from the reef. Conspicuously absent among the reported prey are the many species of comparable size that are numerous close above the reef at night, including apogonids and holocentrids. One can readily see how camouflage and ambush would be especially suited to daylight, but less significant after dark. Randall (1967), basing his generalization on the West Indian situation, characterized the scorpaenids as diurnal. In Hawaii, most species are predominantly nocturnal. In addition to *Pterois sphex* and *Scorpaena coniorta,* which prey largely on benthic crustaceans, as described above, other members of the family that appear on the reef in greater numbers at night include *Dendrochirus brachypterus, Scorpaenodes parvipinnis,* and *Scorpaena ballieui.* Among feeding scorpaenids, camouflage does not seem to play the important role at night that it does during the day. When these predators are abroad after dark they often contrast markedly with their surroundings. Although fishes do not seem to be significant prey at night, the behavior of these nocturnal scorpaenids indicates that their tactic remains a short lunge from a resting position to capture prey that have inadvertently come within range.

ORDER PERCIFORMES

Family Serranidae: sea basses

Sea basses are prominent on most tropical reefs, but the family has no representatives native to shallow Hawaiian reefs (Gosline and Brock, 1960). Nevertheless, the widespread Indo-Pacific serranid *Cephalopholis argus* has been introduced into Hawaii from the Society Islands, the first time in 1956, and has since become well established in Kona.

Cephalopholis argus Bloch and Schneider

This solitary fish, numerous on Kona reefs, swims close among overhanging ledges and crevices during the day, but is seen less often at night. Because it generally is wary of humans, lack of nocturnal observations could mean that it avoided our diving lights at night.

Although 6 of 10 specimens (319: 232-520 mm) speared at various times of day were empty, no temporal pattern is recognized, as the 6 were taken from early morning to late afternoon. All four that contained food, also taken at various times during the day (on four different occasions over 3 mo), had fed exclusively on fishes. One, taken during midmorning, contained, because of digestion, what was recognizable only as a fish (125 mm). The other three—one collected during midday, and two late in the afternoon—each contained a single moderately digested squirrelfish, *Holocentrus xantherythrus* (80, 110, and 130 mm, respectively). *Holocentrus xantherythrus* congregates under ledges during the day in areas where *C. argus* is active (see the species account for *H. xantherythrus* above), and thus is available as prey for the sea bass at this time. *Cephalopholis argus* has been reported to feed on shrimps as well as fishes in the Marshall Islands (Hiatt and Strasburg, 1960) and on shrimps in the Gilbert Islands (Randall, 1955). In a sample of 98 specimens from Tahiti, Randall and Brock (1960) found that 77.5% contained fishes, whereas 22.5% contained crustaceans (shrimps and crabs).

CONCLUSION.—*Cephalopholis argus* preys on fishes among reef crevices during the day. Its nocturnal habits remain uncertain.

General Remarks on Sea Basses

Diurnal piscivorous habits were reported in *Mycteroperca rosacea* in the Gulf of California,

with peaks during twilight (Hobson, 1965, 1968a). On the other hand, nocturnal habits were noted in *Alphestes multiguttatus* and *Rypticus bicolor* (the latter is often placed in a separate family, the Grammistidae), both of which prey chiefly on benthic crustaceans (Hobson, 1965, 1968a). In the same reports, a fourth sea bass, *Epinephelus labriformis,* was reported to feed by both day and night, chiefly on fishes in daylight and on benthic crustaceans after dark. These data suggest that fishes may be the major prey of sea basses in daylight with crustaceans predominating after dark, a generalization consistent with the limited observations on *Cephalopholis argus* in Kona.

Starck and Davis (1966) noted that serranids of the genera *Epinephelus, Mycteroperca,* and *Petrometopon* behave similarly day and night in the Florida Keys, with probable feeding peaks around sunrise and sunset. Longley and Hildebrand (1941) reported that *Epinephelus morio* feeds during both day and night in the Dry Tortugas, Fla., and Randall (1967) noted that larger serranids in the West Indies feed both day and night, with greatest activity at dawn and dusk. Collette and Talbot (1972), on the other hand, reported *E. guttatus* in the Virgin Islands to be active by day and apparently asleep at night. They also found *E. fulvus* and *E. cruentatus* active in daylight and suspected that these sea basses rest at night. Randall (1967) considered the smaller serranids, in general, to be primarily diurnal. In Florida, Starck and Davis (1966) regarded certain small serranids of such genera as *Diplectrum, Hypoplectrus,* and *Serranus* to be active by day and inactive by night. None of these authors attempted to relate time of activity with kinds of prey.

Family Kuhliidae: aholeholes

Kuhlia sandvicensis (Steindachner)—*aholehole*

This predator occurs in only a few locations within the Kona study area, and there just sparsely, compared to its large numbers elsewhere in Hawaiian nearshore waters. Juveniles and young adults live in tide pools or in schools close to shore (Gosline and Brock, 1960), but the larger adults congregate during the day under low ledges and boulders, usually in water less than 5 m deep farther from shore. They emerge from shelter at nightfall, and the few observed after dark during this study were solitary in the water column over the reef. Gosline and Brock (1960) noted that the adults, at least, are nocturnal, a conclusion consistent with the large eyes of the species.

Of the 13 specimens (164: 132-202 mm) collected, 8 speared during midmorning from under rocky cover contained in their stomachs extensively digested crustacean fragments (including crab megalops), 1 taken under a rock at noon contained only well-digested material scattered through its intestine, and 4 speared under rocks late in the afternoon were empty.

CONCLUSION.—*Kuhlia sandvicensis* is a nocturnal predator that feeds on free-swimming crustaceans.

Family Priacanthidae: bigeyes

Priacanthus cruentatus (Lacépède)—bigeye, *aweoweo*

This priacanthid (Figure 18) is numerous in Kona, where it takes shelter under rocks or coral during the day, often in groups, and is active in the open at night. After emerging from shelter at nightfall, many individuals assemble in schools high in the water column and then migrate offshore. These do not return inshore until about 40 min before sunrise, but a lesser number of other individuals, mostly solitary or in small groups, remain over the inshore reefs throughout the night. All of these fish return to their daytime shelter by 30 min before sunrise, at least many of them to specific home caves (Hobson, 1972).

Forty specimens (173: 115-255 mm) were collected during day and night. All 17 that were speared during morning twilight (shortly after they had reappeared near their diurnal shelter, but before they had taken cover) had relatively fresh prey in their stomachs. Four others were collected from under cover during late morning, and although all had full stomachs, with many items identifiable, digestion was advanced, and most of the material was damaged beyond recognition. The other 19 were collected from caves late in the afternoon, and although only 4 of these had empty stomachs, the material in the other 15 was reduced to unidentified fragments. Items in the 21 specimens containing identifiable material are listed in Table 19.

Hiatt and Strasburg (1960) acknowledged that species of *Priacanthus* generally are thought to be nocturnal, but contested this opinion as far as *P.*

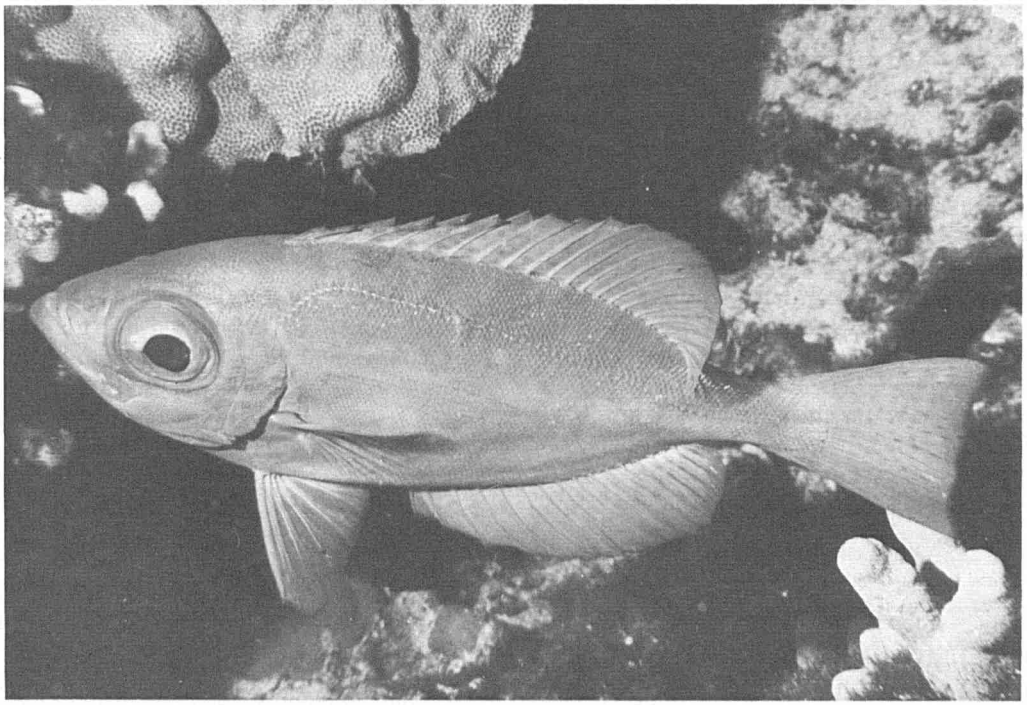


FIGURE 18.—*Priacanthus cruentatus*, a bigeye, showing the plain red coloration typical of this species when among the coral during the day.

cruentatus in the Marshall Islands is concerned. Although conceding the possibility of some nocturnal feeding, they believed that this species captures octopods, a major food there, in reef crevices and caves during the day. This conclusion was heavily influenced by finding food in the stomachs of this priacanthid during the day, but none in stomachs of the nocturnally active holocentrids. As noted above, I found a similar difference between *P. cruentatus* and holocentrids in Kona, but attribute this to the priacanthid retaining food in its stomach longer during digestion than do holocentrids.

Longley and Hildebrand (1941) noted that this circumtropical species feeds chiefly at night in Florida, a conclusion with which Starck and Davis (1966) concurred. In the West Indies, Randall (1967) was of the same opinion, but he also felt that the condition of prey in some specimens indicated diurnal feeding as well; Randall noted that *P. cruentatus* preys mostly on the larger animals in the plankton. Collette and Talbot (1972) concluded that in the Virgin Islands this is a crepuscular species that continues to feed in caves and under ledges during daytime.

Gosline (1965) reported that *P. cruentatus* in

TABLE 19.—Food of *Priacanthus cruentatus*.

Rank	Items	No. fish with this item (n = 21)	Mean percent of diet volume	Ranking index
1	Crab megalops	17	32.3	26.15
2	Cephalopods	8	20.4	7.77
3	Fish	6	11.2	3.20
4	Decapod shrimps	5	3.6	0.86
5	Adult crabs	2	7.6	0.72
6	Mysids	1	0.4	0.02
7	Stomatopods	1	0.1	0.01
Also, crustacean fragments		11	13.4	7.02
	Unidentified fragments	8	11.0	4.19

Hawaii migrates offshore at night. In Florida, however, Starck and Davis (1966) noted only that it is active at night in the same areas where it is sheltered in daylight; they illustrated this species with a mottled color pattern, which they believed to be its nocturnal coloration. The same mottled pattern occurs regularly at night in Kona when the fish is held in the beam of a diving light, and I believe it is a response to the light, rather than a nocturnal coloration—especially because the pattern is intensified upon moving the light progressively closer to the fish. In the absence of a diving light at night, this species is either plain red (as it usually is in daylight), or, more often with individuals in mid-water, overall pale-silver (occasionally this pale-silver coloration is displayed under cover during the day). The blotched pattern is the red and silver hues in combination.

CONCLUSION.—*Priacanthus cruentatus* is a nocturnal predator that feeds on free-swimming organisms, mostly crustaceans and cephalopods.

Family Apogonidae: cardinalfishes

Apogon erythrinus Snyder

After dark, this small solitary cardinalfish is numerous close to basalt reefs in water less than 6 m deep, usually in small sand and cobble pockets. The smaller ones are largely transparent, and transparency remains a characteristic of even the largest individuals, despite an increased pinkish hue (Figure 19). During the day *A. erythrinus* remains out of sight, secreted deep in reef crevices.

Of 14 individuals (36: 22-42 mm) examined, 4 that had been collected together from a deep crevice 4 h after sunrise were empty (rotenone was used to collect these 4, a departure from the standard collecting method necessary here because the species was never visible during the day). The other 10 specimens were speared from among those active in exposed locations on the reef at night (more than 4 h after sunset), and although 2 were empty, the other 8 contained prey in their stomachs.

All eight with material in their stomachs contained crustaceans exclusively. Xanthid crabs

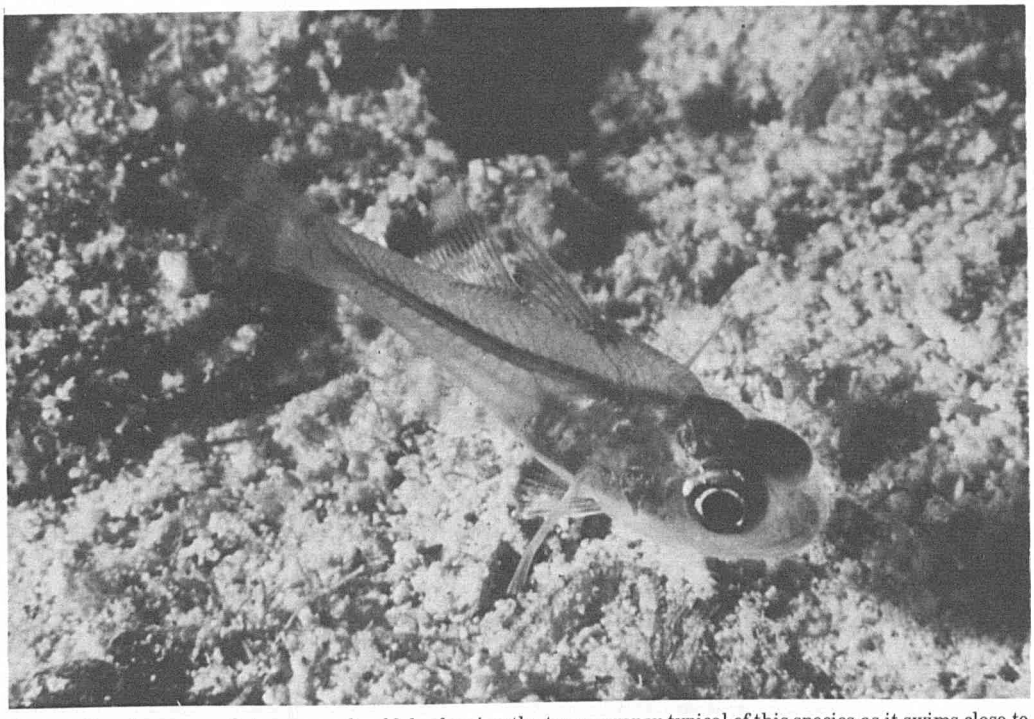


FIGURE 19.—*Apogon erythrinus*, a cardinalfish, showing the transparency typical of this species as it swims close to the reef at night.

were the major item, occurring in five individuals (mean percent of diet volume: 50; ranking index: 31.25). Most of these xanthids were in the megalops stage, except that their abdomens were reflected under their carapaces. The only other identifiable prey, occurring in three specimens, were gammaridean amphipods (mean percent of diet volume: 20; ranking index: 7.5). Four contained unidentified crustacean fragments (mean percent of diet volume: 30; ranking index: 15).

CONCLUSION.—*Apogon erythrinus* is a nocturnal predator that takes mostly benthic crustaceans.

Apogon menesemus Jenkins—*'upapalu*

This species and the very similar *A. snyderi* (below) are the largest and most abundant apogonids in Hawaii (Gosline and Brock, 1960), and they were the apogonids seen most often during the present study. During the day, *A. menesemus* hovers quietly in the deep shadows of reef crevices, but during late evening twilight emerges into the open. Throughout the night solitary individuals hover about 1 m above the coral. On several occasions after dark this cardinalfish struck at the silver barb on my otherwise dark spear: sometimes when this happened the spear was faintly illuminated by my partner's diving light, but other times moonlight provided the only illumination. At first morning light *A. menesemus* moves close to cover on the reef, and during morning twilight returns to its daytime shelter. When under cover during the day its coloration is relatively featureless, but when in the open at night distinctive fin markings appear (Figure 20a and b).

Fifty-nine specimens (114: 90-134 mm) were collected during day and night. Of the 14 that were speared from reef caves during late afternoon, only 2 had food in their stomachs—one contained an extensively digested piece of meat that probably was the remains of prey captured the previous night, whereas the other contained a relatively fresh xanthid crab that appeared to have been captured earlier that day. In comparison, 25 of 40 specimens collected at night, between 3 h after sunset and first morning light, had food in their stomachs—much of it fresh. Finally, of five specimens collected from caves during early morning, within 3 h after sunrise, four had food in their stomachs. Items in the 31 individuals containing identifiable material are listed in Table 20.

Two individuals that each contained just a single xanthid crab are the only ones that indicated exclusively benthic feeding; significantly, one of these was the lone individual, noted above, that appeared to have fed while under cover during the day. The other, collected in the open just 3 h after sunset, may also have taken its prey before leaving shelter in the evening. *A. menesemus* takes mostly free-swimming prey, presumably at its regular nocturnal station above the reef. Nevertheless, judging from the sand mixed with food in one individual collected at midnight, some prey are taken from the sea floor after dark.

CONCLUSION.—*Apogon menesemus* is a nocturnal predator that feeds mostly on free-swimming crustaceans.

Apogon snyderi Jordan and Evermann—*'upapalu*

This cardinalfish cooccurs with the very similar *A. menesemus,* above, but the two species remain at least partially segregated. During the day both species occupy the same caves, but *A. snyderi* is not so deep in the shadows and, in fact, frequently hovers at the entrances. Like *A. menesemus, A. snyderi* emerges into the open during evening twilight, but during the night stays closer to the sea floor; furthermore, whereas *A. menesemus* mostly remains over coral, *A. snyderi* tends to move over the sand patches within the reef and in the fringes of the more extensive sand areas adjacent to the reef. On several occasions at night, *A. snyderi* struck at the silver barb on my spear, just as described above for *A. menesemus. Apogon snyderi* does not have prominent nocturnal color features, as does *A. menesemus.* When over sand at night its body has a highly reflective bluish cast, also shown to a lesser extent by *A. menesemus,* but which is largely lost by both species soon after they move over coral or rocks.

Thirty specimens (96: 82-130 mm) were speared during day and night. All 3 that were taken from caves during the afternoon had empty stomachs, whereas of 24 collected in the open at night, between 2 h after sunset and first morning light, 22 had food in their stomachs. The remaining three were collected from caves during the 4 h after sunrise, and while two of these had food in their stomachs, the third was empty. Items in the 24 individuals containing identifiable material are listed in Table 21.

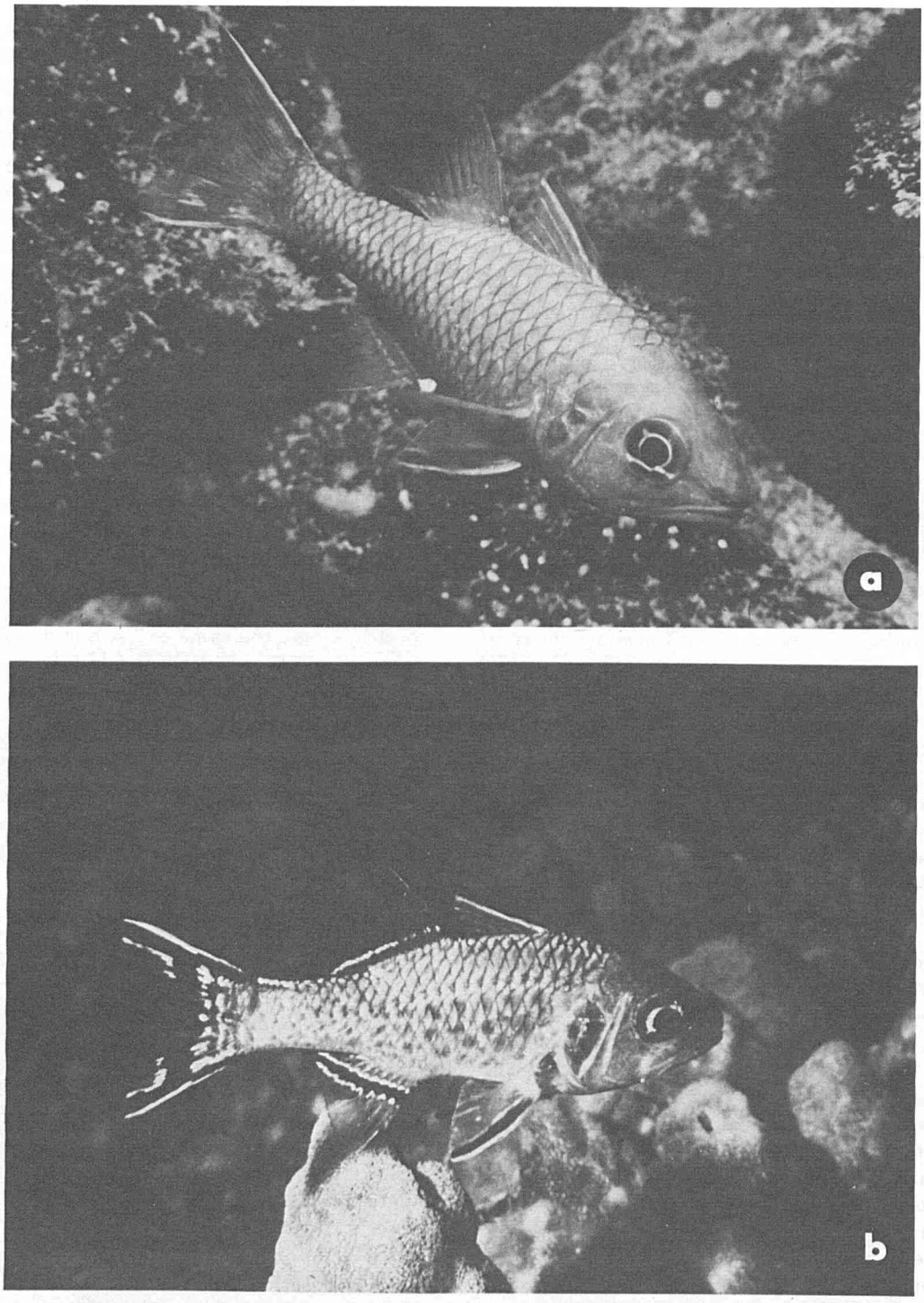


FIGURE 20.—*Apogon menesemus*, a cardinalfish: a, showing its diurnal coloration under a ledge during the day; b, showing its nocturnal coloration as it swims above the reef at night.

TABLE 20.—Food of *Apogon menesemus*.

Rank	Items	No. fish with this item (n = 31)	Mean percent of diet volume	Ranking index
1	Crab megalops	10	17.6	5.68
2	Decapod shrimps	11	15.7	5.57
3	Xanthid crabs	2	6.9	0.45
4	Mysids	3	2.9	0.28
5	Fish	1	2.0	0.07
6	Gammaridean amphipods	1	0.8	0.03
7	Isopods	1	0.2	<0.01
8	Copepods	2	0.1	<0.01
9	Gastropod larvae, echinospira	1	0.1	<0.01
Also, crustacean fragments		20	40.0	25.81
	Unidentified fragments	6	13.7	2.65

TABLE 21.—Food of *Apogon snyderi*.

Rank	Items	No. fish with this item (n = 24)	Mean percent of diet volume	Ranking index
1	Decapod shrimps	12	34.3	17.15
2	Xanthid crabs	6	14.6	3.65
3	Crab megalops	4	7.5	1.25
4	Fish	2	5.6	0.47
5	Mysids	2	2.1	0.18
6	Hippid crabs	1	4.2	0.18
7	Polychaetes	1	2.9	0.12
8	Copepods	1	1.3	0.05
9	Gammaridean amphipods	1	1.3	0.05
10	Sipunculid introverts	1	0.2	<0.01
Also, crustacean fragments		12	25.4	12.70
	Unidentified fragments	1	0.6	0.03

The diet of *A. snyderi,* compared with that of *A. menesemus,* includes a greater proportion of benthic organisms, especially forms from sandy bottom, like hippid crabs. Nevertheless, many of the prey of *A. snyderi* are free-swimming forms that may or may not have been in the water column when captured. The major item, decapod shrimps, were mostly in their planktonic larval stage.

CONCLUSION.—*Apogon snyderi* is a nocturnal predator that feeds on both free-swimming and benthic forms, mostly crustaceans.

General Remarks on Cardinalfishes

Cardinalfishes are widely recognized as being nocturnal. For example, Starck and Davis (1966) reported that all of the apogonids they studied in Florida Keys are nocturnal, and Randall (1967) came to the same conclusion for species in the West Indies; Randall provided food-habit data on two forms, *Apogon conklini* and *A. maculatus,* both of which prey primarily on plankton.

In the Gulf of California, *A. retrosella,* a relatively small nocturnal species (mostly <100 mm long), aggregates above the reef at night, preys on plankton, and its aggregations are more compact under moonlight than on dark nights (Hobson, 1965, 1968a). Although the relatively large *A. menesemus* is solitary when feeding on free-swimming prey above Kona reefs, it remains within about 1 m of the reef, never far from cover.

Another apogonid occasionally seen in Kona, *A. maculiferus,* has behavior more like that of *A. retrosella* in the Gulf of California. *Apogon maculiferus* is abundant on some Hawaiian reefs and attains a length of about 150 mm (Gosline and Brock, 1960). It was not abundant during this study, however, and all those seen apparently were juveniles that ranged between about 20 and 60 mm long. On nights of bright moonlight these small individuals were in aggregations 2 to 3 m above the reef; however, on dark nights they ranged even higher in the water column, their aggregations were more loosely formed, and many of them were solitary. Significantly, limited observations indicate that juveniles of both *A. menesemus* and *A. snyderi* (< 50 mm long) behave

more like these small individuals of *A. maculiferus* than they do like the adults of their own species, so this behavior may be characteristic only of the smaller representatives of all three species.

Finally, a fourth apogonid, *Pseudamiops gracilicauda,* is relatively numerous in Kona, but does not seem to grow longer than about 30 mm. Being such a small species, *P. gracilicauda* generally went unnoticed by me and, in fact, was seen only on dark nights when solitary individuals hovered 1 to 2 m above the reef.

Suyehiro (1942), Hiatt and Strasburg (1960), and Hobson (1965), all reported that certain apogonids cease to feed sometime during reproductive activity. Perhaps this phenomenon accounts for the relatively high incidence of empty stomachs at night in *A. menesemus* from Kona (15 of 40), especially considering that species of other nocturnal groups with similar diets, like the various holocentrids (see above), are almost always full of food at night.

E. H. Chave, University of Hawaii, is currently working on the ecology of Hawaiian apogonids.

Family Carangidae: jacks

The jacks are prominent fishes on Hawaiian reefs, but although many species were seen occasionally during this study, only one, presented below, was observed regularly.

Caranx melampygus Cuvier—blue ulua, *'omilu*

This jack (Figure 21), attains a length of about 1 m in Hawaii (Gosline and Brock, 1960), but most of those present in Kona during this study were less than half this size. During the day it usually is solitary, or in groups of several individuals. Typically, it swims actively about 1 m above the reef in a manner that suggests it is patrolling over a relatively large area. Frequently several of these jacks accompany the large piscivorous goatfish, *Parupeneus chryserydros* (see account for this species, below), probably to capture prey that are driven out of hiding as the goatfish probes the substratum. This jack swims over the reef throughout the day, but occurs there most frequently during early morning and late afternoon

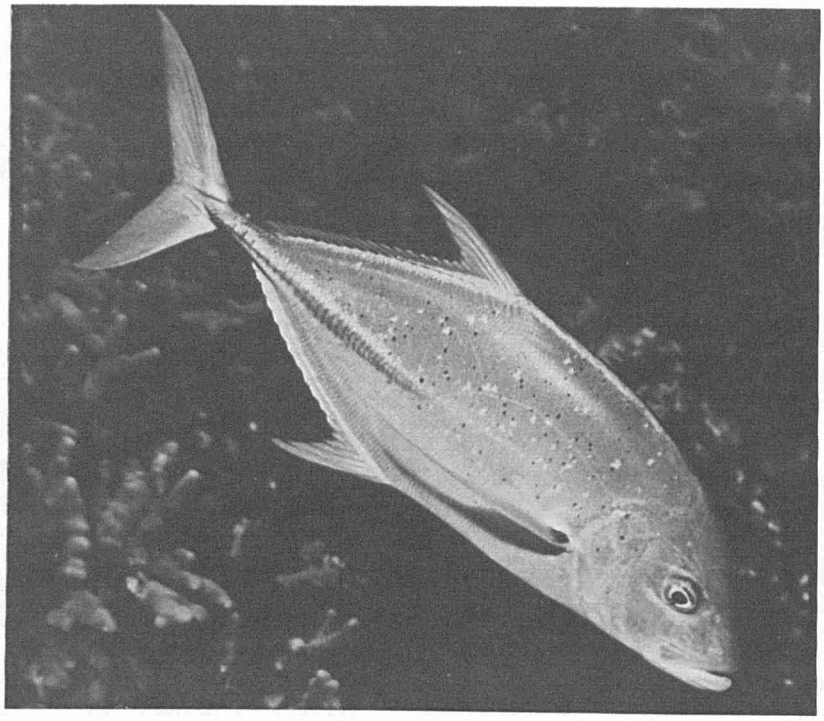


FIGURE 21.—*Caranx melampygus,* a jack, swimming close above the reef during the day.

or evening. It was only occasionally seen at night, perhaps because it avoided our diving lights after dark.

Six specimens (337: 245-570 mm) were collected at various times of the day. The only one (248 mm) that contained relatively fresh prey (three larval fishes, about 10 mm long, and a number of mysids) was collected 3 h after sunrise. A second individual (315 mm), taken shortly after noon, contained in its stomach, an unidentified fish (about 80 mm) and a shrimp, both moderately digested. Three other individuals (245-330 mm) were collected late in the afternoon, and their stomachs contained well-digested fragments—in at least one, the fragments of a fish. The last specimen (570 mm) behaved as if sick when speared early in the afternoon, and its gut was empty. Hiatt and Strasburg (1960) found only fishes in the two specimens of this species that they examined from the Marshall Islands, as did Randall (1955) in the four specimens that he examined from the Gilbert Islands.

CONCLUSION.—*Caranx melampygus* preys on free-swimming fishes and crustaceans, probably most often early and late in the day.

General Remarks on Jacks

Jacks are major predators on many widespread tropical reefs (e.g. Marshall Islands: Hiatt and Strasburg, 1960; Gulf of California: Hobson, 1965, 1968a; Florida Keys: Starck and Davis, 1966; West Indies: Randall, 1967). The larger piscivorous jacks, like *Caranx hippos caninus,* are primarily crepuscular in the Gulf of California (Hobson, 1965, 1968a) and in the Florida Keys (Starck and Davis, 1966).

Family Lutjanidae: snappers

As is true of the sea basses, Hawaiian inshore reefs lack native species of snappers, a family whose members are prominent on shallowwater reefs elsewhere in the tropical Pacific (Gosline and Brock, 1960; Randall and Brock, 1960). Only one species of this family was seen regularly on the Kona study reefs during this project.

Aphareus furcatus (Lacépède)—*gurutsu*

During the day this solitary predator swims slowly, 1 to 2 m above the reef, with never more than a few individuals in any one place. It was not seen at night during this study, perhaps because it avoided our lights. Only once did I see one attack prey: 5 min before sunrise this individual suddenly broke from its patrolling attitude 2 m above the reef and dived among a cluster of small fishes, mostly pomacentrids, that were in the process of emerging from their nocturnal shelters (see Hobson, 1972). The success of the strike was undetermined, but at the instant of attack all small fishes within a radius of about 15 m shot under cover.

Three specimens (253: 244-262 mm) were speared for study. One taken during midafternoon contained a *Plagiotremus goslinei,* a blenny that swims above the reef only in daylight (see account for this species, below); because this prey was relatively fresh, it almost certainly was captured earlier that day. Another *A. furcatus* collected during midafternoon contained moderately digested crab megalops and gammaridean amphipods; although megalops are more typically food of nocturnal predators, the relatively good condition of these small prey indicated they had been collected earlier that day. The third *A. furcatus,* speared during midmorning, was empty. Randall (1955) examined four specimens of this snapper in the Gilbert Islands, and the two with prey contained only fishes.

CONCLUSION.—*Aphareus furcatus* preys on free-swimming fishes and crustaceans during daylight. Its habits at night remain unknown.

General Remarks on Snappers

If *Aphareus furcatus* hunts prey mostly in daylight, it would seem an atypical lutjanid. Generally lutjanids are described as nocturnal fishes (e.g. Hobson, 1965, 1968a: Gulf of California; Starck and Davis, 1966: Florida Keys; Randall, 1967: West Indies).

The efforts that successfully introduced the sea bass *Cephalopholis argus* into Hawaiian waters (see account for that species, above) also included the snapper *Lutjanus vaigiensis*, which now too is well established in Kona. Although *L. vaigiensis* was not numerous in the study area during this work, one school was seen consistently during daylight on irregular visits to a location in Kealakekua Bay, and solitary individuals occasionally were encountered on the reef after dark. Thus, the habits of this fish appear to be similar to those of certain other species of *Lutjanus*

elsewhere; that is, it forms relatively inactive schools during the day, then disperses at nightfall and hunts prey after dark. This pattern is known for *L. argentiventris* in the Gulf of California (Hobson, 1965, 1968a), and for *L. griseus* and others in the tropical Atlantic (Starck and Davis, 1966). Randall and Brock (1960) reported predominantly nocturnal feeding by *L. vaigiensis* in Tahiti and often found this snapper in large aggregations during the day.

Family Sparidae: porgies

Monotaxis grandoculis (Forskål)—*mu*

In Kona, this porgy is most numerous near basalt reefs that are exposed to the prevailing sea. During the day it typically hovers 2 to 3 m above the reef, either in loose aggregations of 4 to 10 fish, or as solitary individuals. When congregated, most individuals display broad bars on their sides dorsally; although this same color pattern occurs frequently in solitary fish, these often are overall pale grey. Those I observed in Kona during the day always seemed inactive; however, Hiatt and Strasburg (1960) reported individuals in the Marshall Islands excavating prey buried in the sand, presumably during daylight. In Kona, *M. grandoculis* disperses from its daytime assemblages at nightfall and forages as solitary individuals throughout the night. After dark, many move into shallower water than is frequented by the species in daylight. The nocturnally active individuals sometimes show the barred color pattern but are most often plain grey (Figure 22).

Of five specimens (312: 244-397 mm) speared during day and night, one that was taken from an aggregation late in the afternoon was empty, whereas all four that were speared at night (later than 4 h after sunset and before first morning light) were full of food, as listed in Table 22.

Although the gut contents were relatively fresh, the shelled items had been reduced to crushed fragments—presumably by the large molarform jaw teeth of this fish.

Prey taken by this porgy in Kona are much the same as taken by the same species in the Marshall Islands (Hiatt and Strasburg, 1960) and Gilbert Islands (Randall, 1955).

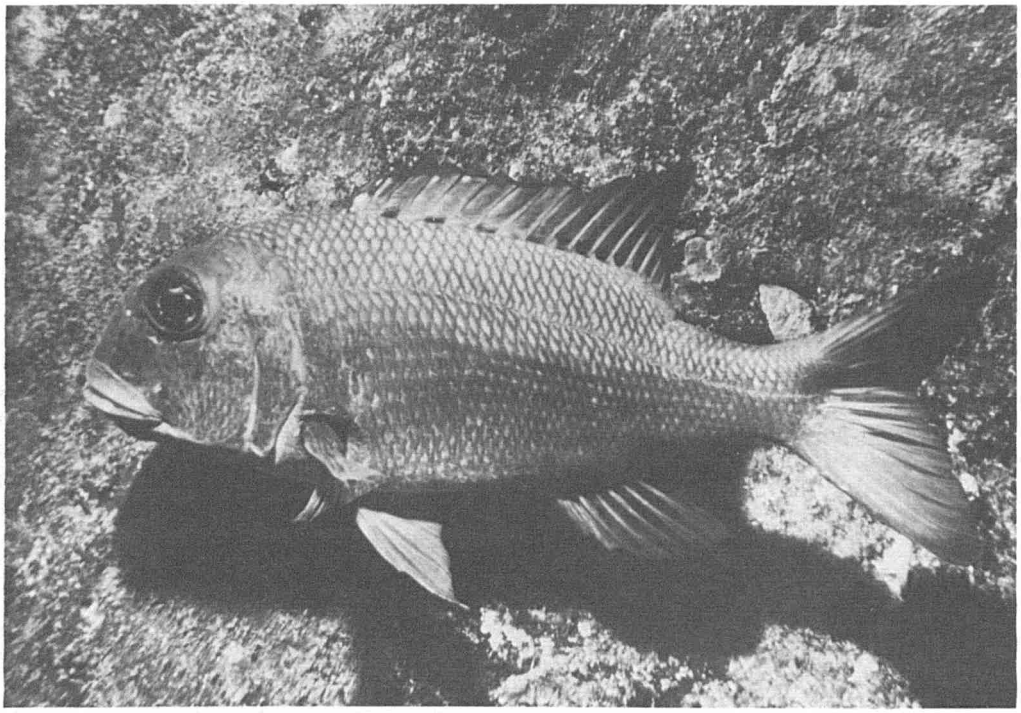


FIGURE 22.—*Monotaxis grandoculis*, a porgy, showing its plain grey coloration as it swims close to the reef at night.

TABLE 22.—Food of *Monotaxis grandoculis*.

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Prosobranch gastropods	4	21.3	21.30
2	Ophiuroids	3	27.1	20.33
3	Echinoids	3	21.3	15.98
4	Opisthobranch gastropods	2	11.8	5.90
5	Pagurid crabs	2	3.8	1.90
6	Polychaetes	1	3.8	0.95
7	Brachyuran crabs	1	2.5	0.63
8	Tunicates	1	2.5	0.63
9	Egg masses (unident.)	1	1.3	0.33
10	Holothurians	1	0.8	0.20
Also, crustacean fragments		1	2.5	0.63
	Algal fragments	1	1.3	0.33

CONCLUSION.—*Monotaxis grandoculis* is a nocturnal predator that feeds on benthic invertebrates, most of them heavily shelled.

General Remarks on Porgies

Porgies are closely related to the snappers, most of which seem to be mainly nocturnal. Nevertheless, porgies have been reported as diurnal, for example species of *Archosargus, Diplodus,* and *Calamus* in the tropical Atlantic (Randall, 1967). Still, Starck and Davis (1966) recognized that species of *Calamus* in Florida may also feed at night. Diurnal habits in porgies may be attributed to their habit of excavating buried prey, which makes available to them certain nocturnal forms that have concealed themselves in the sand during daylight.

Family Mullidae: goatfishes

Mulloidichthys auriflamma (Forskål)—*weke'ula*

During the day this goatfish, which is relatively numerous in Kona, hovers in schools above the reef, or (occasionally) under ledges. Individuals recognized by distinguishing marks occurred in schools at the same locations each day, even though these schools disperse at nightfall. After dark, solitary or in small groups, this species probes with its barbels in the sandy areas adjacent to the reef, and in some of the larger sand patches on the reef. When illuminated by a diving light at night, it often shows a deep reddish hue that seems to be a reaction to the light, not a nocturnal coloration.

Of the 22 individuals (170: 110-235 mm) speared during day and night, all 12 collected from schools during the afternoon were either empty or contained only well-digested fragments, whereas of the 10 collected at night (later than 3 h after sunset and before sunrise), all contained food, including fresh material, as listed in Table 23.

Thus my observations concur with those of Gosline and Brock (1960), who reported that *M. auriflamma* does not feed during the day, but instead schools quietly in certain established areas and then disperses to forage at night.

Although crab megalops, a primary food, are a major element of the plankton, most of those captured by this goatfish probably were taken from the sand.

CONCLUSION.—*Mulloidichtys auriflamma* is a nocturnal predator that feeds on invertebrates that live in the sand.

Mulloidichthys samoensis (Günther)—*weke 'a'a*

This goatfish, widespread in Kona, often hovers in quiet schools over the reef during the day, where it looks much like *M. auriflamma,* above. Although *M. samoensis* is a more elongated fish, the two must be seen together before this distinction is obvious. Sometimes the two species school together, but more often they are segregated. Frequently instead of schooling during the day, *M. samoensis,* but not *M. auriflamma,* moves as solitary individuals or in small groups over sand patches on the reef, and there actively probes with its barbels in the sediment. These active individuals have a color pattern distinct from that of relatively inactive conspecifics in schools. When schooling, *M. samoensis* has a prominent yellow stripe running from eye to tail along its upper sides, as does *M. auriflamma* in similar schools (Figure 23a); however, this stripe is not present (or at least is indistinct) when *M. samoensis* actively

TABLE 23.—Food of *Mulloidichthys auriflamma*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Crab megalops	6	11.5	6.90
2	Ophiuroids	4	14.5	5.80
3	Polychaetes	4	11.7	4.68
4	Xanthid crabs	6	7.0	4.20
5	Prosobranch gastropods	7	4.7	3.29
6	Echinoids	6	4.7	2.82
7	Gammaridean amphipods	5	1.3	0.65
8	Isopods	4	1.1	0.44
9	Ostracods	2	0.6	0.12
10	Sipunculid introverts	1	0.5	0.05
11	Pelycypods	1	0.5	0.05
12	Penaeid shrimps	1	0.5	0.05
13	Portunid crabs	1	0.2	0.02
Also, crustacean fragments		4	8.5	3.40
	Unidentified fragments	2	12.0	2.40
	Algal fragments	1	1.0	0.10
	Sand, foraminiferans, and debris	7	19.7	13.79

forages on the reef, it being replaced by a black spot on the fish's side, below the dorsal fin (Figure 23b).

At nightfall, those individuals of *M. samoensis* that had been hovering over the reef in quiet schools disperse. After dark the species not only continues the activity that some members had pursued over reef sand patches in daylight, but also extends this activity in some areas farther out over the more extensive sandy areas adjacent to the reef. When illuminated by a light at night, *M. samoensis* frequently displays a color pattern of red blotches that seems to be a response to the light, rather than being a nocturnal color feature. Its coloration at night is as described above for foraging individuals in daylight. After a night of foraging, many individuals regroup in the morning, forming schools that reappear in the same locations each day.

Twenty-three specimens (182: 136-283 mm) were speared during day and night. Of four taken during afternoons as they probed sand patches on the reef, swimming in small groups or as individuals, two had full stomachs that included relatively fresh prey; the other two contained only debris. Of three individuals taken while they hovered in schools over the reef during the afternoon, one had an empty stomach, and the other two contained only well-digested fragments. Contrasting data were provided by 16 specimens speared as they actively probed in sand patches on the reef during the 2 h immediately before first morning light, and during the first 30 min of morning twilight. Of these, 11 had full stomachs, including much fresh material, 2 contained only bits of debris, and only 3 were empty. Items in the 13 individuals containing identifiable prey are listed in Table 24.

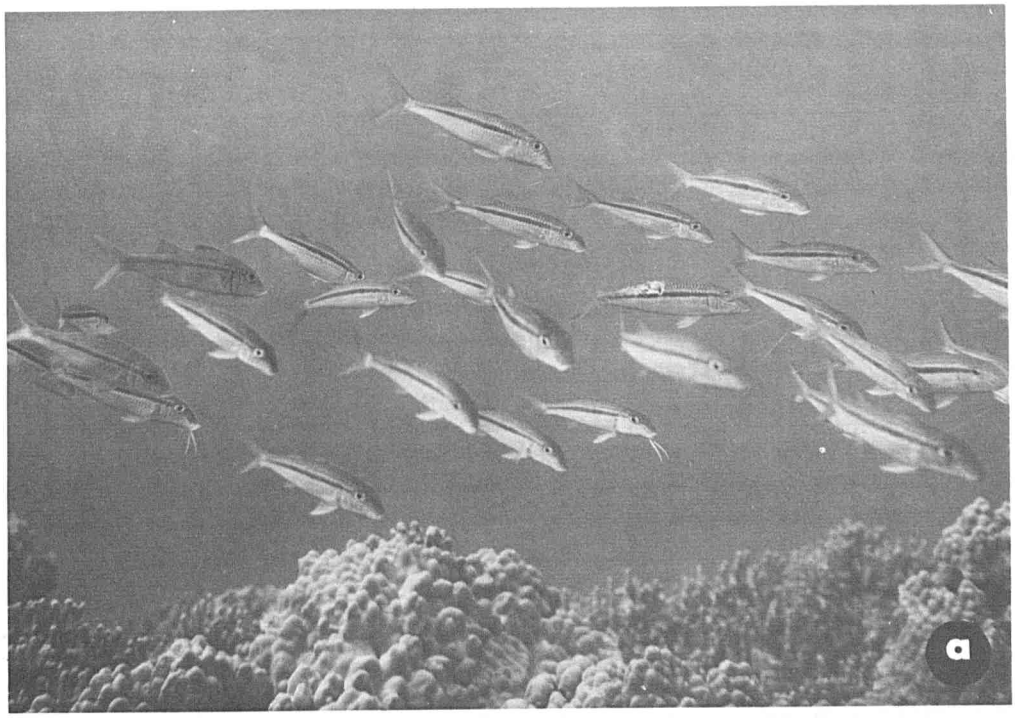
No obvious difference was noted between prey taken during day and night although pertinent data are too few for meaningful comparison. Hiatt and Strasburg (1960) reported that fishes are an important food of this goatfish in the Marshall Islands. Otherwise, they listed foods similar to those taken by the species in Kona.

CONCLUSION.—*Mulloidichthys samoensis* preys on sand-dwelling invertebrates, mostly at night, but to some extent during the day.

Parupeneus multifasciatus (Quoy and Gaimard) —*moano*

This is the most numerous and widespread goatfish on Kona reefs. During the day solitary individuals and groups of two or three actively probe with their barbels among cracks and crevices on the reef, especially in pockets where sand and debris have accumulated. This species is active through twilight, but generally appears inactive after dark, when solitary individuals rest in exposed locations on the reef. To some extent these immobile nocturnal attitudes may be influenced by the diving light, but not to the extent indicated for *P. bifasciatus*, below; certainly the blotched red color pattern often displayed at this time is a reaction to the light. On nights of bright moonlight, at least some individuals of *P. multifasciatus* swim over the reef.

Thirty specimens (162: 125-212 mm) were speared during day and night. Of 14 collected during the hour immediately before first morning



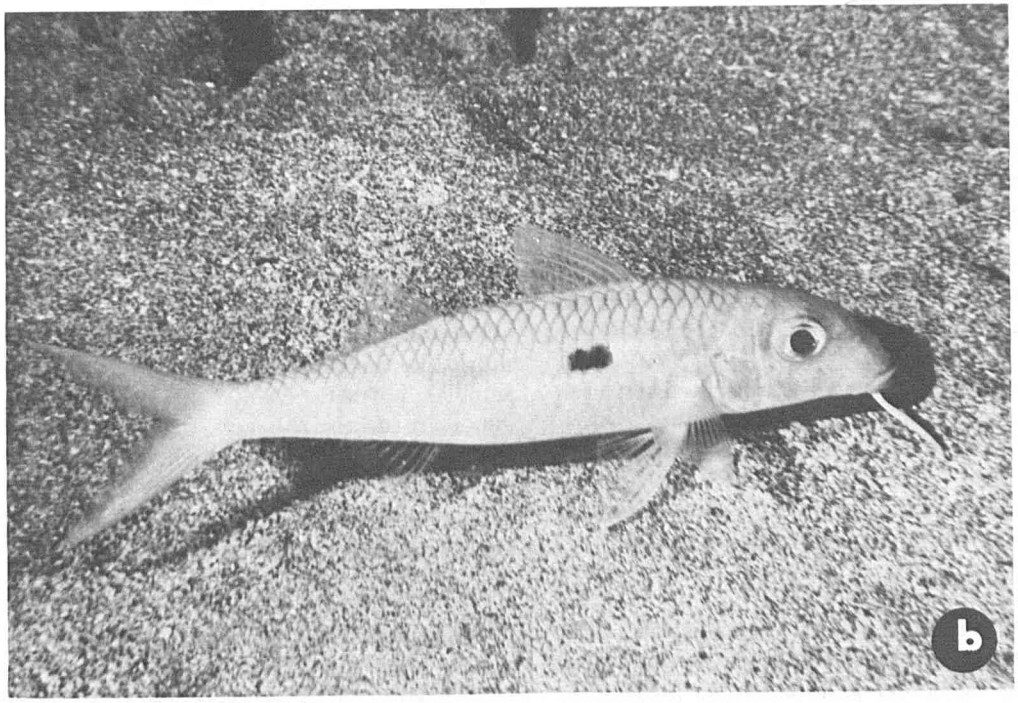


FIGURE 23.—*Mulloidichthys samoensis*, a goatfish: a, with the coloration shown when schooling during the day; b, with the coloration shown when feeding as a solitary individual or in small groups during both day and night.

TABLE 24.—Food of *Mulloidichthys samoensis*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Pelecypods	7	10.0	5.39
2	Polychaetes	5	11.2	4.31
3	Gammaridean amphipods	7	6.7	3.61
4	Prosobranch gastropods	6	3.1	1.43
5	Sipunculid introverts	3	5.4	1.25
6	Crab megalops	3	3.1	0.72
7	Isopods	3	2.8	0.65
8	Hippid crabs	1	0.8	0.06
9	Echinoids	1	0.8	0.06
10	Xanthid crabs	1	0.4	0.03
11	Shrimps	1	0.2	0.02
Also, crustacean fragments		5	7.1	2.73
	Unidentified fragments	3	11.6	2.68
	Sand and debris, including foraminiferans	13	36.8	36.80

TABLE 25.—Food of *Parupeneus multifasciatus*.

Rank	Items	No. fish with this item (n = 18)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	14	30.6	23.80
2	Caridean shrimps	8	15.4	6.84
3	Crab megalops	5	8.6	2.39
4	Prosobranch gastropods	3	1.8	0.30
5	Tanaids	2	0.6	0.07
6	Gammaridean amphipods	2	0.4	0.04
7	Stenopid shrimps	1	0.6	0.03
8	Ostracod	1	0.1	0.01
Also, crustacean fragments		14	29.4	22.87
	Unidentified fragments	1	0.8	0.04
	Debris	7	11.7	4.55

light, and through morning twilight, the stomachs of 12 were empty, but the other 2 contained prey in varying stages of digestion that appeared to have been taken during the night (one night with, the other without, moonlight). In contrast, all 16 specimens speared on the reef during the afternoon contained prey in varying stages of digestion, including fresh material. Items in the 18 containing identifiable material are listed in Table 25.

No obvious difference in diet was noted between the 2 individuals of *P. multifasciatus* that apparently had captured their prey at night and the 14 that had been feeding in daylight; however, the data are too few for a meaningful comparison.

Juveniles of *P. multifasciatus* sometimes aggregate up in the water column where plankton abounds, apparently feeding on these organisms, but none of these individuals were collected. The relatively high incidence of crab megalops in the diet of this and other bottom-feeding goatfishes may reflect some predation on free-swimming forms in the water column, but I believe that at least most of these megalops were taken off the sea floor.

CONCLUSION.—*Parupeneus multifasciatus* is primarily a diurnal predator that takes benthic crustaceans.

Parupeneus bifasciatus (Lacépède)—*munu*

This goatfish, which exceeds 300 mm when fully grown, is especially numerous among basalt boulders—frequently solitary, but also in groups of two or three. In daylight, its actions appear much like those of *P. multifasciatus*, which it resembles, but after dark, when *P. multifasciatus* generally rests on the reefs, *P. bifasciatus* usually moves about. Nevertheless, when *P. bifasciatus* is illuminated by the diving light it often settles immobile onto the reef—an action that complicates assessing its nocturnal activity. Like *P. multifasciatus*, *P. bifasciatus* often displays at this time a blotched red-colored pattern that seems to be a response to the diving light.

Twenty-seven specimens (229: 164-300 mm) were speared during day and night. Of 11 taken as they swam close to the reef during early morning (between first light and 3 h after sunrise), the stomachs of 2 were empty, but the other 9 contained prey in varying stages of digestion, some of

it fresh. Similarly, of 12 individuals collected as they swam close to the reef during afternoons, only 1 had an empty stomach, whereas the other 11 contained prey in varying stages of digestion, some of it fresh. Finally, of four specimens speared at night (between 4 and 5 h after sunset) the stomach of one was empty, but the other three contained prey in varying stages of digestion, some of it fresh.

These data indicate that *P. bifasciatus* feeds regularly during both day and night. Recognizing that the contrasting conditions under which it hunts may be reflected in the composition of its diet, I attempted to distinguish prey that had been taken by day from that taken at night. Although, undoubtedly there is overlap, generally specimens collected during the night and early morning should contain mostly prey captured after dark, whereas specimens taken during afternoons should contain mostly prey taken in daylight.

Thus, the 12 *P. bifasciatus* taken during the night and early morning with identifiable material in their stomachs presumably represent mostly nocturnal feeding. Items in these individuals are listed in Table 26. Using the same rationale, diurnal feeding presumably is reflected in the 11 *P. bifasciatus* collected with identifiable material in their stomachs during afternoons. Items in these individuals are listed in Table 26.

Although xanthid crabs are the major prey day and night, they assume greater relative importance in daylight, as do caridean shrimps. Xanthids and carideans are largely under cover in daylight, where they may be especially vulnerable to this predator's probing actions. Crab megalops become increasingly important to this goatfish at night, but the circumstances surrounding their capture remain uncertain; megalops are the major prey of many nocturnal planktivores, such as *Myripristis* spp. (see accounts for these species, above), but are also taken day and night by predators like certain goatfishes that probe the sea floor.

Based on the above data, fishes seem to be more available as prey to *P. bifasciatus* at night. Prey fishes that could be identified were blennies and pomacentrids, which are diurnal fishes that take cover after dark. Apparently *P. bifasciatus* is adapted to capture these resting diurnal fishes at night, but is less effective in capturing the fishes that are under cover during daylight.

CONCLUSION.—*Parupeneus bifasciatus* hunts prey on the reef during both day and night. Adult crabs and shrimps are more important as prey during the day than at night, whereas the reverse is true of fishes and crab megalops.

Parupeneus porphyreus (Jenkins)—*kumu*

This is the most numerous goatfish on some Hawaiian reefs (Gosline and Brock, 1960), but

TABLE 26.—Food of *Parupeneus bifasciatus*.

Nighttime Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	10	29.0	24.17
2	Fish	6	17.0	8.50
3	Crab megalops	5	19.4	8.08
4	Caridean shrimps	7	8.0	4.67
5	Octopods	2	3.9	0.65
6	Oxyrhynchid crabs	2	1.7	0.28
7	Prosobranch gastropods	2	0.6	0.10
8	Polychaetes	1	0.4	0.03
9	Gammaridean amphipods	1	0.3	0.03
Also, crustacean fragments		7	15.5	9.04
	Debris	2	4.2	0.70
Daytime Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	9	43.3	35.43
2	Caridean shrimps	9	15.5	12.68
3	Crab megalops	3	3.5	0.95
4	Octopods	1	7.1	0.65
5	Grapsid crabs	1	3.9	0.35
6	Oxyrhynchid crabs	1	1.1	0.10
7	Fish	1	0.7	0.06
8	Gammaridean amphipods	2	0.2	0.04
Also, crustacean fragments		8	24.7	17.96

there are relatively few in the Kona study area. During the day this species stays close to cover, where it usually occurs in small groups under ledges. At night solitary individuals are active close among rocks and coral on the reef.

Of the 11 specimens (157: 137-173 mm) collected, 6 speared close to reef crevices late in the afternoon either were empty or contained only a few well-digested fragments, whereas all 5 collected in the same places within 1 h after sunrise had stomachs full of prey, some of it fresh, as listed in Table 27.

CONCLUSION.—*Parupeneus porphyreus* is a nocturnal predator that feeds mostly on benthic crustaceans.

Parupeneus chryserydros (Lacépède)—*moano kea*

The scientific name of this goatfish remains uncertain. I follow Gosline and Brock (1960) in recognizing the nominal *P. chryserydros,* even though some authors (e.g. Lachner, 1960) refer this form to *P. cyclostomus* (Lacépède). Growing to about 600 mm long (Gosline and Brock, 1960), *P. chryserydros* is the largest of the goatfishes occurring regularly on Kona reefs.

During the day, solitary individuals or groups of two to five move over the reef, where their exceptionally long barbels work through the covering on rocky substrata. More often than not, groups of *P. chryserydros* are accompanied by a single jack, *Caranx melampygus,* which follows close behind them. For 1 mo I recorded all sightings of *P. chryserydros* that swam in groups of two or more, and of 24 such groups, 16 were accompanied by a jack. Usually solitary individuals of this goatfish are not thus accompanied, but this too was seen four times during the month. Clearly, it is the jack that maintains the association, probably as a tactic to capture prey driven from cover as the foraging goatfish disturb the substratum. Apparently the jack finds this advantage only with *P. chryserydros,* as it was not seen similarly following other species. Titcomb and Pukui (1952) listed many ancient Hawaiian fish names which they were unable to associate with species recognized today. One of these, *moano ukali ulua,* translates as "moano with ulua following," and probably refers to *P. chryserydros.* Whereas the adults of *P. chryserydros* are followed by the jack, the juveniles of this goatfish frequently swim close beneath various labrids, especially *Thalassoma duperrey,* and here it is the goatfish that maintains the associations, though to what advantage I do not know.

Of the 20 specimens (261: 123-363 mm) collected, all 3 that were speared as they rested on the reef at night (between 4 h after sunset and first morning light) had empty guts, whereas 15 of 17 taken as they swam close to the reef at various times of the day (between midmorning and late afternoon) had prey in their stomachs, and only the other 2 were empty.

Fish were the major item, occurring in 13 of the 15 individuals that contained food (mean percent of diet volume: 83.1; ranking index: 72.02). Other food items were: xanthid crabs in two individuals (mean percent of diet volume: 8.3; ranking index: 1.11), caridean shrimps in one (mean percent of diet volume: 1.3; ranking index: 0.09), and unidentified fragments in two (mean percent of diet volume: 7.3; ranking index: 0.97).

The fishes in the diet ranged between 25 and 102 mm long, and included the following species: *Abudefduf imparipennis* (1), *Cirrhitops fasciatus* (2), *Istiblennius gibbifrons* (1), *Plagiotremus goslinei* (1), *Cirripectus* sp. (4), and a labrid (1). All of these are diurnal fishes that swim close to the reef in daylight, but take cover when a predator approaches. Judging by how *P. chryserydros* feeds,

TABLE 27.—Food of *Parupeneus porphyreus.*

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	5	65.2	65.20
2	Hippid crabs	1	10.0	2.00
3	Caridean shrimps	1	2.0	0.40
4	Prosobranch gastropods	1	0.2	0.04
5	Chitons	1	0.2	0.04
6	Gammaridean amphipods	1	0.2	0.04
Also, crustacean fragments		3	21.2	12.72
	Debris	1	1.0	0.20

small fishes that have taken shelter on its approach probably are detected and even driven out from under cover by the exceptionally long barbels of this goatfish. If the probing barbels do in fact drive small fishes from their hiding places, this would account for the behavior of the jacks that follow them, described above. These same prey fishes also shelter themselves at night when they are inactive, so one might ask why this goatfish does not hunt for them at that time too. As reported above, *P. bifasciatus* preys on some of these same fishes (pomacentrids and blennies) when they are inactive under shelter at night. But capturing a relatively inert diurnal fish that is resting under cover after dark probably presents different problems for a predator than capturing an alert fish that has taken refuge from some specific threat in daylight. It appears that *P. bifasciatus* is adapted to taking these fishes when they rest under cover at night, whereas *P. chryserydros* is adapted to take them when they seek shelter in daylight. After dark, *P. chryserydros* is inactive, resting under reef cover (Figure 24).

Parupeneus cyclostomus in the Marshall Islands, which is closely related to *P. chryserydros,* if not conspecific, was reported by Hiatt and Strasburg (1960), on the basis of 16 specimens, to be an "active feeder on small benthonic fishes," but may prey more heavily on crustaceans than does the Hawaiian form.

CONCLUSION.—*Parupeneus chryserydros* is a diurnal predator that feeds mostly on small fishes.

General Remarks on Goatfishes

Despite their superficial similarity, the various goatfishes behave distinctively. Some, such as *Mulloidichthys auriflamma* and *Parupeneus porphyreus,* are primarily nocturnal; others, including *P. chryserydros* and *P. multifasciatus,* are mostly diurnal; and still others, like *P. bifasciatus* and *M. samoensis,* regularly hunt prey during both day and night. One might suppose that fishes which probe the sea floor for food would be indifferent to changes associated with day and night, but obviously this is not so. Whether a given species of goatfish is primarily diurnal or nocturnal probably relates to the differential day-night habits of its specific prey. That some goatfishes are

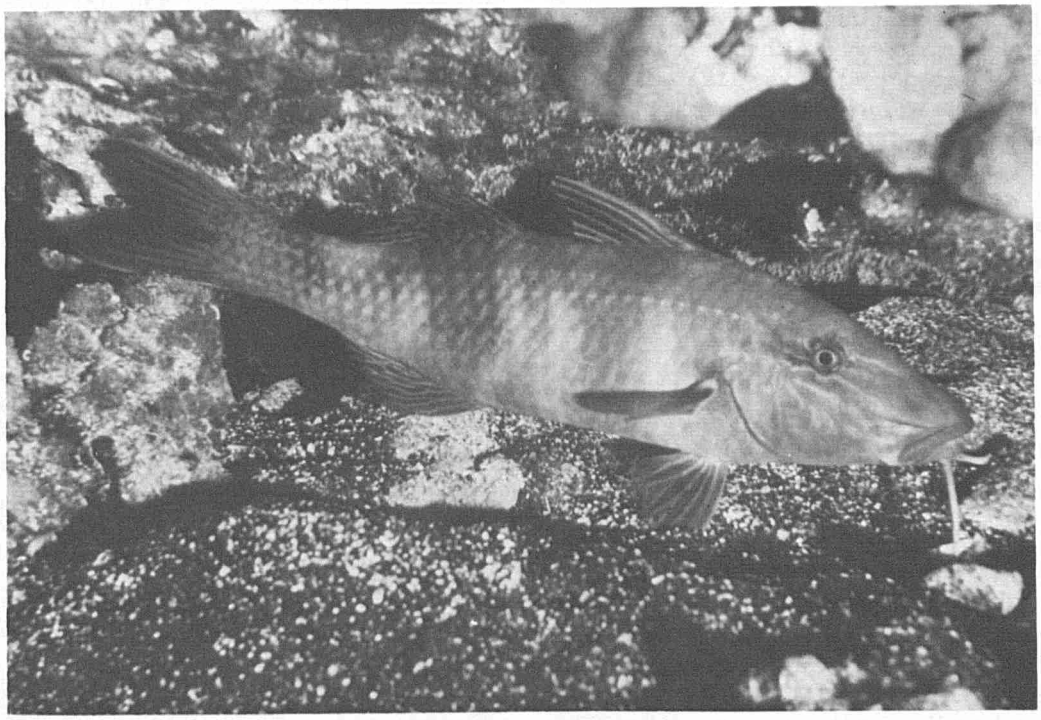


FIGURE 24.—*Parupeneus chryserydros,* a goatfish, resting under a ledge at night, with its exceptionally long chin barbels spread out before it.

nocturnal, whereas other are diurnal, is also recognized from other seas. In Florida, Starck and Davis (1966) suspected that *Mulloidichthys martinicus* feeds at night, whereas they recognized diurnal feeding habits in *Pseudupeneus maculatus*. Longley and Hildebrand (1941), as well as Collette and Talbot (1972), also regarded *M. martinicus* as nocturnal and *P. maculatus* as diurnal. Randall (1967) reported that *M. martinicus* feeds by day as well as night, and described a diet much like that of the two species of *Mulloidichthys* from Kona.

Family Kyphosidae: sea chubs

Kyphosus cinerascens Forskål—*nenue*

In Kona, *K. cinerascens* is most numerous where a basalt reef face confronts the prevailing swell in water deeper than about 8 m. Often over 500 mm long, this fish is active throughout the day—usually in groups of up to 10 or more individuals, and often swimming high in the water column. At night, solitary individuals swimming above the sea floor are often encountered in the same areas.

All three specimens (205: 166-250 mm) collected for study had guts full of a wide variety of benthic algae exclusively. Although two of these fish were taken during midday, the other was taken at night, within 1 h before first morning light. No sedimentary material was mixed in these gut contents, indicating that the algae had been bitten, not scraped, off the rocks, or else had been taken as fragments drifting in mid-water. Hiatt and Strasburg (1960) found the same gut contents in specimens from the Marshall Islands.

CONCLUSION.—*Kyphosus cinerascens* feeds during the day, cropping algae from rocks or taking them as drifting algal fragments. Its nocturnal habits remain uncertain.

General Remarks on Sea Chubs

Sea chubs generally are described as diurnal herbivores (e.g. Longley and Hildebrand, 1941; Starck and Davis, 1966; Randall, 1967). Smith (1907) reported crabs and bivalved mollusks among algae in the diet of *Kyphosus sectatrix* in the Atlantic Ocean, but these items probably were taken incidentally with the algae. Randall (1967) found only algae and a bit of sea grass in *K. sectatrix* from the West Indies. Starck and Davis (1966) reported that *K. incisor* rests in sheltered locations on Floridian reefs at night after having fed on drifting sargassum at the water's surface during the day. In the East Indies, however, William N. McFarland, Cornell University (pers. commun.) observed kyphosids active at night.

Family Chaetodontidae: angelfishes and butterflyfishes

The chaetodontids comprise two distinct groups: the angelfishes, subfamily Pomacanthinae; and the butterflyfishes, subfamily Chaetodontinae. Of the species treated below, the first two are angelfishes, the remainder are butterflyfishes.

Holacanthus arcuatus Gray—angelfish

This angelfish is sparsely distributed on Kona reefs, but being relatively large and distinctive is readily noticed where it occurs. Usually solitary or paired, it swims close among rock ledges and boulders at depths below about 8 m. During the day it picks material from the surface of rocks, but was not seen active at night.

Six specimens (136: 123-150 mm) were speared during afternoons, and all had full stomachs. They had fed almost exclusively on sponges (mean percent of diet volume and ranking index: 98.3). The only other items—algae and hydroids—probably were taken incidentally with the sponges.

CONCLUSION.—*Holacanthus arcuatus* is a diurnal species that feeds on sponges.

Centropyge potteri (Jordan and Metz)—potter's angelfish

An abundant species in coral-rich surroundings, this small angelfish behaves more like some of the damselfishes than it does other members of its family. A given individual limits its movements to restricted, well-defined locations close among fingerlike growths of the coral *Porites compressus*. During the day it swims about, picking at material growing over dead coral. At night it is alert, but secreted deep among the coral, apparently inactive.

All five specimens (80: 69-86 mm long) speared at various times during the day were full of food. Filamentous algae were the major identifiable item in the gut contents of all five (mean percent of

diet volume and ranking index: 41.7). There also was much unidentified debris, including sand and foraminiferans (mean percent of diet volume and ranking index: 42.3) that all five apparently had scraped from the substratum, and which probably included substantial nourishment in the form of organic detritus. The other components of the diet, all minor, were: diatoms in all five (mean percent of diet volume and ranking index: 3.3), sponges in all five (mean percent of diet volume and ranking index: 2.3), and harpacticoid copepods in one (mean percent of diet volume: 0.3; ranking index: 0.06).

CONCLUSION.—*Centropyge potteri* is a diurnal species that feeds on benthic algae and probably on organic detritus.

Forcipiger flavissimus Jordan and McGregor—*lau wiliwili nukunuku 'oi 'oi*

This long-snouted species (Figure 25a), numerous in Kona, and widespread throughout the Indo-Pacific region, was long called *F. longirostris*. Only recently has the distinction between *F. flavissimus* and the true *F. longirostris* (Figure 25b and c; treated below) been recognized (Wheeler, 1964; Randall and Caldwell, 1970). *Forcipiger flavissimus* occurs singly, or, more often, in groups of two or three. It is active throughout the day, especially over coral-rich reefs, where it picks at objects on a variety of surfaces. At night it is alert close among rock and coral cover but apparently inactive.

Twenty-seven specimens (116: 94-137 mm) were speared during day and night. Of 11 that were taken either at night (later than 4 h after sunset) or during early morning twilight, the stomachs of 9 were empty, and those of 2 (collected between 4 and 5 h after sunset) contained only a few well-digested fragments. In contrast, all 16 specimens taken at various times of the day had full stomachs, including relatively fresh material, as listed in Table 28.

Most of the unidentified fragments among the gut contents were relatively fresh pieces that this fish apparently had recently torn from the bodies of larger animals. The similarity of its elongated snout and mouth to a pair of needle-nosed pliers (Figure 26, lower) underscores the adaptiveness of its feeding apparatus to this habit. Even the gripping surfaces on the pliers are paralleled in the snout of *F. flavissimus* by expanded contact-surfaces in both upper and lower jaws—both of which carry multiple rows of short, inwardly curving teeth (Figure 27b).

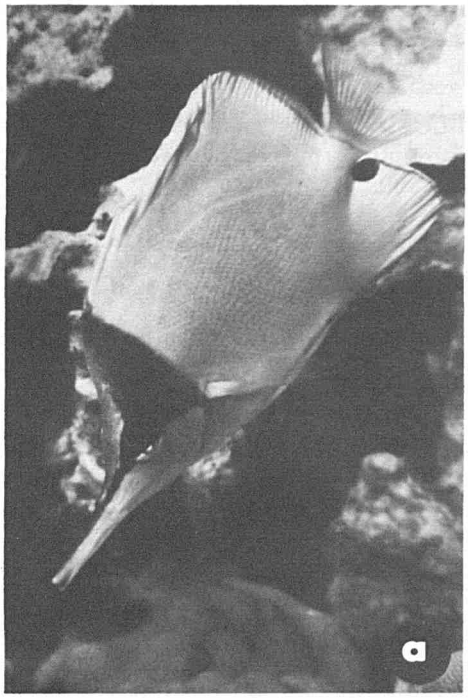
CONCLUSION.—*Forcipiger flavissimus* is a diurnal predator that tears pieces off larger benthic animals.

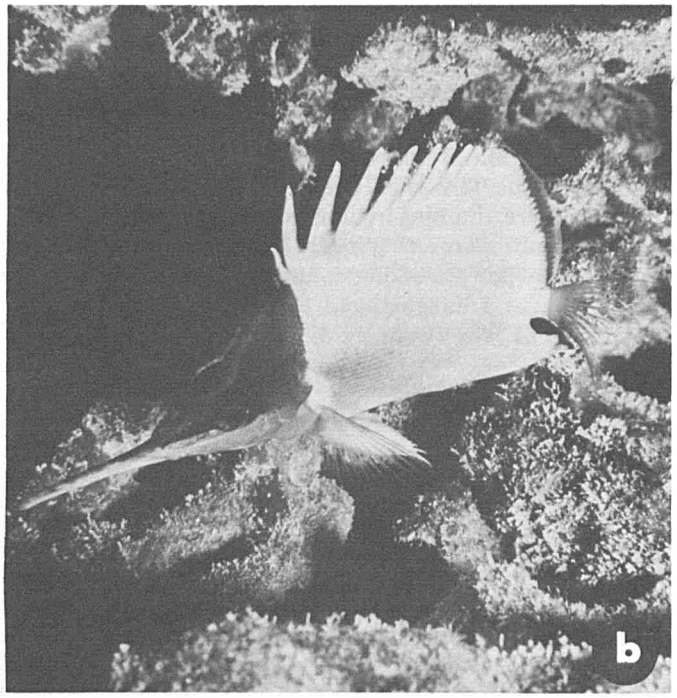
Forcipiger longirostris (Broussonet)—*lau wiliwili nukunuku 'oi 'oi*

This species is relatively numerous in Kona, although it appears to be rare elsewhere in Hawaii. Both color varieties—the yellow form (Figure 25b), which is essentially identical to *F. flavissimus*, discussed above, and the dark brown form (Figure 25c)—were observed regularly throughout the study. Like *F. flavissimus*, *F. longirostris* occurs typically over coral-rich reefs, and the two species overlap extensively; however, in areas where one is numerous, the other occurs less frequently. Despite this, I was unable to relate observed differences in relative numbers to specific habitat differences. *Forcipiger longirostris* is generally larger, but the most obvious morphological distinction between the two lies in the relative lengths of their snouts and in their different mouth structures (Figure 26). Less noticeable, but probably also related to feeding, *F. longirostris* has relatively larger eyes. Like its congener, *F. longirostris* is active on the reef by day, swimming singly or in groups of two or three, and probing with its long snout in cracks and crevices. At night it is close among cover of rocks or coral —alert, but apparently inactive.

Of the 26 specimens (136: 98-162 mm) collected, all 4 that were speared at night (later than 4 h after sunset and before first light in the morning) had empty stomachs, whereas the stomachs of all 22 collected at various times during the afternoon were full (including relatively fresh items). Decapod shrimps were the major prey, occurring in all 22 individuals that contained food (mean percent of diet volume and ranking index: 88.4). Other food items were: pagurid crabs, without the mollusk shell, in two individuals (mean percent of diet volume: 1.9; ranking index: 0.17), fish fragments in one (mean percent of diet volume: 0.5; ranking index: 0.02), and crustacean fragments in nine (mean percent of diet volume: 9.2; ranking index: 3.76).

In contrast to the omnivorous *F. flavissimus*, *F. longirostris* has a restricted diet. It does not tear





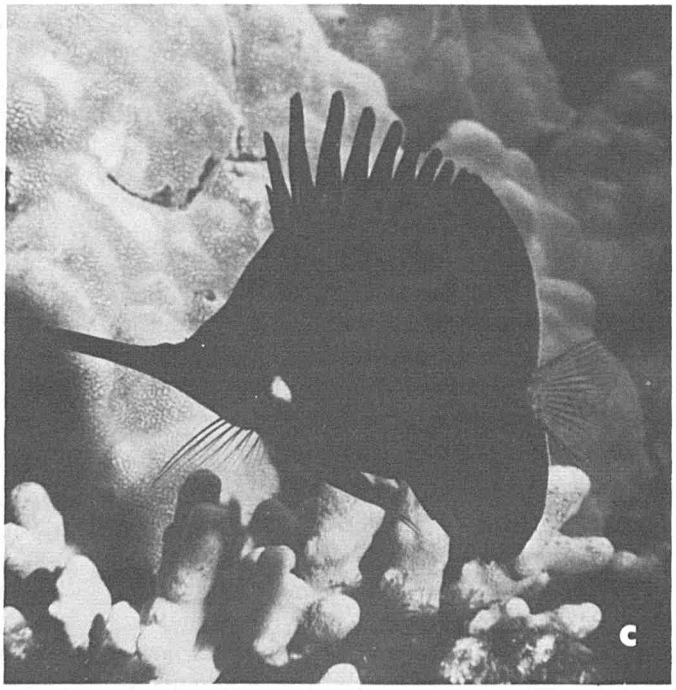


FIGURE 25.—a, *Forcipiger flavissimus*, a longsnouted butterflyfish, active on the reef during the day; b, *F. longirostris* (yellow form), a longsnouted butterflyfish, active on the reef during the day; c, *F. longirostris* (brown form), active on the reef during the day.

TABLE 28.—Food of *Forcipiger flavissimus*.

Rank	Items	No. fish with this item (n = 16)	Mean percent of diet volume	Ranking index
1	Radioles of sabellid polychaetes	10	15.4	9.63
2	Nemerteans	7	11.9	5.21
3	Podia and pedicellaria of echinoids	9	7.0	3.94
4	Calanoid copepods	8	4.1	2.05
5	Tentacles of terebellid polychaetes	7	3.6	1.58
6	Gammaridean amphipods	7	2.3	1.01
7	Hydroids	8	1.0	0.50
8	Caridean shrimps	2	1.3	0.16
9	Caprellid amphipods	4	0.5	0.13
10	Sipunculid introverts	3	0.6	0.11
11	Prosobranch gastropod egg capsules	3	0.5	0.09
12	Crab megalops	2	0.1	0.01
13	Isopods	1	0.1	<0.01
14	Demersal fish eggs	1	0.1	<0.01
Also, crustacean fragments		2	0.9	0.11
	Algal fragments	2	0.2	0.03
	Unidentified fragments	15	50.4	47.25

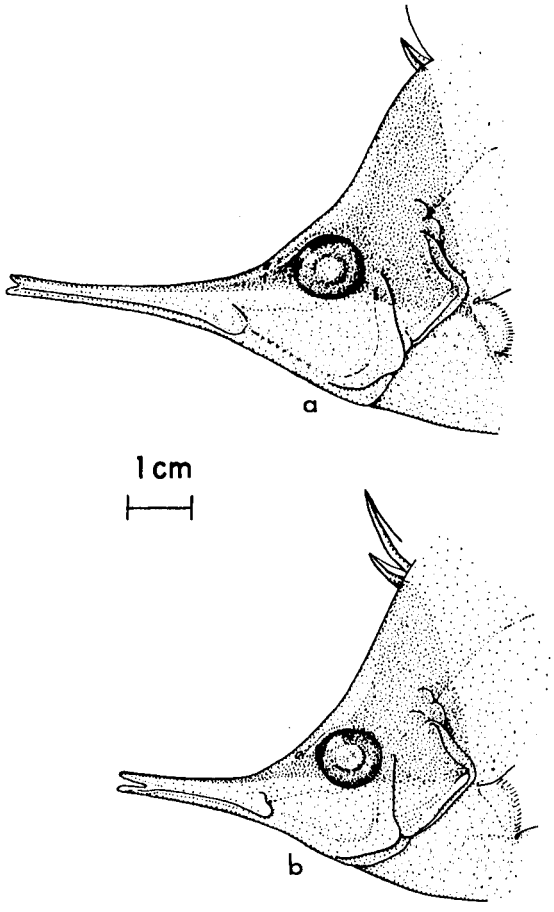


FIGURE 26.—The head and snout of: a, *Forcipiger longirostris*, 102mm long; *F. flavissimus*, 103 mm long. (Note: to discount the size difference in their snouts, lengths were measured from the posterior edge of the maxillary.)

off pieces of larger organisms, as does its congener, but instead takes only whole prey. The sharp difference between their diets is reflected in differing feeding structures. The snout and mouth of *F. longirostris* do not suggest needle-nosed pliers, as do those of *F. flavissimus;* indeed, for *F. longirostris,* the generic name *Forcipiger* (from the Latin *forcipis,* meaning pincers) is a misnomer. Compared with *F. flavissimus,* the mouth of *F. longirostris* is smaller and its jaws do not have the greatly expanded contact surfaces; the teeth are inwardly curved, as in *F. flavissimus,* but are longer and confined to only two or three rows at the front of the mouth (Figure 27a). Clearly, *F. longirostris* is adapted to grasping the tiny prey on which it feeds, but not to tearing pieces free.

CONCLUSION.—*Forcipiger longirostris* is a diurnal predator that takes small benthic animals, mostly decapod shrimps.

Hemitaurichthys thompsoni Fowler

This plain dark-brown chaetodontid seems to be generally rare in Hawaii (Gosline and Brock, 1960), but is numerous in several locations near

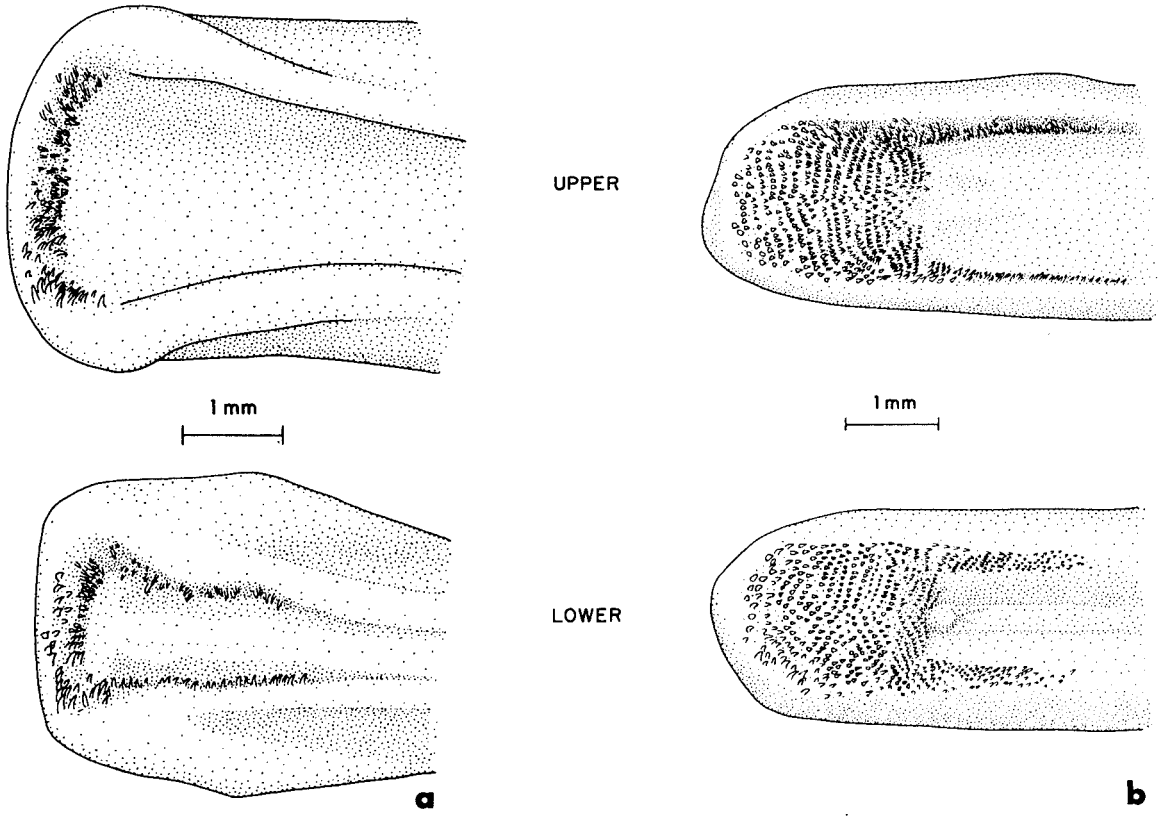


FIGURE 27.—Dentition of: a, *Forcipiger longirostris*; b, *F. flavissimus*.

the outer drop-off at Puuhonua Point, Honaunau. During the day it is active in large aggregations high in the water column, but at nightfall descends to the reef and remains close among cover until morning.

Of the 11 specimens (167: 127-185 mm) collected, all 5 that were taken from under cover on the reef at night (between 4 h after sunset and daybreak) had empty guts, whereas all 6 taken during afternoons from aggregations in midwater were full of food, as listed in Table 29.

I saw no evidence of benthic feeding by this fish. The circumstance that various planktonic copepods made up over 86% of its diet indicates that *H. thompsoni* is a more specialized feeder than its congener *H. zoster* below.

TABLE 29.—Food of *Hemitaurichthys thompsoni*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	6	81.9	81.90
2	Blue-green algae in gelatinous sacs	4	3.5	2.33
3	Cyclopoid copepods	4	3.5	2.33
4	Fish eggs, planktonic	4	1.0	0.67
5	Harpacticoid copepods	4	0.7	0.47
6	Hyperiid amphipods	3	0.3	0.15
7	Gastropods, planktonic	1	0.3	0.05
8	Unidentified egg masses in gelatinous matrix	1	0.2	0.03
9	Mysids	1	0.2	0.03
10	Larvaceans	1	0.2	0.03
Also, unidentified fragments		4	8.2	5.47

CONCLUSION.—*Hemitaurichthys thompsoni* is a diurnal planktivore that takes mostly copepods.

Hemitaurichthys zoster (Bennett)—blackface butterflyfish

Gosline and Brock (1960) stated that the colorful *H. zoster* (Figure 28a) and *H. thompsoni* attain a similar size (about 175 mm), but of those seen during this project, *H. zoster* was consistently smaller. Of the two, *H. zoster* also was by far the more numerous and more widespread. During the day *H. zoster* aggregates much like *H. thompsoni,* especially where the reefs drop abruptly into water deeper than about 10 m. Where *H. thompsoni* occurred, *H. zoster* was always nearby, but mixed aggregations of the two species were never seen. Unlike *H. thompsoni,* which was seen feeding only in mid-water, *H. zoster* sometimes is active in small groups close to the reef. At night *H. zoster* is generally solitary, close among cover in the same areas where it is active in daylight. Although *H. thompsoni* has the same coloration day and night, *H. zoster* displays a color pattern at night that differs strikingly from its daytime coloration (Figure 28a and b).

Twelve specimens (119: 100-128 mm) were collected during day and night. Four were speared during morning twilight from a group milling about close above the reef just prior to rising into mid-water. Two of these, taken 18 and 20 min before sunrise, respectively, both had empty stomachs; the third, taken 15 min before sunrise, contained calanoid copepods in varied stages of digestion; the fourth, taken 10 min before sunrise, contained more than 100 calanoid copepods and assorted other prey in varied stages of digestion. I cannot believe that all these prey had been taken since first light that morning, especially as no feeding was observed, and these fish had not yet risen to their customary plankton-feeding levels. And yet *H. zoster* was never seen above the reef at night. Until additional data are available, these two specimens remain anomalous. The other eight specimens, taken at various times during daylight from small aggregations above the reef, all had full stomachs. Items in the 10 individuals containing identifiable prey are listed in Table 30.

These data indicate that *H. zoster* has feeding habits that are less specialized than those of *H. thompsoni.* Planktonic copepods, constituting almost 62% of its diet, are still the major prey, but are less dominant than in *H. thompsoni.* Furthermore, *H. zoster* appears to feed significantly on benthic prey: the alcyonarian *Sarcothelia edmondsoni* constituted over 60% of the material in each of the three specimens in which it occurred.

CONCLUSION.—*Hemitaurichthys zoster* is chiefly a diurnal planktivore that takes primarily copepods, but also feeds on benthic organisms, especially alcyonarians.

Chaetodon corallicola Snyder

Observations in the western Pacific have indicated that the Hawaiian *C. corallicola* is closely related to, if not conspecific with, the widespread Indo-Pacific *C. kleini.* In Kona, this species is relatively numerous at depths below 20 m along the edge of the outer drop-off. In daylight it generally swims in loosely associated pairs that pick free-swimming organisms from the water column within a meter or so of the reef. At night it remains close among the coral—alert, but apparently inactive.

All 11 specimens (89: 75-96 mm) collected for study during afternoons had full stomachs (including fresh material), as listed in Table 31. The only evidence of bottom feeding among this material is the caprellid amphipods and hydroids, both taken from the same individual.

CONCLUSION.—*Chaetodon corallicola* is primarily a diurnal planktivore that feeds largely on copepods.

Chaetodon miliaris Quoy and Gaimard

Gosline and Brock (1960) noted that *C. miliaris* is one of the commonest inshore fishes. Although it is numerous in shallow water around Oahu, Brock and Chamberlain (1968), using a submarine off that island, found it even more abundant in deeper water. They discovered it to be a dominant form at depths below 120 m, where it hovered in aggregations 15 to 40 m above the sea floor, apparently feeding on plankton. In the Kona study area, this species rarely occurs in water shallower than 20 m, but is numerous along the outer drop-off at 30 m and deeper. During the day it aggregates 2 to 3 m above the reef, where it picks organisms from the plankton. At night it is scattered among the rocks and ledges, alert but apparently inactive.

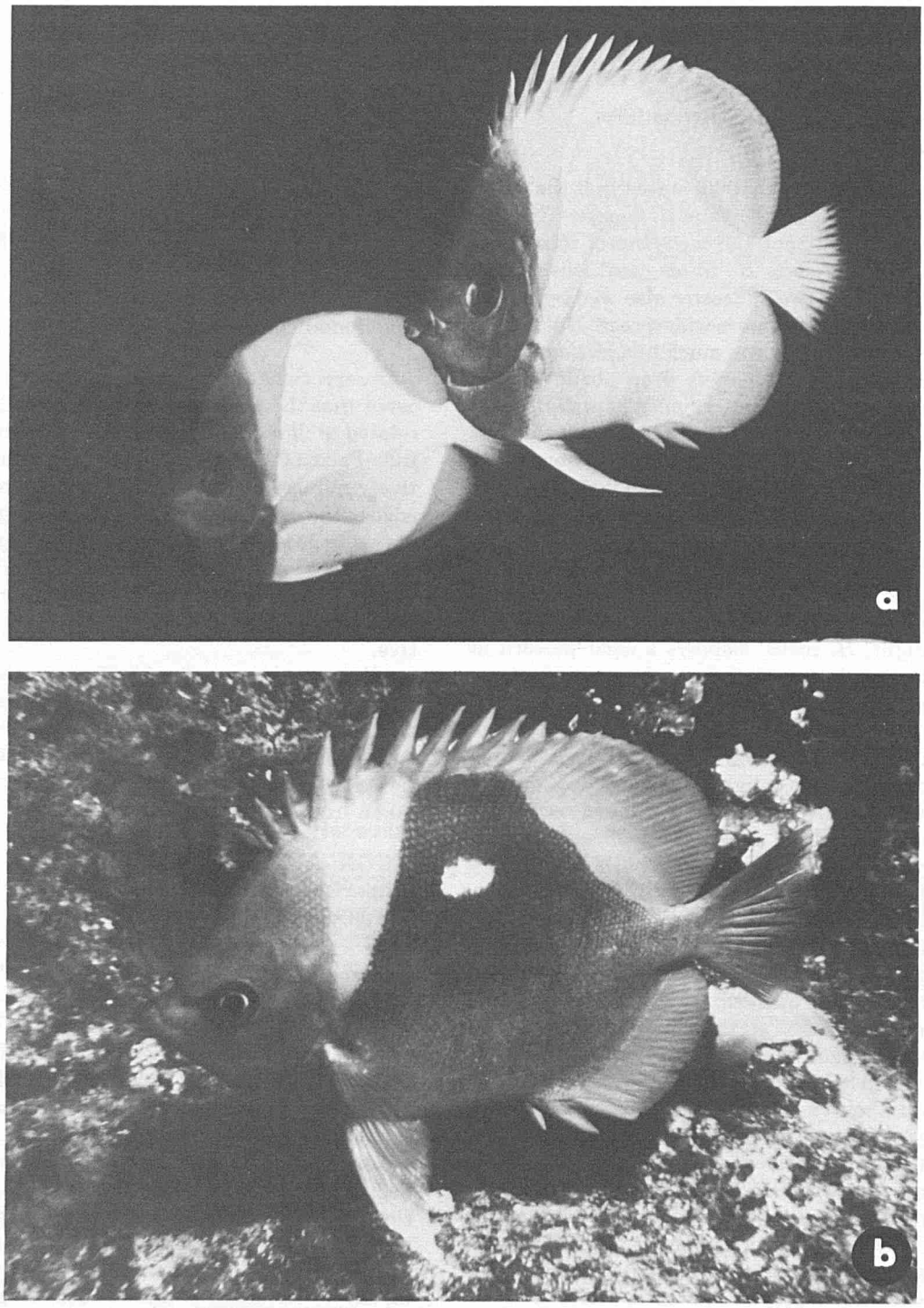


FIGURE 28.—*Hemitaurichthys zoster*, a butterflyfish: a, showing its diurnal coloration while swimming in the water column during the day; b, showing its nocturnal coloration while close to the reef at night.

TABLE 30.—Food of *Hemitaurichthys zoster*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	10	55.3	55.30
2	Alcyonarians	3	18.2	5.46
3	Cyclopoid copepods	8	6.1	4.88
4	Fish eggs, planktonic	6	1.9	1.14
5	Larvaceans	4	1.0	0.40
6	Blue-green algae in gelatinous sacs	3	1.3	0.39
7	Hydroids	2	1.9	0.38
8	Harpacticoid copepods	3	0.3	0.09
9	Gastropod veligers	2	0.3	0.06
10	Penaeid shrimps	1	0.2	0.02
11	Gastropod larvae, echinospira	1	0.1	0.01
12	Pelycypod larvae	1	0.1	0.01
13	Foraminiferans	1	<0.1	<0.01
14	Ostracods	1	<0.1	<0.01
Also, unidentified fragments		5	9.9	4.95
	Crustacean fragments	2	3.2	0.64

TABLE 31.—Food of *Chaetodon corallicola*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	11	52.6	52.60
2	Cyclopoid copepods	11	12.1	12.10
3	Fish eggs, planktonic	9	1.3	1.06
4	Larvaceans	2	5.5	1.00
5	Ostracods	3	0.5	0.14
6	Lobster phyllosomes	3	0.5	0.14
7	Mysids	2	0.3	0.06
8	Caprellid amphipods	1	0.5	0.05
9	Salps	1	0.2	0.02
10	Shrimp larvae	1	0.2	0.02
11	Hydroids	1	0.1	<0.01
12	Gammaridean amphipods	1	<0.1	<0.01
13	Blue-green algae in gelatinous sacs	1	<0.1	<0.01
Also, unidentified fragments		11	26.0	26.00

Of eight specimens (118: 110-125 mm) collected, one that was taken during early morning twilight close among cover contained only a few well-digested fragments, whereas all seven that were active above the reef when taken during the afternoon were full of food (much of it fresh), as listed in Table 32.

CONCLUSION.—*Chaetodon miliaris* is a diurnal planktivore that takes mostly copepods.

Chaetodon quadrimaculatus Gray—four-spot butterflyfish

This butterflyfish is especially numerous where the water is less than 10 m deep over reefs rich in the coral *Pocillopora*. During the day it is active, solitary or paired, close to the sea floor. Feeding strictly on the bottom, it mostly picks at the surface of living coral or in cracks within dead coral and basalt. It occurs in the same areas at night, but though alert, seems relatively inactive.

Twenty-six specimens (92: 43-110 mm) were speared during day and night. All 15 collected during midday were full of food, as were 4 of 5 taken at night during the 2 h immediately before midnight (the fifth was empty). The remaining six were collected at night during the hour immediately before daybreak, and while three of these had empty stomachs, the other three were full. Whether these findings indicate nocturnal feeding or slow digestion remains uncertain. No differences were recognized in composition or condition of gut contents between specimens taken day and night. Items in the 22 individuals containing identifiable material are listed in Table 33.

At least some of the corals taken by this fish probably are soft corals. Most material in the gut appeared as amorphous clumps rich in nematocysts and zooxanthellae. That much of this is soft coral seems likely considering how often *C. quadrimaculatus* nibbles about reef crevices where living stony corals are absent.

TABLE 32.—Food of *Chaetodon miliaris*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	7	68.6	68.60
2	Cyclopoid copepods	7	2.8	2.80
3	Salps	1	3.0	0.43
4	Hyperiid amphipods	3	0.4	0.17
5	Fish eggs, planktonic	3	0.4	0.17
6	Larvaceans	1	0.9	0.13
7	Egg masses in gelatinous sacs	2	0.4	0.11
8	Ostracods	1	0.1	0.01
9	Harpacticoid copepods	1	0.1	0.01
10	Mysids	1	0.1	0.01
Also, unidentified fragments		6	23.2	19.89

TABLE 33.—Food of *Chaetodon quadrimaculatus*.

Rank	Items	No. fish with this item (n = 22)	Mean percent of diet volume	Ranking index
1	Anthozoans (no skeletal material)	22	81.4	81.40
2	Polychaetes (mostly tentacles and fragments)	13	6.2	3.66
3	Hydroids	13	1.6	0.95
4	Sipunculid introverts	7	1.9	0.60
5	Opisthobranch gastropods	3	1.3	0.18
6	Caprellid amphipods	6	0.4	0.11
7	Gammaridean amphipods	4	0.2	0.04
8	Cyclopoid copepods	2	0.1	<0.01
9	Calanoid copepods	1	<0.1	<0.01
10	Mites	1	<0.1	<0.01
11	Demersal eggs	1	<0.1	<0.01
Also, unidentified fragments		5	4.5	1.02
	Algal fragments, including diatoms	12	2.1	1.15

Opisthobranch gastropods had been taken by three of the individuals collected at night. Perhaps significantly, these same opisthobranchs are a major prey of *C. lunula* after dark (see below).

CONCLUSION.—*Chaetodon quadrimaculatus* feeds during the day mostly on corals, but also on polychaetes and other benthic organisms. Some nocturnal feeding is likely.

Chaetodon unimaculatus Bloch—one-spot butterflyfish

This chaetodontid is numerous on shallow reefs exposed to a strong surge where the coral *Pocillopora* is also abundant. Generally occurring in pairs, it is active during the day, picking at the surface of living *Pocillopora*, and to a lesser extent other reef surfaces. At night it is alert, but appears inactive as it hovers close among cover on the reef.

Twenty-six specimens (85: 66-102 mm) were speared during night and day. Of three that were collected during the 2 h immediately before midnight, two had empty stomachs, and the third contained a few well-digested fragments. Of four collected during the hour immediately before daybreak, two had empty stomachs, and two contained only well-digested fragments. Thus, there was no evidence of recent feeding by individuals taken after dark. In contrast, all 19 specimens collected during the day had full stomachs, including fresh material, as listed in Table 34.

The major food item, scleractinian corals (mostly *Pocillopora*), included many skeletal fragments.

CONCLUSION.—*Chaetodon unimaculatus* feeds during the day, mostly on the coral *Pocillopora*.

Chaetodon multicinctus Garrett—pebbled butterflyfish

Chaetodon multicinctus is probably the most numerous chaetodontid on Kona reefs in water

TABLE 34.—Food of *Chaetodon unimaculatus*.

Rank	Items	No. fish with this item (n = 19)	Mean percent of diet volume	Ranking index
1	Scleractinian corals	15	45.3	35.76
2	Sponges	5	12.4	3.26
3	Gammaridean amphipods	4	1.3	0.27
4	Pelycypods	1	3.2	0.17
5	Sipunculid introverts	1	1.6	0.08
6	Calanoid copepods	2	0.3	0.03
Also, unidentified fragments		18	29.1	27.57
	Algal fragments and diatoms	9	6.8	3.22

TABLE 35.—Food of *Chaetodon multicinctus*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Scleractinian coral polyps	11	91.6	91.60
2	Gammaridean amphipods	7	1.8	1.15
3	Sipunculid introverts	5	1.3	0.59
4	Polychaetes (fragments and tentacles)	3	0.4	0.11
5	Hydroids	2	0.2	0.04
6	Calanoid copepods	1	0.1	0.01
Also, unidentified fragments		2	3.4	0.62
	Algal fragments and diatoms	6	1.2	0.66

shallower than 20 m, especially where stony corals abound. During the day it generally occurs in pairs, and is active close to the reef, often picking at living corals—both *Porites* and *Pocillopora*. At night it rests close among cover on the reef, alert but apparently inactive.

Of the 26 specimens (84: 78-94 mm) examined, all 15 that were collected at night (between 4 h after sunset and first morning light) were empty, whereas all 11 that were collected during midday were full of food (including fresh material), as listed in Table 35.

More so than the other butterflyfishes that feed on stony corals, *C. multicinctus* does so without also taking fragments of the surrounding skeleton.

CONCLUSION.—*Chaetodon multicinctus* is a diurnal predator that feeds primarily on scleractinian corals (mostly *Porites* and *Pocillopora*).

Chaetodon ornatissimus Solander—ornated butterflyfish

This butterflyfish is numerous over coral-rich reefs, generally swimming in pairs during the day. It moves from one growth of coral to another, locating and working its mouth over abrasions on the surface of the coral. In this way it feeds on a variety of scleractinian corals, including *Porites*, *Pavona*, and *Cyphastrea*. At night it rests quiet, but alert, close among cover on the reef. Its daytime and nighttime colorations differ strikingly (Figure 29a and b).

Nineteen specimens (119: 95-140 mm) were examined. All eight that were collected at night, later than 4 h after sunset and before first morning light, had the stomachs and anterior half of the intestines empty. All four that were taken during morning twilight—the earliest 25 min before sunrise—had material in their stomachs, but their intestines were empty (apparently they had just begun to feed). Finally, all seven that were collected during midday were full of food.

All 11 specimens with material in their stomachs contained only a thick mucus rich in nematocysts, zooxanthellae, and organic debris (mean percent of diet volume and ranking index: 99.8). The balance of the gut contents was made up of diatoms and a few algal fragments.

It is well known that stony corals increase their production of mucus when injured, so this chaetodontid's habit of seeking out abrasions on coral may explain why its gut contents include so much mucus. This species probably obtains significant nourishment from coral mucus, but judging from the numbers of zooxanthellae and

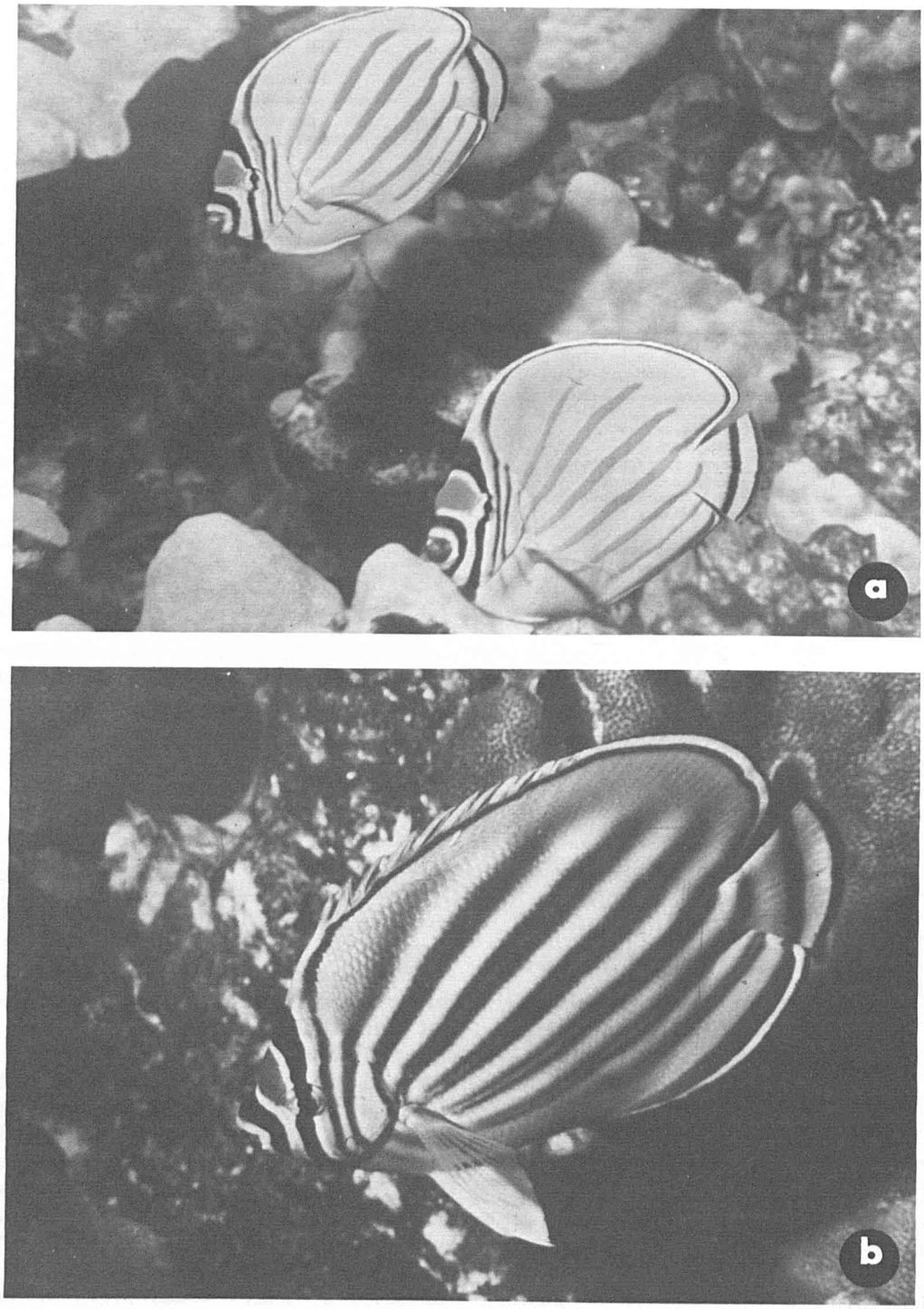


FIGURE 29.—*Chaetodon ornatissimus*, a butterflyfish: a, showing its diurnal coloration while swimming above the reef during the day; b, showing its nocturnal coloration while close to the reef at night.

nematocysts present, at least some coral tissue is also taken (although nothing was found recognizable as such). Presumably at least much of this material had been freshly ingested, because it came from individuals that were actively feeding when collected. Johannes (1967) and Coles and Strathman (in press) have shown there are significant quantities of organic material in coral mucus that could nourish a wide range of animals, including fishes. A similar butterflyfish, *Chaetodon trifasciatus,* not numerous in Kona, has feeding behavior similar to *C. ornatissimus.*

CONCLUSION.—*Chaetodon ornatissimus* is a diurnal fish that feeds on coral during the day, obtaining significant nourishment from coral mucus.

Chaetodon auriga Forskål

In Kona this chaetodontid is less abundant than many of its congeners. Generally paired, it swims close to the reef in daylight, occasionally picking at objects on the sea floor. At night it is alert close among ledges and other reef irregularities.

All six specimens (151: 132-160 mm) collected had full stomachs including four taken during the afternoon and two taken on a dark night, 3 h after sunset. All these specimens contained similar prey in what seemed similar condition. The data are too few to draw conclusions regarding nocturnal activity, but suggest that this species may feed after dark. Items in the stomachs of these six specimens are listed in Table 36.

Most of the food items were fragmented, including the unidentified material, and many of them were relatively fresh. Clearly, this chaetodontid obtains most of its food by tearing pieces from larger sessile organisms. Hiatt and Strasburg (1960) found similar prey in *C. auriga* from the Marshall Islands.

CONCLUSION.—*Chaetodon auriga* preys on a wide variety of benthic organisms during the day, obtaining most of its food by tearing off pieces of larger sessile animals. It also seems to feed to some extent after dark.

Chaetodon fremblii Bennett—blue-striped butterflyfish

This butterflyfish is most numerous where large basalt boulders are interspersed with small pockets of sand. Sometimes paired, but more often solitary, this chaetodonid picks at objects on the rocks and in the sand during the day. At night it occurs close among cover, alert but seemingly inactive.

Fourteen specimens (103: 86-120 mm) were speared during day and night. All eight collected during the afternoon had full stomachs, whereas the two taken from among rocks at night, between 4 and 5 h after sunset, were empty. On the other hand, three others collected together among the rocks during morning twilight, about 25 min before sunrise after a moonless night, had material in their stomachs. Two of them contained only a few well-digested fragments that could have been

TABLE 36.—Food of *Chaetodon auriga.*

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Alcyonarians	5	31.0	25.83
2	Terebellid polychaete tentacles	6	18.4	18.40
3	Gastropod egg masses	6	8.8	8.80
4	Errant polychaete fragments	5	5.4	4.50
5	Sabellid polychaete radioles	4	2.2	1.47
6	Echinoid podia	4	2.0	1.33
7	Caridean shrimps	4	1.4	0.93
8	Anemones	1	4.0	0.67
9	Sponges	1	3.1	0.52
10	Sipunculid introverts	3	0.4	0.20
11	Gammaridean amphipods	3	0.4	0.20
12	Hydroids	1	0.2	0.03
13	Serpulid polychaete fragments	1	0.2	0.03
Also,	Unidentified fragments	6	20.7	20.70
	Algal fragments	3	1.8	0.90

taken the previous day, but in the third individual a wide variety of differentially digested items indicated either nocturnal feeding or unusually slow digestion. A fourth individual taken during morning twilight was empty. Items in the eight specimens containing identifiable material, much of it fragments torn from larger sessile animals, are listed in Table 37.

CONCLUSION.—*Chaetodon fremblii* preys on a wide variety of benthic organisms during the day, obtaining much of its food by tearing off pieces of larger sessile animals. With some uncertainty, it seems largely inactive after dark.

Chaetodon lunula (Lacépède)—masked butterflyfish

This butterflyfish, one of the more numerous in Kona, is most abundant where a coral-crested reef face falls among basalt boulders, yet occurs in a variety of habitats. Setting it apart from all other chaetodontids reported here, I never saw this species feed during the day. It generally hovers close to the reef in daylight, sometimes solitary, or in twos or threes, and often in large aggregations (Figure 30). These aggregations form day after day in the same locations, and several occurred in the same places over the entire 15-mo period of the study. The aggregations disperse at nightfall, and after dark the species scatters over the reef, either solitarily, or in twos or threes.

Of the 26 specimens (134: 112-150 mm) examined, all 14 speared at night (more than 4 h after sunset), or during morning twilight, had stomachs full of food in varying stages of digestion, much of it fresh; the other 12 were collected during afternoons (some from the daytime aggregations), and although they too had full stomachs, the contents generally were further digested. There was no recognizable difference in the composition of the diet between specimens collected during each of these three periods. Items in the stomachs are listed in Table 38.

Clearly, *C. lunula,* like *C. auriga* and *C. fremblii,* habitually tears pieces off the bodies of larger sessile animals, but, more so than the others, also takes whole organisms. In fact, its major prey, based on these data, are opisthobranch gastropods, which it takes whole. The opisthobranchs are mostly one form of Anaspidea and one form of Cephalaspidea. Significantly, all individuals of *C. lunula* that contained what seemed to be freshly ingested opisthobranchs were speared at night. Opisthobranchs in *C. lunula* speared during the afternoon were consistently far digested. These opisthobranchs are mostly about 4 to 10 mm long, and are relatively solid pieces of meat that may take longer to digest than many other kinds of food. Similarly, the polychaete heads and prosobranch gastropod heads taken by this fish are relatively dense pieces of meat that probably resist digestion (the shells of the prosobranch gastropods were never present—only the heads, which this butterflyfish apparently is adept at snipping off). Smaller organisms that would be rapidly digested like the amphipods and isopods, generally, but with two exceptions, were absent in specimens speared during the afternoon. Generally then, the stomach contents appeared to have been taken mostly at night. Finally, it may be significant that the eyes of *C. lunula* are relatively larger than the eyes of all other species of this genus studied at Kona.

TABLE 37.—Food of *Chaetodon fremblii.*

Rank	Items	No. fish with this item (n = 8)	Mean percent of diet volume	Ranking index
1	Terebellid polychaete tentacles	6	25.0	18.75
2	Sipunculid introverts	6	15.0	11.25
3	Gammaridean amphipods	8	10.1	10.10
4	Errant polychaete fragments	4	3.1	1.55
5	Hydroids	2	2.9	0.73
6	Isopods	3	1.6	0.60
7	Gastropod egg capsules	1	3.6	0.45
8	Caprellid amphipods	1	2.3	0.29
9	Acorn worms	1	2.3	0.29
10	Opisthobranch gastropods	1	1.4	0.18
11	Caridean shrimps	1	0.1	0.01
12	Gastropod opercula	1	0.1	0.01
Also, unidentified fragments		6	21.3	15.98
	Algal fragments	7	11.2	9.80

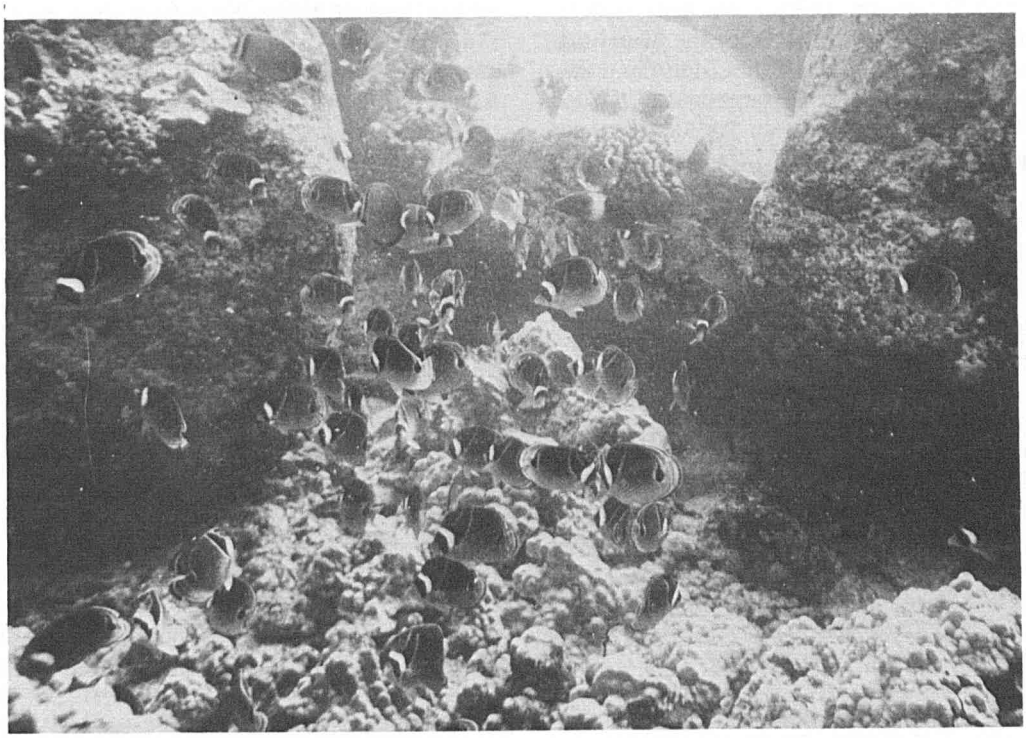


FIGURE 30.—Diurnal aggregation of *Chaetodon lunula*, a butterflyfish.

TABLE 38.—Food of *Chaetodon lunula*.

Rank	Items	No. fish with this item (n = 26)	Mean percent of diet volume	Ranking index
1	Opisthobranch gastropods	21	29.2	23.58
2	Terebellid polychaete tentacles	11	8.7	3.68
3	Errant polychaete fragments	17	2.2	1.44
4	Sipunculid introverts	9	1.7	0.59
5	Polychaete heads	8	1.9	0.58
6	Prosobranch gastropod heads	7	0.7	0.19
7	Gammaridean amphipods	9	0.3	0.10
8	Holothurians	2	1.3	0.10
9	Fish eggs	2	1.1	0.08
10	Caridean shrimps	4	0.3	0.05
11	Echinoid podia	4	0.2	0.03
12	Alcyonarians	2	0.3	0.02
13	Sabellid polychaete radioles	3	0.2	0.02
14	Caprellid amphipods	3	0.1	0.01
15	Crustacean eggs	1	0.2	<0.01
16	Tanaids	2	0.1	<0.01
17	Hydroids	2	0.1	<0.01
18	Anemones	1	0.1	<0.01
19	Calanoid copepods	1	0.1	<0.01
20	Crabs	1	0.1	<0.01
21	Tunicates	1	0.1	<0.01
Also, unidentified fragments		24	50.3	46.43
	Algal fragments	5	0.5	0.10
	Crustacean fragments	4	0.2	0.03

Hiatt and Strasburg (1960) noted only tips of coral polyps in one *C. lunula* from the Marshall Islands. Although the diet of this individual diverges sharply from that of representatives in Kona, one cannot speculate on its significance from one specimen.

CONCLUSION.—*Chaetodon lunula* preys on benthic invertebrates, especially opisthobranchs, at night.

General Remarks on Angelfishes and Butterflyfishes

The two Hawaiian angelfishes, *Holacanthus arcuatus* and *Centropyge potteri,* have feeding habits that set them apart from the butterflyfishes. *Holacanthus arcuatus* is the only chaetodontid that feeds strictly on sponges, and *C. potteri* is the only one that takes just algae and detritus. Thus the Hawaiian situation parallels that in the tropical Atlantic, where species of *Holacanthus* and of *Pomacanthus* (another genus of angelfish) feed mostly on sponges and where species of *Centropyge* feed almost exclusively on algae and detritus (Randall, 1967). Similarly, Hiatt and Strasburg (1960) reported a strictly herbivorous diet for *C. flavissimus* in the Marshall Islands.

Although butterflyfishes in Kona are more strictly predators in the conventional sense than are the angelfishes, Hiatt and Strasburg (1960) reported *Chaetodon reticulatus* in the Marshall Islands to be strictly herbivorous. That species is seen only occasionally in Kona, and so was not included in the present study. Otherwise, Hiatt and Strasburg found scleractinian corals and polychaetes to be the major food of butterflyfishes in the Marshall Islands, and this is in broad accord with the habits of certain species in Kona. Randall (1967) reported that West Indian butterflyfishes feed primarily on anthozoans and the tentacles of polychaetes, again paralleling the habits of certain Kona species. On the other hand, the number of planktivorous butterflyfishes in Kona seems on a scale without parallel in published accounts of other reef areas.

Chaetodontids have been widely described as diurnal fishes, e.g. in the tropical Atlantic (Starck and Davis, 1966; Collette and Talbot, 1972), and in the Gulf of California (Hobson, 1965, 1968a). Although diurnal habits are generally characteristic of chaetodontids in Kona, the fact that at least one, *Chaetodon lunula,* is nocturnal and that several others feed at least somewhat after dark may reflect increased interspecific pressures associated with the large number of *Chaetodon* species on Kona reefs. I treat the nine most numerous species of *Chaetodon* here, but also saw five others during this study.

Family Pomacentridae: damselfishes

Plectroglyphidodon johnstonianus Fowler and Ball

This solitary species is most numerous where stony corals abound. During the day it swims close to the reef, each individual seemingly associated with a particular location, and here it picks frequently at the substratum, especially around coral. At night it is secreted deep among the coral, relatively inactive, but alert.

Of the eight specimens (60: 39-70 mm) examined, the stomachs of two that were speared among the coral shortly before dawn contained only a few well-digested fragments (probably material that had been ingested during the previous day), whereas the stomachs of all six taken during midday were full of food, much of it fresh.

The major food item in all six was anthozoans: nematocysts and zooxanthellae, with tissue fragments and mucus, but no skeletal material (mean percent of diet volume and ranking index: 94.3). All other items made up only a minor part of the diet: algal fragments in three (mean percent of diet volume: 2; ranking index: 1), sipunculid introverts in one (mean percent of diet volume: 0.2; ranking index: 0.03), and unidentified fragments in four (mean percent of diet volume: 3.5; ranking index: 2.33). Because *P. johnstonianus* is closely associated with scleractinian corals, these probably are the anthozoans so prominent in its diet. However, specific identifications of the fragmented gut contents remain uncertain, and because direct observations of feeding are limited, other anthozoans may also be involved. In any event, the observations indicate that this fish is adept at snipping off pieces of anthozoan tissue and mucus without taking any of the surrounding skeletal material.

CONCLUSION.—*Plectroglyphidodon johnstonianus* is a diurnal predator that feeds chiefly on anthozoans.

Pomacentrus jenkinsi Jordan and Evermann

This species is one of the more widespread and numerous in Kona, especially in relatively quiet water over coral and rocks. During the day, individuals are scattered among reef irregularities, each seemingly associated with specific locations, and here they pick at coral and rock surfaces. At night they hover under cover, remaining alert but relatively inactive until shortly after first light, when diurnal activity is resumed.

Twenty-two specimens (89: 80-100 mm) were collected during day and night. All 12 that were speared as they swam close to the reef during midday were full of food, much of it fresh, whereas of 5 that were speared in reef crevices at night (between 4 and 5 h after last evening light), the stomachs of 3 were empty and those of the other 2 contained only a few well-digested, unidentified fragments. Finally, of five active individuals that were collected during morning twilight and during the first 30 min after sunrise, two were empty, and three contained in their stomachs a few fresh fragments that appeared to have been recently ingested. The 15 specimens that contained at least some fresh material had consumed the items listed in Table 39.

The amorphous organic fragments that constituted the bulk of the gut contents in this fish were in part items that had been digested beyond recognition; however, most of this material appeared to be detritus—organic deposits—that had been scraped from the reef. Gosline and Brock (1960) noted that *P. jenkinsi* inhabits quiet water, where it feeds on algae, and perhaps detritus. Hiatt and Strasburg (1960) also found this fish in quiet water in the Marshall Islands and reported it to be primarily a herbivore that feeds occasionally on small fishes.

CONCLUSION.—*Pomacentrus jenkinsi* is a diurnal omnivore that takes mostly organic detritus, algae, and small animals from reef surfaces.

Abudefduf sindonis (Jordan and Evermann)

This damselfish occurs where basalt boulders are swept by a strong surge. Activity is limited to daylight; at night it remains under cover among the rocks.

All five specimens (91: 81-102 mm) were speared during the day, and their guts were full of the material listed in Table 40, much of it fresh. The amorphous organic fragments, the major food item, probably are largely detritus from the reef, such as is also taken by *Pomacentrus jenkinsi*, discussed above. Where a strong surge sweeps the boulder habitat, *A. sindonis* replaces *P. jenkinsi* in depths shallower than about 3 m.

Gosline and Brock (1960) noted that *A. sindonis* seems restricted to surge areas among lava rocks and appears to be omnivorous.

CONCLUSION.—*Abudefduf sindonis* is a diurnal omnivore that takes mostly organic detritus, algae, and small animals from the substratum.

Abudefduf sordidus (Forskål)—*kupipi*

Although juveniles of *A. sordidus* are prominent in tide pools, the adults, which are the largest of the Hawaiian pomacentrids, seem to occur only where a precipitous basalt reef face confronts a prevailing swell. In this situation large individuals of this species are fairly numerous among rocky crevices and close to boulders at the base of the reef. Generally a solitary fish, *A. sordidus* is

TABLE 39.—Food of *Pomacentrus jenkinsi*.

Rank	Items	No. fish with this item (n = 15)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	15	24.1	24.10
2	Sponges	6	5.7	2.28
3	Calanoid copepods	1	4.6	0.31
4	Errant polychaetes	2	2.0	0.27
5	Fish eggs, demersal	2	1.0	0.13
6	Cyclopoid copepods	4	0.4	0.11
7	Gammaridean amphipods	2	0.2	0.03
8	Barnacle cirri	1	0.1	<0.01
9	Pelecypod mollusks	1	0.1	<0.01
Also, amorphous organic fragments		15	60.1	60.10
	Sand	4	1.7	0.45

TABLE 40.—Food of *Abudefduf sindonis*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	5	39.4	39.40
2	Polychaetes	4	2.2	1.76
3	Gammaridean amphipods	4	2.2	1.76
4	Caridean shrimps	1	7.0	1.40
5	Cyclopoid copepods	4	1.0	0.80
6	Hydroids	1	1.0	0.20
7	Sipunculid introverts	1	0.2	0.04
8	Insects	1	0.2	0.04
Also, amorphous organic fragments		5	46.8	46.80

TABLE 41.—Food of *Abudefduf sordidus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	5	35.0	35.00
2	Crabs	4	20.0	16.00
3	Sponges	4	12.2	9.76
4	Prosobranch gastropods	4	9.2	7.36
5	Gammaridean amphipods	5	4.4	4.40
6	Prosobranch gastropod eggs	2	1.2	0.48
7	Tanaids	3	0.6	0.36
8	Hydroids	2	0.4	0.16
9	Bryozoans	2	0.4	0.16
10	Polychaetes	2	0.4	0.16
11	Pycnogonids	2	0.4	0.16
12	Insects	1	0.4	0.08
Also, unidentified fragments		5	15.4	15.40

active only during daylight, close to the substratum. After dark it is secreted under rocky cover, alert but relatively inactive.

All five specimens (147: 129-160 mm) were speared during midday, and their guts were full of the material listed in Table 41, much of it fresh. Gosline and Brock (1960) reported that the young of *A. sordidus* are very prominent tide-pool inhabitants and that the omnivorous adults apparently live just outside of the reef edge.

CONCLUSION.—*Abudefduf sordidus* is a diurnal omnivore that takes chiefly algae and small animals from the substratum.

Abudefduf imparipennis (Sauvage)

This pomacentrid is numerous on shallow, surge-swept reefs where exposed basalt is dotted by the coral *Pocillopora meandrina*. It is a solitary, bright-eyed little fish that is active in daylight, and does not swim away from the substratum. Appearing tense and alert, even when hovering motionless at the base of a coral head, its movements are short but rapid darts from one spot to another. At night it takes shelter deep within reef crevices.

All 15 specimens (42: 29-50 mm) were active on the reef during the day when collected, and all contained food, including fresh material, as listed in Table 42. Gosline and Brock (1960) noted that this fish seems to occur over all rocky areas in the surge zone, and that it appears to be entirely carnivorous, with the predominant food organism being a polychaete annelid.

CONCLUSION.—*Abudefduf imparipennis* is a diurnal predator that feeds mainly on small benthic crustaceans and polychaetes.

Abudefduf abdominalis (Quoy and Gaimard)—*maomao*

This damselfish is most numerous where basalt boulders lie at the base of a vertical reef face in water 5 to 10 m deep. During daylight it hovers in aggregations high in the water column close to the

TABLE 42.—Food of *Abudefduf imparipennis*.

Rank	Items	No. fish with this item (n = 15)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	12	12.6	10.08
2	Polychaetes	7	17.6	8.21
3	Cyclopoid copepods	9	7.1	4.26
4	Sipunculid introverts	8	1.9	1.01
5	Fish eggs, demersal	3	3.1	0.62
6	Unidentified eggs, demersal	4	1.8	0.48
7	Opisthobranch gastropods	2	1.7	0.23
8	Diatoms	6	0.5	0.20
9	Algae fragments	2	0.8	0.11
10	Prosobranch gastropod eggs	1	0.8	0.05
11	Isopods	2	0.4	0.05
12	Sponge spicules	1	0.3	0.02
13	Caprellid amphipods	1	<0.1	<0.01
14	Harpacticoid copepods	1	<0.1	<0.01
15	Caridean shrimps	1	<0.1	<0.01
16	Mites	1	<0.1	<0.01
17	Insects	1	<0.1	<0.01
Also, unidentified fragments		15	50.9	50.90

TABLE 43.—Food of *Abudefduf abdominalis*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	10	54.0	54.00
2	Cyclopoid copepods	8	6.5	5.20
3	Fragments of algae	4	2.6	1.04
4	Fish eggs, planktonic	4	2.0	0.80
5	Polychaetes	4	1.9	0.76
6	Decapod shrimps	4	1.7	0.68
7	Larvaceans	1	4.0	0.40
8	Harpacticoid copepods	4	0.8	0.32
9	Gelatinous clumps of blue-green algae	2	1.3	0.26
10	Pelecypod larvae	2	0.2	0.04
11	Penaeid shrimp larvae	1	0.2	0.02
12	Gastropod veligers	1	0.1	0.01
13	Naupilius larvae	1	0.1	0.01
Also, unidentified fragments		9	24.6	22.14

reef, where it picks organisms from the plankton. Although members of an aggregation are close to one another, each feeds independently. The plankters are taken with what seems to be a visually directed action in which the fish suddenly thrusts both jaws forward, then immediately retracts them. Presumably the sudden expansion of the oral cavity sucks the prey in.

A given aggregation maintains station over a particular location although its position in the water column is influenced by several factors. Fish size is important, because the larger individuals tend to be farther above the reef than the smaller ones. Prevailing light is another factor; thus, when clouds pass in front of the sun, and light diminishes, individuals of all sizes descend closer to the reef. In addition, the appearance of a large predator, or some other disturbance, intermittently sends this fish diving to cover on the reef. However, after such an event it quickly returns to its feeding stations in the water column.

As light progressively fades late in the day, this species gradually descends to the reef so that by evening twilight it is sheltered among the coral (Hobson, 1972). On dark nights it remains under cover, relatively inactive but alert; however, under bright moonlight it swims in exposed positions close to the reef. Then, during morning twilight, it begins to ascend to its daytime feeding stations in the water column (Hobson, 1972).

Of 14 specimens (142: 105-162 mm) examined, the 4 that were speared as they hovered among the rocks on dark nights (between 4 and 6 h after sunset) contained only well-digested fragments, whereas all 10 that were speared from mid-water aggregations during afternoons had their stomach full of food (including much fresh material), as listed in Table 43.

CONCLUSION.—*Abudefduf abdominalis* is a diurnal planktivore that preys primarily on copepods.

Dascyllus albisella Gill

Where corals are abundant, this damselfish is numerous to depths of at least 35 m. During daylight, it aggregates in the water column and picks small organisms from the plankton, much as does *Abudefduf abdominalis,* described above, and its aggregations rise and fall in the water column in response to the same variables that influence that species. Also like *A. abdominalis, D. albisella* descends to the reef during evening twilight and spends the night close among the rocks—under cover on dark nights, and in exposed positions when there is moonlight.

Twelve specimens (79: 42-95 mm) were collected during day and night. The six that were speared shortly before first morning light as they hovered among the coral contained only a few well-digested fragments (five were taken after nights of bright moonlight, one after a dark night). On the other hand, the six that were collected from aggregations in the water column during afternoons had stomachs full of food, including much fresh material as listed in Table 44.

Gosline and Brock (1960) reported that *D. albisella* occurs in small schools around certain large coral heads and listed stomach contents as follows: shrimp and crab larvae, mysids, and calanoid copepods.

CONCLUSION.—*Dascyllus albisella* is a diurnal planktivore that takes primarily larvaceans and copepods.

Chromis vanderbilti (Fowler)

This, the smallest pomacentrid in Kona, is numerous where exposed basalt ledges are interspersed with coral. During the day it aggregates in the water column, but even under bright sunlight rarely moves more than 50 cm above the reef. On overcast days it generally remains sheltered, and shortly before sunset is the first planktivorous damselfish to descend to cover on the reef (Hobson, 1972). At night, it usually remains out of sight deep within reef crevices, and in the morning is the last pomacentrid to appear.

All 12 specimens (38: 17-46 mm) taken from feeding aggregations during midday had stomachs full of food, including fresh material, as listed in Table 45.

CONCLUSION.—*Chromis vanderbilti* is a diurnal planktivore that takes primarily copepods and larvaceans.

Chromis leucurus Gilbert

Gosline and Brock (1960) considered *C. leucurus* to include two distinct color phases: in one the body is very dark anteriorly and abruptly white posteriorly; in the other, the whole body, except black pectoral base and white caudal fin, is mostly plain orange-brown. Although I followed this judgment when making the fish counts, the probability that at least two species are represented, and that neither one may in fact be *C. leucurus,* is currently under study by John E. Randall, B. P. Bishop Museum, and Stanley Swerdloff, Government of American Samoa. In any event, the specimens collected for study of food

TABLE 44.—Food of *Dascyllus albisella.*

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Larvaceans	6	43.1	43.10
2	Calanoid copepods	6	11.2	11.20
3	Cyclopoid copepods	6	9.2	9.20
4	Gelatinous clumps of blue-green algae	4	7.2	4.80
5	Fragments of algae	4	1.5	1.00
6	Decapod shrimp larvae	2	2.2	0.73
7	Fish eggs, planktonic	2	1.1	0.37
8	Hydroid fragments	1	0.2	0.03
9	Pelecypod larvae	1	0.2	0.03
10	Gammaridean amphipods	1	0.2	0.03
11	Harpacticoid copepods	1	0.2	0.03
Also, unidentified fragments		5	23.7	19.75

TABLE 45.—Food of *Chromis vanderbilti*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	11	30.5	27.96
2	Larvaceans	8	21.7	14.47
3	Cyclopoid copepods	12	8.8	8.80
4	Polychaetes	5	0.9	0.38
5	Fish eggs, planktonic	4	0.9	0.30
6	Decapod shrimps	2	1.7	0.28
7	Harpacticoid copepods	3	1.1	0.28
8	Siphonophores	1	1.7	0.14
9	Gelatinous clumps of blue-green algae	2	0.5	0.08
10	Ostracods	1	0.5	0.04
11	Hyperiid amphipods	1	0.1	0.01
Also, unidentified fragments		12	31.1	31.10

habits, below, all represent the orange-brown form.

Of the two, the orange-brown form is the more numerous in Kona, but both abound over coral-rich reefs, often together in plankton-feeding aggregations that hover within 1 m of the substratum during the day. As is true of *Abudefduf abdominalis* and *Dascyllus albisella,* described above, *C. leucurus* remains closer to the reef when light is diminished, and dives to cover when threatened (Figure 31). At night it generally is out of sight within crevices.

All five specimens (57: 37-70 mm) speared during midday had their stomachs full of food, including fresh material, as listed in Table 46.

Swerdloff (1970a) described the behavior of two spatially related species of *Chromis* in the Marshall Islands, *C. leucurus,* and *C. dimidiatus,* and reported their food to be calanoid copepods, fish eggs, and larval tunicates.

CONCLUSION.—*Chromis leucurus* is a diurnal planktivore that takes primarily copepods and larvaceans.

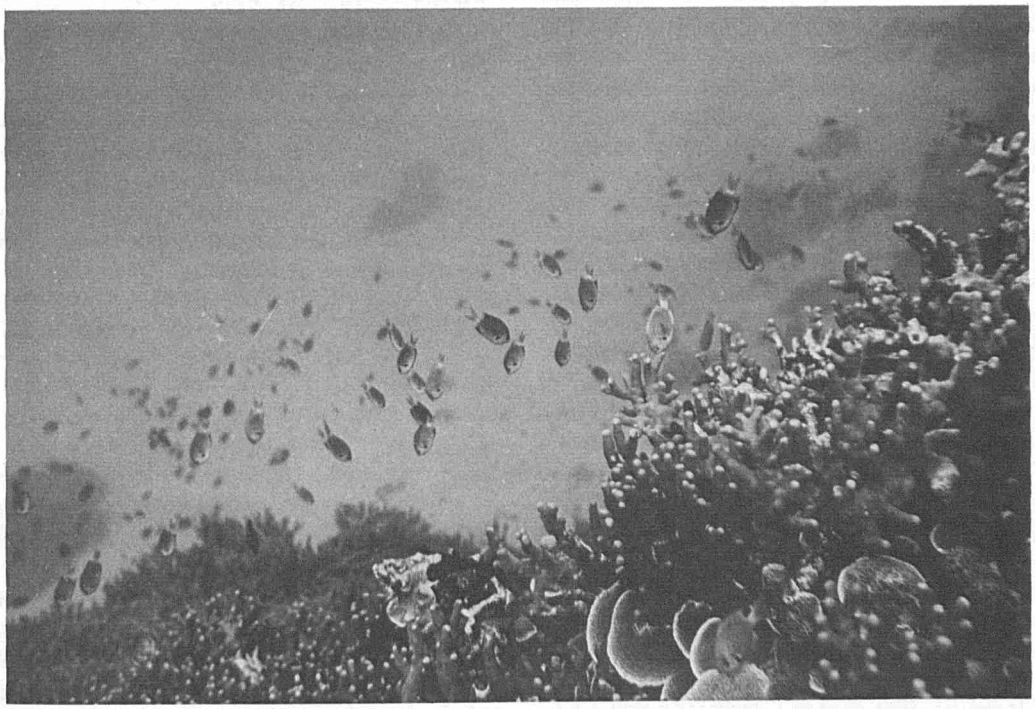


FIGURE 31.—Members of an aggregation of *Chromis leucurus,* a damselfish, having been threatened, dive from their plankton-feeding location in the water column toward shelter among the coral below.

TABLE 46.—Food of *Chromis leucurus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Cyclopoid copepods	5	19.0	19.00
2	Larvaceans	3	22.0	13.20
3	Calanoid copepods	3	4.0	2.40
4	Fish eggs, planktonic	4	2.8	2.24
5	Gelatinous clumps of blue-green algae	3	3.6	2.16
6	Fragments of algae	2	2.0	0.80
7	Harpacticoid copepods	1	0.4	0.08
Also, unidentified fragments		5	46.2	46.20

TABLE 47.—Food of *Chromis verater*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	5	29.6	29.60
2	Larvaceans	4	36.0	28.80
3	Cyclopoid copepods	5	2.2	2.20
4	Fish eggs, planktonic	3	2.4	1.44
5	Decapod shrimps	1	7.0	1.40
6	Siphonophores	1	0.8	0.16
7	Mysids	1	0.4	0.08
8	Chaetognaths	1	0.4	0.08
9	Polychaetes	1	0.2	0.04
10	Harpacticoid copepods	1	0.2	0.04
Also, unidentified fragments		5	20.8	20.80

Chromis verater Jordan and Metz

This damselfish is one of the more prominent fishes over both coral and basalt reefs in Kona at depths below about 15 m. During the day it swims in plankton-feeding aggregations that hover 2 to 5 m above the reef, where changing light levels and the appearance of certain predators produce effects much as described above for *Abudefduf abdominalis* and other planktivorous pomacentrids. Also as in these other species, *C. verater* passes the night among cover on the reef, relatively quiet but alert. It moves about under moonlight, but rests in crevices on dark nights.

Of the seven specimens (120: 100-141 mm) examined, two that were collected from among cover on the reef shortly before first morning light (one after a night of bright moonlight, the other after a dark night) contained only a few well-digested fragments, whereas, all five speared from aggregations above the reef during afternoons were full of food (including fresh material), as listed in Table 47.

Swerdloff (1970b), who recognized that *C. verater* inhabits relatively deep water, reported the following categories of prey in 13 specimens from one collection on the island of Oahu (ranked as percent of the diet): copepods, 71.5%; tunicates, 17.6%; malacostracans, 4.7%; mollusks, 2.5%; fish eggs, 1.7%; and siphonophores, 1.7%. He also presented additional data of food habits, as he compared the ecology of *C. verater* with that of its congener *C. ovalis* see below).

Gosline and Brock (1960) noted that *C. verater* occurs in deeper water than other Hawaiian pomacentrids. This conclusion was later supported by Brock and Chamberlain (1968) who, making observations from a submarine, found *C. verater* to be the most abundant reef fish around rocky outcrops at a depth of 70 m.

CONCLUSION.—*Chromis verater* is a diurnal planktivore that takes primarily copepods and larvaceans.

Chromis ovalis (Steindachner)

This species is less numerous in Kona than any of the other planktivorous damselfishes described above. It occurs over irregular substrata of exposed basalt interspersed with coral at depths between 5 and 20 m. During the day it aggregates 2 to 5 m above the reef—at about the same level as *C. verater,* with which it often forms mixed groups (Swerdloff, 1970b). Its reactions to changing light and threatening situations are as described above

TABLE 48.—Food of *Chromis ovalis*.

Rank	Items	No. fish with this item (n = 2)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	2	47.5	47.50
2	Larvaceans	2	7.5	7.50
3	Cyclopoid copepods	2	3.0	3.00
4	Mysids	1	2.5	1.25
5	Decapod shrimps	1	2.5	1.25
Also, unidentified fragments		2	37.0	37.00

for *Abudefduf abdominalis* and for other planktivorous pomacentrids; its nocturnal behavior also is like that described for these other species.

Of six specimens (124: 121-138 mm) examined, all four that were speared among corals shortly before first morning light (two after dark nights, two after moonlit nights) contained only a few well-digested fragments, whereas two that were speared from aggregations above the reef during midafternoon were full of food (including fresh items), as listed in Table 48.

Swerdloff (1970b) reported the following categories of prey in eight *C. ovalis* from one collection on the island of Oahu (ranked as percent of the diet): copepods, 60.1%; tunicates, 16.9%; malacostracans, 9.5%; mollusks, 9.5%; polychaetes, 2.3%; fish eggs, 0.8%; and siphonophores, 0.8%. Gosline and Brock (1960) reported "a mass of copepods" in the stomach of one individual of this species.

CONCLUSION.—*Chromis ovalis* is a diurnal planktivore that takes primarily copepods.

General Remarks on Damselfishes

Pomacentrids are widely recognized as being active by day and relatively inactive at night. For example, they were so described in the Gulf of California (Hobson, 1965, 1968a), and also in the tropical Atlantic (Starck and Davis, 1966; Collette and Talbot, 1972). Food-habit data from the various members of this family in areas as widely separated as the West Indies (Randall, 1967) and the Marshall Islands (Hiatt and Strasburg, 1960) show widely divergent habits: some are strictly herbivorous, others are omnivorous, and still others are strictly carnivorous.

The habitat of each pomacentrid in Kona is especially well defined. Two major categories exist: those that forage on the bottom and those that feed in the water column.

BOTTOM FEEDERS.—Pomacentrids that forage on the sea floor have especially diverse diets. Algae and organic detritus are the major foods of many, especially among species of *Pomacentrus* (Hiatt and Strasburg, 1960; Randall, 1967). In Kona, *P. jenkinsi* is in this category, but *P. pavo* in the Marshall Islands is primarily a predator on small fishes and crustaceans (Hiatt and Strasburg, 1960). The diets of species of *Abudefduf* appear even more diverse. *Abudefduf sindonis* in Kona has food habits similar to those of *P. jenkinsi*, but the highly omnivorous *A. sordidus* forages on a wide variety of benthic animals and plants, whereas the predaceous *A. imparipennis* takes mostly benthic crustaceans and polychaetes. *Abudefduf saxatilus* in the West Indies is, according to Randall (1967), "one of the most diversified of all fishes in its food habits," feeding as it does on a wide assortment of plants and animals from both sea floor and water column. Similarly, *A. troschelii* in the Gulf of California feeds on zooplankton and bits of algae from the water column, as well as organisms from the substratum (Hobson, 1968a).

WATER-COLUMN FEEDERS.—Planktivorous pomacentrids are prominent on coral reefs throughout tropical seas. Their characteristic mid-water aggregations have been described in the Indian Ocean (Eibl-Eibesfeldt, 1962), central Pacific (Hiatt and Strasburg, 1960), Gulf of California (Hobson, 1965, 1968a), and the tropical Atlantic (Starck and Davis, 1966). In the Bahamas, Stevenson (1972) showed that the height in the water column at which *Eupomacentrus partitus* feeds on plankton is determined largely by light and current. The progressive ascent of planktivorous pomacentrids into the water column during morning twilight, as they rise to their mid-water feeding grounds, and their subsequent descent to the reef during evening twilight, has been described in Kona (Hobson,

1972) and the West Indies (Collette and Talbot, 1972).

Some of these planktivorous pomacentrids, for example *Abudefduf saxatilus* and *A. troschelii,* noted above, also forage part time on the sea floor. However, most of them, including the species of *Chromis* and *Dascyllus,* are specialized as predators on zooplankton, especially copepods. Examples include the representatives of these genera on Kona reefs, described in the present report, as well as others from the central Pacific (Hiatt and Strasburg, 1960) and tropical Atlantic (Randall, 1967).

Family Cirrhitidae: hawkfishes

Paracirrhites arcatus (Cuvier)—*pili ko'a*

This hawkfish is numerous in areas richly overgrown by the coral *Pocillopora meandrina.* Typically, it rests immobile on the coral heads during day, and takes shelter among the coral branches at night. Individuals shorter than about 50 mm are among the coral branches day and night, whereas those longer than about 90 mm frequently occur on the other hard substrata—perhaps because they are too large to fit between the branches of most *Pocillopora* heads. *Paracirrhites arcatus* moves only infrequently—a short dash to capture prey, or when threatened.

Forty-five specimens (82: 49-101 mm) were collected during day and night. The nighttime situation is reflected in the 17 that were speared during the 2 h before first morning light (13 on moonlit nights, 4 on dark nights). Of these, 16 (52 to 95 mm) were resting among branches of *Pocillopora,* whereas the other (99 mm) was amid a fingerlike growth of *Porites compressus.* The stomachs were empty in 13 and contained only well-digested fragments in 3. The last individual, taken during new moon, contained a caridean shrimp that probably had been captured that night.

The daytime situation is reflected in the 12 individuals speared during afternoons, all perched in exposed positions on the reef when collected. Ten of these (71 to 101 mm) rested on *Pocillopora,* and two (95 and 97 mm) rested on rocks. Ten had stomachs full of food, much of it fresh, and although the remaining two had empty stomachs, their intestines were full.

Specimens collected at other times of day and night offer less conclusive data. Of nine speared at night (between 3 and 5 h after sunset), seven were deep among coral branches, but two rested in exposed positions (the latter situation was only rarely seen). Six of these had food in their stomachs, but although the material was well-digested in five, the sixth was full of a species of cyclopoid copepod that often swarmed around our diving lights for about 30 min, an hour or so after last evening light. Finally, of the seven speared within 2 h after sunrise as they rested on top of *Pocillopora* heads, four had the stomachs empty and three contained fresh prey. Identifiable material occurred in 20 of the 46 specimens examined, as listed in Table 49.

Hiatt and Strasburg (1960), reporting on this species from the Marshall Islands, remarked that it habitually lies motionless on the upper surface of living coral heads and listed a diet of crustaceans and fishes.

CONCLUSION.—*Paracirrhites arcatus* is a diurnal predator that feeds primarily on xanthid crabs and other benthic crustaceans.

Paracirrhites forsteri (Bloch and Schneider)—*hilu pili ko'a*

This hawkfish is numerous in coral-rich areas, where it rests immobile in exposed positions on the reef during the day (Figure 32). Its attitude is

TABLE 49.—Food of *Paracirrhites arcatus.*

Rank	Items	No. fish with this item (n = 20)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	43.3	25.98
2	Decapod shrimps	6	15.5	4.65
3	Fish	3	10.5	1.58
4	Ophiuroids	1	5.0	0.25
5	Calapid crabs	1	4.3	0.22
6	Cyclopoid copepods	1	4.0	0.20
7	Crab megalops	2	1.8	0.18
8	Gammaridean amphipods	2	0.5	0.05
9	Calanoid copepods	1	0.3	0.02
Also, crustacean fragments		6	13.5	4.05
	Unidentified fragments	1	1.3	0.07

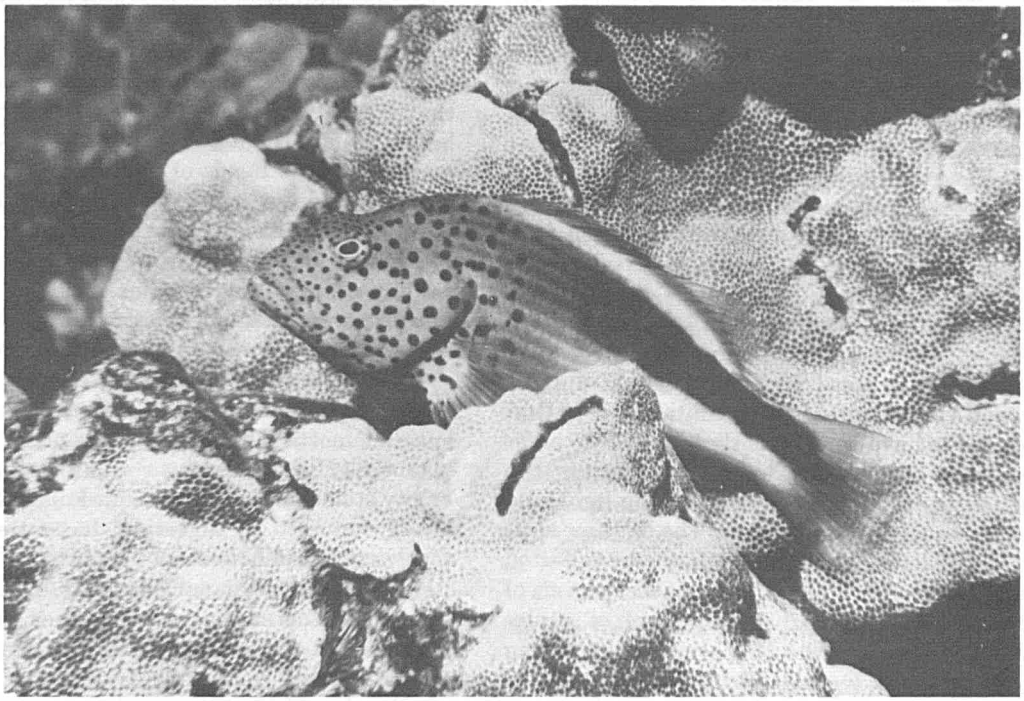


FIGURE 32.—*Paracirrhites forsteri,* a hawkfish, seated on the reef during the day.

much like that of *P. arcatus,* above, but it occurs widely on different hard surfaces, rather than being mostly associated, as is *P. arcatus,* with one type of coral. In the manner typical of hawkfishes, *P. forsteri* moves only infrequently, attacking prey that have come within range of a short, explosive dash. Such attacks were seen only during the day; at night *P. forsteri* generally is out of sight in reef crevices.

Thirty-six specimens (139: 93-181 mm) were collected during day and night. Of the 28 that were speared as they rested during midday on a variety of reef substrata, 18 contained food in the stomach, much of it relatively fresh (although in 1 the material was reduced to unidentifiable fragments). In contrast, among eight others that were speared from deep within reef crevices during the 2 h immediately before first morning light, four had empty stomachs and three contained only well-digested fragments; only the eighth specimen contained relatively fresh prey—a shrimp, *Saron marmoratus*—that appeared to have been taken that night.

Fish were the major prey, occurring in 14 of the 21 individuals that contained identifiable material (mean percent of diet volume: 66.6; ranking index: 44.4). Other food items were: caridean shrimps in four (mean percent of diet volume: 16.2; ranking index: 3.09), xanthid crabs in one (mean percent of diet volume: 4.8; ranking index: 0.23), and unidentified crustacean fragments in three (mean percent of diet volume: 12.4; ranking index: 1.77). The only identifiable fish among the gut contents was a wrasse, *Thalassoma duperrey.* Three of the four individuals containing caridean shrimps had preyed on *Saron marmoratus.* Of the larger shrimps (to about 50 mm), this was the one most frequently seen after dark, but only one of these, noted above, appeared to have been captured at night. Perhaps significantly, the specimens of *P. forsteri* that were examined had preyed on either fishes or crustaceans, but never on both.

Hiatt and Strasburg (1960), citing the similarity in habits between *P. forsteri* and *P. arcatus,* noted that the diet of *P. forsteri* runs more to fishes than crustaceans. I agree with them that this difference probably relates to the size difference between these two congeners.

CONCLUSION.—*Paracirrhites forsteri* is a diurnal predator that preys mostly on small fishes.

Cirrhitops fasciatus (Bennett) — *'o'opu kaha 'iha 'i*

This hawkfish is numerous on both coral and basalt reefs, and unlike the two species of *Paracirrhites,* above, occurs in exposed positions at night as well as during the day. In typical hawkfish fashion, it generally rests immobile on the substratum, except when attacking prey; thus, it is difficult to differentiate periods of activity from periods of inactivity.

Twenty-three specimens (76: 39-91 mm) were collected during night and day. Seven of nine speared from exposed positions under moonlight between 4 and 5 h after sunset contained prey that appeared to have been recently ingested. In addition, three of six individuals taken during the hour immediately before first morning light also contained relatively fresh prey. The daytime situation is reflected by specimens that were collected during afternoons, where the stomachs from six of eight individuals contained prey, much of it relatively fresh. Items in the 16 specimens containing identifiable prey are listed in Table 50.

CONCLUSION.—*Cirrhitops fasciatus* regularly feeds during both day and night, mostly on xanthid crabs and other benthic crustaceans.

Cirrhitus pinnulatus (Bloch and Schneider)— *po'o pa'a*

This hawkfish is numerous at depths of less than 5 m in and around crevices on surge-swept basalt reefs (Figure 5). Corals in this habitat are mostly isolated heads of *Pocillopora meandrina* and encrusting patches of *Porites compressus.* As do other hawkfishes, *C. pinnulatus* generally rests motionless on the substratum. During the day it usually remains under at least partial cover; at night it more frequently occurs in exposed positions on the reef.

All 32 specimens (152: 103-221 mm) that were examined were resting immobile on the reef when speared, most of them partially concealed in crevices. Of 17 taken during the afternoon, 14 had empty stomachs, and 3 contained material extensively damaged by digestion. In contrast, of 15 that were taken between 1 h before first morning light and 2 h after sunrise, only 4 had empty stomachs, whereas each of the other 11 had the stomach full of food, much of it fresh. Items in the 14 individuals containing identifiable material are listed in Table 51.

Most of the xanthid crabs among these gut contents were *Trapezia,* a genus common among branches of the coral *Pocillopora.* Hiatt and Strasburg (1960) also reported a crab of this genus in one *C. pinnulatus* that they examined from the

TABLE 50.—Food of *Cirrhitops fasciatus.*

Rank	Items	No. fish with this item (n = 16)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	7	30.9	13.52
2	Decapod shrimps	5	20.9	6.53
3	Crab megalops	2	7.8	0.98
4	Ophiuroids	1	6.3	0.39
5	Octopods	1	6.3	0.39
6	Gammaridean amphipods	1	0.6	0.04
Also, crustacean fragments		5	22.2	6.94
	Unidentified fragments	1	5.0	0.31

TABLE 51.—Food of *Cirrhitus pinnulatus.*

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	11	60.0	47.14
2	Oxyrhynchan crabs	3	7.5	1.61
3	Decapod shrimps	3	2.9	0.62
4	Ophiuroids	1	7.1	0.51
5	Octopods	1	7.1	0.51
6	Echinoids	1	3.2	0.23
7	Pagurid crabs	1	1.1	0.08
Also, crustacean fragments		3	11.1	2.38

Marshall Islands. Randall (1955) reported only brachyuran crabs in the diet of two specimens that he examined from the Gilbert Islands.

CONCLUSION.—*Cirrhitus pinnulatus* is a nocturnal predator that hunts mostly xanthid crabs.

Family Labridae: wrasses

Bodianus bilunulatus (Lacépède) — *'a'awa*

This relatively large, solitary wrasse occurs only infrequently on the shallow reefs in Kona as it lives mostly at depths below 15 m. Two individuals (172 and 283 mm) were speared during midafternoon as they moved actively among coral at 25 m along the outer drop-off, and the guts of both were full of crushed mollusks.

CONCLUSION.—*Bodianus bilunulatus* feeds on mollusks during the day.

Cheilinus rhodochrous Günther—*po'ou*

This labrid is numerous over both coral and rocky substrata deeper than about 10 m. It is a solitary species that hovers close to the reef during the day and takes shelter in the reef at night. Several times larger individuals attempted to take fish that were impaled on my spear, and twice they succeeded despite my attempts to drive them away.

Among 16 specimens (175: 129-242 mm) collected during afternoons, 6 contained only a few well-digested fragments posteriorly in the gut, and most of the material in the other 10 was far digested. Fish were the major prey, occurring in 4 of the 10 individuals that contained identifiable material (mean percent of diet volume: 40; ranking index: 16). Other food items were: decapod shrimps in three (mean percent of diet volume: 30; ranking index: 9), brachyuran crabs in one (mean percent of diet volume: 8; ranking index: 0.8), unidentified crustacean fragments in two (mean percent of diet volume: 12; ranking index: 2.4), and other unidentified fragments in two (mean percent of diet volume: 10; ranking index: 2). The only fish that could be identified was a pomacentrid, *Pomacentrus jenkinsi,* and the only identifiable shrimp was *Saron marmoratus*. Generally *C. rhodochrous* preys on large organisms, but because it crushes them upon ingestion, identifications are difficult. Presumably crushing the food items accelerates digestion, thus contributing to the poor condition of this material. However, because all these specimens were collected during afternoons, the advanced digestion could also reflect early morning feeding.

Cheilinus rhodochrous is a stalking predator, equipped by a relatively large mouth and pair of large canine teeth at the front of each jaw to hunt prey that are relatively larger and more active than those taken by most other labrids. Most of the specimens that were examined contained a single large prey organism, indicating that feeding is infrequent and that each successful attack provides enough nourishment to sustain the predator for some time.

CONCLUSION.—*Cheilinus rhodochrous* is a diurnal predator that stalks relatively large fishes and crustaceans. It may have peaks in feeding early and late in the day, but is inactive at night.

Pseudocheilinus octotaenia Jenkins

This small species is one of the more numerous labrids on coral-rich reefs at depths to at least 30 m, but its large numbers are difficult to appreciate because it occurs close among the many narrow interstices of the reef. It is strictly a diurnal species that takes shelter in the reef at night.

All 12 specimens (77: 50-95 mm) taken during afternoons had material in their stomachs, but the food items were difficult to identify because they were small and had been crushed when ingested. Thus, most of the gut contents of all 10 individuals that contained recognizable material can be listed only as unidentified crustacean fragments (mean percent of diet volume and ranking index: 71.9). Items that could be identified are: brachyuran crabs in three (mean percent of diet volume: 22; ranking index: 6.6), echinoids in one (mean percent of diet volume: 5; ranking index: 0.5), demersal fish eggs in one (mean percent of diet volume: 1; ranking index: 0.1), and copepods in one (mean percent of diet volume: 0.1; ranking index: 0.01).

CONCLUSION.—*Pseudocheilinus octotaenia* is a diurnal predator that feeds mostly on brachyuran crabs and other benthic crustaceans.

Labroides phthirophagus Randall

This small wrasse (most are less than 100 mm long) is specialized to pick ectoparasites from the

bodies of other fishes at well-defined cleaning stations (Figure 33). Usually two or several of these cleaners are active at each station. It is a diurnal species that shelters in reef crevices at night (Hobson, 1972).

This is the major cleaner fish on Hawaiian reefs, and its habits are well known (e.g. Randall, 1958; Youngbluth, 1968; Losey, 1971; Hobson, 1971). Because the activity of this species has been extensively documented, it was only incidentally observed during the present study.

CONCLUSION.—*Labroides phthirophagus* cleans ectoparasites from the bodies of other fishes during the day.

Thalassoma duperrey (Quoy and Gaimard) — *hinalea lauwili*

This is probably the most ubiquitous fish on Kona reefs (Figure 33): it is numerous everywhere, from the surge-swept reef tops to the outer drop-off on both coral-rich and exposed basalt substrata. In the daytime fish counts along transect lines, *T. duperrey* ranked among the five most numerous species in all the sampled habitats. An opportunist, it is consistently the first fish to appear when a sea urchin has been crushed, or when a rock has been overturned and vulnerable organisms exposed. Sometimes it follows close to the feeding jaws of scarids to snap up prey uncovered when these herbivores disturb the substratum. This wrasse is adapted to a wide range of habits: it forages in the water column when plankton are abundant, but mostly picks organisms off a variety of substrata. It is strictly a diurnal species that shelters in reef crevices at night (Hobson, 1972).

Many of the juveniles are cleaners and maintain stations at certain prominent coral heads. On one survey 5 m deep along approximately 1 km of the north shore of Honaunau Bay, I found a cleaning station maintained by these fish at every large head of *Porites pukoensis* that was of a distinctive mustardlike hue and characterized by golf-ball-sized nodules separated by narrow, shallow depressions. The general extent of this cleaner's relationship to this type of coral was not determined, but I saw cleaning stations nowhere else during the survey. Because the juveniles of *T. duperrey* always discontinued cleaning when a human was near, incidental observations of this activity were rare. And, as noted above in discussing *Labroides*

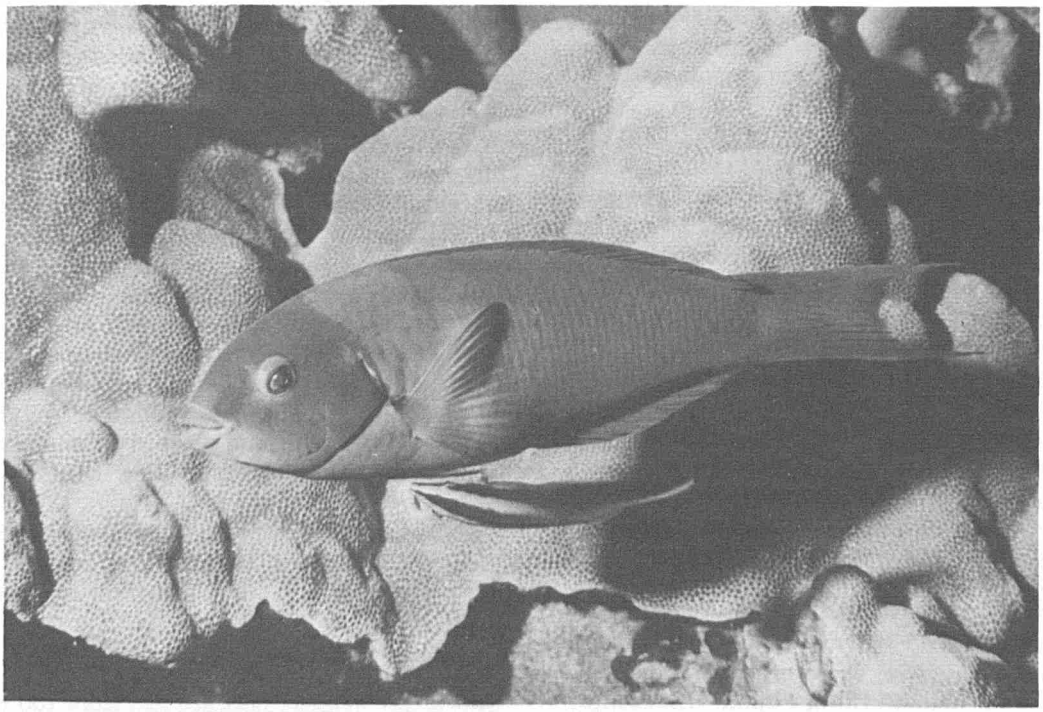


FIGURE 33.—A wrasse, *Thalassoma duperrey*, being cleaned by another wrasse, *Labroides phthirophagus*.

phthirophagus, my observations of cleaning were mostly incidental. Nevertheless, it was evident that cleaning by *T. duperrey* is mostly an activity of juveniles. Adults clean only infrequently, and not at well-defined cleaning stations.

To indicate the food of the post juveniles of this species, 24 specimens, 125 (103-146) mm long, were speared during the day as they swam actively over the reef. All contained identifiable items, as listed in Table 52. In contrast with the diet of most fishes examined during this study, no single item or certain few items predominate in the diet of *T. duperrey,* a circumstance that undoubtedly relates to its populating a wide range of habitats.

CONCLUSION.—*Thalassoma duperrey* is a diurnal predator that feeds on a very wide range of shelled organisms, most of them benthic.

Thalassoma fuscus (Lacépède)—*hou*

This species was shown by numerous observations of spawning aggregations to include the nominal *T. umbrostigma* (which represents the juveniles and females). It is a fish of shallow water along rocky, surge-swept shores and is one of the most numerous species on the shallow reef flats. Generally it does not occur in water deeper than about 5 m and is strictly a diurnal fish that shelters in reef crevices after dark.

All 14 specimens (132: 60-200 mm) speared as they swam on the reef during daylight contained identifiable food material, as listed in Table 53. Hiatt and Strasburg (1960) reported on two specimens of this species (as *T. umbrostigma)* in the Marshall Islands: one had consumed a stomatopod, the other a fish. Randall (1955) reported (also as *T. umbrostigma*) that one specimen taken in the Gilbert Islands contained a crab.

CONCLUSION.—*Thalassoma fuscus* is a diurnal predator that feeds mostly on crabs and mollusks.

Halichoeres ornatissimus (Garrett)—*la'o*

In Kona this labrid is nowhere particularly numerous, yet it occurs regularly in all inshore habitats. It is generally solitary and swims close to cover during the day. At night it is out of sight, presumably resting in crevices or under the sand.

All 13 specimens (96: 76-115 mm), speared during daylight, had a full gut that included fresh material, as listed in Table 54. Food items more than about 4 mm in greatest dimension were crushed, and this included most of the mollusks. Probably at least much of the unidentified material constituted fragmented molluscan soft parts. This fish plucks small benthic organisms off the substratum, including some forms, like the didemnid tunicates, that are attached to the reef.

TABLE 52.—Food of *Thalassoma duperrey.*

Rank	Items	No. fish with this item (n = 24)	Mean percent of diet volume	Ranking index
1	Gastropod mollusks	9	7.5	2.81
2	Echinoids	3	7.9	0.99
3	Brachyuran crabs	3	6.1	0.76
4	Pelecypod mollusks	3	5.0	0.63
5	Gammaridean amphipods	9	1.5	0.56
6	Calanoid copepods	2	6.3	0.53
7	Tanaids	6	1.3	0.33
8	Cyclopoid copepods	4	1.4	0.23
9	Scleractinian corals	2	2.5	0.21
10	Polychaetes	2	2.1	0.18
11	Ophiuroids	2	1.5	0.13
12	Tunicates	2	1.5	0.13
13	Isopods	2	0.9	0.08
14	Fish eggs	2	0.6	0.05
15	Caprellid amphipods	2	0.4	0.03
16	Pagurid crabs	2	0.4	0.03
17	Foraminiferans	1	0.2	<0.01
18	Sipunculid introverts	1	0.2	<0.01
19	Fish	1	0.2	<0.01
20	Unidentified eggs	1	<0.1	<0.01
Also, crustacean fragments		11	9.4	4.31
	Algae fragments	8	11.5	3.83
	Unidentified material	15	31.5	19.69

TABLE 53.—Food of *Thalassoma fuscus*.

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Brachyuran crabs	7	35.5	17.75
2	Mollusks	5	17.2	6.14
3	Octopods	1	7.1	0.51
4	Ophiuroids	1	5.0	0.36
5	Polychaetes	2	1.8	0.26
6	Sipunculid introverts	2	1.4	0.20
7	Crab megalops	1	2.8	0.20
8	Fish	1	2.5	0.18
9	Gammaridean amphipods	3	0.7	0.15
10	Cyclopoid copepods	3	0.6	0.13
11	Calanoid copepods	1	1.4	0.10
12	Isopods	1	0.1	<0.01
Also, crustacean fragments		2	3.7	0.53
	Unidentified fragments	8	20.2	11.54

TABLE 54.—Food of *Halichoeres ornatissimus*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Mollusks	6	13.5	6.23
2	Gammaridean amphipods	7	7.7	4.15
3	Colonial diatoms	4	6.9	2.12
4	Didemnid tunicates	3	8.8	2.03
5	Tanaids	5	1.5	0.58
6	Harpacticoid copepods	4	1.7	0.52
7	Sipunculid introverts	3	1.2	0.28
8	Ophiuroids	1	3.1	0.24
9	Cyclopoid copepods	2	0.8	0.12
10	Polychaetes	1	1.5	0.12
11	Isopods	2	0.5	0.08
12	Demersal eggs	1	0.8	0.06
13	Echinoids	1	0.4	0.03
14	Ostracods	1	0.1	<0.01
Also, crustacean fragments		7	10.8	5.82
	Sand and foraminiferans	3	4.5	1.04
	Algal fragments	2	1.2	0.18
	Unidentified fragments	10	35.0	26.92

The widespread occurrence of this fish probably relates to the fact that no single item, or certain few items, especially predominate in its diet. This is true to an even greater degree in the ubiquitous *Thalassoma duperrey,* above, but is unlike most fishes on Kona reefs.

CONCLUSION.—*Halichoeres ornatissimus* is a diurnal predator that picks a wide variety of small benthic animals from the sea floor.

Stethojulis balteata (Quoy and Gaimard) — *'omaka*

This wrasse is most numerous on the shallow reef flats and on some of the reefs richly overgrown with corals. During the day it swims close to rocks or coral, at which it periodically picks. At night it rests in reef crevices, or buried in the sand.

All five specimens (90: 76-102 mm) collected during daylight had a gut full of material, some of it fresh, as listed in Table 55. The major food items—small crustaceans shorter than about 4 mm—were mostly intact. Larger items, such as some of the gastropods, were crushed.

CONCLUSION.—*Stethojulis balteata* is a diurnal predator that mostly picks small crustaceans and gastropods off the sea floor.

Anampses cuvier Quoy and Gaimard—*'opule*

Although this wrasse occupies all inshore reef habitats in Kona, it is most numerous where the sea floor consists of basalt boulders. During the day, solitary individuals swim close to the substratum, where they inspect the surface, and frequently pluck at the low growth of algae on the

TABLE 55.—Food of *Stethojulis balteata*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Harpacticoid copepods	5	19.4	19.40
2	Prosobranch gastropods	4	15.6	12.48
3	Gammaridean amphipods	3	8.6	5.16
4	Tanaids	3	5.0	3.00
5	Foraminiferans	2	2.4	0.96
6	Isopods	2	2.4	0.96
7	Polychaetes	1	4.0	0.80
8	Echinoids	1	1.0	0.20
9	Sipunculid introverts	1	0.6	0.12
10	Cyclopoid copepods	1	0.4	0.08
Also, crustacean fragments		5	15.0	15.00
	Sand and debris	4	10.2	8.16
	Unidentified fragments	4	15.4	12.32

TABLE 56.—Food of *Anampses cuvier*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	10	28.9	24.08
2	Mollusks	10	18.1	15.08
3	Polychaetes	3	4.3	1.08
4	Xanthid crabs	3	1.8	0.45
5	Fish eggs, demersal	1	5.0	0.42
6	Echinoids	2	1.9	0.32
7	Tanaids	3	0.3	0.08
8	Isopods	3	0.3	0.08
9	Didemnid tunicates	2	0.3	0.05
Also, crustacean fragments		9	14.1	10.58
	Sand and foraminiferans	4	4.3	1.43
	Algal fragments	3	1.9	0.48
	Unidentified fragments	8	18.8	12.53

rocks. Much sand has accumulated here, and periodically they pause during their foraging to blow a small cloud of sand and debris from their mouths. At night this wrasse is out of sight, presumably resting in reef crevices.

All 12 specimens (169: 110-225 mm) speared during daylight had a gut full of material, much of it fresh, as listed in Table 56. The gammaridean amphipods, all shorter than 3 mm, were the major prey of even the largest individuals. Furthermore, the mollusks, which were the only other significant prey, were mostly prosobranch gastropods also shorter than 3 mm.

Undoubtedly, the small size and other characteristics of these prey are reflected in the feeding morphology of *A. cuvier* and its congeners, certain features of which set them apart from most other labrids in Kona. In dentition, the species of *Anampses,* with two flattened teeth projecting forward from the front of each jaw, are unlike those of any other genus of Hawaiian fishes (Gosline and Brock, 1960). Obviously this specialized dentition effectively captures gammarideans that inhabit the low stubble of algae overgrowing most basalt boulders. Compared with most other labrids, species of *Anampses* have the pharyngeal teeth reduced, which is expected considering the relatively small proportion of crushed items in the diet. The food items are mostly so small they need not be crushed upon ingestion. Gammarideans and certain other prey of similar size regularly pass intact through the pharynx of even those labrids with well-developed pharyngeal teeth (see accounts of other labrids in this report).

CONCLUSION.—*Anampses cuvier* is a diurnal predator that mostly plucks small benthic organisms, especially gammarideans, from rocky substrata.

Coris gaimard (Quoy and Gaimard)—*hinalea lolo*

This wrasse is most numerous where the reef is interspersed with small patches of sand. It forages in this sand during daylight, usually close to the base of rock or coral. Of all the wrasses treated in this report, this one is the most adept at excavating buried organisms. Moving its head sidewise, it effectively overturns small stones or digs in the

TABLE 57.—Food of *Coris gaimard*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Mollusks	9	72.2	72.20
2	Echinoids	3	9.8	3.27
3	Crabs	1	2.2	2.44
4	Didemnid tunicates	1	0.6	0.07
5	Gammaridean amphipods	1	0.2	0.02
Also, crustacean fragments		5	15.0	8.33

TABLE 58.—Food of *Macropharyngodon geoffroy*.

Rank	Items	No. fish with this item (n = 8)	Mean percent of diet volume	Ranking index
1	Prosobranch gastropods	8	37.8	37.80
2	Foraminiferans	8	35.3	35.30
3	Harpacticoid copepods	2	0.4	0.10
4	Gammaridean amphipods	1	0.1	0.01
Also, crustacean fragments		2	0.6	0.15
	Sand and algae	5	8.4	5.25
	Unidentified fragments	6	17.4	13.05

sand, exposing hidden prey. It is not seen at night, when presumably it is buried in the sand, or secreted in reef crevices.

All nine specimens (117: 81-164 mm), speared during daylight, contained relatively fresh material, but items longer than a few millimeters were crushed so extensively that precise identifications were difficult. The gut contents are itemized in Table 57.

CONCLUSION.—*Coris gaimard* is a diurnal predator that mostly excavates mollusks and other prey that are buried in the sand.

Macropharyngodon geoffroy (Quoy and Gaimard)

This solitary little wrasse is widespread on Kona reefs, but is nowhere numerous. It swims close among coral and rocks during daylight, but is not seen after dark, when presumably it secretes itself in reef crevices, or under the sand.

All eight specimens (99: 74-120 mm) collected during the day had the gut full of the items listed in Table 58, almost all crushed.

The exceptionally large pharyngeal teeth of this wrasse obviously are adapted to a diet of heavily shelled organisms. The specimens examined, which had fed mostly on gastropods and foraminiferans, are undoubtedly representative. The foraminiferans were almost all *Marginospora vertebralis,* which is an abundant benthic form on shallow reefs in the Marshall Islands (Cushman, Todd, and Post, 1954).

CONCLUSION.—*Macropharyngodon geoffroy* is a diurnal predator that feeds mostly on benthic gastropods and foraminiferans.

Gomphosus varius Lacépède—bird wrasse, *hinalea 'i'iwi*

This wrasse is numerous on shallow surge-swept reefs, especially where the coral *Pocillopora meandrina* abounds. During daylight solitary individuals swim among the coral heads, probing with their elongated snouts among the coral branches. At night the species lies quietly in reef crevices.

All 12 specimens (142: 114-180 mm) collected during the day had their guts full of the items listed in Table 59. Most of this material was crushed. The xanthid crabs were mostly *Trapezia* sp. They and the alpheids are species that live among the branches of *P. meandrina*. Hiatt and Strasburg (1960) noted that this labrid's major prey in the Marshall Islands are xanthids and alpheids that live in the interstices of ramose corals. Randall (1955) similarly reported alpheid shrimps and also stomatopods in the diet of this species (as *G. tricolor)* in the Gilbert Islands.

Gomphosus varius takes relatively large motile prey, and with its large mouth does not pluck them from the substratum in the manner characteristic of the many other wrasses that prey on relatively tiny or sessile organisms. Rather, this wrasse vigorously wrests its prey from the reef crevices in which they are secreted.

TABLE 59.—Food of *Gomphosus varius*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	7	37.9	22.11
2	Alpheid shrimps	2	6.7	1.12
3	Pelecypods	1	4.2	0.35
4	Gastropods	2	2.1	0.35
Also, crustacean fragments		8	25.8	17.20
	Unidentified fragments	4	23.3	7.77

CONCLUSION.—*Gomphosus varius* is a diurnal predator that takes relatively large crustaceans from reef crevices.

General Remarks on Wrasses

Kona reefs, like tropical reefs the world over, are populated by a diverse array of wrasses, most of them with strong pharyngeal teeth adapted to crush hard-bodied prey. *Macropharyngodon geoffroy,* for example, preys on more heavily armored prey—in this case mollusks and foraminiferans. Others, like *Anampses cuvier,* have the pharyngeal teeth less developed and prey mostly on tiny crustaceans. Some of the wrasses, especially *Thalassoma duperrey,* are highly opportunistic, and these tend to be the most widespread and have the most varied diets.

It is well known that wrasses are active only during the day; at night they rest in reef crevices and under the sand (Longley and Hildebrand, 1941; Gosline and Brock, 1960; Hobson, 1965, 1968a, 1972; Starck and Davis, 1966; Collette and Talbot, 1972). They are among the first diurnal fishes on the reef to seek cover at day's end, and among the last to leave cover in the morning (Hobson, 1965, 1968a, 1972; Collette and Talbot, 1972).

Family Scaridae: parrotfishes

Scarus sordidus Forskål—*uhu*

This is one of the more numerous parrotfishes in Kona, especially over coral-rich reefs. During the day, it swims actively close to the substratum, often in groups. With its parrotlike beak, it scrapes away the fine filamentous algae that grows over the surface of dead coral, especially *Porites*. Although frequently it scrapes up to the edge of living coral, it stops there (Figure 34). During twilight, this species migrates in schools from one part of the reef to another, but the migratory pattern remains unclear (Hobson, 1972).

At night *S. sordidus* rests solitarily in reef crevices. Because some parrotfishes are known to secrete a mucous envelope around themselves at night (Winn, 1955), during a series of night observations over 3 mo I estimated the standard length of each resting parrotfish, and noted whether or not it was encased in mucus. During these observations, 20 individuals of this species were seen, estimated to be between 150 and 350 mm long. All eight that appeared to be shorter than 300 mm were in mucous envelopes, whereas all six without envelopes were judged to be longer than 300 mm. The other six, all estimated to exceed about 300 mm long, were in envelopes. Thus, all the smaller individuals, but only some of the larger ones, were in envelopes.

The guts of all seven *S. sordidus* (195: 150-213 mm) that were speared during midday were full of bits of algae, mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae constituted less than 20%). No evidence was found in these specimens of coral tissues or mucus (the latter is prominent in the gut contents of fishes known to feed on coral), even though Hiatt and Strasburg (1960) reported that coral polyps constituted the major food of this parrotfish in the Marshall Islands. These authors stated (p. 103): "Scraping living coral heads seems to be its predominant mode of feeding." This observation contrasts with mine in Kona, where *S. sordidus* avoids the living coral when feeding.

CONCLUSION.—*Scarus sordidus* is a diurnal herbivore that feeds mostly by scraping fine benthic algae that have overgrown the surface of dead coral.

Scarus taeniurus Valenciennes—*uhu*

My observations of their social interactions render it clear that the two forms Schultz (1969) distinguished in Hawaii as *S. taeniurus* and *S. forsteri* are conspecific and that his "*S. forsteri*" represents the large male of the species.

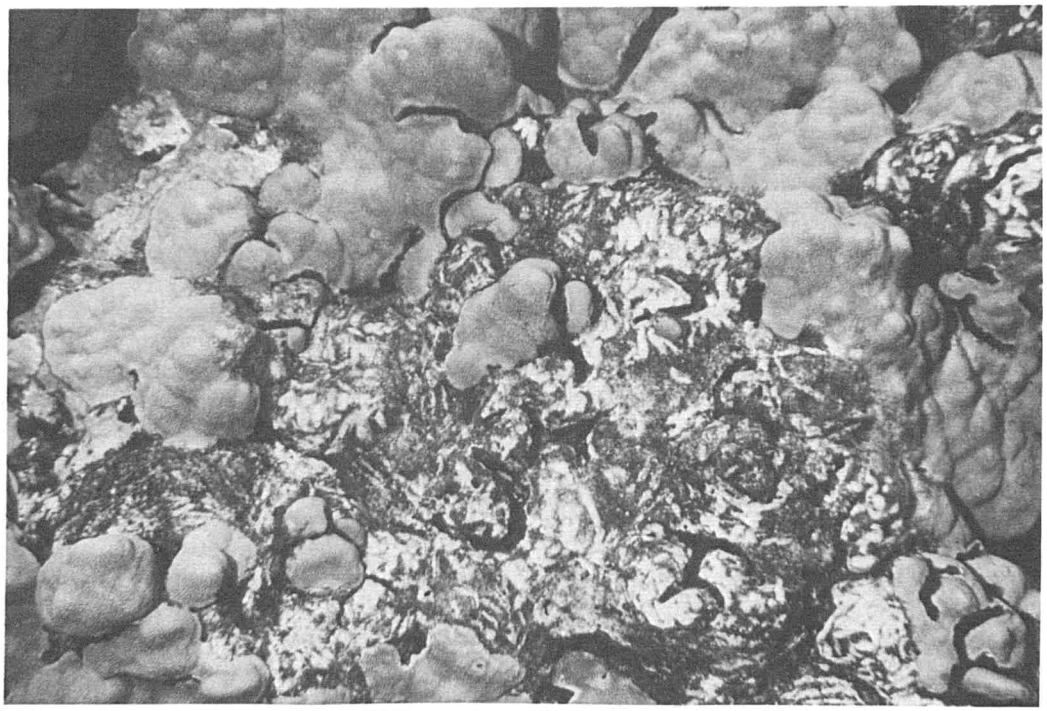


FIGURE 34.—Area of the reef showing scrape marks made by the teeth of grazing parrotfishes, mostly *Scarus sordidus*. Note that grazing has occurred only where dead coral is overgrown with algae—no living coral has been scraped.

This, the smallest Hawaiian species of *Scarus* (not exceeding a length of about 300 mm), is by far the most numerous parrotfish over exposed basalt on shallow reef flats and adjacent reef faces. The smaller juveniles and females, usually in aggregations, tend to occupy the shallow flats, the larger, distinctively hued males, which are usually solitary, tend to occupy the reef faces. This species is like *S. sordidus* in grazing during the day; however, whereas *S. sordidus* usually scrapes algae from the surface of dead coral, *S. taeniurus* ordinarily scrapes algae from the surface of rocks.

At night *S. taeniurus* rests in reef crevices. During the series of night observations in which I checked the incidence of mucous envelopes, all 11 *S. taeniurus,* which were less than 300 mm long, were in envelopes (Figure 35).

The two individuals (150 and 243 mm) that were collected during midday were full of bits of algae, mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae made up less than 20%), with no evident trace of coral tissue or mucus.

CONCLUSION.—*Scarus taeniurus* is a diurnal herbivore that usually feeds by scraping benthic algae from rock surfaces.

Scarus rubroviolaceus Bleeker—*uhu palukaluka*

During the day this parrotfish ranges over the reef, usually in mixed groups of several males and females. It occurs on all the inshore reefs, but mostly on rock substrata. Generally, using the sides of its jaws, it takes one bite and then withdraws a few centimeters before approaching for another bite.

At night *S. rubroviolaceus* rests in reef crevices. While surveying the incidence of mucous envelopes in resting parrotfishes (see accounts for *S. sordidus* and *S. taeniurus* above), of the nine *S. rubroviolaceus* that were observed, including both males and females approximately 200 to 500 (mean 394) mm long, none were in envelopes (Figure 36). Because the large and distinctive males of *S. rubroviolaceus* are not numerous, I came to recognize some individuals. These often returned

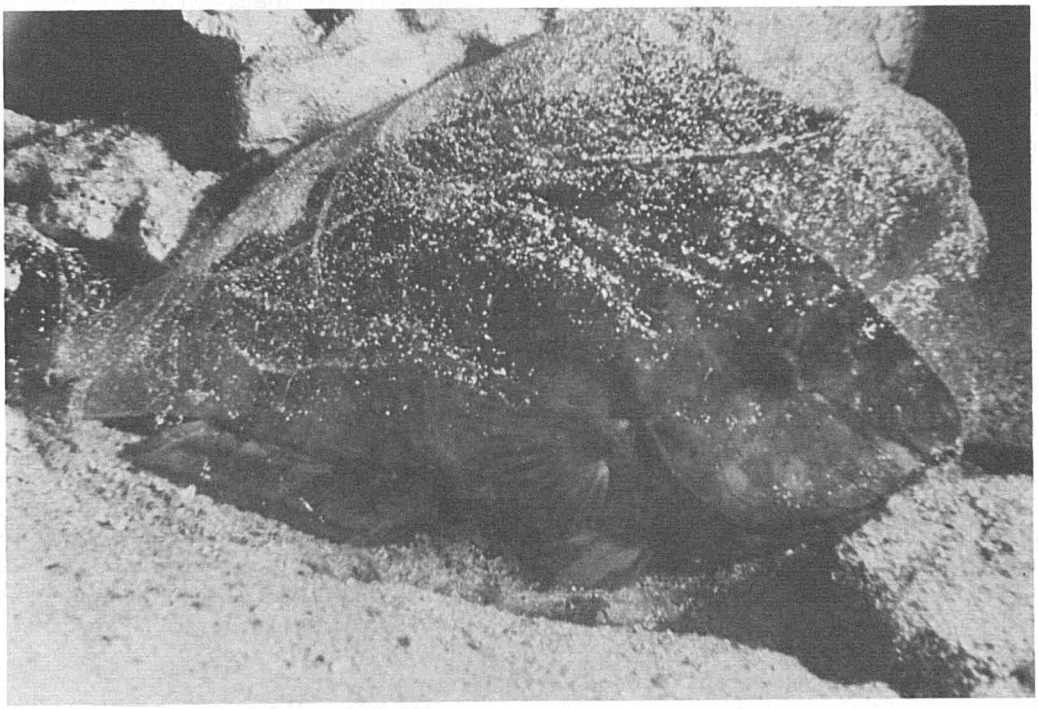


FIGURE 35.—*Scarus taeniurus,* a parrotfish, resting in a mucous envelope at night, a habit apparently shared by all members of this relatively small species.

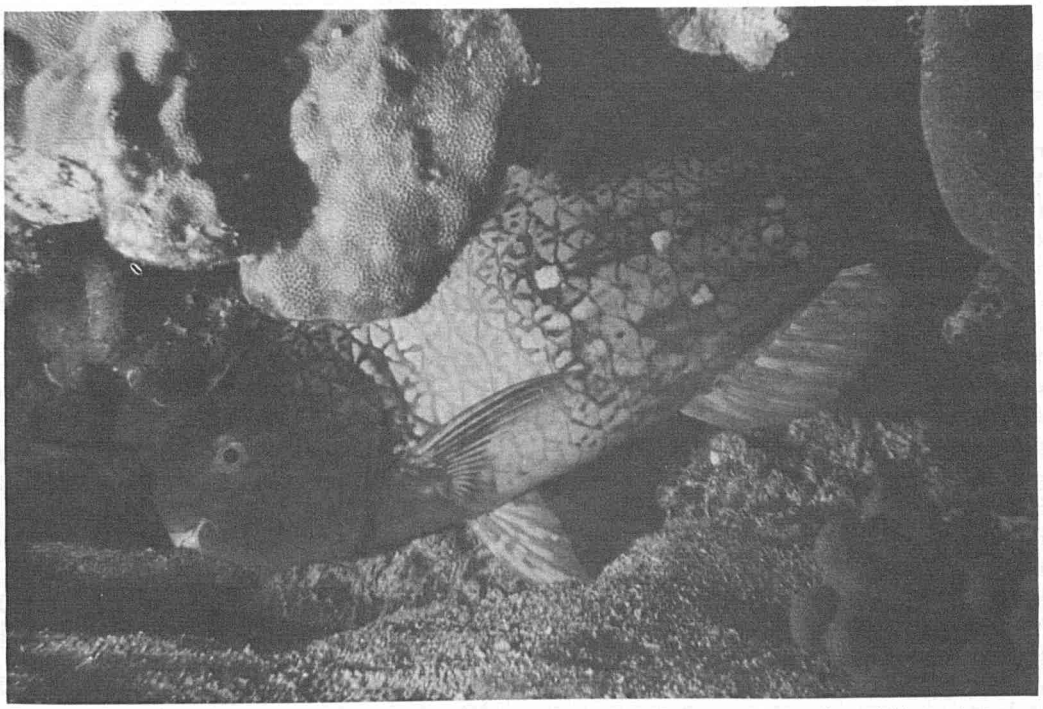


FIGURE 36.—*Scarus rubroviolaceus,* female, a parrotfish, resting under a ledge at night. Members of this species were never seen in mucous envelopes.

night after night to caves in the same areas, but not necessarily to the same cave, as has been reported for some parrotfishes elsewhere (e.g. Winn and Bardach, 1960; Starck and Davis, 1966).

The guts of two males (340 and 410 mm) that were speared during midday were full of bits of algae mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae constituted less than 20%), with no evident trace of coral tissue or mucus.

CONCLUSION.—*Scarus rubroviolaceus* is a diurnal herbivore that typically scrapes benthic algae from rock surfaces.

General Remarks on Parrotfishes

It is well known that parrotfishes are quiescent at night. They have been thus described in the tropical Atlantic (Winn, 1955; Winn and Bardach, 1959, 1960), eastern Pacific (Hobson, 1965; Rosenblatt and Hobson, 1969), Hawaii (Hobson, 1972), and elsewhere. Earlier (Hobson, 1965), I suggested that mucous envelopes in resting parrotfishes at night are characteristic of certain small individuals, or of individuals suffering injury or stress. The relation between small size and envelope secretion was also noted by Starck and Davis (1966) and by Casimir (1971). Winn and Bardach (1959) believed that the envelope is a defense against nocturnal predators, especially those that sense prey by olfaction or gustation, as do certain moray eels (Bardach, Winn, and Menzel, 1959). Because the threat from predators increases with decreasing size, obviously the smaller individuals are in greatest need for protection. Similarly, it is known that injured or distressed fishes are particularly attractive to predators (e.g. Hobson, 1968a), so envelope secretion by parrotfishes suffering these conditions is consistent with the idea that the envelopes provide protection. The survey of mucous envelopes in Kona shows a decreasing incidence with increasing size. Nevertheless, Winn and Bardach (1960), working with *Scarus vetula* at Bermuda, found that certain individuals in aquaria produced the envelope irregularly, and Smith and Tyler (1972) found that one individual of that species observed on a reef in the Virgin Islands formed an envelope on some nights, but not on others. Probably this variation within individuals occurs in other species too, but the question was not examined in Kona, where only certain males of *S. rubroviolaceus* were recognized as individuals, and these were never seen in envelopes.

There is controversy over the diet of parrotfishes. Hiatt and Strasburg (1960) reported a diet of living coral not only in *S. sordidus,* as noted above, but also in all other scarids they examined in the Marshall Islands. I found no evidence that any of the species in Kona, including *S. sordidus,* feed on living coral. Randall (1967) similarly concluded that parrotfishes in the West Indies do not feed on living coral; he noted the large amount of sand in the guts of parrotfishes, and suggested that this material, taken purposefully, aids in grinding plant tissue—the primary food —in the pharyngeal mill.

Although I classify all parrotfish species in Kona as herbivores, their large gut loads of calcareous powder, organic slurry, and sand seem too great a proportion of the total contents to have been taken only incidentally, or to be adaptive only because it aids in grinding up plant tissue. There is need to look closer at how parrotfishes utilize the material they ingest.

Family Blenniidae: combtooth blennies

The combtooth blennies are most numerous in tide pools and close to rocky shores, where frequently they are the dominant fishes. However, this report considers only those species that occur regularly in water deeper than 5 m.

Exallias brevis (Kner)—*pao'o kauila*

Because *E. brevis* is distinctively hued and habitually perches in exposed positions during the day (Figure 37), it is frequently noticed even though it is not especially numerous. It rarely leaves the sea floor and usually rests immobile except when scraping the surface of living coral with its comb-like teeth. After dark, it is secreted in reef crevices and seen only occasionally.

Of the 10 specimens (94: 70-106 mm) examined, 2 that were taken from under partial cover at night (between 4 and 5 h after sunset) contained only well-digested fragments, whereas only 1 taken during the day was empty, and the other 7 were full of food, including fresh material. The major item in all seven (over 90% of the contents in each) was scleractinian corals—both skeletal and tissue fragments, along with much mucus. The remaining identifiable items in the diet were fine filamentous algae and diatoms.

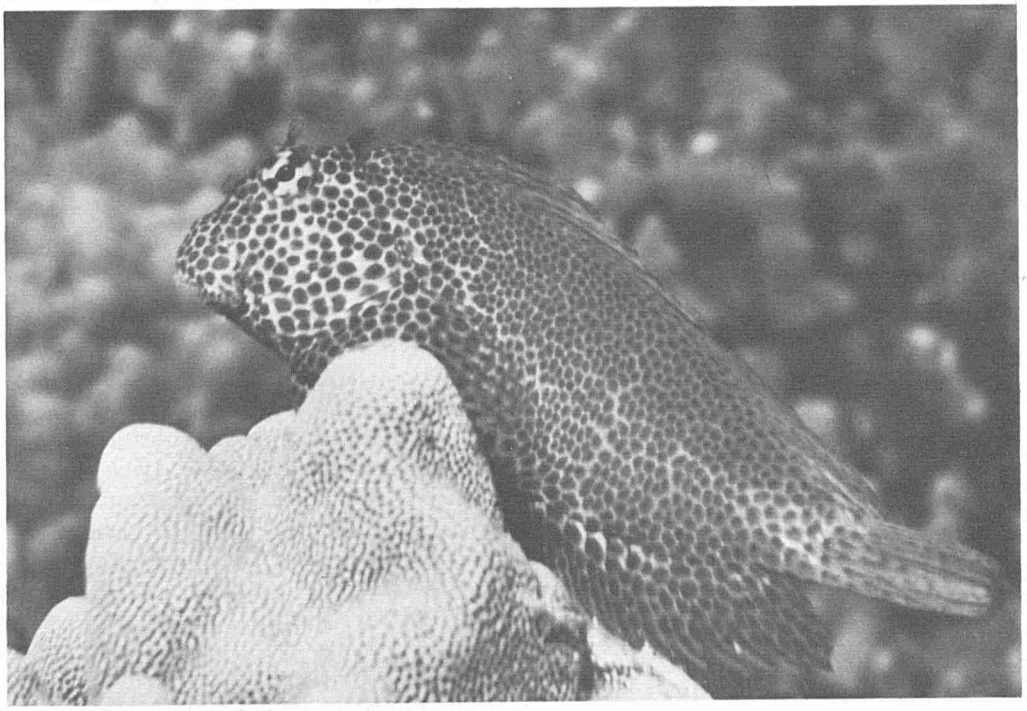


FIGURE 37.—*Exallias brevis,* a blenny, showing typical diurnal attitude.

In contrast to these food data, Hiatt and Strasburg (1960) found only filamentous algae and detritus in the single *E. brevis* (80 mm) that they examined in the Marshall Islands.

CONCLUSION.—*Exallias brevis* is a diurnal species that feeds largely on scleractinian corals, both tissue and mucus.

Cirripectus variolosus (Valenciennes)

During the day, this relatively small blenny moves about close to cover on the reef, remaining in contact with the substratum. Though numerous, it is not seen after dark, when presumably it is secreted in reef crevices.

The guts of both specimens (66 and 80 mm) collected during midday contained filamentous algae (about 40% of the diet volume) and what appeared to be detritus (50 to 60%). In addition, one contained a few scleractinian coral fragments (5%). Except for the coral fragments, the diet of these two individuals was the same as that of one specimen of this species examined by Hiatt and Strasburg (1960) in the Marshall Islands.

CONCLUSION.—*Cirripectus variolosus* is a diurnal species that feeds mostly on algae and detritus.

Plagiotremus goslinei (Strasburg)—sabre-toothed blenny

During the day, *P. goslinei* hovers a meter or so above the reef, from which position it attacks larger fishes that incidentally pass by, striking them unseen from below and behind, much as does *P. azalea* in the eastern Pacific (Hobson, 1968a, 1969). But whereas *P. azalea* usually aggregates when hovering above the reef, *P. goslinei* usually is solitary. No specimens of *P. goslinei* were collected, but presumably it feeds on the mucus and dermal tissue of its victim, as do other species of this genus, including *P. rhinorhynchus* (Wickler, 1960), *P. azalea* (Hobson, 1968a), and *P. townsendi* (Springer and Smith-Vaniz, 1972). These species are called sabre-toothed blennies because each carries in its lower jaw a pair of enormous fangs. Eibl-Eibesfeldt (1955) and Strasburg (1960) believed that these fangs are used in feeding, but Wickler (1960) concluded from work in aquaria

that *P. rhinorhynchus* uses its fangs not to feed, but rather to defend its territory.

Plagiotremus goslinei hovers above the reef during only part of the day. Much of the time it occupies abandoned mollusk and worm tubes on the rocks, and these retreats also serve as resting places at night. In the eastern Pacific, *P. azalea* uses similar tubes in the same way (Hobson, 1968a, 1969).

CONCLUSION.—*Plagiotremus goslinei* is a diurnal predator that feeds on mucus and dermal tissue of larger fishes.

General Remarks on Combtooth Blennies

The combtooth blennies are generally regarded as diurnal. For example, Starck and Davis (1966) did not see members of the family, known to be present, during many night observations on Florida reefs, and Randall (1967) reported the group to be diurnal in the West Indies.

Although food habits remain unknown or uncertain for most combtooth blennies, reportedly many feed by scraping filamentous algae and detritus from rocks. These items predominated in the diet of all four blenniid species that Randall (1967) examined in the West Indies, and in all five studied by Hiatt and Strasburg (1960) in the Marshall Islands. In Kona, this mode of feeding occurs in *Cirripectus variolosus,* but *Exallias brevis* may be exceptional in feeding mostly on the tissue and mucus of scleractinian corals. The significance of coral mucus as food of *E. brevis* may relate to the significance of fish mucus as food for blennies of the genus *Plagiotremus.* Böhlke and Chaplin (1968) suggested that at least some combtooth blennies which scrape algae from rocks may gain most of their nourishment from small organisms living on or around the algae. Clearly, much about blenniid feeding remains unknown. Because these small fishes scrape their food from various substrata, their gut contents are difficult to analyze. One can easily see that species of *Plagiotremus* have a mode of feeding that differs from those of other blenniids, because their manner of taking food is uniquely spectacular. In comparison, differences distinguishing the feeding modes of other combtooth blennies are relatively subtle.

Family Acanthuridae: surgeonfishes

The surgeonfishes are the predominant fishes over most Hawaiian inshore reefs, but this report treats only the two species that feed on zooplankton in the water column. The habits of these two were only superficially touched on by Jones (1968), who provided a thorough treatment of the many species occurring in Kona that take their food directly from the substratum (see general remarks on surgeonfishes, below).

Acanthurus thompsoni (Fowler)

Acanthurus thompsoni (Figure 38) swims in stationary aggregations in the water column above the reef in several locations along the outer drop-off, 20 to 30 m deep. Often mixed with this surgeonfish in these groups are several other species, especially *Chromis verater, C. ovalis,* and *Naso hexacanthus.* At nightfall, *A. thompsoni* descends to the reef below where, inactive but alert, it remains under cover until morning.

Fourteen individuals (141: 128-185 mm) were speared at different times of day and night. All six that were taken from crevices during the hour before daybreak had empty stomachs, whereas, all seven collected from aggregations in the water column at various times during afternoons had full stomachs, including fresh material. Finally, one solitary individual speared during midafternoon close among the coral in about 6 m of water, approximately 200 m from the nearest feeding aggregation, had its stomach empty. The seven individuals with material in their stomachs contained the items listed in Table 60.

The data show a strong trend in the diet toward relatively large, semitransparent, and often gelatinous prey. Some planktivorous fishes from other families feed heavily on one or another of these prey, as does the pomacentrid *Chromis verater,* which feeds heavily on larvaceans (see species account, above). But in none of these others is the diet similarly dominated by an array of such prey. However, the sparse information on the food habits of *A. thompsoni* given by other authors does not show this trend. Gosline and Brock (1960) reported only mollusk eggs and copepods, whereas Jones (1968) noted copepods, crab zoea, crab megalops, and mysids. But these reports did not indicate how many specimens were examined, nor the relative proportion of each type of prey in the diet. Most important, they did not indicate how much of the gut contents remained unidentified. The major food items that I found in *A. thompsoni* are types quickly rendered unidentifiable by digestion, and thus easily missed if the sample is not fresh.

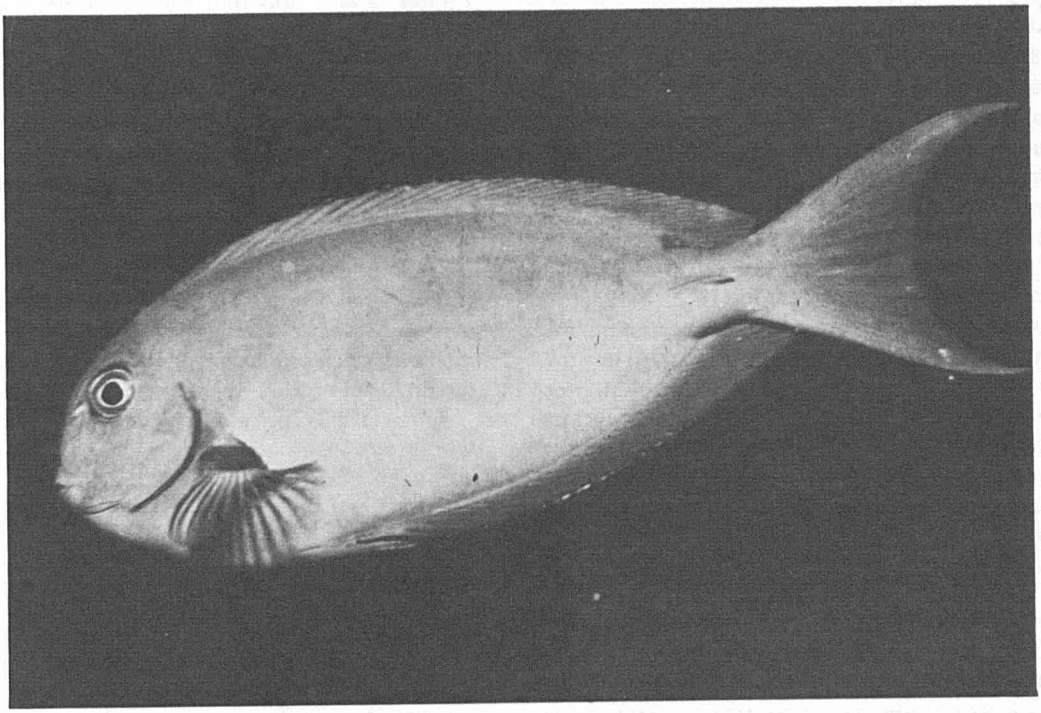


FIGURE 38.—*Acanthurus thompsoni*, a zooplanktivorous surgeonfish. In comparison with its bottom-feeding congeners, this species carries its more upturned mouth higher on its head, its body is more fusiform, and its tail is more deeply lunate. These morphological tendencies occur in many unrelated zooplanktivorous fishes.

CONCLUSION.—*Acanthurus thompsoni* is a diurnal planktivore that feeds mostly on semitransparent, often gelatinous, organisms—especially chaetognaths, salps, siphonophores, and larvaceans.

Naso hexacanthus (Bleeker)—*kala*

During daylight, this relatively large surgeonfish swims above the outer drop-off in schools that periodically range farther offshore to yet unknown distances. Brock and Chamberlain (1968) found this species at depths below 120 m when diving in the research submarine *Asherah*, but it is not known whether these fish had migrated from shallower water or are of deepwater populations, although the latter possibility seems the more probable. Generally, individuals in less than 10 m of water over inshore reefs during the day are relatively small, and swim in groups of

TABLE 60.—Food of *Acanthurus thompsoni*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Chaetognaths	6	37.1	31.80
2	Salps	7	18.6	18.60
3	Siphonophores	4	10.0	5.71
4	Larvaceans	5	7.4	5.29
5	Calanoid copepods	4	8.6	4.91
6	Gelatinous egg masses	2	1.7	0.49
7	Gelatinous clumps of blue-green algae	2	1.6	0.46
8	Fish eggs, planktonic	2	1.3	0.37
9	Hyperiid amphipods	3	0.7	0.30
10	Polychaetes	2	0.9	0.26
11	Decapod shrimps	1	0.3	0.04
12	Harpacticoid copepods	1	0.1	0.01
Also, unidentified fragments		4	11.7	6.69

only a few individuals, often close to the substratum. Most representatives seen inshore are not feeding, but rather move uniformly together closely spaced in schools. When they do feed, the schools are abandoned for aggregations in which loosely spaced individuals act independently.

During evening twilight many individuals move in from deeper water over the shallower parts of the reef. Larger representatives are in the shallows only after dark. On dark nights, the species is scattered close among rocks and corals, relatively inactive, but alert. However, on moonlit nights some swim above the reef in small groups.

Sixteen individuals (261: 202-392 mm) were speared at various times of night and day. Because larger individuals are less accessible, especially during the day, the sample is biased toward smaller members of the species. All four solitary individuals taken close among rocks or coral at night (later than 4 h after sunset and before daybreak) had empty stomachs, whereas only one of nine others taken from schools above the reef at various times of day had material in its stomach, and this one came from a school that had just appeared over the reef from offshore during midafternoon. Finally, all three that had been observed feeding when speared above inshore reefs (on three afternoons over 2 mo) had full stomachs. Items in the four individuals whose stomachs contained food are listed in Table 61.

Like *Acanthurus thompsoni*, this acanthurid feeds mostly on semitransparent, often gelatinous, prey. Of the four that contained food, the three taken from inshore feeding aggregations were relatively small fish (233-238 mm) whose major food was planktonic fish eggs. Perhaps significantly, there were no fish eggs in the fourth specimen, which had just appeared over the reef from offshore. This individual was larger than the others, about 300 mm long, but was collected within 30 min of one of them. The major item in its stomach was filamentous red algae, which did not occur in the smaller three. Only chaetognaths and larvaceans occurred in the stomachs of all four specimens. These limited data suggest there may be distinctive differences in diet and feeding grounds over the size range of individuals sampled.

The high incidence of empty stomachs among individuals over the inshore reefs during the day, as well as at night, suggests that many may feed offshore, and be relatively inactive, or at least not feeding, when they are inshore.

Jones (1968) included *N. hexacanthus* with *A. thompsoni* when reporting the diet of copepods, crab zoea, crab megalops, and mysids noted above. My comments concerning the reported diet of *A. thompsoni* (see above) apply equally here.

CONCLUSION.—*Naso hexacanthus* is a diurnal planktivore that takes mostly semitransparent, often gelatinous, prey—especially chaetognaths, larvaceans, and fish eggs. Limited data suggest that drifting pieces of filamentous algae may also be important.

General Remarks on Surgeonfishes

Surgeonfishes are widespread on tropical reefs, and usually are described in a general way as herbivores (e.g. in the Bahamas by Böhlke and Chaplin, 1968; and in the West Indies by Randall, 1967). Jones (1968) grouped the many Hawaiian surgeonfishes according to their habitats and methods of foraging. In categorizing the bottom-foraging species, not studied by me, he defined three types of habitats, and listed the surgeonfishes characteristic of each: 1) The turbulent

TABLE 61.—Food of *Naso hexacanthus*.

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Chaetognaths	4	21.3	21.30
2	Fish eggs, planktonic	3	25.0	18.75
3	Larvaceans	4	16.3	16.30
4	Filamentous red algae	1	18.4	4.60
5	Decapod shrimps	3	2.3	1.73
6	Calanoid copepods	2	2.3	1.15
7	Siphonophores	2	2.0	1.00
8	Polychaetes	1	1.3	0.33
9	Hyperiid amphipods	1	0.5	0.13
10	Mollusk veligers	1	0.3	0.08
11	Gammaridean amphipods	1	0.3	0.08
Also, unidentified fragments		2	10.0	5.00

waters of the surge zone are frequented by four species of *Acanthurus* (*achilles, glaucopareius, guttatus,* and *leucopareius*). 2) The sand patches on deeper, more tranquil reefs are home to four species of *Acanthurus* (*dussumieri, mata, olivaceus,* and *xanthopterus*). 3) Finally, basalt and coral substrata on reefs below the surge zone (to a depth of about 90 m) are inhabited by three species of *Acanthurus* (*nigrofuscus, nigroris,* and *sandvicensis*); two species of *Ctenochaetus* (*hawaiiensis* and *strigosus*); two species of *Zebrasoma* (*flavescens* and *veliferum*; the adults of the latter often occur in the surge zone); and three species of *Naso* (*brevirostris, lituratus,* and *unicornis*).

In erecting categories according to foraging types, Jones (1968) classified the bottom feeders either as browsers or grazers. The browsers are described as "strictly herbivores that bite and tear off bits of multicellular benthic algae, generally without ingesting any of the inorganic substratum." Browsing surgeonfishes include those characteristic of the surge zone and those characteristic of subsurge reefs, except for the two *Ctenochaetus*. The browsing species of *Acanthurus* and *Zebrasoma* feed chiefly on fine filamentous algae, whereas the browsing species of *Naso* tend to feed on the leafy and fleshy forms.

Surgeonfishes classified by Jones (1968) as grazers are described as "Fishes that purposely pick up large quantities of the substratum while feeding. . . irrespective of whether the material is rasped away from rocks, or picked up as loose sand." This category includes the surgeonfishes characteristic of the sand patches, all of which are species of *Acanthurus,* and the two reef-dwelling species of *Ctenochaetus*. The sand-patch *Acanthurus* species pick up mouthfuls of sand, whereas the reef-dwelling *Ctenochaetus* species ingest sediment that has accumulated over rocks and dead coral. In examining these sediment-packed guts, Jones found material from the two groups distinguishable by particle size—being coarse and grainy in the sand-patch *Acanthurus,* fine and silty in the reef *Ctenochaetus*. He concluded that the major food of both groups are diatoms and detritus that have accumulated around the particles in the surface layers of the sediment.

Surgeonfishes are widely recognized to be active by day and relatively inactive at night (e.g. in the Gulf of California by Hobson, 1965; and in the Florida Keys by Starck and Davis, 1966). Although quiescent, these nocturnally resting acanthurids are most often described as alert; however, Collette and Talbot (1972) reported that *Acanthurus coeruleus* sleeps while sheltered among coral at night in the Virgin Islands. In the Gulf of California, *Prionurus punctatus* aggregates above the reef on bright moonlit nights (Hobson, 1965), as does *Naso hexacanthus* in Kona.

Family Zanclidae: moorish idol

Zanclus canescens (Linnaeus)—moorish idol, *kihikihi*

The moorish idol (Figure 39a) is closely related to the surgeonfishes, and some ichthyologists (e.g. Greenwood et al., 1966) consider it to be a member of that family. It lacks the caudal spine common to all surgeonfishes, however, and most classifications assign it to the monotypic family Zanclidae.

This fish is numerous in all Kona inshore habitats, where it swims over the reef during the day, usually in groups of four to six individuals. When feeding, it regularly probes the narrow cracks and crevices of the reef with its elongated snout. At night it is relatively inactive, but alert, close among rocks or coral, and at this time its coloration differs strikingly from that displayed in daylight (compare Figure 39a and b).

Of 21 specimens (108: 74-137 mm) speared at various times of day and night, all 9 that were collected at night (later than 4 h after sunset and before sunrise) had empty stomachs, whereas all 12 that were taken during the day (between mid-morning and late afternoon) had full stomachs that included fresh material. Items in the specimens containing identifiable material are listed in Table 62.

The sponges, which greatly predominate in the diet, were all small species that presumably live in narrow reef crevices. This fish appears to be specialized in this diet, although Randall (1955) reported only algae in two specimens from the Gilbert Islands.

CONCLUSION.—*Zanclus canescens* is a diurnal species that feeds mostly on small sponges.

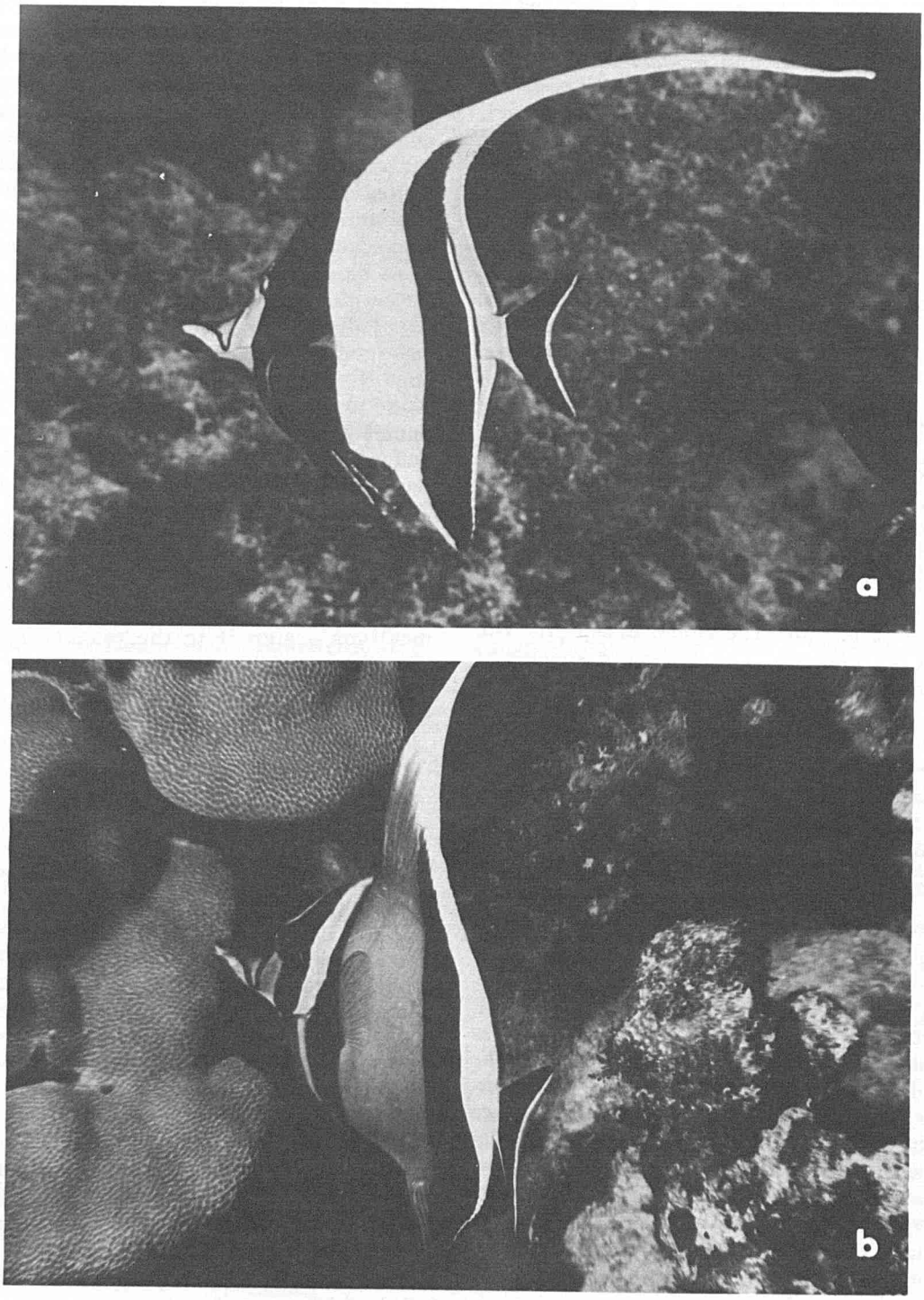


FIGURE 39.—*Zanclus canescens*, the moorish idol: a, showing diurnal coloration while swimming over the reef during the day; b, showing nocturnal coloration while close to the reef at night.

TABLE 62.—Food of *Zanclus canescens*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Sponges	12	84.5	84.50
2	Coralline algae	12	5.7	5.70
3	Other algae	12	5.6	5.60
4	Bryozoans	8	1.1	0.73
5	Pelecypod mollusks	8	0.9	0.60
6	Gammaridean amphipods	6	0.5	0.25
7	Polychaetes	4	0.6	0.20
8	Foraminiferans	3	0.3	0.08
9	Hydroids	2	0.2	0.03
10	Barnacle cirri	2	0.2	0.03
11	Didemnid tunicates	1	0.2	0.02
12	Tanaids	1	0.1	<0.01
13	Decapod shrimps	1	0.1	<0.01

ORDER PLEURONECTIFORMES

Family Bothidae: left-hand flounders

Bothus mancus (Broussonet)—*paki'i*

This flatfish is most numerous lying immobile where rocks are interspersed with small patches of sand. It changes its coloration to match closely that of whatever substratum it happens to lie on, rocks or sand. When on sand, it is frequently buried except for its eyes. No change was noted in the overt behavior of this fish between day and night.

Eight specimens (223: 137-277 mm) were speared at various times of the day. Both individuals collected within an hour after sunrise were empty, whereas of six taken during afternoons, two were empty and four contained well-digested fish remains that appeared to have been in the stomachs at least several hours when collected.

Hiatt and Strasburg (1960) reported this flounder on both rocks and sand in the Marshall Islands and noted a diet comprised primarily of fishes that live in sandy areas adjacent to coral. Most prey species listed by them are fishes (balistids, labrids, pomacentrids, and blennies) that probably are active in exposed positions only during daylight. They believed that *B. mancus* responds only to moving prey; if so, at least most of its prey, which rests at night, would not be available after dark. The prey listed by Hiatt and Strasburg also included two species of apogonids, members of what seems to be a universally nocturnal group; however, during daylight these particular apogonid species congregate in exposed positions close among the coral, where they would seem available to diurnal predators.

CONCLUSION.—*Bothus mancus* preys on small fishes during the day. Its nocturnal habits remain uncertain.

General Remarks on Left-hand Flounders

Bothids are the most numerous flatfishes on tropical reefs. In the West Indies, Randall (1967) found fishes the major prey of *Bothus lunulatus* and *B. ocellatus,* both of which occur on sand patches around coral reefs, often largely buried. In the Florida Keys, Starck and Davis (1966) found *B. ocellatus* in sandy areas of all reef zones, and although they did not examine its food habits, they inferred from its behavior that it preys after dark on the various small nocturnal invertebrates active on the sand at night.

ORDER TETRAODONTIFORMES

Family Balistidae: triggerfishes

Melichthys niger (Bloch)—*humuhumu 'ele'ele*

During the day, *M. niger* typically hovers in loosely spaced aggregations several meters above the reef. Each individual independently picks material drifting in the mid-waters. It is a wary animal that dives to holes in the reef when alarmed. It enters these same holes at nightfall and rests there on its side until morning.

All seven individuals (165: 122-195 mm) speared from among those active above the reef during the day were full of food, as listed in Table 63. The major food items are fragments of fleshy algae—filamentous and foliaceous—probably most of which are drifting in the mid-waters when taken. This triggerfish feeds at least occasionally on the sea floor, as indicated by the relatively high

TABLE 63.—Food of *Melichthys niger*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Fleshy algae	7	52.3	52.30
2	Coralline algae	7	18.7	18.70
3	Calanoid copepods	5	2.7	1.93
4	Caridean shrimps	4	1.1	0.63
5	Harpacticoid copepods	4	0.6	0.34
6	Scleractinian coral	1	2.1	0.30
7	Insects	2	0.4	0.11
8	Foraminiferans	2	0.3	0.09
9	Heteropods	2	0.3	0.09
10	Cyclopoid copepods	1	0.6	0.09
11	Crab megalops	1	0.4	0.06
12	Mollusk veligers	1	0.1	0.01
13	Naticid gastropods	1	0.1	0.01
14	Ostracods	1	0.1	0.01
15	Gammaridean amphipods	1	0.1	0.01
16	Fish eggs, planktonic	1	0.1	0.01
Also, sand		1	2.9	0.41
	Unidentified fragments	6	17.1	14.66

proportion of coralline algae in its diet and also by the stony coral, bitten off in chunks, in one individual; nevertheless, most of its food is planktonic. Certainly the relatively minor status of the many zooplankters in the above list far understates their relative significance to this fish. The ranking is biased toward the more bulky items; thus, one algal fragment, in terms of volume, may be equivalent to a hundred or more copepods. And yet the effort expended in taking the algal fragment may have been no greater than that expended in taking a single copepod. A given volume of copepods (and many other zooplankters) probably is far more nutritious than the same volume of algae.

In the West Indies, this circumtropical triggerfish similarly feeds on algae and zooplankton in the mid-waters, taking the algae from the benthos, or as drifting fragments (Randall, 1967).

CONCLUSION.—*Melichthys niger* is a diurnal omnivore that feeds mostly on drifting algal fragments and zooplankton, along with some benthic vegetation.

Xanthichthys ringens (Linnaeus)

This triggerfish (Figure 40) is one of the most numerous fishes at depths below 25 m along the outer drop-off. Like so many fishes that concentrate in this location, it aggregates in the water column and picks plankton, an activity that is limited to daylight; at nightfall, it shelters in reef crevices, where it rests on its side until morning.

Of the 11 specimens (125: 98-145 mm) speared during day and night, 2 that were collected from reef crevices during the last hour before daybreak were empty, whereas all 9 that were taken from mid-water aggregations at various times during the day were full of food, as listed in Table 64.

I found no evidence that this triggerfish takes food from the sea floor. Like *Melichthys niger, X. ringens* is circumtropical (Böhlke and Chaplin, 1968); perhaps the planktivorous habits of these two triggerfishes permit survival over long periods in the open sea where their bottom-feeding relatives would perish. Gosline and Brock (1960), whose data were mostly from relatively shallow water, reported *X. ringens* uncommon in Hawaii. The large numbers of this species occurring along the outer drop-off in Kona, however, indicates a habitat in Hawaii similar to that in the West Indies, where it rarely occurs in less than 35 m of water, but is one of the most numerous fishes below that depth (Randall, 1968).

CONCLUSION.—*Xanthichthys ringens* is a diurnal planktivore that feeds mostly on calanoid copepods.

Rhinecanthus rectangulus (Bloch and Schneider)—*humuhumu nukunuku a pua'a*

This triggerfish is most common on shallow, surge-swept, basalt reefs. It is a solitary fish that swims close to the reef top during the day, picking at organisms on the bottom. A wary animal, it quickly takes refuge in the reef when threatened.

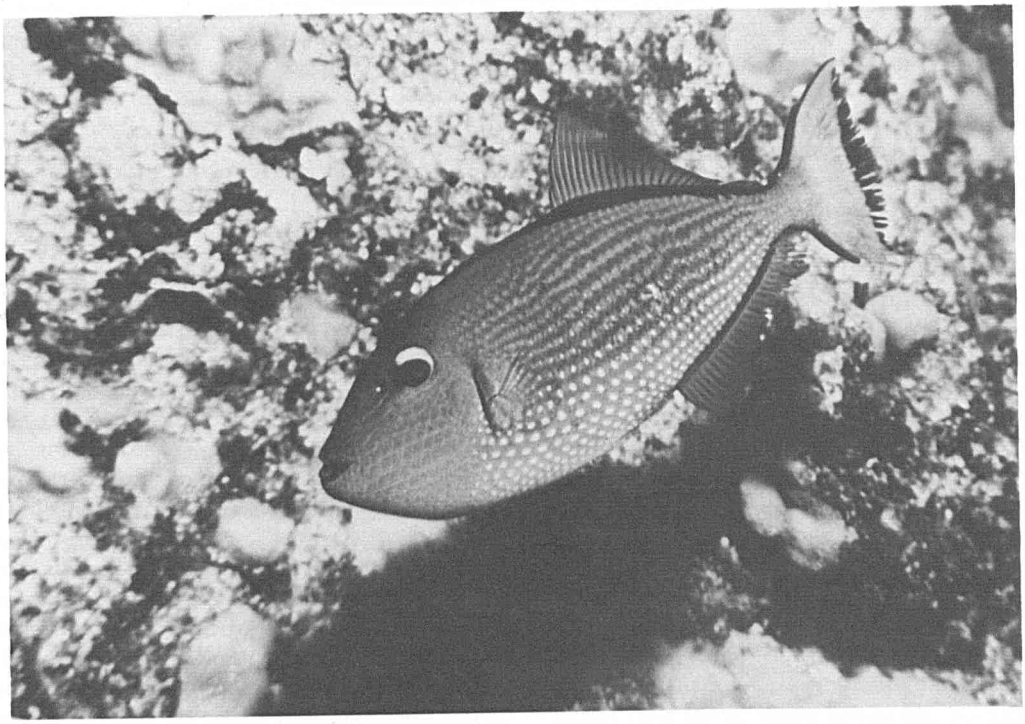


FIGURE 40.—*Xanthichthys ringens*, a zooplanktivorous triggerfish. In comparison with bottom-feeding triggerfishes, this species has a more upturned mouth that is higher on its head, and its body is more fusiform. Both features are widespread among zooplanktivorous fishes.

Its shelters, like those of *Melichthys niger*, above, are small enough so that the fish can wedge itself in by locking its large dorsal spine erect. Each individual fish seems to resort to a specific hole that serves as a refuge by day, and also as a resting place at night when the species is inactive.

All nine individuals (142: 114-170 mm) speared at various times of the day from among those active close to the reef were full of food, as listed in Table 65. Food items were mostly small organisms between 1 and 6 mm in their greatest dimension, taken intact; the few exceptions are fragments of about this size from larger organisms.

Hiatt and Strasburg (1960) found this species numerous on shallow reefs in the Marshall Islands and reported a crustacean and algal diet similar to that of the species in Kona.

TABLE 64.—Food of *Xanthichthys ringens*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	9	43.9	43.90
2	Mollusk veligers	6	0.8	0.53
3	Fish eggs, planktonic	2	1.4	0.31
4	Chaetognaths	2	1.3	0.29
5	Siphonophores	2	1.2	0.27
6	Pteropods	2	1.2	0.27
7	Ostracods	4	0.6	0.27
8	Cyclopoid copepods	1	0.8	0.09
9	Heteropods	2	0.3	0.07
10	Hyperiid amphipods	2	0.2	0.04
11	Gammaridean amphipods	1	0.2	0.02
Also, crustacean fragments		4	4.6	2.04
	Unidentified fragments	9	43.5	43.50

TABLE 65.—Food of *Rhinecanthus rectangulus*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	9	19.4	19.40
2	Didemnid tunicates	9	8.6	8.60
3	Filamentous algae	6	7.8	5.20
4	Xanthid crabs	4	6.7	2.98
5	Polychaetes	4	6.3	2.80
6	Decapod shrimps	5	4.2	2.33
7	Tanaids	4	2.9	1.29
8	Coralline algae	4	2.6	1.16
9	Prosobranch gastropods	4	2.4	1.07
10	Echinoids	3	2.9	0.97
11	Isopods	3	2.6	0.87
12	Bryozoans	2	0.7	0.16
13	Caprellid amphipods	1	0.6	0.07
14	Pelecypods	1	0.3	0.03
15	Crab megalops	1	0.2	0.02
Also, crustacean fragments		4	6.2	2.76
	Unidentified fragments	7	25.6	19.91

TABLE 66.—Food of *Sufflamen bursa*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Echinoids	9	9.1	9.10
2	Gammaridean amphipods	7	8.3	6.46
3	Polychaetes	8	4.6	4.09
4	Prosobranch gastropods	9	3.8	3.80
5	Brachyurans	5	4.8	2.67
6	Sponges	8	2.6	2.31
7	Tanaids	6	2.8	1.87
8	Opisthobranchs	6	2.3	1.53
9	Cyclopoid copepods	9	1.2	1.20
10	Isopods	7	1.3	1.01
11	Ostreid pelecypods	7	1.0	0.78
12	Caridean shrimps	3	0.8	0.27
13	Foraminiferans	4	0.4	0.18
14	Ostracods	4	0.4	0.18
15	Crab megalops	2	0.3	0.07
16	Bryozoans	1	0.1	0.01
17	Sipunculid introverts	1	0.1	0.01
18	Harpacticoid copepods	1	0.1	0.01
19	Barnacle cirri	1	0.1	0.01
20	Mites	1	0.1	0.01
Also, crustacean fragments		5	3.8	2.11
	Algal fragments	5	1.2	0.67
	Unidentified fragments	9	50.8	50.80

CONCLUSION.—*Rhinecanthus rectangulus* is a diurnal omnivore, feeding mostly on gammaridean amphipods and other small organisms.

Sufflamen bursa (Bloch and Schneider)—*humuhumu umauma lei*

This is the most numerous and widespread triggerfish on Kona reefs. A solitary species, active by day close to rocks and coral, it picks at organisms on the sea floor. It is less inclined to seek cover in reef crevices than are *Melichthys niger* and *Rhinecanthus rectangulus,* above, but nevertheless is a wary animal that shys away from humans. At night it is inactive, resting on its side under cover on the reef until morning.

Thirteen individuals (140: 109-164 mm) were speared at various times of day and night. The four that were collected in darkness as they rested in reef crevices during the last 2 h before daybreak were empty, whereas the nine that were collected at various times during the day as they swam over the reef were full of food, as listed in Table 66. As was true of the food of *R. rectangulus,* these food items, including the echinoids, are mostly small animals between 1 and 6 mm in their greatest dimension, taken intact; the exceptions are fragments of about this size from larger organisms. Unlike the omnivorous *R. rectangulus,* however, *S. bursa* seems to be strictly carnivorous (the few algal fragments among its gut contents probably were taken incidentally along with prey). No

single item greatly predominates in its diet, a circumstance that may relate to its widespread occurrence in a variety of habitats.

CONCLUSION.—*Sufflamen bursa* is a diurnal predator that feeds on a variety of benthic animals.

General Remarks on Triggerfishes

The balistids are known for their powerful jaws and sharp cutting teeth, which enable them to prey on a variety of armored invertebrates denied as food to most other fishes (Randall, 1967). Most triggerfishes seem to make full use of this equipment: in the Virgin Islands *Balistes vetula* preys on the large echinoid *Diadema* (often attacking this sea urchin from its oral surface, where the spines are shortest) and on relatively large queen conchs, *Strombus,* which it crushes upon ingestion (Randall, 1967). Similarly, in the Marshall Islands several triggerfishes use their powerful feeding apparatus to crush mollusks and hard-shelled crustaceans, as well as to break off the tips of cespitose corals (Hiatt and Strasburg, 1960). *Rhinecanthus rectangulus* and *Sufflamen bursa* in Kona may be exceptional among bottom-foraging balistids in that they feed so heavily on small organisms, ingested intact. On the other hand, it may be that the high proportion of unidentified fragments in the guts of both species are the crushed remains of larger organisms not properly ranked among the data. Nevertheless, the capacity to feed on tiny organisms is probably well established among the balistids, as demonstrated by the exclusively zooplanktivorous habits of *Xanthichthys ringens.*

Triggerfishes are well known to be active by day and to rest under cover at night, usually lying on their sides. Diurnal habits were reported in balistids of the Gulf of California (Hobson, 1965, 1968a) and the West Indies (Randall, 1967). Collette and Talbot (1972) described *Balistes vetula* sleeping at night in exposed positions on reefs in the Virgin Islands, and Earle (1972) reported that in the Virgin Islands *B. vetula* frequently returns nightly to the same hole in the reef. There is at least some activity among triggerfishes on moonlit nights, however, as for example in *B. polylepis* in the Gulf of California (Hobson, 1965), but it is unknown whether this activity involves feeding.

Family Monacanthidae: filefishes

Cantherines dumerili (Hollard)—*'o'ili*

During daylight, this filefish swims several meters above coral-rich reefs, usually in loosely associated pairs that move, often on their sides, back and forth in restricted, well-defined areas. Because it swims in the water column and because it is relatively large, this filefish is a conspicuous component of the fauna, even though relatively few occur on the reef. Despite the time it spends in mid-water, *C. dumerili* was observed feeding only on the sea floor, where it bites off the tips of coral branches. During evening twilight it settles into holes in the reef, where it remains inactive until morning.

All eight individuals (200: 171-240 mm) speared from among those hovering above the reef during midday were full of food. Scleractinian corals were the major food items, occurring in seven of the eight specimens (mean percent of diet volume: 80; ranking index: 70), always as chunks of *Pocillopora* and *Porites,* about 4 mm in diameter. Other food items were: echinoids, all tips of the clublike spines of *Heterocentrotus mammillatus*, in two (mean percent of diet volume: 7.4; ranking index: 1.85), a variety of bryozoans, both encrusting and arborescent, that were almost the total contents of one (mean percent of diet volume: 12.5; ranking index volume: 1.56), and pelecypods in one (mean percent of diet volume: 0.1; ranking index: 0.01).

Hiatt and Strasburg (1960) found that of the two specimens of this species (reported as *Amanses carolae)* that they examined in the Marshall Islands, one had fed on scleractinian corals exclusively, whereas the other had mixed a coral diet with sponges and algae. Apparently this species does not feed during the considerable time that it spends in the water column, as its diet seems to comprise only benthic organisms.

CONCLUSION.—*Cantherines dumerili* is a diurnal predator that feeds mainly on scleractinian corals.

Cantherines sandwichiensis (Quoy and Gaimard)—*'o'ili lepa*

This, the most numerous filefish in Kona, especially on basalt reefs in less than 10 m of water, is a solitary fish that swims close over the reef during

TABLE 67.—Food of *Cantherines sandwichiensis*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Filamentous algae	7	35.7	35.70
2	Coralline algae	7	32.1	32.10
3	Didemnid tunicates	7	6.1	6.10
4	Gammaridean amphipods	6	4.0	3.43
5	Scleractinian corals	2	5.0	1.43
6	Sponges	2	2.2	0.63
7	Diatoms	3	1.1	0.47
8	Bryozoans	2	1.0	0.29
9	Hydroids	2	0.4	0.11
10	Polychaetes	1	1.4	0.20
11	Ostreid pelecypods	2	0.6	0.17
12	Caprellid amphipods	2	0.6	0.17
13	Gastropod eggs	1	0.3	0.04
14	Prosobranch gastropods	1	0.3	0.04
15	Tanaids	1	0.1	0.01
16	Ophiuroids	1	0.1	0.01
Also, unidentified fragments		5	8.3	5.93
	Sand	1	0.7	0.10

TABLE 68.—Food of *Pervagor spilosoma*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Scleractinian corals	5	35.8	29.83
2	Filamentous algae	4	19.3	12.87
3	Coralline algae	6	7.7	7.70
4	Sponges	1	3.3	0.55
5	Polychaetes	2	1.5	0.50
6	Echinoids	3	0.8	0.40
7	Gammaridean amphipods	3	0.7	0.35
8	Tanaids	2	0.5	0.16
9	Diatoms	2	0.3	0.10
10	Fish eggs	1	0.5	0.08
11	Hydroids	2	0.3	0.10
12	Opisthobranch gastropods	1	0.2	0.03
13	Ostracods	1	0.2	0.03
14	Cyclopoid copepods	1	0.2	0.03
15	Crab megalops	1	0.2	0.03
16	Ophiuroids	1	0.2	0.03
Also, unidentified fragments		5	28.1	23.41
	Sand	1	0.2	0.03

the day, picking at objects on the bottom. During evening twilight, it moves from sight and is not visible at night when presumably it rests in reef crevices.

All seven individuals (116: 84-132 mm) speared from among those active close to the reef during the day were full of food, much of it fresh, as listed in Table 67.

CONCLUSION.—*Cantherines sandwichiensis* is a diurnal omnivore that feeds on a wide variety of benthic algae and invertebrates.

Pervagor spilosoma (Lay and Bennett)—*'o'ili 'uwi'uwi*

This, the most colorful filefish in Kona, as well as the smallest of the three considered there, is most numerous on coral-rich reefs. It is a solitary fish, active close among the corals in daylight, but not seen after dark when presumably it rests in reef crevices.

Of the seven specimens (85: 64-120 mm) collected, one that was speared close to coral just before sunrise (the first individual of the species to appear that morning) had an empty gut, whereas all six that were speared from among those active on the reef between midmorning and midafternoon were full of food, as listed in Table 68.

As is true of *Cantherines dumerili*, above, the major food of this filefish is scleractinian coral; however, whereas *C. dumerili* bites off relatively large chunks of coral, each containing many polyps, *P. spilosoma* seems to pluck at only one polyp at a time, as do certain chaetodontids. Nevertheless, judging from its gut load of skeletal

fragments, *P. spilosoma* does not neatly snip off the polyps so much as coarsely gouge them from their thecae.

CONCLUSION.—*Pervagor spilosoma* is a diurnal omnivore that feeds mainly on scleractinian corals, to a lesser extent on algae and other benthic invertebrates.

General Remarks on Filefishes

In summarizing their treatment of monacanthids in the Marshall Islands, Hiatt and Strasburg (1960:105) stated: "There is no question that filefishes derive the bulk of their nutriment from living corals." All of the *Oxymonocanthus longirostris* (a widespread Indo-Pacific species that does not occur in Hawaii) examined by them contained only coral polyps, with no skeletal material. Their account indicates that this species, which has a very long, narrow snout, with teeth protruding from its mouth as long, cupshaped incisors, may be among the most highly specialized of coral-feeding filefishes. On the other hand, Randall (1967) found corals to be insignificant as food for West Indian filefishes; of the six species he examined, corals were in the diet of only one, and only as a minor component. According to Randall, the West Indian filefishes take a diverse array of benthic organisms: Algae and sea grasses are major items, along with a variety of benthic invertebrates. Thus, *Cantherines sandwichiensis* in Kona has a diet much like the West Indian species described by Randall, whereas *C. dumerili* takes largely corals in Kona, just as Hiatt and Strasburg reported it and other filefishes doing in the Marshall Islands. Clearly, many filefishes, especially certain Indo-Pacific species, feed heavily on corals, whereas various other filefishes find their food from among other elements of the benthos.

Filefishes are recognized as being diurnal. For example, Starck and Davis (1966) described *C. pullus* as resting at night wedged in rocky holes on reefs in Florida.

Family Ostraciontidae: boxfishes

Ostracion meleagris (Shaw)—*pahu*

This boxfish is widespread on nearshore reefs in Kona, but is nowhere numerous, except occasionally in some parts of the boulder habitat. During the day it swims, slowly, close among rocks and coral, now and then picking at the substratum. I saw several in the same places at night, but at the time felt they had been disturbed from resting places by my activity. It was difficult to appraise the nocturnal behavior of this species, owing to its relatively low numbers on the reef and the reduced visibility after dark, and because the few observations were somewhat ambiguous.

Of the six individuals (65: 43-80 mm) collected, one speared within 15 min after sunrise as it swam close to the reef had an empty gut, whereas all five taken under similar circumstances, except later in the day (between late morning and late afternoon) had food throughout the gut. The items in the foregut are listed in Table 69.

CONCLUSION.—*Ostracion meleagris* feeds on benthic invertebrates during the day. Its nocturnal status remains uncertain, although tenuous data indicate relative inactivity after dark.

General Remarks on Boxfishes

Boxfishes in the tropical Atlantic generally are described as active during both day and night (Starck and Davis, 1966; Earle, 1972; Collette and Talbot, 1972). Tunicates, the major prey of *Ostracion meleagris* in Kona, were ranked either

TABLE 69.—Food of *Ostracion meleagris*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Didemnid tunicates	3	42.8	25.68
2	Polychaetes	2	13.0	5.20
3	Algae	2	7.4	2.96
4	Sponges	1	2.0	0.40
5	Pelecypods	1	1.0	0.20
6	Prosobranch gastropods	1	1.0	0.20
7	Copepods	1	0.4	0.08
Also, sand and debris		1	6.0	1.20
	Unidentified fragments	2	26.4	10.56

first or second as prey of three of the five West Indian boxfishes studied by Randall (1967). Furthermore, polychaetes and sponges also were found to be important prey in the Atlantic species just as they are in *O. meleagris* from Kona. In the Marshall Islands, the major foods of *O. cubicus* are mollusks, polychaetes, and algae (Hiatt and Strasburg, 1960).

At least some boxfishes, including *O. meleagris* in Hawaii (Gosline and Brock, 1960; Thomson, 1964), release a substance that is toxic to other fishes. This may give them some immunity from predation, as suggested for some tropical Atlantic species by Randall (1967).

Family Tetraodontidae: balloonfishes

Arothron hispidus (Linnaeus)—*'opu hue, keke*

This solitary balloonfish is widespread on Kona reefs, but is nowhere numerous. In daylight it frequently hovers inactively several meters above the reef, although just as often it swims slowly among the rocks and coral. After dark it continues to swim actively, close to the reef.

Nine individuals (253: 187-332 mm) were speared during day and night. The guts of two were empty: one of these was hovering high in the water column during early afternoon when collected; the other was swimming close among rocks during the hour immediately before first morning light. All of the other seven, taken as they swam close to the reef—five during midday, two during midnight—contained identifiable material, as listed in Table 70. The tunicates taken by this balloonfish include several benthic species, both compound and simple forms; the echinoids are the crushed tests and spines of echinometrids and cidarids; the asteroids are mostly tips of the appendages from *Linckia*.

Generally the items are hard-bodied forms that remain recognizable for a relatively long time after ingestion; nevertheless, material from the two individuals collected at night appeared fresher overall than that from the individuals collected during midday.

In the Marshall Islands, the single *A. hispidus* examined by Hiatt and Strasburg (1960) had fed on much the same material as listed above, except that it also had ingested some living scleractinian corals.

CONCLUSION.—*Arothron hispidus* preys on a variety of benthic invertebrates, especially those having a hard or leathery external covering. Limited evidence indicates it is active during both day and night.

Arothron meleagris (Bloch and Schneider)—*'opu hue, keke*

Like its congener *A. hispidus*, above, the solitary species *A. meleagris* (Figure 41) is widespread on Kona reefs, but is nowhere numerous. It does not hover inactively above the reef during the day as *A. hispidus* often does, and on the few occasions when it was seen at night—always under ledges or in crevices—*A. meleagris* seemed inactive. During daylight it swims slowly among the rocks or corals.

Eleven individuals (221: 146-393 mm) were collected during the day. Of three whose guts were empty, two were speared as they swam close to the reef within an hour after sunrise, and one was taken from a small cave during midafternoon. The remaining eight, taken as they swam close to the reef during midday, all contained identifiable material. Seven of these had taken scleratinian corals (mean percent of diet volume: 43.1; ranking index: 37.71), mostly small chunks of encrusting

TABLE 70.—Food of *Arothron hispidus*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Tunicates	5	33.7	24.07
2	Echinoids	5	28.1	20.07
3	Ophiuroids	3	13.4	5.74
4	Asteroids	3	8.3	3.56
5	Brachyurans	2	6.4	1.83
6	Sponges	1	2.9	0.41
7	Hydroids	1	2.9	0.41
8	Prosobranch gastropods	1	0.1	0.01
9	Pagurid crabs	1	0.1	0.01
Also, algae		1	0.3	0.04
	Unidentifiable fragments	3	3.8	1.63

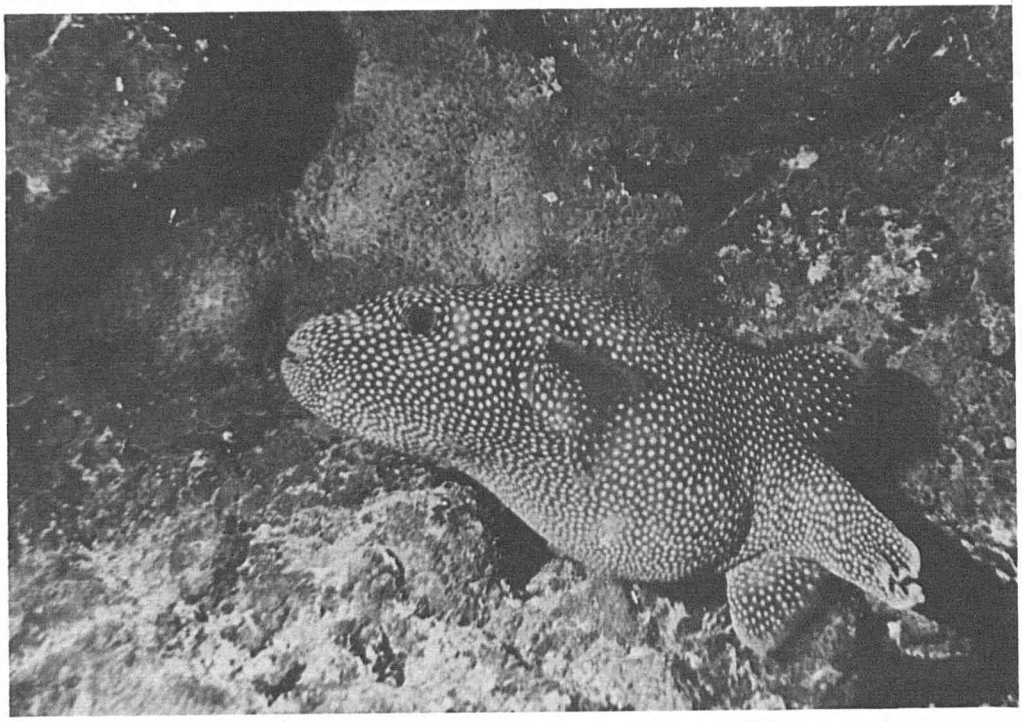


FIGURE 41.—*Arothron meleagris,* a balloonfish. By inflating its saclike body with water, this slow-swimming fish increases its size, which presumably decreases its vulnerability to predators.

Porites, whereas six had taken tunicates (mean percent of diet volume: 44.4; ranking index: 33.3), all of them a large colonial form with a heavy black integument that, like the coral, encrusts on rocks. The only other recognizable items were pectinid pelecypods in one (mean percent of diet volume: 0.6; ranking index: 0.08). Three contained unidentifiable fragments (mean percent of diet volume: 11.9; ranking index: 4.46). Thus, these data indicate that, compared with *A. hispidus, A. meleagris* is a relatively specialized feeder. The three *A. meleagris* that Hiatt and Strasburg (1960) examined in the Marshall Islands had fed almost exclusively on living corals.

CONCLUSION.—*Arothron meleagris* is a diurnal predator that feeds mostly on corals and tunicates which encrust on rocks.

General Remarks on Balloonfishes

The dentition of tetraodontids consists of heavy plates, two in each jaw, that form a sharp beak. With this exceptionally strong apparatus, these fishes crush an array of armored organisms that are unavailable as prey to most other fishes (Hiatt and Strasburg, 1960).

Family Canthigasteridae: sharpbacked puffers

Canthigaster amboinensis Bleeker — *pu'u ola'i*

This pufferfish occurs chiefly in relatively shallow water where there is much exposed basalt. It is a solitary fish, active close to the sea floor during the day, but only infrequently in view after dark, when, presumably, it generally retires to reef crevices.

All 11 individuals (69: 31-91 mm) that were speared at various times during daylight contained identifiable material (much of it fresh), as listed in Table 71.

CONCLUSION.—*Canthigaster amboinensis* is a diurnal omnivore that feeds mostly on coralline algae and various hard-bodied invertebrates.

TABLE 71.—Food of *Canthigaster amboinensis*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Coralline algae	10	42.5	38.64
2	Filamentous algae	8	9.4	6.84
3	Scleractinian corals	6	7.7	4.20
4	Pectinid pelecypods	2	7.8	1.42
5	Brachyurans	2	7.3	1.33
6	Ophiuroids	2	4.9	0.89
7	Echinoids	4	2.4	0.87
8	Sponges	5	1.3	0.59
9	Prosobranch gastropods	4	0.6	0.22
10	Bryozoans	2	0.6	0.11
11	Sipunculid introverts	2	0.3	0.05
12	Foraminiferans	3	0.2	0.05
13	Gammaridean amphipods	2	0.2	0.04
14	Didemnid tunicates	1	0.3	0.03
15	Polychaetes	1	0.2	0.02
Also, unidentified fragments		6	14.3	7.80

TABLE 72.—Food of *Canthigaster jactator*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Coralline algae	3	15.7	7.85
2	Prosobranch gastropods	4	11.2	7.47
3	Sponges	3	6.8	3.40
4	Scleractinian corals	2	10.0	3.33
5	Filamentous algae	5	3.7	3.08
6	Didemnid tunicates	3	6.0	3.00
7	Sipunculid introverts	3	4.3	2.15
8	Echinoids	2	5.5	1.83
9	Bryozoans	2	1.3	0.43
10	Brachyurans	2	1.3	0.43
11	Diatoms	3	0.7	0.35
12	Foraminiferans	2	0.3	0.10
13	Ophiuroids	1	0.3	0.05
14	Ostracods	1	0.2	0.03
15	Gammaridean amphipods	1	0.2	0.03
16	Isopods	1	0.2	0.03
17	Caridean shrimps	1	0.2	0.03
Also, crustacean fragments		1	5.0	0.83
	Sand	3	1.5	0.75
	Unidentified fragments	5	25.6	21.33

Canthigaster jactator (Jenkins)

This small pufferfish lives mostly where corals are well developed. Like its congener *C. amboinensis*, above, it is mostly solitary, although sometimes several occur together. It swims close among the coral during daylight, but is only occasionally in view at night, probably because it usually rests in reef crevices after dark. Once during the predawn hours, as noted above, I observed a nocturnally active moray eel, *Gymnothorax petelli*, grasping one of these puffers between its jaws.

Thirteen individuals (50: 40-70 mm) were speared at various times of day and night. Four were taken during daylight, and these were the only ones that had material in the anterior third of their gut, much of it relatively fresh. In two others taken at night (one 4 h after sunset, the other during the last hour before daybreak), food was confined to the posterior two-thirds of their guts, but much of it was still largely identifiable. In comparison, the remaining seven, collected either at night (more than 4 h after sunset), or during morning twilight, were empty. Items in the six specimens that contained identifiable material are listed in Table 72.

CONCLUSION.—*Canthigaster jactator* is a diurnal omnivore that feeds mostly on coralline algae and various hard-bodied benthic invertebrates.

Remarks on Sharpbacked Puffers

The canthigasterids are widely recognized as omnivorous fishes that feed on benthic plants and

invertebrates (e.g. in the tropical Atlantic by Randall, 1967; and in the western Pacific by Hiatt and Strasburg, 1960). Most investigators have considered them diurnal. Smith and Tyler (1972) described *Canthigaster rostratus* sleeping at night on reefs in the Virgin Islands; Collette and Talbot (1972) also suspected *C. rostratus* to be nocturnally inactive, and suggested that some they saw swimming at night had been disturbed by their lights. To Starck and Davis (1966), however, at least some individuals of *C. rostratus* appeared to be nocturnally active in the Florida Keys; however, they recognized that this species is active in daylight as well.

Family Diodontidae: spiny puffers

Diodon holocanthus Linnaeus — *kokala*

This spiny puffer is numerous in Kona, where it frequently swims close above the reef at night; nevertheless, I never saw one there in daylight. Undoubtedly, it is under shelter during the day, probably deep within the coral caverns that honeycomb much of the reef. In the Gulf of California, where the rocky sea floor offers mostly ledges and relatively shallow caves, one often sees the nocturnally active *D. holocanthus* resting in these places during the day.

All five individuals (211: 175-239 mm) that were speared as they swam in exposed locations on the reef after dark contained identifiable material in their guts, much of it relatively fresh. Prosobranch gastropods, which occurred in all five specimens, were the major food item (mean percent of diet volume and ranking index: 54.1), with pagurid crabs also important prey of all five (mean percent of diet volume and ranking index: 24). Other food items were: echinoids, all *Echinometra mathaei,* in four (mean percent of diet volume: 18; ranking index: 14.4), and ophiuroids in two (mean percent of diet volume: 3.9; ranking index: 1.56). Although this material had been crushed by the powerful jaws and beaklike dentition of the fish, it was apparent that at least many of the gastropod shells actually had housed pagurid crabs; thus the pagurids, not the gastropods themselves, may have been the major food. It remains uncertain how many living gastropods are in fact taken, although opercula among the gut contents showed that living gastropods are important prey.

This circumtropical species has a similar diet in the Atlantic Ocean, as determined by Randall (1967), who also listed prosobranch gastropods as the major food item. He listed pagurid crabs too, but did not suggest that some of the gastropods on his list may have been shells that housed these crabs.

Diodon holocanthus is nocturnal in the Florida Keys, where it stays under ledges or in holes during the day, but emerges at night to feed on various invertebrates, particularly larger shelled forms (Starck and Davis, 1966).

CONCLUSION.—*Diodon holocanthus* is a nocturnal predator that feeds mostly on prosobranch gastropods and pagurid crabs.

Diodon hystrix Linnaeus—*kokala*

During the day, *D. hystrix* either is secreted under ledges, or hovers inactively high in the water column, often several together. At night, solitary individuals (Figure 42) swim in exposed locations close above the reef, especially among basaltic boulders.

Of the 16 individuals (263: 244-333 mm) speared during day and night, only 4 had empty guts, and these were collected during late afternoon, either from holes under rocks, or as they hovered in the water column. The only ones that carried food in the anterior third of their gut were taken at night—two during the hour before midnight and one 2 h before daybreak. Although the anterior third of the gut was empty in the other nine, all carried material posteriorly, which, composing entirely shelled organisms, was readily identifiable: two of these specimens were collected at night—one at midnight, the other just before daybreak; the remaining seven were taken during the day—four of them in the morning, three early in the afternoon. In all, 12 specimens contained identifiable prey.

Echinoids, including both cidarids and echinometrids, occurred in 11 of the 12 specimens and were the major food item (mean percent of diet volume: 55; ranking index: 50.42). Prosobranch gastropods, present in 11 (mean percent of diet volume: 27.1; ranking index: 24.84), were ranked second, and pagurid crabs, also present in 11 (mean percent of diet volume: 12.9; ranking index: 11.83), were ranked third. Thus, the diet includes items similar to those taken by *D. holocanthus,* above, but ranked in a different order. As is true of the material from *D. holocanthus,* many of the gastropod shells had housed pagurid crabs, but the

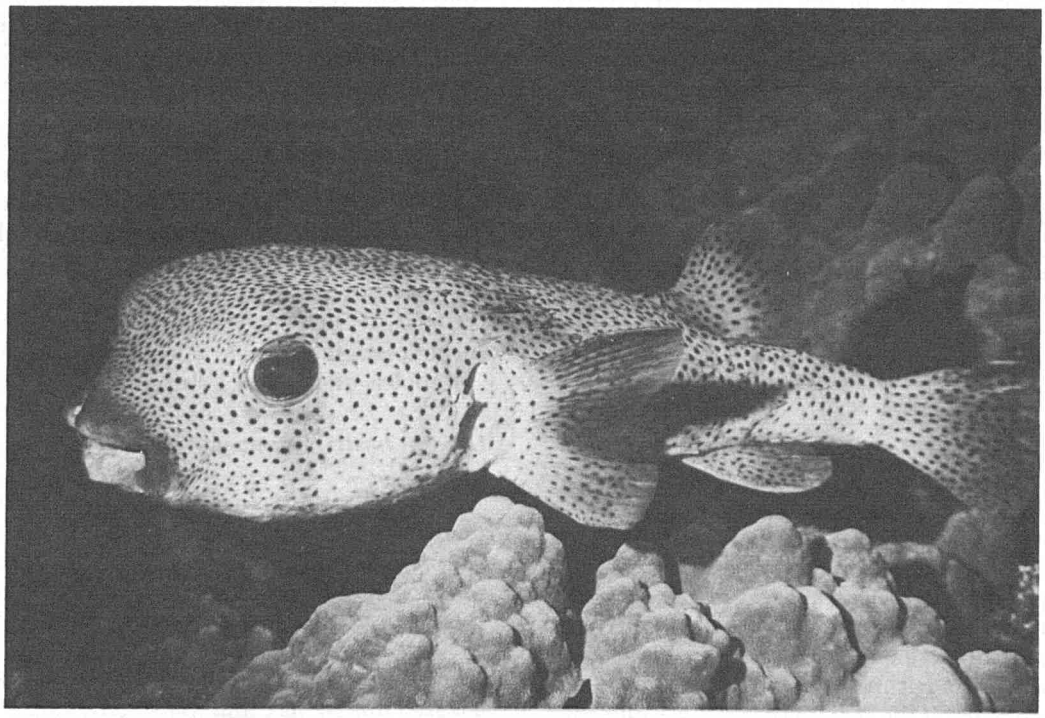


FIGURE 42.—*Diodon hystrix,* a spiny puffer, swimming above the reef at night. With its heavy, beaklike dentition, this fish crushes its shelled prey.

number remains unknown. Nevertheless, the pagurids may actually rank second as prey even though the opercula among this material show that living gastropods are important prey. One *D. hystrix* also contained ostreid pelecypods (mean percent of diet volume: 0.8; ranking index: 0.07), and one contained unidentified fragments (mean percent of diet volume: 4.2; ranking index: 0.35).

Randall (1967) similarly found echinoids the major food of this circumtropical species in the West Indies. For this species as well as *D. holocanthus,* Randall listed gastropods and pagurids separately, without suggesting that some of the gastropods may have been only shells which housed pagurids. Randall recognized that *D. hystrix* feeds partly by night, but believed it to be primarily diurnal. Starck and Davis (1966), however, reported strictly nocturnal habits for *D. hystrix* in the Florida Keys.

The strong, sharp spines that cover *D. hystrix* and *D. holocanthus* are perhaps their most distinctive morphological characteristic. These spines lie flat against their bodies most of the time, but when the bodies inflate with water—a regular response to threats—the spines stand straight out. Although this formidable defense probably deters most predators, the slow-moving *Diodon* would be ready prey for those predators able to tolerate the spines and inflated body. In Hawaii, the tiger shark, *Galeocerdo cuvieri,* regularly preys on full-grown adults of *D. hystrix* (Tester, 1963).

CONCLUSION.—*Diodon hystrix* is a nocturnal predator that feeds mostly on echinoids, and to a lesser extent on prosobranch gastropods and pagurid crabs.

General Remarks on Spiny Puffers

The teeth in both upper and lower jaws of the diodontids are fused together to produce a solid, heavy beak, and this apparatus enables them to crush some of the larger, heavily shelled prey that are beyond the capacity of other fishes—even their relatives the balloonfishes.

The nocturnal habits of the two species of *Diodon,* described above, may be a family characteristic. Starck and Davis (1966) reported that two species of *Chilomycterus* in Florida—*antillarum* and *schoepfi*—are active at night and inactive during the day.

DISCUSSION

The habits of fishes on Kona reefs exemplify the habits of fishes on coral reefs around the world. The following discussion relates these habits to the evolution of fishes on modern tropical reefs, stressing the selective pressures that have shaped the diverse array of forms coexisting on these reefs today. I refer to some of these forms as more advanced, or specialized than others, even though all are products of an equally long evolution, and each is well adaptated to its own specific way of life. Some, nevertheless, have diverged more than others from the generalized carnivores that gave rise to them all, and in this fact lies the basis for the discussion.

The categories erected for presentation have indistinct, overlapping limits, and some species are discussed under one category, rather than another, quite arbitrarily. Nevertheless, the synthesis presented, though an oversimplification, provides a frame of reference within which new information may be assessed. Reemphasizing a point made above, this report deals only with individuals of the various species that behave as adults.

Coral Reefs as a Habitat for Fishes

Most fishes that inhabit coral reefs are among the more recently evolved teleosts (Schaeffer and Rosen, 1961; and others). Indeed, much of the diversity among higher teleosts expresses adaptations to reef habitats. Of the fishes observed along Kona transect lines (Table 7), 98.5% are acanthopterygians.[8]

To properly appreciate the relation of modern coral-reef fishes to their habitat, one should be familiar with the history of tropical reefs. The following outline is based on Newell (1971).

The evolution of tropical reefs can be traced through a fossil record that reaches back into the Precambrian. By the Mid-Ordovician, over 400 million years ago, animal communities had become associated with coral-algal reefs. A succession of reef communities then evolved during subsequent geological history, each with its own characteristic assemblage of animals, and each achieved marked stability before crashing into oblivion during worldwide environmental upheavals. Between each of these periods of stable reef communities, a long time passed without known reefs.

The scleractinian corals, which dominate modern reefs, first appeared during the Triassic, and by Jurassic times, about 150 million years ago, the lithothamnion-scleractinian reef community was well established. Significantly, the teleostean radiation also began during the Jurassic (Gosline, 1971), indicating that their history may closely interrelate with that of the lithothamnion-scleractinian reef community. But Smith and Tyler (1972) suggested that the preacanthopterygian teleosts and their forebearers were maladapted to reef conditions. They contended that fishes entered reef habitats only upon acquiring certain of the morphological advances that marked the first appearance of acanthopterygians early during the Cretaceous, over 100 million years ago. Newell (1971), on the other hand, believed that fishes have had a much longer history as reef inhabitants. He attributed their absence in the fossil record of early reefs to their skeletal remains having been "destroyed by scavengers that abound in this strongly oxidizing environment."

It is unquestioned, nevertheless, that early acanthopterygian fishes—the Beryciformes—were better adapted than were their predecessors for reef habitats. Their increased success probably was based mostly on increased maneuverability and a more adaptive feeding mechanism—the features which Smith and Tyler (1972) felt were especially suited for coral reefs. Patterson (1964) underscored this point when he concluded that most skeletal differences between acanthopterygians and their primitive elopidlike ancestors resulted from changes that permitted the fish better maneuverability: most significant, the fins, given increased rigidity by replacing the anterior soft rays with spines, were more effectively positioned, and the body was shortened and deepened. The advances these fishes made in their feeding mechanism was especially significant, as attested by Schaeffer and Rosen (1961), who stated: "It is primarily the acanthopterygian

[8]Because most of the transect counts were made in daylight, there is a bias toward the more advanced forms in numbers of species (the greater incidence of diurnally secretive habits among the more primitive forms, and of diurnally exposed habits among the more highly evolved forms, is discussed below). Even so, however, the preponderance of acanthopterygians is overwhelming, especially if one also considers numbers of individuals. On Kona reefs such advanced groups as the labrids, pomacentrids, and acanthurids are among the species with the largest numbers of individuals. And although among the nonacanthopterygians the numerous muraenid eels are not properly represented in the counts, neither are such nocturnal acanthopterygians as the numerous holocentrids.

mouth that has given rise to the enormous variety of specialized feeding mechanisms for which teleosts are so well known. Presumably, the evolution of the acanthopterygian jaw mechanism promoted the successful exploitation of food sources that previously were largely unavailable to actinopterygian fishes." They referred to the protrusible premaxillary of acanthopterygians, which permits them to project their upper jaw at food. Fishes with this mouth construction can accommodate the shape and size of the mouth opening more appropriately to the shape of the food item than can fishes without a protusible premaxillary (Alexander, 1967; Gosline, 1971).

During the Cretaceous, in which the beryciforms flourished, the ecological role of the scleractinian corals was challenged by a group of bivalved mollusks, the rudists, which underwent an extraordinary radiation and became the center of a highly successful and widespread reef community. But at the end of the Cretaceous, about 70 million years ago, these and other reef communities collapsed in sweeping extinctions associated with the worldwide biological revolution that marked the close of the Mesozoic (Newell, 1971).

Tertiary seas over most of the world were without known coral-reef communities until lithothamnion-scleractinian reefs underwent a second major radiation during the Eocene, about 50 million years ago (Newell, 1971). The communities that developed in association with these reefs are essentially those of our time. And in what would seem a related phenomenon, the explosive radiation of acanthopterygians into the types that inhabit modern reefs also occurred during the Eocene (Patterson, 1964). Of the families living on reefs today, only a relatively few can be traced back in time earlier than the Eocene (Berg, 1940), and yet by the end of that period, which spanned about 15 million years, representatives of almost every major type of modern fish had appeared (Romer, 1966).

This most recent proliferation of acanthopterygians probably radiated from a line of generalized percoidlike carnivores that had arisen from among the Beryciformes during the late Cretaceous (Gosline, 1966). Above, I note that 98.5% of the fishes seen on Kona transect lines are acanthopterygians; more specifically, 90.4% are acanthopterygians that have reached, or passed, the percoid level of structural development, and 75.5% belong to the order Perciformes (see footnote 7). Only the holocentrids represent the ancestral Beryciformes. In fact, worldwide the Holocentridae, and a few species of Anamalopidae, are the only representatives of this once prolific order that have survived on nearshore reefs.

Obviously the percoid level of development has been highly successful. Gosline (1971) pointed out: "In no single way does it seem to differ from that of the now unimportant, perhaps relic Beryciformes from which it was presumably derived. Possibly the percoids have developed some distinct and as yet unknown biological advantage over the Beryciformes, but for the moment one can only assume that the percoids represent a successful integration of minor advances." The minor advances which Gosline cited include increased maneuverability and adaptability of the protrusible jaw mechanisms, which are refinements on those same features adaptive to reef living that probably gave the Beryciformes an advantage over their progenitors.

Generalized Carnivores: Main Line of Teleostean Evolution

From early Mesozoic times the main line of actinopterygian evolution has progressed through a series of generalized carnivores; with each step forward, the basic feeding mechanism has improved, and the potential for adaptive radiation has increased (Schaeffer and Rosen, 1961). Although this progression has been marked by periodic bursts of specialized offshoots, the primary stem, the generalized carnivore, has remained relatively conservative (Gosline, 1959).

The generalized predator, in simplified form, has a large mouth and is adapted to directly approach, and seize, prey that are fully exposed to the attack. Its prey are small enough to be manipulated, yet large enough to be grasped; moreover, the prey are not sealed in heavy armour, nor do they carry strong spines, spicules, or other noxious components for which the unspecialized digestive tract of the generalized predator is maladapted. Although even the most primitive of today's predators have acquired at least some feeding specializations, the closer one approximates this simplified form, the closer its feeding habits fit this description.

With the generalized predaceous feeding mechanism being a relatively conservative morphological link between periods of adaptive radiation in actinopterygian fishes, one would expect

conservative predatory behaviors to be associated with this morphology, and just such behaviors are centered around nocturnal and crepuscular feeding habits. The nocturnal habit involves mostly predation on small, motile crustaceans, the crepuscular habit mostly predation on smaller fishes. Together, crustaceans and fishes are the two major types of prey taken by the generalized predator.

Nocturnal and crepuscular habits among generalized carnivores are discussed separately in the following sections. The separation is artificial, as is the delimitation of a third category, that dealing with generalized carnivores that feed regularly by day. In fact, as illustrated below, the behavior patterns associated with these three types of activity are closely interrelated.

Generalized Carnivores as Nocturnal Predators

Early in the evolving relation between fishes and their prey, the evolutionary lines of many small, vulnerable organisms probably increasingly shifted activity to periods of darkness. There scarcely could be a more elementary solution for animals threatened by active, visually orienting predators. And because effective defense adjustments in prey pressure predators to modify their offense, it seems certain that various predators early aquired means to follow their prey into the night. Thus, in predatory fishes the nocturnal habit itself would be a specialization, but a specialization probably adopted in early preteleostean times that has permitted much of the continued widespread success of the generalized predaceous feeding mechanism.

The smaller generalized carnivores on reefs today find their major prey among the abundant crustaceans, which, as follows from the above, are mostly nocturnal animals that expose themselves at night (Longley, 1927; and others). Many generalized predators that would feed on these organisms have found nocturnal habits adaptive, because only after dark does their straightforward attack find suitable prey in the required exposed position. In this feeding relation, the relatively small size of the crustaceans undoubtedly has influenced the size of the predatory fishes, most of which are of small to medium size (less than about 300 mm long).

Most nocturnal fishes in Kona prey on benthic crustaceans, especially xanthid crabs; however, a number are adapted to take crustaceans and other forms from the water column. The prey of these fishes are mainly relatively large zooplankters (a broad, perhaps loose concept of the term "zooplankton" is used in this report), like crab megalops, that are most abundant in the water column at night. Adults of most nocturnal planktivorous fishes in Kona do not feed significantly on the many small plankters, like calanoid copepods, that predominate in the water column during both day and night.

The extent to which the more primitive reef fishes feed at night seems not properly appreciated. Nocturnal habits are widespread among basal percoids, whereas diurnal habits tend to be characteristic of certain more specialized offshoots. Even if one considers only families that occur in Kona, all nearshore species of the Kuhliidae, Priacanthidae, and Apogonidae seem to be nocturnal, as are many species among the Serranidae, Carangidae, Lutjanidae, Sparidae, and Mullidae.

Probably the nocturnal habits of these more generalized percoids were inherited from ancestral beryciforms. The Holocentridae are the major representatives of this once diverse order on nearshore reefs today, yet as illustrated by their prominence in Kona, they nonetheless are numerous, widespread, and obviously successful. All of them for which there are data are nocturnal, and there is no reason to believe that this is not a primitive characteristic. The anamalopids, which are the only other beryciforms on nearshore reefs, also are nocturnal (e.g. Harvey, 1922). Presumably these modern beryciforms have competed successfully with nocturnal forms among the more advanced teleosts by having refined certain features that are highly adaptive to feeding in the dark. Thus, although much of their anatomy is essentially that of their ancestors, they have acquired highly specialized features—at least many of them sensory—that have permitted more effective use of this equipment. All other present-day beryciforms live in the twilight zone of middepths or in the deep sea, and their suitability to the diminished light of this habitat suggests that their shallowwater ancestors perhaps were nocturnal (Richard H. Rosenblatt, Scripps Institution of Oceanography, pers. commun.). Perhaps during the Cretaceous certain more specialized beryciforms possessed diurnal habits, much as many specialized perciforms do today. But if so, these

probably did not survive the widespread extinctions that decimated reef communities at the close of the Mesozoic.

If, as suggested, many reef fishes close to the main line of actinopterygian evolution long ago assumed nocturnal habits in answer to the nocturnal habits of their prey, then one is not surprised to find that widespread predator-prey relations are centered around the nocturnal habit and that the participants are mostly among the more generalized members of the reef community. One especially widespread activity pattern is displayed by the many fishes that assemble in schools on or close to nearshore reefs during the day, then disperse at nightfall and feed on small organisms that become exposed after dark. This is the basic activity pattern of many carangids, lutjanids, pomadasyids, and sciaenids—all among the more generalized perciforms (Hobson, 1965, 1968a, 1972, 1973).

In addition to these basal percoids, it is significant that of the relatively few fishes of preacanthopterygian groups associated with modern reefs, many either follow this pattern themselves, or closely relate as predators to other fishes that do (see next section). A diurnally schooling-nocturnally active pattern is especially widespread, if not universal, among the inshore clupeids, order Clupeiformes—as described earlier for *Harengula thrissina*, an exceedingly numerous fish close to shore in the Gulf of California (Hobson, 1965, 1968a). Starck and Davis (1966) found this same pattern in all five clupeids that they studied on reefs in Florida, and I observed it in *Herklotsichthys punctatus* in the Marshall Islands (unpubl. data). Pertinent information on nearshore clupeids is limited because so few investigators have distinguished between diurnal and nocturnal activity; nevertheless, there are at present no data refuting the generalization that these fishes feed at night.

There are fewer of these diurnally schooling, nocturnally active fishes on Kona reefs than on most other tropical reefs, perhaps for reasons discussed earlier (Hobson, 1972). Still, the pattern is well defined there in certain of the mullids, genus *Mulloidichthys,* and in the lutjanid *Lutjanus vaigiensis,* and is especially apparent in the atherinid *Pranesus insularum,* just as in its congener *P. pinguis* of the Marshall Islands (Hobson and Chess, 1973)—both of the preacanthopterygian order Atheriniformes.

Generalized Carnivores as Crepuscular Predators

In the same way that many generalized predators are nocturnal because suitable prey are most available to them after dark, other generalized predators—those that prey mostly on smaller fishes—are primarily crepuscular because that is when these prey become most vulnerable to their mode of attack (Hobson, 1968a). Moreover, just as is true of the nocturnal forms, the crepuscular piscivores, which also are among the more generalized of the reef fishes, experience certain long-established predator-prey relations. Significantly, many of these crepuscular piscivores are members of the same basal percoid families, the Serranidae, Carangidae, and Lutjanidae, that have produced some of the nocturnal predators discussed above. Many of the crepuscular piscivores, however, tend to be larger than the nocturnal species, which might be expected, inasmuch as the nocturnal fishes are among their major prey (Hobson, 1968a). Schools of nocturnal carangids, pomadasyids, mullids and, especially, clupeids, are well-known targets of such piscivores.

During the twilight periods of greatest piscivorous activity (Hobson, 1968a, 1972), these nocturnal fishes are still in their diurnal schools. And although the schools effectively protect them from predators during most of the day (Manteifel and Radakov, 1961; Eibl-Eibesfeldt, 1962; Hobson, 1968a), this protection is reduced during twilight (Hobson, 1968a). At this time of maximum danger from predators, most other smaller reef fishes, both diurnal and nocturnal, are under cover; thus, the schooling fishes, which are still in the water column, become the most numerous prey of proper size exposed to the space-demanding attacks of the generalized piscivores (Hobson, 1968a). After dark, the smaller fishes seem relatively safe from at least most such predators (Hobson, 1973), but during the changeover between day and night, they are vulnerable (Hobson, 1968a; Munz and McFarland, 1973).

The large piscivores are exceptionally abundant in certain parts of the Gulf of California where the diurnally schooling, nocturnally active fishes are numerous (Hobson, 1968a). As suggested earlier (Hobson, 1972), the relatively few such large predators on Hawaiian reefs, compared with most other tropical areas, may relate to the relative dearth in Hawaii of schooling prey.

Thus, a major activity pattern of these large piscivores closely interrelates with a major activity pattern of the smaller nocturnal predators. For this reason, and because so many members of the two groups are closely related taxonomically, it is apparent that the crepuscular pattern probably has had a longevity comparable to that of the nocturnal pattern. A good indication of this long history exists in the Gulf of California, where the day-night activity pattern of the nocturnal clupeid *Harengula thrissina* closely interrelates with the crepuscular activity not only of certain basal percoids, but also of *Elops affinis,* order Elopiformes, a member of the most primitive of all extant teleostean genera (Hobson, 1968a).

Generalized Carnivores as Diurnal Predators

Thus, nocturnal or crepuscular habits are adaptive for many generalized carnivores. Others with basically the same feeding mechanism, however, have acquired morphological and behavioral characteristics suited to capture small, motile crustaceans and, especially, fishes in daylight. Despite the fact that crustaceans are most exposed to direct attacks at night, and smaller fishes generally are most vulnerable to such attacks during twilight, various predators are equipped to exploit the exceptions to these generalizations.

True, selective pressures applied by generations of visually orienting predators have refined the defense mechanisms that protect so many prey organisms during daylight. But there are occasional lapses in all these defenses when the prey are briefly vulnerable. For example, nocturnal organisms resting under a thin layer of sand occasionally betray their presence by moving. And small fishes that usually are within retreating distance from cover sometimes stray too far into the open; or others, enjoying the security of a school, occasionally drift too far from their fellows. Still others, normally alert to surrounding danger, are momentarily distracted. At such times, these organisms are open to attack. But normally such events fail to occur in the presence of large, free-swimming predators that are actively hunting. Potential prey are sensitive to cues that mark the hunting predator, and take defensive action when a hunter appears—cryptic forms stop moving, others move closer to cover, and schooling forms draw themselves closer together (Hobson, 1965, 1968a). Above all, in this alerted state the prey are less likely to make a defensive mistake. This does happen occasionally, of course, as when large carangids swim slowly among schooling prey for hours during the day without an aggressive move, and then suddenly attack —presumably having sensed a vulnerable target (Hobson, 1968a). Probably this offensive tactic depends on the prey eventually becoming conditioned to the predator's presence, and finally making a mistake. But it seems unlikely that such predators could depend on these relatively infrequent successes. They remain best suited for crepuscular attacks.

The problem of being within striking range when prey are momentarily available during the day because of a defensive lapse is probably best solved by those predators that lie in wait under concealment—the ambushers—or by those that stalk. Both tactics have produced some highly specialized forms that are more appropriately considered in the next section. However, many of those that use concealment to ambush their prey look much like the nocturnal or crepuscular predators discussed above, and so are considered here.

This is especially true among certain basal percoids, like the serranids. For example, many species of *Epinephelus* ambush prey from a concealed position, and much of this activity occurs in daylight (Hiatt and Strasburg, 1960; and others). Most of these predators are cryptically hued for a sedentary existence among rocks or coral—usually they are brown or grey, with the hues often arranged in blotches or spots. Such predators rest unseen until a small organism within striking distance makes a defensive error.

Generalized predators adapted for this tactic are well known to feed regularly during both day and night, as exemplified by certain species of *Epinephelus* (Longley and Hildebrand, 1941; Starck and Davis, 1966; Hobson, 1968a). There is evidence, however, that feeding habits of these predators differ between day and night. In the Gulf of California, *E. labriformis* preys almost entirely on crustaceans at night, but heavily on fishes during the day (Hobson, 1968a). I have already commented on the increased vulnerability of small crustaceans at night; apparently fishes are more vulnerable to the predatory tactics of this fish in daylight. The diurnal piscivorous habit of *Cephalopholis argus* (*Epinephelus argus* of some authors, e.g. Smith, 1971) in Kona is consistent with this probability.

Predators having obvious morphological and behavioral specializations that increase their proficiency as ambushers or as stalkers are considered in the next section.

Specialized Offshoots from the Main Line of Teleostean Evolution

Most fishes inhabiting tropical reefs today, as exemplified by species in Kona, represent specialized offshoots from the main teleostean line.

Predators Specialized to Ambush Prey

As emphasized in the introductory remarks, the categories erected in this discussion overlap. This is especially true of predators that ambush their prey. By using this tactic, predators with the generalized feeding mechanism increase their capacity to capture prey in daylight. But many ambushers, like certain species of *Epinephelus,* are so similar in both morphology and habits to many of the nocturnal and crepuscular forms discussed above that one can only arbitrarily distinguish them as being specialized in this activity. Nevertheless, some forms have retained the generalized feeding mechanism while diverging widely from the primitive form in other respects. And the divergence is based on features that better adapt these fishes for the ambushing tactic.

The synodontids, order Myctophiformes, which are prominent ambushers in Kona, as they are on most other tropical reefs, are products of an evolutionary offshoot that diverged from the main line at a preacanthopterygian level. Thus, the ambushing tactic has had a long history. The scorpaenids, order Scorpaeniformes, and the bothids, order Pleuronectiformes, both of whose Kona representatives include specialized ambushers, belong to groups that diverged from the mainstream near the percoid level (Gosline, 1971; and others). Significantly, the adults of all these forms seem to be primarily piscivorous during the day.

The synodontids, scorpaenids, and bothids that ambush their prey have acquired characteristics that camouflage them as they lie on the sea floor. Clearly, it is important for these predators to go unseen by their victims. In this respect, many of the cirrhitids, order Perciformes, might seem a puzzle. An example from Kona is *Paracirrhites forsteri* (Figure 32), which preys mostly on smaller fishes during the day. Although attacking prey in much the same manner as other ambushers, this colorful fish is clearly visible as it rests in exposed positions on the reef. Selection, in this case, may have in fact favored coloration that attracts attention. Conceivably this could be an effective offensive characteristic, just so long as its use among predators is limited. It is well known that certain small fishes are attracted to conspicuous objects on the sea floor—one needs only to place a small, shiny artifact on the bottom to see this. Perhaps *P. fosteri* actually finds prey among small fishes that approach to investigate its conspicuous features.

Predators Specialized to Stalk Prey

Many predators specialized to stalk prey in the water column belong to groups whose ancestors diverged from the main teleostean line below the percoid level. Characteristically, they have long, attenuated bodies. Among species whose behavior in Kona is described above are the trumpetfish, *Aulostomus chinensis*, and the cornetfish, *Fistularia petimba*—both of the order Gasterosteiformes.

Two other highly specialized stalkers on Kona reefs were not included in the species accounts above because observations on them were infrequent; these are the needlefish, *Strongylura gigantea,* order Atheriniformes, and the barracuda, *Sphyraena barracuda,* order Perciformes. The various species of needlefishes and barracudas are widespread on tropical reefs, and their stalking habits are well documented. Hiatt and Strasburg (1960) reported that *Strongylura gigantea* feeds on small fishes in the Marshall Islands by "drifting up to them and suddenly lashing out with its jaws." On the basis of similar observations in the tropical Atlantic, Randall (1967) reported that needlefishes are almost exclusively piscivorous, and that they "drift slowly into range of one of their prey before making a quick rush." Regarding barracudas, Hiatt and Strasburg (1960) told of *Sphyraena genie* in the Marshall Islands "drifting solitary near the surface stalking its prey" and stated that "it surprises its victim with a sudden lunge." Randall (1967) noted that barracudas in the tropical Atlantic feed primarily on fishes during the day, a statement probably true of at least most stalking predators.

Predators Specialized to Seek Prey in Reef Crevices

Here I am concerned primarily with muraenid eels, order Anguilliformes, and the brotulids, order Gadiformes. Members of both groups, but the eels in particular, have elongated bodies suited to maneuvering through the crevices that honeycomb coral reefs. Their similar morphologies led early Hawaiians to group eels and brotulids together by the generic term *puhi*. There are a number of other secretive forms on Kona reefs—small inconspicuous fishes like the pseudochromid *Pseudogramma polyaccanthus*, which were occasionally visible at night during this study—but because I have little knowledge of their habits they are not considered here.

The muraenid eels are products of an evolution that has diverged widely from the main teleostean line: today they possess many specialized features that equip them for hunting in reef crevices. The primary specializations, for example their exceptionally solid skulls, are adaptive for wedging through small openings, and they can back out of any hole they enter (Gosline, 1959, 1971). Many of the morays, and at least some of the brotulids, for example *Brotula multibarbata* in Kona, are nocturnal; however, other morays are diurnal. Obviously hunting conditions in reef crevices differ between day and night.

Reef crevices are havens for numerous creatures. Many diurnal forms rest there at night, some of them virtually asleep, and many nocturnal forms shelter themselves there in daylight (Hobson, 1968a, 1972). Moreover, most reef animals find refuge in these crevices when they are injured or distressed; obviously, sheltering in reef crevices is adaptive for prey threatened by the many predators on the surface of the reef. But it is equally obvious from their long successful history on tropical reefs that eels have acquired adaptive means to exploit such prey.

Predators with Sensory Specializations That Detect Concealed Prey

In this category I am concerned with the mullids, order Perciformes, which are prominent on Kona reefs. Their distinctive sensory chin barbels permit them to locate prey that go undetected by other fishes. And, like the muraenid eels, above, their numbers include both diurnal and nocturnal forms, as well as species that hunt effectively during both day and night. This fact, and the great diversity in their prey, shows that mullids, with their distinctive modes of feeding, have available to them a broad range of predatory activity denied most other fishes.

Although seeking refuge under rocks, algae, or sand is adaptive for many small animals approached by a predator, this tactic probably plays to the advantage of some mullids. For example, the diurnal *Parupeneus chryserydros* preys mostly on small diurnal fishes that typically take cover when threatened. This mullid may use its exceptionally long barbels not only to locate such animals, but also to drive them into the open.

Many small organisms that seek cover when threatened rest in the same refuges when they are inactive, and at such times may be prey for other mullids, notably *P. bifasciatus*. This species seems to feed with equal effectiveness day and night, although its food habits differ between these two periods. In this respect, a comparison with the serranid *Epinephelus labriformis* in the Gulf of California is insightful. As noted above, *E. labriformis* also feeds regularly day and night, taking mostly crustaceans after dark and small fishes in daylight; thus, its food habits agree with the generalization that crustaceans are most vulnerable at night, and fishes most vulnerable in daylight. *Parupeneus bifasciatus* seems to be a successful exception to this generalization, because it takes fishes more often at night than during the day and crustaceans more during the day than at night. Apparently, *P. bifasciatus* is specialized to capture prey that rest under cover, safe from predators with generalized feeding equipment.

Thus, at least some mullids find prey among animals that have sheltered themselves in the reef, just as do some of the muraenid eels, so that, like the eels, they have gained advantage from what generally are successful defensive behaviors in their prey. But whereas the eels probe deep into reef interstices, the mullids confine their activity to the superficial covering on the reef.

Predators Specialized to Take Prey Among the Plankton During the Day

There are clear distinctions between diurnal and nocturnal planktivorous fishes on coral reefs, with the diurnal species inactive at night and the nocturnal species inactive during the day (Hobson, 1965, 1968a, 1972; Starck and Davis, 1966). Emery (1968) showed that the composition of

plankton over reefs in Florida also differs between day and night, a fact undoubtedly related to the diurnal-nocturnal dichotomy among the planktivorous fishes. As described above, planktivorous fishes that feed in the water column at night, for example *Myripristis* and *Apogon,* have the generalized carnivore's large mouth and prey largely on the relatively large plankters, like crab megalops, that are mostly in the water column above the reef after dark.

Although a large array of plankters inhabit the water column during the day, generally they seem too small for adults of the large-mouthed nocturnal planktivores. Significantly, diurnal planktivores all have a small mouth, and their major prey, calanoid copepods, are generally smaller than the prey of their nocturnal counterparts. Moreover, diurnal planktivores among adult reef fishes generally are among the more advanced teleosts, having attained, or passed, the percoid level of development. There are no basal percoids among the prominent diurnal planktivores in Kona, but in the tropical Atlantic certain serranids, lutjanids, and pomadasyids specialized in this habit are numerous (Starck and Davis, 1966; Randall, 1967). Most diurnal planktivores on coral reefs, however, are among the higher Perciformes. These include the pomacentrids, which probably include a higher proportion of planktivorous species than any other major family of coral-reef fishes. The balistids, order Tetraodontiformes, are among the most advanced teleosts and include several specialized diurnal planktivores: species of *Melichthys* and *Xanthichthys ringens* are prominent on coral reefs over much of the tropical world.

Many unrelated species that forage on zooplankton in the water column during the day display convergent morphologies. Features characteristic of these fishes were identified by Davis and Birdsong (1973), who did not distinguish between diurnal and nocturnal forms, however. Drawing examples from the tropical Atlantic Ocean, they illustrated certain unrelated planktivorous fishes, for example *Paranthias furcifer* (a serranid) and *Chromis cyanea* (a pomacentrid), that, on casual inspection, look more like one another than they do members of their own families that feed on the benthos. The similarity among these unrelated forms is based mainly on their common increased tendency toward a fusiform body, a deeply incised (forked or lunate) caudal fin, and a small, upturned mouth that gives their heads a characteristic appearance. Presumably diurnal planktivores that tend toward a more fusiform body and deeply incised caudal fin—both well-known characteristics of rapid-swimming oceanic fishes—can swim faster than relatives in which these tendencies are less developed. Considering the many active predators at large during the day, increased speed clearly is adaptive for small reef fishes that swim at that time in open water, high above the sheltering reef. The advantage of the upturned mouth may be indirect: Rosenblatt (1967) acknowledged Walter A. Starck II for pointing out that this mouth construction gives the fish a shortened snout, which permits close-range binocular vision—an obvious advantage in capturing tiny organisms in the water column. A number of diurnal planktivorous fishes in Kona possess one or more of these characteristics, as described and illustrated above (e.g. Figures 38 and 40).

Significantly, none of the nocturnal planktivores in Kona tend toward having either a more fusiform body, or a more deeply incised caudal fin. In fact, planktivorous squirrelfishes of the genus *Myripristis* are actually deeper bodied than their bottom-feeding relatives of the genus *Holocentrus,* and the caudal fins of most are less deeply incised (compare, for example, Figures 11a and 14). If, as suggested above, these features gain selective advantage in the planktivores by providing added speed to elude predators in open water, then their absence among forms that rise into the water column after dark is consistent with the contention (above, and Hobson, 1973) that small free-swimming fishes face a much diminished threat from predators at night. Many of the nocturnal species, including species of *Myripristis,* have the sharply upturned mouth; but it is a large structure, as noted above, suited to taking the larger zooplankters that appear in the water column after dark.

Not all of the diurnal planktivores in Kona tend toward fusiform bodies, deeply incised caudal fins, or sharply upturned mouths. None of these features occur in the planktivorous chaetodontids, for example *Hemitaurichthys zoster* (Figure 28a), which nevertheless are well suited to feed on copepods, and other tiny zooplankters in the water column by day. Obviously many conflicting pressures have differentially affected the morphologies of the various fishes that forage on tiny organisms in the mid-waters.

Predators Specialized to Prey on Benthic Invertebrates During the Day

A wide variety of fishes prey on benthic invertebrates during the day. They include most of the labrids, chaetodontids, balistids, canthigasterids, monacanthids, ostraciontids, and tetraodontids, as well as many of the pomacentrids, blenniids, and others—all of them higher perciforms or tetraodontiforms. Their prey are among the more prominent invertebrates on the reef, including such sessile forms as sponges, coelenterates, and tunicates; and also various slow moving animals like echinoids and gastropods. Typically, these prey are fortified with toxic or noxious components, like spines, spicules, nematocysts, or tough, fibrous components; or they are encased in heavy armour. Because of these defensive features, fishes that prey on such forms must have specialized feeding structures or techniques—the unspecialized feeding apparatus of generalized predators is maladapted for this task. Also unavailable to generalized predators are the many very small organisms whose capture requires delicate manipulations or movements for which large-mouthed fishes are unsuited. Moreover, many of these prey are diurnally cryptic or secretive, thus requiring still additional specializations to capture them in daylight.

Thus, fishes that successfully feed on most benthic reef invertebrates during the day are advanced species whose evolution has been mostly one of perfecting means to feed in daylight on prey that are beyond the capacity of fishes with generalized feeding equipment. Certain mullids, discussed above, are adapted to feed on many of these prey, but mullids use nonvisual means, whereas fishes considered here are primarily visual feeders.

These are fishes that have passed the percoid level of development. The evolution of the percoid morphology, especially with its highly adaptive feeding mechanism, gave fishes added potential to adjust to a wide variety of feeding situations. But although percoids appeared first during the Cretaceous (Patterson, 1964), not until modern reef communities appeared during the Eocene (Newell, 1971) does it appear they began to fully realize this potential.

Bakus (1964, 1966, 1969) concluded that the secretive habits and defensive structures of many benthic invertebrates on coral reefs today, including sponges, didemnid tunicates, and others, are the result of predation pressures from fishes. Whether or not this is so, certainly the array of specialized feeding habits and structures that characterize diurnal bottom-feeding fishes on coral reefs are mostly adaptations which cope with specific defensive characteristics of their prey. Because predation pressures lead to defensive adjustments in prey, and these in turn stimulate further offensive modifications in predators, it is not surprising that the diverse array of defenses in benthic invertebrates today is matched in the fishes that feed on them by an equally diverse array of solutions. These solutions to invertebrate defenses are manifest in the extremely varied feeding structures and behaviors that occur among diurnal fishes. Most diurnal fishes specialized for diets of benthic invertebrates have relatively small mouths, but beyond this their feeding morphologies have diverged widely.

Sessile invertebrates seem to be significant prey only during the day, perhaps because an animal must move to be sensed by most predaceous fishes at night (Hobson, 1968a). Thus, the few highly specialized fishes that feed on sponges are strictly diurnal. In Kona, the chaetodontid *Holacanthus arcuatus* feeds on some of the larger sponges that encrust in exposed locations on rocks, whereas the zanclid *Zanclus canescens* uses its elongated snout to feed on some of the smaller sponges that are attached within crevices or depressions on the reef. Randall and Hartman (1968), in studying sponge-feeding chaetodontids and monacanthids in the West Indies, noted that sponges cannot be digested by most fishes, and concluded that these organisms have become available as food for only a few highly specialized teleosts in geologically recent times.

Some diurnal predators, for example *Forcipiger flavissimus, Chaetodon auriga,* and *C. fremblii,* among chaetodontids in Kona, habitually tear off pieces of larger sessile invertebrates, including polychaetes, tunicates, and alcyonarians. The analogy drawn above between the snout and jaws of *F. flavissimus* and a pair of needle-nosed pliers underscores the suitability of this fish's feeding morphology for its feeding habit.

One of the most obvious potential foods for carnivorous bottom-feeding fishes on coral reefs would seem to be the corals themselves. Nevertheless only some of the most advanced teleosts exploit this resource. In Kona, coral eaters include certain chaetodontids, pomacentrids, and blenniids (all higher Perciformes) and certain

monacanthids and tetraodontids (all Tetraodontiformes). In pointing out that coelenterates are not food for fishes in most marine communities, Hiatt and Strasburg (1960) cited various specialized features of fishes that prey on corals in the Marshall Islands: for chaetodontids and monacanthids that snip off individual polyps, they listed the produced snouts, small terminal mouths, and fine protruding incisiform teeth; for tetraodontids and balistids that bite off larger pieces of coral, they noted very heavy, strong dentition. All fishes that feed on coral, including those that feed heavily on coral mucus, seem to be diurnal. Obviously a predator that bites off large chunks of coral, or which scrapes away mucus, would find diurnal habits adaptive—its food is equally accessible day or night, and its own activity would benefit from daylight. On the other hand, the polyps of some coral species are most expanded at night, suggesting that perhaps predators that would snip them off might find them most accessible after dark; however, the precise manipulations involved in this activity probably require the light of day, because without exception all such predators are diurnal.

Daylight and precise manipulations also seem required of predators that pluck tiny cryptic organisms, notably amphipods, from amid benthic cover. An example from Kona is the labrid *Anampses cuvier,* whose prey are amphipods and other organisms too small for large-mouthed generalized predators of comparable size. Taking such prey requires a specialized tactic and feeding mechanism. Characteristically such predators hover within a few centimeters of the substratum, inspecting the surface. When they spot prey —perhaps through movement or an unusual contour—they take it in a characteristic plucking manner.

Probably this way of plucking tiny prey from a substratum preadapted precursors of those fishes that are specialized as cleaners. Most cleaner fishes, which include certain labrids, pomacentrids, and chaetodontids, pluck various materials, mostly ectoparasitic crustaceans, from the bodies of other fishes. Possessing both the necessary techniques and morphology, certain fishes in this category were prepared to adopt the cleaning habit when their concept of a suitable feeding substratum broadened to include the bodies of other fishes (Hobson, 1971). A few species, like *Labroides phthirophagus* in Kona, are specialized as cleaners, having refined both their feeding morphologies and techniques to more efficiently practice this habit. All known cleaner fishes are diurnal.

Most of the invertebrate prey of diurnal fishes are insignificant as prey of nocturnal fishes. However, the specializations that permit certain diurnal fishes to seek out secretive prey in daylight make available to them at that time some of the forms—motile crustaceans in particular—that are important prey of various generalized predators after dark. For some fishes, the adaptations that permit them to take crustaceans and other forms from under reef cover in daylight are morphological. Thus, the chaetodontid *Forcipiger longirostris* and the labrid *Gomphosus varius* both have elongated snouts with which they reach deep into reef crevices for crustaceans. In other fishes the adaptations that make secretive prey available are more strictly behavioral. Thus, the labrid *Thalassoma duperrey* follows close to the feeding jaws of large herbivores and other fishes that disturb the substratum, and snaps up tiny crustaceans driven from cover. This behavior is widespread, occurring in other wrasses in Kona and also in the Gulf of California (Hobson, 1968a). Some species lower on the evolutionary scale seem to have similar behavior: as suggested above, the carangid *Caranx melampygus* may enjoy this advantage by following the mullid *Parupeneus chryseydros,* as may the aulostomid *Aulostomus chinensis* by accompanying grazing schools of acanthurids—in these two situations, however, the prey seem to be mostly small fishes.

Some diurnal predators excavate buried prey, as when the labrid *Coris gaimard* overturns small stones with its snout and feeds on animals thus exposed. And in the eastern Pacific the balistid *Sufflamen verres* uncovers prey buried in the sand by exposing them with a jet of water from its mouth, or by rapidly undulating dorsal and anal fins while lying on its side, thereby generating currents that sweep the sand away (Hobson, 1965, 1968a). Similarly, the ostraciontid *Lactophrys triqueter* in the tropical Atlantic by jetting water from its mouth uncovers prey buried in the sand (Longley, 1927).

Related Problems of Species Recognition.—The enormous potential for varied feeding adaptations in these advanced teleostean groups has led to the occurrence on most coral reefs of large numbers of closely related species that seem to have diverged from one another chiefly on the basis of differing food habits. For example, 14 species of the genus

Chaetodon occur together on Kona reefs—all very similar in general body form, but with distinctive differences in diet and related morphology. Obviously, such situations can exist only if, in addition to having acquired adaptations suited to specialized diets, closely related forms have also acquired effective barriers to interbreeding. Central to this is the ability of each individual to recognize others of its own kind, which probably relates to the circumstance that most species in this category have highly visible species-specific color patterns.

It is logical that diurnal fishes would employ visual cues to identify one another. But the distinctive nocturnal colorations of many chaetodontids suggest that members of some species need to recognize each other after dark as well. Nocturnal colorations that occur among chaetodontids in Kona tend to accentuate a contrast, thus making them more visible at lower light levels (e.g. Figures 28a and b; 29a and b). Although the nocturnal colorations of some fishes, such as those that become mottled, make them more difficult to see in the dark (Schroeder, 1964), certain chaetodontids in Kona seem to be effecting a nocturnal display. This phenomenon appears most pronounced among fishes in the present category, but others show it as well; for example, in Kona certain of the nocturnal squirrelfishes, *Holocentrus* (Holocentridae: Beryciformes) display characteristic white bars or spots at night that are more visible under reduced light than their daytime colorations would be (e.g. Figure 12a and b). Probably one can generalize only to the extent that distinctive day/night colorations in coral reef fishes reflect distinctive day/night situations.

Fishes Specialized to Feed on Vegetation

Vegetation, which carpets much of the rocky sea floor inshore, would seem ready food for fishes. Yet relatively few species utilize this resource, even though, as in Kona, they often predominate on tropical reefs. The herbivorous habit is an advanced trait among marine fishes, a fact recognized by Hiatt and Strasburg (1960).

In general, herbivorous fishes on coral reefs share many characteristics with the diurnal predators that are specialized to prey on benthic invertebrates, discussed in the previous section. Like the fishes grouped together in that category, at least most coral reef herbivores are active by day and relatively inactive at night; furthermore, they too tend to be colorful animals that have small mouths which are part of highly evolved feeding systems. In fact, several families of fishes span both categories; for example, the Chaetodontidae, Pomacentridae, Blenniidae, Balistidae, Monacanthidae, and others include gradations of species from some that are strictly carnivorous, to others that feed on both plants and animals, to still others that are strictly herbivorous. Within these groups, which have favored plasticity in feeding habits and structures, it seems that characteristics adaptive to plucking benthic invertebrates from the sea floor have been modified in some species for grazing on plants.

Nocturnal Activity Among Advanced Teleosts

Not all the more advanced fishes are diurnal. The chaetodontid *Chaetodon lunula* seems to be nocturnal in Kona, and at least some of its congeners—notably *C. quadrimaculatus* and *C. auriga*—may feed to some extent after dark. But these are exceptional cases in an overwhelmingly diurnal group. As suggested above, nocturnal activity in these instances may relate to competition among the exceptionally large number of *Chaetodon* species that cooccur on Kona reefs.

Nocturnal habits cannot be regarded as exceptional where they occur among the diodontids, however, because night feeding seems to be the rule in this family. And these members of the order Tetraodontiformes are among the most highly evolved of all reef fishes. The prey of *Diodon hystrix* and *D. holocanthus* in Kona —large echinoids, gastropods, and pagurid crabs—are more exposed at night than during the day. And because they are relatively large and move at least intermittently after dark, one can predict they would be suitable quarry for nocturnal predators having means to crush heavy armour. These are large prey, so a predator must carry its crushing mechanism in its mouth, rather than in its throat—as do many of the labrids and other predators that feed on smaller mollusks and echinoids during the day. The highly evolved diodontids accomplish this job with their powerful crushing jaws, but the problem has also been solved at a more primitive level by certain basal percoids. In Kona, the nocturnal sparid *Monotaxis grandoculis*, with its molariform dentition, has feeding habits similar to those of the diodontids, but with less emphasis on heavily armoured forms. Clearly, the diodontids, with more powerful jaws and heavier dentition, are better adapted

than the sparids for this particular task. Of even more primitive stock than the sparid, the muraenid eel *Echidna zebra* has crushing dentition, but its prey seem to be primarily large crabs that it takes regularly from reef crevices in daylight. There is no evidence that it can crush the heavy gastropods so prominent in the diets of the more advanced sparids and diodontids.

CONCLUSIONS

1. The feeding relationships of fishes on coral reefs in Kona, Hawaii, follow essentially the same pattern as do feeding relationships of fishes on coral reefs elsewhere.

2. Nocturnal habits have had a long history in teleostean fishes, and are widespread among the more generalized forms, including many of the clupeids, holocentrids, serranids, kuhliids, priacanthids, apogonids, lutjanids, and others. These large-mouthed predators find night feeding adaptive because that is when their prey—mostly small, motile crustaceans—are in exposed locations and thus vulnerable to their straightforward attack.

3. Piscivorous predators that have a generalized feeding mechanism, and which attack with a straightforward charge, for example certain large carangids, are mostly crepuscular.

4. Certain piscivorous predators that have a generalized feeding mechanism feed effectively during the day, as well as during twilight, by ambushing or stalking their prey. The ambushers, which include certain synodontids, serranids, scorpaenids, and bothids, typically have cryptic morphology, coloration, and behavior. The stalkers, which include the aulostomids, fistulariids, belonids, and sphyraenids, typically have long, attenuated bodies.

5. In acquiring features adaptive for hunting in reef crevices, muraenid eels have become highly successful, capitalizing on the otherwise effective shelter-seeking habits of small reef animals. Although many small reef animals become more vulnerable to eels when they shelter in reef crevices, they find these refuges adaptive when resting, injured, or distressed, because they are relatively safe here from the even greater threat from predators that exists on the surface of the reef.

6. The mullids use their distinctive sensory barbels to locate prey that are sheltered under the superficial covering of the reef and adjacent sand. Some mullids are best adapted to capture such prey at night, others to capture such prey in daylight, and some feed effectively during both day and night. At least some use their barbels not only to detect prey, but also to drive them into the open.

7. Most fishes on Kona reefs, like fishes on coral reefs elsewhere, are among the more recently evolved teleosts, having reached, or passed, the percoid level of structural development.

8. The adaptability of the perciform feeding apparatus has given rise to a wide variety of forms that have diverged from one another primarily on the basis of differing food habits. Much of this diversity has resulted from adaptations that cope with specific defensive characteristics of the organisms on which these fishes feed.

9. Just as nocturnal and crepuscular habits predominate among the more generalized coral-reef fishes, diurnal habits predominate among the more advanced, specialized forms, including most of the higher Perciformes, and Tetraodontiformes. Some of the most advanced of all, however, including the diodontids, are nocturnal.

10. Some higher teleosts, including certain chaetodontids, labrids, and balistids, have specializations that permit them to capture, during daylight, nocturnal forms hidden under cover. Such prey include forms like motile crustaceans that expose themselves at night, and at that time become the major prey of generalized nocturnal fishes.

11. Some advanced teleosts, including certain chaetodontids, labrids, and pomacentrids, are specialized to pluck tiny prey, such as amphipods, from among vegetation and other benthic cover. These prey are too small, and too cryptic, to be taken after dark or by predators with a large mouth. This plucking habit preadapted certain species for cleaning ectoparasites and other material from the bodies of other fishes.

12. Fishes that prey mostly on sessile invertebrates, like sponges and coelenterates, are highly evolved diurnal species, including certain chaetodontids, pomacentrids, balistids, and monacanthids. These predators have specialized feeding structures and techniques that handle various noxious or toxic defensive features in their prey, including spines, spicules, nematocysts, tough fibrous tissues, and heavy armour. And they take these sessile animals in daylight because only moving prey are effectively sensed by visually feeding predators after dark.

13. Characteristics developed in feeding on sessile benthic invertebrates have been modified in some fishes for grazing on benthic vegetation. Thus, many families, for example the Chaetodontidae, Pomacentridae, Balistidae, and Monacanthidae, include some strictly carnivorous forms that prey on benthic invertebrates, other forms that feed on both benthic invertebrates and vegetation, and still others, strictly herbivorous, that only graze on benthic vegetation.

14. On coral reefs there is no sharp distinction between fishes that feed on sessile invertebrates and those that graze on benthic vegetation: species in both categories tend to be colorful diurnal fishes with a small mouth that is part of a highly evolved digestive apparatus.

15. The plasticity in feeding habits and structures characteristic of higher teleosts that feed on benthic organisms has led to the multiplicity of closely related, and morphologically similar species that live together on coral reefs. This situation could not have evolved without effective barriers to interbreeding, which in turn requires that individuals recognize others of their own kind from among many very similar forms. This requirement has been met by having developed highly visible, species-specific color patterns. The distinctive nocturnal color patterns of some forms, for example *Zanclus* and certain chaetodontids, indicate that, although they are diurnal, certain of them need identifying features at night, as well as during the day.

16. The small mouth of higher teleosts is adaptive for feeding on the smaller plankters, like calanoid copepods, that compose the vast majority of organisms in the water column. This characteristic distinguishes diurnal planktivores, including certain pomacentrids, chaetodontids, and balistids, from the nocturnal planktivores, which include certain holocentrids and apogonids. Most nocturnal planktivores have the larger mouth of the generalized predators, and most of them feed primarily on the larger plankters, like crab megalops and mysids, that are most numerous in the water column over the reef at night.

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THE EFFECTS OF DIETARY α-TOCOPHEROL AND TUNA, SAFFLOWER, AND LINSEED OILS ON THE FLAVOR OF TURKEY

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ABSTRACT

Turkeys were fed varying levels of α-tocopherol acetate and oils containing linolenates (linseed and tuna oils). As expected, these oils caused a fishy flavor to develop in the turkey carcass, and α-tocopherol fed concomitantly, greatly retarded development of this fishy flavor, but did not affect the uptake of linolenates by the turkey carcass. These and other observations pointed to the conclusion that linolenates do not by their simple presence in turkey carcass cause fishy flavor, but that perhaps their in vivo and/or postmortem oxidation are responsible for the development of this flavor.

Several investigators have reported that fishy flavors develop in poultry carcass when diets are supplemented with oils, such as linseed oil (Klose et al., 1951) and fish oil (Neudoerffer and Lea, 1966, 1967, 1968; Miller et al., 1967a, 1967b; Miller and Robisch, 1969; Dreosti, 1970; Opstvedt, Olsen, and Urdahl, 1970; Opstvedt, Nygard, and Olsen, 1970, 1971). The latter investigators showed that this off flavor is related to the linolenate content of the oil, especially the long chain homologues. Miller and Robish (1969) showed that fishy flavors were eliminated with the withdrawal of fish oils and substitution of a more saturated fat (like tallow) in the diet. Lineweaver (1970) reported that practical experience has shown that the amount of fish oil in the diet of poultry should not exceed 0.3% if fishy flavors are to be avoided. However, it was not clear whether the specific character of the oil (ω3 fatty acid content) was a factor to be considered.

Lea et al. (1966), Dreosti (1970), and Opstvedt et al. (1971) reported that antioxidant-treated fish meal is more likely to cause fishiness than untreated meal. They reasoned that the unsaturated fatty acids of the untreated meal become oxidized and, perhaps, polymerized, thereby becoming unavailable for uptake in the tissue.

The research of Mecchi, Pool, Beham, Hamachi, and Klose (1956) showed that the stability of turkey fat closely paralleled the tocopherol content of the fat. Other work by Mecchi, Pool, Nonaka, Klose, Marsden, and Lillie (1956) whereby chickens and turkeys were fed varying levels of dietary tocopherol, further substantiated that in fact tocopherol uptake was possibly singularly important to the stability of carcass fat. These findings are corroborated in more detailed studies by Webb, Marion, and Hayse (1972) and Webb, Brunson, and Yates (1972).

Dreosti (1970) and Opstvedt et al. (1971) reported that dietary α-tocopherol acetate supplementation (above levels required to prevent nutritional disease) significantly reduced fishy flavors in poultry fed fish oils.

It is clear that dietary oils containing ω3 fatty acids do in some way contribute to fishy flavors in poultry and that α-tocopherol acetate supplementation reduces the development of this flavor. It is not clear how ω3 fatty acids, when ingested by poultry, result in fishy flavored carcasses or how α-tocopherol reduces the development of this flavor. This paper reports on the fatty acid composition of extracted lipids and on the flavor of the meat from turkeys fed fish oil and linseed oil to 6 wk and to 8 wk of age using safflower oil or beef fat to bring diets into lipid isocaloric balance. Supplemental tocopherol acetate was added to some of the diets. The flavor of adult turkeys fed tuna oil for 2 wk was also observed.

While it is not a practice to raise turkeys to only 6 and 8 wk of age or to feed fish oil midstream for only 2 wk, it was convenient and expedient for the present study. Additionally, observations can be made on the relative uptake of dietary fats and the influence of metabolic rate.

EXPERIMENTS

Oils

Linseed oil, refined safflower oil, freshly rendered beef fat, and fresh polished tuna oil (albacore) were obtained unstabilized. The oils were

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deaerated under vacuum and twice flushed with nitrogen. To part of each oil was added 0.3125% ethoxyquin (this will give 125 ppm when added to diet). The stabilized oils were again evacuated, flushed under nitrogen, and stored at −26°C until use. The rendered beef fat was stored at −26°C until used.

Feed

The following basal diet was used in the feeding of turkeys:

Ingredients	*% of diet*
Soybean oil meal (50%)	50.00
Mineral mix	2.58
Vitamin mix (in corn starch)	1.00
$CaHPO_4 \cdot 2H_2O$	1.70
$CaCO_3$	1.90
Choline Cl (50%)	0.40
DL-Methionine	0.20
Ground corn	38.42

Diets contained 10 mg vitamin E (*dl*-α-tocopherol acetate) per kilogram and 0.66 ppm sodium selenite. Oils were preweighed and stored at −26°C under nitrogen before incorporation into diets. Diets were mixed with the oils every 1 or 2 wk and stored in a refrigerator and fed fresh daily.

Diets and Feeding

Experiment I

Eighty White Broad Breasted poults (unsexed) were fed chick starter (about 7% fish meal) on day 1. On days 2 and 3, they were fed one-half starter and one-half basal diet. On day 4, they were divided into eight groups of 10 turkeys each, equally distributed by weight, and fed to 6 wk of age on the following experimental diets:

Group	*Oil supplement to basal diet*[1]
1	4% SO
2	4% SO + 125 ppm EMQ
3	1% SO + 3% LO
4	1% SO + 3% LO + 125 ppm EMQ
5	3.5% SO + 0.5% TO
6	3.5% SO + 0.5% TO + 125 ppm EMQ
7	3% SO + 1% TO
8	3% SO + 1% TO + 125 ppm EMQ

[1]SO = safflower oil; EMQ = ethoxyquin, an antioxidant; LO = linseed oil; TO = tuna oil.

Experiments II and III

Eighty-one White Broad Breasted poults were obtained sexed (male only) for Experiments II and III. Starter diet containing 7% fish meal was fed day 1, and one-half starter and one-half basal diet were fed on days 2 and 3. On day 4, the poults were divided into nine groups of nine turkeys each, equally distributed by weight. Groups 1 through 8 were fed the experimental diets described below for 8 wk. These turkeys constituted Experiment II. Group 9 was fed the basal diet without oil supplementation to 14 wk of age and was then divided into three groups of three turkeys each which were designated as Groups A, B, and C. For 2 wk (until 16 wk of age), Group A was fed Diet 1 (control 4% beef fat) and Groups B and C were fed Diets 3 and 5 (3% beef fat + 1% tuna oil and 2% beef fat + 2% tuna oil), respectively. These turkeys constituted Experiment III.

Group	*Oil supplement to basal diet*[1]
1	4% BF
2	3.5% BF + 0.5% TO
3	3% BF + 1% TO
4	3% BF + 1% TO + 200 mg vitamin E/kilogram
5	2% BF + 2% TO
6	2% BF + 2% TO + 200 mg vitamin E/kilogram
7	3% SO + 1% TO
8	2% SO + 2% TO
9	No oil supplement until 14 wk of age

[1]BF = beef fat; TO = tuna oil; vitamin E = *dl*-α-tocopherol acetate; SO = safflower oil.

Sampling and Analysis

All turkeys were sacrificed at the appropriate time by cutting the jugular vein with an electrified knife and bleeding for 2 min. The turkeys were then scalded at 60°C, defeathered, eviscerated, dressed, packed in ice overnight, vacuum sealed, blast frozen, and stored at −30°C for about 4-6 wk. All birds were halved in the frozen state, with half being reserved for chemical analyses and half for baking and subsequent organoleptic analyses.

The halves for chemical analyses were thawed overnight in a 2°C cold room. Thighs and breasts were removed and minced individually after removal of skin and subcutaneous fat. Minced thighs and breasts from individual birds were

wrapped in Saran[4] film and aluminum foil, identified, and stored at −30°C until analyzed.

Oil content was determined on composites of 18-g samples of the individual thighs and breasts from each bird by the modified method of Smith, Ambrose, and Knobl (1964). Methyl esters for gas-liquid chromatography (GLC) analyses were prepared from the same oil extract by the method of Metcalfe, Schmitz, and Pelka (1966). The GLC column was 10% diethylene glycol adipate on Gas Chrom Q. GLC conditions were as follows: column, 196°C; injector, 250°C; flame ionization detector, 300°C; carrier gas flow, 24.6 cm^3/min.

Organoleptic analyses for the turkeys in Experiment I were performed by ranking. The panelists ranked four samples per session (of which one sample was a control). Comments about off flavors, if present, were solicited (e.g., fishy, oxidized, rancid, etc.). In Experiments II and III, organoleptic analyses were performed by scoring, using a balanced incomplete block technique. Analyses of variance and a Duncan multiple range test were calculated for Experiment II. Regression equations were calculated for breast and thigh meat and skin for Experiment III.

RESULTS AND DISCUSSION

Experiment I

All turkeys in Experiment I seemed to have grown normally and to have been in good nutritional health. The mean dressed weight was 991 g, with no significant weight differences between groups.

Table 1 gives the results of GLC analyses and lipid content (grams/100 g) of breast and thigh meat from the turkeys fed linseed and tuna oils to 6 wk of age. As expected, the thigh contained nearly twice the amount of lipid as the breast, (about 2% and 1% extracted lipid, respectively). The distribution of the methyl esters of fatty acids showed consistently higher percentages of C16:0, C18:0, C20:4, C22:5, and C22:6 in the breast, but higher C18:3 (when present in the diet), C18:2 and C18:1 in the thigh for all treatments. The lipid composition of the leg and breast reflect generally that of the dietary oils.

Results of organoleptic evaluation of the turkeys are reported in Table 2. The scoring (by rank) shows that 1% tuna oil imparts off flavor (slight) in breast and thigh meat and somewhat the same trend is indicated for odor evaluation, especially in the breast meat. But no clear trend is indicated for the skin. In general, flavor was judged as excellent. Ofttimes, there were no clear differences in a given set of comparisons. There were only a few scattered comments that described the flavor as fishy. No consistent differences were found between samples with and without ethoxyquin.

The lack of the development of positive fishy flavor in this experiment was unexpected since the oils fed to the turkeys contained high levels of linolenic acid (linseed oil, ca. 57% C18:3 ω3)or one of its longer-chained homologues (tuna oil, ca. 32% C22:6ω3). Fishy flavors have been induced in poultry by other investigators using oils that contained far less linolenates than used in this exper-

[4]Reference to a company or product name does not imply approval or recommendation of the product by the U.S. Department of Agriculture or the National Marine Fisheries Service, NOAA, to the exclusion of others that may be suitable.

TABLE 1.—Methyl ester fatty acid composition[1] of linseed oil and tuna oil and lipids extracted from turkeys[2] fed to 6 wk of age diets containing varying levels of safflower, linseed, and tuna oils with and without ethoxyquin.

Fatty acid	Linseed oil	Tuna oil	1B	1T	2B	2T	3B	3T	4B	4T	5B	5T	6B	6T	7B	7T	8B	8T
C16:0 + Iso C16:0	5.3	14.2	18.4	12.1	18.2	13.6	19.0	11.5	15.7	11.1	17.5	12.5	19.0	14.0	18.5	13.0	17.5	13.1
C18:0	3.8	5.5	12.3	8.4	13.0	9.0	14.9	10.1	11.9	6.7	12.8	8.5	12.6	7.5	10.3	8.9	9.5	5.7
C18:1	18.1	15.8	10.2	13.9	9.1	16.6	11.4	15.7	14.6	18.8	10.3	14.2	9.5	14.8	9.3	13.7	11.7	17.3
C18:2	15.0	4.8	37.8	52.0	40.3	47.1	28.6	35.3	33.5	36.9	33.7	49.2	34.2	48.5	32.5	46.0	38.8	48.0
C18:3ω3	57.8	—	—	—	—	—	4.1	14.6	10.5	19.6	—	—	—	—	—	—	—	—
C20:4ω6	—	3.0	12.0	6.3	10.1	5.6	7.1	4.0	4.3	1.9	8.9	4.8	9.1	3.9	8.9	4.3	5.6	2.6
C20:5ω3	—	7.9	—	—	—	—	2.3	—	—	—	—	—	—	—	1.8	—	—	—
C22:3ω3	—	—	2.5	—	2.3	—	—	—	—	—	—	—	—	—	—	—	—	—
C22:5ω3	—	1.8	—	—	—	—	3.4	—	2.2	—	—	—	—	—	—	—	—	—
C22:6ω3	—	32.5	—	—	—	—	3.9	—	1.9	—	7.9	3.7	7.9	3.2	11.6	5.2	8.9	4.0
% lipid, g/100 g tissue	—	—	0.88	1.87	0.92	2.12	0.95	1.86	1.40	3.01	1.22	2.12	1.02	2.29	0.92	1.97	1.17	3.03

[1]Fatty acids in amounts of 2% or less omitted. B = Breast meat; T = thigh meat.
[2]All groups of turkeys were fed a basal diet plus an oil supplement for 6 wk. Group 1 = 4% safflower oil (SO), Group 2 = (same as 1) + 125 ppm ethoxyquin (EMQ), Group 3 = 1% SO + 3% linseed oil (LO), Group 4 = (same as 3) + 125 ppm EMQ, Group 5 = 3.5% SO + 0.5% tuna oil (TO), Group 6 = (same as 5) + 125 ppm EMQ, Group 7 = 3% SO + 1% TO, Group 8 = (same as 7) + 125 ppm EMQ.

TABLE 2.—Taste panel scores (rank) on breast and thigh meat and skin of turkeys fed to 6 wk of age diets containing varying levels of safflower oil, linseed oil, and tuna fish oil with and without ethoxyquin.

Group[1]	Breast meat	Thigh meat	Skin
	Odor[2]		
	Without antioxidant		
1, 4% SO	1.9	2.4	2.9
3, 3% LO	2.4	3.0	2.6
5, 0.5% TO	2.5	1.9	2.3
7, 1% TO	3.2	2.8	2.4
	With antioxidant		
2, 4% SO	1.9	2.2	2.5
4, 3% LO	2.6	2.2	2.7
6, 0.5% TO	2.1	2.4	2.2
8, 1% TO	3.5	2.9	2.7
	Flavor[2]		
	Without antioxidant		
1, 4% SO	1.9	2.3	2.5
3, 3% LO	2.4	[3]3.2 (4F)	[3]3.0 (1F)
5, 0.5% TO	2.7	2.1	1.9
7, 1% TO	3.0	[3]2.4 (1F)	[3]2.6 (1F)
	With antioxidant		
2, 4% SO	2.3	1.9	2.6
4, 3% LO	2.3	2.3	2.9
6, 0.5% TO	2.1	2.4	2.1
8, 1% TO	[3]3.3 (2F)	[3]3.3 (1F)	2.5

[1]All groups of turkeys were fed a basal diet plus an oil supplement for 6 wk. Group 1 = 4% safflower oil (SO), Group 2 = (same as 1) + 125 ppm ethoxyquin (EMQ), Group 3 = 1% SO + 3% linseed oil (LO), Group 4 = (same as 3) + 125 ppm EMQ, Group 5 = 3.5% SO + 0.5% tuna oil (TO), Group 6 = (same as 5) + 125 ppm EMQ, Group 7 = 3% SO + 1% TO, Group 8 = (same as 7) + 125 ppm EMQ.
[2]Rank 1 = least off odor or off flavor.
[3]F = number of fishiness comments.

iment (Miller and Robish, 1969; Dreosti, 1970; Opstvedt, Nygard, and Olsen, 1970).

Some suggestions may be offered as to why no clear fishy flavors were induced, even though there was uptake of linolenates in the turkey carcass. For example, the use of safflower oil to achieve lipid isocaloric balance may have depressed the uptake of linolenates. Edwards and May (1965) observed this effect when they fed mixtures of corn and menhaden oil. Certainly the metabolism of the young birds (in this experiment 6 wk of age) must be considered. Their cell turnover is considerably higher than that of adult birds; phospholipid (an integral part of cell membranes) turnover is proportional to mitotic rate, and long-chained fatty acids are more readily found in phospholipids.

Experiment II

As before, all turkeys appeared to be in good nutritional health. The mean dressed weight was 1,377 g for turkeys fed to 8 wk of age.

Table 3 shows the results of fatty acid (methyl esters) determination by GLC of lipids extracted from the breast of turkeys fed fish oil and safflower oil to 8 wk of age. The fatty acids C20:5ω3 and

TABLE 3.—Methyl ester fatty acid composition of tuna oil and lipids extracted from the breast of turkeys[1] fed to 8 wk of age diets containing varying levels of tuna oil and beef fat or safflower oil with and without vitamin E (*dl*-α-tocopherol acetate) supplementation.

Fatty acid	Tuna oil[2]	% distribution in extracted oil							
		Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8
C14	3.1	0.7	1.0	0.7	0.5	0.4	0.5	0.3	0.5
C14:1	—	0.2	0.2	0.1	0.1	0.1	0.1	0.0	0.1
C15	—	0.2	0.2	0.2	0.2	0.3	0.2	0.1	0.2
Iso C16	—	3.3	3.3	3.1	3.5	3.9	3.7	2.6	3.3
C16	—	14.8	14.3	14.3	13.7	14.5	14.3	15.2	14.9
C16:1	4.7	1.1	1.2	0.9	0.6	0.6	0.9	0.3	0.6
C17	—	0.5	0.6	0.5	0.6	0.8	0.7	0.7	0.7
Iso C18	—	1.7	1.4	1.4	2.1	1.3	1.6	0.7	0.9
C18	5.5	15.4	14.9	15.0	15.3	14.9	14.6	13.6	11.2
C18:1	15.8	20.8	18.9	17.4	15.7	14.7	14.9	11.1	12.8
C18:2	4.8	24.8	20.6	19.9	18.5	18.0	18.1	30.9	28.9
C18:3	—	0.8	0.7	0.5	0.3	0.5	0.5	0.5	0.7
C20:4	3.0	6.6	5.9	6.5	7.4	6.2	6.4	8.8	6.5
C20:5	7.9	0.7	2.4	3.3	3.4	4.2	4.3	1.8	3.3
C22:5	1.8	1.2	1.6	1.5	1.6	2.0	1.5	1.0	1.0
C22:6	32.5	3.3	10.3	11.9	13.4	14.9	15.5	9.2	11.8
Others	21.0	3.9	2.5	2.8	3.1	2.7	2.2	3.2	2.6
% lipid, g/100 g tissue	—	0.89	0.95	0.98	0.86	0.84	0.90	0.93	0.84

[1]All groups of turkey were fed a basal diet plus an oil supplement for 8 wk. Group 1 = 4% beef fat (BF), Group 2 = 3.5% BF + 0.5% tuna oil (TO), Group 3 = 3% BF + 1% TO, Group 4 = (same as 3) + 200 mg/kg vitamin E, Group 5 = 2% BF + 2% TO, Group 6 = (same as 5) + 200 mg/kg vitamin E, Group 7 = 3% safflower oil (SO) + 1% TO, Group 8 = 2% SO + 2% TO.

TABLE 4.—Methyl ester fatty acid composition of lipids extracted from the cooked breast of turkeys[1] fed to 8 wk of age diets containing varying levels of beef fat and tuna oil with and without vitamin E (*dl*-α-tocopherol acetate) supplementation.

Fatty acid	% distribution in extracted oil		
	Group 1	Group 5	Group 6
C14	0.8	1.1	0.9
C14:1	0.1	0.3	0.2
C15	0.2	0.3	0.3
Iso C16	2.7	2.3	1.8
C16	15.9	16.6	15.9
C16:1	0.8	2.2	1.7
C17	0.6	0.9	0.8
Iso C18	1.6	1.4	1.1
C18	17.1	14.1	14.5
C18:1	19.1	21.2	18.8
C18:2	22.5	19.3	19.7
C18:3	0.6	0.9	0.8
C20:4	5.1	3.4	4.7
C20:5	1.8	2.5	3.1
C22:5	1.0	1.1	1.1
C22:6	6.6	9.2	11.5
% lipid, g/100 g tissue	1.10	1.15	1.10

[1]All groups of turkeys were fed a basal diet plus an oil supplement for 8 wk. Group 1 = 4% beef fat (BF), Group 5 = 2% BF + 2% tuna oil, Group 6 = (same as 5) + 200 mg α-tocopherol acetate per kilogram.

C22:6ω3 increase as the amount of tuna oil increases in the diet. Safflower oil added to Diets 7 and 8 seemed to reduce the uptake of these fatty acids. Tocopherol acetate supplementation did not seem to have any effect on the uptake of ω3 fatty acids. Fatty acid distribution analyses (Table 4) on lipids extracted from cooked turkey breast from Groups 1, 5, and 6 show that α-tocopherol did not have an effect on the relative stability of the long-chain fatty acids during cooking.

The results of taste panel evaluations (Table 5) show that, while α-tocopherol supplementation did not change the ω3 fatty acid distribution, it greatly reduced fishy flavor as judged by the taste panel. Opstvedt, Nyard, and Olsen (1970) also reported these findings. On the other hand, safflower oil (used to achieve isocaloric balance) reduced the uptake of ω3 fatty acids, but there were no differences in flavor when compared to the flavor of turkeys fed the same amount of tuna oil but using beef fat for isocaloric balance. There was a strong relationship between the amount of C20:5ω3 and/or C22:6ω3 and fishy flavor when no α-tocopherol or safflower oil supplementation was present in the diets. This agrees with the findings of Neudoerffer and Lea (1966, 1967), Miller et al. (1967a), Miller and Robish (1969), and Dreosti (1970). However, a comparison of the fatty acid distributions and lipid contents found by these investigators with those in this experiment and Experiment I, shows that the levels of C20:5ω3 and C22:6ω3 present when fishy flavors are detected are higher in these experiments. We should also note that the fish oils used by other investigators contained about 2-12% C22:6ω3, while the tuna oil used in these experiments contained 32% C22:6ω3.

Experiment III

These 16-wk-old turkeys had been fed diets containing 3% beef fat plus 1% tuna oil and 2% beef fat plus 2% tuna oil for the 2 wk prior to slaughter. The control diet contained 4% beef fat. All turkeys apparently enjoyed good nutritional health and the mean dressed weight was 3,585 g.

TABLE 5.—Mean[1] taste panel scores[2] and Duncan's multiple range test of mean scores on thigh and breast meat and skin of turkeys fed to 8 wk of age diets containing varying levels of tuna fish oil and beef fat or safflower oil with and without vitamin E (*dl* α-tocopherol acetate) supplementation.

Group[3]	Breast meat	Group[3]	Thigh meat	Group[3]	Skin
5, 2% TO + 2% BF	3.91	8, 2% TO + 2% SO	3.56	8, 2% TO + 2% SO	3.37
8, 2% TO + 2% SO	3.35	5, 2% TO + 2% BF	3.28	5, 2% TO + 2% BF	2.69
3, 1% TO + 3% BF	3.04	6, 2% TO + 2% BF + E	2.41	3, 1% TO + 3% BF	1.99
2, 0.5% TO + 3.5% BF	2.94	2, 0.5% TO + 3.5% BF	2.20	6, 2% TO + 2% BF + E	1.98
6, 2% TO + 2% BF + E	2.48	7, 1% TO + 3% SO	2.03	7, 1% TO + 3% SO	1.69
7, 1% TO + 3% SO	2.30	3, 1% TO + 3% BF	1.85	1, 4% BF	1.27
1, 4% BF	1.33	4, 1% TO + 3% BF + E	1.22	2, 0.5% TO + 3.5% BF	1.26
4, 1% TO + 3% BF + E	1.24	1, 4% BF	0.95	4, 1% TO + 3% BF + E	1.04
$S_{\bar{x}}$	0.228		0.211		0.252

[1]Means connected by a common line are not significantly different at the 0.05 probability level.
[2]1 = no fishy flavor, 5 = very fishy.
[3]All groups of turkeys were fed a basal diet plus an oil supplement for 8 wk. Group 1 = 4% beef fat (BF), Group 2 = 0.5% tuna oil (TO) + 3.5% BF, Group 3 = 1% TO + 3% BF, Group 4 = (same as 3) + 200 mg/kg vitamin E (E) Group 5 = 2% TO + 2% BF, Group 6 = (same as 5) + 200 mg/kg vitamin E, Group 7 = 1% TO + 3% safflower oil (SO), Group 8 = 2% TO + 2% SO.

TABLE 6.—Methyl ester fatty acid composition of lipids extracted from the thighs of turkeys[1] fed from 14 wk to 16 wk of age diets containing varying levels of beef fat and tuna oil.

Fatty acid	% distribution in extracted oil		
	Group A	Group B	Group C
C14	0.4	1.0	1.0
C14:1	0.1	0.1	0.1
C15	0.1	0.2	0.2
Iso C16	1.9	2.1	1.6
C16	17.7	16.8	18.7
C16:1	5.8	1.8	1.9
C17	0.3	0.5	0.6
Iso C18	0.9	0.8	0.7
C18	10.6	13.8	12.1
C18:1	21.7	20.3	20.4
C18:2	30.7	26.4	26.2
C18:3	1.6	1.3	1.5
C20:4	5.2	6.2	5.0
C20:5	0.2	0.9	1.4
C22:5	0.5	0.8	0.7
C22:6	0.5	4.5	6.1
% lipid, g/100 g tissue	2.10	2.12	2.55

[1]All turkeys were fed a basal diet without oil supplement to 14 wk of age and to 16 wk of age with oil. Group A = 4% beef fat, Group B = 3% beef fat + 1% tuna oil, Group C = 2% beef fat + 2% tuna oil.

Fatty acid distributions and percent extracted lipids from the thighs of these turkeys are shown in Table 6. (The same analyses were not possible for the breast meat because it was used in another experiment.) As before, the amount of C22:6ω3 increased as the amount of fish oil in the diet increased. It is of interest that the lipid level was only slightly higher in the 16-wk turkeys fed fish oil for 2 wk than in the 6- or 8-wk turkeys fed from day 4 to slaughter. Yet, the percent of C22:6ω3 was less than half that of the 8-wk birds, while the flavor reported in Table 7 was at least as fishy, if not more so.

In conclusion, if consideration is given to 1) the effects of α-tocopherol on (reducing) the fishy flavor, while not affecting the uptake of linolenates, and 2) the different levels of long-chain linolenates present when fishiness is detected, one has to reason that the long-chained ω3 fatty acids do not of themselves cause fishy flavor by their simple presence. It is plausible that the fishy flavors result at least in part from the oxidation (in vivo? postmortem?) of linolenates and that α-tocopherol limits the oxidation. It is further colorable that the amount of linolenate oxidation needed to produce fishy flavor may be smaller than the inherent error in fatty acid analyses and therefore, no differences would be observed in the amount of linolenates in the carcass of turkeys fed fish oils with and without α-tocopherol.

TABLE 7.—Mean taste panel scores[1] and regression equations (% tuna fish oil supplement vs. mean taste panel scores) for thigh and breast meat and skin of turkeys fed diets containing varying amounts of beef fat and tuna oil.

Group[2]	Breast meat	Thigh meat	Skin
A, control	1.44	1.11	1.06
B, 1 TO	2.06	2.50	1.89
C, 2 TO	3.28	4.11	2.94
$S_{\bar{x}}$	0.26	0.21	0.28
Regression equations:			
$y = 1.343 + 0.917X$			
$y = 1.074 + 1.500X$			
$y = 1.018 + 0.944X$			

[1] = no fishy flavor, 5 = very fishy.
[2]All groups of turkeys were fed a basal diet without oil supplementation to 14 wk of age and to 16 wk with oil. Group A = 4% beef fat, Group B = 3% beef fat + 1% tuna oil (TO), Group C = 2% beef fat + 2% TO.

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ZOOGEOGRAPHY OF THE GENUS *NEMATOSCELIS* (CRUSTACEA, EUPHAUSIACEA)

K. GOPALAKRISHNAN[1]

ABSTRACT

The International Indian Ocean Expedition provided zooplankton samples to study the distribution and seasonal changes in numerical abundance of *Nematoscelis* in the Indian Ocean. Distributional boundaries of species of this genus in the Atlantic and Pacific oceans were determined mainly on the basis of mid-water trawls. All seven species of this genus occur in the Pacific, whereas only five species are present in the Indian and four in the Atlantic. Two forms ("old" and "new") of *N. gracilis*, considered to be ecophenotypes, but distinguished on the basis of morphological differences observed in the petasma, occupy the tropical Indo-Pacific subregion. The "old form" is most abundant in the oxygen-poor waters of the Arabian Sea, Bay of Bengal, and also in the eastern tropical Pacific. The "new form" is mostly confined to areas of the South Equatorial Current. The present study indicates that *N. gracilis* does not occupy the equatorial zone of the Atlantic Ocean, but "new forms" are transported from the Indian Ocean up to the southern tip of South Africa. *Nematoscelis atlantica* is distributed in the central water masses of the Pacific and Indian oceans, whereas in the Atlantic its distribution extends also to the equatorial zone. *Nematoscelis microps* and *N. tenalla* are warmwater species and are distributed between lat. 40°N and 40°S, although lacking in most areas of low oxygen water. *Nematoscelis lobata* has restricted distribution in the region of the Philippines. *Nematoscelis megalops* occupies the circumpolar transitional regions of the Southern Hemisphere and also the subarctic and transition subregions of the North Atlantic. *Nematoscelis difficilis* is endemic to the North Pacific transition zone. The basins of Timor and Banda Seas and their associated straits in the Indo-Australian Archipelago appear to allow inter-ocean gene flow among populations of *N. gracilis*, *N. Microps*, and *N. tenella*. A similar communication exists between Atlantic and Indian Ocean populations of these species through the oceanic waters around the tip of South Africa.

Zoogeography of the order Euphausiacea is reasonably well known for the Pacific Ocean (Brinton, 1962). The study on the distribution of euphausiids in the Indian Ocean is still in its preliminary phase. Available data from this ocean are adequate to make possible estimates of species ranges only. The role of the biological program during the International Indian Ocean Expedition (IIOE) (1960-65) was to provide materials from wide areas of the ocean to facilitate a better understanding of distributions of many zooplankton taxa in the Indian Ocean. Therefore, in the present study it was decided to put more effort into understanding the geographical distribution and seasonal abundance of Indian Ocean species of *Nematoscelis* than those from the Pacific and Atlantic oceans. Preliminary observations on the distribution of Euphausiacea as a whole were made by Gopalakrishnan and Brinton (1969). Subsequently, Brinton and Gopalakrishnan (1973) brought the distributional information up to date on the basis of IIOE samples studied up to that time.

Ocean-wide records of species of euphausiids in the Indian Ocean come from three major expeditions: the Percy Sladen Trust Expedition (Tattersall, 1912), the Deutsche Tiefsee Expedition (Illig, 1930), and the John Murray Expedition (Tattersall, 1939). Studies on the regional fauna are available for the eastern waters of South Africa (Boden, 1951), Red Sea, Arabian Sea, and Bay of Bengal (Ponomareva, 1964, 1968). Species of *Nematoscelis* of the southwest coast of India were provided by Sebastian (1966). Only four of the seven species of this genus have been reported from the Indian Ocean: *N. gracilis, N. megalops, N. microps,* and *N. tenella.* The present study confirms the presence of a fifth species, *N. atlantica,* in the southern Indian Ocean. *Nematoscelis megalops* was described by Boden (1951) from the southern African waters. Three females of this species were reported by Illig (1930) from southwest of Ceylon in the northern Indian Ocean. The present investigation does not confirm its distributional range in that region.

Nematoscelis difficilis is an endemic species of

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the transition zone in the North Pacific and is not reported from anywhere else. Previous studies on the distribution of all seven species of *Nematoscelis* in the Pacific Ocean are summarized by Brinton (1962).

Only four species of *Nematoscelis* have been reported from the Atlantic Ocean. Moore (1952) studied ocean-wide distributions of many euphausiids in the North Atlantic Ocean, including *N. microps* and *N. megalops*. Einarsson (1945) also reported *N. megalops* from the northeastern Atlantic. From the Mediterranean Sea *N. megalops, N. microps,* and *N. atlantica* were reported by Ruud (1936) and Casanova-Soulier (1968). Incorporating all previous records Mauchline and Fisher (1969) have provided a generalized picture of the distribution of *Nematoscelis* in the Atlantic Ocean. Gopalakrishnan (1973) examined the pattern of vertical distribution of *Nematoscelis* species of the Pacific Ocean.

METHODS AND MATERIALS

The Indian Ocean portion of the present study of *Nematoscelis* is based on samples collected during the IIOE. This expedition was a collaborative venture in which 10 countries participated and 16 vessels collected zooplankton samples as part of the biological program during 1960-65. The composite pattern of stations occupied during 70 cruises provided coverage of most geographical provinces of the Indian Ocean (Figure 1a, b). A standard procedure was followed by all participating vessels for collecting zooplankton samples. Accordingly, each sample was obtained by using the Indian Ocean Standard Net (IOSN) which was specially devised for the IIOE (Currie, 1963). It is a ring net with a mouth area of 1 m² and a length of 5 m. The straining surface is nylon gauze of 0.33-mm mesh. Hauls were as nearly vertical as possible, from approximately 200-m depth to the

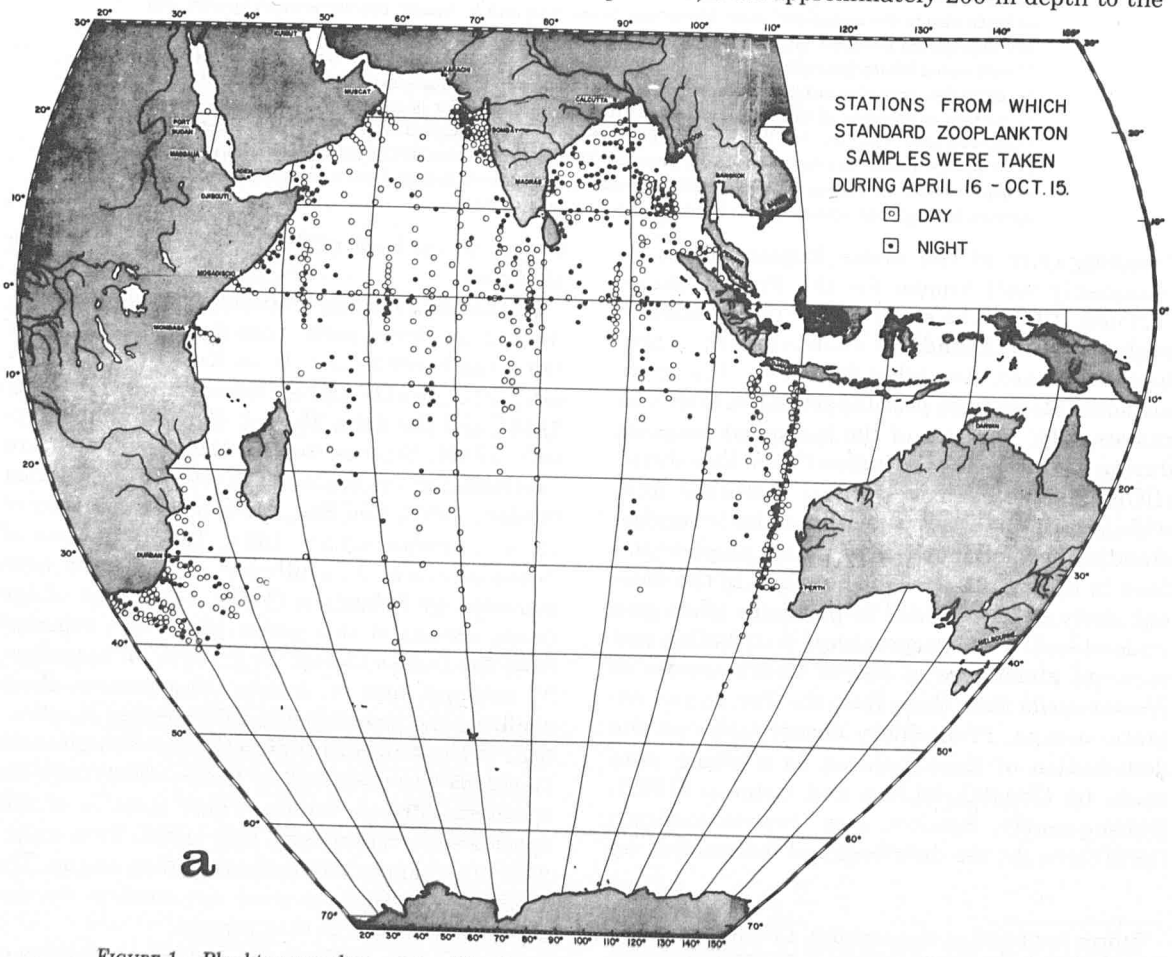


FIGURE 1.—Plankton samples examined for *Nematoscelis* of the Indian Ocean: a - SW Monsoon period.

surface. Assuming 0° wire angle the net would be expected to filter approximately 200 m³ of water; but 0° wire angle was rarely attained at sea. Moreover, Tranter and Smith (1968) showed that the initial filtering efficiency of this net is 0.96; subsequent clogging does not reduce the filtering volume significantly.

Plankton samples collected according to these procedures are classified as "standard." In waters over the continental shelf where the depth was less than 200 m, the net was usually hauled up from within a few meters of the bottom; such collections were also treated as standard since the full water column was filtered. Samples collected from less than approximately 200-m depth in the open ocean, where the depth was far greater than 200 m, were designated as "nonstandard."

All samples were processed and sorted at the Indian Ocean Biological Centre situated in Cochin, India. The list of plankton samples processed at this center is included in a handbook to the international collections (Indian Ocean Biological Centre, 1969). The locality, time, and depth of haul at each station are given in this list, along with total displacement volume of the sample and fraction of each sample that was sorted into major taxa. At the sorting center a 3- to 4-ml portion of each sample was sorted into its constituent major taxa after removing large individuals from the sample. Individuals in each group were then counted to give an estimate of numbers in the whole sample. The sorted fractions ranged from 5% to 90% of the whole sample on the basis of the initial displacement volume of the sample. Further details of the sorting procedure were described by Hansen (1966). The unsorted portion (archive) of all samples were deposited at the Indian Ocean Biological Centre. About 215 of them were examined during the present study in order to check whether the fractionating proce-

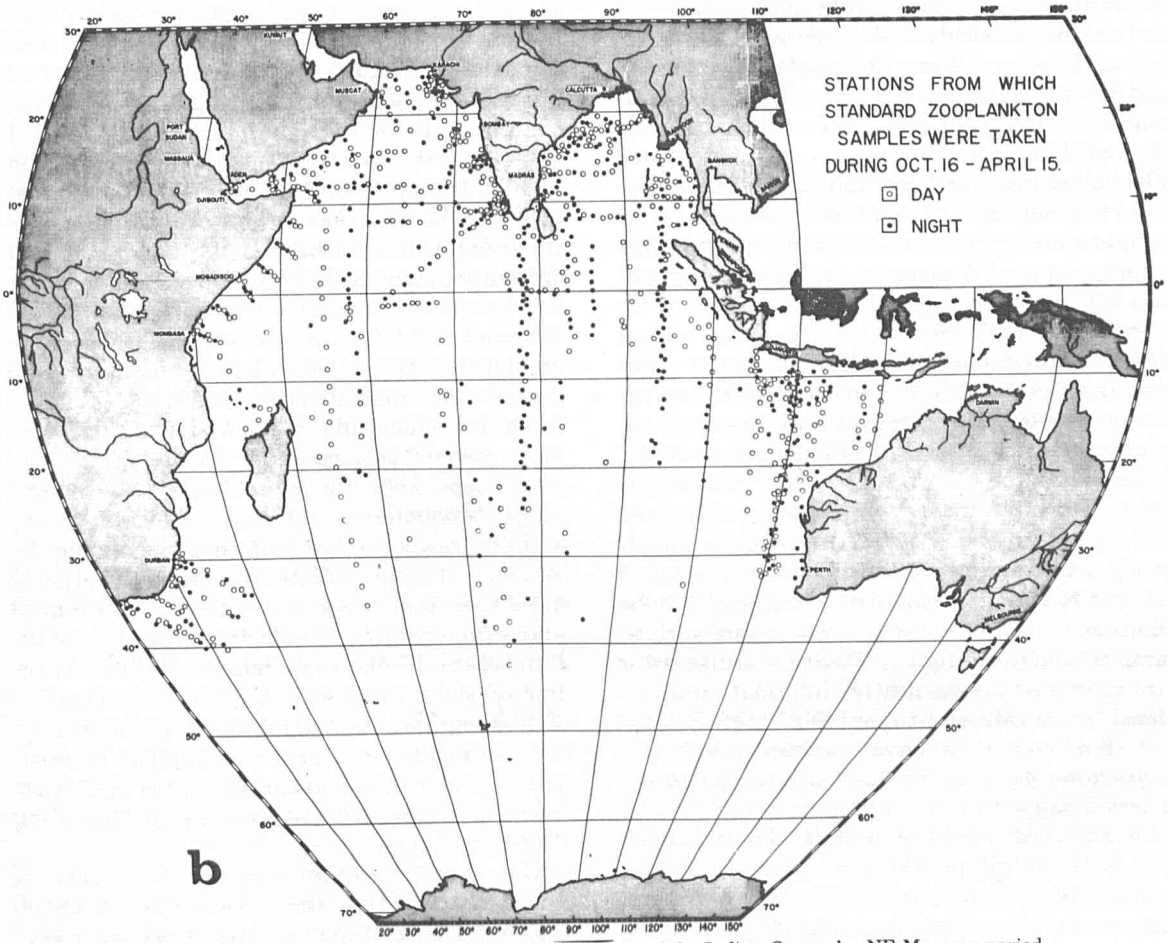


FIGURE 1.—Plankton samples examined for *Nematoscelis* of the Indian Ocean: b - NE Monsoon period.

dure was efficient enough to retain all species of *Nematoscelis* present in the whole sample. Only 26 archives were found to have contained one or more species not present in their subsamples. Therefore it is assumed that the subsampling procedure was usually adequate.

The wind system over the Indian Ocean is monsoonal. The two monsoon phases are designated as the Southwest (SW) and Northeast (NE) monsoons, indicating the predominant wind directions in the northern Indian Ocean during each phase. The bulk of the samples were grouped into two categories: those collected during 16 April to 15 October falling in the SW monsoon and those collected during 16 October to 15 April falling in the NE monsoon. The period 16 April to 15 October generally agrees with that of the wind regime of the SW monsoon (Wooster, Schaefer, and Robinson, 1967).

Of the 1,927 samples processed at the Indian Ocean Biological Centre, 1,732 samples were examined for the study of *Nematoscelis*. Of these, 879 samples were taken during the SW monsoon and 853 during the NE monsoon. Since a comparison of day and night catches of total euphausiids showed differences in day and night estimates (Gopalakrishnan and Brinton, 1969), it was decided to group day and night counts separately for each season. There were 401 night and 478 day samples for the SW monsoon period and 413 night and 440 day samples for the NE monsoon.

In order to fill gaps in certain geographical areas, some samples collected by using gear other than the IOSN have also been used in the preparation of charts. *Kistna* cruises 2 to 6 used an organdy net with 50-cm mouth diameter. *Natal* cruises 1 and 4 used the N-70 net with 70-cm mouth diameter. These samples were standardized for comparing with IOSN samples: the organdy net samples were multiplied by a factor of 5.1 and N-70 net samples by a factor of 2.6. In addition to these samples, 26 nonstandard surface samples taken during the *Patanela* cruise were also examined for qualitative information. *Argo* Monsoon Expedition stations 9-27 (ref. Snyder and Fleminger, 1972) have also been used in the preparation of present charts. These samples were collected using 1-m nets.

The observed differences between day and night catches of adult euphausiids are due to the fact that during day time many species either migrate to deeper layers or are able to dodge the net. Total euphausiids were 1.5-2.0 times more abundant in night samples than in day samples (Gopalakrishnan and Brinton, 1969). The mouth area of the IOSN is only 1 m^2 and it is probable that many large zooplankters can avoid the net. However, most samples taken at night contained many adult euphausiids, including some of the large thysanopods that migrated into the upper layer. All species of *Nematoscelis* are smaller than most *Thysanopoda* species. It is reasonable to believe that the IOSN tows taken at night would have been adequate to representatively sample adult species of *Nematoscelis*.

The present distributional study of *Nematoscelis* in the Indian Ocean is limited to the upper 200 m only. The geographical distribution of each species of this genus is compared with the pattern of water circulation in the upper layer. Larvae and juveniles of all *Nematoscelis* species are confined to the upper 200-m layer during both day and night, whereas adults undertake diurnal vertical migration (Gopalakrishnan, 1973). During daytime the distribution of adults extends from the upper 200-m layer to about 600-800 m; but at night, because of their upward migration, the range extends from the surface to about 400-600 m only, with the maximum above 200 m in most geographical regions. It is therefore probable that the IOSN would have caught adults better at night than during the day. For this reason only night samples were considered in charting the distribution of adults. However, a few trawls (Isaacs-Kidd Mid-water trawl) fished from depths greater than 200 m, were also used for examining overall geographical range. Station positions of these are included in Figures 7, 11, and 18. Most of these reached as deep as ca. 900-1,000 m, somewhat deeper than the lower limit of the vertical range of *Nematoscelis*. The geographical coverage of these trawls was not sufficient to examine the influence of deep circulation on the distribution of species. A total of 286 mid-water trawl samples were examined from the Pacific, Atlantic, and Indian oceans. [Collections from the Pacific and Indian oceans are located at the Scripps Institution of Oceanography. Collecting data regarding many of these appear in Clarke (1963).] The approximate boundaries of distribution of each species are shown on the basis of present evidence, including literature records.

The distributional ranges of species of *Nematoscelis* in the Atlantic Ocean were based on specimens sorted from fractions of plankton samples obtained by the Woods Hole Oceanographic

Institution. Most of the samples were from the North Atlantic. Charts were prepared for each species of *Nematoscelis*; but the abundance is expressed only as the percentage of the total *Nematoscelis* present in the aliquot, because the aliquot itself was an unknown quantitative fraction of the whole sample. *Atlantis II* and *Chain* cruises took samples using a 75-cm net from above 100 m; *Delaware* samples were also taken from similar depths, but by using 1-m nets. Lusiad VII cruise in the South Atlantic collected samples from 200 m to surface. In all, 217 plankton samples were examined from the Atlantic Ocean.

HYDROGRAPHY OF THE INDIAN OCEAN

In the upper strata of the sea, the general circulation may be related to the prevailing wind system. This wind-driven oceanic circulation affects and modifies the distribution of water masses in the upper strata; the wind-driven circulation penetrates into deeper layers and can be recognized at intermediate depths (Reid, 1965). The thermohaline circulation, caused by density differences in the ocean due to heat and water exchanges with the atmosphere, is thought to be responsible for formations of deepwater masses and the deep circulation (Neumann and Pierson, 1966). As a result of these types of circulations, properties such as temperature, salinity, oxygen, and nutrients show distinct features in their distributions in different oceanic areas, providing different characteristic habitat conditions for individual species or communities of organisms.

Since a major part of the present study deals with the seasonal distributions of Indian Ocean species of *Nematoscelis,* it is pertinent to provide a general background of the available information on the monsoonal seasons prevailing over the Indian Ocean. The surface currents of the Indian Ocean during the monsoon periods are described by Taft (1971) and for the present study I will follow his discussion of the wind and current patterns (see Neumann and Pierson, 1966, and Taft, 1971, for illustrations of surface currents of the Indian Ocean). Hydrographical changes associated with the monsoon are well documented for the Arabian Sea (Wooster et al., 1967). During the NE monsoon the northeast winds of the Northern Hemisphere cross the Equator into the Southern Hemisphere, there becoming northwesterly. This monsoon phase is established in November and persists through March; its maximum intensity is in January. During this phase a broad doldrum belt develops at about lat. 5°S to lat. 10°S between weak northerly winds and the southeast trade winds. In the SW monsoon, southeast trades from the Southern Hemisphere cross the Equator and gradually turn into southerly and southwesterly directions in the Northern Hemisphere. Winds are especially intense during this period near the African, Somali, and Arabian coasts. The SW monsoon is well established in May and persists through September. It is most intense in July.

The onset of monsoon periods in the Indian Ocean is found to be symmetrical in time (Wooster et al., 1967; Taft, 1971). Each period lasts for 5 mo; April and October are transition periods. Because of these short periods of transition in the monsoon system, it was decided to divide each April and October period into two halves and add the first half of April and the latter half of October to NE monsoon. The latter half of April and the first half of October were similarly added to the SW monsoon period. The overall winds and surface currents are far stronger in the SW monsoon than in the NE monsoon.

The surface circulation plays an important role in the distribution of planktonic animals in the ocean. In the Indian Ocean the surface circulation is subjected to a longer seasonal change than in other oceans. The outstanding features of the surface circulation are: 1) currents that follow in a more or less zonal direction far from the continents, and 2) currents near continental coasts. During the NE monsoon the North Equatorial and the South Equatorial currents flow westward and the Equatorial Countercurrent flows eastward between these two currents. Unlike those in the Pacific and Atlantic, the countercurrent in the Indian Ocean is situated in the Southern Hemisphere. This is related to the position of the doldrums south of the Equator. The South Equatorial Current, after reaching the African coast, contributes water to the Agulhas Current flowing southwest and also to the eastward flowing Countercurrent. During the NE monsoon the Somali Current, flowing southwest with a speed of about 100 cm/s, merges into the Mozambique Current (Neumann and Pierson, 1966), thereby bringing many tropical species as far south as lat. 35°-40°S along the coast of Africa. At this time the surface current off the southwest coast of India is also weak and flows in a southeast direction. In the Bay

of Bengal the general circulation is counterclockwise. Unlike in the Pacific and Atlantic oceans, there is little evidence of an eastern boundary current in the Indian Ocean along the west coast of Australia. According to Wyrtki (1973), water movements in this region are weak and variable and most of the northward flow is situated farther offshore between long. 95°E and 105°E. In the Indian Ocean the Equatorial Undercurrent is also seasonal, being more pronounced during the NE monsoon than in the opposite season (Taft and Knauss, 1967; Taft, 1971).

At the onset of the SW monsoon the surface currents in the Indian Ocean change dramatically. The westward flowing North Equatorial Current is replaced by an eastward flowing Southwest Monsoon Current, thereby reversing the surface circulation in that region. Together with the Somali Current it is the outstanding current in these latitudes. The surface current north of lat. 5°S is then directed eastward and the Equatorial Countercurrent is not distinguishable as a separate flow. This is contrary to the conditions prevailing in other oceans where the intensity of the Countercurrent reaches a maximum during this period. The Somali Current, now flowing northeast as an intense western boundary current, extends to about lat. 8°N. The current transports southern forms into the Arabian Sea thereby serving to increase the faunal complexity of the region. In addition, enrichment of surface water north of the current produces zooplankton blooms. North of lat. 8°N the data suggest that this current leaves the coast and turns eastward (Taft, 1971). The South Equatorial Current becomes intensified in the western Indian Ocean; near the African coast it contributes to part of the northern flow. This brings species of the southern latitudes close to the Equator in the western Indian Ocean and even occasionally farther north to about lat. 10°N along the western boundary. During the SW monsoon the flow off the Arabian coast is toward the east and northeast but is much less intense than the Somali Current. This flow starts in April and is reported to persist until August. The southeastward flow off the southwest coast of India remains the same as in the NE monsoon. In this region the current flows northward only for 2 mo and it is essentially opposite to the prevailing wind stress. Taft (1971) pointed out that the circulation in the eastern Arabian Sea is therefore influenced by thermohaline processes.

During the SW monsoon three areas are prominent in the Arabian Sea for upwelling: off the Somali, Arabian, and southwest Indian coasts. There is evidence that the upwelling off the Arabian coast is wind driven; that off the Somali coast is partly wind driven and partly due to dynamic constraint on the current (Taft, 1971); and that off the coast of southwest India is due to the dynamic response which involves tilting of the thermocline up toward the coast (Darbyshire, 1967; Banse, 1968). The cool surface waters off the coasts of Arabia and Somalia during the SW monsoon are clear indication of intense upwelling (See Wyrtki, 1971:45). Along the western Indian Ocean Düing (1971) commented on the presence of many offshore anticyclonic and cyclonic vortices which are indicated by alternating highs and lows of dynamic height persisting through both monsoon phases. Taft (1971) singled out the importance of these vortices in the mixing processes of the near-surface waters which would increase the rate of nutrient enrichment of the surface layer. In the western Arabian Sea such enrichments are maximum during the June-August period (Table 1). High values of NO_3-N and SiO_3-Si persist for a longer period along the coast of Somalia than off the Arabian coast. The plankton atlas of the IIOE (Indian Ocean Biological Centre, 1968) shows that the maximum abundance of zooplankton is also associated with these upwelling areas.

The distribution of surface temperature during the NE monsoon indicates no cool surface water in

TABLE 1.—Surface nutrients at four coastal regions of the Arabian Sea. A = off the coast of Arabia, lat. 20°N; B = off the coast of India, lat. 20°N; C = off the coast of Somalia, lat. 10°N; D = off the coast of southwest India, lat. 10°N. All values are in μg-at/l. (Data from Wooster et al., 1967.)

	Dec.-Feb.				Mar.-May				June-Aug.				Sept.-Nov.			
Nutrients	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
PO_4-P	0.75	0.25	0.25	0.50	>0.25	0.25	0.25	0.25	>2.0	0.50	1.0	>0.25	>1.0	>0.25	1.0	0.25
NO_3-N	all values <2.5				all values <2.5				>25.0	2.50	>15.0	<2.5	<2.5	<2.5	15.0	<2.5
SiO_3-Si	all values 5.0				all values <5.0				>20.0	<5.0	>20.0	<5.0	10.0	<5.0	>15.0	<5.0

the Arabian Sea (see Wyrtki, 1971:38). Isotherms slope southwestward toward the African coast. During this period no upwelling is observed off the southwest coast of India, although the Ekman theory would predict upwelling in this area since the surface winds blow equatorward and parallel the coast. Taft (1971) suggested that this may be due to the low speed of the northeasterly wind.

In the Bay of Bengal upwelling has been reported to occur seasonally along the east coast of India and west coast of Burma (La Fond, 1954, 1957; Banse, 1960; La Fond and La Fond, 1968). During the early part of the NE monsoon, the northeasterly winds displace subsurface water offshore along the Burmese coast. Wyrtki (1961) also reported upwelling along the coast of Burma and Thailand during the December-February period. The general surface circulation of the Bay of Bengal is clockwise during January through July and it becomes counterclockwise from August to December (La Fond and La Fond, 1968). The southwesterly winds prevail over the northern Bay of Bengal in March and over the entire region in April. During these months an intense upwelling is noticed along the east coast of India (La Fond and La Fond, 1968). In this region, along with the nearshore occurrence of dense water, the average sea level also reaches a minimum height during this period (La Fond, 1954).

A remarkable feature of the Indian Ocean is the rapid attenuation of dissolved oxygen with depth; at 200 m values become 0.2 ml/l or less in the Arabian Sea and Bay of Bengal (Wyrtki, 1971). Vinogradov and Voronina (1961) and Vinogradov (1968) have discussed the association of low zooplankton biomass within the oxygen minimum layer in the Arabian Sea. North-south and east-west transects in the Arabian Sea indicate that oxygen values as low as 0.1 ml/l occur below 200 m during both seasons (Figure 2A, B). According to Wyrtki (1971) the concentrations of oxygen in the minumum layer do not vary seasonally, although the depth of this layer changes. The vertical profile at four north-south transects across the equatorial Indian Ocean show the occurrence of very low oxygen concentrations below 100 m (Figure 3). Since these profiles were taken during different months, it appears that this feature persists throughout the year.

The vertical distribution of temperature along four north-south transects (same transects as shown in Figure 3) indicates that the thermocline is situated between 75 and 100 m in the regions north of lat. 10°S. The South Equatorial Current

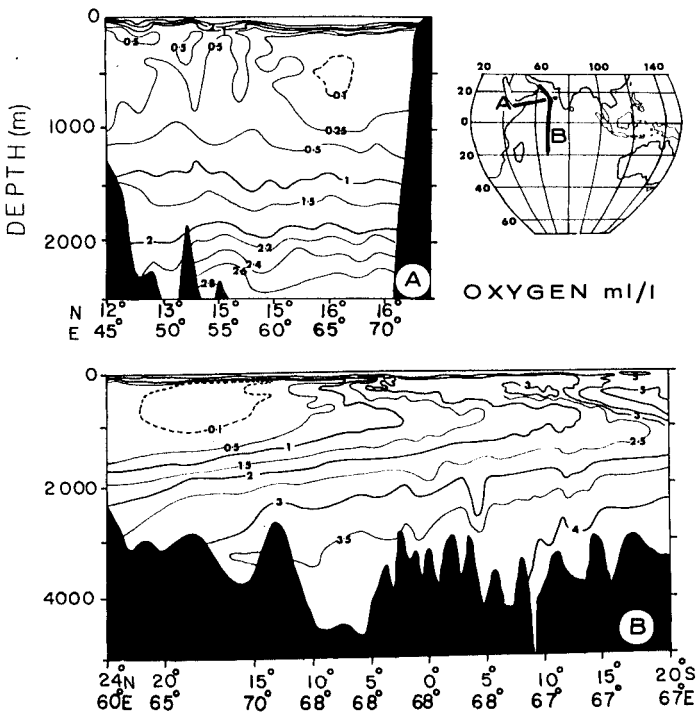


FIGURE 2.—Vertical distribution of oxygen in the Arabian Sea: A. East-west transect along lat. 11°N, long. 45°E to lat. 16°S, long. 72°E (July-August); B. North-south transect along lat. 24°N, long. 60°E to lat. 20°S, long. 67°E (November-May). (Charts reproduced from Wyrtki, 1971.)

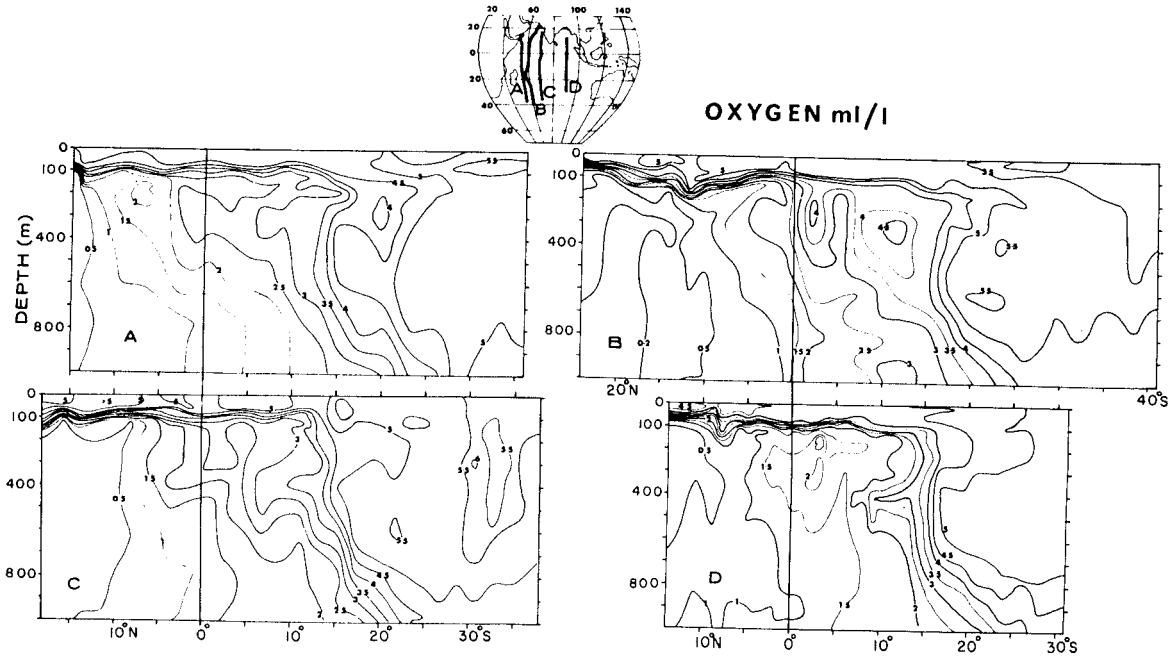


FIGURE 3.—Vertical distribution of oxygen along four north-south transects in the Indian Ocean: A - lat. 14°N to 36°S at long. 55°E (February-March); B - lat. 24°N to 41°S at long. 60°E (August-November); C - lat. 18°N to 37°S at long. 70°E (May-July); D - lat. 13°N to 30°S at long. 92°E (August-September). (Charts reproduced from Wyrtki, 1971.)

flows along the zone where the thermocline slopes upward toward the Equator between lat. 10°S and 20°S. The general distribution of subsurface isotherms is more or less similar across the full breadth of the equatorial region.

Wyrtki's figure (1971:38) indicates the presence of cold surface water in the northern part of the Bay of Bengal during the NE monsoon. Banse (1960) pointed out that the cold surface water in this region may not be attributed to upwelling, but to a high rate of evaporation caused by the dry air from the continent. The coasts of northwest Australia and Java are other regions reported to have seasonal upwelling. Wyrtki (1961) pointed out that there was intense upwelling in these two areas during the SW monsoon.

It is postulated that in the Indian Ocean wind-driven equatorial upwelling is less intense than in the Atlantic and Pacific oceans and may be totally absent (Taft, 1971). The absence of substantial peaks in the zooplankton biomass along the equatorial regions of the Indian Ocean is consistent with the idea of there being little equatorial upwelling, compared at least with the Pacific (King and Demond, 1953; Reid, 1962; Heinrich, 1968) and the Atlantic (Hentschel, 1933).

In the Indian Ocean seasonal changes in surface salinity are more pronounced in the Arabian Sea and the Bay of Bengal than in any other region (see Wyrtki, 1971). Throughout the year the surface salinity was greater in the Arabian Sea than in the Bay of Bengal. During the NE monsoon surface salinity becomes very low (30-33‰ in the Bay of Bengal; advection of low-salinity water occurs from the Bay of Bengal toward the western Indian Ocean. As the Monsoon Current develops during the SW monsoon, a tongue of high-salinity water flows eastward.

RESULTS

Geographical Distribution of *Nematoscelis gracilis*

Indian Ocean

Two forms considered to be ecophenotypes of *N. gracilis* are recognized to occur in the Indian Ocean: an "old form" which is identical in morphological character to the typical form described by Hansen (1910) from waters of the Indo-Australian Archipelago, and a "new form" which

is distinguished from the typical form on the basis of the difference in dimension of the proximal process of the petasma. In the old form the proximal process does not reach the distal end of the median lobe, whereas in the new form it is extremely long, reaching far beyond the distal end of the median lobe. The proximal process of the old form is serrated at the distal end and that of the new form is without any serration. There is also an apparent size difference between the two forms; the body length of the old form is found to be significantly larger than that of the new form. Moreover, the upper lobe of the eye of the new form is narrower than that of the old form. Along the equatorial zone, where the distributions of the two forms overlap, another form, which is recognized to be "intermediate" of the old and new forms with regard to the length of the proximal process, is also encountered. All three forms are distinguishable only in mature adults: males on the basis of structural differences of the petasma and females on the basis of differences in the body lengths and eye shape. Further discussion of them will appear in a forthcoming taxonomic paper (manuscript).

Nematoscelis gracilis is by far the most abundant species of *Nematoscelis* in the tropical regions of the Indian Ocean, including the Arabian Sea and the Bay of Bengal (Figures 4, 5). Along the full extent of the ocean at the Equator this species was found to be distributed between lat. 20°N and 20°S. The southern limit extended farther south along the regions of the western and eastern boundary currents, the Mozambique Current, and the West Australian Current, respectively. Larvae and juveniles were caught year-round from all geographical areas within the distributional range of the species. Therefore, spawning apparently occurred everywhere within that range. Larvae consisted of metanauplii, calyptopes, and furcilias; metanauplii were undoubtedly underestimated since they (body length <1 mm) could have been washed away through mesh apertures of the net.

During the NE monsoon maximum numbers of larvae and juveniles per sample were caught off the coast of southeast India (Figure 4a). For example, during *Kistna* cruise 26, 840 individuals were caught at station 704 (lat. 13°N, long. 81°E); and 764 individuals from station 705. Four stations had numbers exceeding 300 per sample from the same area. However, during the SW monsoon maximum abundance was in the western Indian Ocean north of the Equator (Figure 4b). Both larvae and juveniles were absent from the northern and northeastern Arabian Sea. There the oxygen concentration in the subsurface waters is as low as 0.1 ml/l (see Figure 2B). They were also absent to the north of lat. 10°N along the west coast of India; but during the NE monsoon they were caught as far north as lat. 15°N in the coastal waters of southwest India. The North Equatorial Current, flowing westward, has a northwestward component after passing the southern tip of India during the early part of the NE monsoon, bringing a spawning population of this species as far north as lat. 15°N. In the area of the Mozambique Current, larvae and juveniles were caught only as far south as lat. 30°S.

Adults of the old form are confined mostly to the Arabian Sea and the Bay of Bengal and the new form to areas of the Southwest Monsoon Current and the South Equatorial Current which is situated south of the Equator. During the NE monsoon old forms are frequently caught in the areas of the North Equatorial Current, whereas new forms occur only in the Equatorial Countercurrent and south of it. The two forms overlap in distribution along the northern boundary of the Countercurrent from east of long. 75°E. In the eastern Indian Ocean the distribution of old forms extends farther south (as far as lat. 14°S) (Figure 5a). "Intermediate forms" were encountered all along the overlapping zone. They were present along the western and eastern boundaries of the ocean. Most transport of the intermediate forms to the west is through the North Equatorial Current. In the South Equatorial Current it was found only at one station (*Koyo Maru* cruise 14, station 19: lat. 13°49′S, long. 94°16′E). In the western Indian Ocean there was no overlap in distribution of the forms, and the new forms did not occur north of the Equator. Moreover, during this period the Somali Current flows southwestward so that it brings the old form as far south as lat. 3°S. Therefore, the pattern of distribution of the two forms in the upper layer may be influenced by the direction of water flow in the equatorial current system which is subject to seasonal changes. During the NE monsoon no samples were taken from the Mozambique Current area north of lat. 30°S. However, mature adults of the new form were caught in one sample taken from the southeast coast of Africa (*Natal* cruise 6, day station 161: lat. 34°21′S, long. 26°21′E). Thus it appears likely that the Mozambique Current, which is stronger during the NE monsoon than in the opposite season (as judged

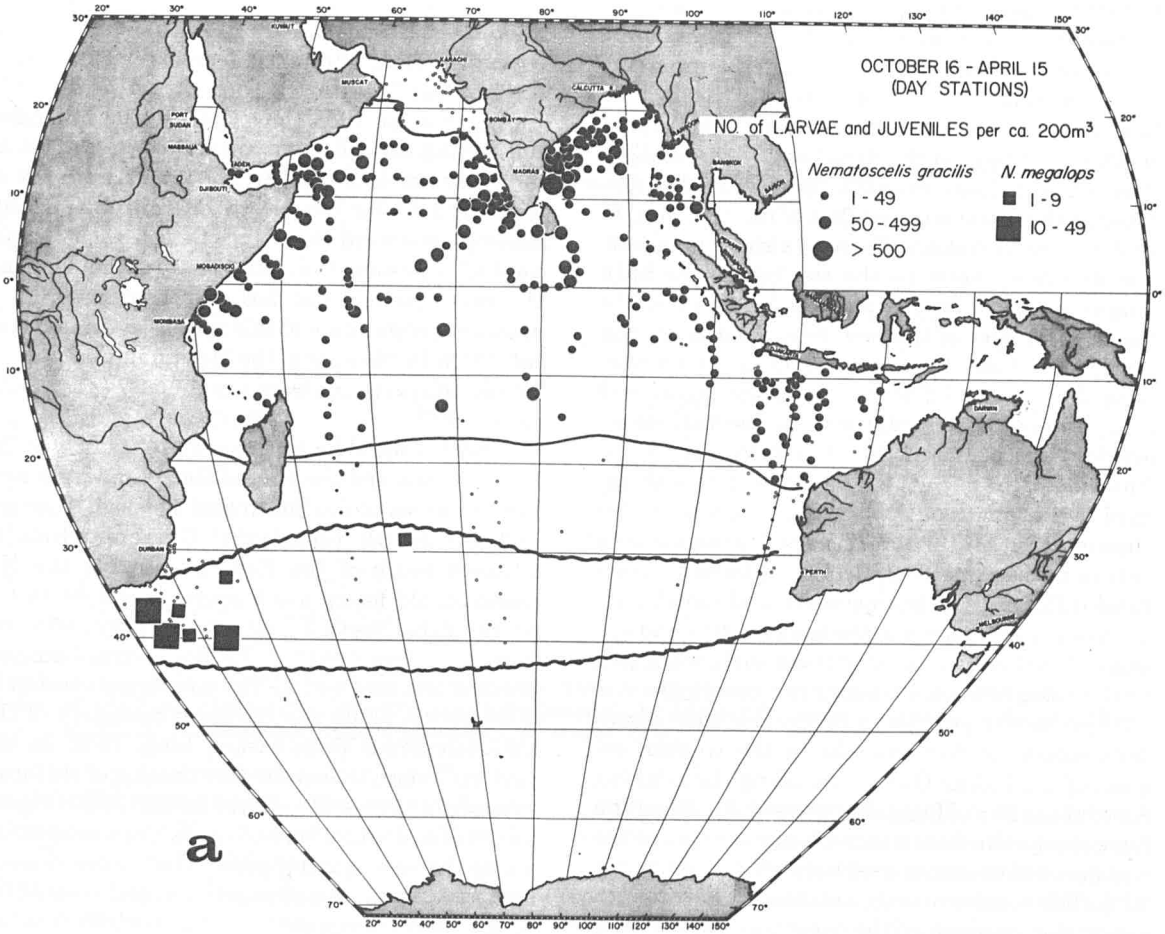


FIGURE 4.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis gracilis* and *N. megalops* in the Indian Ocean: a - NE Monsoon period. (Solid lines represent approximate distribution boundaries of *N. gracilis* and wavy lines represent those of *N. megalops*.)

from Figures 14.1 and 14.2 of Neumann and Pierson, 1966) and to which the South Equatorial Current contributes, transports some of the new forms to the south and the Agulhas Current transports them to the tip of South Africa.

During the SW monsoon the distribution of the new form is much broader in the west than in the east (Figure 5b). As the strong Somali Current begins to flow northeastward, a great deal of Southern Hemisphere water is brought to the north along the African coast. Thus the population of the new form is brought north of the Equator. It was caught as far north as lat. 8°N along the coast of Somalia; but it did not reach the upwelling areas of the Arabian coast. It has been suggested that the Somali Current turns eastward after reaching lat. 8°N and joins the Southwest Monsoon Current flowing east (Taft, 1971); the distribution of the new form in the upper layer follows the same pattern (Figure 5b). Except in the area of the Somali Current, the overlapping zone was confined to the eastern ocean. The intermediate forms were distributed across the equatorial ocean. In the region of the Mozambique Current new forms were found as far south as lat. 30°S.

Populations of the old form in the Bay of Bengal and the Arabian Sea show seasonal changes in the abundance of larvae and juveniles (Figure 6). All the available IIOE plankton samples from these two areas were used to prepare these monthly frequency distributions. In the Bay of Bengal the highest frequency of calyptopis larvae was observed in February, whereas in the Arabian Sea it

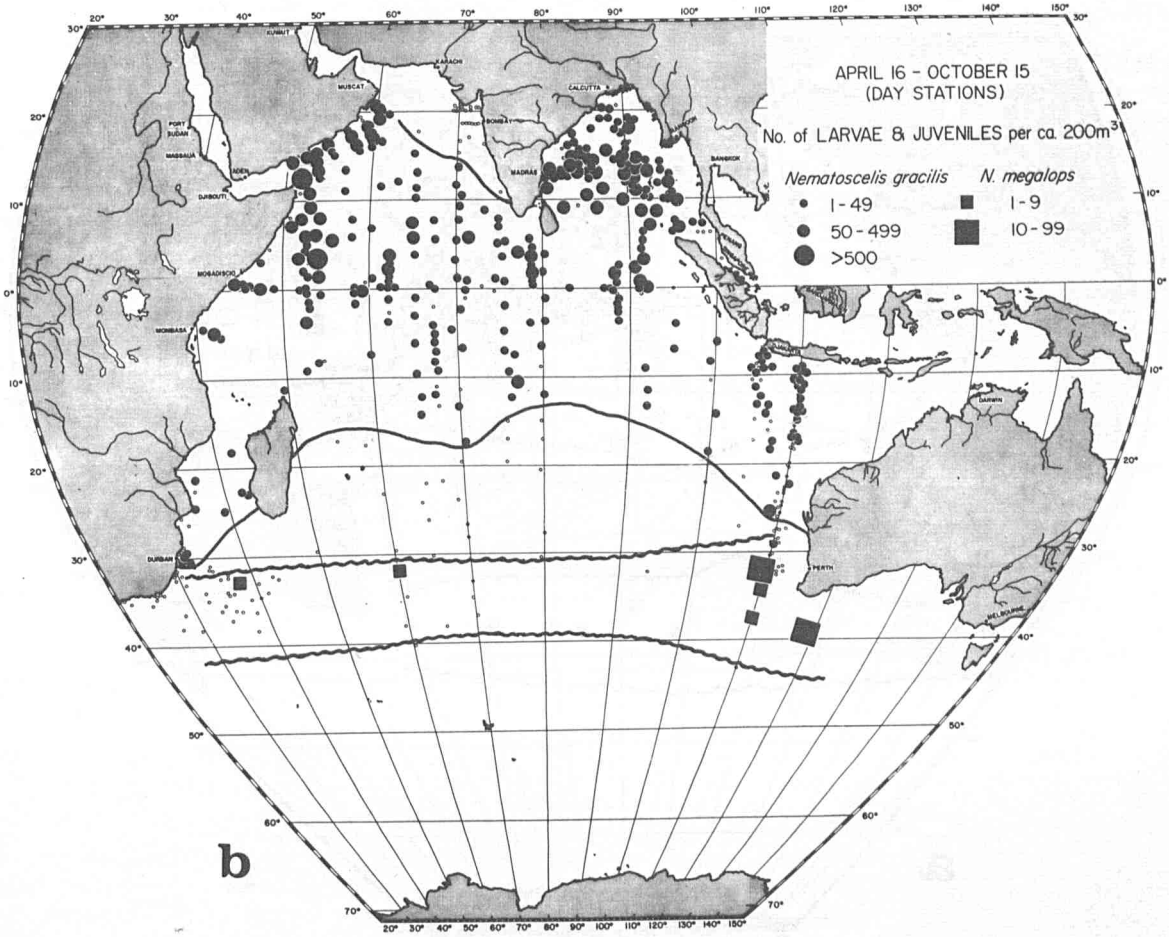


FIGURE 4.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis gracilis* and *N. megalops* in the Indian Ocean: b - SW Monsoon period. (Solid lines represent approximate distribution boundaries of *N. gracilis* and wavy lines represent those of *N. megalops*.)

was during August and December. (In both areas metanauplii were clearly underestimated.) A Student's t-test carried out on means of developmental stages during February, August, and December indicated that the frequencies of larvae in the Bay of Bengal were significantly different ($P < 0.01$) from those in the Arabian Sea during the same months. Frequencies during other months were not significantly different between the two populations. Since most of the developmental stages were caught each month, it appears that spawning is continuous; only the rate of production is subjected to seasonal changes.

The distributional patterns of the two forms of *N. gracilis* so far discussed are based on adults caught from the upper 200-m layer. As pointed out before, the vertical distribution of this species extends much greater than this depth. Figure 7a shows the distributions of new and old forms based on deeper samples. Evidently these are similar to those based only on the upper layer samples (cf. Figures 5, 7a). Both forms were caught from the same station only near the Equator, and intermediate forms were found only at the areas of overlap near the Equator.

Atlantic Ocean

Nematoscelis gracilis has not been reported from the tropical Atlantic Ocean, nor was it found in any collections examined during the present survey. The only record from the Atlantic Ocean was from the southwest coast of Africa (Lusiad VII-IKMT, station 63-539, lat. 33°47′S, long.

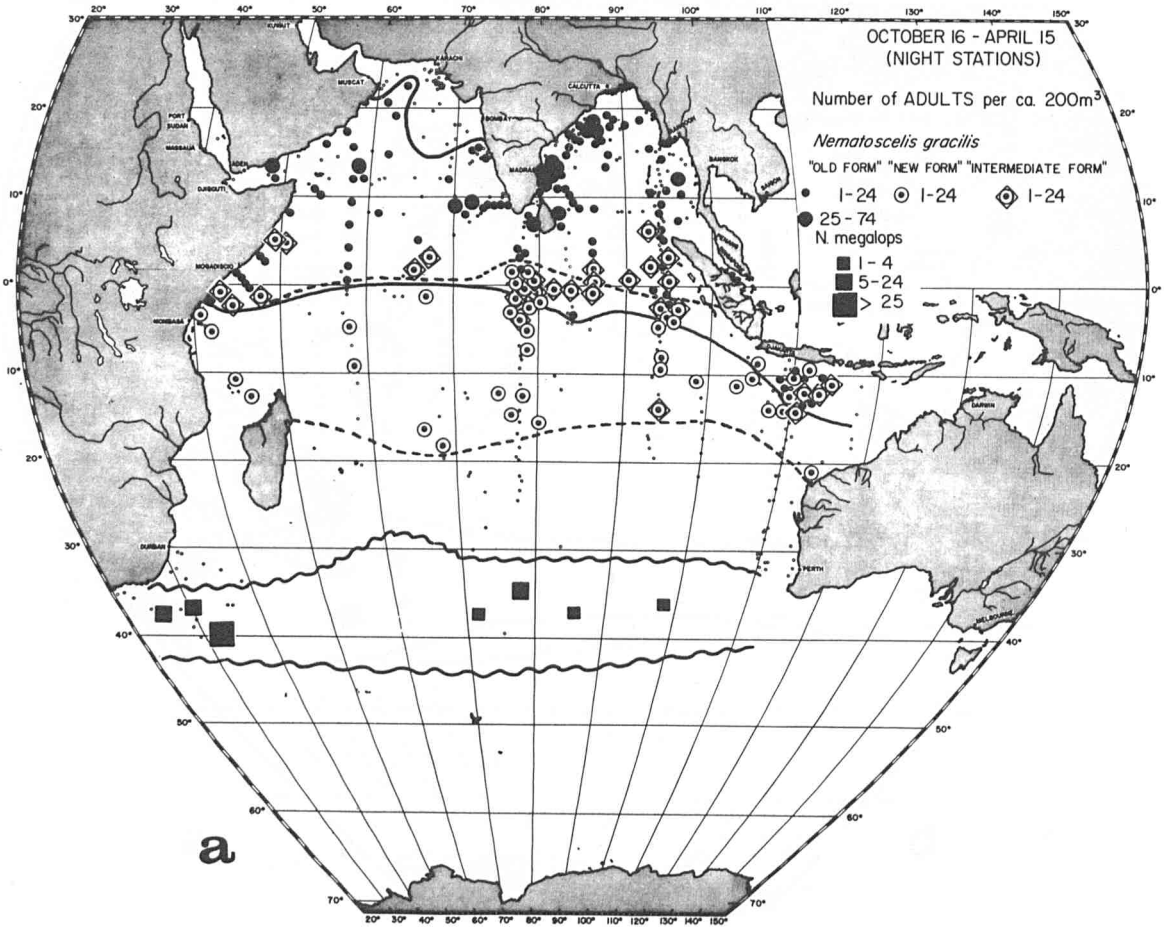


FIGURE 5.—Locality records and nighttime abundance of *Nematoscelis gracilis* and *N. megalops* adults in the Indian Ocean: a - NE Monsoon period. (Solid lines represent approximate boundaries of distribution of *N. gracilis* "old form," broken lines represent those of "new form," and wavy lines those of *N. megalops*.)

15°47′E, 5 June 1963). (See Figure 14b.) Three adult males and one female belonging to the new form were caught at this station, but no old form was found. Probably these new forms were transported westward by the Agulhas Current (Figure 7a).

Pacific Ocean

Nematoscelis gracilis is recorded from the equatorial zone of the Pacific (Brinton, 1962). Populations of this species were also shown to have been carried by the Kuroshio system to as far as lat. 40°N, east of Japan. The numerical density was found to be much higher in the east than in the west. In the present survey based on midwater trawls from the Pacific, a similar pattern of distribution was observed (Figure 7a). The new forms were also found to occur in the Pacific, but only south of the Equator. There Reid (1965) recognized an eastward flow at about 400-800 m (on the basis of acceleration potentials at 125 cl/ton (lat. 2°-8°S) and 80 cl/ton (lat. 8° - 20°S) δ T). However, in the eastern Pacific the same latitudes are occupied by old forms where Reid (1965) and Love (1972) reported a narrow tongue of low oxygen, as low as 0.2-0.5 ml/l, extending westward. The contour of oxygen concentration of 0.5 ml/l extended as far west as long. 130°W between the Equator and lat. 10°S (at 160 cl/ton δ T surface, 150-200 m). This may account for the fact that new forms do not reach eastward to the coasts of Chile and Peru. The association of old forms with oxygen-poor

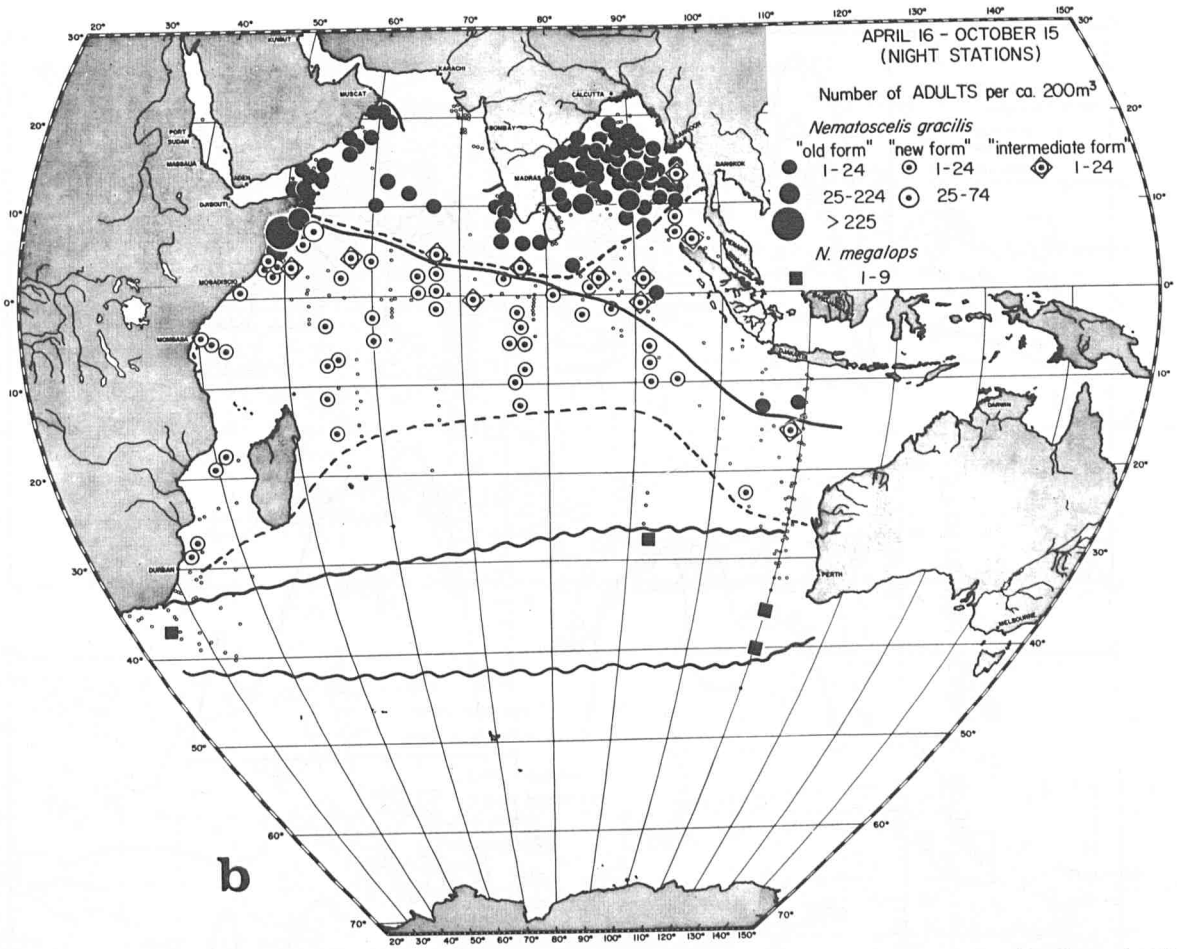


FIGURE 5.—Locality records and nighttime abundance of *Nematoscelis gracilis* and *N. megalops* adults in the Indian Ocean: b - SW Monsoon period. (Solid lines represent approximate boundaries of distribution of *N. gracilis* "old form," broken lines represent those of "new form," and wavy lines those of *N. megalops*.)

water is evident from these comparisons. *Nematoscelis gracilis* old form is the dominant *Nematoscelis* species occurring in the eastern tropical Pacific. Along the coasts of Peru and Chile this form is now known to be distributed as far south as lat. 33°S (personal observation in a sample collected by Antezana). Only old forms were found in the China Sea and in oceanic waters of the Kuroshio system. However, the new and old forms cooccurred in the Timor, Banda, Celebes, Halmahera, and Molucca seas. The Indian Ocean populations of both forms are therefore in continuity with those of the Pacific. In the Pacific the eastern and western populations of the species as a whole are linked along the equatorial zone between lat. 0° and 10°N (Brinton, 1962). Brinton has pointed out that the lat. 20°N-20°S range of *N. gracilis* in the east and the lat. 10°N-10°S range in the west corresponds reasonably well to the range of the equatorial water mass (Sverdrup, Johnson, and Fleming, 1942).

Geographical Distribution of *N. megalops*

Indian Ocean

Nematoscelis megalops was recorded during the IIOE between lat. 30°S and 45°S. This is the area of transition between subantarctic and Indian Central water (Sverdrup et al., 1942). The number of samples collected from this zone is too scanty to permit a seasonal study. Larvae, juveniles, and adults were caught during both seasons along the

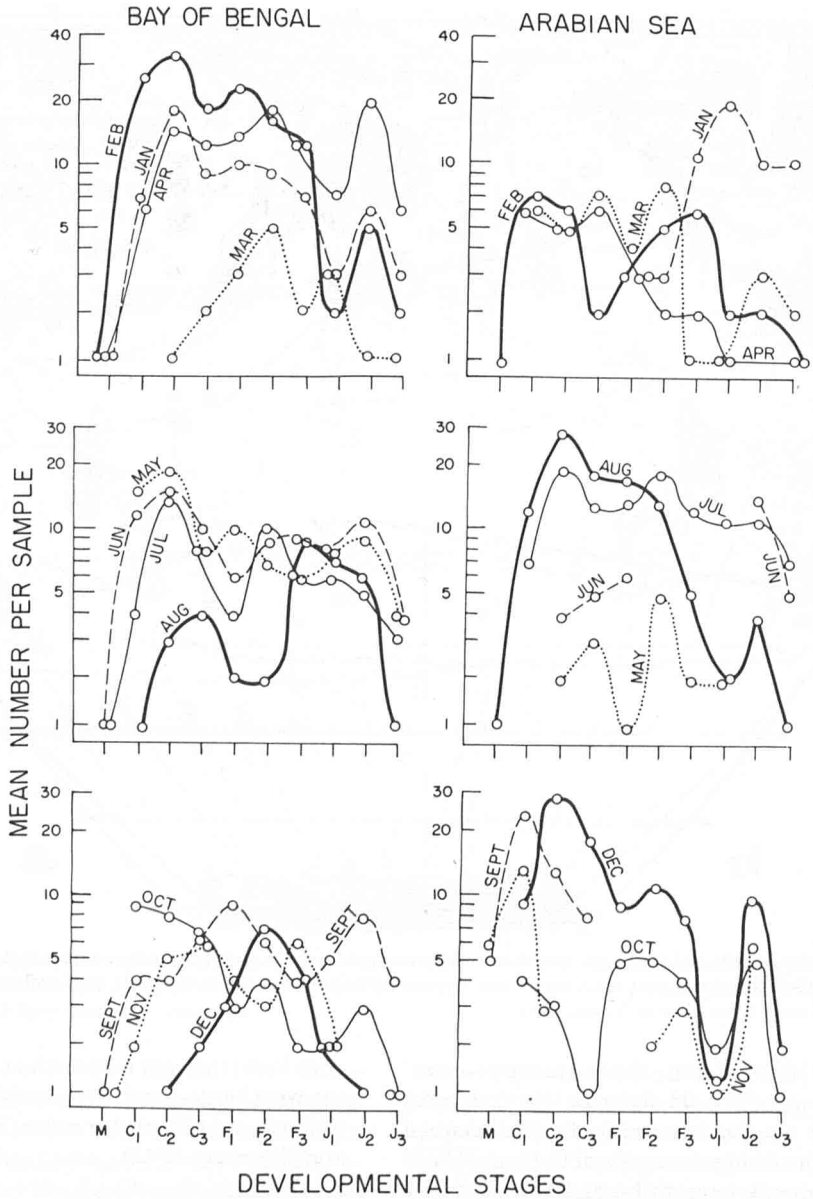


FIGURE 6.—Frequency distribution of developmental stages of *Nematoscelis gracilis* "old form" in the Bay of Bengal and the Arabian Sea. (Number of samples used to calculate monthly averages ranged from 11 to 18.)

full extent of the transition zone (Figures 4, 5). In the western Indian Ocean, the maximum number of larvae (as many as 280 larvae per sample) was caught during October 1962 (*Natal* cruise 5). In the east, *Diamantina* cruise 3/62 caught up to 90 larvae per sample during September 1962. Although Boden (1954) reported this species in the region of the Mozambique Current, I did not find it in meter-net samples or mid-water trawls taken north of lat. 34°S in waters of southeast Africa (Figure 7b). (Trawls were made during the October-November period.) However, the northern boundary of distribution appears to lie between lat. 28°S and 30°S. The northernmost record of this species was at lat. 28°18′S, long. 62°33′E (*Vitiaz* 36, station 5323).

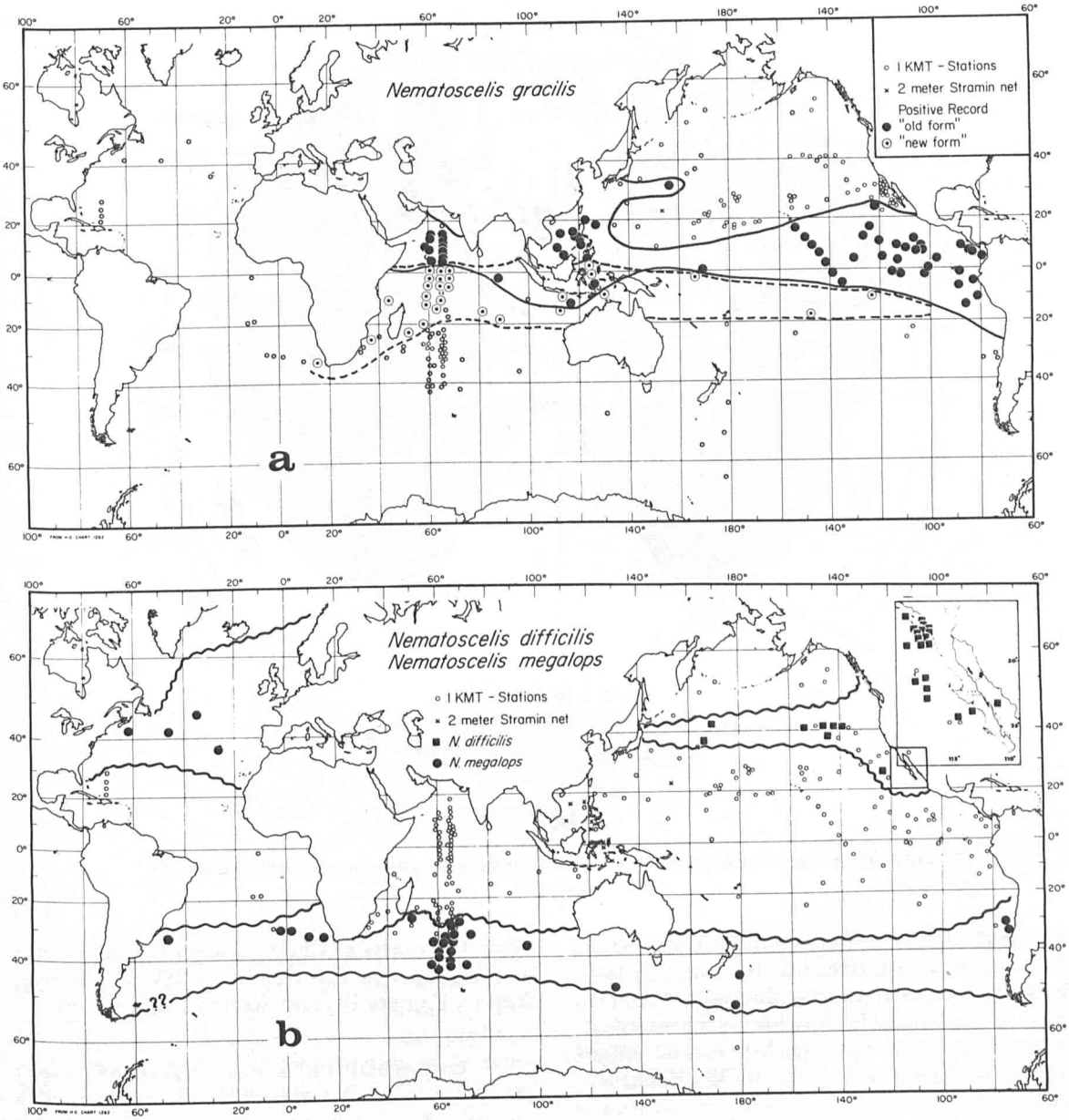


FIGURE 7.—Worldwide distribution of *Nematoscelis* based on mid-water trawls: a - *N. gracilis* "old" and "new" forms; b - *N. difficilis* and *N. megalops*. (Solid lines represent approximate boundaries of distribution of old form, broken lines represent those of new form, and wavy lines represent distributional boundaries of *N. difficilis* and *N. megalops*. Boundaries are based on literature records and present evidence.)

Atlantic Ocean

Nematoscelis megalops appears to have a wider north-south range in the Atlantic than in other oceans. The southernmost record in the North Atlantic was in the region of the Canary Current (Figure 8a). Larvae and juveniles were frequently caught between lat. 40°N and 53°N. Literature records of this species in the North Atlantic are as far north as lat. 68°N (Zelikman, 1964). Moore (1952) recorded this species from lat. 35°N to 55°N. It occurs in the Mediterranean Sea (Ruud, 1936). In the South Atlantic it was collected by the Lusiad Expedition between lat. 25°S and 30°S

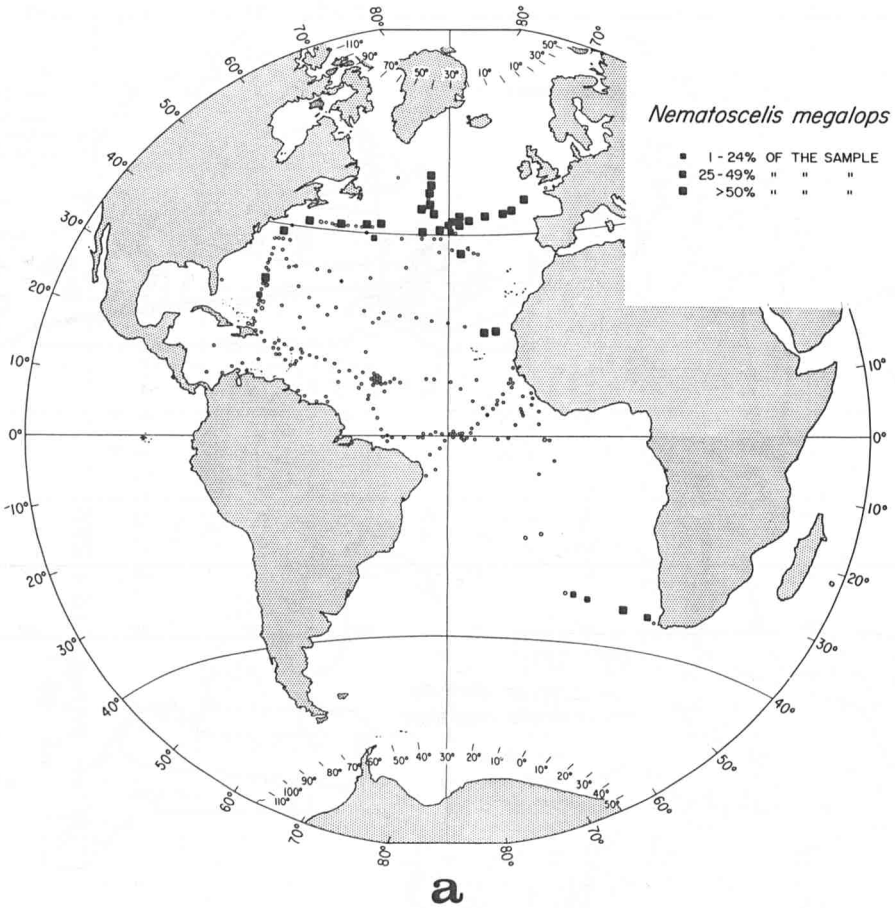


FIGURE 8.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: a - *N. megalops*.

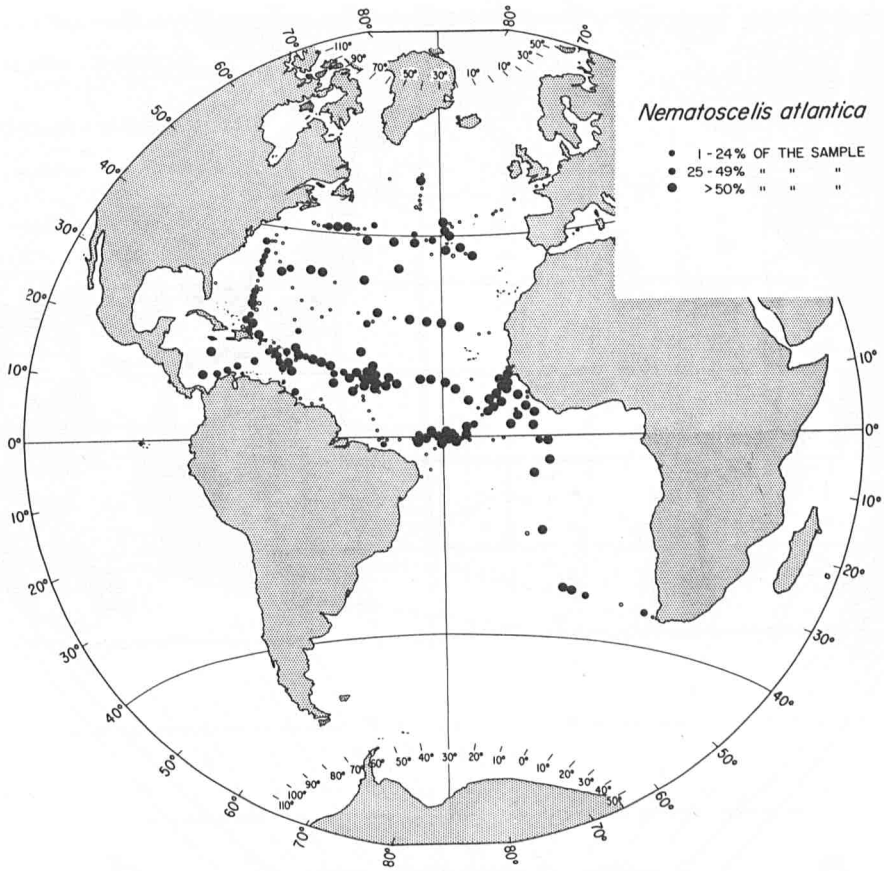
(Figure 8a). Boden (1954) recorded this species from the Benguela Current as far north as lat. 22°S. From the western part of the South Atlantic no data is available. The only literature record is from the Brazil Current area, between lat. 45°S and 50°S and long. 62°W and 68°W (Ramirez, 1971).

Pacific Ocean

Nematoscelis megalops and *N. difficilis* are a recognized sibling species pair, occupying transoceanic belts of the transition zones of the South and North Pacific oceans respectively (Brinton, 1962). During the Downwind Expedition, Brinton found *N. megalops* distributed between lat. 33°S and 48°S in midocean. The Monsoon Expedition caught it as far south as lat. 54°21′S (Figure 7b). Along the coasts of Chile between lat. 30°S and 50°S this species was caught by MV-65 (*Anton Bruun*), Piquero III, and Scorpio I expeditions.

Geographical Distribution of *N. difficilis*

Nematoscelis difficilis is endemic to the North Pacific, occupying the North Pacific Drift and the California Current (Figure 7b). It was reported during Transpacific Expedition from seven stations located east of Japan (Brinton, 1962). In the present study it was found in mid-water trawls from near lat. 40°N between long. 130°W and 160°W. Along the North American coast, the distribution extends northward to lat. 51°N (Banner, 1949) and southward to lat. 20°N (Brinton, 1962). It is common in the cold water of the California



b

FIGURE 8.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: b - *N. atlantica*.

Current and caught frequently in mid-water trawls in the San Diego Trough area. This species was also caught in the Gulf of California by the Vermilion Sea Expedition; however, this population is believed to be separated, perhaps seasonally, from that on the west side of Baja California due to the influx of warm water from the south at the mouth of the Gulf (Brinton, 1962). Literature records and present evidence indicate that the ranges of *N. megalops* and *N. difficilis* do not overlap.

Geographical Distribution of *N. atlantica*

Indian Ocean

This species has not been reported previously from the Indian Ocean. In the IIOE collections there were frequent occurrences of this species, but only in the midlatitudes (lat. 15°-40°S) of the Southern Hemisphere (Figure 9a, b). *Nematoscelis atlantica* lives in the region of the Indian Ocean central water mass. Larvae and juveniles were caught from most stations occupied within the range of distribution of the species. Moreover, there were no obvious differences between seasonal distributions. IIOE samples included many adults from west of Australia and the Agulhas Current (Figure 10a, b). In the mid-water trawls it was caught between lat. 11°S and 42°S along long. 60°E (Figure 11a).

Atlantic Ocean

Nematoscelis atlantica was observed in many samples from the North Atlantic (Figure 8b). Un-

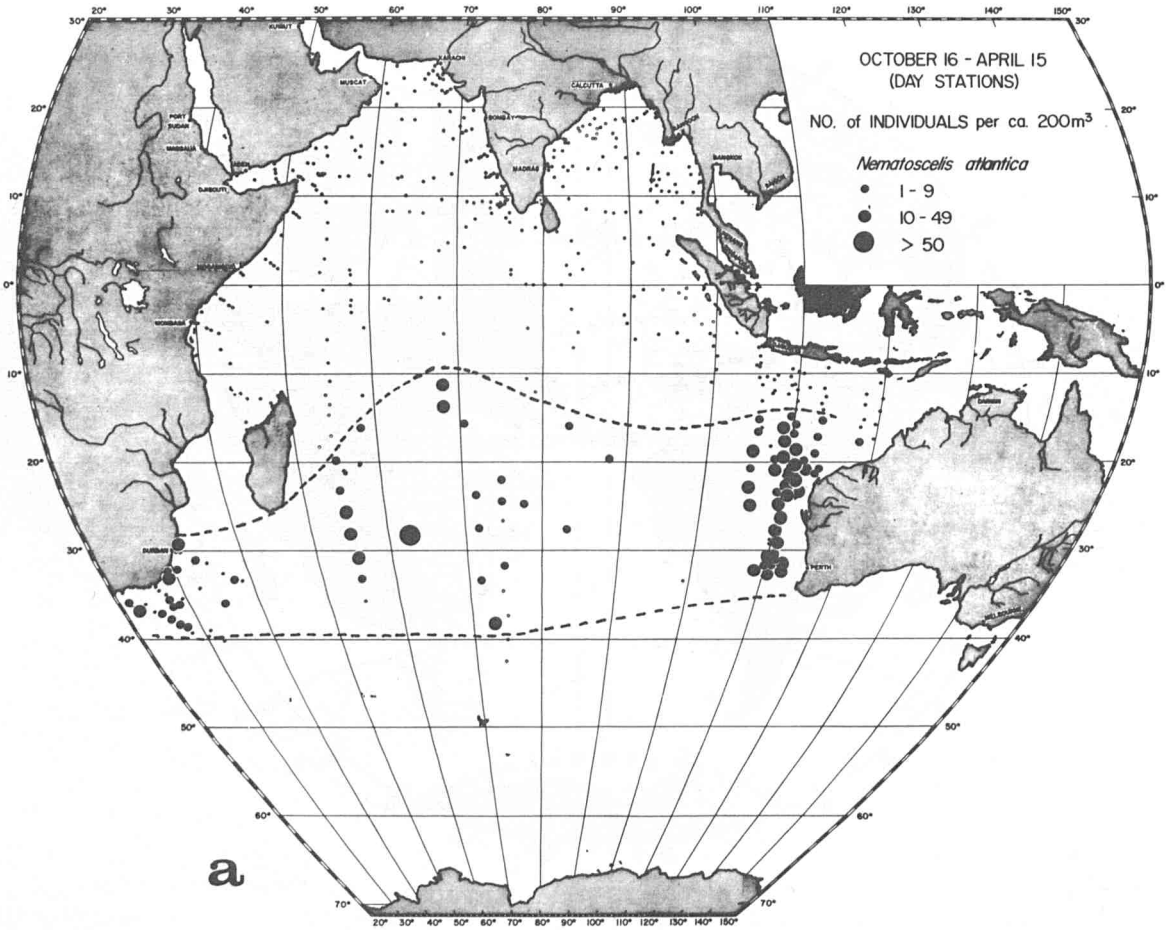


FIGURE 9.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis atlantica* in the Indian Ocean: a - NE Monsoon period.

like in the Pacific and Indian oceans, this species also occupies the Atlantic equatorial zone providing communication between North and South Atlantic populations. The German South Polar Expedition (Zimmer, 1914) first recorded the north-south continuity of *N. atlantica* in the Atlantic. In the eastern Atlantic between the Equator and lat. 40°N, *N. atlantica* constituted over 50% of the total *Nematoscelis* present in each sample. The northernmost record was at lat. 52°N (*Atlantis II*-9, station 371). This species was not reported previously from the North Atlantic central gyre (Mauchline and Fisher, 1969). In the present collection many larvae, juveniles, and mature adults were recorded from this area. Mediterranean Sea records come from Ruud (1936) and Casanova-Soulier (1968). In the South Atlantic it was present in the Lusiad collections (Figure 11a). Literature records in the South Atlantic show that it occurs in the Benguela Current, extending as far as lat. 40°S (Mauchline and Fisher, 1969). No samples were available from the areas of the Argentine Basin.

Pacific Ocean

In the Pacific, *N. atlantica* lives in the central water masses of both hemispheres (Figure 11a). The approximate boundaries of distribution are between lat. 13° and 38° in each hemisphere (Brinton, 1962). It was not caught in the Naga collections from the Indo-Australian Archipelago. The North Pacific population of this species appears to be separated from those of the South Pacific and Indian Ocean regions. It may be possible that communication exists between Indian and South Pacific populations through the oceanic waters south of Australia.

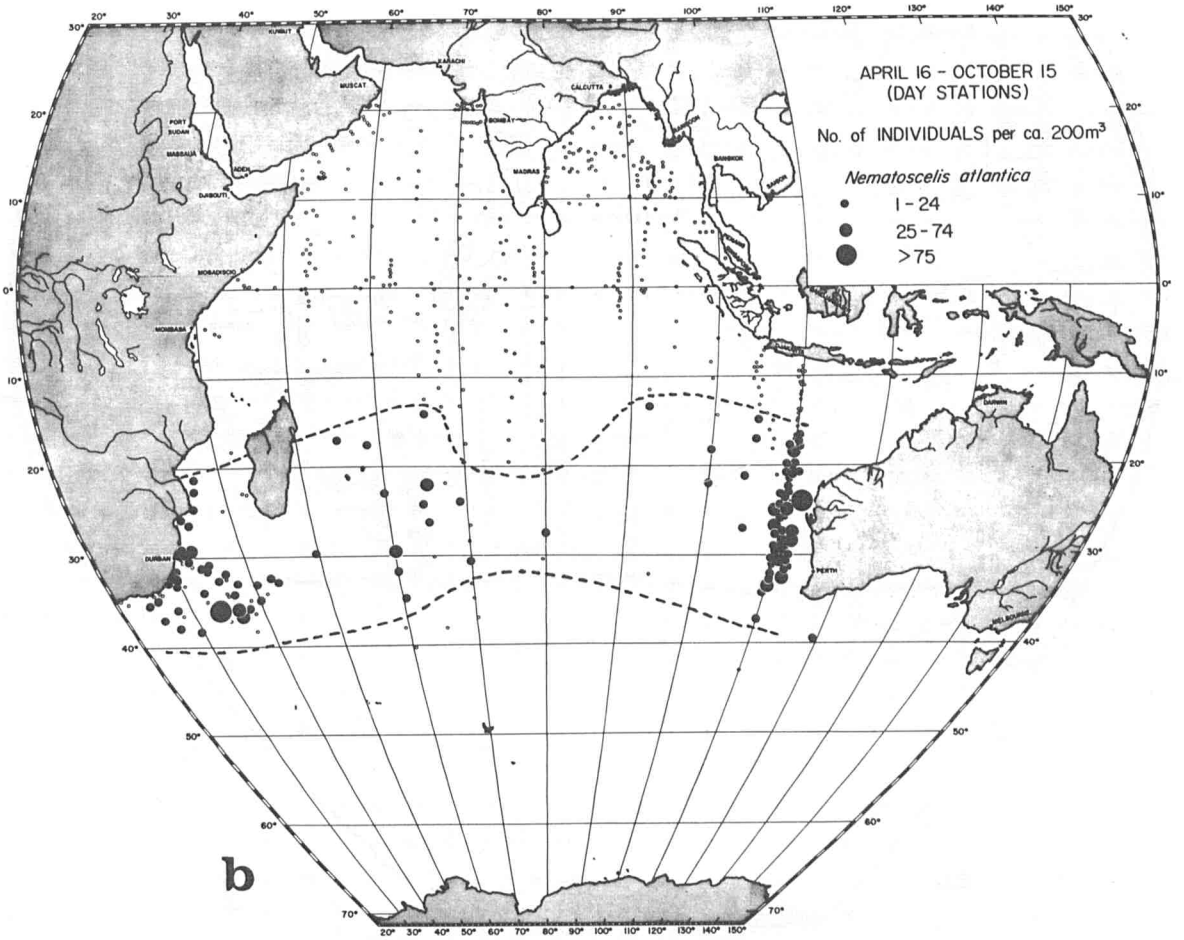


FIGURE 9.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis atlantica* in the Indian Ocean: b - SW Monsoon period.

Geographical Distribution of *N. microps*

Indian Ocean

Nematoscelis microps has wider ranges of distribution than *N. gracilis* and *N. atlantica*. This species penetrates the Arabian Sea and the Bay of Bengal only at their western and eastern sides respectively (Figure 12a, b). The northernmost record of this species in the western Arabian Sea was at lat. 14°N and that in the eastern side of the Bay of Bengal at lat. 19°N off the coast of Burma. It does not live in the poorly oxygenated subsurface waters of the Arabian Sea and Bay of Bengal. In midocean the northern boundary does not extend north of lat. 6°N and the southern boundary not beyond lat. 30°S. It was caught less frequently from the southern central gyre south of lat. 10°S. *Nematoscelis microps* is a predominant species of the South Equatorial Current and the West Australian area. The Agulhas Current apparently brings it around the tip of South Africa.

There was not much seasonal change in the distribution of this species in the Indian Ocean. Larvae and juveniles were present in the Somali Current area during both monsoon seasons but were carried as far north as lat. 14°N only during the SW monsoon. They were present throughout the year in the Andaman Sea area. During the NE monsoon adults were not caught in the Somali Current area north of the Equator, whereas they were present as far north as lat. 12°N during the opposite season when the flow is northeastward (Figure 13a, b). Adults occurred in the North Equatorial Current area during the NE monsoon

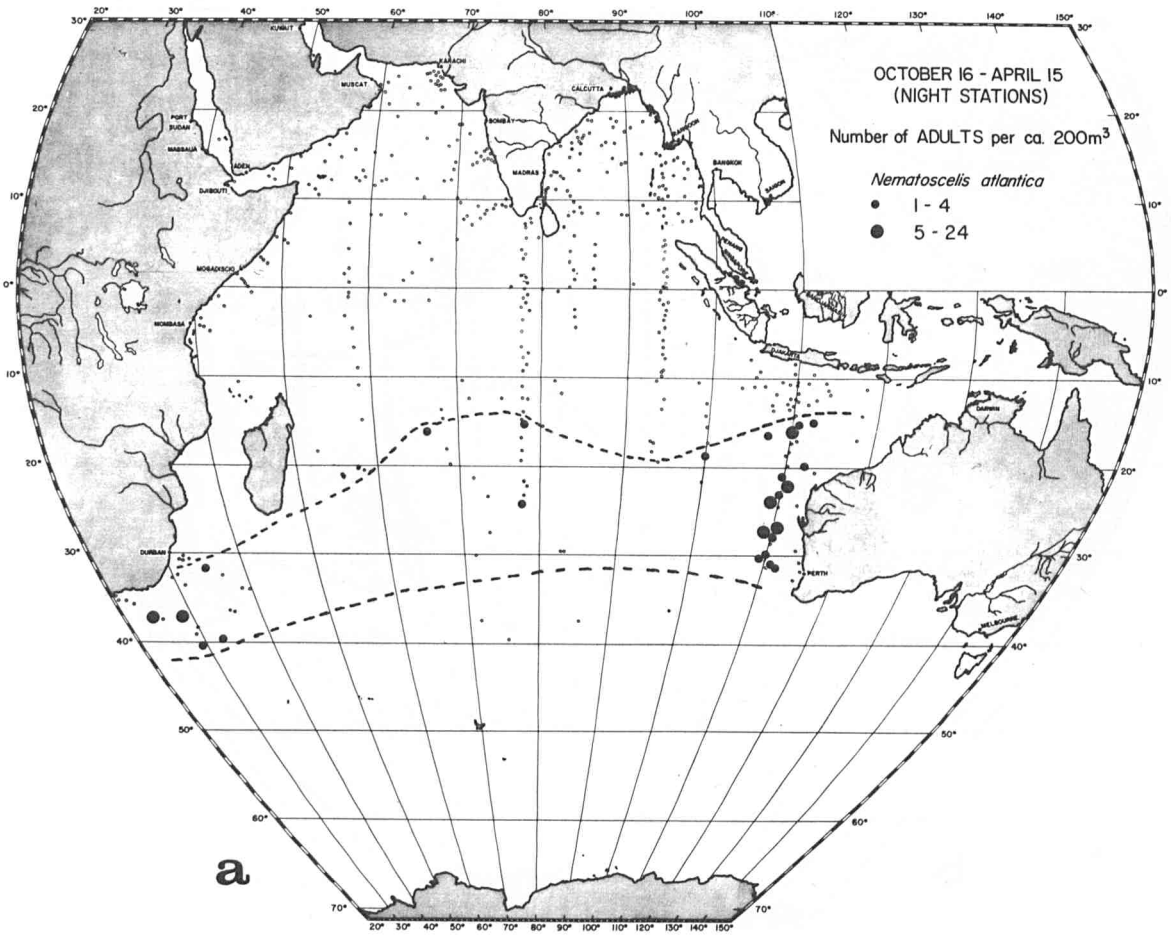


FIGURE 10.—Locality records and nighttime abundance of *Nematoscelis atlantica* adults in the Indian Ocean: a - NE Monsoon period.

but were not caught there during the opposite season when the Monsoon Current replaces the North Equatorial Current. During the SW monsoon none of the stations north of the Equator between long. 50°E and 90°E contained adult specimens (Figure 13b). Evidently this species does not reach the coast of India. In the mid-water trawls *N. microps* was caught between lat. 10°N and 41°S (Figure 11b), but north of lat. 2°N this species was caught from only one station (*Anton Bruun* cruise 3, station 146, lat. 10°09′N, long. 59°55′E).

Atlantic Ocean

From the Atlantic Ocean there are literature records of scattered occurrences of this species between lat. 40°N and 40°S. Moore (1952) reported that this species occurred in the western Atlantic north of the equator to lat. 40°-45°N, in the region of the Gulf Stream. The most northerly record in the eastern ocean was from lat. 59°39′N (Illig, 1930), although most other records lie south of lat. 40°N. In the present survey it was caught between the Equator and lat. 40°N and was relatively more abundant in the western ocean than in the east (Figure 14a). It was not present in many samples taken from the North Atlantic central gyre. There were a few doubtful records of this species from the Mediterranean Sea (Ruud, 1936; Bacescu and Mayer, 1961). In the South Atlantic it was caught by Lusiad and *Atlantis II* - 31 expeditions (Figure 11b).

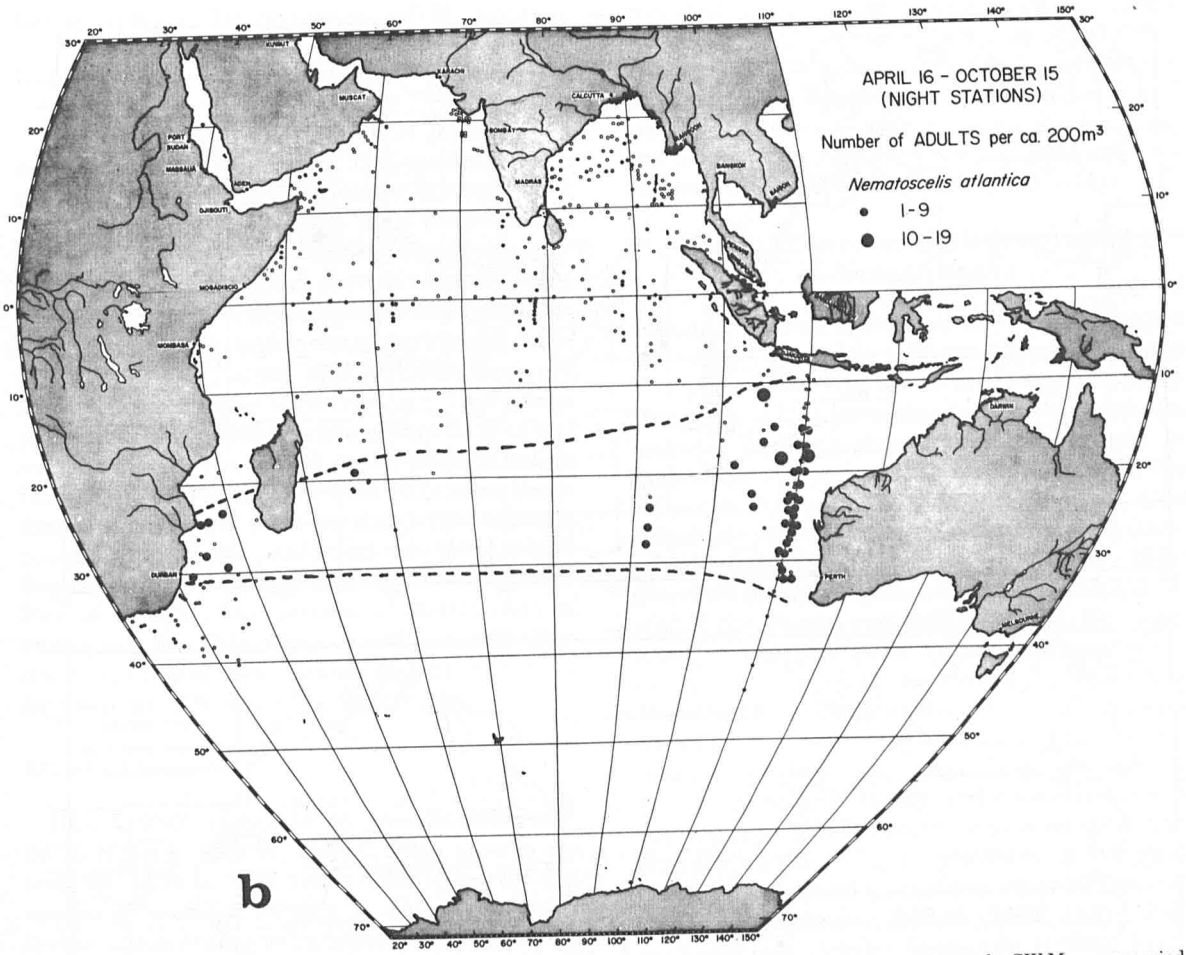


FIGURE 10.—Locality records and nighttime abundance of *Nematoscelis atlantica* adults in the Indian Ocean: b - SW Monsoon period.

Pacific Ocean

North and South Pacific populations of *N. microps* are in communication with each other across the western equatorial Pacific (Figure 11b). This species is absent along the eastern boundary currents (California Current and Peru Current) and also from the poorly oxygenated subsurface waters of the eastern tropical Pacific. *Nematoscelis microps* was also caught less frequently in the eastern North Pacific central water mass than in the western North Pacific central water mass. In the equatorial region this species is known to occur only west of long. 110°W (Brinton, 1962). It is also recorded from the China Sea and the regions of the Timor, Molucca, and Banda seas. The populations of the Indian and Pacific oceans are probably in communication with each other through the straits of Timor, Banda, Molucca, and Halmahera.

Geographical Distribution of *N. lobata*

Hansen (1916) described *N. lobata* from the Philippines. He found it at only two localities: lat. 13°43′N, long. 121°E and lat. 7°07′N, long. 125°40′E. *Nematoscelis lobata* appears to be endemic to the semi-isolated seas around the western side of the Philippines. In the present survey it was caught mostly from the Sulu Sea area (Naga Expedition) (Figure 15). At station S11B-205, five mature males and six females were caught in a 2-m-net collection, 0-500 m (lat. 6°35′N, long.

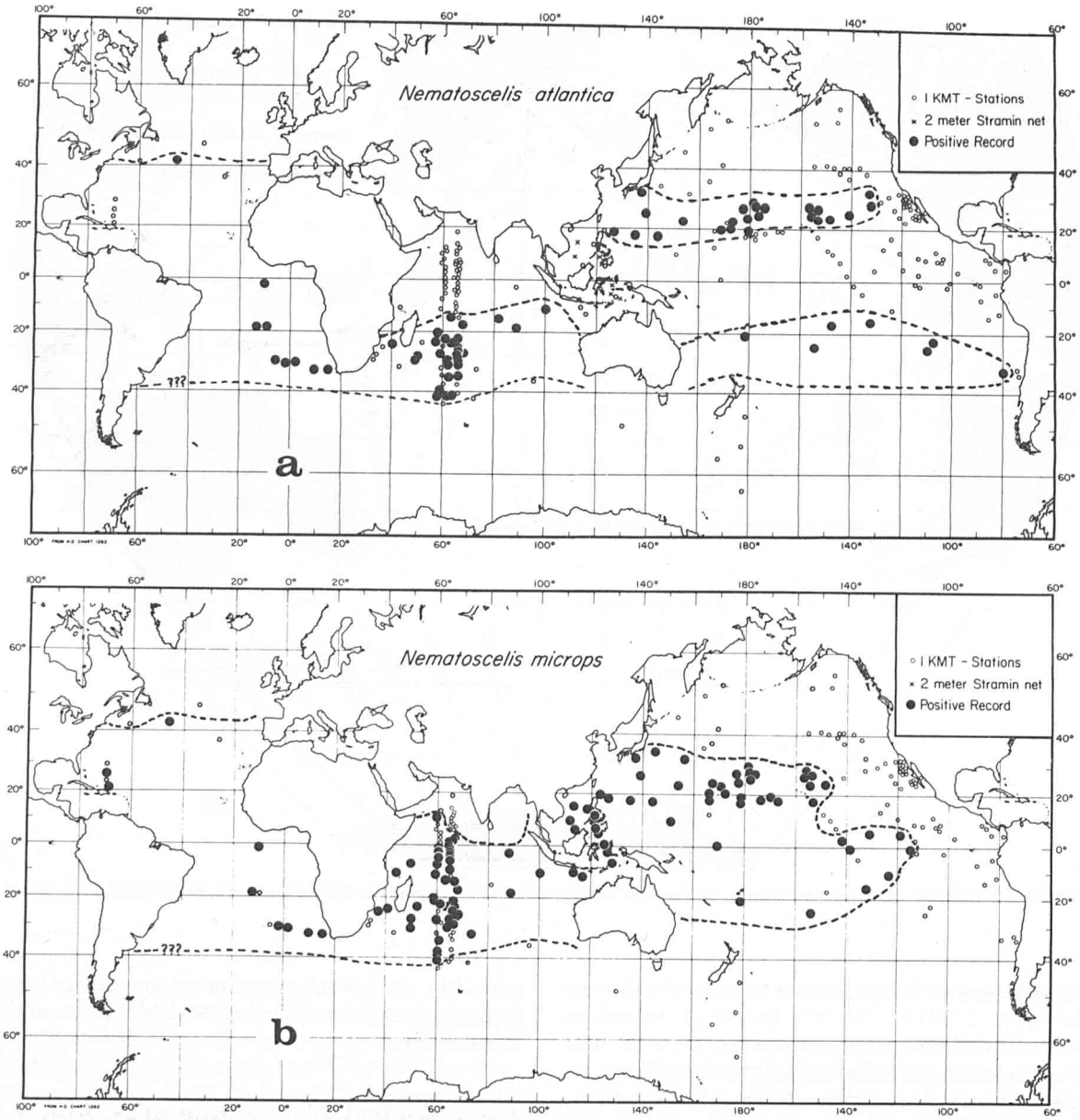


FIGURE 11.—Worldwide distribution of *Nematoscelis* based on mid-water trawls: a - *N. atlantica*; b - *N. microps*. (Broken lines represent approximate boundaries of distribution of the species based on literature records and present evidence.)

122°27′E; 29 April 1961). At six other stations only mature females were caught. The petasma, particularly the broad median lobe with its convex inner and outer margins, is an excellent diagnostic feature of this species. The shape of the keel on the carapace of both sexes is also different from other *Nematoscelis* species. *Nematoscelis lobata* is not reported from any other place, including the Siboga collections from the East Indian Archipelago and the Troll Expedition collections made along the eastern coast of the Philippines (Figure 15). This species appears to be absent from the South China Sea and the Gulf of Thailand (Brinton, manuscript).

Geographical Distribution of *N. tenella*

Indian Ocean

The geographical distribution of *N. tenella* is similar to that of *N. microps*. This species lives in the equatorial and central water masses of all oceans. In the Indian Ocean most records came from between lat. 7°N and 38°S except in the eastern and western boundary current areas (Figures 16a, b; 17a, b). It was most frequently caught in the equatorial zone and in the eastern ocean south of the Equator. Larvae and juveniles occurred throughout the range of distribution. There were no seasonal differences in the distribution of larvae and juveniles; however, in the western Indian Ocean north of the Equator they were more abundant during the SW monsoon than in the opposite season. This species penetrates into the Arabian Sea only in the western side. It is absent from the Bay of Bengal. The pattern of distribution of adults was like that of larvae and juveniles (Figure 17a, b). Mid-water trawls caught *N. tenella* between lat. 8°N and 40°S (Figure 18).

Atlantic Ocean

Illig (1930) recorded *N. tenella* from lat. 59°39′N, long. 8°49′W, but all other records are from lat. 35°N to 35°S. Lewis (1954) reported this species off southern Florida. In the present study larvae and juveniles were found to be more abundant in the western North Atlantic than on the eastern side (Figure 14b). Around lat. 40°N, its northern limit, it was caught in five plankton samples. It has not been reported from the Mediterranean Sea. In the South Atlantic this species was found in the Lusiad collections off South Africa. No samples were available from the western South Atlantic nor has it been reported from that region. It is also not known whether this species occurs in the Benguela Current.

Pacific Ocean

Nematoscelis tenella lives in both hemispheres of the Pacific, lat. 35°N-34°S. It does not occupy the more coastal areas of the California Current or its southward extension into the eastern equatorial region (Figure 18). It is also scarce in the region of the Peru Current (Brinton, 1962). In midocean, Brinton recorded it as far south as lat. 34°S. This species appears to be more abundant in the northern central gyre than in the south. It occurs farther east in the tropical belt than *N. microps*. The north-south range is continuous across the Equator. It is a common species in the South and East China seas and also in the Banda, Molucca, and Timor seas. Apparent communication exists between the Indian and Pacific populations.

Faunal Zones and Biogeography of *Nematoscelis*

Faunal regions of the oceanic environment are not as well defined as in the terrestrial habitats. The oceanic environment, as distinguished by Hedgpeth (1957), consists of a system of zonally oriented hydrographic provinces arranged in latitudinal succession within each ocean. In the Atlantic Ocean, Dahl (1894) recognized four epipelagic faunal regions: arctic, subarctic (temperate), subtropical, and tropical. Steuer (1933) described a similar system of classification but included the Pacific and Indian oceans. He recognized circumpolar arctic, circumequatorial tropical, and circumpolar antarctic on a global scale. The arctic region was subdivided into a circumpolar subregion as well as Atlantic and Pacific subarctic subregions. The antarctic region includes the circumpolar antarctic and subantarctic subregions. The tropical region was subdivided into Atlantic and Indo-Pacific provinces. A system of classification based on this and other subsequent works [for example: Deacon (1933, 1937); Radzikhovskaya (1965); Stepanov (1965); Frost (1969); McGowan (1971)] is adapted here and shown in Table 2. The division of the epipelagic environment into faunal zones agrees with the distributional patterns of many planktonic organisms [see McGowan (1971) for examples]. Species of *Nematoscelis* occupy one or more of the subregions (Table 3). As mentioned before, *N. difficilis* is endemic to a zone of transition between subarctic and central water in the North Pacific. Even though this zone (Johnson and Brinton, 1963) does not have as well defined a temperature-salinity envelope as other water masses, it maintains endemic species, as well as the densest part of the overall populations of some subarctic and central species. Evidence is accumulating for the existence of a unique water body in this zone with characteristic hydrographical and faunal properties (McGowan, 1971). The extent and location of an analogous transition zone in the North Atlantic, if such exists, is not

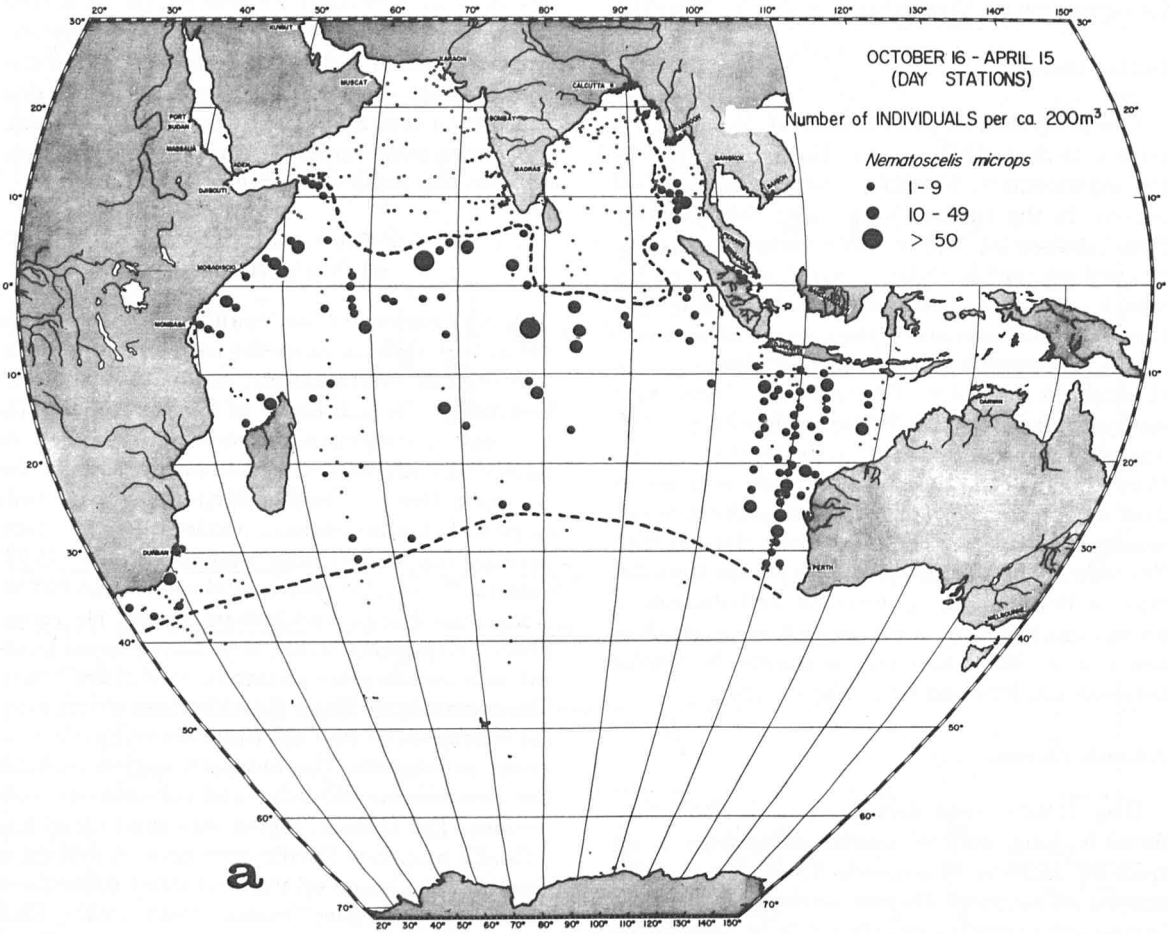


FIGURE 12.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis microps* in the Indian Ocean: a - NE Monsoon period.

TABLE 2.—Biogeographical zones of the oceanic environment.

Zones	Terminology (Regions)	Latitude (approximate)	Subregion
Northern Cold Water	Circumpolar Arctic	>67°N	
	Subarctic (Cold Temperate)	45°-67°N	Subarctic Atlantic Subarctic Pacific
Northern Transitional	———	35°-45°N	Transitional North Atlantic Transitional North Pacific
Warm Water	Northern Subtropical (Warm Temperate)	23°-35°N	Subtropical North Atlantic Subtropical North Pacific
	Tropical	23°S-23°N	Tropical Atlantic Tropical Indo-West Pacific Eastern Tropical Pacific
	Southern Subtropical (Warm Temperate)	23°-35°S	Subtropical South Atlantic Subtropical South Pacific Subtropical South Indian
Southern Transitional	———	35°-45°S	Circumpolar Transitional Region of the Southern Hemisphere
Southern Cold Water	Circumpolar Subantarctic (Cold Temperate)	45°-67°S	
	Circumpolar Antarctic	>67°S	

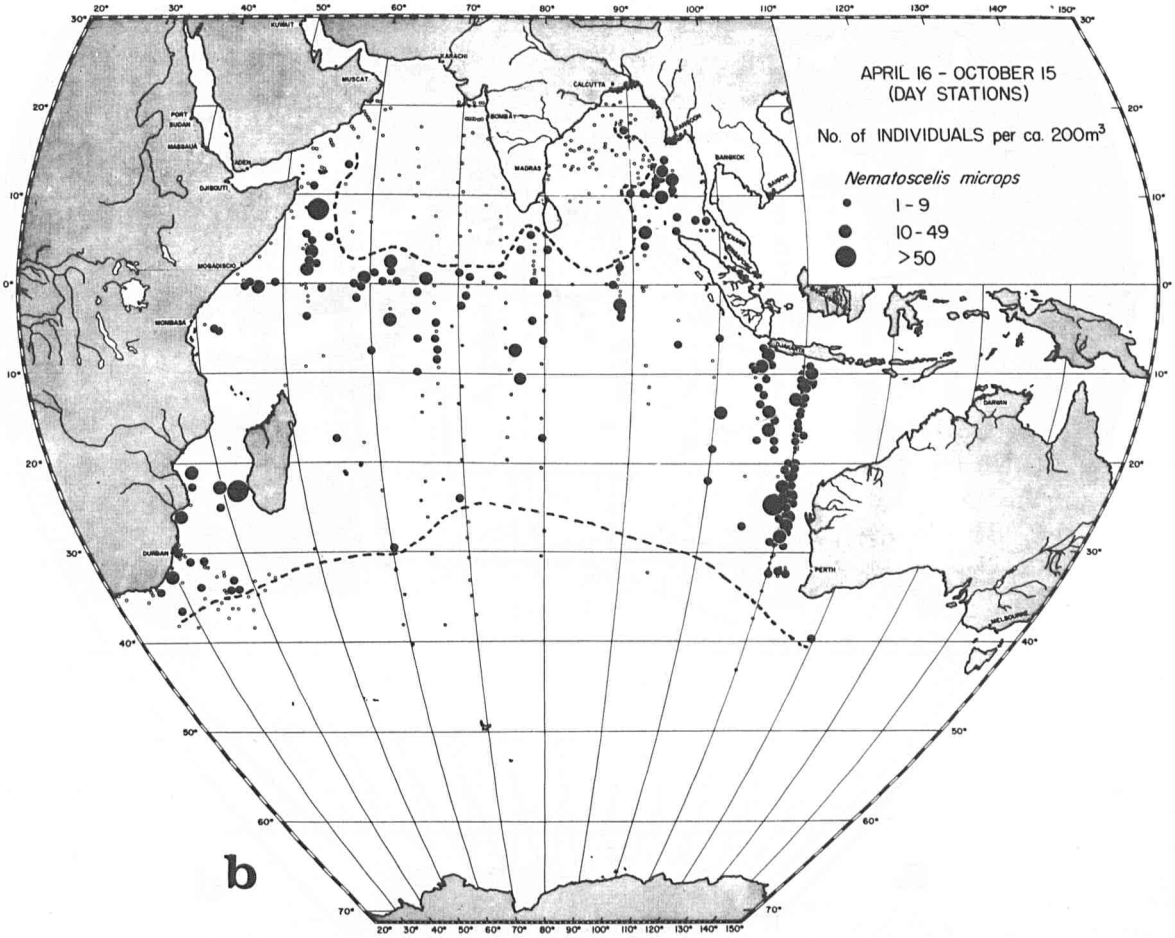


FIGURE 12.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis microps* in the Indian Ocean: b - SW Monsoon period.

TABLE 3.—Biogeographical zones of the oceanic environment and the distribution of *Nematoscelis*. *Both new and old forms. **Old forms only. ***New form expatriate adults only. ****New forms in Mozambique Current area only.

Subregions	*N. difficilis*	*N. megalops*	*N. atlantica*	*N. gracilis*	*N. microps*	*N. tenella*
Subarctic Atlantic		x				
Transitional North Atlantic		x				
Transitional North Pacific	x					
Subtropical North Atlantic		x	x		x	x
Subtropical North Pacific			x		x	x
Tropical Atlantic			x		x	x
Tropical Indo-West Pacific				x*	x	x
Eastern Tropical Pacific				x**		x
Subtropical South Atlantic			x	x***	x	x
Subtropical South Pacific			x		x	x
Subtropical South Indian			x	x****	x	x
Circumpolar Transitional Region of the Southern Hemisphere		x				

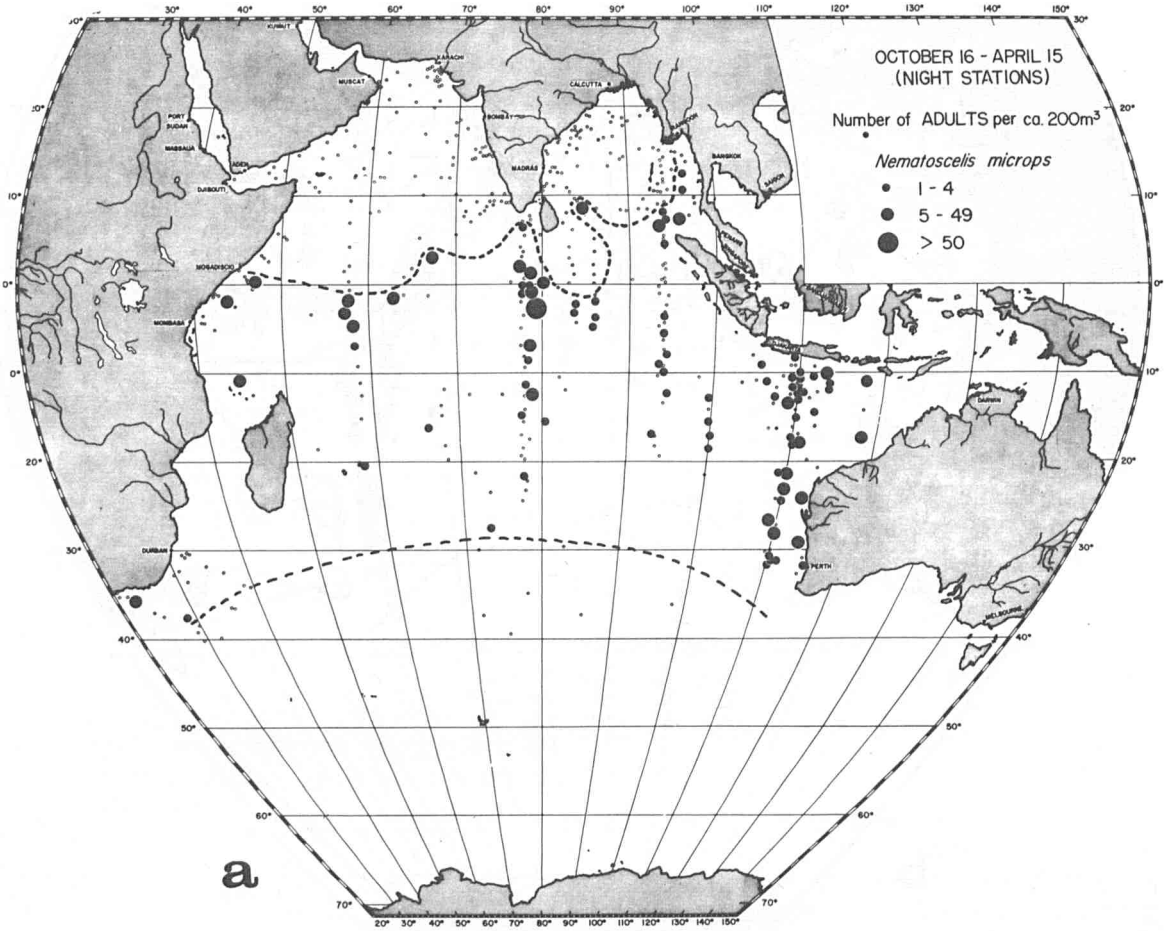


FIGURE 13.—Locality records and nighttime abundance of *Nematoscelis microps* adults in the Indian Ocean: a - NE Monsoon period.

clearly understood. However, lat. 35°-45°N, corresponding to the North Pacific transition, seems to be the extent of the region in the North Atlantic where *N. megalops* (instead of *N. difficilis*) is the most common *Nematoscelis*. *Nematoscelis atlantica, N. microps,* and *N. tenella* also appear in the transition zone of the North Atlantic but not in the corresponding zone in the North Pacific. The northeasterly North Atlantic Current carries warmwater species farther north into the transition zone or even beyond to the subarctic subregion. For example, the present survey recorded *N. atlantica* from lat. 52°N (*Atlantis II*-9, station 371). Outside of its main zone in the North Atlantic, *N. megalops* occasionally occurs in the subtropical and subarctic subregions. It is also the most common *Nematoscelis* species of the circumpolar transitional regions of the Southern Hemisphere, while *N. atlantica*, *N. microps*, and *N. tenella* also were occasionally caught there, from the Indian Ocean sector.

The eastern tropical Pacific Ocean is considered a subregion of the warmwater zone because of its characteristic hydrographical and faunal properties. *Nematoscelis gracilis* old form is part of that faunal assemblage. The Indo-West Pacific and eastern tropical Pacific subregions were considered separate from the Atlantic tropical subregion (Ekman, 1953). The distribution of *N. gracilis* and *N. atlantica* presents evidence for this. *Nematoscelis microps* and *N. tenella* are warmwater species, occupying both tropical and subtropical regions (Table 3). Many warmwater planktonic species are restricted to tropical latitudes, whereas others are found only outside of this region (examples in Bieri, 1959; Brinton, 1962; Alvariño, 1965; Baker, 1965; McGowan, 1971). In this respect *N. gracilis* is tropical and *N. atlantica*

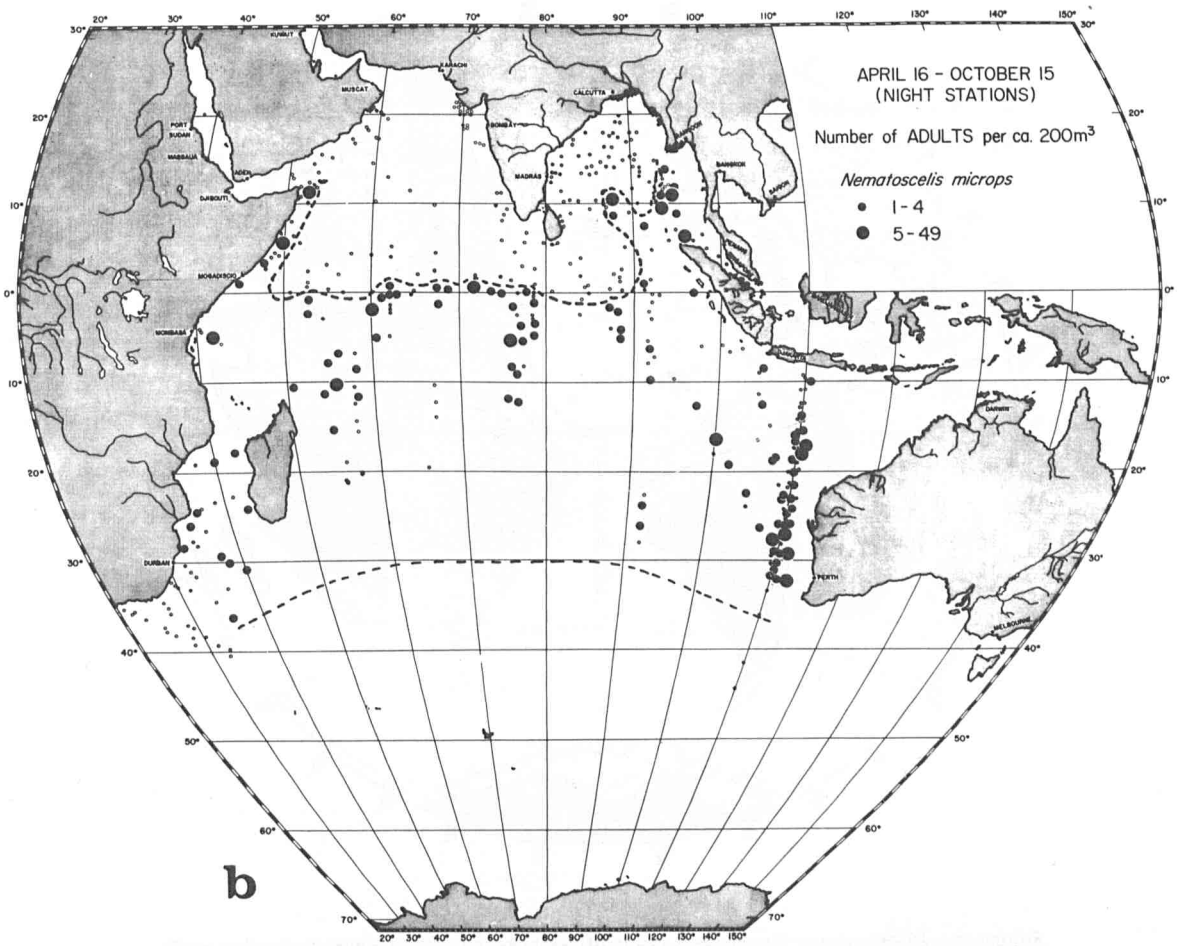


FIGURE 13.—Locality records and nighttime abundance of *Nematoscelis microps* adults in the Indian Ocean: b - SW Monsoon period.

is subtropical. Because the boundaries between the full breadth of tropical and subtropical regions are not well defined hydrographically, it is usually difficult to correlate species' distributional pattern to the hydrographical zones of these two areas.

DISCUSSION

The distributions of *Nematoscelis* species are associated with general hydrographical features in each ocean. In the Indian Ocean the seasonality in abundance of this genus is more pronounced in the Northern Hemisphere than in the south; and it is probably related to changes in monsoonal regimes. The hydrographical features of the Arabian Sea and Bay of Bengal limit the northern boundary of distribution of all species of *Nematoscelis* except *N. gracilis* old form. There appears to be a general break in the north-south midocean distribution of *N. microps* and *N. tenella* near the equatorial zone of the Indian Ocean. Their northern boundary of distribution corresponds to the approximate southern extent of oxygen-poor waters (<1 ml/l) of the Arabian Sea and the Bay of Bengal.

Wyrtki (1973) proposed a division of the Indian Ocean into three circulation systems: a seasonally changing monsoon gyre, a southern subtropical anticyclonic gyre, and the antarctic waters with the Circumpolar Current. One unique feature of the Indian Ocean is the persistence of a hydrochemical front at about lat. 10°S, separating the high-nutrient, low-oxygen content waters of the monsoon gyre from the low-nutrient, high-oxygen content waters of the subtropical gyre. The existence of such a front is very well reflected by the chemical characteristics of the subsurface water

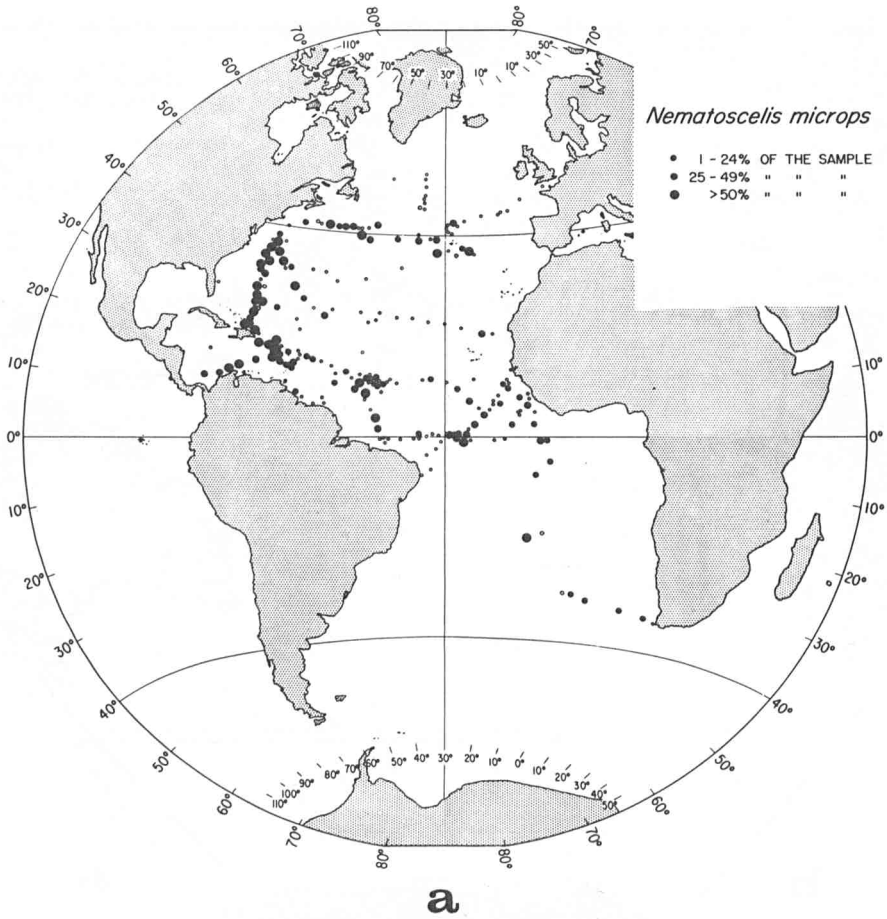
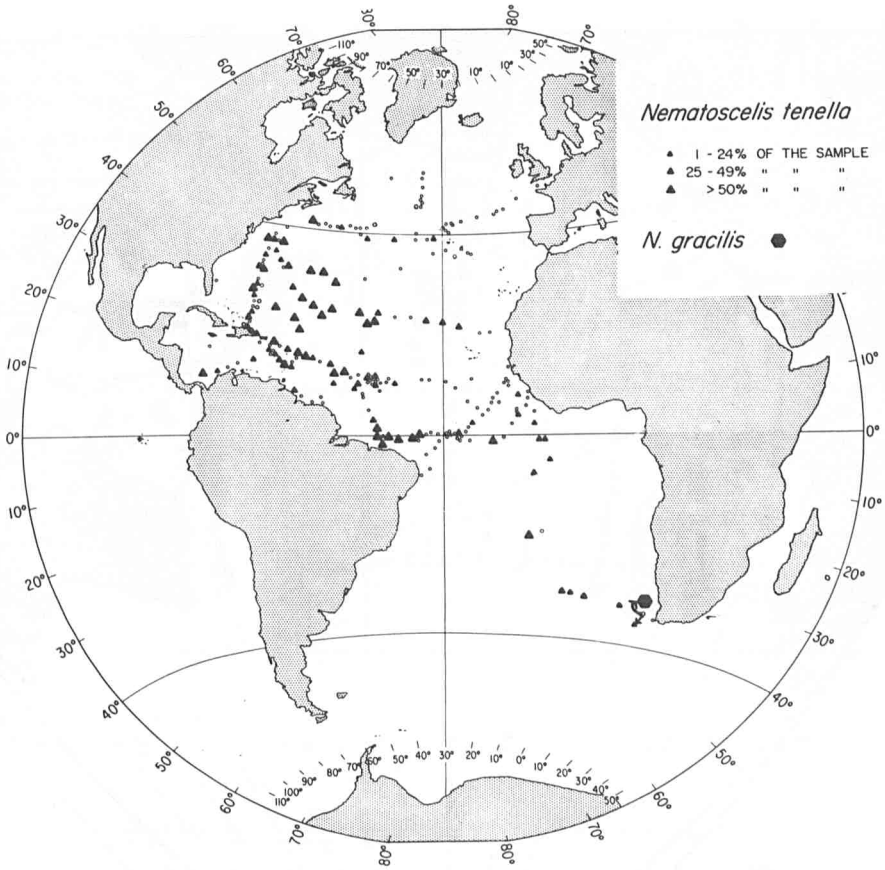


FIGURE 14.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: a - *N. microps*.

(Wyrtki, 1973). The boundaries of distribution of many zooplankton species appear to fall within this zonal band. This is also the area of the northern boundary of the subtropical species *N. atlantica*. Evidently the southern boundary of *N. gracilis* new form is not confined to this zone; since the South Equatorial Current carries it as far south as lat. 20°S. The subtropical convergence located at about lat. 40°-41°S separates the southern subtropical anticyclonic gyre and the antarctic circumpolar water. This is the region of the southern boundary of distribution of both the subtropical species *N. atlantica* and the warmwater species *N. microps* and *N. tenella*.

Brinton and Gopalakrishnan (1973) recognized different euphausiid faunal assemblages in the Indian Ocean, each of which is bounded mainly around lat. 10°N, 0°, 10°S, 25°-30°S. Latitude 10°N delimits the northern distribution of not only *N. microps* and *N. tenella* but also other euphausiid species such as *Euphausia tenera, Thysanopoda monacantha, T. tricuspidata, Nematobrachion flexipes, Stylocheiron abbreviatum,* and *S. longicorne* (Brinton and Gopalakrishnan, 1973). Therefore, the Arabian Sea and Bay of Bengal north of lat. 10°N contains large numbers of only *N. gracilis* old form along with *Stylocheiron indicum, S. carinatum, S. affine, Pseudeuphausia latifrons, Euphausia diomediae,* and *E. distinguenda*. In both the Arabian Sea and the Bay of Bengal a low level of oxygen (as low as 0.1 ml/l) persists year-round in the upper oxygen minimum layer (Wyrtki, 1971). However, temperature and salinity vary seasonally in these areas. The surface salinity ranges are 30-33‰ for the Bay of Bengal and 34-37‰ for the Arabian Sea. Biologi-



b

FIGURE 14.—Distribution of *Nematoscelis* in the Atlantic Ocean based on plankton samples: b - *N. tenella* and *N. gracilis*.

cal and oceanographical differences between these two parts of the Indian Ocean were discussed by Panikkar and Jayaraman (1966). Throughout the year *N. gracilis* old form maintains spawning populations in these two areas.

Nematoscelis gracilis new and old forms, *N. microps*, and *N. tenella* are part of the faunistic assemblage between lat. 0° and 10°S. The occurrence of *N. gracilis* new form in the mid-Pacific agrees with the distribution of *Euphausia pseudogibba* and *Thysanopoda subaequalis* in the zone lat. 10°-20°S (cf. Brinton, 1962:212). South of lat. 25°-30°S, *N. gracilis* is replaced by *N. atlantica*. Other species of this zone are *Euphausia brevis*, *E. mutica*, *Stylocheiron suhmii*, and *Thysanopoda subaequalis*. In the Indian Ocean all of these central species, including *N. atlantica*, occur only in the Southern Hemisphere.

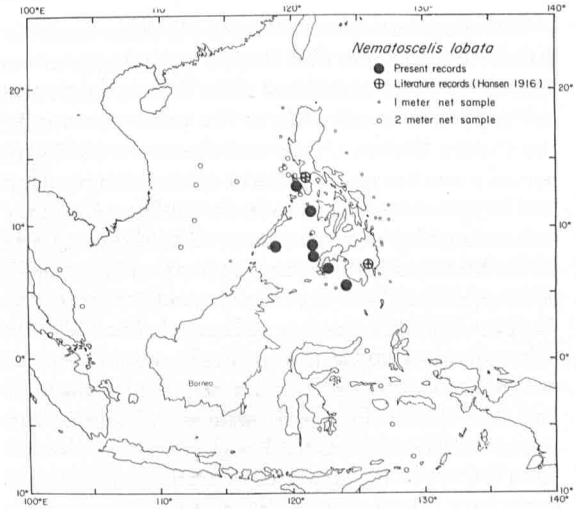


FIGURE 15.—All known records of *Nematoscelis lobata*.

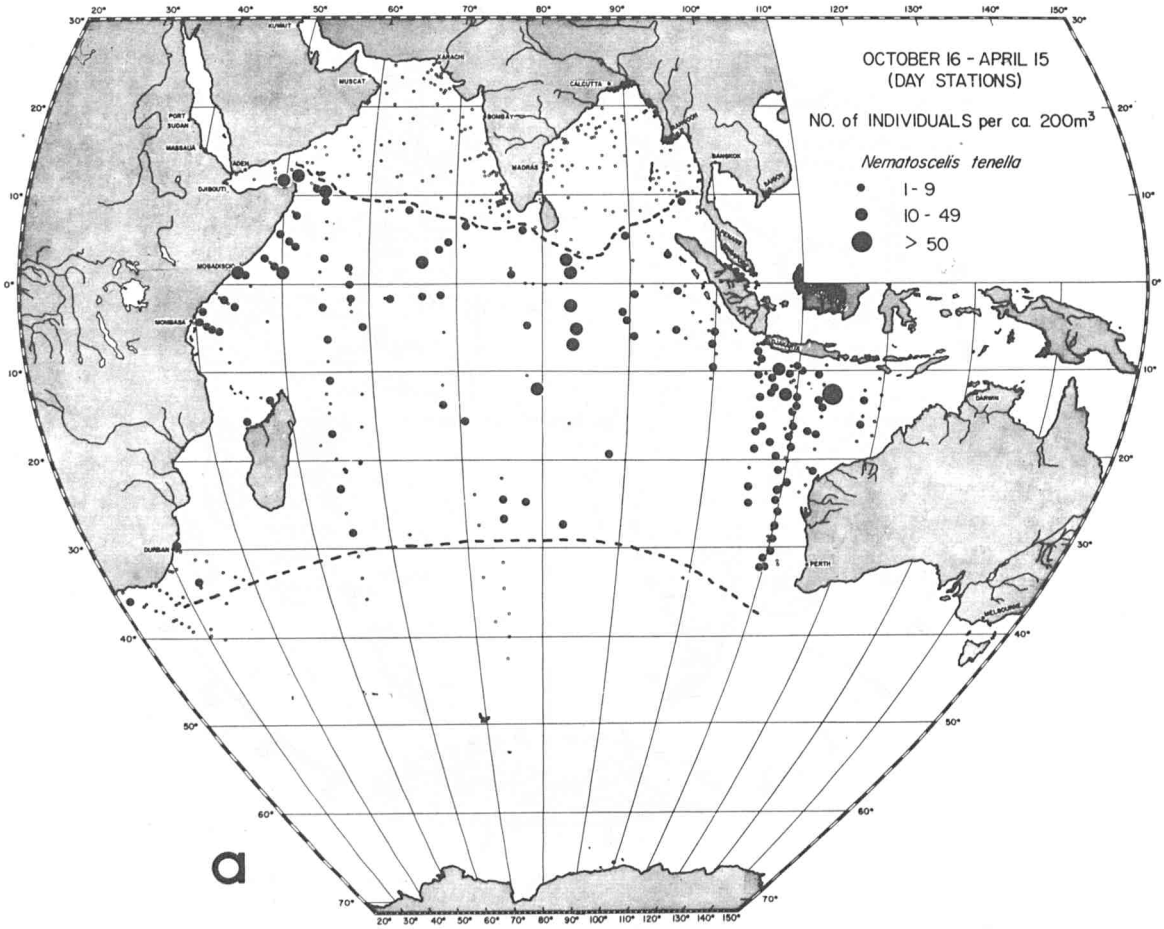


FIGURE 16.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis tenella* in the Indian Ocean: a - NE Monsoon period.

The distributions of *N. gracilis* new and old forms in the Indian and Pacific oceans appear respectively to be associated with areas of high and low oxygen concentration in the water column. In the Indian Ocean, Gibbs and Hurwitz (1967) reported a similar association of species distribution and oxygen concentration in the water column for two mesopelagic fish species, *Chauliodus pammelas* and *C. sloani*. Like *N. gracilis* old form, *C. pammelas* is only in the oxygen-poor waters of the Arabian Sea and the Bay of Bengal. The old form is largely confined to the tropical areas where the oxygen concentration in the upper minimum is less than 2 ml/l (Figure 3); whereas the new form occurs in those equatorial regions where the oxygen values in the upper minimum layer is never less than 1 ml/l. Since the adults have to pass through the oxygen minimum layer during their diurnal migrations, the old forms might have attained physiological adaptations to the lower oxygen levels. It has been documented experimently (Teal and Carey, 1967) that *Euphausia mucronata*, one of the common residents in the oxygen-poor waters of the Peru-Chile Current, can withstand the stress of oxygen pressure as low as that in the oxygen minimum layer.

Low oxygen values in the upper minimum layer of the tropical Indian and Pacific oceans reflect the presumed high productivity of the surface layers (Vinogradov and Voronina, 1961; Longhurst, 1967). Old forms occur in these areas of high zooplankton abundance, particularly in the eastern tropical Pacific, Arabian Sea, and Bay of Bengal. Reid (1962) plotted the distribution of zooplankton abundance in the Pacific. In the area of the North Equatorial Current the zooplankton biomass is

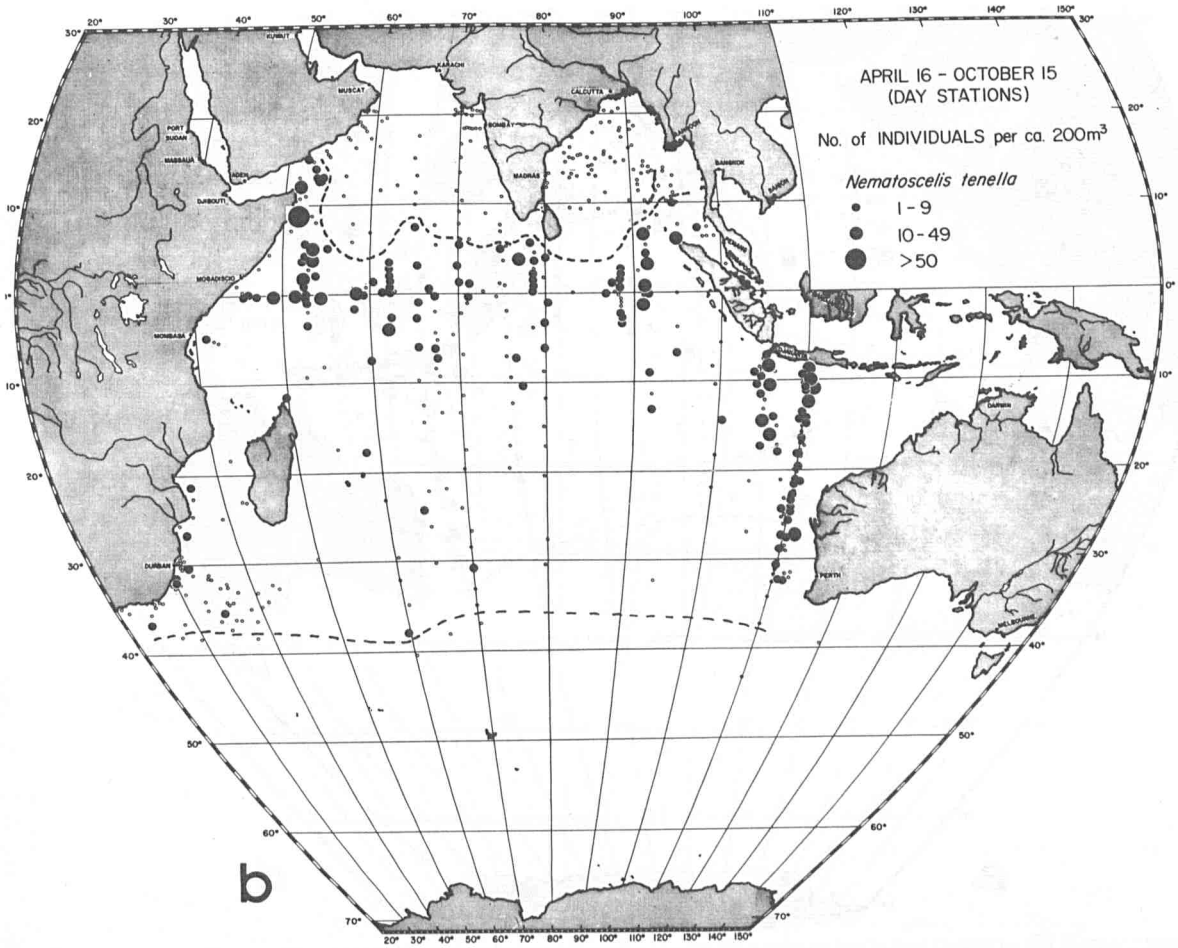


FIGURE 16.—Locality records and daytime abundance of larvae and juveniles of *Nematoscelis tenella* in the Indian Ocean: b - SW Monsoon period.

much higher than in the area of the South Equatorial Current. Correspondingly, *N. gracilis* old forms are distributed in the northern part of the equatorial current systems and new forms to the south in less rich waters. The same relationship exists in the Indian Ocean [cf. the International Indian Ocean Expedition Plankton Atlas. Indian Ocean Biological Centre (1968)].

Each form of *N. gracilis* is considered to be an ecophenotype. Mayr (1971) recognized ecophenotype as a nongenetic modification of the phenotype in response to an environmental condition. However, the observed morphological differences, associated with reproductive structures, suggest the possibility of genetic divergence of the two demes. The intergradation (intermediate forms) along the overlapping zones suggest incomplete genetic isolation.

Nematoscelis gracilis old forms in the northern part of the Indian Ocean differ from those of the eastern tropical Pacific in that the Indian Ocean forms are smaller in size. The degree of similarity of these two populations is expressed quantitatively in a separate paper.

Brinton (1962) pointed out that most of the inter-ocean waterways in the Indo-Australian Archipelago, (e.g., the Strait of Malacca, Sunda Strait, and Torres Strait) are too shallow (<100 m) to allow interoceanic transport of the oceanic euphausiid species. The deep pathway is through the straits of Molucca and Halmahera, and the Banda and Timor seas. Even central species like *Euphausia mutica* are found along this route. *Nematoscelis gracilis* new and old forms, *N. microps*, and *N. tenella* show similar communication between Pacific and Indian Ocean populations.

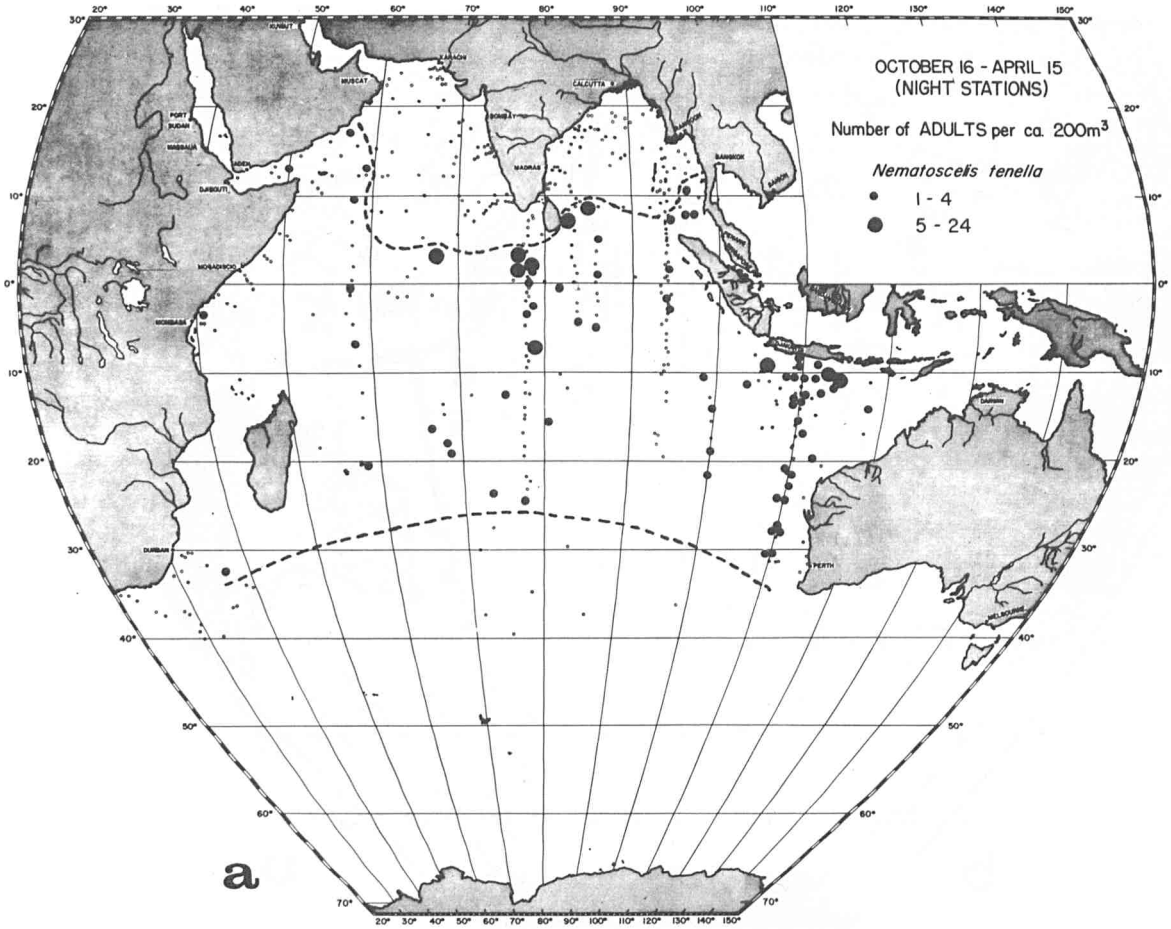


FIGURE 17.—Locality records and nighttime abundance of *Nematoscelis tenella* adults in the Indian Ocean: a - NE Monsoon period.

However, the absence of *N. atlantica* from the region of the Indo-Australian Archipelago suggests the lack of inter-ocean communication of this species. Moreover, *N. lobata,* which is morphologically most similar to *N. atlantica,* is endemic to a part of this region, mainly the Sulu and Celebes seas. These basins are connected with the open ocean by relatively shallow channels. This region is well known for its endemic species. Gilbert and Hubbs (1920) pointed out that the peculiar characteristics of the isolated basin of the Sulu Sea might have caused the evolution of many fish species. Because of morphological similarities and non-overlapping distribution (geographical isolation), *N. lobata* and *N. atlantica* may have derived from the same stock.

The North Pacific central population of *N. atlantica* is also isolated from its southern counterpart. However, it is not known whether the disjuncts are genetically different. Analyses performed by both numerical and conventional ways indicate no morphological differences.

Another region of importance in considering gene flow between Indian and Pacific populations is the South Australian Basin and the Tasman Sea. The Bass Strait between Australia and Tasmania is probably too shallow to allow passage of adult oceanic euphausiids. However, larvae and juveniles may be transported across this passage. The only route for adults is south of Tasmania, but this is almost certainly too far south for the tropical-subtropical species including *N. tenella, N. microps,* and *N. atlantica.* Evidence from south of Australia (Monsoon Expedition, long. 120°E-175°W) indicates that populations of *N. megalops* are in communication between the South Pacific and Indian oceans. The Pacific population evidently does not mix with the South At-

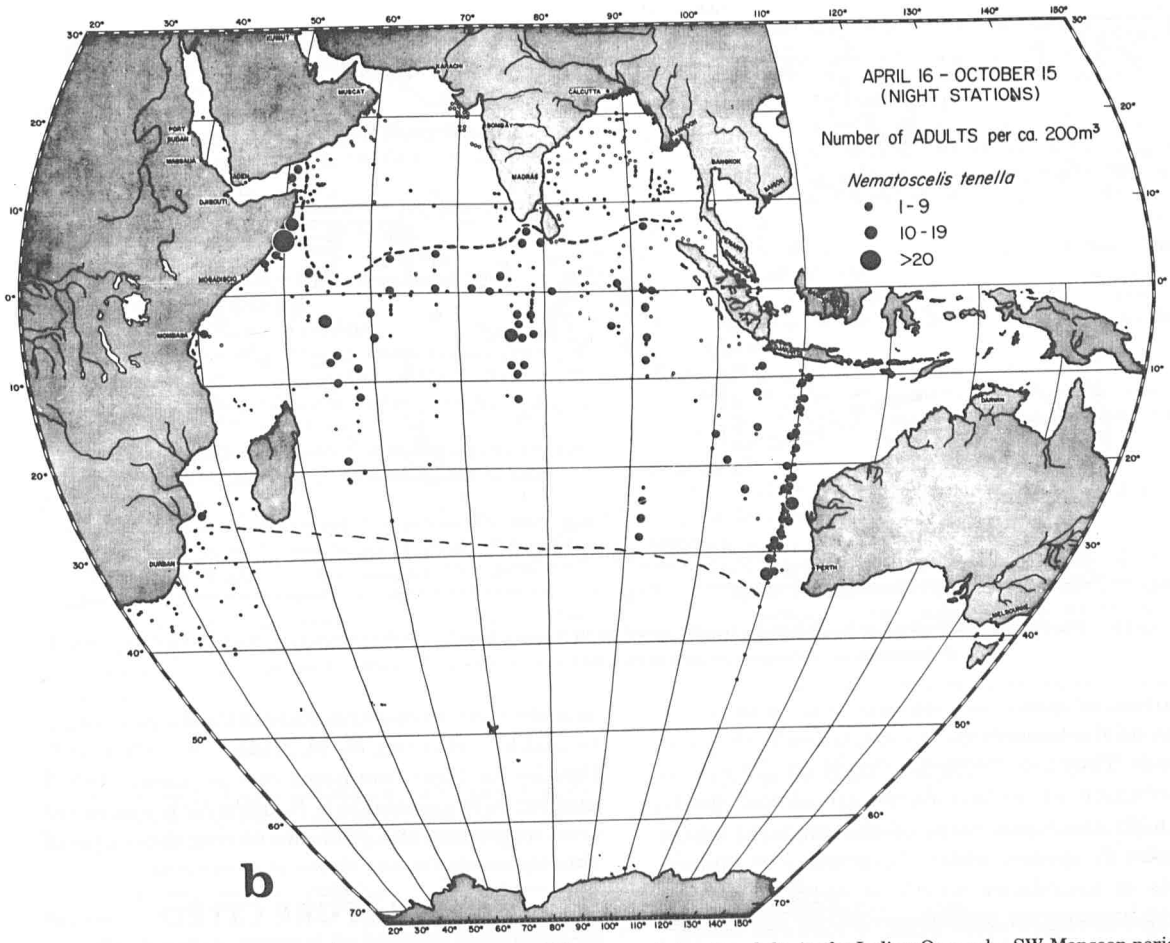


FIGURE 17.—Locality records and nighttime abundance of *Nematoscelis tenella* adults in the Indian Ocean: b - SW Monsoon period.

lantic counterpart at the Drake Passage (Antezana, manuscript). The morphological differences between *N. megalops* and *N. difficilis* already reflect presumed genetic differences.

Atlantic populations of *N. atlantica*, *N. microps*, and *N. tenella* are not in direct communication with their respective counterparts in the Pacific, but the North and South Atlantic populations are in communication at the Equator. It appears that the Atlantic and Indian Ocean populations of these species are in at least seasonal communication around the tip of South Africa.

A further aspect of the zoogeography of *Nematoscelis* in the Atlantic lies in the fact that *N. atlantica*, not *N. gracilis*, occupies the equatorial belt, permitting north-south continuity of the species. Atlantic expatriates of *N. gracilis* new form are found only off southwest Africa, probably transported by the Mozambique Current. The cool Benguela Current region may then limit northern transport of this tropical form, or the low oxygen (0.5 ml/l) in the minimum layer of the current, lat. 10°S and 15°S (Bubnov, 1966), might be a barrier to the new forms as it appears to be in the northern Indian Ocean.

There are similarities between distributions of species of *Nematoscelis* and those of other zooplankters. For example, the distribution of *N. megalops* is like that of a copepod, *Clausocalanus ingens* (Frost, 1969) and *Thysanoessa gregaria* (Brinton, 1962); horizontal boundaries of *N. microps* and *N. tenella* are like those of other tropical-subtropical species, *C. mastigophorus* and *Stylocheiron carinatum*. It is likely that both biological (species interaction) and physical [water mass, Sverdrup et al. (1942)] reasons are responsible for the numerous similarities.

McGowan (1971) classified the patterns of dis-

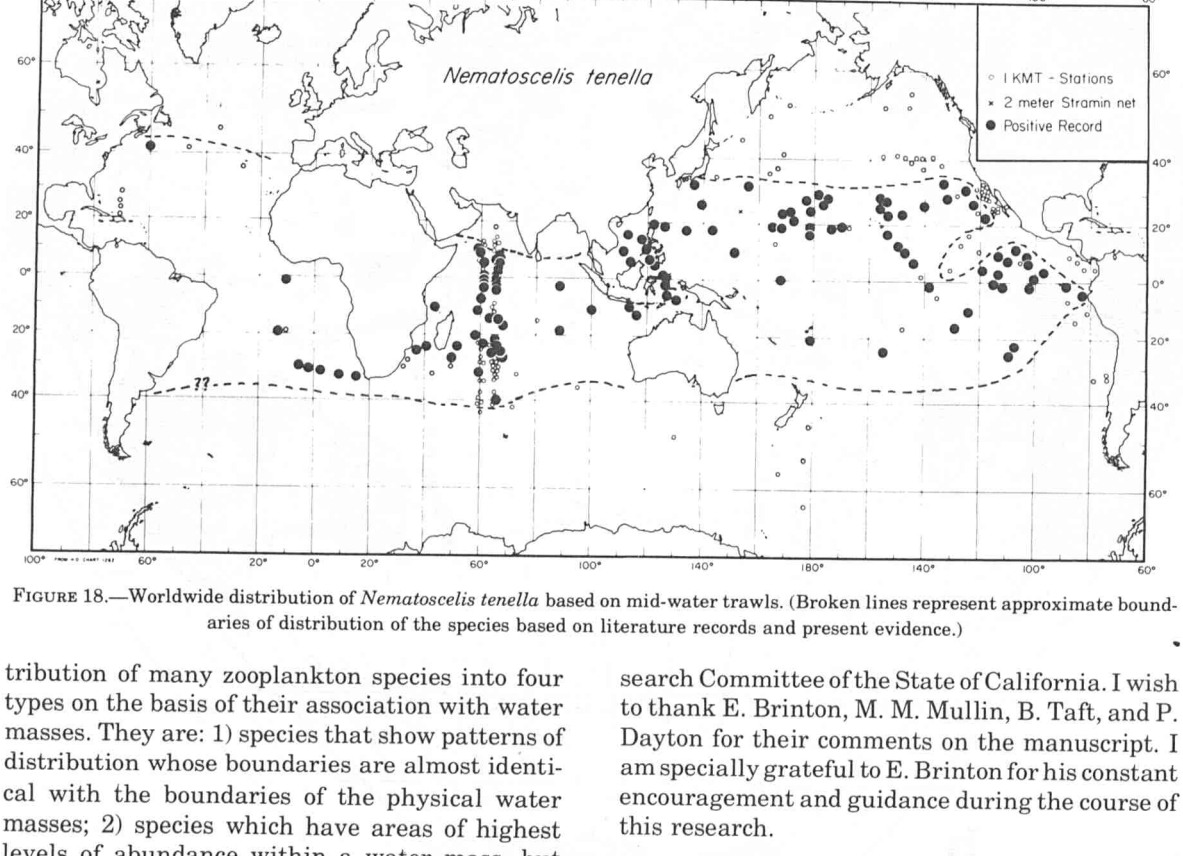


FIGURE 18.—Worldwide distribution of *Nematoscelis tenella* based on mid-water trawls. (Broken lines represent approximate boundaries of distribution of the species based on literature records and present evidence.)

tribution of many zooplankton species into four types on the basis of their association with water masses. They are: 1) species that show patterns of distribution whose boundaries are almost identical with the boundaries of the physical water masses; 2) species which have areas of highest levels of abundance within a water mass, but whose boundaries extend somewhat beyond the boundary of the water mass; 3) species that have distributions throughout several water masses; and 4) species having limited distributions in parts of some water masses. *Nematoscelis gracilis* and *N. atlantica* fall in the first category, *N. megalops* in the second, and *N. tenella* and *N. microps* in the third. *Nematoscelis difficilis* is restricted to the North Pacific transition zone whereas *N. megalops* is distributed in the central, transitional, and subarctic water masses of the Atlantic and in the southern transitional zones of the Indian and Pacific oceans.

ACKNOWLEDGMENTS

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VARIATION OF THE SURFACE GEOSTROPHIC FLOW IN THE EASTERN INTERTROPICAL PACIFIC OCEAN

MIZUKI TSUCHIYA[1]

ABSTRACT

A sequence of seven maps is presented to show the distribution of geopotential anomaly at the sea surface in the eastern intertropical Pacific Ocean. Each map represents a 2-mo period during the EASTROPAC expedition from February 1967 to April 1968.

The most striking feature revealed by these maps is the variation of the North Equatorial Countercurrent in response to the annual variation of the atmospheric circulation. In February-April (both 1967 and 1968), when the atmospheric intertropical convergence zone (ITCZ) lay near its southernmost position at lat. 2°-6°N, the Countercurrent was discontinuous and was rapidly changing in intensity. In August-September, when the ITCZ lay near its northernmost position at lat. 11°-15°N, the Countercurrent was strong, broad, and extended east all the way to the coast of Costa Rica.

In southern summer a weak and narrow eastward current was indicated along about lat. 10°S between long. 112° and 90°W within the westward flow of the South Equatorial Current. This current is so weak that it is probably buried in the westward Ekman drift due to the southeast trades and can be observed only when the trade winds are unusually weak.

An eastward current, which can be interpreted as the Equatorial Undercurrent breaking the sea surface, was indicated within about 2° of the equator in April-May, when the southeast trades were relatively weak near the equator.

The distributions of relative geostrophic flow in February-March 1967 and February-April 1968 were remarkably similar over the entire study area.

The purpose of this paper is to present a sequence of seven maps (Figures 1-7) showing the distribution of geopotential anomaly at the sea surface of the eastern intertropical Pacific Ocean from February 1967 to April 1968 and to discuss the variations of the circulation revealed by these maps. Each map represents a 2-mo period during the EASTROPAC expedition, which was an international cooperative oceanographic investigation coordinated by the Bureau of Commercial Fisheries (now National Marine Fisheries Service).

Prior to EASTROPAC a considerable number of expeditions took place in the eastern intertropical Pacific Ocean; consequently, its principal oceanographic features were reasonably well known (e.g., Wooster and Cromwell, 1958; Bennett, 1963; Wyrtki, 1966, 1967; Tsuchiya, 1968; Stroup, 1969). However, the accumulated data were too sparse in time and space to give insight into monthly or seasonal variations in the distribution of oceanographic properties. The EASTROPAC expedition was designed to acquire data to bring to light these time variations.

The expedition was divided into seven 2-mo cruise periods. During each period, a single-ship or multiship cruise was carried out. Multiship cruises took place in February-March, August-September 1967, and February-April 1968. These cruises covered the area between lat. 20°N and 20°S (15°S in August-September 1967) and from the coast of the American continents westward to long. 119°W (126°W in February-March 1967). Single-ship cruises took place in April-May, June-July, October-November 1967, and December 1967-January 1968 in time intervals between the multiship cruise periods. Each of these cruises covered the area between lat. 20°N and 3°S and between long. 98° and 119°W.

Details of the observational program, the list of participating vessels, and track charts have been published in the EASTROPAC atlas (Love, 1972a).

DATA

Almost all EASTROPAC stations with observations to 500 m or deeper were used in this study. These stations are listed in Table 1 and can be identified on the track charts included in the EASTROPAC atlas (Love, 1972a).

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TABLE 1.—List of stations used in Figures 1-7.

Ship and cruise	Stations	Dates	Number of stations used	Data type[1]	Figure number
Argo 11	2, 25-328	25 Jan.-2 Mar. 1967	152	a	Fig. 1
Jordan 12	2-284	12 Feb.-21 Mar. 1967	129	a	
Rockaway 13	1-265, 318-342	1 Feb.-20 Mar. 1967	129	b	
Alaminos 14	1-101, 110-159, 194-267, 301, 309, 332, 333, 340-342	31 Jan.-3 Apr. 1967	143	a, b	
			Total 553		
Jordan 20	5-264	13 Apr.-24 May 1967	129	a	Fig. 2
Jordan 30	8-264	17 June-27 July 1967	149	a, c	Fig. 3
Washington 45	7-206, 282-387	6 Aug.-15 Sept. 1967	177	a	Fig. 4
Undaunted 46	2-189	16 Aug.-22 Sept. 1967	141	a	
Rockaway 47	1-40, 49-113, 124-258, 268-382, 402-527	1 Aug.-23 Sept. 1967	212	b	
			Total 530		
Jordan 50	5-249	20 Oct.-26 Nov. 1967	126	a	Fig. 5
Jordan 60	2-289	21 Dec. 1967-28 Jan. 1968	166	a	Fig. 6
Washington 75	1-144, 187-258	18 Feb.-8 Apr. 1968	160	a	Fig. 7
Jordan 76	1-255	21 Feb.-30 Mar. 1968	131	a	
Rockaway 77	6-103, 113-278, 302-438, 475-571	30 Jan.-18 Apr. 1968	263	b	
			Total 554		

[1]a: STD digital data logger; b: STD analogue charts; c: Nansen-bottle casts.

Temperature and salinity data used for computing geopotential anomaly were collected with in situ salinity-temperature-depth recorders (STD) except for those from EASTROPAC cruise *David Starr Jordan* 30, on which a breakdown of the STD necessitated the use of Nansen bottles during the last half of the cruise. Most of the STD data were obtained from digital data loggers, but some were digitized from analogue charts (Table 1). The method of processing STD data is described in the EASTROPAC atlas (Love, 1972a).

From these temperature and salinity data, geopotential anomaly at the sea surface was computed with reference to 500 db. Because of relatively homogeneous water at depths greater than 500 m in the intertropical ocean, this reference is believed to be adequately deep for estimating the geostrophic current at the sea surface. The unit of geopotential anomaly is chosen to be joule per kilogram (abbreviated J/kg; equivalent to dynamic decimeter).

Computed geopotential anomaly was plotted on each map, and smooth isopleths were drawn at intervals of 1.0 or 0.5 J/kg. The base map is a Mercator projection and was adapted from U.S. Navy H. O. 526 and 823.

THE SURFACE GEOSTROPHIC FLOW

The surface geostrophic flow revealed by the maps of geopotential anomaly is described below. A comparison of these maps with other maps based on long-term averages of set and drift of ships is also made. The atlas of the monthly average surface currents in the eastern North Pacific published by the U.S. Navy Hydrographic Office (H. O. 570, 1947) and the atlas of the quarterly average surface currents in the South Pacific published by the Meteorological Office (M. O. 435, 1939) are pertinent to the comparison. There are also monthly drift charts by Cromwell and Bennett (1959) for the northern hemisphere and those by Puls (1895) and Wyrtki (1965) for both hemispheres. The charts by Cromwell and Bennett are simply a different presentation of the H. O. 570 charts for the area east of long. 120°W and south of lat. 30°N. Puls' charts show the current direction and relative intensity for the area between lat. 20°N and 10°S. Wyrtki's charts are based on averages over 1-degree squares, but it is not clear how he smoothed or interpolated the original 1-degree averages to obtain the current patterns shown on his charts.

Various sources of errors and disparities in the geostrophic calculation and set-and-drift observations should be kept in mind. Geopotential anomaly computed from oceanographic data may include short-period density fluctuations that are not necessarily associated with fluctuations of the actual current. The calculation of geostrophic flow neglects the direct frictional effect of wind stress.

On the other hand, set-and-drift observations are affected by strong winds, sea, swell, and tidal currents.

South Equatorial Current Region

The South Equatorial Current is well defined west of long. 90°W on the maps for February-March 1967, August-September 1967, and February-April 1968 (Figures 1, 4, and 7). South of lat. 10°S the direction of geostrophic flow is predominantly to the northwest, whereas the drift charts (Meteorological Office, 1939; Wyrtki, 1965) for the corresponding months indicate that the surface current flows almost due west in this region. This disagreement may be due to the effect of the Ekman drift. The trade winds in this area are from the southeast to east, so that if the Ekman drift is added to the geostrophic flow, the resultant surface current would be nearly to the west.

North of lat. 10°S the South Equatorial Current becomes more zonal and flows almost due west. In February-March 1967 (Figure 1) the westward flow of the South Equatorial Current extends across the equator to about lat. 5°N, and the current near the equator west of the Galápagos Islands is also westward. In April-May 1967 (Figure 2) the westward flow of the South Equatorial Current is interrupted by an eastward current within about 2° of the equator. Puls' (1895) charts of the surface current for March and April clearly show an eastward current at the equator between long. 110°W and the Galápagos Islands. Such an eastward current can be interpreted as the Equatorial Undercurrent breaking the sea surface during local weakening of the easterly trades (Cromwell, Montgomery, and Stroup, 1954; Montgomery, 1962; Montgomery and Stroup, 1962:59-60). Jones (1969) has presented evidence of a surfacing of the Undercurrent on the basis of direct current measurements made at long. 98°W in April 1968 (EASTROPAC cruise *Thomas Washington* 75). The distribution of geopotential anomaly from this cruise, however, does not suggest a surfacing of the Undercurrent (Figure 7).

On the other maps (Figures 3-7) flow is westward from the equator to about lat. 5°N, and in some longitudes an eastward current is revealed just south of the equator, because geopotential anomaly does not show a minimum at the equator but a few degrees of latitude south of the equator. The same distribution of geopotential anomaly can be seen on Bennett's (1963, Figure 6) map based on EASTROPIC data. This distribution is associated with a thermocline ridge that tends to occur at lat. 1°-3°S (instead of the equator) in the eastern Pacific. This southward displacement of the ridge from the equator is clearly evident on many of EASTROPAC vertical sections of temperature or thermosteric anomaly and maps of the topography of the 300-cl/t isanosteric surface, which lies close to the center of the thermocline (Love, 1971, 1972b, 1973, in press). According to Cromwell's (1953) simple model of the wind-driven meridional circulation, the direction of the wind near the equator determines the position of the maximum divergence of the Ekman transport in the surface layer. He points out that the meridional component of the southeast trades shifts the maximum divergence, which would correspond to a ridge of the thermocline, to the south of the equator.

The eastward geostrophic flow between the equator and the ridge was first discussed by Austin (1960) and later commented upon by Stroup (1969:35). It is not certain, however, that the actual surface current is eastward south of the equator. Estimates of the magnitudes of terms in the equation of motion suggest that the southward pressure gradient is in approximate balance with the northward component of wind stress. The M. O. 435 drift chart for the May-July quarter shows very weak easterly components just south of the equator at long. 100°-110°W between strong westward currents to the north and south. The drift charts for the other quarters show no evidence of an eastward current south of the equator.

The southern-summer maps (Figures 1 and 7) exhibit a weak eastward current along about lat. 10°S from long. 112°W to about 90°W. Examination of vertical sections of temperature and maps of surface temperature in the EASTROPAC atlas (Love, 1972a, in press) indicates that this current is associated with a slight southward shoaling of a shallow summer thermocline and with a meridional temperature gradient developed during summer between a pool of warm surface water south of the equator and cold surface water farther south that appears to be coming from the Chile Current (Wooster, 1970). This suggests that the eastward geostrophic current along lat. 10°S is found only in southern summer. (It is interesting to note that the North Equatorial Countercurrent, which flows east at roughly the same latitude in the northern hemisphere, is most strongly developed during the same season, i.e., northern

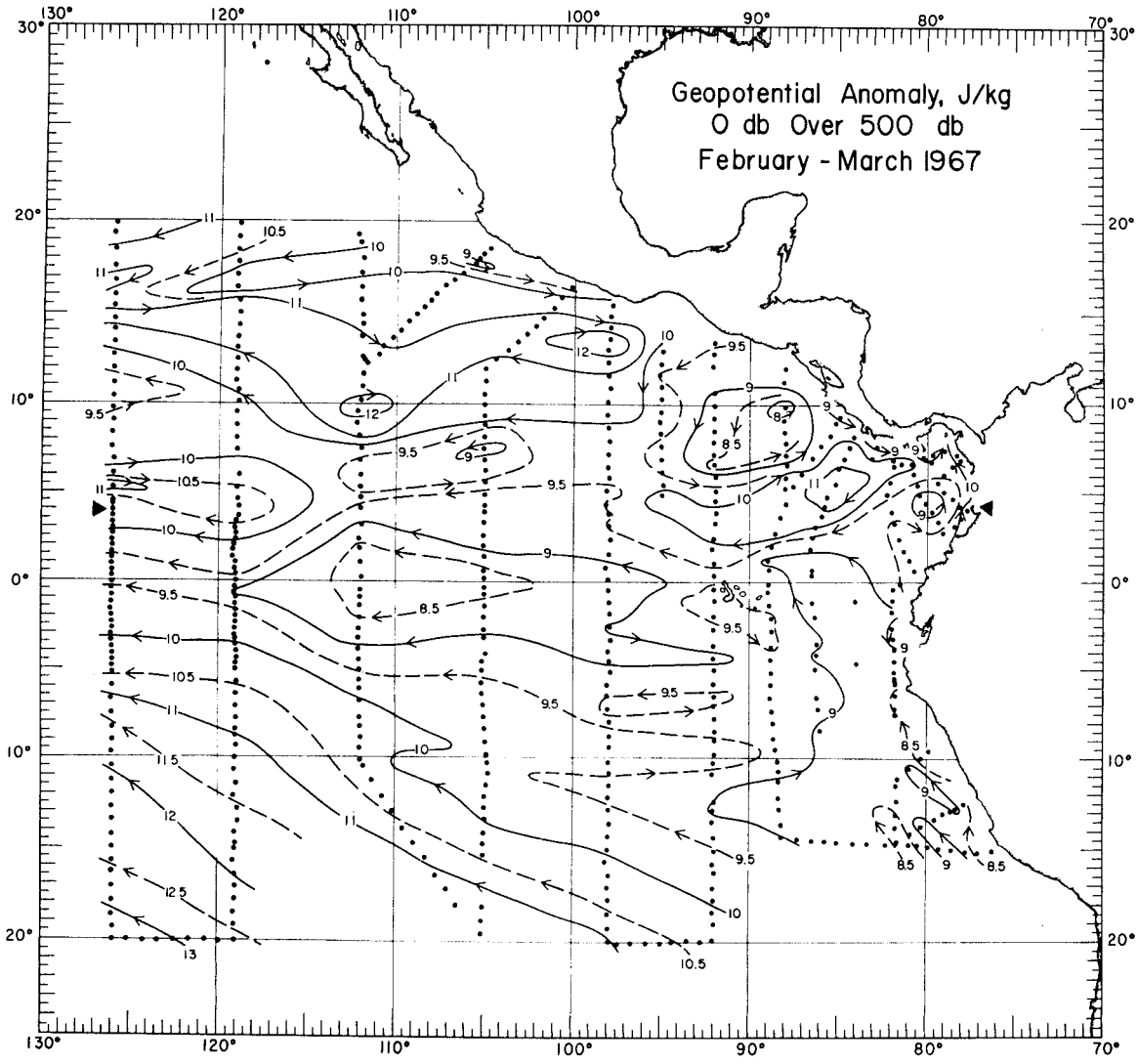

FIGURE 1.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in February-March 1967. EASTROPAC cruises *Argo* 11, *David Starr Jordan* 12, *Rockaway* 13, and *Alaminos* 14. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

summer.) However, the coverage of the southern-winter map (Figure 4) is limited to lat. 10°S, and this suggestion cannot be confirmed by winter data. None of the drift charts examined shows an eastward current near this latitude in the eastern South Pacific, but their data are too sparse to draw a definite conclusion. Because of its low speed, the countercurrent, indicated by the distribution of geopotential anomaly (Figures 1 and 7), may well be buried in the westward Ekman drift due to the prevailing southeasterly trades and may be observed only when the trade winds are unusually weak.

Peru Current

In the region south of the equator and between long. 90°W and the coast of South America, the distribution of geopotential anomaly is irregular, and its spatial variation is not large (Figures 1, 4, and 7). This distribution suggests a dominance of weak and broad flow with small-scale irregularities such as eddies and countercurrents (Wooster and Reid, 1963; Wyrtki, 1963). Partly because of this fact and partly because of a rather inadequate orientation of ship tracks in this area, contouring is difficult; there are many other ways

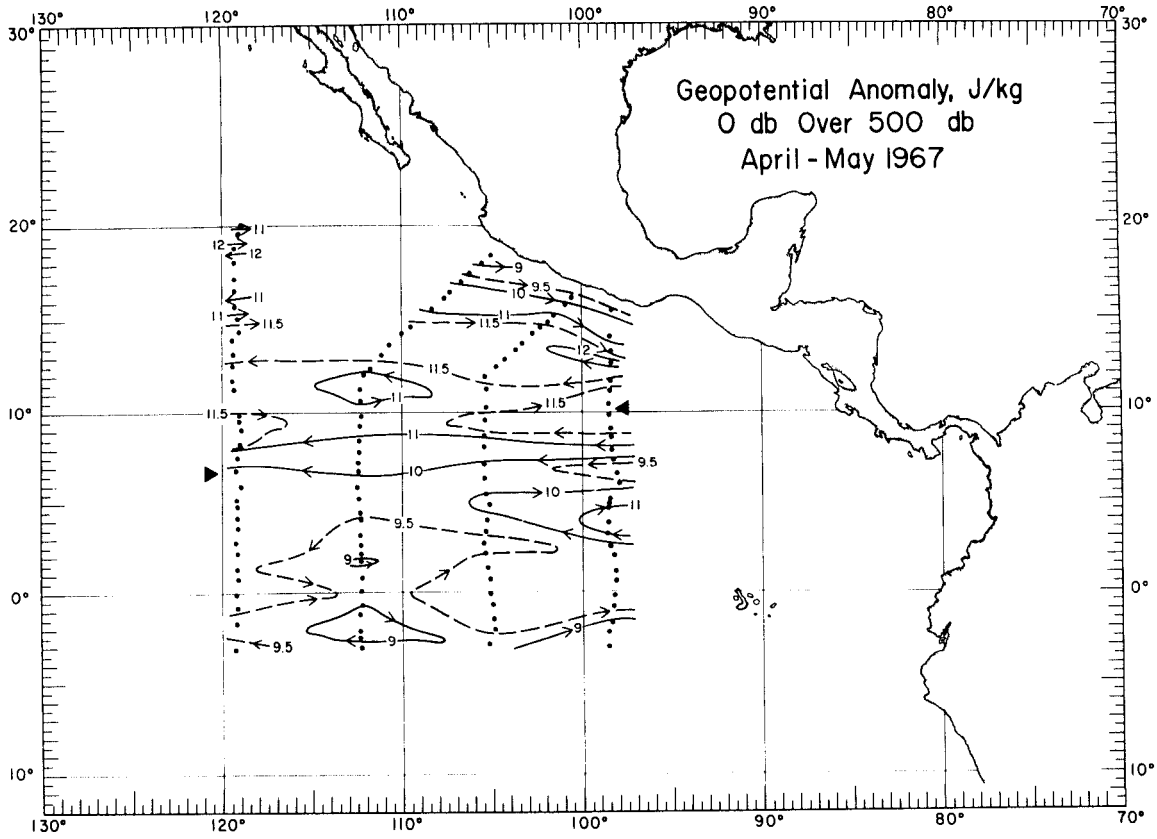

FIGURE 2.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in April-May 1967. EASTROPAC cruise, *David Starr Jordan* 20. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

to draw isopleths. Consequently, the deduced geostrophic-flow pattern is not everywhere reliable. Nevertheless, the general trend of flow indicated by the present maps is parallel to the coast and toward the equator. There is not much change in general flow patterns during the EASTROPAC period.

Eastern Boundary Currents in the Northern Hemisphere

In this region flow also tends to follow the coastline. On the map for February-March 1967 (Figure 1), there is an indication of a northward current, the Colombia Current (Wooster, 1959; Stevenson, 1970), flowing close to the coast of Colombia toward the Gulf of Panama. On the maps for August-September 1967 and February-April 1968 (Figures 4 and 7) the distribution of stations is inadequate for defining the Colombia Current.

Off Costa Rica the direction of flow varies, depending on the development of an anticyclonic eddy farther offshore. The strong southeastward flow indicated by the map for February-March 1967 (Figure 1) is associated with the northern edge of an anticyclonic eddy centered at lat. 5°N, long. 85°W. A similar anticyclonic eddy is observed in February-April 1968 (Figure 7), but is centered at lat. 5°N, long. 88°W, farther west than in 1967; and the flow near the coast of Costa Rica is northwestward. As Puls (1895:24 and 27), Cromwell (1958), and Wyrtki (1965) have noted, their drift charts also show a well-developed anticyclonic eddy in this area from February to March. This anticyclonic eddy seems to be a normal feature in these months. In August-September (Figure 4), when no such anticyclonic eddy develops, the area off the coast of Costa Rica is dominated by the northwestward return flow of the North Equatorial Countercurrent.

A cyclonic circulation is well developed around the Costa Rica thermal dome centered near lat.

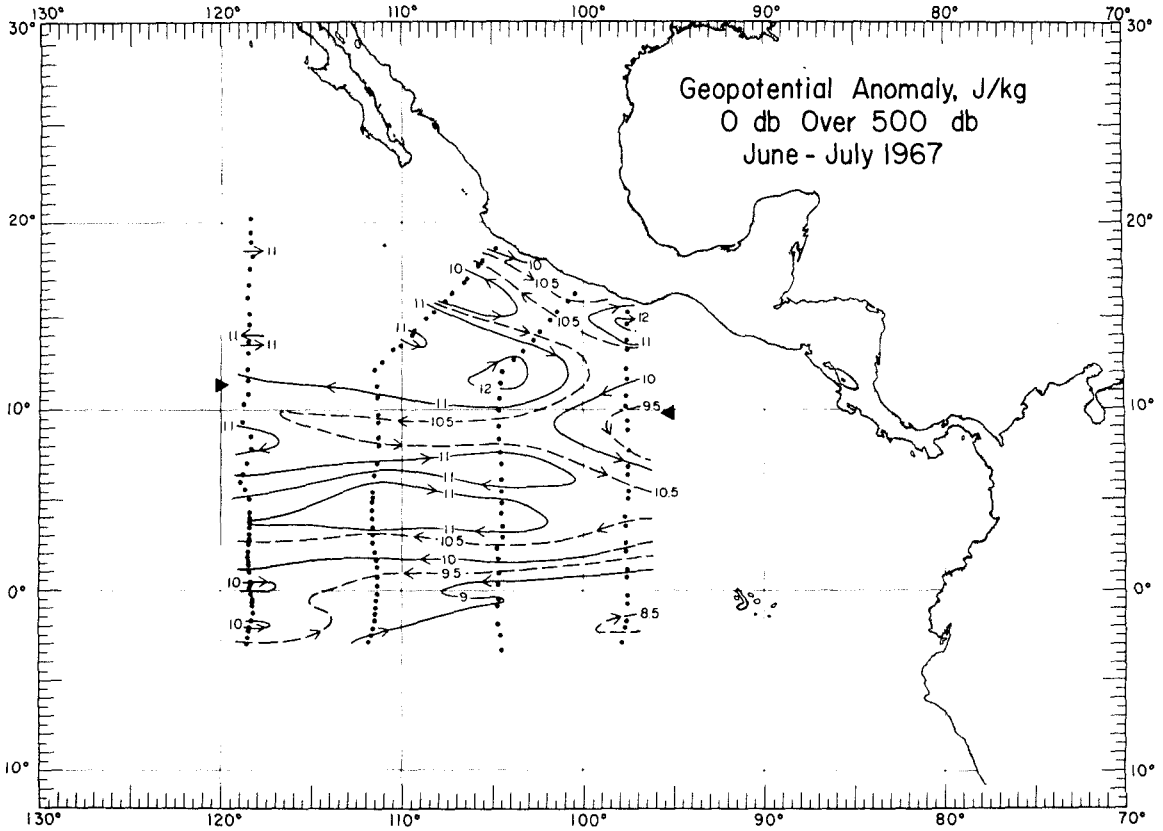

FIGURE 3.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in June-July 1967. EASTROPAC cruise *David Starr Jordan* 30. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

9°N, long. 89°W (Brandhorst, 1958; Cromwell, 1958; Wooster and Cromwell, 1958; Wyrtki, 1964) in February-March 1967 and February-April 1968 (Figures 1 and 7), but is less well defined in August-September 1967 (Figure 4).

Between Costa Rica and Cape Corrientes (lat. 20°N), nearshore flow is generally northwestward in August-September (Figure 4), when the North Equatorial Countercurrent is strongly developed. In the other months (Figures 1-3 and 5-7) flow is southeastward from Cape Corrientes at least as far south as the Gulf of Tehuantepec (lat. 16°N). This sense of flow is in agreement with that found on the H. O. 570 drift charts except for June-July, when the nearshore current is northwestward on the drift charts. Puls' (1895) charts, however, indicate easterly components of flow near the coast between Cape Corrientes and the Gulf of Tehuantepec in all months of the year.

North Equatorial Countercurrent

Previous studies (e.g., Wyrtki, 1965) have indicated that the North Equatorial Countercurrent is subject to a large variation in response to that of the atmospheric circulation, particularly the annual meridional migration of the intertropical convergence zone (ITCZ). During EASTROPAC the North Equatorial Countercurrent exhibited a high level of variability in position and intensity. The Countercurrent was weak and discontinuous in February-April 1967 and 1968, when the ITCZ lay near its southernmost position at lat. 2°-6°N. It was strong, broad, and extended all the way to the coast of Costa Rica in August-September 1967, when the ITCZ lay near its northernmost position at lat. 11°-15°N. (The position of the ITCZ during EASTROPAC can be inferred from surface-wind charts in the EASTROPAC atlas.

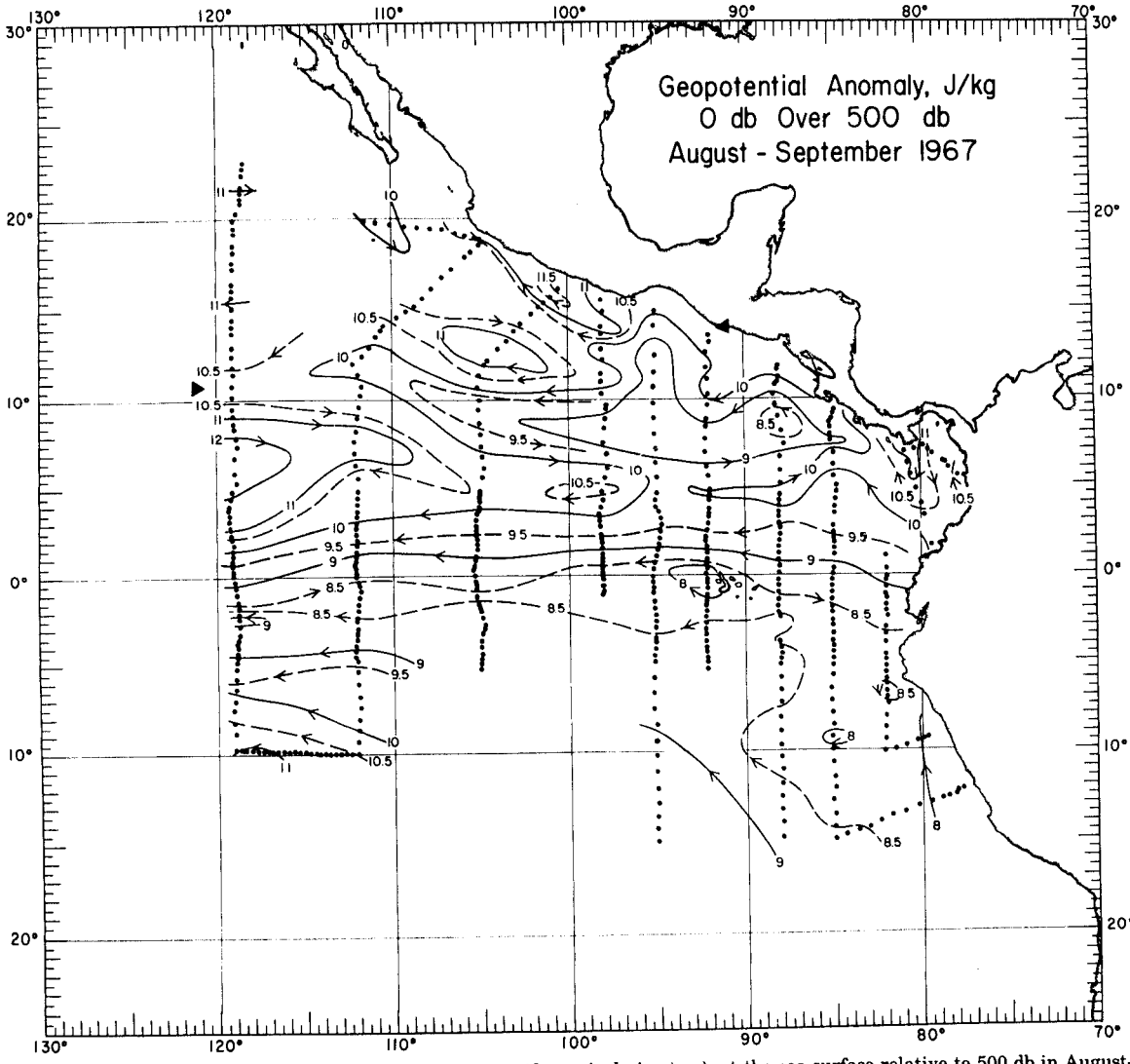

FIGURE 4.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in August-September 1967. EASTROPAC cruises *Thomas Washington* 45, *Undaunted* 46, and *Rockaway* 47. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

The position at the easternmost and westernmost meridional sections is indicated by triangles on each map in Figures 1-7.)

In February-March 1967 (Figure 1) the North Equatorial Countercurrent is present between lat. 5° and 8°N[2] at long. 126° and 119°W, but it is practically missing at long. 112°W and only weakly developed at long. 105°W. At long. 98°W the Countercurrent is entirely absent. From long. 95° to 85°W a strong eastward current, which can be identified as the North Equatorial Countercurrent, is found along lat. 5°-6°N between the cyclonic and anticyclonic eddies mentioned earlier. In April-May (Figure 2) no countercurrent is found at long. 119°, 112°, and 105°W, but a strong countercurrent is indicated between lat. 4° and 7°N at long. 98°W. In April-May the ITCZ starts returning to the north and is located north of lat. 6°N.

The development of the North Equatorial Countercurrent in February-April 1968 (Figure

[2]Near the northern edge of the North Equatorial Countercurrent, flow is usually weak, and the current boundary is not always well defined by the distribution of geopotential anomaly. The northern boundary cited here is that of the band of strong current. Weak eastward flow may extend farther north.

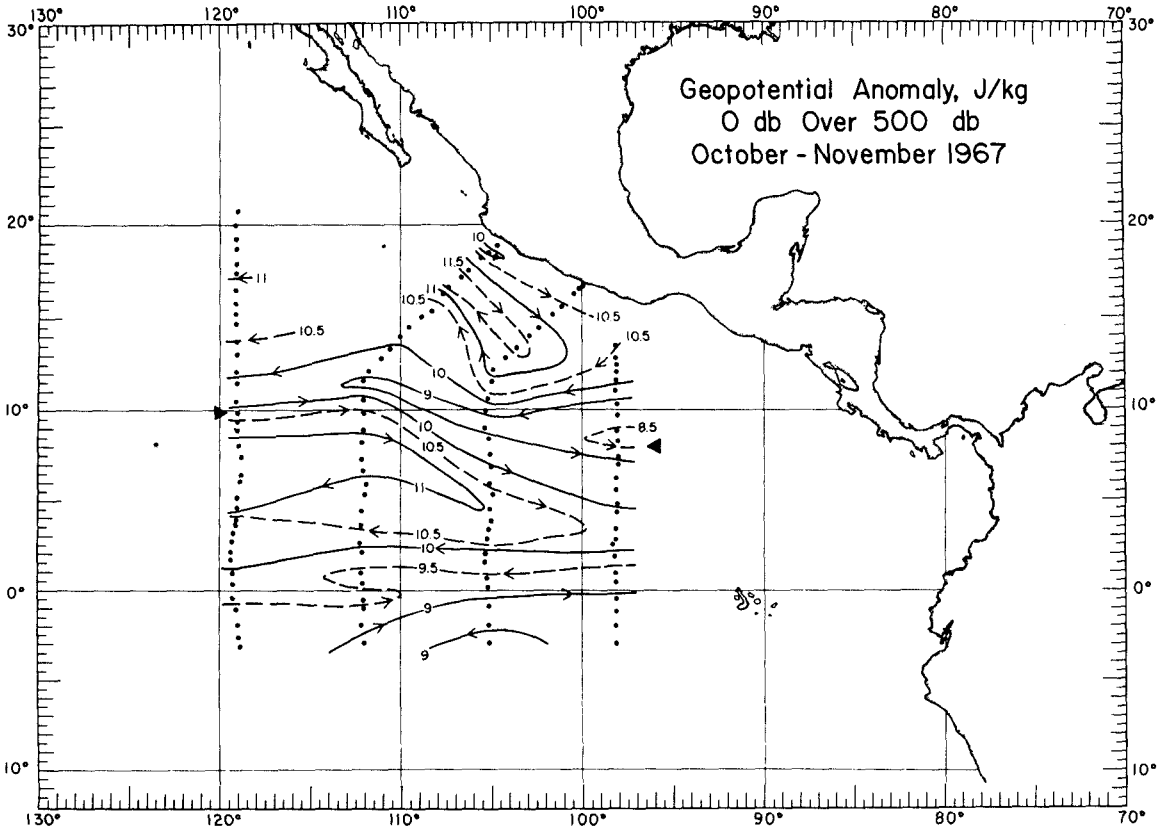

FIGURE 5.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in October-November 1967. EASTROPAC cruise *David Starr Jordan* 50. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

7) is much like that in February-April 1967 (Figure 1). In 1968 the Countercurrent is present between lat. 4° and 7°N at long. 119°, 112°, and 105°W, but is not found at long. 98° and 95°W. Farther east at long. 88° and 85°W the Countercurrent is strongly developed along lat. 5°-8°N between cyclonic and anticyclonic eddies similar to those observed in 1967.

By June-July 1967 (Figure 3) the North Equatorial Countercurrent is well established between lat. 6° and 10°N on all four meridional sections. In Figure 3 a weak eastward current, separated from the Countercurrent by a narrow band of westward flow, can be seen about 200 km south of the southern boundary of the Countercurrent. This secondary countercurrent represents a surfacing of a narrow but stable subsurface eastward current, which has its maximum speed at a depth of 50-200 m just south of the North Equatorial Countercurrent (Tsuchiya, 1972).

In August-September (Figure 4) the North Equatorial Countercurrent is fully developed and extends east to the coast of Costa Rica, where it turns to the northwest along the coast. In these months the Countercurrent is wider and is located farther north than in the February-April periods of 1967 and 1968. In August-September it lies between lat. 7° and 11°N at long. 119° and 112°W and between lat. 5° and 10°N east of long. 105°W (Figure 4). About the same condition continues through November (Figure 5), although the ITCZ starts shifting south in October. In December-January (Figure 6) the Countercurrent starts moving south, following the ITCZ's southward shift, which began 2 mo earlier.

The variation of the North Equatorial Countercurrent revealed by the present maps of geopotential anomaly generally agrees with the results of set-and-drift observations discussed by Puls (1895), Cromwell and Bennett (1959), and Wyrtki (1965).

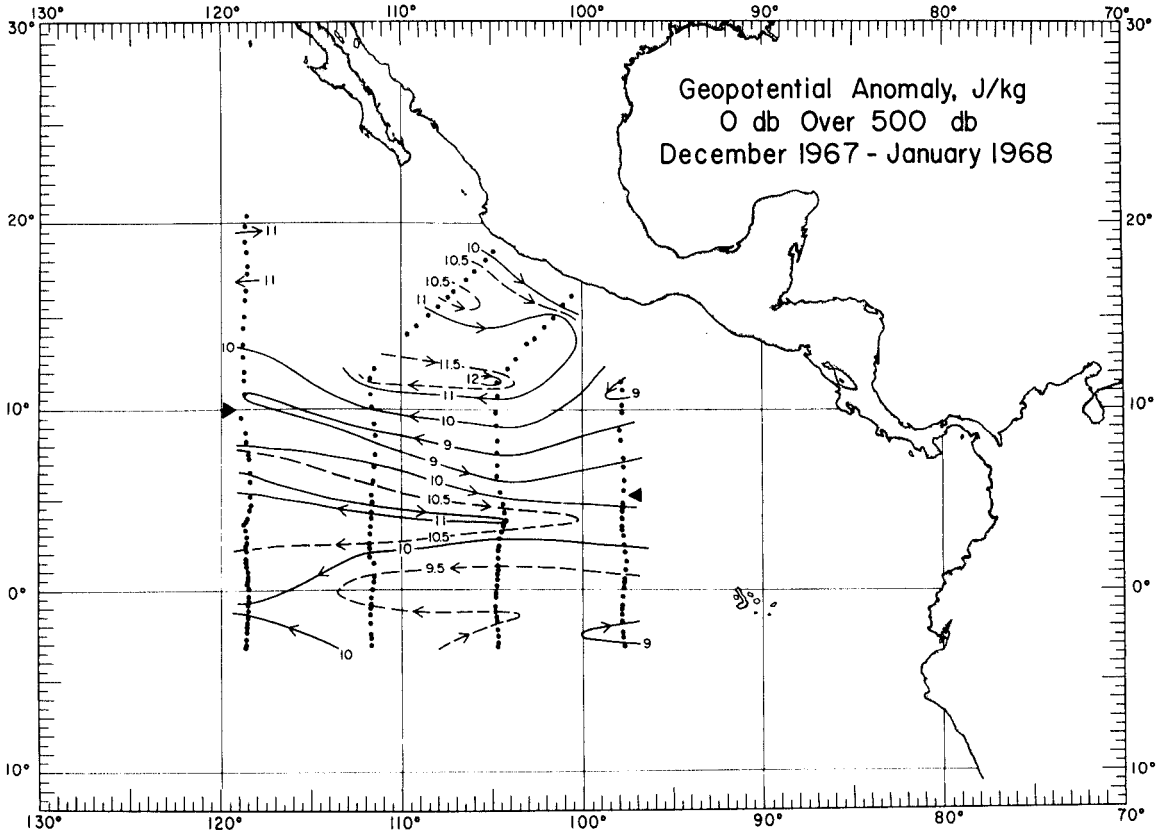

FIGURE 6.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in December 1967-January 1968. EASTROPAC cruise *David Starr Jordan* 60. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

North Equatorial Current Region

North of the North Equatorial Countercurrent, the North Equatorial Current is found on all seven maps (Figures 1-7). On the maps for February-March 1967 and February-April 1968 (Figures 1 and 7) the westward flow of the North Equatorial Current starts off the Gulf of Tehuantepec with a major contribution of water coming from the northwest along the Mexican coast. Water coming from the southeast appears to return to the east forming a cyclonic eddy around the Costa Rica thermal dome.

In February-March 1967 (Figure 1) the North Equatorial Current is interrupted by a continuous eastward flow indicated along lat. 15°N from long. 126°W to the coast of Mexico, where it turns to the south to feed the North Equatorial Current. This eastward flow is broadly developed at long. 112°W and extends from lat. 10° to 18°N. There is a suggestion that a similar eastward flow is present in April-May 1967 and February-April 1968 (Figures 2 and 7). Reid's (1961) map of the surface geostrophic flow also indicates an eastward current at about the same latitude from long. 130° to 95°W, but his data in this area are principally from northern fall and winter. The surface drift charts (Puls, 1895; U.S. Navy Hydrographic Office, 1947) do not show such an eastward flow west of long. 110°W, possibly because of the westward Ekman drift and leeway of ships due to the strong northeasterly trades.

On the map for August-September (Figure 4) the North Equatorial Current starts off the coast of Costa Rica. East of long. 100°W it is fed almost entirely by the return flow of the North Equatorial Countercurrent, which is fully developed in these months.

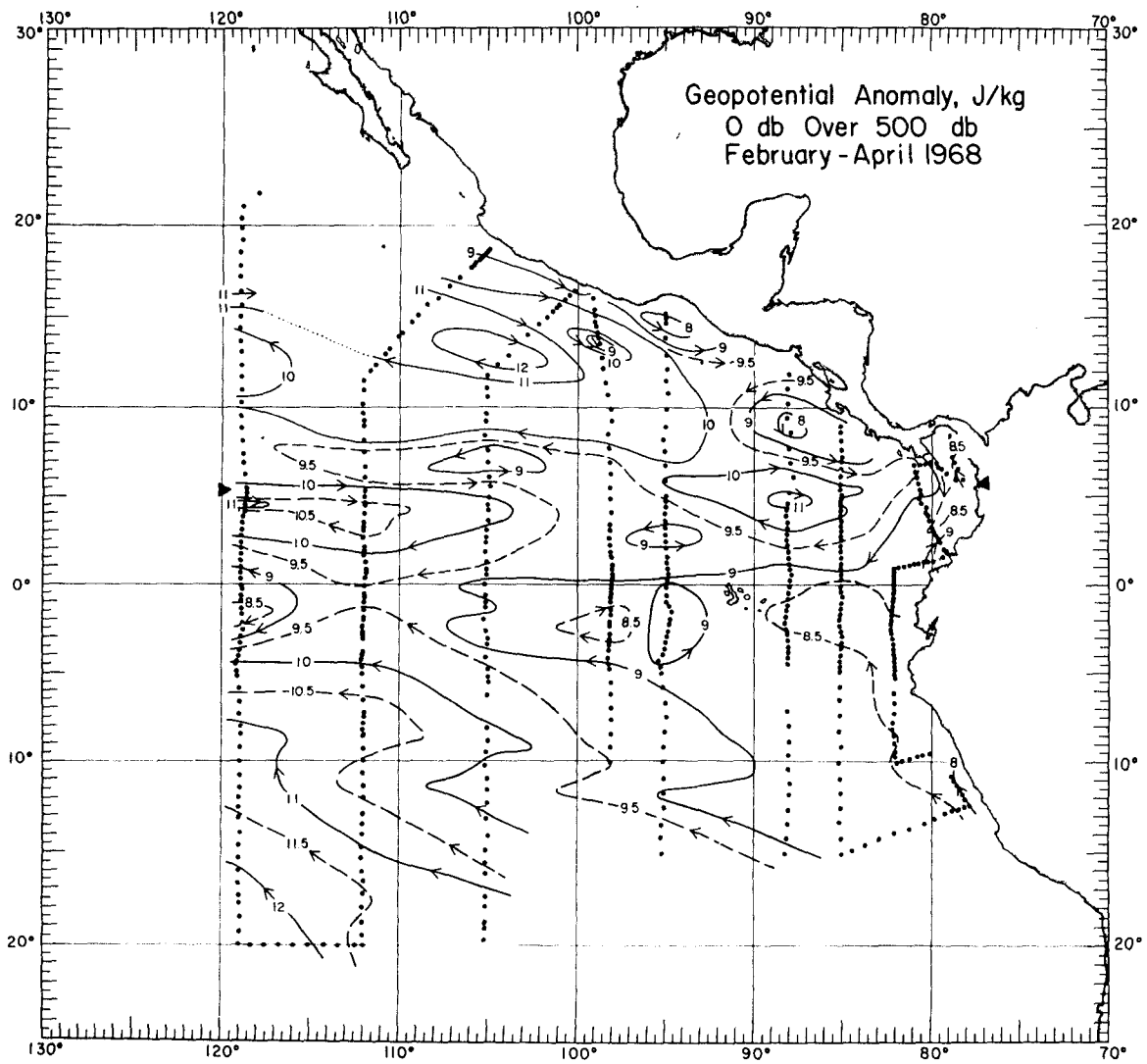

FIGURE 7.—Geopotential anomaly, in joules per kilogram (dynamic decimeters), at the sea surface relative to 500 db in February-April 1968. EASTROPAC cruises *Thomas Washington* 75, *David Starr Jordan* 76, and *Rockaway* 77. The position of the intertropical convergence zone at the eastern and western ends of the map is indicated by triangles.

DISCUSSION

As was noted earlier, geopotential anomaly computed from oceanographic data contains short-period nongeostrophic fluctuations of the mass field, but there is no way of removing them from the data. Consequently, not all of the features indicated by the present maps may be real. Despite this problem, EASTROPAC data are unique in their time and space coverage and in the close spacing of stations on tightly coordinated ship tracks and, thus, reveal some interesting features that have not been observed previously.

A zonal discontinuity of the North Equatorial Countercurrent in the months when the ITCZ lies near its southernmost position is suggested by the monthly average drift charts (U.S. Navy Hydrographic Office, 1947; Wyrtki, 1965); however, the present maps (Figures 1, 2, and 7) are the first to show it on the basis of quasi-synoptic oceanographic data from the entire eastern intertropical North Pacific. (It is highly unlikely that the breakup of the Countercurrent as shown on

these maps is an artifact of short-period fluctuations of the mass field.) In these months the Countercurrent shows a drastic change in intensity; its rapid disappearance and reappearance on this sequence of maps (Figures 1-3, 6, and 7) are remarkable. The maps demonstrate that the Countercurrent can either disintegrate or reestablish itself on a time scale less than 2 mo.

A comparison of the present maps (Figures 1-7) with meteorological charts in the EASTROPAC atlas (Love, 1971, 1972a, 1972b, 1973, in press. See also the position of the ITCZ indicated at the eastern and western ends of each map.) reveals a rather good correlation between the positions of the North Equatorial Countercurrent and the ITCZ. The northern boundary of the Countercurrent (minimum of geopotential anomaly) coincides approximately with the ITCZ except in February-March and August-September. In February-March the southern boundary of the Countercurrent, if it is present, more nearly coincides with the ITCZ; in August-September the ITCZ is located far to the north of the northern boundary. This finding is in agreement with what can be seen on Wyrtki's (1965) long-term average charts.

There is a high degree of similarity in geostrophic-flow patterns between February-March 1967 (Figure 1) and February-April 1968 (Figure 7). The major features are much the same for the two maps; even the development of the cyclonic and anticyclonic eddies off Costa Rica, the discontinuity of the North Equatorial Countercurrent near long. 98°W, and the eastward flow along about lat. 10°S are similar. In view of the large variations observed between the two cruise periods, this similarity is perhaps surprising. The only notable difference is the latitude of the minimum of geopotential anomaly near the equator (discussed in the preceding section) west of the Galápagos Islands; the minimum is located at the equator in 1967 (Figure 1), while it is located a few degrees south of the equator in 1968 (Figure 7). The southward shift of the minimum in Figure 7 is probably due to the more southerly trade winds near the equator in 1968 than in 1967 (Cromwell, 1953).

The eastward current indicated along about lat. 10°S on the southern-summer maps (Figures 1 and 7) is of particular interest, because no previous data from the eastern Pacific have suggested it. This countercurrent is very weak (the average geostrophic speed from seven meridional sections is 7 cm/s) and was not noticed in earlier examination of vertical sections based on EASTROPAC data (Tsuchiya, 1972). It is a narrow and thin current (about 50 m thick) and is completely separate from a subsurface eastward current which has its maximum speed at a depth of 70-200 m and which flows along about lat. 6°S (Stroup, 1969; Tsuchiya, 1972).[3] More data are needed to determine the relation of this surface eastward countercurrent with the South Equatorial Countercurrent, which is well developed near lat. 10°S at the sea surface of the central and western Pacific (Reid, 1959, 1961; Merle, Rotschi, and Voituriez, 1969; Rotschi, 1970; Tsuchiya, 1970; Donguy and Rotschi, 1970). As was mentioned in the preceding section, the former countercurrent is defined only between long. 112°W and long. 90°W and is not found in the west of the EASTROPAC area.

ACKNOWLEDGMENTS

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[3]A detailed report on this subsurface eastward countercurrent is being prepared for publication elsewhere.

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THERMOREGULATORY BEHAVIOR AND DIEL ACTIVITY PATTERNS OF BLUEGILL, *LEPOMIS MACROCHIRUS*, FOLLOWING THERMAL SHOCK

THOMAS L. BEITINGER[1]

ABSTRACT

Individual bluegill were allowed to thermoregulate for 3 days in a temperature-preference apparatus and then were exposed for 30 min to one of three temperature treatments: 21.0°, 31.0°, or 36.1°C. Fish exposed to 31°C served as controls for handling procedures. Thermoregulatory performance of surviving fish was monitored for an additional 3 days. Pretreatment results indicated mean lower and upper avoidance temperatures of 29.3° and 33.1°, and 31.2°C as the midpoint of the preferred range. All 20 fish exposed to 21° and 31°C survived treatment and demonstrated no significant differences between pretreatment and posttreatment thermoregulatory performance. Thirty-five percent of fish (7 of 20) exposed to 36.1°C died during treatment. Fish surviving the 36.1°C treatment retained the ability to thermoregulate; however, their mean lower and upper avoidance temperatures increased 0.6° and 0.7°C, respectively. Activity patterns were typically diurnal, but variable, in all three treatment groups. Immediately after treatment, the activity of fish exposed to 21° and 36.1°C was markedly decreased. Thereafter, activity tended to be higher in the 21°C group and lower in the 36.1°C group than during the pretreatment period.

Opportunities for temperature shock occur wherever sharp temperature gradients are present. Fish may be exposed to a sudden temperature change when penetrating the thermocline; in areas containing springs, upwellings or natural allochthonous inputs of water; in sharp horizontal temperature gradients characteristic of shallow waters; and during the passage of weatherfronts. Also, fish species migrating through or residing within waters under the influence of electric generating companies may be subjected to sudden temperature changes.

Investigations concerning thermal shock of fishes have mainly been limited to descriptions of morbidity stages and determinations of species' lethal temperatures. Noteworthy exceptions are studies by Sylvester (1972) and Coutant (1972a, b, 1973) that demonstrate enhanced vulnerability of thermally stressed fishes to predation. Fish mortalities owing to natural and artificially induced temperature shock have been reported in marine, estuarine, and freshwater environments (Gunther, 1936; Gunter, 1941; Huntsman, 1942; Gunter and Hildebrand, 1951; Bailey, 1955; Threinen, 1958; Colton, 1959; Alabaster, 1963; Clark, 1969), but the majority of work has involved laboratory determinations of thermal resistance.

An important question is: does a sublethal temperature shock disrupt subsequent thermoregulatory behavior of a fish? The objective of this study was to assess effects of temperature shock upon the thermoregulatory ability, selected temperatures, and locomotor activity patterns of individual bluegill, *Lepomis macrochirus*.

MATERIALS AND METHODS

Specimen

Juvenile bluegill (mean length 86.3 mm, range 72-105 mm) were captured during summer with electroshocking gear from Lake Wingra (Dane County, Wis.) and maintained in the laboratory at 25°C under constant photoperiod (LD 14:10 with 0.5 h dawn and dusk intervals) for at least 2 wk prior to experimentation. Throughout the preexperimental and experimental periods fish were fed pelleted food daily at 1630 h ± 15 min.

Apparatus

The thermoregulatory apparatus was derived from that of Neill and Magnuson (in press) with temperature control and rate-change modi-

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fications reported by Beitinger et al. (in press). The design (Neill, Magnuson, and Chipman, 1972) substitutes a temperature gradient over time for the spatial gradient typical of most temperature preference studies and allows an individual fish to serve as its own tank thermostat. Each 50-liter test tank was divided into halves with a molded fiber glass partition. A tunnel in the partition allowed the fish to choose between halves differing by a fixed 2°C temperature interval. When a fish selected the higher temperature, the temperature of the tank increased at a constant rate of 3°C/h while the 2°C differential between halves remained constant. When the fish moved to the cooler tank half, the temperature decreased at the same rate (3°C/h) until the fish again moved to the warmer tank half. By moving from one side to the other, a fish was able to control the temperature to which it was exposed. For this study, a potential temperature range of 4° to 55°C was available.

Temperatures of each tank half were monitored by a thermistor-wheatstone bridge circuit connected to a multichannel analog recorder. Avoidance temperatures (i.e., turnaround temperatures), preferred temperature range and midpoint of the preferred range (midpoint temperature) were the same as defined by Neill and Magnuson (in press). During the experiment, tunnel passes, recorded on an event recorder, were utilized as a measure of fish activity.

PROCEDURE

One fish was introduced per tank and allowed to experience the static system for 2.5 days with the tank halves set at 24° and 26°C. The test period then began and tank temperature control was relinquished to each fish. Thermoregulatory performance during the second, third, and fourth days constituted the pretreatment data. Then fish were removed and individually subjected to a sudden temperature change in 3.5-liter cylindrical chambers. The water in each chamber was well aerated and "conditioned" with 150 ml of that fish's thermoregulatory tank water. High temperature treatment was 36.1 ± 0.1°C and low temperature treatment was 21.0 ± 0.1°C. For control purposes, a third group of fish was treated at 31.0± 0.1C, a temperature approximating the preferred range midpoint for bluegill. A series of cursory experiments indicated that fish body temperatures equilibrated to the treatment temperature during exposure. Fish were randomly allocated to the three treatment temperatures. Following a 30-min exposure, each surviving fish was returned to its respective thermoregulatory tank for an additional 3-day posttreatment period. Thermoregulatory tank temperatures at fish reentry were the same as those at fish removal. Finally, fish were isolated and observed for 1 wk for possible latent effects.

RESULTS

Prior to treatment, there were no statistically significant differences in thermoregulatory performance among the three groups (Kruskal-Wallis one way analysis of variance; Siegel, 1956; lower and upper avoidance temperatures, midpoint temperature, and width of preferred range, all $P>0.20$). Fish had mean lower and upper avoidance temperatures of 29.3° and 33.1°C and mean preferred range width of 3.8°C. The

TABLE 1.—Lower and upper avoidance temperatures, preferred range midpoint and width, pretreatment and posttreatment, for each of the three groups. Means ± standard deviations are given.

Item	Controls 31.0°C	Cold shocked 21.0°C	Heat shocked 36.1°C	Grand mean
N	10	10	[1]12	
Lower avoidance temperature, °C:				
Pretreatment	29.4 ± 0.7	29.2 ± 0.9	29.4 ± 0.9	29.3
Posttreatment	29.4 ± 0.8	29.1 ± 1.0	30.0 ± 0.8	
Upper avoidance temperature, °C:				
Pretreatment	33.1 ± 0.6	33.1 ± 0.5	33.1 ± 0.9	33.1
Posttreatment	33.1 ± 0.7	33.1 ± 0.5	33.8 ± 0.9	
Midpoint of preferred range, °C:				
Pretreatment	31.3 ± 0.6	31.2 ± 0.6	31.2 ± 0.8	31.2
Posttreatment	31.2 ± 0.7	31.1 ± 0.7	31.9 ± 0.8	
Width of preferred range, °C:				
Pretreatment	3.7 ± 0.6	3.8 ± 0.7	3.7 ± 0.7	3.7
Posttreatment	3.6 ± 0.5	4.0 ± 0.8	3.8 ± 0.5	3.8

[1]One fish survived treatment but died during the first posttreatment night, owing to electronic failure.

midpoint of the preferred range was 31.2°C (Table 1).

Pretreatment and posttreatment comparison of preferred range midpoints for individual fish are illustrated in Figure 1. Of the 20 control and cold-treated fish (1b, a), 18 had posttreatment midpoint temperatures within 0.3°C of their pretreatment values. None of the individual control fish had significant pretreatment and posttreatment changes in mean avoidance temperatures (t-test, $P>0.05$). Among the cold-treated fish, two had significant downward changes in lower avoidance temperatures and one had a significant downward change in its upper avoidance temperature. In the control and cold-treated groups, five fish each had lower posttreatment midpoint temperatures; however, there were no significant trends (Wilcoxon matched pairs, signed ranks; controls and cold-treated $P>0.10$).

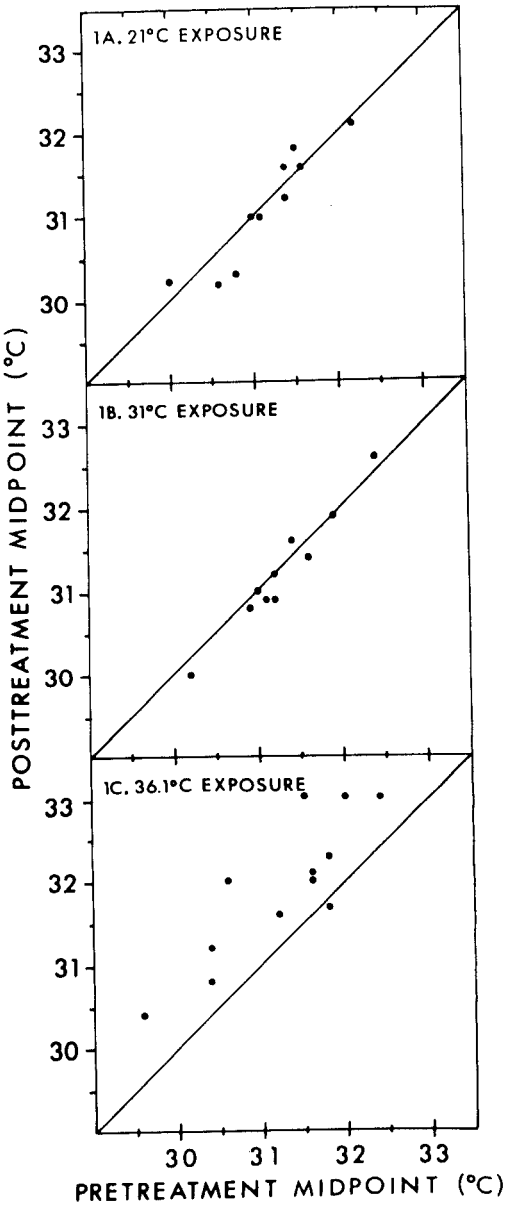

FIGURE 1.—Mean preshock and postshock midpoints of preferred range for individual bluegills in each of the treatment groups. Points falling on the 45° line indicate no change in midpoint temperatures.

Eleven of the twelve heat-treated fish had higher posttreatment midpoint temperatures (Figure 1c). This trend was highly significant (Wilcoxon matched pairs, signed ranks, $P<0.01$). The mean posttreatment midpoint temperatures for heat-treated fish during each of the 3 days were 31.9°, 32.0°, and 31.9°C, indicating no return towards the pretreatment preference level.

Whereas all of the control and cold-treated fish survived the treatment process, 7 of the 20 fish (35%) exposed to 36.1°C died during treatment. All fish that died lost equilibrium early in the treatment and were dead within 5 min. The mean pretreatment midpoint temperature of those that died was significantly lower than that of the survivors (Mann-Whitney U test $P<0.05$); however, temperatures experienced immediately prior to exposure were the same for both groups.

Although visual observations during the posttreatment period of this study were limited to avoid disturbing the fish, the typical immediate posttreatment behavior of both the heat- and cold-treated fish was submissive; often fish were hiding behind objects in their experimental tanks. However, at the feeding time, 4.5 h following exposure, nearly all fish actively fed.

A distinct diurnal pattern of activity was observed for each of the treatment groups throughout the 6-day experiment (Figure 2). Daytime hourly activities were typically two to three times higher than nighttime activities. The median activity (tunnel passes) of the cold- and, particularly, heat-treated fish dropped appreciably the hour following exposure (Figure 2). For general activity comparisons (Figure 3a, b) diurnal and nocturnal periods were separately analyzed (dawn and dusk excluded). With the pretreatment activity of each group serving as its own control, a series of Mann-Whitney U tests, with ties correction and z transformation were performed

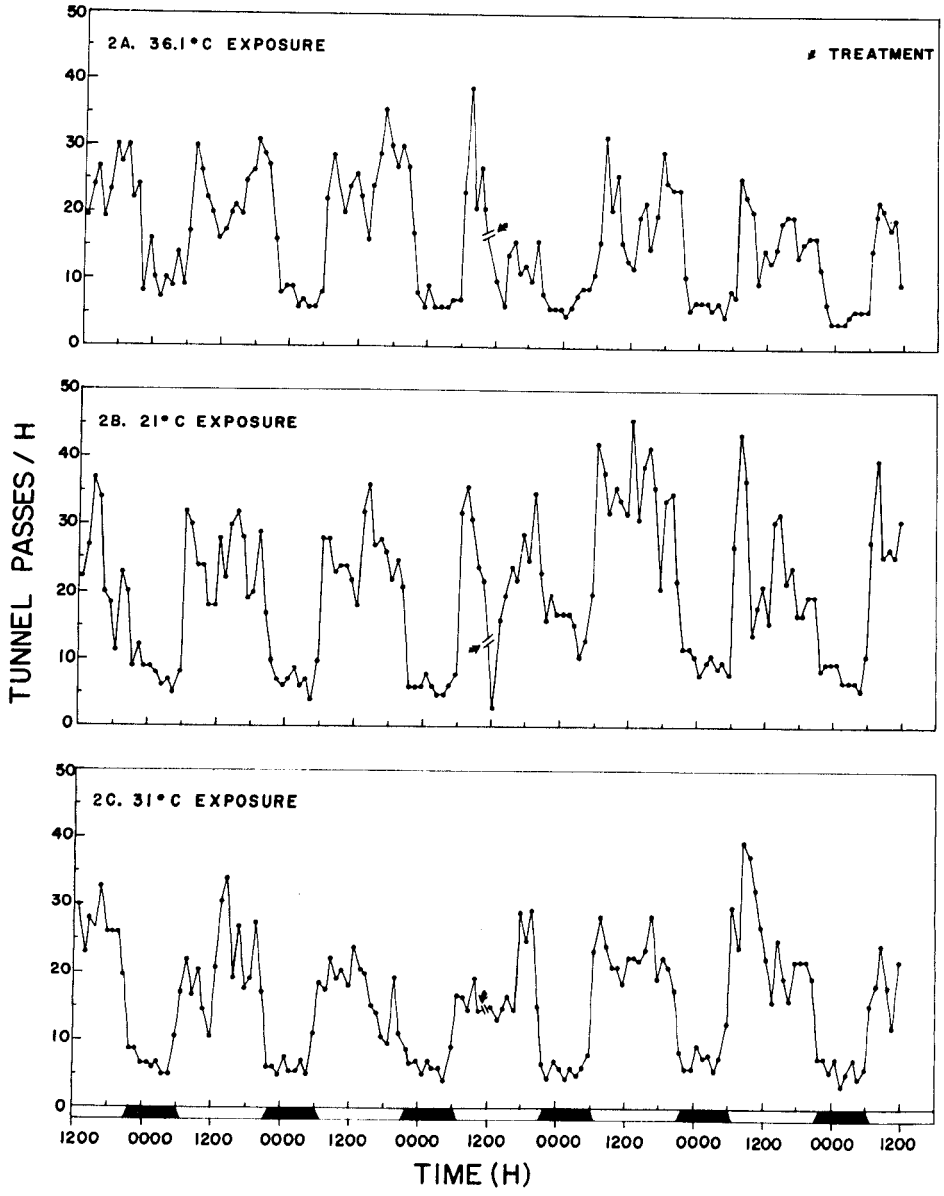

FIGURE 2.—Median hourly tunnel passes by fish throughout the entire 6-day experiment for each treatment group. The arrow indicates time of treatment.

to compare the 3-day pretreatment and 3-day posttreatment median hourly activities. The pretreatment and posttreatment activity levels of the control group were not significantly different. The daytime posttreatment activity of cold-treated fish, although higher and more variable, was not significantly changed; however, night activity increased ($P<0.001$). Heat-treated fish demonstrated the greatest change in activity. Both night and daytime activities decreased ($P<0.01$, $P<0.001$ respectively).

DISCUSSION

Combined pretreatment data demonstrate that the 32 test bluegills maintained their environmental temperatures within well-defined limits relative to the available temperature range. The

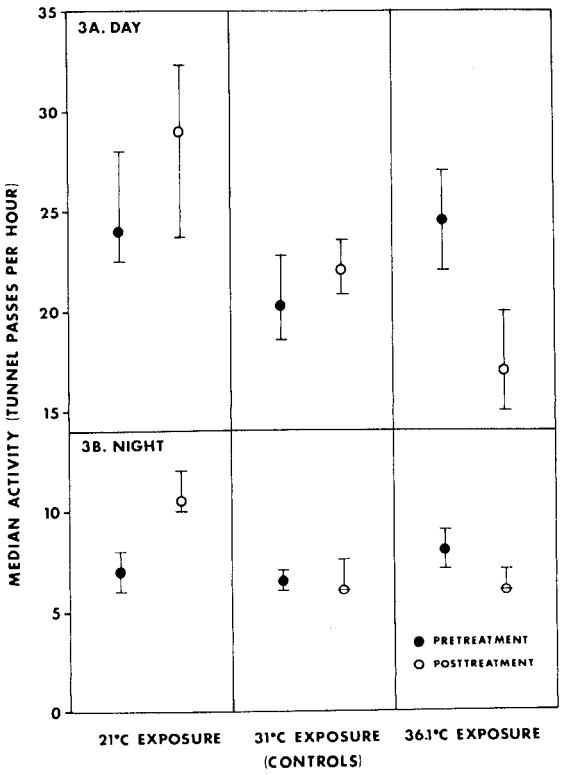

FIGURE 3.—Medians (circles) and 95% confidence limits for pretreatment and posttreatment bluegill hourly activities for the three treatment groups. Day and night activities are presented separately.

calculated midpoint of the preferred range, 31.2°C, is similar to that of Neill and Magnuson (in press), 30.4° and 0.8°C below the final temperature preferendum for bluegill reported by Fry and Pearson (1952).[2] The effect of sudden temperature stress on thermoregulatory behavior has not been previously examined. However, several other external factors have been reported to influence temperature preferenda, including season (Sullivan and Fisher, 1953; Zahn, 1963; Barans and Tubb, 1973), light intensity (Sullivan and Fisher, 1954), starvation (Javaid and Anderson, 1967) and exposure to chlorinated hydrocarbons (Ogilvie and Anderson, 1965; Peterson, 1973).

Pretreatment and posttreatment comparisons in the grouped control data clearly indicate no change in thermoregulatory performance. The Δt experienced by control fish was minimal and changes, if any, could be ascribed to handling or time-dependent variations in temperature preference.

Cold- and heat-treated fish actually experienced two temperature shocks. One occurred when the fish were introduced into the treatment chambers and the second when they were returned to their experimental tanks. Both cold and heat treatments were conducted at temperatures actively avoided by fish while in their thermoregulatory tanks.

Cold exposure did not significantly change any of the four measured parameters of thermoregulatory behavior. These fish experienced a Δt of approximately 10°C, but the exposure temperature, 21°C, is near the middle of the tolerance zone for bluegill. That these fish did not select lower temperatures was expected, owing to the slow rate of downward temperature acclimation characteristic of fishes (Brett, 1944, 1946). The lethal rates of temperature increase are at least 20 times the corresponding lethal rates of temperature decrease for bluegill (Speakman and Krenkel, 1971). Apparently, the 30-min exposure was not sufficient to change the acclimation state and, hence, the preferred temperature range of these fish.

Fish exposed to 36.1°C experienced a smaller Δt (about 5°C) during treatment, but this exposure was to within approximately 0.5°C of the bluegill's incipient upper lethal temperature (Hart, 1952; Cairns, 1956). The ability of surviving bluegills to thermoregulate was not deleteriously affected by the 30-min exposure to 36.1°C, however, statistically significant changes in avoidance and midpoint temperatures did occur. Thus, the thermoregulatory performance of bluegill was influenced more by exposure either to 1) temperatures closer to lethal limits than exposure to large Δt's per se or to 2) temperatures above rather than those below, the acclimation state of the fish.

Of the three exposure temperatures, only 36.1°C resulted in fish mortality. The pretreatment midpoint temperatures of these fish were significantly lower than those of fish surviving heat treatment, indicating a relationship between preferred and upper lethal temperatures. That a considerable proportion, 35%, of fishes exposed to 36.1°C died, is more important to the population than the observation that surviving

[2]Fry, F. E. J., and B. Pearson. 1952. Some temperature relations of the pumpkinseed and bluegill sunfish. Unpubl. manuscr., 10 p. Ont. Fish. Res. Lab. R.R. 2, Maple, Ont., Can.

fish had a 0.7°C increase in preferred range following exposure.

Use of tunnel passes as an index of locomotor activity is discussed by Beitinger et al. (in press). The diurnal activity pattern continued after treatment in all three groups (Figure 2). Immediately subsequent to treatment, a marked decrease in activity occurred in cold- and heat-treated fish but not in the control group (Figure 2). This decrease might help explain the increased susceptibility of thermally shocked fish to predation reported by Coutant (1972a, b, 1973) and Sylvester (1973). Hocutt (1973) found that exposure to rapid temperature changes, as large as 12°C below and 8°C above ambient temperatures, resulted in decreased swimming performance in juvenile largemouth bass, *Micropterus salmoides*; spotfin shiner, *Notropis spilopterus*; and channel catfish, *Ictalurus punctatus*.

Due to their mobility and acute temperature sensitivity, fishes are able to avoid environments of unfavorable temperatures. If trapped at these temperatures, fish possess the ability to resist thermal death. Ecologically, resistance ability affords a fish the opportunity to escape potentially lethal conditions at least until they lose equilibrium. Fish are exposed to stressful conditions when existing within their thermal resistance zone or when experiencing large temperature changes. The major objective of this research was to examine the thermoregulatory performance of bluegill following "high" and "low" thermal exposure. Nevertheless, the 35% mortality among 36.1°C treated fish and the severe depression in immediate posttreatment activity of both the 21.0° and 36.1°C treated fish were the two most ecologically important findings. All fish surviving treatment retained the ability to behaviorally thermoregulate, hence, disruption of thermoregulatory behavior is not a likely outcome of thermal shock in fishes.

ACKNOWLEDGMENTS

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DENSITY DISTRIBUTION OF JUVENILE ARCTIC COD, *BOREOGADUS SAIDA*, IN THE EASTERN CHUKCHI SEA IN THE FALL OF 1970

JAY C. QUAST[1]

ABSTRACT

The Arctic cod, *Boreogadus saida*, is a key element in the ecosystem of the Arctic Ocean. Juveniles, principally young-of-the-year, were taken by Isaacs-Kidd mid-water trawl at night during September and October 1970 in the eastern Chukchi Sea. Their average concentration was about 28/1,000 m^3 and their average biomass about 0.7 metric ton/km^2 of ocean surface. In 20 stations (representing about 30 x 10^3 km^2, or 8,714 square nautical miles), the number of juvenile cod (N) per standard haul (about 8,223 m^3 of water filtered per haul) increased with depth in meters (D) at about the same rate [$\log_{10}(N + 1) = 0.0669D$]. Yet the depth at which equivalent concentrations occurred varied over a range of 38 m between stations. The zone of increased concentration with depth, called a density structure, appears to be the nighttime relict of a graded negatively phototactic response to sunlight by the juvenile cod during preceding daylight. Apparently the structure was vertically displaced after dark by wind-induced upwelling and downwelling. The juvenile cod may have originated in the northwestern Bering Sea, off Arctic Siberia, or within the Chukchi Sea, and probably had recycled in the Chukchi Sea prior to capture.

This study of biomass and distribution of juvenile Arctic cod, *Boreogadus saida* (Lepechin), in the Chukchi Sea is an outgrowth of the Western Beaufort Sea Ecological Cruise of 1970 (WEBSEC-70) sponsored by the U.S. Coast Guard. My original objective was to explore the fishes of the marine ecosystem in the Arctic Ocean east of Point Barrow, Alaska, and if possible to quantify the occurrence of important forms. Because of an early southward shift of the arctic ice pack, the study was moved to the eastern Chukchi Sea. The sampling schedule—date, location, depth of water, and number and types of hauls—is given in Table 1 and Figure 1. The species of fish and where they occurred are summaried in Quast (1972).

Juvenile Arctic cod and Pacific sand lance, *Ammodytes hexapterus* Pallas, were virtually the only fish species trawled in the surface and mid-depths at night. The cod occurred at every station; also they were more numerous and had a larger biomass than the sand lance—a subjective estimate suggests a minimum 10 fold difference in both respects. Although sand lance were chiefly taken at the surface, the number of Arctic cod usually increased with depth. Because of the apparent importance of the Arctic cod in the off-bottom marine ecosystem of the eastern Chukchi Sea during WEBSEC-70, I further analyzed their data to estimate their numbers and biomass over the study area.

General life history, distribution, and literature on Arctic cod are summarized by Andriyashev (1954:195-198). The species is circumpolar and occurs to or nearly to the North Pole. Off Alaska, it occurs along the Arctic coast, in the Chukchi Sea, and in the Bering Strait; it also has been recorded in the winter from Norton Sound and the Gulf of Anadyr. Although most authors term the species "pelagic," "demersal" is probably better because adults appear to be associated with a shallowwater substrate, whether it be ocean bottom over the continental shelf or the undersurface of ice. Maximum size is about 320 mm total length (TL). Association with low temperatures is an important characteristic: Rass (1968: 136) gives the thermal environment of eggs as 0° to 2°C, of larvae as 2° to 5°C, and of fry as 5° to 7°C and probably higher. During WEBSEC-70, specimens of 0-age fish occurred at −1.5° to 3.5°C. According to Andriyashev (1954), Arctic cod mature when about 4 yr old and 190 mm TL; they spawn near coasts, principally in January

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TABLE 1.—Station data for trawl collections in the eastern Chukchi Sea during WEBSEC-70.

Station	Date and inclusive time (Bering Standard)	Approximate position		Depth of water (m)	Hauls		
		Lat. N	Long. W		No.	Type[1]	Depths (m)[2]
10	27 Sept. (1917-2207)	70°04′	165°57′	44	4	R	11
14	29 Sept. (0518-0817)	70°17′	165°02′	51	4	R	11
16	29 Sept. (1721-2002)	70°16′	163°58′	53	4	R	11
20	30 Sept. (1740-2025)	70°20′	163°24′	42	4	R	12
22	1 Oct. (1734-2103)	70°20′	163°25′	35	4	R	12
25	2 Oct. (1731-2036)	70°07′	163°14′	33	4	R	12
30	4 Oct. (1756-2137)	69°58′	164°07′	31	5	M	2,5,10,13,19
32	5 Oct. (1831-2104)	69°48′	163°49′	26	4	R	12
37	6 Oct. (1727-1956)	70°07′	167°36′	49	4	R	12
41	7 Oct. (1752-2014)	69°57′	167°31′	44	4	M	10,10,12,22
45	8 Oct. (1816-2058)	69°57′	168°38′	44	4	M	2,9,13,20
51	9 Oct. (1744-2024)	69°36′	167°36′	48	4	M	2,7,14,20
56	10 Oct. (1940-2229)	69°14′	166°53′	44	4	M	2,9,18,23
61	11 Oct. (1755-2015)	69°05′	166°13′	29	4	M	8,13,16,23
65	12 Oct. (1755-2016)	69°21′	166°45′	36	4	M	8,13,16,22
70	13 Oct. (1735-1958)	69°12′	167°38′	39	4	M	8,13,18,22
74	14 Oct. (1723-1946)	69°35′	164°29′	22	4	M	2,8,13,18
80	15 Oct. (1814-2055)	69°27′	164°43′	30	4	M	2,8,13,22
88	16 Oct. (1917-2205)	68°55′	166°47′	45	4	M	2,11,24,40-45
92	17 Oct. (1733-2014)	68°36′	167°41′	54	4	M	2,13,17,33

[1]M = multidepth hauls with 1.8-m (6-foot) Isaacs-Kidd mid-water trawl, and R = replicate hauls at single depth.
[2]Depth at depressor.

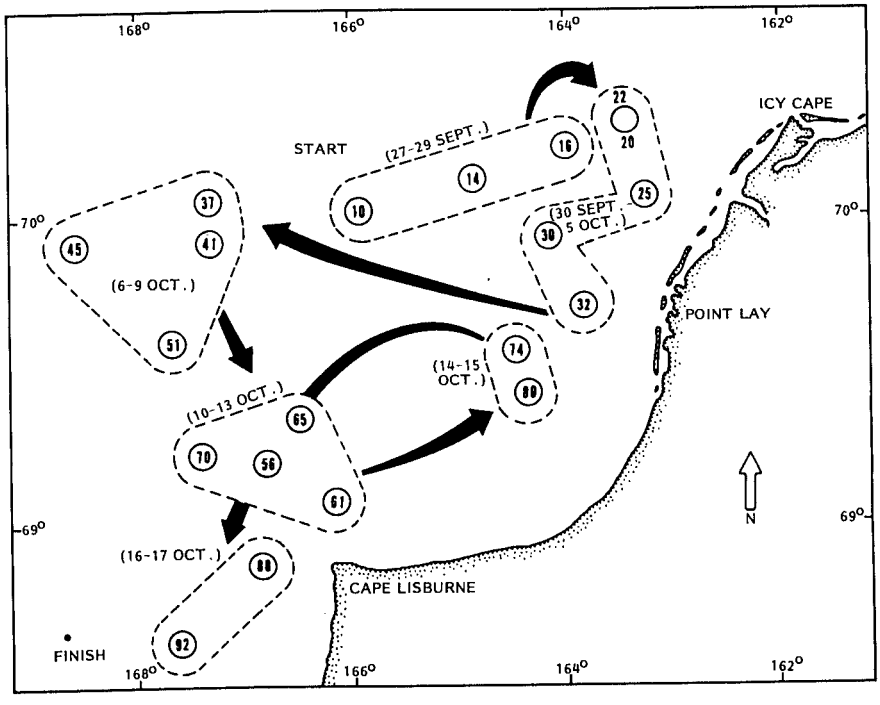

FIGURE 1.—Sequence and position of IKMT stations (circles) in the eastern Chukchi Sea in 1970. Dashed lines indicate time spans for groups of stations.

and February, and their eggs are large—approximately 1.5-1.9 mm in diameter. Rass (1968:136) adds that the first larvae appear in the sea in May-July; the larval stage (5.4-15.0 mm) lasts about 2 mo (in the Barents and Siberian Seas through June-July); and transition to juveniles is at 30-50 mm, in August.

Arctic cod appear to be a key species in the ecology of the arctic seas. They are widespread, locally abundant, and probably are a major element of the secondary consumer level in the trophic pyramid. Ponomarenko (1967:8) found that cod larvae and fry fed successively on copepod eggs, nauplii, and copepodites, and

Hognestad (1968:130) reported that adults trawled from the eastern Barents Sea in September 1966 fed principally on the copepod *Calanus finmarchicus*. In turn, Arctic cod are important as forage for higher level consumers. Andriyashev (1954:194-198) cites literature records for predation on Arctic cod by a long list of species, including char, saffron cod, flounders, sculpins, seals, walrus, beluga, sea gulls, alcids, and skuas. Tuck (1960:166) stresses the importance of Arctic cod in the diet of common and thick-billed murres of the polar basin, whose total populations contain at least 15 million birds (p. 51).

METHODS

Studies with the 1.8-m (6-foot) Isaacs-Kidd mid-water trawl (IKMT) involved 81 30-min tows (at depth) at 20 stations (Table 1). All stations were occupied for periods of about 2 h or more, and all but one started at late dusk or dark. The IKMT was similar in dimensions to the trawl tested and figured by Friedl (1971); it had a section of coarse mesh (3.8-cm bar) preceding 0.6-cm bar mesh. The cross-sectional area at the mouth was calculated as 2.87 m^2 and at the beginning of the 0.6-cm mesh as 1.55 m^2. To compensate for the possibility that fish would be herded into the small-mesh section by the coarse anterior mesh, a middle value between the two cross-sectional areas, 2.21 m^2, was arbitrarily used as the effective cross-sectional area of that portion of the net that captured juvenile cod. Calculation of the horizontal and vertical dimensions of the net swath was simplified by treating the effective cross-sectional area as a square—1.49 m on a side. Tows were standardized at 2 nautical miles (3,704 m) at depth by maintaining a vessel speed of 4 knots (estimated by engine revolutions) over 30 min. The resulting horizontal swath was calculated as 5,519 m^2 and the volume filtered as 8,223 m^3. At least four tows were made at each station, either at the same depth or at four different depths (Table 1)—two on one bearing and the remainder on its reciprocal.

Sampling followed a zigzag pattern (Figure 1) before a southward-advancing ice front. Because blocks of ice are sometimes difficult to see or become too abundant to avoid, mid-water trawling at night even in the presence of light pack ice is hazardous. The trawl can be seriously damaged or lost outright if a large block of ice becomes trapped beneath a trawl warp and causes the trawl to be lifted to the surface where the ice would be fed into its mouth at trawling speed. Consequently, trawling was usually done in the relatively open water of broad leads or ahead of the ice pack.

Two types of IKMT station were occupied. In one type (eight stations), nektonic organisms at a single depth within stations were sought by conducting four "replicate" hauls at 11 or 12 m (Table 1). In the other type (12 stations), the vertical distribution of nektonic organisms was sought by making four or five hauls at different depths (Table 1); the depths, which were usually verified with a bathykymograph, were selected after study of a Simrad[2] echogram (Model ER2—38 kHz). No reliable association was detected between presence or absence of bands on echograms and catch at those depths.

Data obtained on juvenile Arctic cod in the IKMT hauls included counts, range of standard lengths, and volumes. When large numbers of cod were captured, usually the total volume was measured and the number of cod was estimated from the average volume per individual in a subsample. When there appeared to be negligible differences in size of cod between hauls, the average volume per individual in one haul was used to estimate the number of juveniles in a volume taken in another haul at the same station.

RESULTS

The juvenile Arctic cod appeared to be principally of 0 age-class (young-of-the-year), based on a comparison between length frequencies of the Chukchi specimens and age-length data reported in the literature. For the comparison, the Chukchi data were converted from standard to total length by a regression based on data from the Chukchi Sea specimens (Table 2), because the measurement employed for data in the literature was not specific and therefore was assumed to be total length (the measurement usually used in fishery studies). Modal size of the Chukchi Sea specimens was 44 mm, slightly higher than the average size for age 0 cod, 35 mm, from the Barents Sea and Spitzbergen cited by Hognestad (1968:130). The

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Regressions of total length and volume on standard (body) length (X) in juvenile Arctic cod from eastern Chukchi Sea. Least squares fit to power equation, $Y = aX_b$, for 83 specimens over sizes 30<SL mm<74.

Measurement (Y)	a	b	Correlation coefficient
Total length (mm)	1.4429	0.9478	0.996
Volume (ml)	0.4454×10^{-4}	3.1678	0.984

upper limits of nearly all size distributions by haul from the Chukchi Sea, 35 of 40, were below the mean size for age I cod cited by Hognestad. Because the cod from the Chukchi Sea were captured in September and October, at a later date than Hognestad's specimens, there is little doubt that most specimens captured in the eastern Chukchi Sea were age 0.

Homogeneity of sampling variance was then examined in the data on frequency of occurrence of juvenile cod in the hauls by comparing within-station (single depth) standard deviations from the replicate stations. Three hauls also were included from one multidepth station because they were taken at about the same depth, 11 m, as the hauls at the replicate stations. Standard deviation appeared to be proportional to the mean in the comparisons (Table 3), strong evidence that the sampling variance was not homogeneous. The variance appeared to be stabilized by logarithmic transformation of the frequencies [$\log_{10}(N + 1)$] which then passed Bartlett's test (Table 3). As a result, the logarithmic transformation was applied to the analysis of frequencies.

The frequency data were examined by analysis of variance to determine the significance of between-station differences in population density. Data from multidepth stations were not used because these stations were not standardized for depth. Significant between-station differences were present (Table 4), evidence that there were important horizontal differences in density of Arctic cod over the sampling area, at least at depths of 11-12 m.

TABLE 4.—Analysis of variance of numbers (transformed) of juvenile Arctic cod in IKMT hauls at eight replicate stations in eastern Chukchi Sea.

Source	*d.f.*	*S.S.*	*M.S.*	*F*
Among stations	7	10.60984	1.51569	8.84; $P<0.001$
Within stations	24	4.11693	0.17154	—
Total	31	14.72677	—	—

Capture rate of juvenile cod consistently increased with depth and the slope of regressions of number of captures on depth was similar among the multidepth stations. Also, regressions at the stations appeared to bear no direct relationship to salinity structure nearby (Figure 2). Significance of differences between the regressions was tested by analysis of covariance with the result that differences in slope were judged as insignificant. Differences in level, however, did appear to be significant (Table 5). Apparently concentration of juvenile Arctic cod increased at about the same logarithmic rate (0.0669) with depth, but the depth at which a given concentration occurred varied between stations. This triangular area on the plots (Figure 2), with its apex toward the surface, was regarded as the graphic analog of the relationship between concentration and depth in the juvenile cod; it was termed a "density structure." Evidently the density structure was relatively stable relative to the time span of sampling at a station (about 2 h) because the structure was always evident despite the depth sequence of hauls (Figure 2).

TABLE 3.—Comparison of means, standard deviations, and variances for raw and transformed frequencies of occurrence [$\log_{10}(N + 1)$] of juvenile Arctic cod between replicate stations in eastern Chukchi Sea. Data arranged in order of increasing means in the transformed data.

Station	No. replicate hauls	Raw data			Transformed data		
		Mean	SD	Variance	Mean	SD	Variance[1]
37	4	3.3	4.0373	16.3	0.4758	0.4273	0.1826
32	4	6.3	5.4406	29.6	0.7751	0.3079	0.0948
14	4	20.8	22.0681	487.6	1.0397	0.7333	0.5377
25	4	23.3	31.9312	1,019.6	1.1380	0.5011	0.2511
20	4	51.8	47.7169	2,276.9	1.6159	0.3260	0.1063
22	4	57.0	56.3090	3,170.7	1.6399	0.3516	0.1236
16	4	62.5	28.2436	797.7	1.7612	0.2347	0.0551
41	[2]3	277.7	202.5075	41,009.3	2.3101	0.4795	0.2299
10	4	258.0	87.2221	7,607.7	2.3954	0.1453	0.0211

[1]Bartlett's Test for Homogeneity (Sokal and Rohlf, 1969:370, 371): $\chi^2 = 4.004$, $P>0.5$.
[2]A multidepth station in which three hauls were at approximately 11 m.

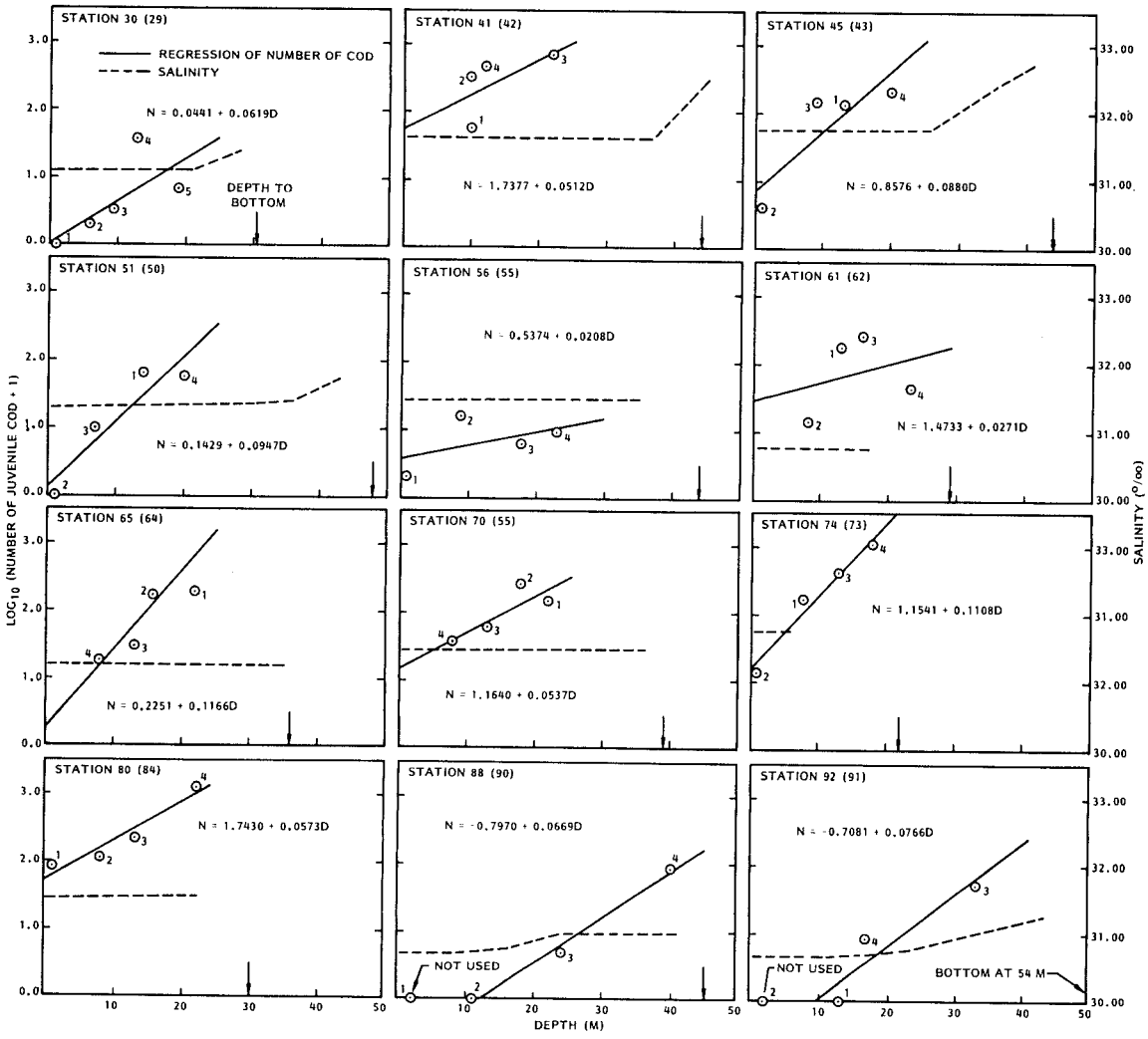

FIGURE 2.—Depth distribution of juvenile Arctic cod and salinity at the 12 multidepth stations. Salinities from the nearest oceanographic station (number in parentheses) from Ingham and Rutland (1972) and U.S. National Oceanographic Data Center. Numbers on points indicate sequence of hauls. Regressions of number of cod (N) on depth in meters (D) fitted by least squares. Pooled slopes for all data = 0.0669.

TABLE 5.—Analysis of covariance on data for abundance and depth of juvenile Arctic cod at 12 multidepth stations in eastern Chukchi Sea.

Source	*d.f.*	*S.S.*	*M.S.*	*F*
1. Individual regressions	23	3.91335	0.17015	—
2. Difference between 1 and 3 for testing slopes	11	1.48432	0.13494	(2)/(1) = 0.79; n.s.
3. Individual regressions fitted with a common slope	34	5.39767	0.15876	—
4. Difference between 3 and 5 for testing levels	11	23.56263	2.14206	(4)/(3) = 13.49; $P<0.005$
5. Regressions fitted to a single line	45	28.96030	—	—

DISCUSSION

Possible Causes of the Density Structure and Its Vertical Displacement

The steady increase of number of cod in the density structure with depth indicated a graded rather than a threshold response to some environmental factor, because if the response depended on a threshold, one would expect a sudden increase in density of juvenile cod when that threshold was reached. Salinity relationships in the water column did not appear to be a cause of the density structure because the water column was usually nearly isohaline through the region of greatest change in concentration of juvenile cod (Figure 2)—the density structure evidently persisted despite forces that contributed to oceanic mixing. Predation by aquatic predators did not seem to be a reasonable cause because the only evident potentially effective fish or invertebrate predator on the cod was large jellyfish, which occurred in approximately equal numbers throughout the water column. Reaction of the juvenile cod to a pressure gradient also was dismissed, for reasons discussed below.

A graded negative phototaxis either in the juvenile cod or, possibly, in the prey they were following seemed to offer the best hypothesis for the cause of the density structure and its variations. A gradient of increasing darkness with depth could coincide closely with the gradient for increase in number of cod. This type of gradient is illustrated in Figure 3 (shown here for the English Channel—the slope in regard to perception by the cod should be dependent on turbidity as well as the spectral sensitivity of the juvenile cod). Under this hypothesis the density structure of juvenile cod found at night was a relict of earlier daylight hours, during which the density structure was maintained despite turbulence, upwelling, and downwelling. With onset of darkness the means of orientation by the fish was removed and the density structure was elevated or depressed, depending on whether it occurred in cells of upwelled or downwelled water. The density structure presumably persisted into the early night when most hauls were made because of the short period of time elapsing before trawling began and also because the cod were relatively inactive at the low sea temperatures

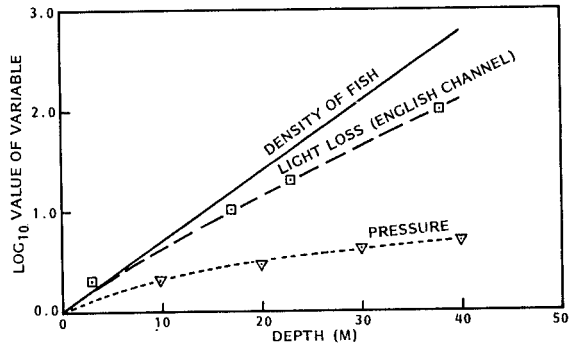

FIGURE 3.—Conformity of the variables—density of juvenile Arctic cod, loss of light (blue-green, English Channel), and pressure at increasing depths. Regression of fish with depth (D), $\hat{N} = 0.0699D$, where $\hat{N}$ = most likely number of fish in a trawl swath (see text); index of light loss based on $I = \log_{10}(1/p \times 100)$, where p = percent of illumination at surface, from data of Nicol (1960:22); and pressure (atmosphere) based on an increase of 1 atm/10-m depth, after Nicol (1960:22).

(−1.5° to 3.5°C). The freshly trawled specimens were markedly inactive. The validity of the gradient hypothesis possibly could have been evaluated further had trawl data been available for daylight hours. Data on vertical distribution of zooplankton were not available because sampling was entirely by vertical tows (Wing, in press).

Orientation by the cod to a pressure gradient was dismissed as an explanation of the density structure for two reasons: the shape of the curve of pressure on depth differs from that of the density structure (Figure 3), and orientation to a pressure gradient should be the same during the day as at night and should not allow the density structure to be elevated or depressed.

If the density structure were a result of behavior in the juvenile cod, it may have been evolved in response to predation by birds. Undoubtedly, such predation is a factor of tremendous ecological importance to juvenile cod, primarily during summer when bird populations are at their peak. Arctic piscivorous birds form a spectrum of depth capabilities, and because their feeding is based at the surface, intensity of predation should decline with depth, i.e., complement the density structure. Watson and Divoky (1972) give an extensive list of bird species observed in the Chukchi Sea during WEBSEC-70, the majority of which are either recorded as predators or are assumed to have, and to make use of, the potential for predation on juvenile Arctic cod. Included are loons, slender-billed shearwater, pelagic

cormorant, red phalarope, glaucous gull, herring gull, ivory gull, black-legged kittiwake, Ross's gull, Sabine's gull, murres, guillemot, Kittlitz's murrelet, parakeet auklet, and horned puffin. Swartz (1966:674) estimated a population of about 600,000 piscivorous birds (adults and fledglings) at Cape Thompson, which is south of Cape Lisburne, in 1960; murres and kittiwake gulls accounted for 90% of the population. He estimated that the birds consumed approximately 13.5×10^3 metric tons of food during their breeding season. Tuck (1960:166) found that Arctic cod were the most important fish in the diet of murres, as did Swartz (1966:667) in his studies at Cape Thompson. Tuck cited depth records for murres which indicate that they are able to feed throughout the entire water column over the shelf portion of the Chukchi Sea. Since the birds at Cape Thompson are undoubtedly only a small fraction of the birds that utilize the southern Chukchi Sea, predation on fishes by birds must be intense over the entire region. However, bird predation could not have been a direct cause of the density structure during WEBSEC-70 because most birds appeared to have left the region prior to the time of our visit.

The hypothesis of negative phototaxis in juvenile Arctic cod had further appeal—it seems congruent to presumed needs for lowering vulnerability to predation by birds during summer when subsurface illumination is high while allowing for vertical foraging by the cod when illumination is low. Because piscivorous birds undoubtedly are visual feeders, directed or passive movement toward the surface by juvenile cod at night should not be counterselective. During the prolonged periods of low illumination of arctic winter, and under ice cover, juveniles presumably would be able to occupy the entire water column over the continental shelf. However, because larger juveniles, about 15 cm TL, were commonly seen in daylight near ice that had been broken by the icebreaker, negative phototaxis of the juveniles, if present, must decrease with growth in favor of life near a substrate. Changes from a pelagic to demersal existence during early growth stages is a commonplace in fishes.

Upwelling and downwelling seemed a plausible explanation of the differences in depth noted for the density structure. Salinity of the upper water column and an index of elevation or submergence of the density structure, explained below, showed good correlation (Table 6). The index was obtained for each station by algebraically projecting the pooled value for slopes of all regressions of number vs. depth, multidepth and replicate stations, through the station data, to the hypothetical apex of the density structure at the station. If the apex lay above the ocean surface (e.g., Figure 2, stations 41 and 70), the converted amount in meters was negative and was taken as the amount the density structure was elevated. If the apex lay below the ocean surface (e.g., Figure 2, stations 88 and 92), the converted amount in meters was positive and was taken as the amount the density structure was submerged. For each replicate station the regression was based on a point determined by depth of trawling and the average number of juvenile cod captured at the station. All indices for salinity were based on data for 10-18 m because this zone was the common depth of the replicate hauls; however, the water column was usually nearly isohaline from the surface to considerably below this depth (Figure 2).

Two sources of upwelling seemed possible—an accelerated current around the Cape Lisburne-Point Hope headland and wind over the sampling

TABLE 6.—Comparison of hypothetical elevation of the density structure of juvenile Arctic cod at the trawl stations taken at late dusk or after dark, based on density distribution of cod at each station, with surface salinity at a nearby station. Stations in order from greatest submergence (positive values) to greatest elevation (negative values) of the density structure. Projections for the multidepth stations were based on the data of Figure 2 fit to the standard slope of 0.0669; methods for obtaining projections from the replicate data are explained in the text.

IKMT station and type [1]	Indicated level of apex in meters	Closest oceanographic station	Average salinity at 10-18 m
88(M)	11.9	90	30.72
92(M)	10.5	91	30.67
37(R)	4.9	36	31.65
32(R)	0.5	31	30.85
30(M)	-0.7	29	31.11
51(M)	-2.1	50	31.32
65(M)	-3.4	64	31.19
25(R)	-5.0	24	31.00
56(M)	-8.0	55	31.43
20(R)	-12.2	19	31.72
22(R)	-12.5	19	31.72
45(M)	-12.8	43	31.76
16(R)	-15.3	18	31.11
74(M)	-17.3	73	31.77
70(M)	-17.4	55	31.43
61(M)	-22.0	62	30.76
10(R)	-24.8	9	31.56
41(M)	-26.0	42	31.63
80(M)	-26.1	84	31.47
	$r = -0.514$; $P<0.05$		

[1]M = multidepth station; R = replicate station.

area. Both should produce transient cells of upwelling and downwelling, but the wind-caused cells should have broader distribution.

Currents apparently flow predominantly northward in the southern Chukchi Sea and accelerate around headlands (Fleming and Heggarty, 1966: 744). Therefore, at an early stage in analysis, it appeared that the density structure of juvenile cod encountered during WEBSEC-70 may have been a result of bird predation off the Cape Lisburne-Point Hope headland or in Kotzebue Sound with subsequent vertical displacement of the density structure in an eddy north of Cape Lisburne. However, this hypothesis was rejected because, as mentioned previously, birds were not abundant during WEBSEC-70; most of them had probably left the region at least a month previously. Moreover, oceanic mixing should quickly dissipate a density structure that formed near the cape. The apparent occurrence of the structure over the entire sampling area indicated that it 1) was quite permanent, 2) was probably maintained by the juvenile cod, and 3) was not in very large measure induced by currents around Cape Lisburne. These requirements were satisfied by the hypothesis of negative phototaxis and wind-induced upwelling.

Horizontal Density Distribution of Juvenile Cod

Regardless of possible origins of the density structure or reasons for its vertical displacement, it was necessary to take the vertical elevation of the density structure (Table 7) into consideration when estimating the concentration and biomass of juvenile cod at each station. This correction was accomplished by regarding the density structure as a unit that extended downward 47 m (the depth equivalent on the density structure of the highest number of cod sampled) in undisturbed water. The structure would be truncated in its upper part by the ocean surface when raised, or truncated in its lower part when it intersected the ocean bottom because of lowering of the structure or shallowness of the sea. Thus, for a structure that appeared to be raised 10 m in the water column, the number of cod remaining in the structure was taken as the number that occurred between 10 and 47 m in an entire structure. If a structure appeared to be truncated by the ocean bottom for 17 m, the number of cod remaining in the structure was taken as the number between 0 and 30 m in an entire structure. Estimation of the density of

TABLE 7.—Reconstruction of numbers of juvenile cod beneath a standard swath at the IKMT stations, eastern Chukchi Sea.

Station (type)	Depth of tows (m)	Average $\log_{10}(N + 1)$	Indicated level of apex in meters[1]	Density structure: Depth of base (m)	Density structure: Juvenile cod (no.)	Depth of water (m)	No. cod below density structure	Total for column beneath swath
10(R)	11	2.3954	-24.8	22.2	4,698	44	7,883	12,581
14(R)	11	1.0397	-4.5	42.5	5,184	51	3,222	8,406
16(R)	11	1.7612	-15.3	31.7	5,138	53	8,073	13,211
20(R)	12	1.6159	-12.2	34.8	5,179	42	2,729	7,908
22(R)	12	1.6399	-12.5	34.5	5,176	35	([2])	5,366
25(R)	12	1.1380	-5.0	42.0	2,462	33	([2])	2,462
30(M)	—	regression	-0.7	46.3	1,268	31	([2])	1,268
32(R)	12	0.7751	0.5	47.5	547	26	([2])	547
37(R)	12	0.4758	4.9	51.9	4,162	49	([2])	4,162
41(M)	—	regression	-26.0	21.0	4,595	44	8,717	13,312
45(M)	—	regression	-12.8	34.2	5,173	44	3,714	8,887
51(M)	—	regression	-2.1	44.9	5,181	48	1,175	6,356
56(M)	—	regression	-8.0	39.0	[3]5,190	44	1,895	7,085
61(M)	—	regression	-22.0	25.0	4,891	29	1,516	6,407
65(M)	—	regression	-3.4	43.6	2,798	36	([2])	2,798
70(M)	—	regression	-17.4	29.6	5,088	39	3,563	8,651
74(M)	—	regression	-17.3	29.7	2,681	22	([2])	2,681
80(M)	—	regression	-26.1	20.9	4,586	30	3,449	8,035
88(M)	—	regression	11.9	58.9	1,492	45	([2])	1,492
92(M)	—	regression	10.5	57.5	3,968	54	([2])	3,968

[1]Negative values indicate apex above the surface.

[2]Stations at which hypothetical depth of bottom of density structure is deeper than the bottom. The number of juvenile cod represented by the overlap is subtracted from the total.

[3]In some instances the number of juvenile cod estimated for a density structure that was truncated at the surface was slightly higher than the theoretical number in an entire density structure. This discrepancy seems to be due to rounding errors in the integrations about the point where the parabolic equation approaches and forms a small angle with the x-axis. Since very few juvenile cod were present in the apex of the density structure, the error is small and probably unimportant.

juvenile cod below the presumed density structure was a problem because data from near bottom were not available for many stations. Therefore, the density of juvenile cod below the structure was assumed to be the maximum calculated for the density structure (i.e., that at 47 m in an entire structure). The possible error in estimating biomass of juvenile Arctic cod at the stations under this assumption was not judged to be serious because the sampling area was so shallow that the bottom of the density structure was usually close to the ocean bottom.

Although the transformed data on cod abundance vs. depth were useful for analyzing the density structure at the stations, back transformation of the estimates offered problems of interpretation. At present there appears to be no practical procedure for back transforming the variance and estimates of a logarithmic-arithmetic regression. Consequently, the density structure was redescribed from the untransformed data by fitting a parabolic regression with least squares (Figure 4). The variables were

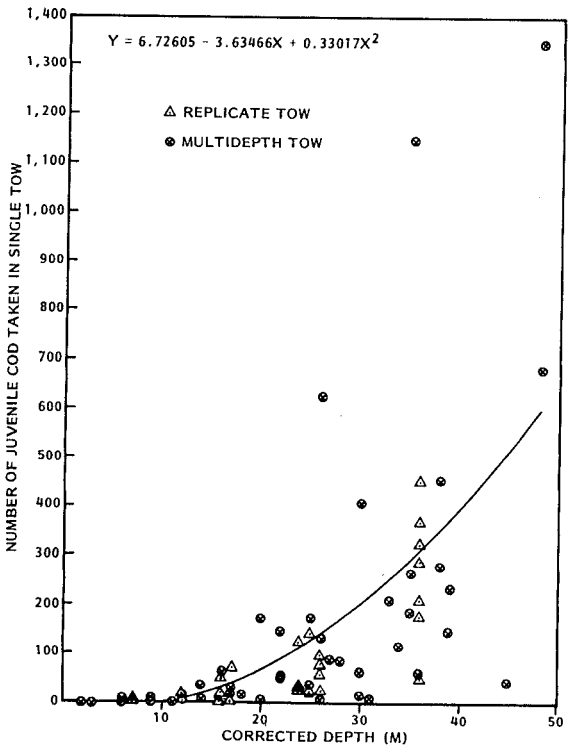

FIGURE 4.—Number of juvenile Arctic cod per Isaacs-Kidd tow, the depths corrected for apparent emergence or submergence of the density structure (Tables 6 and 7). Weighted regression ($1/X^2$) fitted by least squares.

weighted by the inverse of the corrected depth squared because the variance of number of cod vs. depth appeared to be linearly related to the square of the corrected depth. The result was

$$Y = 6.72605 - 3.63466X + 0.33017X^2$$

and its integration

$$Y^* = \int_U^L Y\ (X)\ dX$$

$$= 4.51413\ (L - U) - 1.21968\ (L^2 - U^2) + 0.07386\ (L^3 - U^3)$$

where Y = most likely estimate of number of cod in a tow at corrected depth.
X = corrected depth in meters.
Y^* = most likely estimate of the number of cod over the depth interval U-L in a trawl swath.
U = upper (shallower) level of depth interval, where $0 \leq U \leq L \leq 47$.
L = lower (deeper) level of depth interval.

Accordingly, the density structure contained approximately 5,186 juvenile cod over its depth range (0-47 m) over the area of a trawl swath. The most likely estimate of maximum density, at 47 m, was 379 cod/m of depth over the area of a trawl swath (5,519 m^2).

Under these assumptions, composite estimates of the number of juvenile Arctic cod in the water column beneath a standard trawl swath was calculated for all IKMT stations (Table 7). Totals for each station were obtained by adding the number of juvenile cod estimated for that section of the water column occupied by the density structure—5,186 over 47 m of depth except when the structure was truncated by the surface or bottom—to the hypothetical number in the column below the structure, or 379/m of depth. For the replicate stations, where only one depth was sampled, the hypothetical depth of the structure was obtained by comparing the average catch (log transformed data) at the trawling depth with the catch (log transformed data) that would be expected at that depth if the apex of the density structure coincided with the ocean surface. If this comparison indicated that the apex of the hypothetical structure was projected above

the ocean surface (indicated by minus values for level of apex in Tables 6 and 7) or below the ocean bottom, then the appropriate adjustments, discussed previously, were made. As a result, estimates of juvenile cod at the IKMT stations were influenced by both an inferred height of the density structure and the depth of water beneath the structure. Stations in relatively shallow water and with a deeply submerged density structure had the lowest estimates, and stations in water deeper than average and with density structures that reached to the surface had the highest. The average for all stations was 28.5 juvenile cod/1,000 m³ (Table 8).[3]

Biomass of juvenile Arctic cod in the area surveyed by WEBSEC-70 was estimated by converting the overall average concentration to volume and weight. Average volume of individuals in samples was 0.618 ml, with no apparent size segregation with depth (Figure 5). If we assume that the specific gravity of the cod approximated unity (actually they were heavier), then the stations averaged 17.6 g of juvenile cod/1,000 m³. If we take the area surveyed in the eastern Chukchi Sea as approximately 30 x 10^3 km² (8,714 square nautical miles) and the average depth as 40.0 m (the average for the 20 IKMT stations), then approximately 12 x 10^{11} m³ of ocean were contained in the sampling area. Thus, it appears that 211.2 × 10^8 g of fish were represented by this volume, or 211.2 × 10^2 metric tons, for an average of 0.7 metric ton/km² of ocean surface.

Where did the juvenile cod originate? Likely sources appear to be the Bering Sea, the East Siberian Sea, or the Chukchi Sea itself. The northwestern part of the Bering Sea has particularly low temperatures (Zenkevitch, 1963:824, 825) and water from the Gulf of Anadyr tends to flow northeastward (Zenkevitch, 1963:821). The East Siberian Sea, of course, also has low temperatures and apparently has an eastward-flowing current

[3]This compares with an arithmetic average of 7.3/1,000 m³ for the replicate hauls and 19.5 for the multidepth hauls—an average of 13.4 for all hauls. Thus, simple arithmetic averaging would seriously underestimate the value obtained under the hypothesis of density structure with upwelling and downwelling. Even higher values would be obtained if it is assumed that the density structure continued to increase at the same logarithmic rate below its depth of 47 m until the bottom was reached, instead of having the increase truncated at 47 m. This approach would require extrapolation well beyond all observed values for fish densities and would not be fully consistent with the welling part of the hypothesis.

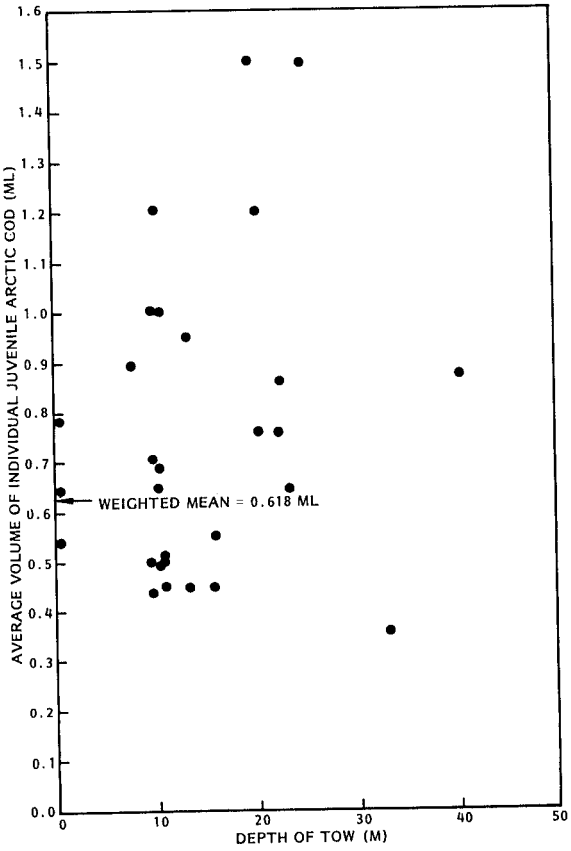

FIGURE 5.—Relation of average volume (milliliters) of individual juvenile Arctic cod in IKMT tow to depth of capture, eastern Chukchi Sea.

TABLE 8.—Estimated volume of water and number of juvenile cod beneath a standard swath at the IKMT stations, eastern Chukchi Sea.

Station	Volume of water beneath trawl swath (m³)	Juvenile cod/1,000 m³
10	242,836	51.8
14	281,469	29.9
16	292,507	45.2
20	231,798	34.1
22	193,165	27.8
25	182,127	13.5
30	171,089	7.4
32	143,494	3.8
37	270,431	15.4
41	242,836	54.8
45	242,836	36.6
51	264,912	24.0
56	242,836	29.2
61	160,051	40.0
65	198,684	14.1
70	215,241	40.2
74	121,418	22.1
80	165,570	48.5
88	248,355	6.0
92	298,026	13.3
Weighted average	—	28.5

into the Chukchi Sea (Zenkevitch, 1963:262). The near absence of high-arctic zooplankton in the eastern Chukchi Sea (Zenkevitch, 1963:268), verified during WEBSEC-70 by Wing (in press), is only weak evidence that the cod did not originate in the East Siberian Sea: the cod probably spawned in January and February (Rass, 1968:136), approximately 8 mo before WEBSEC-70, and it seems possible that the juveniles could have lost their arctic ecological associates over that period of time. In any event, the apparent short time that cod spent in some sections of the Chukchi Sea—about 10 days in the southeastern part according to the oceanographic data of Fleming and Heggarty (1966: 724)—and the time elapsed between spawning and capture at our IKMT stations is evidence that the juvenile cod either originated at considerable distances from the Chukchi Sea or had been cycled in the Chukchi Sea. Since there is reason to believe that a portion of the Chukchi Sea circulates in a counterclockwise gyre (Zenkevitch, 1963:262), similar cycling of eggs and larvae seems possible.

SUMMARY

1. Twenty stations in the eastern Chukchi Sea between Icy Cape and Cape Lisburne were sampled with a 1.8-m (6-foot) Isaacs-Kidd mid-water trawl (IKMT) during September and October 1970.

2. Only two species of fish occurred in any abundance in the middle and upper water column at night, juvenile Pacific sand lance and juvenile Arctic cod (mostly age 0). Because the Arctic cod were most abundant and were distributed through most of the water column, their occurrence was given a detailed analysis.

3. Two types of IKMT stations were occupied; one in which hauls were replicated at the same depth, and another in which hauls were made at several depths. All stations but one (a replicate station) were occupied starting at late dusk or at night.

4. The standard deviation in frequency of juvenile cod occurrence at the replicate stations seemed to be proportional to the means. The variance was stabilized by $\log_{10}(N + 1)$ transformation of the data.

5. Analysis of variance of the transformed data from the replicate stations disclosed significant between-station variation in number of cod occurring at 11-12 m.

6. Number of juvenile cod per unit volume of water increased with depth at all multidepth stations.

7. Analysis of covariance on regressions of cod abundance ($\log_{10}$ transformed) vs. depth disclosed no significant differences in slope of the regressions between stations but significant differences in level.

8. The characteristics of slope and level in the regressions for multidepth stations described a depth region of logarithmic increase in concentrations of juvenile cod. This region was at a different depth at some stations than at others and was called a density structure.

9. It appeared that the density structure resulted from a graded rather than a threshold response to subsurface illumination. Such a response seems to be a suitable behavioral strategy for lessening predation by piscivorous birds.

10. The hypothesis is presented that the density structure was formed during daylight hours and that differences in its vertical displacement between stations at night were caused by wind-induced upwelling or downwelling.

11. Average number of juvenile cod calculated for the stations was 28/1,000 m^3 or approximately 0.7 metric ton/km^2 of ocean surface.

12. The origin of juvenile cod could have been in the northeastern Bering Sea, the East Siberian Sea, the Chukchi Sea, or all three. Regardless of origin, a cycling of eggs and larvae within the Chukchi Sea seems likely.

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DESCRIPTION OF EGGS AND LARVAE OF SCALED SARDINE, *HARENGULA JAGUANA*[1, 2]

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ABSTRACT

Eggs and larvae of scaled sardine, *Harengula jaguana*, were described from specimens reared in the laboratory. Meristics, morphometrics, osteology, and pigmentation were examined as development proceeded. Transformation of larvae to the juvenile stage was complete at 22 to 24 mm standard length. During transformation outstanding features included forward movement of the dorsal fin, shortening of the gut, and forward movement of the anal fin. Eggs and larvae of scaled sardine were compared with those of other clupeids that may occur in the same areas. An illustrated series of scaled sardine eggs and larvae, including details of the caudal fin, was presented to show changes that occur during development.

Scaled sardines, *Harengula jaguana* Poey, are common clupeids in the tropical western Atlantic (Rivas, 1963). Until recently they were known as *H. pensacolae* Goode and Bean, 1879, but Whitehead (1973) has concluded that the correct name for the species is *Harengula jaguana* Poey, 1865. Scaled sardines prefer coastal habitats and have been reported from New Jersey to Brazil; they are abundant in the Gulf of Mexico (Briggs, 1958; Rivas, 1963; Berry, 1964b). Despite their common occurrence, larvae have not been described. Matsuura (1972) has described artificially fertilized and planktonic eggs of this species. Fecundity, maturation, and spawning of scaled sardines recently were reported by Martinez (1972). Eggs have been collected in south Florida, and the larvae reared to juvenile sizes in the laboratory (Houde and Palko, 1970; Detwyler and Houde, 1970; Saksena and Houde, 1972). Eggs and larvae from these experiments have provided us with material to describe early development.

Scaled sardines support a small bait fishery in south Florida and are important forage for predatory fishes like Spanish mackerel, *Scomberomorus maculatus* (Klima, 1959). They are caught for human consumption throughout the West Indies and are canned in Cuba and Venezuela (Rivas, 1963). Scaled sardines are one of the clupeid species that may have potential to support reduction fisheries in the tropical Atlantic.

Eggs and larvae of other species attributed to the genus *Harengula* have been described. Uchida et al. (1958) described larvae and juveniles of *H. zunasi* from Japan, and Takita (1966) described eggs and newly hatched larvae of that species. Whitehead, Boeseman, and Wheeler (1966) stated that this species is in fact a *Sardinella*, based on skeletal characters. Marchal (1967) included *H. rouxi* in his key to some west African clupeid eggs and larvae. Berry (1964a) and Berry and Whitehead (1968) restricted the genus *Harengula* to members having paired hypomaxillary bones. Neither *H. rouxi* nor *H. zunasi* have hypomaxillaries, and both species presumably belong in the genus *Sardinella*.

METHODS

Eggs were collected in surface tows of plankton nets near Miami Beach and in Biscayne Bay, Fla. during 1969 through 1971. A total of 10 embryos and 165 larvae from rearing experiments were preserved in 5% Formalin[6] to describe

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[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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development. Rearing methods have been described (Houde and Palko, 1970; Saksena and Houde, 1972). Scaled sardines can be reared successfully at temperatures from 21° to 33.5°C (Saksena, Steinmetz, and Houde, 1972), and salinities have ranged from 29 to 37‰. Larvae and juveniles up to 38.7 mm standard length are included in this description, but we have reared scaled sardines to more than 100 mm in some experiments.

Morphometrics

Eggs and larvae were measured with an ocular micrometer in a dissecting microscope. The following measurements were made:

Total length (TL)—Tip of snout to end of caudal fin.

Standard length (SL)—Tip of snout to tip of notochord on small larvae, before notochord flexure; tip of snout to base of hypural plate on larger larvae, after notochord flexure. Unless otherwise noted, all references to lengths of larvae in text refer to standard lengths.

Preanus length—Tip of snout to anus, measured along midline. This measurement is equivalent to preanal fin length for specimens that have the anal fin developed.

Predorsal length—Tip of snout to origin of dorsal fin, measured along midline of body.

Prepelvic length—Tip of snout to origin of pelvic fins, measured along midline of body.

Head length—Tip of snout to posterior margin of otic capsules in yolk-sac larvae; tip of snout to opercular margin in older larvae.

Snout length—Tip of snout to anterior margin of eye.

Eye diameter—Horizontal distance between anterior and posterior edges of the fleshy orbit.

Body depth—Vertical height of the body at the pectoral symphysis.

Meristics

Fin rays were counted in each of the developing fins (Table 4). Myomeres were counted and designated as follows:

Total myomeres.

Preanal myomeres: number anterior to the anus.

Postanal myomeres: number posterior to the anus.

Predorsal myomeres: number anterior to the dorsal fin origin.

Postdorsal—preanal myomeres: number between the posterior insertion of the dorsal fin and the anus.

Osteology

Sequence of ossification was determined from a total of 16 specimens ranging in length from 4.8 to 22.4 mm. They were cleared with trypsin and stained with alizarin using the method of Taylor (1967). Development of the caudal fin bones was examined in detail. Ossification of fin rays, vertebrae, and head bones also was examined.

DESCRIPTION

Description and Occurrence of Embryos

Ten fertilized eggs from plankton collections were spherical, ranging from 1.55 to 1.78 mm in diameter (mean = 1.66 mm). They had a single, light yellow oil globule ranging from 0.07 to 0.10 mm in diameter (mean = 0.09 mm). Measurements did not differ from artificially fertilized eggs described by Matsuura (1972). Embryos were well developed when preserved (Figure 6A), and yolk diameters ranged from 0.63 to 0.72 mm at that time. The perivitelline space was wide, averaging 58% of the egg diameter for the 10 preserved specimens. In living embryos, the yolk is clearly segmented, but segments are difficult to see in preserved specimens. The chorion is thin, unpigmented, and unsculptured; it is fragile and easily broken compared to most teleost eggs. Preserved embryos had no discernible pigment. Living embryos, just prior to hatching, had tiny melanophores, which were difficult to see, in a paired dorsolateral series near the dorsal midline.

Embryos that were collected from mid-May through July were well developed by noon when our collections were examined (Figure 7). Surface water temperatures were 28°C or higher in the spawning area. Spawning presumably occurs only at night because embryos are all at similar stages of development when collected in the morning. Hatching usually began by late after-

noon, less than 24 h after the presumed spawning time.

The spawning season extends from February through July near Miami, based on our collections of planktonic eggs. Spawning may occur within Biscayne Bay from late February through early May but is confined to more offshore areas later in the season. Biggest egg collections were made about 4 km east of Miami Beach during May and June. Martinez (1972) confirmed the spawning season of scaled sardines by determining gonad indices and examining ovarian maturation of adults collected throughout the year from south Florida.

Description of Larvae

Body Shape

Larvae were 2.4 mm at hatching. The head was bent over the large, nearly spherical yolk sac. Yolk was absorbed and the body axis straightened during the next 12 h at 26° to 28°C. By 12 to 15 h after hatching, larvae were typically clupeoid (Figure 8A). They were elongate, thin larvae averaging 4.4 mm at 15 h after hatching. The gut was a long straight tube at this stage. Little growth occurred during the first 3 days after hatching. Thereafter, growth was rapid and temperature-dependent (Saksena et al., 1972). Larvae retained the typically elongate and rodlike shape until they transformed to juveniles when they became deeper bodied and laterally compressed. Proportional measurements of larvae in relation to standard length are given in Table 1.

Yolk Absorption and Gut Differentiation

Absorption of the nearly spherical yolk mass in newly hatched larvae was rapid at 26° to 28°C. The oil globule was located ventrally and just posterior to the middle of the yolk mass in newly hatched larvae (Figure 8A). By 48 h after hatching the yolk sac and oil globule had been absorbed, and larvae were actively feeding. The gut was a straight tube at 15 h after hatching (Figure 8A), but a distinct foregut and hindgut were present at 2 days (Figure 8B). By 4 days (at about 5.0 mm) the hindgut appeared to be composed of a series of adjacent muscular rings, typical of clupeid larvae.

Total Length and Standard Length

Standard length was used to examine development of scaled sardine larvae with respect to other morphometric data. The relation between standard length and total length (Table 1, Figure 1) was not linear over all sizes of larvae that were available. Standard length decreased relative to total length as larvae grew. Standard length was about 97% TL for larvae between 4 and 8 mm TL but decreased to 85% TL for larvae between 8 and 25 mm TL. The ratio averaged about 83% TL for individuals longer than 25 mm TL. The observed decrease between 8 and 25 mm TL was related to development of the caudal fin, particularly notochord flexure and hypural plate development.

Preanus Length

Preanus length averaged 83% SL at 15 h after

TABLE 1.—Summary of relationships between total lengths (TL) and standard lengths (SL), and proportional measurements relative to standard lengths for larvae used to describe *Harengula jaguana* development. Proportions are from data fitted by eye to relationships in Figures 1 to 5.

TL (mm)	SL (mm)	SL:TL	Preanus length: SL	Predorsal length: SL	Body depth: SL	Head length: SL	Snout length: SL	Eye diameter: SL	Prepelvic length: SL
4.3	4.2	0.977	0.833	—	0.064	0.119	0.017	0.045	—
6.2	6.0	.968	.867	—	.067	.133	.025	.042	—
8.2	8.0	.978	.888	0.680	.064	.138	.031	.041	—
10.8	10.0	.926	.890	.648	.081	.157	.036	.041	—
13.0	12.0	.923	.900	.626	.087	.167	.040	.043	0.440
15.4	14.0	.909	.864	.600	.100	.185	.047	.050	.447
18.5	16.0	.865	.838	.556	.125	.204	.052	.056	.466
20.8	18.0	.865	.822	.517	.142	.217	.057	.057	.467
23.1	20.0	.866	.780	.478	.162	.240	.066	.064	.462
25.6	22.0	.859	.764	.441	.184	.264	.072	.073	.465
29.0	24.0	.828	.775	.417	.219	.262	.072	.075	.482
31.5	26.0	.825	.758	.404	.236	.260	.072	.077	.485
33.6	28.0	.833	.750	.408	.245	.257	.071	.075	.481
36.0	30.0	.833	.750	.410	.252	.257	.071	.074	.482
38.5	32.0	.831	.750	.409	.262	.250	.071	.073	.482

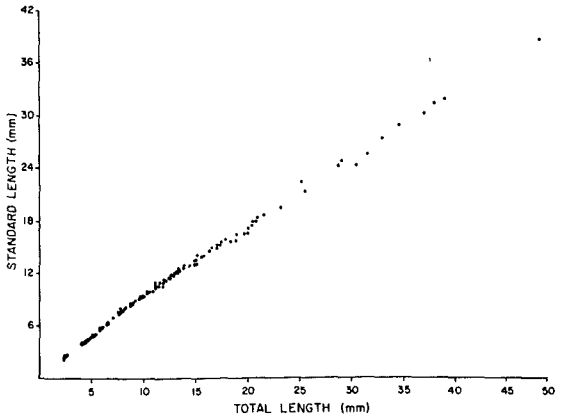

FIGURE 1.—Relation between standard length and total length for larvae of *Harengula jaguana*.

hatching and increased to about 90% SL when larvae were 12 mm (Table 1, Figure 2). A gradual decrease in preanus length occurred in larger larvae. At 22 mm, preanus length was 76% SL; juveniles 28 to 32 mm had preanus lengths that averaged 75% SL. Decreasing preanus length in larger larvae was caused by shortening of the gut during transformation to the juvenile stage.

Head Length

Head length increased relative to standard length from 12% at 4.2 mm to 26% at 22.0 mm (Table 1, Figure 3). The ratio was constant at 25 to 26% SL for specimens between 22 and 38.7 mm, which falls within the range of variation in head lengths reported for juvenile and adult *H. pensacolae pensacolae* (Rivas, 1950).

Eye Diameter

Eye diameters averaged 4.0 to 4.5% SL for specimens 4.2 to 12 mm (Table 1, Figure 4). A rapid increase in eye diameters from 4.3 to 7.3% SL occurred in specimens 12 to 22 mm. Eye diameters on specimens longer than 22 mm varied, but no increasing trend relative to standard length was observed. A 38.7-mm specimen had an eye diameter of 7.8% SL. Eye diameters were variable for larvae of a given length (Figure 4); for example, at 12 mm, eye diameters varied from about 3.5 to 5.5% SL. Rivas (1950) and

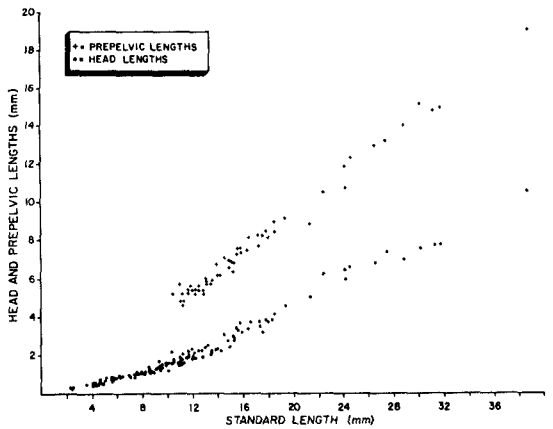

FIGURE 3.—Relation of head length and prepelvic length to standard length for larvae of *Harengula jaguana*.

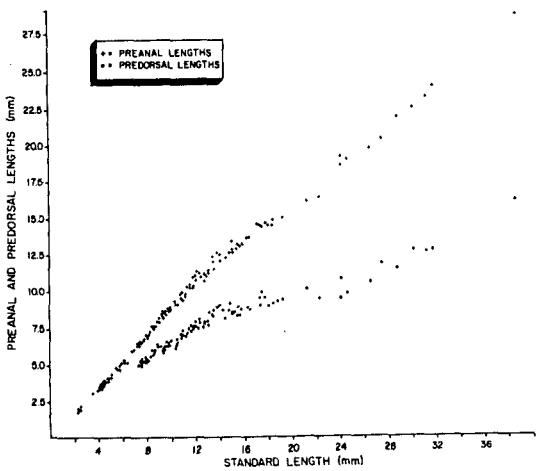

FIGURE 2.—Relation of preanal length and predorsal length to standard length for larvae of *Harengula jaguana*.

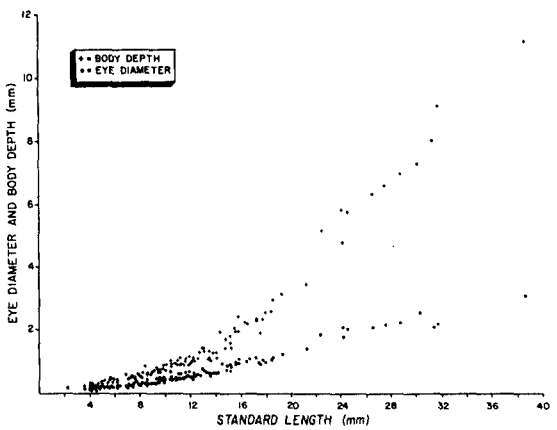

FIGURE 4.—Relation of eye diameter and body depth to standard length for larvae of *Harengula jaguana*.

Storey (1938) found eye diameters to be variable for juvenile and adult *H. pensacolae.*

Snout Length

Snout length increased from 1.7 to 7.2% SL for larvae between 4.2 and 22.0 mm (Table 1, Figure 5). It remained constant for longer larvae at about 7.2%, which is within the range of variation for juvenile and adult *H. pensacolae* (Rivas, 1963). Like eye diameters, snout lengths varied considerably for larvae of a given size; for example, at 12 mm, snout length varied from about 3.1 to 4.8% SL.

Body Depth

Body depth at the pectoral symphysis was constant at about 6.5% SL for larvae from 4.2 to 9.0 mm. Body depth then increased rapidly from 7.0 to 21.9% SL for specimens between 9.0 and 24.0 mm SL. A slow increase continued to occur for larger individuals (Table 1, Figure 4).

Predorsal Length

Predorsal lengths, as measured from the snout to the first developing ray in the dorsal fin, were recorded on specimens 7.5 mm and longer, when the rays began to develop. The dorsal fin moves forward as development proceeds, causing predorsal length to decrease from 68.0% SL to 41.7% SL for larvae between 7.5 and 24.0 mm (Table 1, Figure 2). Predorsal lengths averaged 41% SL for specimens longer than 24.0 mm.

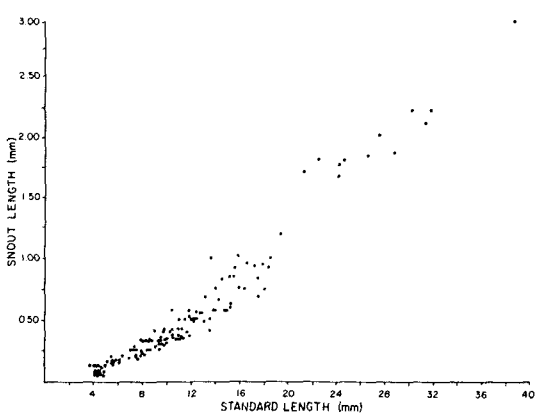

FIGURE 5.—Relation of snout length to standard length for larvae of *Harengula jaguana.*

Prepelvic Length

Prepelvic lengths were measured on larvae that had pelvic fin buds or fins. At 11 to 12 mm, prepelvic lengths averaged about 44% SL, increasing to 46% SL for larvae up to 22 mm (Table 1; Figure 3). Prepelvic lengths averaged 48% SL for specimens between 24 and 38.7 mm. Pelvic fins moved slightly posterior as larvae transformed to juveniles, causing the observed small increase in prepelvic length.

Meristics

Myomeres

Total numbers of myomeres ranged from 39 to 42; most larvae had 40 or 41. Numbers of myomeres and distribution of myomeres in relation to other body parts can be useful for identifying clupeid genera (Ahlstrom, 1968). Total myomeres could be counted accurately on 144 of our larvae. Frequencies were as follows:

Number of myomeres	39	40	41	42
Frequency	2	68	67	7

The mean number of myomeres was 40.56 ($S_{\bar{x}} = 0.2861$).

Distribution of myomeres in relation to the dorsal fin and anus was examined for larvae in 2-mm size classes (Table 2). Preanal myomeres decreased as larvae grew from about 35 for the smallest larvae to 27 at transformation. Postanal myomeres increased from a mean number of 5.7 for the smallest larvae to more than 12 for transformed specimens. Shortening of the gut during development accounted for the observed changes in preanal and postanal myomere counts. Mean numbers of predorsal myomeres decreased rapidly from about 25 to 10 as development proceeded, reflecting the anterior movement of the dorsal fin. Considerable variation in predorsal myomere numbers was present for larvae of a given length (Table 2). Postdorsal-preanal myomeres ranged from 5 to 7 for larvae of all sizes, but the mean number tended to decrease as larvae grew from 8 to 22 mm.

Fin Development

Newly hatched larvae had a fin fold that invested much of the body and which persisted in

TABLE 2.—Distribution of myomeres relative to other body parts for *Harengula jaguana* larvae.

Size class (mm, SL)	Preanal myomeres			Postanal myomeres			Predorsal myomeres			Postdorsal-preanal myomeres		
	Number of specimens	Mean	Range	Number of specimens	Mean	Range	Number of specimens	Mean	Range	Number of specimens	Mean	Range
4.0- 6.0	34	34.85	34-36	36	5.67	5-7	—	—	—	—	—	—
6.1- 8.0	16	35.00	34-36	17	5.53	5-7	11	24.82	23-26	12	6.67	5-7
8.1-10.0	22	34.68	33-36	22	6.09	5-7	22	23.41	22-25	22	6.50	5-7
10.1-12.0	18	33.72	32-35	18	6.89	6-8	18	21.61	20-24	18	6.00	5-7
12.1-14.0	15	33.47	32-35	15	7.20	6-8	15	21.07	20-23	15	5.67	5-7
14.1-16.0	12	32.08	30-34	12	8.25	7-9	12	18.75	16-22	12	5.42	5-6
16.1-18.0	6	31.67	31-33	6	8.50	8-9	6	17.17	16-19	6	5.50	5-6
18.1-20.0	4	31.00	31	4	9.25	9-10	4	15.25	15-16	4	5.50	5-6
20.1-22.0	1	29.00	29	1	11.00	11	1	13.00	13	1	5.00	5
>22.0	4	27.25	26-28	4	12.75	12-14	4	10.00	8-11	4	6.25	6-7

part until larvae were about 16 mm. Pectoral fin buds were present at hatching (Figure 8A), but no other fins were developed at this stage. An opaque area in the fin fold was the first indication of median fin development. Rayed fins developed in the following sequence: dorsal, caudal, anal, pelvics, pectorals. Fin rays first develop as cartilaginous structures; thus, the sizes of larvae at which full complements are present may be smaller than the sizes at which rays are fully ossified. Tables 3 and 4 summarize fin development sequence of scaled sardine larvae, and details are discussed in the osteological development section.

Median fin development usually was completed at 16.0 mm. Dorsal fin rays first appeared between 7.0 and 7.5 mm. A full complement of 17 to 19 rays was present at 14.0 to 17.0 mm. Principal caudal rays were first seen at 7.4 to 8.0 mm, and the full complement of 19 usually was attained at 10.0 mm. Some specimens as small as 8.5 mm had the full complement of principal caudal rays; a few specimens did not have a full complement until they were longer than 11.0 mm. Secondary caudal rays developed at 10.8 to 12.8 mm, and the full complement of 8 or 9 dorsal and 7 ventral secondary caudal rays was present at 16.5 to 19.0 mm. Notochord flexure, which occurs during caudal fin development, began at the same size that principal caudal rays first developed. Anal fin rays usually began to develop at 9.0 to 9.3 mm, but two specimens 8.5 to 9.0 mm had some anal rays. A full complement of 17 or 18 anal rays was present at 13.0 to 15.0 mm. Although principal caudal and anal fin rays began to develop after dorsal fin rays, the dorsal was the last median fin to attain its full ray complement.

Paired fins began to develop after median

TABLE 3.—Summary of fin development sequence in larvae of *Harengula jaguana*.

Fin	Buds first appear	Standard length (mm)[1] Rays first appear	Standard length (mm)[1] Full complement of rays	Number of rays in fully developed fin
Dorsal	—	7.0 to 7.5	14.0 to 16.0	17 to 19
Caudal				
Principal	—	7.4 to 8.0	8.5 to 11.0 (most by 10.0)	19
Secondary	—	10.8 to 12.8	16.5 to 19.0	8 or 9 dorsally 7 ventrally
Anal	—	9.0 to 9.3 (rarely at 8.5 to 9.0)	13.0 to 15.0	17 or 18
Pelvic	11.0-12.0 (rarely at smaller size)	13.0 to 14.0 (rarely at <13.0)	14.6 to 17.8 (most by 15.5)	7 or 8 (usually 8)
Pectoral	<4.0	15.0 to 16.0 (rarely at smaller size)	18.5 to 19.5	14 to 16

[1]Rays were present at the tabulated lengths, but not necessarily ossified at those sizes.

TABLE 4.—Some meristic characters of larval and juvenile *Harengula jaguana*.

Standard length (mm)	Caudal rays	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays
2.3-6.9	No elements present on 48 specimens in this size range				
7.0	—	5	—	—	—
7.3	No elements present on this specimen				
7.4	3	6	—	—	—
7.4	—	6	—	—	—
7.5	—	8	—	—	—
7.5	—	3	—	—	—
7.6	No elements present on this specimen				
7.6	—	9	—	—	—
7.7	—	7	—	—	—
7.8	2	9	—	—	—
7.9	3	8	—	—	—
7.9	5	9	—	—	—
8.0	—	8	—	—	—
8.0	2	5	—	—	—
8.1	3	6	—	—	—
8.3	6	11	—	—	—
8.5	19	14	3	—	—
8.6	6	11	—	—	—
8.6	10	11	—	—	—
8.6	—	2	—	—	—
8.9	4	8	—	—	—
9.1	15	8	—	—	—
9.1	15	12	5	—	—
9.4	8	12	3	—	—
9.4	19	12	8	—	—
9.4	19	13	5	—	—
9.4	10	9	3	—	—
9.5	15	10	—	—	—
9.5	3	9	—	—	—
9.7	19	12	8	—	—
9.7	19	12	8	—	—
9.8	19	14	6	—	—
9.8	17	13	7	—	—
9.8	19	12	6	—	—
10.0	19	14	9	—	—
10.0	8	10	—	—	—
10.4	19	14	9	—	—
10.4	18	16	15	—	—
10.5	19	15	10	—	—
10.5	19	13	10	—	—
10.9	14	11	2	—	—
10.9	19	16	12	—	—
11.0	17	14	3	—	—
11.0	17	9	3	—	—
11.2	19	14	11	—	—
11.3	19	16	12	—	—
11.3	19	15	11	—	—
11.5	19	13	10	—	—
11.7	19	17	4	—	3
11.7	19	13	9	—	—
11.9	19	14	13	—	—
11.9	19	16	15	11	5
12.0	19	14	10	—	—
12.1	19	14	8	—	—
12.2	19	16	13	—	—
12.3	19	15	9	—	—
12.4	19	14	8	—	—
12.7	19	15	12	—	—
12.8	19	15	12	—	—
12.8	19	15	10	—	—
13.0	19	17	17	9	5
13.1	19	17	16	—	2
13.1	19	17	15	—	6
13.5	19	14	11	—	—
13.6	19	15	9	—	—
13.7	19	16	12	—	—
13.9	19	17	11	—	—
14.0	19	16	12	—	—
14.2	19	16	14	—	—
14.6	19	17	17	12	7
14.9	19	16	16	—	4
14.9	19	17	16	—	6
15.2	19	17	17	—	7
15.2	19	17	17	5	6
15.2	19	18	15	—	3
15.5	19	17	15	10	8
15.6	19	18	15	10	7
15.8	19	17	17	13	7
15.9	19	17	17	—	7
16.4	19	18	17	11	7
16.6	19	17	17	12	8
17.3	19	19	17	14	8
17.4	19	19	17	13	8
17.5	19	18	17	—	6
17.8	19	18	17	12	6
18.0	19	18	17	12	7
18.4	19	18	18	13	8
18.6	19	18	16	15	7
19.3	19	17	17	14	8
21.3	19	18	17	15	8
22.4	19	17	17	14	8
24.2	19	17	18	14	8
24.2	19	18	17	15	7
24.7	19	18	18	14	7
26.7	19	17	18	14	8
27.5	19	18	18	15	7
28.9	19	17	18	15	8
30.2	19	17	18	15	8
31.4	20	18	17	16	8
31.8	19	17	18	14	8
38.7	19	17	17	15	7

fins. Rayless pectoral fins were present soon after hatching, but rays usually did not develop until larvae were 15.0 to 16.0 mm. One specimen had some pectoral rays at only 11.9 mm, but this was unusual. Full complements of 14 to 16 pectoral rays were attained at 18.5 to 19.5 mm. Pectorals were the last fins to complete development. Pelvic fins first appeared as buds when larvae were 11.0 to 12.0 mm; most specimens had pelvic buds at 11.3 mm. Pelvic rays usually began to develop at 13.0 to 14.0 mm, but one 11.7-mm specimen had rays. A full complement of 7 or 8 (usually 8) pelvic rays was present at 14.6 to 17.8 mm. Most specimens had complete pelvic fins by 15.5 mm.

Scales

Scale development apparently occurred at 21 to 22 mm. No specimens from 18.5 to 21.2 mm were scaled. The illustrated specimen 21.3 mm (Figure 10C) was fully scaled as were 4 specimens from 22.4 to 24.2 mm.

Osteological Development

Sixteen cleared and stained specimens provided a record of sequence of development of skeletal structures in scaled sardine larvae. Bones stain as a result of calcification, but many bones, though unstained, were discernible before

calcification as distinct cartilaginous structures. Our four smallest specimens (4.8, 6.2, 6.5, and 8.9 mm) showed no evidence of staining and only slight indication of developing bone structures. Our first specimen to show clear evidence of stain uptake and well-formed cartilaginous structures was 10.9 mm. The only bone which was stained in this specimen was the cleithrum. The next bones to stain (an 11.5-mm specimen) were the maxillaries, dentaries, principal caudal fin rays, hypurals, and parhypural. Ossification then proceeded rapidly as larvae grew.

The Caudal Fin Complex

Clupeids have a complex caudal fin, and for descriptive purposes we follow the terminology of Nybelin (1963). The adult caudal fin has the following structures: 2 ural vertebrae, 6 hypurals, a parhypural associated with the first preural vertebra, 19 principal caudal rays (the lower and upper are unbranched, the remainder branched), 2 or 3 epurals, 3 pairs of uroneurals, 8 or 9 dorsal secondary caudal rays, 7 ventral secondary caudal rays, and a modified neural arch and spine on the first preural vertebra. In a 9.9-mm specimen the parhypural and the first four hypurals were visible (but not stained) as distinct cartilage entities (Figure 6A). A noticeable gap was present between the second and third hypural which persisted to the adult stage and separated the 9 lower from the 10 upper principal caudal rays.

The association of individual principal caudal fin rays with the parhypural and hypurals was nearly constant. Our method of counting principal caudal rays was anterior to posterior or, after notochord flexion, ventral to dorsal. The hypurals were counted similarly. The first two principal rays articulated with the parhypural, rays 3 to 7 articulated with the first hypural (in specimens larger than 15.0 mm ray 8 also associated with this hypural); rays 8 and 9 with the second hypural; rays 10 to 14 with the third hypural; rays 15 and 16 with the fourth hypural; rays 17 and 18 with the fifth hypural; and ray 19 with the sixth hypural. Rays 1 and 19 were stained deepest, and staining decreased medially indicating that rays 9 and 10 were the last to ossify although these rays were the first to develop.

In the 11.5-mm specimen (Figure 6B) there was a slight indication of ossification of the first pair of uroneurals and the neural arch of the first preural vertebra. The hypurals were all stained as was the parhypural and hemal spine of the second preural vertebra. In the 11.9-mm specimen the first uroneural pair was well stained as was the second uroneural pair, and the second ural centrum was deeply stained. The second uroneural lay just posterior to the second ural vertebra along the plane of the notochord. The first uroneural originated above an area that became the first preural centrum, but there was no indication of the centrum at 11.9 mm. The first uroneural extended along the notochord over the second ural centrum and ended midway along the second uroneural. The second uroneural extended from the second ural centrum to the origin of the sixth hypural. Two other structures were discernible but not stained at 11.9 mm—the hemal spines of the second and third preural vertebrae and the posteriormost ventral secondary caudal fin ray.

In the 12.0-mm specimen, little change occurred. In the 12.4-mm specimen, all the structures mentioned above were more deeply stained, and the neural and hemal spines of the second preural vertebra (though this vertebra is undifferentiated) were stained (Figure 6C). Of particular interest in this specimen was the marked similarity of the hemal spine of the second preural vertebra to the parhypural. Nybelin (1963) considered the parhypural to be a hemal spine, and our observation bears this out in as much as the caudal artery goes through this bone rather than over it. Monod (1968) has referred to the hemal spine of the first preural centrum as the parhypural bone and Hollister (1936) considered this bone to be a hypural. We use the term parhypural because it has characteristics of both a hypural bone and a hemal spine. During its development, it closely resembles a hypural and in fact is joined to the first hypural (see Figure 6D), and it bears two principal caudal rays. Both spines of the two preural vertebrae are flattened bones with developing hemal arches between the spine base and the notochord. In the 14.0-mm specimen, the first preural centrum and the two ural centra were stained as was the lower portion of the second preural centrum. The posteriormost ventral secondary caudal ray was stained. A neural arch was visible, though unstained on the first pre-

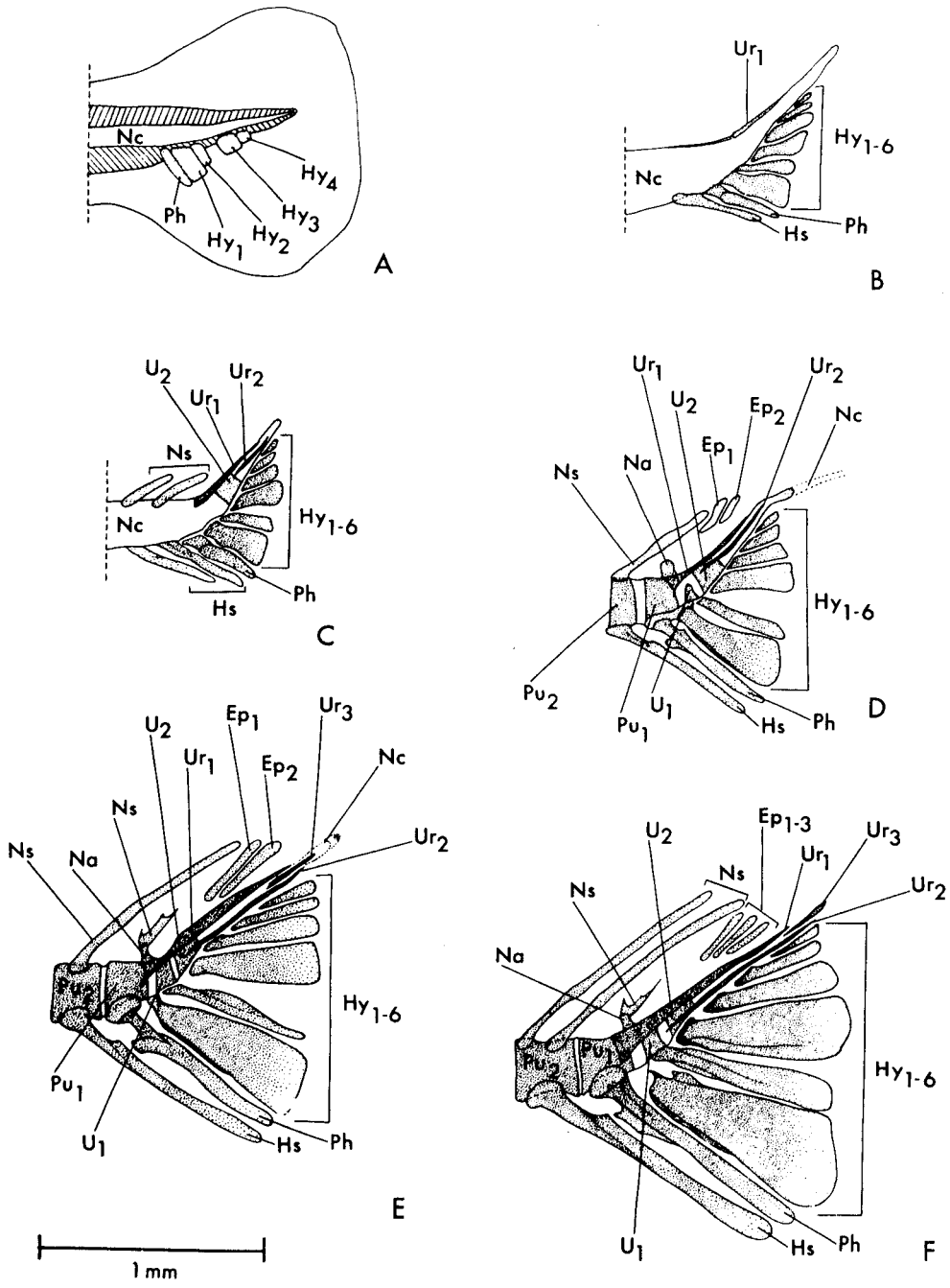

FIGURE 6.—Development of the caudal fin structures in larvae of *Harengula jaguana*. Fin rays are omitted from the illustrations to show the supporting structures more clearly. Standard length of specimens: A, 9.9 mm; B, 11.5 mm; C, 12.4 mm; D, 14.9 mm; E, 18.0 mm; F, 19.3 mm. Abbreviations: HY_{1-6} = hypurals, Ep_{1-3} = epurals, U_1 and U_2 = ural vertebrae, P_{u1} and P_{u2} = preural vertebrae, Hs = hemal spine, Nc = notochord, U_{r1}-U_{r3} = uroneurals, Ns = neural spine, Na = neural arch, Ph = parhypural.

ural centrum and was not connected to the first uroneural base.

In the 14.9-mm specimen major features included an ossified area on the notochord posterior to the sixth hypural (Figure 6D). This structure apparently was temporary; it was not the third uroneural and it was not as clearly observed in larger specimens. Four upper secondary caudal rays were visible though only the posteriormost was stained. Three lower secondary caudal rays also were present with only the posteriormost stained. Two epurals were barely discernible and were not stained. The "hemal archlike" bone of the parhypural changed shape and appeared as a forked bone which received the spine of the parhypural between its forks. This small hemal archlike bone also supported the first hypural and abutted the first preural centrum, the notochord between the first preural centrum and the first ural centrum, and the first ural centrum itself. The third hypural abutted the second ural centrum, and the remaining hypurals abutted the notochord. At this stage, it was obvious that the first uroneural was fused to the first preural centrum. The second uroneural was free and never fused with any bone.

In the 15.6-mm specimen, seven upper secondary caudal rays and four ventral secondary caudal rays were stained. Two epurals were visible but weakly stained. An anteriorly directed flange or expansion had developed on the base of the parhypural. Its supporting hemal arch structure was distinct and not fused with the flange. The neural arch on the first preural vertebra was beginning to ossify. In the 16.6-mm specimen, the third uroneural was visible, lying lateral to the second uroneural. It was shaped like the second uroneural but was much smaller and appeared as a well ossified splintlike bone. The ossified area above the sixth hypural that was noted in the 14.9-mm specimen was not present. Three epurals were visible but not ossified. The full complement of secondary caudal rays was present—eight upper, seven lower.

In the 18.0-mm specimen, several significant changes were evident (Figure 6E). First, only two epurals were present, and they were slightly stained. This probably was the result of individual variation since three were observed in the 16.6-mm specimen. The neural arch of the first preural vertebra had developed an upward projecting spinelike process. This neural arch lay over the posterior dorsal surface of the first preural centrum between the bases of the left and right first uroneural. We did not verify that the dorsal nerve passes through this arch; thus this neural arch and spine of the first preural vertebra could be some other bone. Fusion had not taken place between the neural arch and the first uroneural bases in this specimen. The first hypural no longer touched the first preural centrum, and a remnant of its hemal archlike base remained between the vertebra and the hypural. The first or anteriormost upper and lower secondary caudal fin rays lay parallel to the body axis rather than slightly vertical as in smaller specimens. The third uroneural lay immediately above and posterior to the second uroneural.

Little difference was noted between the 19.3-mm and the 18.0-mm specimen except for the complete absence of the hemal archlike support of the first hypural in the larger specimen (Figure 6F). Three epurals were present but were still only faintly stained. Without doubt, these were the last components of the caudal fin to ossify. In this specimen, there were nine upper and seven lower secondary caudal rays. The second preural vertebra had the anomalous condition of bearing two neural spines.

All three uroneurals are paired and obviously provide rigid support for the notochord as the tail develops. As a result, the first and second uroneurals are among the first tail bones to ossify. The ossified first uroneural fuses to the first preural centrum after the centrum becomes ossified. The other uroneurals were not fused to any bone in the *Harengula* we examined nor were they fused to other bones in large larvae of *Opisthonema* (Richards, Miller, and Houde, 1974).

Dorsal and Anal Fins

Ossification of dorsal fin rays was first observed in the 11.9-mm specimen. Twelve rays in the midregion of the developing fin were faintly stained. Supporting pterygiophores for these rays also were faintly stained. About eight unstained anal rays were visible, but no supporting pterygiophores were seen. In the 12.4-mm specimen, 12 dorsal rays also were stained but these were the last 12 rays of the fin. Supporting pterygiophores for these rays also were stained.

The anal fin rays showed only slight staining. The 14.0-mm specimen had 15 ossified dorsal rays and pterygiophores; the anal had 11 unstained rays and pterygiophores. At this size, the vertebrae were countable and the dorsal rays were over the 24th to 29th vertebrae. The anal fin was beneath the 34th to 38th vertebrae. In the 14.9-mm specimen, 17 ossified dorsal rays were present and were over the 20th to 27th vertebrae. The anal fin had 15 faintly stained rays and visible but unstained pterygiophores. This fin was under the 33rd through 38th vertebrae. In the 15.6-mm specimen, the anal fin pterygiophores were well ossified. Seventeen dorsal pterygiophores supported 18 rays (1 pterygiophore supported the first 2 rays), and 14 anal pterygiophores supported 15 ossified anal rays (1 pterygiophore supporting the first 2 rays). In that specimen, the dorsal fin was over the 19th to 27th vertebrae, the anal under the 33rd to 37th vertebrae. In the 16.4-mm specimen, 18 dorsal and 16 anal ossified rays were present. The first few pterygiophores of each fin were faintly stained. The dorsal fin was over the 18th to 25th vertebrae, the anal under the 32nd to 38th vertebrae. In the 18.0-mm specimen, there were two ural vertebrae in the caudal region. In the 12.0-mm specimen, the middle vertebrae were visible because the ventral portions of their centra were ossified. In the 12.4-mm specimen, 20 vertebrae anterior to the dorsal fin were ossified. Neither the first few vertebrae nor the last several were ossified. The 14.0-mm specimen had the first vertebra faintly stained, the next 36 were complete, the next 3 were visible but unstained, and the last had only the lower half of the centrum stained. In this specimen, a few neural arches near the middle of the vertebral column were lightly stained. The first 10 hemal spines also were slightly stained as were the 2 preceding the parhypural. In the 14.9-mm specimen, all neural spines and hemal spines were lightly stained. Pleural ribs were first observed in the 15.6-mm specimen on the 8th to 16th vertebrae. From density of stain, it appears that they develop in a posterior to anterior direction.

Head Bones

The many skull bones were difficult to describe. A detailed analysis of general developmental changes in skull development has been completed for the related Atlantic thread herring, *Opisthonema oglinum* (Richards et al., 1974). The maxillaries and dentaries of scaled sardines ossified at 11.5 mm. At this time, the maxillary bore five small teeth. These teeth were too small to be shown in the illustrations. Teeth were added with growth—8 teeth at 14.0 mm, 14 teeth at 14.9 mm, 17 teeth at 15.6 mm. Teeth were observed on the dentary only on the 15.6-mm specimen, where two were observed. Dentary teeth apparently are a temporary feature. Teeth also were present on the basihyal; the 15.6-mm specimen had two large teeth, and the 16.6-mm specimen had three teeth on this bone. These teeth, like the dentary teeth, apparently are temporary larval structures. They were also seen as temporary structures in the larvae of *O. oglinum* (Richards et al., 1974). The premaxillaries were first visible in the 14.9-mm specimen, and the posterior supramaxillaries were first seen in the 16.6-mm specimen. The anterior supramaxillaries and the hypomaxillaries had still not developed in our 19.3-mm specimen but were present in our 22.4-mm specimen. Berry (1964a) reported hypomaxillaries to be developed in a 16-mm specimen of *Harengula thrissina* from the eastern Pacific.

Pigmentation

Melanophore distribution on preserved scaled

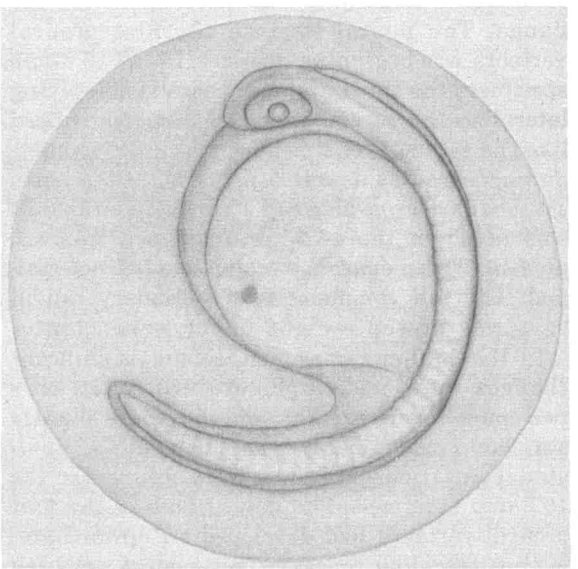

FIGURE 7.—Late stage egg of *Harengula jaguana*.

sardine larvae is similar to that of other clupeid larvae. Pigmentation varied somewhat among individuals of the same size, but a general pattern was always present. Some variation resulted because individual melanophores could be in either a contracted or expanded state. Illustrated specimens have pigmentation that is typical of most larvae of those sizes (Figures 8 to 10). In life, numerous yellow chromatophores were present, usually as internal pigmentation, but these were not illustrated.

Head Region

Pigmentation was sparse on the head of scaled sardine larvae until they attained 15 mm. Eyes became pigmented when larvae were 4 to 5 mm, at 30 to 40 h after hatching. At the same time, from two to four melanophores developed near the pectoral symphysis. These usually consisted of one just anterior to the symphysis and a pair immediately posterior to it. They were retained throughout larval development. One or two melanophores usually were present at the base of the pectoral fins when larvae were 6.5 mm or longer. From one to four stellate melanophores first appeared over the hindbrain at 7 to 8 mm. This number gradually increased as larvae grew, but some specimens had only a single melanophore at 14 mm. On specimens longer than 15 mm, melanophores became numerous over the midbrain and hindbrain. One or two deeply imbedded melanophores were visible through the otic capsules on most specimens longer than 8 mm. One or two stellate melanophores frequently appeared on the cheek when larvae were 14 mm. This number often increased to several at 15 to 18 mm. Tiny melanophores developed on the snout and lower jaw of larvae that were 14 to 17 mm. Melanophore numbers increased

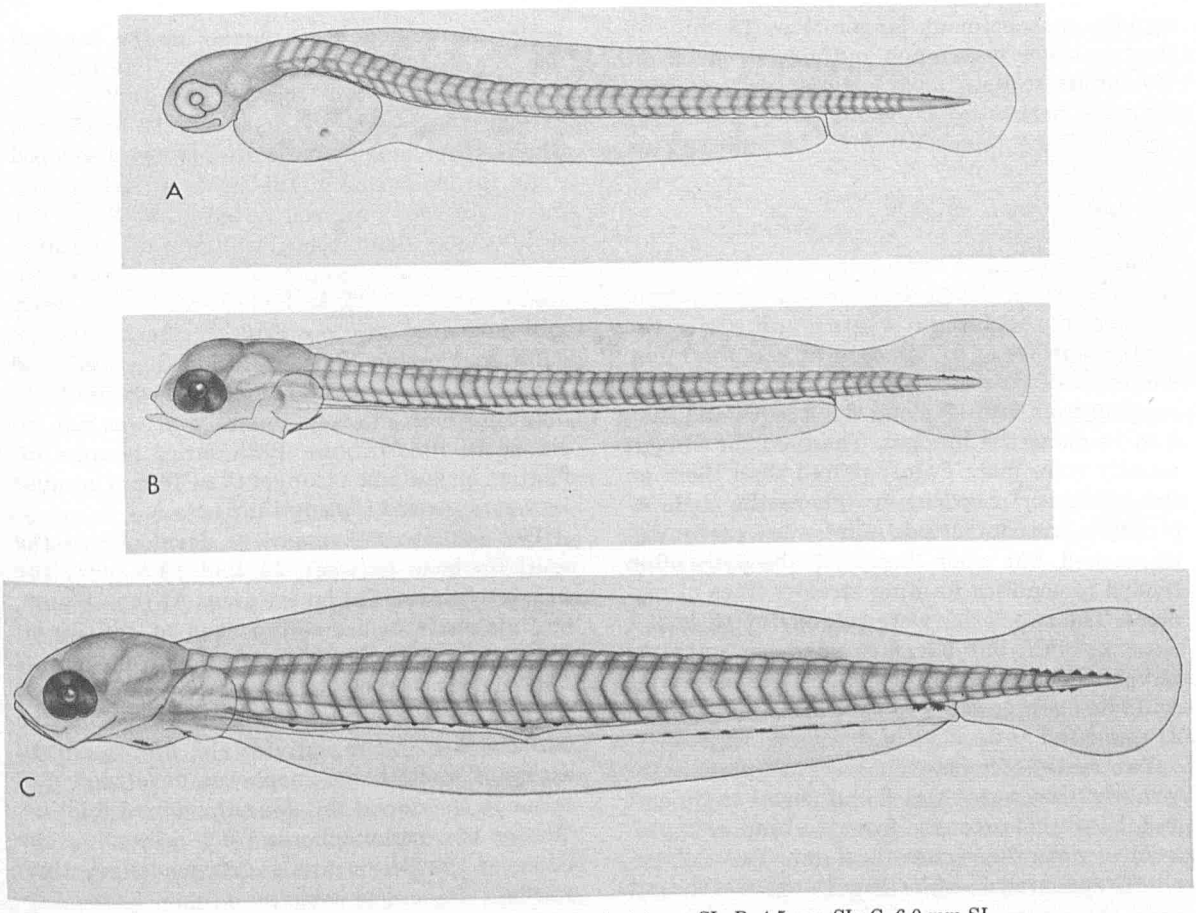

FIGURE 8.—Larvae of *Harengula jaguana*: A, 4.4 mm SL; B, 4.5 mm SL; C, 6.0 mm SL.

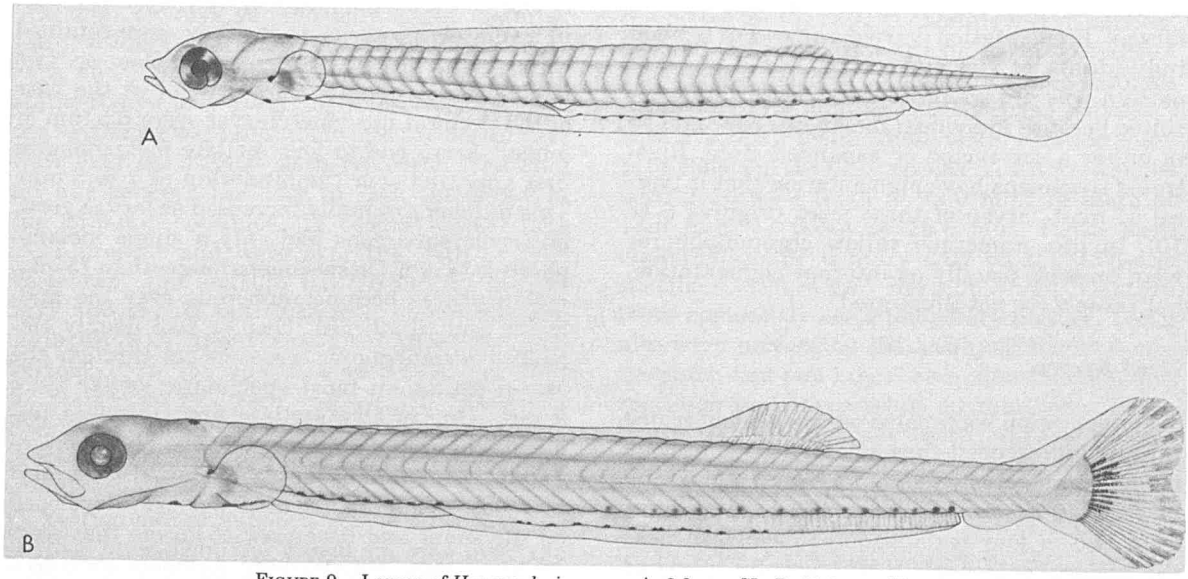

FIGURE 9.—Larvae of *Harengula jaguana*: A, 8.9 mm SL; B, 11.5 mm SL.

rapidly on specimens longer than 18 mm, although there was much individual variation. Numerous stellate melanophores were present over the brain, on the snout, jaws, and cheek region of specimens between 18 and 24 mm.

Gut and Trunk Region

Paired series of melanophores, typical of clupeid larvae, developed over the dorsolateral surface of the foregut region and along the ventral surface of the hindgut at about 4.5 mm. Numbers of pairs in the series were variable, ranging from 7 to 12 along the foregut and from 8 to 14 along the hindgut. Those on the foregut usually were more evenly paired than those on the hindgut. In specimens where the melanophores were contracted, pairs were easily distinguished, but when dispersed, the pairs often tended to coalesce forming streaky lines of pigment. The two series were retained until larvae were 21 mm, but became indistinct on some larvae between 18 and 21 mm. No distinct series could be distinguished on specimens longer than 21 mm.

Two series of melanophores were present internally. One series was found dorsal to the gut and the second extended from the hindbrain posteriorly along the vertebral column. Two melanophores appeared near the dorsal surface of the gut near the anus at 4 to 5 mm, from which the series of melanophores dorsal to the hindgut began to develop at 5 to 6 mm. The number gradually increased from as few as 2 to 5 to as many as 34 when larvae were 12 to 15 mm. The first melanophores in this series developed near the posterior of the hindgut; additional melanophores developed anterior to those. The series along the vertebral column first appeared at 10 to 12 mm, and numbers gradually increased to about 25. Melanophores in this series first appeared just posterior to the hindbrain; additional melanophores developed posterior to them. The vertebral series was difficult to distinguish in most specimens and was not included in illustrations. Both series became indistinct on specimens longer than 18 mm because larvae increased in body thickness.

Two stellate melanophores developed at the anal fin base between 11 and 13.5 mm. The number increased as larvae grew. At 14 to 15 mm, stellate melanophores appeared at the dorsal fin base, the numbers increasing from one or two to eight or more at 18 mm. Between 18 and 21 mm, a few melanophores developed in the dorsal fin of most individuals, and a paired series of stellate melanophores developed posterior to the dorsal fin along the dorsal midline. One or two melanophores were present at the bases of the pelvic fins in larvae longer than 15 mm.

Stellate melanophores began to appear on the

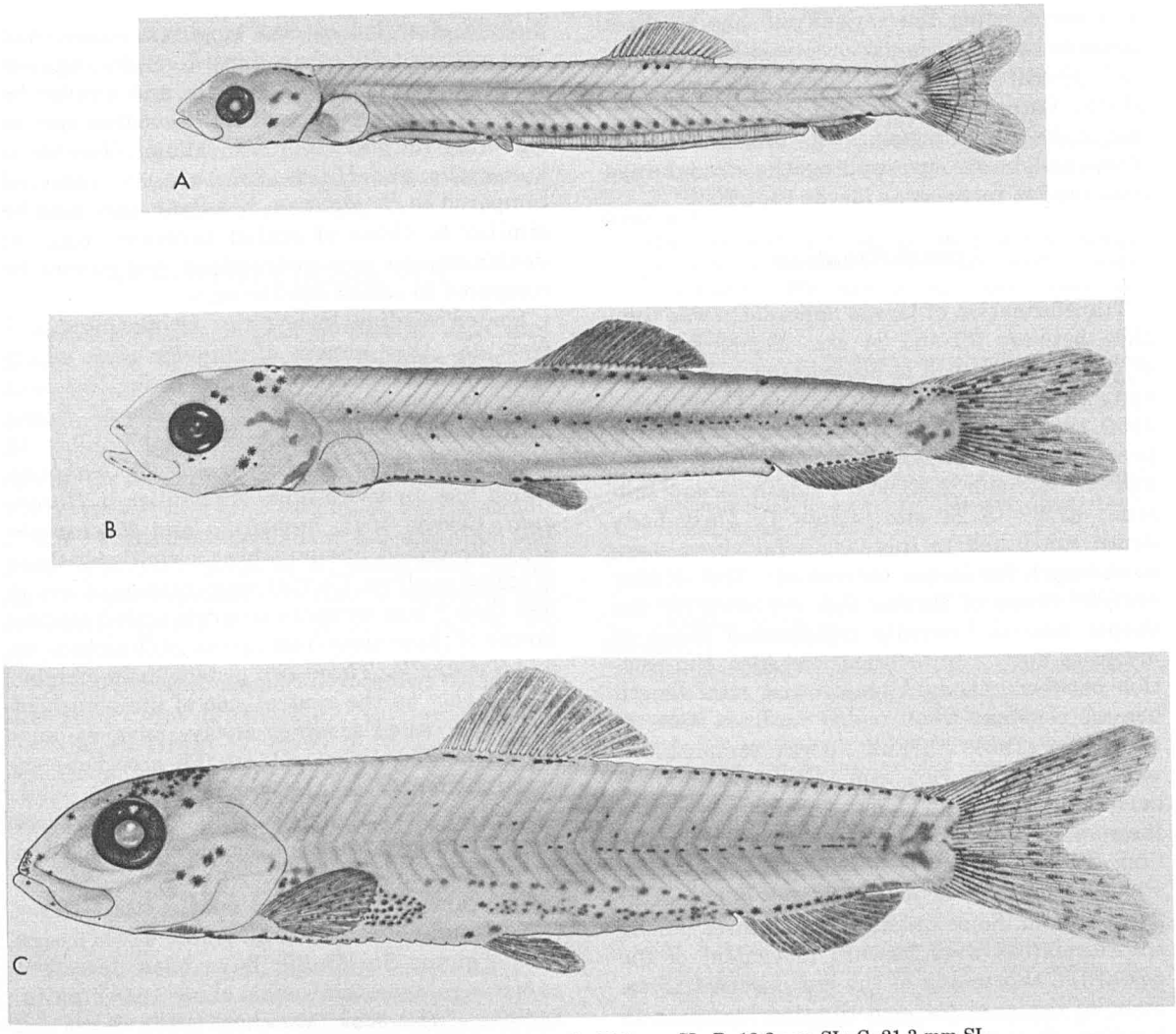

FIGURE 10.—Larvae of *Harengula jaguana*: A, 16.1 mm SL; B, 18.8 mm SL; C, 21.3 mm SL.

sides of most larvae between 16 and 17 mm. The first of these developed posterior to the dorsal fin along the lateral midline of larvae. Numbers increased as larvae grew, spreading anteriorly, dorsally, and ventrally so that most individuals had numerous melanophores scattered over their sides by 22 mm. The epaxial myomeres of specimens longer than 22 mm usually were outlined by melanophores that were concentrated along the myosepta. Silver coloration began to appear along the ventral and ventrolateral areas of the trunk at 22 to 24 mm. By 28 mm few melanophores could be discerned below the midline on sides of juveniles because of the accumulation of guanine in that area. At this stage, scaled sardines resemble large juveniles and adults because of their predominantly silver color.

Caudal Region

Newly hatched larvae, 4 to 4.5 mm, had three or four melanophores along the dorsal tip of the notochord. In the first 48 h after hatching, the number of melanophores in that area ranged from three to six. During the same time from one to three melanophores developed along the ventral tip of the notochord in some specimens. As caudal rays began to develop at 8 to 10 mm, pigment migrated from the notochord tip to the

area surrounding the rays. From one to three deeply imbedded melanophores were present near the hypural plate when larvae reached 11 to 16 mm. Larger specimens had similar pigmentation in the caudal region except that the number of melanophores surrounding the caudal rays continued to increase as larvae grew.

Transformation

Transformation of larvae apparently was complete between 22 and 24 mm. Scaled sardines of 22 mm conformed to descriptions of juveniles and adults in most respects (Storey, 1938; Rivas, 1950, 1963). Proportional measurements relating preanal length, predorsal length, head length, and eye diameter to standard length became constant at 22 to 24 mm (Table 1). Only body depth continued to increase relative to standard length for larger individuals. The slender rodlike shape of larvae was replaced by the deeper bodied, laterally compressed shape of juveniles during transformation. Also, the relation between standard length and total length became constant when scaled sardines were 22 to 24 mm (Table 1). Full fin ray complements were present by 19.5 mm (Table 3), slightly before the dorsal and anal fins had completed their movements during transformation. Scales first developed at 21 to 22 mm, and the typical silvery coloration of juveniles was apparent at 22 to 24 mm. Some outstanding features during transformation were forward movement of the dorsal fin, shortening of the gut, forward movement of the anal fin, and relative increases in head length, snout length, eye diameter, and body depth.

COMPARISONS

Eggs and larvae of scaled sardines can be distinguished from those of similar genera in south Florida marine waters. Houde and Fore (1973) have prepared a guide that will help to identify eggs and larvae of some clupeid fishes, including scaled sardines, from the Gulf of Mexico.

Scaled sardine eggs are larger than those of other clupeid genera from south Florida. Only scaled sardines have eggs larger than 1.50 mm diameter. Eggs of *Opisthonema oglinum, Sardinella anchovia, Brevoortia* spp., and *Etrumeus teres* rarely exceed 1.35 mm diameter. The oil globule of scaled sardine eggs is smaller than that reported for other clupeid genera. Eggs of *Etrumeus* have no oil globule and cannot be confused with scaled sardines. Two other species of *Harengula* may occur near Miami. *Harengula humeralis* and *H. clupeola* are not common compared to *H. jaguana*, but their eggs may be similar to those of scaled sardines. Eggs of *Jenkinsia* spp. are undescribed and cannot be compared to scaled sardine eggs.

Scaled sardine larvae can be distinguished from all other genera of clupeids with which they might cooccur, except perhaps for *Jenkinsia* spp., which are undescribed. Myomeres do not exceed 42 in *Harengula* larvae, but number 45 or more in other genera, except for *Jenkinsia* which has myomere numbers similar to *Harengula*. Larvae of *H. humeralis* and *H. clupeola* are undescribed, but probably are similar to those of scaled sardines. Caudal pigmentation of larvae less than 9 mm serves to separate scaled sardine larvae of those sizes from larvae of *Opisthonema* and *Sardinella*. Those two genera have melanophores only on the ventral side of the notochord tip while scaled sardines always have melanophores on the dorsal side of the notochord tip and frequently on the ventral side as well. *Brevoortia* larvae have caudal pigmentation like that of *Harengula*, but they rarely have fewer than 45 myomeres.

Eggs and larvae of two species that Berry (1964a) and Whitehead et al. (1966) would assign to the genus *Sardinella* have been described as *Harengula zunasi* (Uchida et al., 1958; Takita, 1966) and *H. rouxi* (Marchal, 1967). Eggs and larvae of *H. zunasi* from Japanese waters (Uchida et al., 1958; Takita, 1966) closely resemble those of *H. jaguana*. Egg diameters and oil globule diameters of *H. zunasi* average slightly larger than for *H. jaguana*, but the very wide pervitelline space and exceptionally small oil globule are similar in the two species. Pigmentation is present only on the ventral side of the notochord tip in *H. zunasi* larvae, thus differing from *H. jaguana*. Both *H. zunasi* and *H. jaguana* larvae have less than 45 myomeres—43 in *H. zunasi*, usually 40 or 41 in *H. jaguana*. Marchal's (1967) *Harengula* (= *Sardinella*) *rouxi* eggs and larvae also more closely resemble those of *H. jaguana* than other clupeid eggs and larvae that we have observed from Florida waters. Eggs of *H. rouxi* are smaller than *H. jaguana*,

but relative widths of the pervitelline space and the oil globule diameters are similar. *H. rouxi* and *H. jaguana* larvae have similar pigmentation at the notochord tip. Myomeres range from 43 to 45 in *H. rouxi*, which is higher than for *H. jaguana* but lower than the number observed in most other clupeids.

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EGG AND LARVAL DEVELOPMENT OF THE ATLANTIC THREAD HERRING, *OPISTHONEMA OGLINUM*[1,2]

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ABSTRACT

The egg and larval development of Atlantic thread herring, *Opisthonema oglinum*, is described, based on wild-caught eggs and laboratory-reared larvae. This description includes morphological details of the egg and osteological development, changes in body shape and pigmentation, and significant features of transformation of the larval development stages. The egg is 1.10 to 1.28 mm in diameter with a single oil globule. Ossification commences in the larvae when they attain 10 mm in standard length and all bones have at least begun to ossify by 20 mm. During transformation (15 to 25 mm), the larvae assume juvenile characteristics; particularly evident during this period is the anterior movement of the dorsal and anal fins from their posterior larval positions to their medial adult positions.

The Atlantic thread herring, *Opisthonema oglinum* (Lesueur), is a clupeid fish commonly found in the subtropical and tropical waters of the western Atlantic Ocean, but the eggs and larvae of this species have not been described previously. In 1968, Atlantic thread herring were reared from eggs in the Tropical Atlantic Biological Laboratory, Miami, Fla. (now the Southeast Fisheries Center), and a complete developmental series was obtained (Richards and Palko, 1969). This paper describes the egg and morphological development of the reared larvae. We used a dynamic approach, similar to that of Moser and Ahlstrom (1970), to describe the sequential development of characters, instead of a static approach in which a few selected sizes of larvae are described in detail. Larvae reared under laboratory conditions provide unusually good specimens for studies of this kind.

The major purpose of describing eggs and larvae is to provide information so that they may be identified in field collections. Identification is very difficult among the clupeids because all of the larvae are very similar in appearance. This group is further complicated by the many species that occur. In the western North Atlantic 15 genera, representing about 36 species, are found. Three genera are distinctive since they are found in fresh water, or at least spawn and develop in fresh to brackish water. Five other genera are distinctive because of their long anal fin, and one poorly known genus because of its very few vertebrae. However, approximately 17 species remain represented by seven genera, which are very similar in appearance. These genera are *Clupea* (one species), *Etrumeus* (one species), *Jenkinsia* (three species), *Brevoortia* (four species), *Opisthonema* (two species), *Harengula* (three species), and *Sardinella* (three species). Some species within these genera are imperfectly known (Berry, 1964). At our laboratories, three other species have now been reared besides *O. oglinum*—*Sardinella anchovia, Brevoortia smithi, and Harengula jaguana*—and descriptions of these are in preparation. Except for *Sardinella*, it appears now that *O. oglinum* can be separated from all of the other genera on the basis of meristic characters. *Brevoortia* is similar in most meristic characters, but its anal fin is found nearly below the posterior end of the dorsal fin, unlike *Opisthonema*. The eggs are very similar to one another, but size and spawning times are helpful in separating the species. Much detailed work is needed to work out these identification problems, not only for the eggs and larvae but for the adults as well. A recent paper gives useful information on these identification problems (Houde and Fore, 1973).

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MATERIALS AND METHODS

Eggs that were used for descriptive purposes were collected in 1971 and 1972 during ichthyoplankton surveys in the eastern Gulf of Mexico. Twenty-three eggs in varying stages of development were examined and measured. Eggs from the laboratory rearing experiment were lost and consequently could not be described.

We selected only the best specimens for this study by eliminating fish with pronounced body curvature and those in poor condition. We used 53 of the 197 available specimens. Forty-two of these specimens were measured with an ocular micrometer of a dissecting microscope to provide data on body proportions. Seventeen of the specimens were cleared and stained to provide meristic data and osteological data. Specimens shown in the illustrations were among those cleared and stained for verification of the fin-ray counts. Staining procedures followed those of Taylor (1967).

During development, *O. oglinum* undergoes some pronounced changes in structure. These changes are difficult to adequately define, particularly the metamorphic stages. We have followed the definitions used by Moser and Ahlstrom (1970), and we have also taken into account Ahlstrom's (1968) comments on the subject. Our yolk-sac larvae were lost, so our description commences with the larval period. The period between the larval period and juvenile period is termed the transitional stage, following Moser and Ahlstrom (1970). At the beginning of the transitional period (about 15 mm standard length), the animals commence metamorphosis into juveniles.

Our methods of counting and measuring closely follow Moser and Ahlstrom, but for convenience are defined as follows:

Body length—In early stage larvae and in those undergoing notochord flexion, the body length is the distance from the tip of the snout to the tip of the notochord. After the hypural complex is developed the standard length measurement is used, i.e., the distance from the tip of the snout to the posterior margin of the hypural elements. While the notochord is undergoing flexion and the hypural elements are developing, this estimated standard length measurement is denoted in the tables.

Eye diameter—Maximum width of the pigmented eye measured on the horizontal axis.

Snout length—Distance from the tip of the snout to the anterior edge of the orbit.

Head length—Distance from the tip of the snout to the posterior edge of the opercle.

Length of dorsal and anal fin bases—Distance from the origin of the first ray to the point where the posterior part of the last ray contacts the body.

Snout to origin of dorsal fin—Identical to the predorsal length defined by Hubbs and Lagler (1958).

Snout to origin of pelvic fin—Distance from the tip of the snout to the pelvic fin base.

Snout to origin of anal fin—Distance from the tip of the snout to the origin of the anal fin (in small larvae, before the anal fin develops, this measurement is defined as the distance from the tip of the snout to the end of the gut; it can be used as gut length for all larvae and small juveniles).

Origin of dorsal fin to base of caudal rays—Distance from origin of the dorsal fin to the end of the hypural plate.

Body depth—Vertical depth of the body measured at the origin of the pelvic fins (in larvae that have not developed pelvic fins, the midpoint of the body is used).

Origin of anal fin to base of caudal rays—Distance from origin of the anal fin to the end of the hypural plate.

Origin of pelvic fin to base of caudal rays—Distance from origin of the pelvic fin to the end of the hypural plate.

DESCRIPTION OF THE EGGS

Twenty-three eggs ranged from 1.10 to 1.28 mm in diameter (mean = 1.19 mm). The chorion is thin and fragile, unsculptured, and unpigmented. A single oil globule is present, ranging from 0.12 to 0.16 mm in diameter (mean = 0.15 mm). As in most clupeid eggs, the perivitelline space is wide, and the yolk mass is vaguely segmented. For 10 embryos at the blastodisc stage the yolk diameter averaged 59% of the egg diameter, while for 13 advanced embryos the yolk diameter averaged only 53% of the egg diameter. A paired dorsolateral series of tiny melanophores is present on embryos that are about to hatch (Figure 1). *Opisthonema* eggs

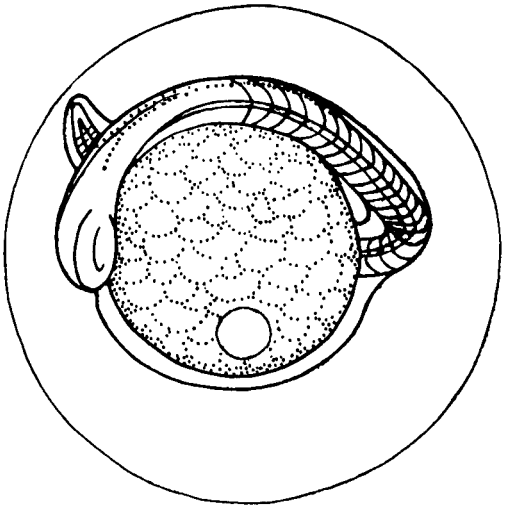

FIGURE 1.—*Opisthonema oglinum* egg.

are similar to those of most other clupeids (e.g., Reintjes, 1962; Simpson and Gonzalez, 1967) but differ markedly in total egg diameter and oil globule diameter from *Harengula* spp., with which they may cooccur. Houde, Richards, and Saksena (1974) reported that the diameter of *Harengula jaguana* eggs was never less than 1.50 mm, and that the oil globule diameter never exceeded 0.10 mm.

MORPHOLOGY OF LARVAE

Meristic values were obtained and these are shown in Table 1. To describe the change in shape and to note changes in various structures, 13 measurements were made. These are shown in Table 2. The larvae are also illustrated for several selected sizes (Figures 2 to 8). *Opisthonema oglinum* larvae, prior to the start of the transition to juveniles, are very slender larvae with a well-developed finfold and long gut. Prior to notochord flexion gut length averages about 86% of the body length. During notochord flexion this increases to 91% because body length is slightly reduced. The abruptness of this flexing is evidenced in the measurement of origin of anal fin to base of caudal rays in Table 2. After notochord flexion this distance is smaller due to the upturning of the notochord. Following flexion (10 mm SL) the gut averages 92% of standard length up until transformation commences at 15 mm SL. At that time there is a gradual shortening of the gut until it becomes about 75% of the standard length as a juvenile. The large finfold decreases at about the time of notochord flexion and is almost lost by the time the anal fin is well differentiated at 13 mm SL, except for a remnant beneath the foregut (Figures 2 to 4).

The first fin to form is the pectoral fin but, as described later under the osteology section, it is not the ossified pectoral fin of the juvenile. The caudal fin, dorsal fin, and anal fin all develop within the finfold itself, and their development is discussed in the osteology section. The pelvic fin is the last fin to be discernible as a small fleshy protuberance at 14 mm SL.

At first, the gut is a straight simple tube. At 5 mm SL it can be differentiated into a foregut and hindgut. The hindgut becomes ridged or banded with tissue, which is quite evident in Figure 4 of a 13.7-mm SL specimen. This ridging is still evident through much of the transitional period (Figure 5).

The most striking feature of development is the anterior migration of the dorsal fin during transformation. The fin nearly has its full complement of rays before this commences and like the shortening of the gut and anterior advancement of the anal fin, it is a rapid change. It is more striking than the latter since the fin is so visible. The predorsal length averages more than 60% of the body length until about 17 mm, then it rapidly decreases to an average of 43% of body length when transformation is completed. The position of both the dorsal and anal fin in relation to the vertebrae also vividly demonstrates this movement (Table 3). The fin movement begins at 15 mm. At that size, the anal fin origin begins to move forward from its position under vertebra 38 (Table 3 and Figure 6) to its final position under vertebrae 33 to 34 at 24 mm (Table 3 and Figure 7). Similarly, the origin of the dorsal fin is transferred forward over vertebra 23 (Table 3 and Figure 6) to over vertebra 15 when larvae measure 19 and 25 mm (Table 3 and Figure 7). To about 20 mm, there are 21 predorsal myomeres and no ossified predorsal bones (free interneurals), but shortly thereafter eight predorsals become ossified.

One character which may be instrumental in separating the various genera and possibly species of clupeids is the distance between the dorsal and anal fins. For practical reasons, the best way to determine this distance is to count

TABLE 1.—Meristic characters of larval and juvenile *Opisthonema oglinum*.

SL (mm)	Caudal rays	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Length of last dorsal ray as fraction of prior longest ray	Gillrakers			Scutes		Vertebrae
							Epibranchial	Cerato-branchial	Hypo-branchial	Pre-pelvic	Post-pelvic	
3.8-7.4	Nothing countable on 4 specimens in this size range.											
8.4	17	11	—	—	—	—	—	—	—	—	—	—
9.0	18	9	—	—	—	—	—	—	—	—	—	46
9.6	18	9	—	—	—	—	—	—	—	—	—	44
10.0	19	13	—	—	—	—	—	—	—	—	—	—
10.4	19	15	—	—	—	—	—	—	—	—	—	45
10.5	19	—	9+	—	—	—	—	—	—	—	—	—
10.7	19	13	—	—	—	—	—	—	—	—	—	46
12.1	18	15	—	—	—	—	—	—	—	—	—	—
12.5	—	16	7±	—	—	—	—	10	—	—	—	45
13.5	19	17	12	—	—	—	—	—	—	—	—	—
13.7	19	17	16	—	—	0.5*X*	—	—	—	—	—	—
14.2	19	16	14	—	—	—	—	—	—	—	—	—
14.3	19	14	—	—	—	—	—	8	—	—	—	—
14.3	19	17	10	—	—	—	—	—	—	—	—	46
curved	19	16	16	—	4	—	—	10	—	—	—	—
15.5	19	20	19	—	—	—	—	—	—	—	—	—
15.6	19	20	14	—	5	—	3	13	2	—	—	45
16.2	19	19	19	—	6	0.5*X*	—	—	—	—	—	—
16.9	19	17	17	—	4	—	—	—	—	—	—	46
17.1	19	19	19	—	5	—	—	10	—	—	—	45
17.2	19	18	18	5	5	—	—	—	—	—	—	45
17.4	19	18	19	—	6	—	—	—	—	—	—	—
17.7	19	19	19	—	6	0.5*X*	—	—	—	—	—	—
17.7	19	18	16	—	4	—	—	—	—	—	—	—
18.4	19	19	19	—	5	—	3	13	—	—	—	46
19.3	19	19	17	9	6	0.5*X*	6	12	6	—	—	—
19.7	19	20	21	15	8	0.6*X*	6	13	4	—	—	45
20.3	19	21	19	13	8	0.7*X*	8	12	8	8	0	—
21.1	19	20	21	14	8	0.6*X*	10	17	10	11	2	46
23.4	19	20	22	16	8	0.7*X*	10	15	9	7	0	—
23.8	19	20	21	15	6	0.7*X*	11	16	10	12	9	—
24.4	19	20	21	14	8	—	11	16	7	14	2	45
24.8	19	22	23	16	8	0.8*X*	12	16	11	18	13	—
25.3	19	18	21	16	8	0.7*X*	10	15	12	13	5	—
25.9	19	20	20	15	8	0.7*X*	13	16	11	17	13	46
26.2	19	20	21	16	8	0.5*X*	13	16	13	18	15	46
27.0	—	21	24	16	8	1.3*X*	16	20	16	18	15	46
27.1	—	20	23	16	—	1.0*X*	14	18	16	17	14	46
27.1	—	20	23	15	—	1.0*X*	15	19	15	18	15	46
27.3	—	20	23	16	—	1.1*X*	15	18	14	18	15	46
28.2	—	20	21	17	—	—	15	18	14	18	15	46
30.0	—	22	22	16	8	1.1*X*	15	18	14	19	14	—
30.8	19	21	21	17	8	1.2*X*	18	18	16	17	14	45
34.9	19	22	23	17	8	1.8*X*	20	22	20	18	16	46
46.8	—	21	21	15	8	2.0*X*	31	25	32	16	16	—
54.0	19	20	25	16	8	2.5*X*	34	27	32	18	16	47

the number of myomeres between the end of the dorsal fin to the origin of the anal fin. In *O. oglinum* larvae less than 16 mm, we counted 8, 9, or 10 myomeres between the two fins. Transforming larvae and small juveniles (17 to 25 mm) had from 5 to 7 myomeres between the fins. We were unable to count these numbers with accuracy in specimens longer than 26 mm.

In life the larvae are very transparent and gradually become opaque during transformation because of an increase in pigmentation and a compacting of the visceral cavity. Other than the gross features of the gut mentioned above, the development of the visceral organs was not considered in the present study, but we assume that abrupt changes take place. The swim bladder first appears during transformation. Before transformation, a cavity develops above the anterior end of the hindgut (just posterior to the pelvic fins) in larvae as small as 10 mm, but a definite swim bladder is not apparent until the larvae are 15 mm long. In living larvae the swim bladder is well defined.

OSTEOLOGICAL DEVELOPMENT

Larvae of *O. oglinum* undergo no ossification of any parts before they measure about 10.0 mm SL (all body lengths will be given in standard length unless otherwise indicated). In the youngest cleared and stained larva examined (4.1 mm TL, total length), the cranial bulb was outlined, as were the lower jaw, hyoid apparatus, and dorsal and caudal fin lobes (Figure 2). All these

TABLE 2.—Measurements of larvae and juveniles of *Opisthonema oglinum*. Specimens between dashed lines are undergoing notochord flexion.

Body length	Eye diameter	Snout length	Head length	Length of dorsal fin base	Length of anal fin base	Snout to origin of dorsal fin (predorsal)	Snout to origin of pelvic fin	Snout to origin of anal fin	Origin of dorsal fin to base of caudal rays	Body depth	Origin of anal fin to base of caudal rays	Origin of pelvic fin to base of caudal rays
3.6	0.20	0.10	0.60	—	—	—	—	3.1	—	0.20	0.50	—
4.1	0.18	0.10	0.53	—	—	—	1.9	3.4	—	0.25	0.63	2.0
4.6	0.20	0.10	0.60	—	—	—	2.0	3.9	—	0.20	0.63	2.5
5.2	0.23	0.13	0.73	—	—	—	2.4	4.4	—	0.33	0.63	2.7
7.3	0.25	0.18	0.90	0.35	—	4.8	3.2	6.5	2.2	0.50	0.75	4.1
7.4	0.25	0.18	1.0	0.38	—	5.0	3.3	6.6	2.3	0.60	0.78	4.1
9.1	0.35	0.28	1.1	0.75	—	5.9	4.0	8.1	3.4	0.95	0.95	5.0
9.7	0.35	0.30	1.2	0.85	—	6.5	4.2	8.8	3.3	0.85	0.95	5.4
10.0	0.35	0.27	1.2	0.94	—	6.8	4.4	9.2	3.4	0.95	0.95	5.6
10.1	0.43	0.38	1.5	1.3	—	6.4	4.4	9.4	3.9	1.0	0.63	5.6
10.4	0.38	0.35	1.7	1.5	0.25	6.3	4.6	9.6	3.9	1.1	0.83	5.8
10.7	0.40	0.40	1.7	1.3	0.35	6.7	4.7	9.7	3.9	1.0	1.0	6.0
12.1	0.45	—	—	—	—	7.9	5.2	11.1	—	—	1.0	6.9
12.8	0.50	0.48	2.0	1.7	0.45	8.1	5.8	11.6	4.9	1.1	1.2	7.2
12.9	0.53	0.48	2.1	1.9	0.75	8.2	5.9	11.4	5.2	1.3	1.6	7.2
13.7	0.55	0.73	2.8	1.9	0.63	8.9	6.2	12.4	5.0	1.6	1.4	7.6
14.0	—	—	—	—	—	9.0	6.3	12.6	5.3	—	—	8.0
14.0	0.58	0.63	2.6	2.1	0.60	8.8	5.8	12.9	5.5	1.7	1.4	8.5
15.0	0.63	0.68	2.7	2.1	0.95	9.0	6.7	13.2	6.0	1.6	1.8	8.4
15.8	0.63	0.78	3.0	2.2	0.88	10.0	7.1	13.8	6.3	1.7	1.9	8.8
16.2	0.63	0.60	3.0	2.4	1.0	9.7	7.0	13.9	6.5	1.7	2.1	8.9
16.8	0.80	0.68	3.2	2.6	1.1	10.2	7.7	14.9	6.9	1.9	2.2	9.1
17.1	0.65	0.73	3.1	2.6	1.0	10.0	7.4	15.3	6.9	1.9	2.1	9.5
17.7	0.70	0.75	3.3	2.7	1.2	10.7	8.5	15.3	7.1	2.0	2.4	9.2
17.7	0.80	0.85	—	—	—	10.4	8.1	15.4	—	—	2.3	9.6
18.4	0.83	0.76	3.5	2.9	1.3	10.9	8.8	16.1	7.8	2.5	2.3	9.6
19.3	1.1	—	—	—	—	10.9	9.3	16.3	—	—	3.0	10.0
19.7	1.1	0.85	3.9	3.1	1.8	10.5	9.0	16.6	9.2	2.6	3.1	10.7
20.3	1.2	1.1	4.9	3.5	2.1	10.0	9.8	16.8	10.0	3.3	3.5	10.5
23.4	1.4	1.5	6.0	4.0	3.4	10.7	11.5	18.0	13.1	4.6	5.4	11.9
23.8	1.7	1.6	6.1	4.0	3.7	10.7	12.1	18.1	13.0	4.7	5.7	11.7
24.4	1.5	1.6	6.4	3.7	3.6	12.0	11.9	18.6	12.5	4.4	5.8	12.5
24.8	1.7	1.9	6.7	4.4	4.5	11.0	13.0	18.7	14.0	5.5	6.1	11.8
25.3	1.7	1.7	6.6	4.5	4.2	11.5	12.7	18.9	14.0	4.8	6.4	12.6
26.2	1.5	1.8	6.6	4.0	3.9	12.0	12.6	19.7	14.2	4.8	6.5	13.6
27.0	1.9	1.6	6.4	4.3	4.3	12.3	13.5	19.7	14.7	5.7	7.3	13.5
27.1	1.8	1.9	7.3	4.4	4.4	11.6	14.2	20.2	15.5	5.8	6.9	12.9
27.1	1.9	1.7	6.7	4.0	4.0	11.4	13.3	20.3	15.8	4.5	6.8	13.8
27.3	1.6	1.8	6.8	4.1	4.3	11.8	14.0	19.9	15.5	5.0	7.0	13.3
28.2	1.9	1.9	7.3	4.3	4.2	12.5	14.3	20.7	16.7	5.0	7.0	13.9
30.0	2.3	2.4	8.5	5.0	5.0	13.0	15.5	22.8	16.8	8.3	8.2	14.5
30.8	2.2	2.4	8.0	5.0	5.0	13.4	15.7	22.9	17.3	7.7	7.9	15.1

structures were clear, however, indicating no ossification. The first structures to ossify were the dentaries and maxillaries when specimens measured about 10.0 mm (bone nomenclature follows Mead and Bradbury, 1963). Almost simultaneously, the very thin cleithral ring (cleithrum, supra-cleithrum, and postcleithrum) and the hypurals began to ossify very slightly. At sizes between 12 and 13 mm, the skull bones began to ossify, as did the vertebral rings. As size increased, various other parts of the fish began to ossify—the caudal fin rays, parts of the branchial apparatus (ceratobranchials, hypobranchials, epibranchials), and the dorsal and anal fin rays; skull bones ossified further (Figure 3). At about 20 to 22 mm, essentially all bony structures of the larvae had at least begun to ossify, and some were well developed.

Vertebral development

No ossification took place before 10 mm, but cartilaginous structures were visible. At the time of notochord flexion, seven hypural elements were formed (four superior and three inferior elements including the parhypural). In specimens measuring 10.5 mm, the hypurals were weakly ossified but the seven elements were distinct. The first vertebral centra to ossify was the first preural centrum and the ventral portion of the centra of the first and second ural centra. This differs somewhat from the development noted in

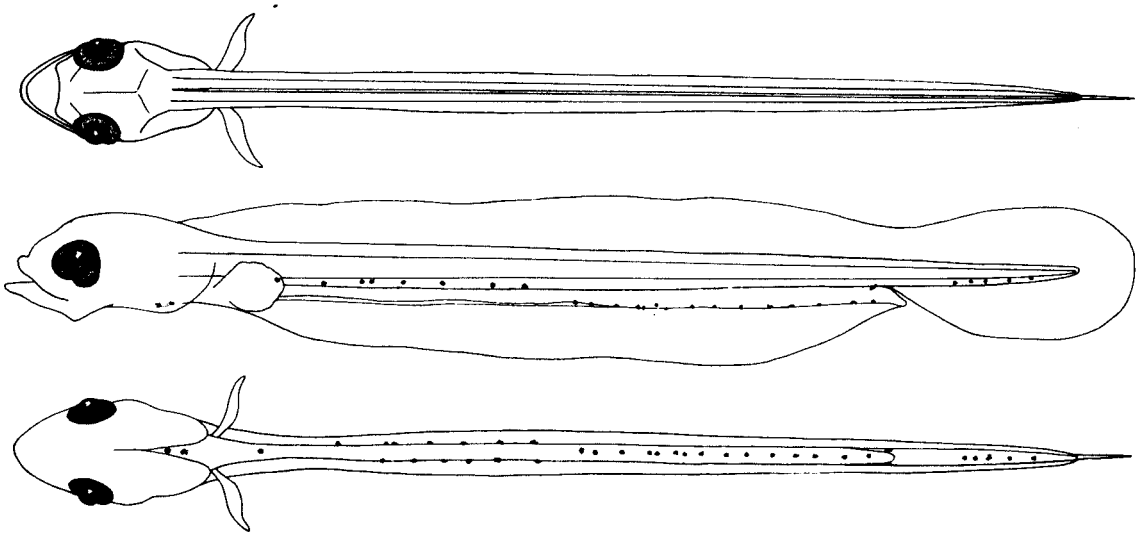

FIGURE 2.—*Opisthonema oglinum* larva 4.0 mm total length.

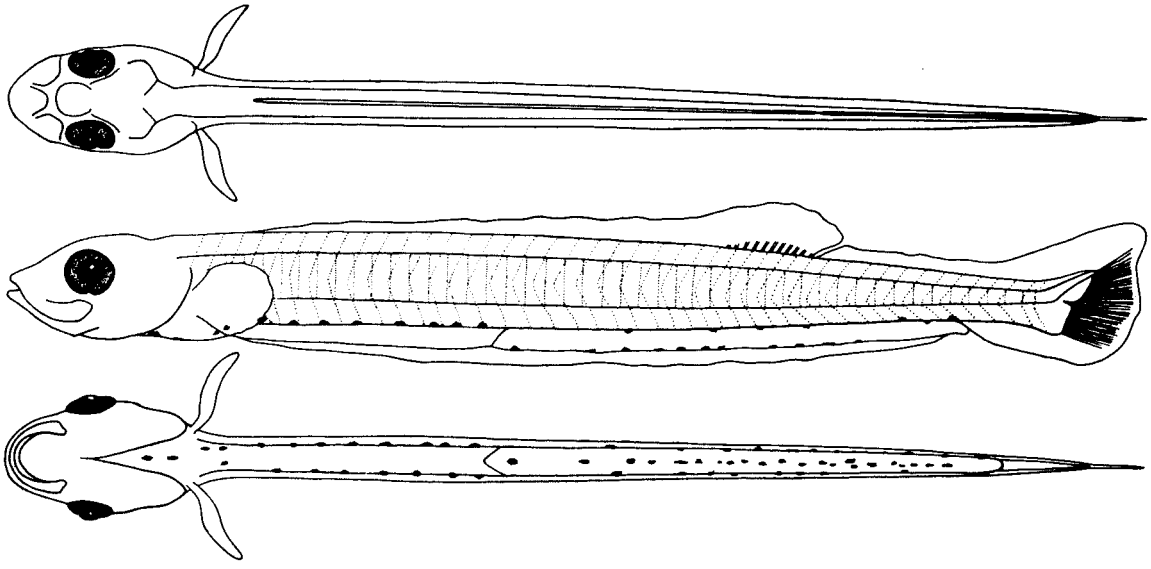

FIGURE 3.—*Opisthonema oglinum* larva 10.7 mm standard length.

H. jaguana by Houde et al. (1974). They noted that the second ural vertebra ossified first. Epural development displayed some variation (two instead of the normal three in some specimens), as was also noted in *Harengula* by Houde et al. (1974). Hollister (1936) noted this variation in *Harengula* but not in *Opisthonema*. Other than these differences, caudal development was essentially the same for *Opisthonema* and *Harengula*. For a more complete account, consult Houde et al. (1974).

At 10.5 mm, ossification also started on vertebrae 12 through 40. This ossification starts on the dorsal and ventral surfaces of the centra, thus making it quite easy to count vertebrae. The degree of ossification of these vertebrae indicates that the middle ones were most ossified, with ossification proceeding anteriorly and posteriorly. By 12.5 mm, dorsal and ventral ossification of the centra is complete on vertebrae 2 through 41, while only the ventral centrum surface has ossified on the first vertebra and the

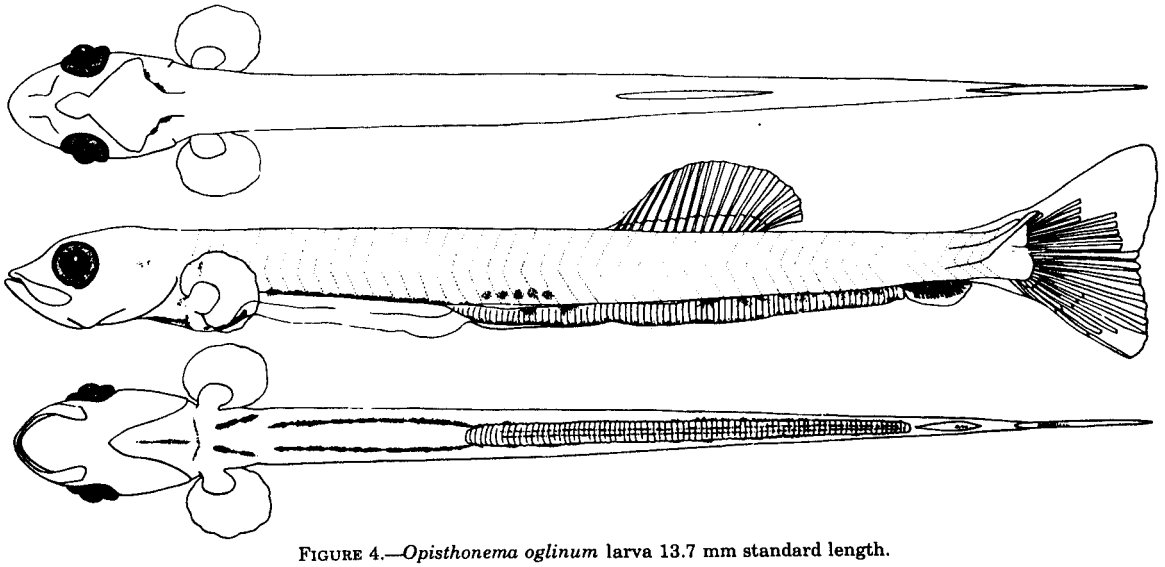

FIGURE 4.—*Opisthonema oglinum* larva 13.7 mm standard length.

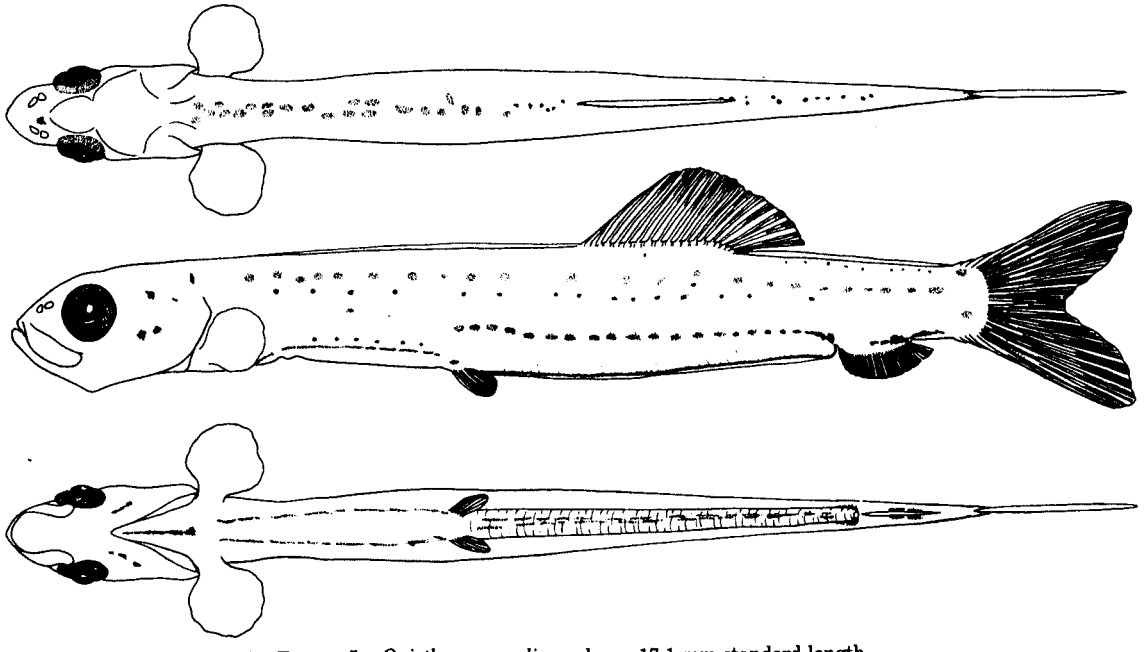

FIGURE 5.—*Opisthonema oglinum* larva 17.1 mm standard length.

three preceding the ural centra. These three centra immediately anterior to the first preural were wider ventrally and had large spaces between the vertebral segments. At 15.5 mm, all vertebral centra were partially ossified and evenly spaced with narrow spaces between. In the first preural and ural centra, the three rings of ossification had widened, but the middle ring was still wider ventrally than dorsally. (This asymmetrical shape of the ossified rings of the vertebrae associated with the caudal region obviously corresponds to flexion of the notochord. The ventral surface is longer after flexion than the dorsal surface and, consequently, to keep the

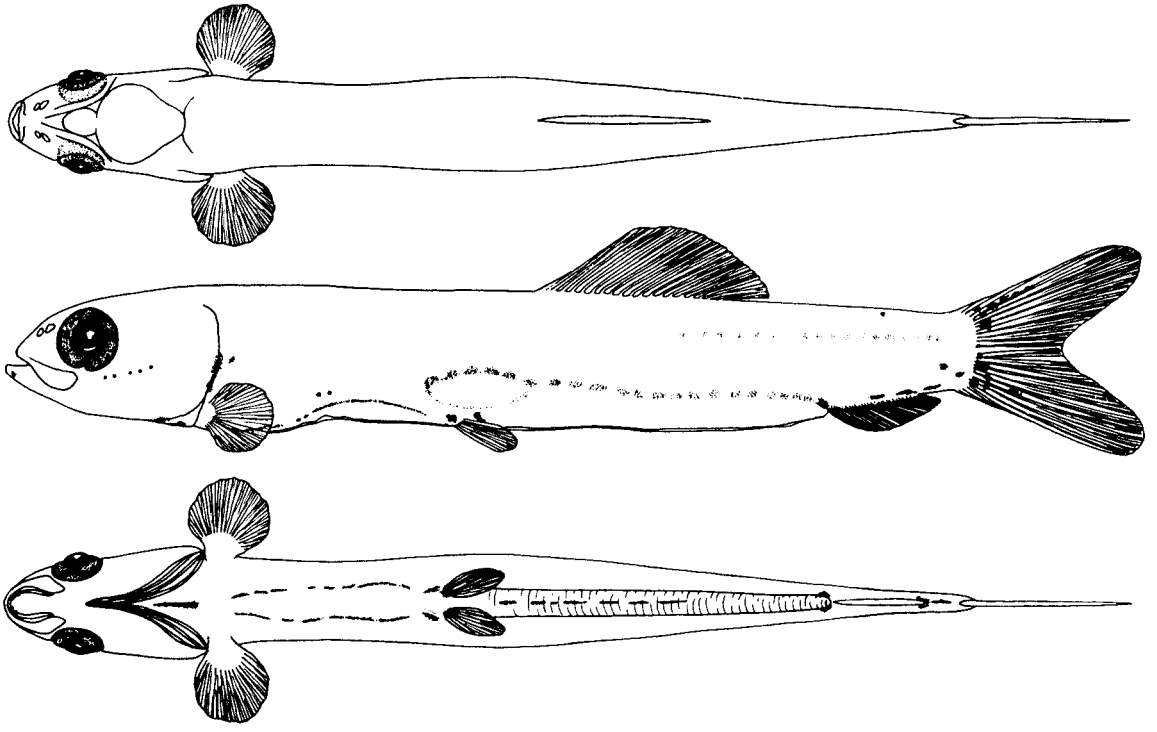

FIGURE 6.—*Opisthonema oglinum* larva 19.7 mm standard length.

spaces between ossified segments equal, the segments ossify in a wedgelike shape.) By 17.1 mm, the three rings had widened appreciably and the spaces had narrowed.

Neural and hemal spines ossify in a posterior to anterior direction. Neural spines are well formed over the last three centra, which precede the first preural well before ossification on the centra is completed. By 17.1 mm, ossification of these elements is just complete to below the dorsal fin, and by 22 mm they are all ossified.

Fin Development

The earliest fin development was of the caudal and dorsal fins, more-or-less as lobes, at about 4 mm TL. This early development may be due to a rearing abnormality since fin development is seldom seen in field-caught larvae less than 7 mm SL. Increasing numbers of caudal and dorsal rays were defined at lengths from 6 to 8.4 mm, but were not clear enough to count until our 8.4-mm specimen (17 caudal and 11 dorsal rays, Table 1 and Figure 3). Between 8.4 and 10.0 mm, the final two caudal rays were differentiated to complete the adult complement of 19 principal cartilaginous rays (10 superior and 9 inferior).

Rays continued to be added to the dorsal fin: 16 were present at 12.5 mm and 18 to 20 were present from 15 to 20 mm (Table 1, Figures 4 through 7). As growth proceeded, one or two more rays were added to complete the adult complement of 21 or 22 dorsal rays (Figure 8). In adult *Opisthonema*, the last ray of the dorsal fin is elongate—more than twice as long as the next longest ray. Until about larval size of 20 mm, the last ray was half as long as the longest ray, but from then on it began to elongate. From about 27 mm, the last ray grew longer than the prior longest ray (Table 1).

The anal fin formed later than the dorsal, from a thickening of the ventral finfold in the relatively short space between the anus and the caudal fin (Figure 3). At 10.5 mm, the fin rays had begun to differentiate and nine rays could be counted. Ossified rays increased rapidly to 14, 15, or 16 at about 14 mm, after which rays were added more slowly to sizes from 15 to 20 mm. Between 14 and 20 mm, counts of 17 to 20 rays

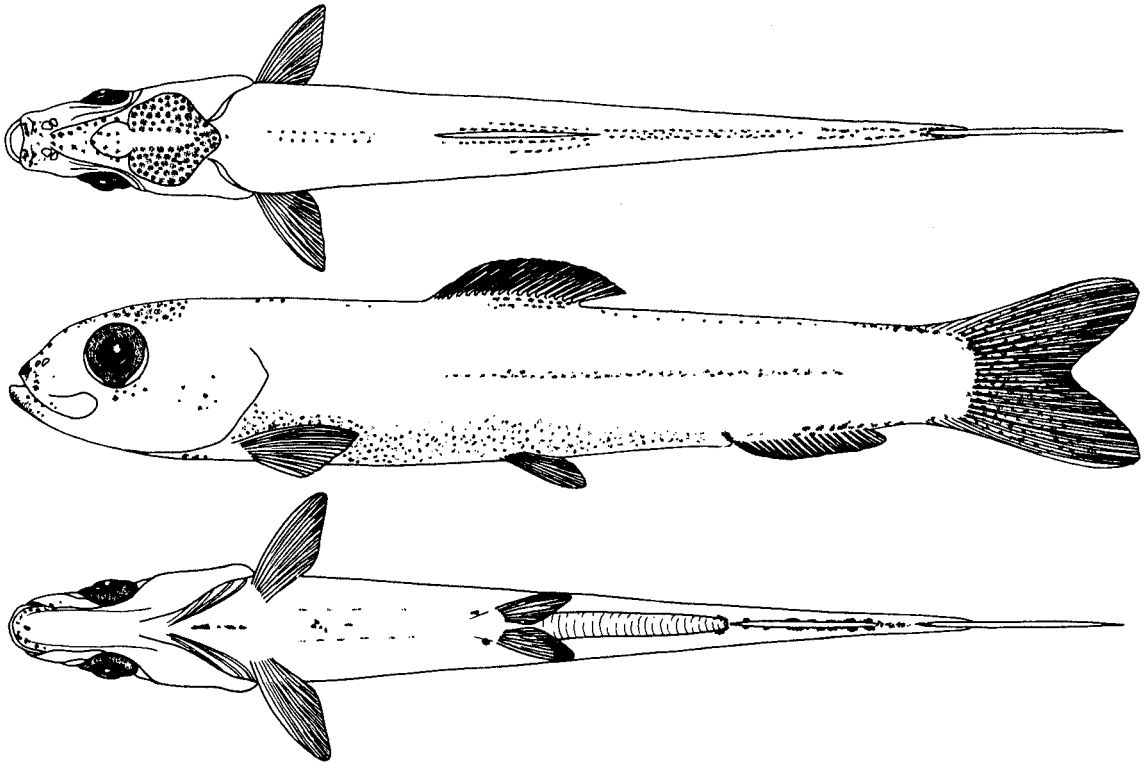

FIGURE 7.—*Opisthonema oglinum* juvenile 24.4 mm standard length.

were produced (Figure 7). Only about three or four more rays were added, from 20 mm, until the adult complement of 21 to 25 anal rays was reached at 30 mm and over (Table 1, Figure 8).

The pectoral fin appeared as a small, fan-shaped structure just behind the cleithral ring, but this structure enlarged gradually (Figures 2 to 7). [Within the fan, "ray areas" differentiated soon thereafter, but these had no apparent relation to where rays actually ossify.] Ossified rays first appeared at about 17 mm (five rays; see Table 1) and quickly increased to about 10 rays at 19 mm. The rounded fan shape of the pectoral fin changed into the pointed shape characteristic of adults between 19 and 23 mm (Figure 7). At 21 mm, specimens had about 13 or 14 rays, and the adult complement of 15 to 17 rays was reached at 23 to 25 mm. The sequence of ray ossification was in a dorsal (uppermost) to ventral (lowermost) direction.

Ossified pelvic rays appeared earlier than the pectoral rays. At about 13 mm, larvae had about four rays (Table 1), and at about 15 mm they had five or six (Figure 5). The number of rays seemed to remain static for about the next 5 mm of growth (10 specimens in the 15 to 20 mm size range), but rather suddenly two more rays appeared at about 20 mm (Table 1, Figure 7). The pelvic ray count held constant, though size increased to 50 mm, but in adults a ninth ray is added as a flattened, segmented ray closely adnate to the second (formerly most lateral) ray to produce nine total rays. In our larger (30 to 54 mm) specimens (Figure 8) the flattened first ray does not appear to be present. If it is, the ray is so tightly attached to the second ray that the two seem to be a single unit.

Cephalic Development

No ossification of any bones appeared before specimens reached about 10.0 mm. In larvae as small as 4.1 mm TL, the cranial bulb, dentaries, and hyoid bones were visible as cartilaginous elements. At about 10.0 mm, the maxillaries and dentaries were easily distinguished and began to show slight ossification (by stain uptake). The jawbones more-or-less steadily increased in

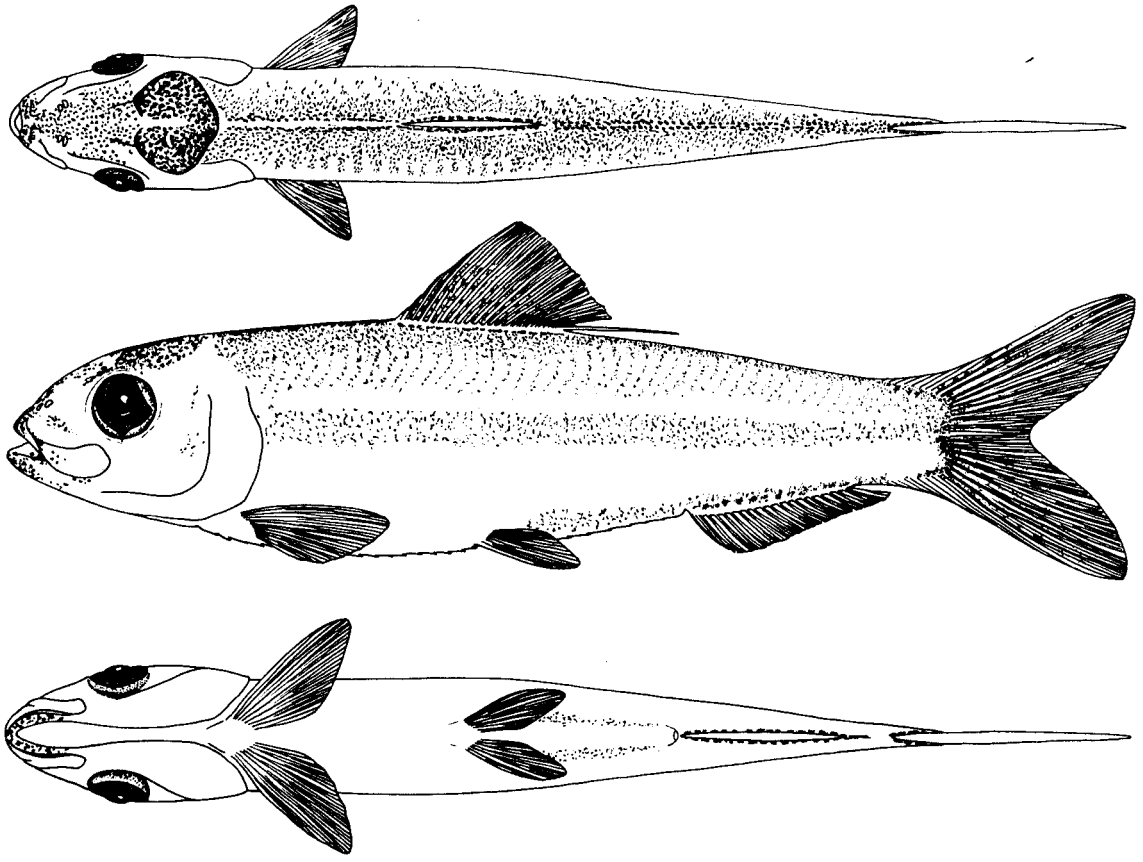

FIGURE 8.—*Opisthonema oglinum* juvenile 30.8 mm standard length.

size and became more heavily ossified; at about 14 mm, small teeth were found on the ventral edge of the maxillaries and the anterodorsal edge of the dentaries. Concommitantly, the hyoid apparatus continued to develop steadily, particularly the ceratohyals and hypohyals, which were quite distinct and slightly ossified by 14 mm. By about 17 mm, the two supramaxillaries were differentiated and partly ossified but had not obtained their characteristic adult shapes. The premaxillaries also were partly formed and ossified as two distinctly separate units close to the anterior tips of the maxillaries. By 19 mm, the articular was well developed but not fully ossified. The posterior supramaxillary was almost completely ossified but not the anterior supramaxillary. Maxillaries maintained an ossified posterior edge (the region of growth), and the teeth on the ventral edges were still prominent. The ceratohyals and urohyal were more ossified, and two small centers of heavy ossification were present in the hypohyals. One structure of interest was the presence of teeth on a few specimens on the basihyal. In a 12.0-mm specimen, two large erect teeth were noted; a 15.6-mm specimen had one such tooth, which was also present on a 17.1-mm specimen. No such teeth were evident on a 25.9-mm specimen, indicating that these teeth may be variable and limited in occurrence. Houde et al. (1974) noted the presence of these temporary teeth in *Harengula*. The branchiostegals ossified in the following sequence: fourth branchiostegal slightly ossified at 15.5 mm; fourth well ossified at 17.1 mm; fourth, third, and second ossified; first visible as cartilage; fifth and sixth not visible at 19.7 mm. By the time specimens reached 24 mm, six well-ossified branchiostegals were present, the supramaxillaries were ossified but the posterior supramaxillary had not reached a complete adult shape, all the hyals were partly ossified, the well-developed premaxillaries were ossified and

TABLE 3.—Position of dorsal and anal fins during the transformation period in larvae of *Opisthonema oglinum*.

SL (mm)	Dorsal origin over vertebra	2d dorsal pterygiophore opposite neural arch	Anal origin under vertebra	1st anal pterygiophore opposite haemal arch
15.5	25	21	38	36
17.1	23	—	37	35
17.2	22-23	20	38-39	36
18.4	23	20	38	35-36
19.7	20	17	36	34
21.1	16	12	—	—
24.4	16	11	33	30
25.9	15-16	11	33	30
26.2	16	11	33-34	30
27.0	14	9	32	29
27.1	15	11	33	30
27.1	15	10	33	30
27.3	14	10	33	30
28.2	15	10	33	30
30.8	15-16	10	33	30
34.9	15	10	34	30
54.0	15	9	34	30

joined at the anterior tip of the upper jaw, and the maxillaries appeared to be fully formed.

At about 10 mm, the cleithral ring was obvious as a thin ring of ossified bone almost encircling the head and forming a posterior line of demarkation. The three bones that actually form this ring are the supracleithrum, cleithrum, and postcleithrum, which developed fairly uniformly to about the time the pectoral fin began to develop ossified rays (about 15 to 17 mm). Thereafter, the cleithrum became the dominant element.

A cartilaginous cranial bulb was visible in our smallest larvae, but no elements were differentiated or ossified until about 12 mm. At that size, bone elements (e.g., the sphenotics, parietals, epiotics, and pterotics) were slightly outlined. Between 12 and 13 mm, the vomer and parasphenoid began to show considerable ossification, and the pterotic and prootic bullae were differentiated by ossification of the surrounding bones. The frontals began to form when specimens measured about 15 mm, and about 19 mm they were partly ossified (but not fully formed), and sensory canals were present within the bones. Canals also formed at the 19-mm size in the prootics and sphenotics, and the prootic bulla was the most obvious structure in the skull because of the heavily ossified bone around it.

The quadrate and the pterygoids had begun to form by 19 mm, and the articular had increased in size but was not yet fully ossified. At about 21 mm, the nasals began to form as thin, small plates at the anterior ends of the frontals. Formation of supraorbitals had also begun, the anterior one being moderately well developed and quite separate from the posterior one. At the 21-mm size, it also appeared that most of the head bones were at least partly formed, and ossification ranged from slight to considerable. By 25 mm, the prootic bulla was well encased in heavy bone, the sclerotics had begun to ossify along with the supraorbitals, the ethmoids had begun to form and ossify at the anterior ends of the frontals and just behind and above the premaxillaries, the vomer was quite large and well ossified, most sensory canals were partly to fully formed and encased in bone, the postorbitals had begun to form, and the pterotic bulla (which lagged far behind the prootic in development) began to grow larger. From 25 mm through the juvenile period, growth of the skull bones was restricted primarily to an increase in size and consolidation within the several multibone complexes; the dorsal and lateral frontoparietal foramina decreased in size as the bones increased, and the characteristic striae of the dorsal surface of the frontoparietals began to form; the pterotic bulla finally became larger than the prootic by about 34 mm; and the palatines began to ossify. During the 30- to 50-mm range, most of the cranial structures assumed their adult configuration, the dorsal frontoparietal foramina completely closed up, and the lateral foramina became reduced in relative size.

The elements of the opercular complex—primarily the opercle and preopercle—began to differentiate at about 15 mm. Shortly thereafter the subopercle and interopercle began to form and by 21 mm most of the opercular series appeared to be about halfway ossified; the interopercle seemed to be the most weakly ossified. By 25 to 26 mm, the interopercle had grown to articulate with the quadrate and angular and the hyals. The other opercular bones had become quite well developed, but the posteroventral edges remained unossified, evidently to permit continuous growth.

Branchial Development

The ceratobranchials were the first elements to develop in the branchial system, becoming evident at about 10 mm. By about 12 to 13 mm, the ceratobranchials showed a slight uptake of stain, indicating that they had begun to ossify. At 14 mm, the hypobranchials had begun to differentiate, and a few unossified rakers were visible on the ceratobranchials.

The ceratobranchials, the first, second, and third epibranchials, and the hypobranchials all developed as more-or-less straight rods (although the epibranchials also developed small dorsal extensions for attachment of suspensory ligaments). The first rakers appeared on the ceratobranchials at about 12 mm (Table 1) and held almost constant between 10 to 13 rakers to about 17 mm. Two or three rakers appeared on the epibranchials and hypobranchials when larvae reached about 15 mm. The numbers of rakers on all three elements gradually increased with the numbers on the epibranchials and hypobranchials almost equal but from two to four lower than on the ceratobranchials, up to about 30 mm (Table 1). At the 30-mm size, all three bones had an equal number of rakers, but beyond that size the ceratobranchials seemed to lag behind the epibranchials and hypobranchials by five or six rakers. In adults, the hypobranchials and ceratobranchials are almost equal in numbers of rakers (30 to 45), producing lower branch counts of 60 to 90, but the epibranchial rakers almost equal the combined lower branch counts.

The fourth epibranchial (E4) was the first to develop a slight vertical extension when specimens measured about 14 mm; the shape of the fourth epibranchial at this stage is more-or-less like an inverted "T"—the crossbar (the basal shaft) is ventral and the vertical segment extends dorsally from it. On the dorsal and posterior edges a developing cartilaginous capsule (see Miller, 1969; Figure 2, for the adult configuration of the capsule) is fused to the developing E4 bone; this capsule is also joined to the epiceratobranchial "elbow." A vertical slit is present in the posterior side of the capsule, and the two raker series that will eventually grow throughout the length of the lumen of the epibranchial organ begin growing along the sides of the posterior slit. Dual fourth epibranchial raker series are present, with the lateral series growing along the ventrolateral edge of the fourth epibranchial bone, outside the epibranchial organ, and the medial fourth epibranchial series is enclosed in the organ along the anterolateral edge of the slit in the cartilaginous capsule. The single fifth epibranchial series grows along the posteromedial edge of the slit. By 15.5 mm, the vertical extension on E4 had grown much heavier and the characteristic posterior foramen had formed (see Miller, 1969; Figures 2 and 4). Three raker tubercles were present along the edges of the posterior slit (which had just begun to form). By 17 mm, the cartilaginous capsule had begun to increase in size, and by 19 mm there were four or five raker tubercles in the posterior slit. Almost no ossification had yet appeared on the fourth epibranchial, and the posterior foramen was quite large. Ossification began at about 20 mm, and by about 25 mm the posterior end of the basal shaft had expanded vertically (it resembled an axe blade), and the vertical shaft had also broadened and ossified quite heavily. At this stage there were about eight rakers along the edges of the posterior slit. When larvae measured 26 mm, the lumen of the organ had begun to form; it extended anterodorsally within the cartilaginous capsule from the bridge of the posterior slit, and 10 rakers appeared along each edge. One or two rakers were present in the developing lumen. By 30 mm, the lumen had elongated to about one-third of a full loop [the epibranchial organ in *Opisthonema* is the continuous-tube type (see Bertmar, Kapoor, and Miller, 1969; Miller, 1969) in which the lumen and included rakers extend for a full loop in adults] and there were about 15 to 20 rakers in the lumen. By 35 mm, the lumen was about a half of a full loop and

had curved anteriorly beyond the width of the vertical shaft of E4. About 30 rakers were present in each series at this stage and the epibranchial organ and E4 bone were assuming adult configuration. Estimates made on adult specimens indicate that in a full-loop, continuous-tube epibranchial organ, the definitive number of rakers in the included medial E4 and single E5 series each at least equal the total of rakers on the whole first gill arch. There are about 120 rakers in adults 100 mm or longer (Berry and Barrett, 1963). We may therefore infer that the number of rakers in the epibranchial organ increases gradually with increasing size of the fish, to about 120 or more in each series.

PIGMENTATION

Melanophores were present along the ventral midline in the smallest specimens studied (4 mm) —one or two melanophores beneath the heart just anterior to the pectoral symphysis, and a paired row along the base of the hindgut (that portion of the gut posterior to the site of the pelvic fins) continuing to the anus, and a row on the ventral midline posterior to the anus. A dorsolateral row of melanophores occurred on each side of the foregut (that portion of the gut anterior to the pelvic fin region). The eye was pigmented but no other melanophores were present (Figure 2). By 10 mm, the posterior ventral row was distributed along the posterior edge of the hypural bones, and a few internally placed melanophores appeared dorsolaterally on each side of the hindgut. The remaining melanophore pattern was basically unchanged (Figure 3). By 15 mm, the melanophores had developed into streaks of pigment along the base of the isthmus, dorsolaterally along the anterior gut, along the base of the posterior gut, and on each side of the base of the anal fin. Internal melanophores above the posterior gut had taken on a well-defined, broken-lined pattern and had begun to advance anteriorly, particularly forming a slight arch in the area of the swim bladder (Figure 4). Melanophores appeared on the cleithrum near the hindbrain, and the hypural melanophores at first clustered on the bases of the lower lobe of the caudal fin but, by 17 mm, melanophores appeared on both lobes of the caudal fin. Between 15 and 24 mm (transformation period), melanophores varied somewhat in time of appearance. In some specimens a melanophore appeared medial to the left nostril (Figure 5, dorsal view). Melanophores appeared both dorsally and ventrally on the swim bladder as it developed (Figure 6). During this period melanophores also began to appear on the dorsum, first posterior to the dorsal fin, then anteriorly. Melanophores also appeared along the lateral midline and over the hypural bones internally. The internal pigment associated with the vertebral column of these larvae is quite pronounced, particularly during transformation. A few internal melanophores over the posterior centra were first noted in a cleared and stained 12.1-mm specimen. By 15 mm, one or two melanophores or groups of melanophores were noted above each vertebra. The melanophores over the anterior vertebrae are lost or reduced by 19 mm. Some individual variation, however, is evident in both the internal and external pigmentation. The dorsal external pigmentation is noticeably reduced in the 19.7-mm specimen (Figure 6) as compared to the 17.1-mm specimen (Figure 5). The expanded state of most melanophores (a probable result of rearing under continuous illumination) makes detailed counts of melanophore patches quite difficult. Following transformation, melanophores were visible over the brain and on the jaws as well as in increasing quantities on the dorsum, lateral midline, over the gut, and in the caudal fin rays (Figure 7). By 30 mm, the dorsal pigment had increased, the foregut pigment was lost, and melanophores were seen in the dorsal fin—essentially the adult pattern (Figure 8).

In life, the larvae are transparent and the only noticeable features are the heavily pigmented eyes. The gut is usually noticeable because of the food contained in it. In larger larvae, the swim bladder is decidedly noticeable as a bubble above the gut (Figure 6). Melanophores are invisible until the specimen is examined under magnification.

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THE INFLUENCE OF TEMPERATURE ON LARVAL AND JUVENILE GROWTH IN THREE SPECIES OF SOUTHERN CALIFORNIA ABALONES[1]

DAVID L. LEIGHTON[2]

ABSTRACT

Larvae of the abalones *Haliotis rufescens*, *H. corrugata*, and *H. fulgens* displayed most rapid growth and best survival at 15°-18°, 18°-21°, and 20°-23°C, respectively. Survival of larvae and postlarvae was poor above these optimal ranges. However, juveniles 3 mo to 1 yr old were tolerant of a broader temperature range. The warm-water species, *H. fulgens*, increased in shell length at an average rate of 88 μ per day at 26°C. Mean shell elongation rates were 77 and 64 μ per day in *H. rufescens* and in *H. corrugata* at their respective optima.

An expanding body of literature exists concerning aspects of the biology and culture of the abalone *Haliotis* (e.g., Sakai, 1962; Oba, 1964; Tamura, 1966; Imai, 1967; Tanaka, 1969; Shibui, 1971a; and McBeth, 1972, which succeeded the pioneering studies of Murayama, 1935, and Ino, 1952). In these studies little attention was directed to problems of larval development, and essentially no information has been obtained on the limitations imposed by temperature on growth and survival of larvae and postlarvae with the single exception of the observations on *H. sorenseni*, reported by Leighton (1972). In 1962, Kan-no and Kikuchi related results of a 3-wk experiment in which juvenile *H. discus hannai* were reared at five different temperatures, but most investigators have merely reported the range of temperature prevailing during observations (e.g., Oba, 1964; Shibui, 1971b).

This paper describes results of experiments in which groups of larvae, postlarvae, and juveniles were reared at a series of temperatures encompassing the natural range to examine the influence of these factors on development and survival. Larvae were obtained from three American west coast species spawned in the laboratory: The red abalone, *H. rufescens*, the pink abalone, *H. corrugata*, and the green abalone, *H. fulgens*.

MATERIAL AND METHODS

Ripe abalone were collected off southern California by diving. In transportation to the laboratory, care was taken to avoid subjecting the animals to desiccation or other physical shock which might have induced premature release of gametes. Adult abalone were allowed a laboratory "conditioning period" of about 2 wk before attempts were made to induce spawning. Water temperature in tanks containing abalone of both sexes was raised approximately 5°-8°C above ambient, following the thermal shock method of Ino (1952) and Oba (1964); a procedure which was only occasionally successful. Most productive spawnings in terms of quantity and viability were those which occurred spontaneously in the laboratory. Natural cues and events associated with "mass spawnings" are not well understood (Owen and Meyer, in press) and were not investigated in this study.

Fertilized eggs were collected as soon as possible after their release. The eggs, which settle rather rapidly, were siphoned or pipetted into freshly filtered seawater (Cuno filter unit,[3] ca. 5 μ) at the same temperature as that of the spawning environment. Repetition of the process several times, each time using freshly filtered seawater, was usually sufficient to wash eggs free of excess sperm and debris. Incubation was carried out at ambient temperatures and larvae treated as described elsewhere (Leighton, 1972).

While some experiments were performed with eggs at early cleavage stages, most observations

[1]This work is a result of research sponsored by NOAA Office of Sea Grant U.S. Department of Commerce, under Grant #UCSD 2-35208 with the Institute of Marine Resources in cooperation with California Marine Associates, Cayucos, Calif. The study was carried out in the aquarium laboratory of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif.

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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were initiated with newly hatched trochophore larvae. Trochophores normally hatched from eggs at 15°-18°C within 12 to 18 h. Shortly after hatching, larvae swim to the surface (negative geotaxis) and are easily drawn into a pipette for transfer to experimental containers.

Thermal influence on development and survival of larvae and postlarvae was observed using a temperature gradient apparatus; an aluminum block (30 × 15 × 150 cm) bored to accommodate replicate series of test tubes (25 ml). Cooling coils and heating elements at opposite ends maintained a temperature differential (range: 7°-31°C) with but slight fluctuation (±0.5°C per gradient position) over the course of the average experiment (2-4 wk). The apparatus is similar to that used with *H. sorenseni* larvae (Leighton, 1972) and has been thoroughly described elsewhere (Thomas, Scotten, and Bradshaw, 1963).

In the typical experiment duplicate series of 10 tubes, each tube containing 20 ml of seawater, were placed in the thermal gradient with 50 eggs or larvae. Incubation was carried out in darkness. A foam urethane cover insulated the apparatus. Inspection of the tubes was made daily during the first week and on alternate days thereafter to determine the stage of development attained. As abalone larvae are lecithotrophic, feeding was not necessary until settlement. At that time a mixture of three species of pennate diatoms (*Nitzschia* spp.) was supplied.

Studies on postlarvae were also conducted using the temperature gradient block. Between two and five individuals were placed in each tube. Postlarvae 1-2 mo of age were picked individually from walls of culture containers (Pyrex beakers or polyethylene pails) using a finely bevelled applicator stick. Several drops of the diatom culture were added to each tube twice weekly over the usual 2-wk observation period.

To examine the effect of temperature on the success of juveniles, groups of 8-12 individuals were reared in six 10-liter polyethylene containers maintained at 12°, 15°, 18°, 21°, 24°, and 27°C (±1.0°). Water was continuously aerated and the entire volume exchanged once a week. Food was either a mixture of unicellular and filamentous algae cultured within each container under illumination of a fluorescent lamp or fronds of the brown alga, *Egregia laevigata,* collected in fresh condition every 3-4 days. Growth of juvenile abalones was measured for month-long intervals in these experiments.

Progeny of each spawning were maintained in the laboratory for over 1 yr providing comparative information on juvenile growth rate in aquaria. Diatoms and minute filamentous algae served as food during their first few months. Older juveniles were provided larger algae, *Egregia laevigata, Eisenia arborea, Macrocystis pyrifera,* and *Laminaria farlowii.*

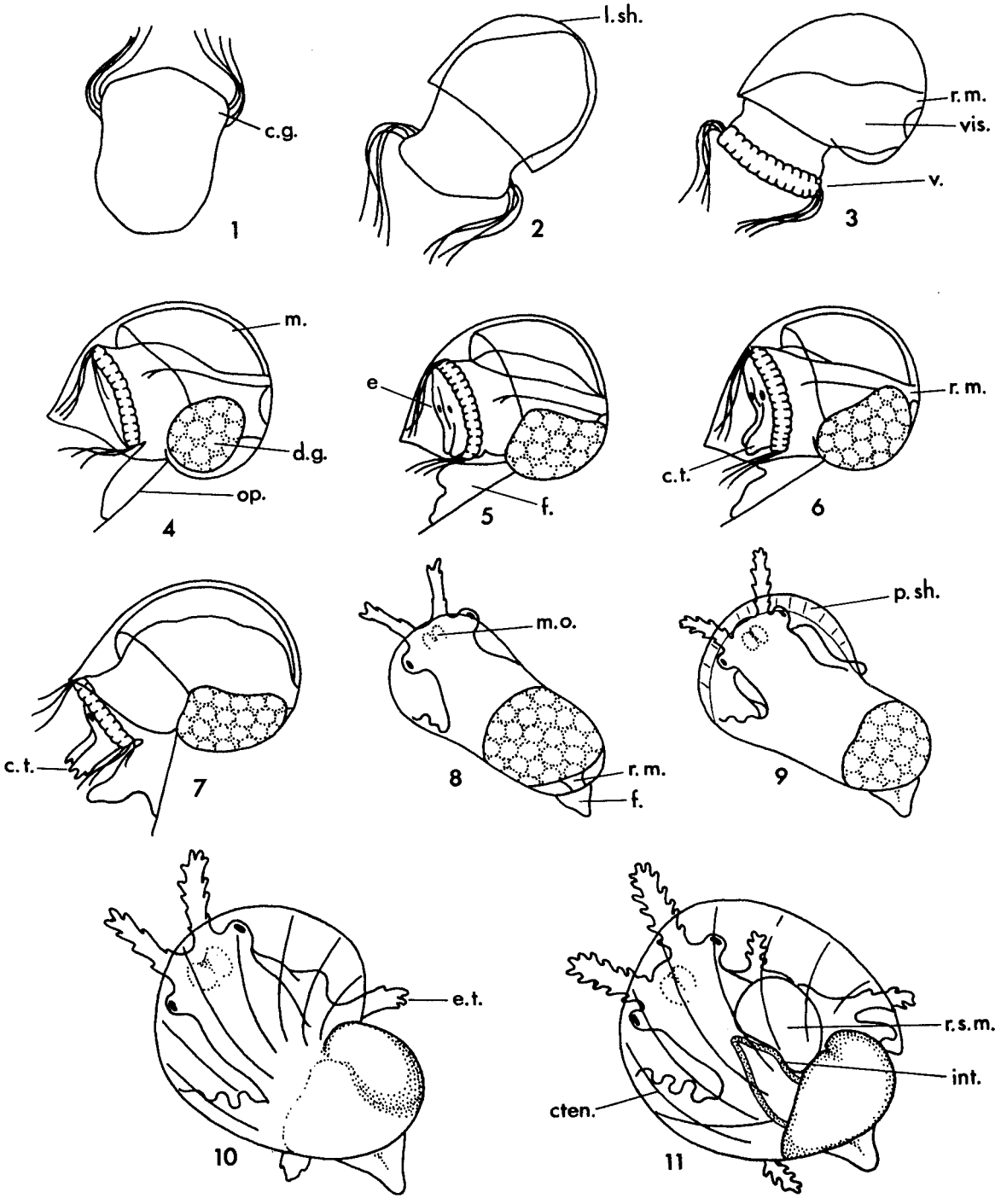
DEVELOPMENTAL FEATURES OF LARVAE, POSTLARVAE, AND JUVENILES

While morphogenesis is gradual and does not progress in a stepwise manner, various stages of larval and postlarval development are recognizable. Development rate was measured in terms of the time required for larvae to first gain features distinctive to each stage. Eleven such stages are passed from trochophore larva to circular-shelled postlarva (Figure 1). Settlement (the crawling stage) marks the end of larval life. Postlarval development then begins with the deposition of peristomial shell and persists to formation of the first respiratory pore ("notch stage," Leighton, 1972) at an age of 1-3 mo. Thenceforth to first sexual maturity the abalone may be regarded as juvenile.

FIGURE 1.—1) Trochophore larva after hatching. 2) Cap-shell early veliger larva. 3) Inflate-shell veliger (torsion stage). 4) Early operculate veliger (preeye spot). 5) Incipient cephalic tentacle stage operculate veliger. 6) Midformed cephalic tentacle stage. 7) Digitate or branched cephalic tentacle stage. 8) Crawling and settling stage. 9) Peristomial shell stage postlarva. 10) Midasymmetric shell postlarva. 11) Circular-shell postlarva.

Labelled structures:

c.g.,	ciliated girdle
c.t.,	cephalic tentacle
cten.,	ctenidium
d.g.,	digestive gland
e.,	eye spot
e.t.,	epipodial tentacle
f.,	foot
int.,	intestine
l. sh.,	larval shell
m.,	mantle
m.o.,	mouth with odontophore
op.,	operculum
p.s.,	peristomial shell
r.m.,	retractor muscle
r.s.m.,	right shell muscle
v.,	velum
vis.,	viscera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RESULTS

In the course of the study six batches of larvae were obtained from *Haliotis rufescens,* while three productive spawnings occurred with *H. corrugata* and *H. fulgens.* Year-round spawning in *H. rufescens* was predicted by Boolootian, Farmanfarmaian, and Giese (1962) and Young and DeMartini (1970) from field sampling for gonad indices. I found spawning adults every month of the year (1969-71) in samples taken from Estero Bay (central California) and in the present study with *H. rufescens* from southern California, laboratory spawnings were obtained in January, February, April, September, November, and December. *Haliotis corrugata* and *H. fulgens* spawned only during the months of April, June, and October. Members of the shallowwater species, *H. cracherodii,* held in the laboratory for another study, spawned in early spring and early fall. *Haliotis sorenseni* produced viable gametes only during late winter (Leighton, 1972).

DEVELOPMENT AND HATCHING IN EGGS

At 14°-16°C (ambient for La Jolla during most of the year) eggs of all species hatched within 18-24 h. Generally, development to hatching appeared normal over a rather broad thermal range. At hatching, however, consequences of inappropriate incubation temperatures became pronounced as trochophore larvae at and near thermal limits became highly abnormal in appearance and behavior and usually succumbed within 48 h, particularly at higher temperatures. Bizarre ciliated bodies predominated at high extremes of temperature while retardation and paralysis occurred at lowest temperatures. Commonly torsion was incomplete in larvae held at subnormal temperatures. A consequence of ensuing abnormality and mortality near thermal limits is apparent in the series of curves generated for development during the first several days of larval life. Attrition at upper and lower extremes and relatively high survival and rapid growth at optimal temperatures is reflected in the sharply peaked curves for larval development rate versus temperature. In *H. rufescens,* for example, eggs developed in an apparently normal manner over the range 10°-23°C, but larval growth after hatching became restricted to the comparatively narrow range 13.5°-20.0°C (Figure 2). The apparent shift of the peaks of curves with time to suggest true optima at temperatures about 2°C lower than observed in trochophore larvae was found in all species studied due to supraoptimum mortality.

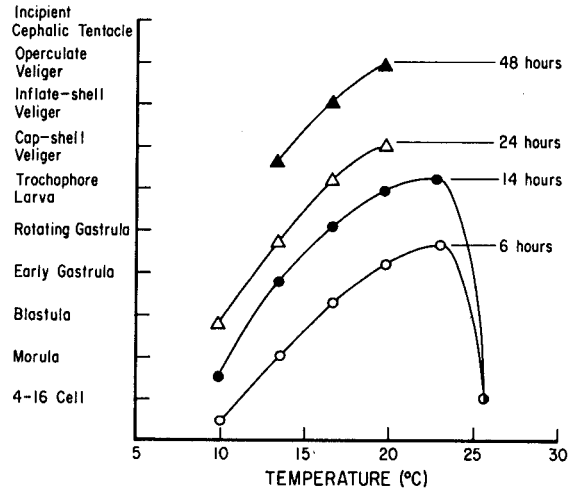

FIGURE 2.—Development of eggs of *Haliotis rufescens* held at different temperatures over a period of 48 h. Mortality occurred above 20°C after 14 h.

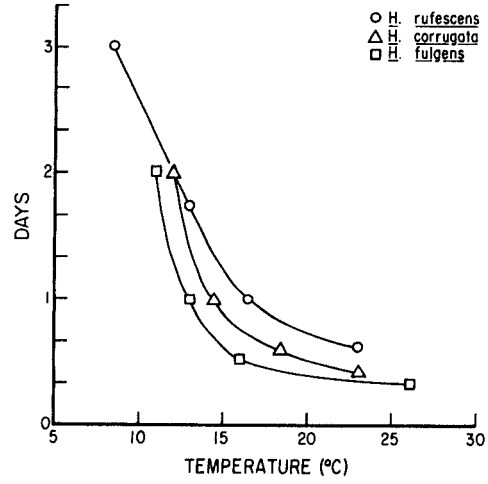

FIGURE 3.—Hatching time for eggs of three species of *Haliotis* incubated at several temperatures.

Hatching time was strongly dependent on temperature and ranged between 10 and 72 h. Both *H. corrugata* and *H. fulgens,* at temperatures supporting rapid but normal growth (their respective thermal optima), reached the point of hatching sooner than did *H. rufescens* (Figure 3). Strongest contrast in specific development rate is seen in the stage attained at supraoptimum temperatures (2°-3°C above optimum). In 2 days: *H.*

rufescens (near 19°C) reached the early (preeye spot) operculate stage, *H. corrugata* (near 23°C) had formed eyespots and cephalic tentacle buds, and *H. fulgens* (near 25°C) had become mid-cephalic tentacle operculates. In the latter, settling was observed as early as 3 days after fertilization.

OBSERVATIONS ON TROCHOPHORE LARVAE

When swimming trochophore larvae rather than developing eggs were introduced to the thermal gradient system, survival was improved. In experiments initiated with fertilized eggs, survival beyond 3 days in the 20-ml tubes was low despite routine addition of dihydrostreptomycin sulfate and sulfanilamide (to final concentration, 10 ppm). Substances within the perivitelline space (including excess sperm) are liberated at rupture of the albumen membrane, frequently promoting fouling. Temperature block studies in which trochophore or veliger larvae were freed of contaminants by repeated transfer and then admitted to the tubes showed reduced mortality.

Haliotis rufescens larvae settled approximately 4 days after fertilization (18°C). However, after 3 wk in the temperature block, only those groups between 14° and 18°C had reached advanced postlarval stages (Figure 4). Settling occurred in some *H. corrugata* larvae within 3.5 days, but postlarvae did not survive (22°-23°C). Most rapid growth and best survival in *H. corrugata* was at 21°-22°C; the circular-shell postlarval stage was reached in 17 days (Figure 5). Settlement began in larvae of *H. fulgens* at 25.5°C in slightly less than 3 days, but again, subsequent success was poor. Those at 22°-23°C, however, settled by the fourth day and progressed to the circular-shell stage in 15 days (Figure 6). There was a close correspondence of curves for development rate vs. temperature obtained with progeny from different spawnings and parentage. Optima described graphically for each species varied within only 1°C for *H. corrugata*, 1.5°C for *H. fulgens*, and 2°C for *H. rufescens*.

Larvae introduced to a thermal gradient as operculate veligers exhibited tolerance to a broader temperature range. Subsequent development rate was, however, slowed. The general retardation may be a shock response to environmental change. The greatly reduced volume provided in the 20-ml tubes and the totally darkened conditions in the temperature block contrast with

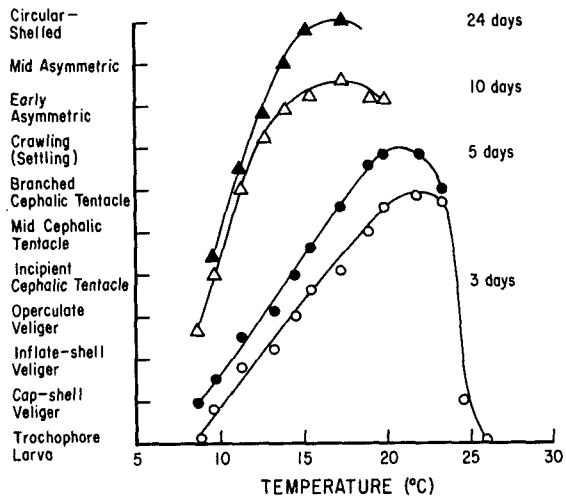

FIGURE 4.—Development of larvae of *Haliotis rufescens* at a series of temperatures when introduced to the thermal gradient as trochophores.

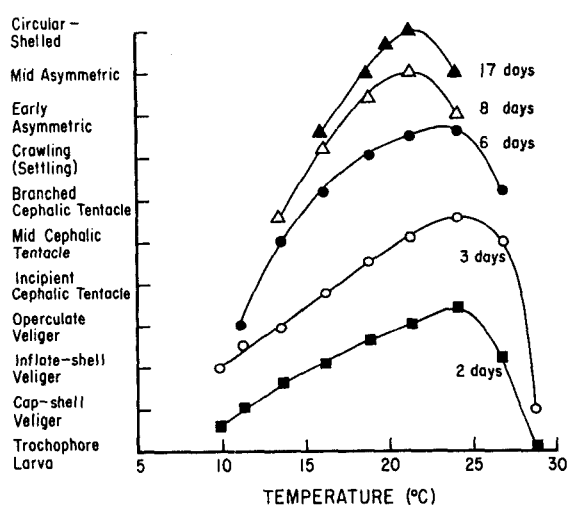

FIGURE 5.—Stages attained by larvae of *Haliotis corrugata* over a period of 17 days. Larvae were placed in the thermal gradient at the trochophore stage.

the 10-liter volume and illumination in the plastic rearing containers. In an experiment illustrating the point, *H. corrugata* eggs, trochophores and operculate veligers were placed in the gradient for 5 days in each case. At 20°-22°C, eggs developed rapidly and early postlarval stages reached in 5 days. However, operculate veligers had not yet reached the crawling stage at an age of 7 days (Figure 7).

In temperature block experiments, survival through settling usually ranged between 50 and

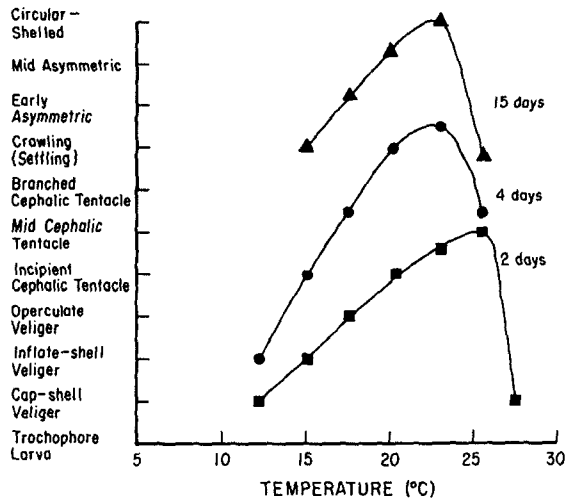

FIGURE 6.—Stages attained by *Haliotis fulgens* larvae incubated at several temperatures for 15 days. The experiment was initiated with trochophore larvae.

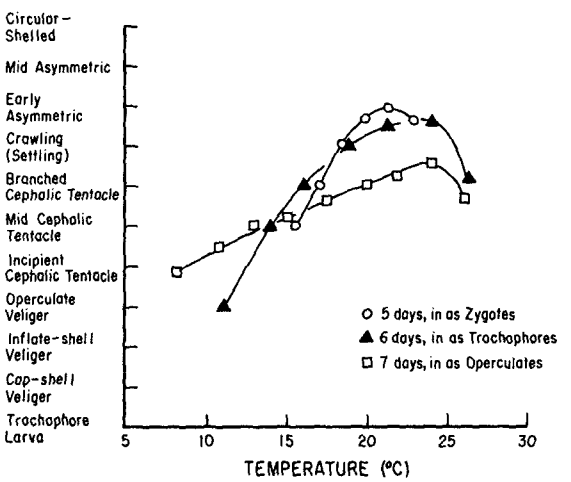

FIGURE 7.—Comparison of development rate and tolerated thermal range in larvae of *Haliotis corrugata* placed in the temperature block at 1, 20, and 48 h after fertilization.

80% within the physiologically acceptable temperature range. High mortality near the upper limit might have been due, in part, to oxygen exhaustion. This was tested by sampling open-top tubes in the block at 22° and 24°C for oxygen content after holding approximately 150 larvae (*H. rufescens*) for 48 h. A decline from 5.8 to 2.9 ml O_2/liter was observed at 22°C in 48 h. Routinely, therefore, only 25 to 50 larvae or eggs were admitted to each tube and once daily tubes were mixed to assure adequate oxygen was available. Subsequently oxygen depletion was not a cause of mortality.

THERMAL TOLERANCE OF POSTLARVAE

Postlarvae ranging in age from 1 to 2 mo were placed (2-5/tube) in the thermal gradient block and provided each 3-4 days a mixture of three species of diatoms (*Nitzschia* spp.). Tubes were checked for survival and growth of postlarvae over periods of 2 wk. Survival was good in all species at colder temperatures, but those at 10°-12°C invariably were lethargic and could not right themselves once overturned. *Haliotis rufescens* survived over the range 10°-19.5°C. *Haliotis corrugata* and *H. fulgens* were tolerant to the same lower temperatures but had different upper limits, 23.5° and 26.0°C, respectively. Typically survival was nearly 100% over a broad intermediate range of temperatures, but declined sharply within 2° of the extremes.

POSTLARVAL AND JUVENILE GROWTH

Specific differences in growth rate of both postlarvae and juveniles under laboratory conditions were measured. When its postlarvae were provided near optimal thermal and feeding environments, *H. fulgens* formed the first respiratory pore in about half the time required by the other species. As the pore is formed, a notch is first seen on the anterior right shell margin. The feature is conspicuous and serves as a convenient point of comparison. The "notch stage" was reached in some rapid-growing *H. fulgens* at an age of 30 days (Table 1).

Variability in growth rate was marked. Groups of juveniles of identical parentage, age, and rearing environment sampled periodically for shell length distribution reflected a broad range and age-increasing standard deviation (Table 2). Shell

TABLE 1.—Age and shell length of postlarval *Haliotis* at formation of the first respiratory pore.

Species	Age (days)	Shell length (mm)	Temperature (°C)
H. rufescens	60-70	1.5-1.8	14-18
H. corrugata	50-60	2.0-2.5	15-22
H. fulgens	30-40	1.7-2.0	16-24
H. sorenseni	55-65	2.0-2.1	[1]14-18

[1]Leighton, 1972.

length at 1 yr of age in four species reared in the laboratory varied over a range greater than 10mm (Table 3).

INFLUENCE OF TEMPERATURE ON GROWTH RATE OF JUVENILES

Several growth experiments were conducted with juveniles of the three species of abalones to gain comparative data and to establish respective temperatures of maximum growth rate. Juveniles were reared for month-long periods in 10-liter plastic containers held at six temperatures between 12° and 30°C. Both *H. corrugata* and *H. fulgens* displayed enhanced growth rate above 20°C. *Haliotis rufescens,* however, grew best below 20°C and, in fact, grew but slightly less at the coldest temperature, 12.5°C (Table 4, Figure 8). *H. fulgens* again showed a superior growth rate. While a mean daily shell growth approaching 90 μ was observed at its temperature of maximum growth rate (26°C), some individuals increased in shell length as much as 130 μ per day.

DISCUSSION

Seven species of *Haliotis* occur in southern California waters ranging vertically from the intertidal to depths over 35 m. Depth distribution is stratified specifically, although in certain areas (i.e., in the presence of localized upwelling) overlapping does occur. Vertical and latitudinal distribution appears most closely related to temperature. The Point Loma (San Diego) shelf from 0 to 35 m supports all California abalone species (Table 5). Colder water species may be found intertidally in northern California (*H. rufescens, H.*

TABLE 2.—Variation in size of juvenile *Haliotis* of identical parentage, age, and growing environment.

Species	Age (months)	Number	Shell length (mm) Mean	Range	SD
H. rufescens	3.7	18	4.4	2.6-6.1	1.06
H. corrugata	5.0	27	9.2	6.8-14.1	2.42
H. fulgens	4.7	70	7.1	3.6-12.0	2.00
H. sorenseni	3.3	19	4.3	3.0-5.6	0.64

TABLE 3.—Size of *Haliotis* at completion of first year growth in the laboratory.

Species	Shell length (mm) Mean	Range	Number
H. rufescens	15.6	9.9-20.0	50
H. corrugata	18.3	12.2-26.4	18
H. fulgens	32.8	30.5-38.9	[1]3
H. sorenseni	13.4	8.0-21.0	19

[1]Recent observations on growth of over 100 juvenile *H. fulgens* suggest the three individuals represented here were exceptionally rapid growers. Projection of growth of juveniles presently 8 mo old suggest the mean size at 1 yr under laboratory conditions may fall closer to 25 mm.

TABLE 4.—Daily shell elongation rate for groups of juvenile *Haliotis* reared for month-long periods at different temperatures (microns/day).

Species and date	Temperature (°C ± 1.5°) 12	15	18	21	24	27	30
H. rufescens							
Oct. 1971	91	61	90	45	32	([1])	
Jan. 1972	36	41	68	61	29		
Mar. 1972	70	64	84	79	35		
Dec. 1972	46	92	67	95	13		
Mean	60.9	64.5	77.3	70.0	27.3		
H. corrugata							
Jun. 1972	26	29	30	46	53		
May 1973	57	55	62	54	60	28	
Jun. 1973		45	72	91	63	68	14
Mean	41.5	43.0	54.7	63.7	58.7	48.0	14.0
H. fulgens							
Mar. 1973	23	29	63	77	119	64	
May 1973	21	21	55	74	88	114	
Jun. 1973		21	56	60	50	86	54
Mean	22.0	23.7	58.0	70.3	85.8	88.0	54.0

[1]*H. rufescens* did not survive in the 27°C containers.

These data are averages for groups of 8 to 15 individuals reared in each of six 10-liter plastic drums. In the case of *H. corrugata* and *H. fulgens*, temperatures were raised throughout for the third experiment to cover the supraoptimal range. Juveniles used in these experiments ranged from 5 to 20 mm.

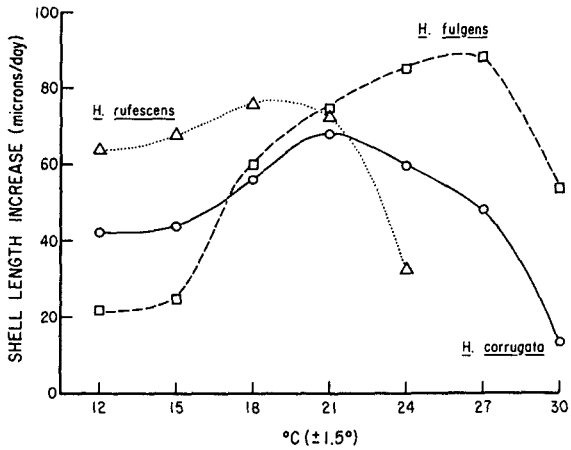

FIGURE 8.—Growth rate of juvenile abalone held for month-long periods at different temperatures. Points are averages for groups of 8 to 15 individuals (see Table 4).

TABLE 5.—Approximate depth distribution of *Haliotis* species off Point Loma (San Diego, Calif.).

Species	Depth range (m)
H. cracherodii	0-2
H. fulgens	0-5
H. corrugata	1-20
H. rufescens	10-25
H. k. assimilis	10-30
H. sorenseni	15-35
H. walallensis	15-35

kamtschatkana, and *H. walallensis* together with the generally shallow water and intertidal *H. cracherodii*). *Haliotis sorenseni*, *H. corrugata*, and *H. fulgens* range from Pt. Conception to central Baja California. *Haliotis cracherodii* and *H. rufescens* occur throughout California and northern Baja California, while *H. k. assimilis* replaces *H. kamtschatkana* in southern California (McLean, 1966).

This study has shown that the thermal requirements, particularly for eggs and early larvae, are exacting. Field distribution of juvenile and adult members of each species correspond with the thermal tolerance range observed in larvae in the laboratory. The range of tolerance increased with larval age. Larvae of *H. corrugata* placed in the thermal gradient as operculate veligers survived a range of 18° (from 8° to 26°C), while those resulting from eggs placed in the same situation were tolerant of a range of only 8° (from 15° to 23°C). The observation is not new nor limited to *Haliotis* (Loosanoff and Davis, 1963). Thus, survival of larvae dispersed in nature is likely dependent on their remaining within a water mass of appropriate temperature and further, settling in areas over which temperature change will not be extreme. Recruitment to marginal environments may rely on the timely influx of advanced veliger larvae. The situation is complicated, no doubt, by acclimation of mature adults near distribution limits.

Most studies in abalone culture have been conducted by Japanese workers concentrating on the species native to northern Japan, *H. discus hannai*. Its broad thermal tolerance (approximately 5°-30°C) and relatively rapid growth at elevated temperatures have attracted the interest of mariculturists. The species exhibits rapid larval development, settling in 3 days at 25°C and reaching the notch stage in 42 days (Kan-no and Kikuchi, 1962). When reared at five temperatures between 5° and 25°C, juvenile *H. d. hannai* displayed daily increments in shell length of 1, 2, 32, 68, and 95 μ, respectively, according to the same report. During winter months when sea temperatures at the coastal hatchery drop below 10°C, cultured juvenile abalone are transferred to a site adjacent the Yogasaki Electric Generating Plant using 26°C water detoured from the effluent stream (Kan-no, pers. commun., McBeth, 1972).

Thermal tolerance and growth characteristics of larvae and juveniles of the Japanese species are similar to that observed in the present study in *H. fulgens*. Of the American species considered here, only *H. fulgens* could be recommended for heated effluent mariculture.

First year growth measured in this study is not considered to approximate growth in nature. Artificial lighting, synthetic materials in rearing tanks, and other factors may have influenced growth, and the growth rate estimates are likely conservative. The general observation of rapid, moderate, and slow growth in *H. fulgens*, *H. rufescens* and *H. corrugata*, respectively, is concluded to reflect specific differences in growth potential.

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LABORATORY STUDY OF BEHAVIORAL INTERACTIONS BETWEEN THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, AND THE CALIFORNIA SPINY LOBSTER, *PANULIRUS INTERRUPTUS*, WITH COMPARATIVE OBSERVATIONS ON THE ROCK CRAB, *CANCER ANTENNARIUS*[1]

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ABSTRACT

Behavioral interactions between *Homarus americanus* and *Panulirus interruptus*, with comparative observations on *Cancer antennarius*, were studied in order to determine the possible effects an introduced population of *H. americanus* would have on the southern California population of *P. interruptus*. Subjects were placed in tanks 3 m in diameter with observational windows equally spaced around the tank perimeter. Three 30-min observation periods were conducted on the lobsters each day for a 5-day precontrol period (*H. americanus* absent), a 10-day experimental period (*H. americanus* present), and a 5-day postcontrol period (*H. americanus* absent). Five replicates of a shelter and no shelter condition were made with five naive *P. interruptus* and one *H. americanus* for each replicate. Agonistic action patterns were recorded for actors and reactors, along with various other behaviors, on data sheets partitioned into 1-min intervals. A large percentage of *Homarus*-initiated behavioral actions in the shelter (44%) and no shelter (39%) conditions involved threat and attack by *H. americanus*. In *Homarus*-initiated interactions, *P. interruptus* was displaced by *H. americanus* 61% of the time in the shelter condition and 63% of the time in the no shelter condition. Although *Panulirus*-initiated interactions occurred much less frequently, the results were similar to the *Homarus*-initiated interactions in that *P. interruptus* was ultimately displaced by threatening and attacking *H. americanus* 92% of the time in the shelter condition and 76% of the time in the no shelter condition. Our results, and those of other studies, are discussed with respect to the potential adverse effects of introducing *H. americanus* into southern California waters. The evidence suggests that such an introduction is inadvisable.

At the present time, there is strong interest from the private sector in introducing the American lobster, *Homarus americanus*, into California waters. This interest arises primarily from the marked downward trend in annual landings of the California spiny lobster, *Panulirus interruptus*, and the high unit value and continuing demand for lobster species in general and in particular for the American lobster, which supports one of the most valuable fisheries in North America. Conditions along the entire California coast appear well within the limits tolerated by larvae, juveniles, and adults of *H. americanus*. Thus, with the recent development of successful mass culture techniques (Hughes, 1968; Ghelardi and Shoop, 1968; Kensler, 1970), the species probably could be established, at least by means of continued stocking (Ghelardi and Shoop, 1972).

Despite the apparent value of the American lobster as a Pacific Coast fishery, there are several potential detrimental effects of introducing it into the Pacific which must be considered (Rathbun, 1888; Ghelardi, 1967). These are: 1) the introduction of disease, parasitic organisms, or other microfauna and microflora harmful to native species and 2) the elimination or reduction in abundance of ecologically similar forms, such as *P. interruptus*, in areas where *H. americanus* might become established.

Introductions of some foreign animals and plants have had very serious effects on native species (Elton, 1958). Thus, there is a great need for effective evaluation and control of exotic species introductions, as recently discussed by Lachner, Robins, and Courtenay (1970). There have been at least 23 attempts to introduce

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H. americanus between Monterey Bay and British Columbia (Ghelardi and Shoop, 1968). The exact reasons for the failure of these introductions are unknown. However, three possible causes were: 1) low stocking density, 2) unsuitability of the locations used for introductions, and 3) possible injuring or weakening of lobsters through mishandling or disease before the introductions (Ghelardi and Shoop, 1968). In the lobster transplants, as in virtually all other attempts to transplant species, there has been little or no effort to evaluate the impact the exotic would have on native species or to control pathogens and other potentially harmful organisms associated with it. Only the recent pilot introduction in British Columbia by Ghelardi and Shoop (Ghelardi, 1967; Ghelardi and Shoop, 1972) considered potential detrimental effects and was conducted on a truly scientific basis.

While it might be argued that one can never determine what the effects of an exotic introduction will be until it takes place, we feel that a serious attempt must be made to evaluate potential adverse effects by laboratory studies before even a small-scale pilot transplant is attempted. During the period 1970-73 we, and others of our group, have conducted a series of studies on the social interactions of *H. americanus* with ecologically similar decapod crustaceans from southern California waters. This paper describes the results of one of our studies concerning interactions between *H. americanus* and *P. interruptus* with comparative observations on *P. interruptus* and the rock crab, *Cancer antennarius*. In it, we have primarily considered agonistic interactions. Other studies have shown that interspecific aggression can be important in regulating the lives of sympatric species (see Aspey, 1971; also Myreberg, 1972a).

METHODS AND MATERIALS

American lobsters were purchased in San Diego from the Gulf of Maine Lobster Corporation. They were quarantined 2 wk in a large holding tank (0.5 × 1.2 × 2.3 m) for effects of gaffkemia or other diseases before being introduced to experimental tanks. California spiny lobsters and rock crabs were trapped in shallow water off the San Diego coast and were either introduced directly into experimental tanks or maintained for short periods in holding tanks of the same size employed for *H. americanus*.

Holding tanks were supplied with fresh running seawater from the Scripps Institution system. The temperature of the water in tanks varied throughout the year in close correspondence with ambient ocean temperatures, from a minimum of 14°C in January to a maximum of 23°C in August. The study began in July 1972 and ended in April 1973. Lobsters and crabs in holding tanks were fed frozen squid, *Loligo opalescens*, and northern anchovy, *Engraulis mordax*, twice a week. No attempt was made to control the photoperiod for these individuals while in the holding tanks. However, they were exposed to the normal day-night cycle during this period from light entering through the walls, roof, and building openings.

Three experimental tanks were used, each 3.04 m in diameter and 1.22 m in height, with a capacity of approximately 9,000 liters. Each tank had four observation windows 68.5 × 48.0 cm positioned equidistant around the perimeter. The tanks were enclosed in lightproof tents made of black Mobil Kordite[3] polyethylene sheeting of 6-mil thickness. Lobsters in the experimental tanks received 11 h of light daily from 0400 to 1500 P.s.t. (Pacific standard time), supplied by two 75-W General Electric floodlights. The experimental subjects were not fed while in the experimental tanks so as to eliminate the variable of interactions for food.

Three experimental conditions were studied. These were: 1) social interaction between *P. interruptus* and *H. americanus* in the absence of shelter, 2) social interaction between *P. interruptus* and *H. americanus* with more shelters than lobsters, and 3) social interaction between *P. interruptus* and *C. antennarius* without shelter. Seven shelters were provided for the experimental condition involving interaction between *P. interruptus* and *H. americanus* with shelter. The shelters, which measured 25 cm in width, 38 cm in length, and 14 cm in height, were made by cutting 76-cm sections of concrete conduit lengthwise and then into 38-cm lengths.

In each experimental condition, five California spiny lobsters and either one American lobster or one rock crab were employed. Five replicates of each experimental condition were made using naive animals for each replicate. The 5:1 ratio used for the *P. interruptus* and *H. americanus*

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

interactions was a compromise between a representative density which might result from a large stocking of *H. americanus* in natural habitats on the southern California coast and the physical limitations of the experimental tanks which prevented using more *P. interruptus*. Both males and females of each lobster species were used for experiments. However, only male *C. antennarius* were used because all females obtained were carrying eggs at the time these experiments were conducted.

Interaction experiments involving *P. interruptus* and *C. antennarius* were employed to help in the process of assessing potential effects *H. americanus* might have on *P. interruptus*. That is, we wanted to establish a behavioral base line by using a clawed decapod crustacean which is naturally sympatric with *P. interruptus*. Thus, the 5:1 ratio used for the *C. antennarius* and *P. interruptus* interactions was employed for comparative purposes.

The *P. interruptus* subjects used ranged in weight from 209 to 911 g, with a mean of 436 g. *Homarus americanus* used weighed from 417 to 635 g, with a mean of 471 g. *Cancer antennarius* used ranged in weight from 560 to 840 g, with a mean of 673 g. California spiny lobsters were assigned to groups by a randomization process. Each group usually consisted of both sexes and individuals which were larger, smaller, and the same size as the single American lobster tested. *Cancer antennarius* used in the experiments weighed more than most of the California spiny lobster subjects with which it was tested. An attempt was made to use *P. interruptus* that weighed between 400 and 600 g for all experiments so that their weight matched the weight of the *H. americanus* available to us. As a result of poor trap catches, however, we were sometimes forced to use *P. interruptus* that were either smaller or larger than the *H. americanus* subjects.

Each of the 15 separate experiments consisted of three observation periods. These were called the precontrol, experimental, and postcontrol periods. For the social interaction experiments involving *P. interruptus* and *H. americanus*, precontrol observations were taken for 5 days, experimental observations were taken for 10 days, and postcontrol observations were taken for 5 days. For the experiments involving social interactions between *P. interruptus* and *C. antennarius*, the precontrol, experimental, and postcontrol observation periods were all 5 days in duration. For the precontrol observation period, only individuals of *P. interruptus* were present in the experimental tanks. Upon completion of the precontrol period, an *H. americanus* or *C. antennarius* was introduced into the tank. Following the experimental observation period, the *H. americanus* or *C. antennarius* was removed and the postcontrol observations of *P. interruptus* taken.

For *P. interruptus* and *H. americanus* experiments, three 30-min observation periods were conducted daily for each tank. These 30-min observation periods were taken between 0800 and 1000 (4-6 h after the onset of the lights), 1200 and 1400 (8-10 h after the onset of the lights), and 1510 and 1700 h (10 min-1 h 50 min after the lights went off) P.s.t. for precontrol, experimental, and postcontrol periods. In the experiment involving *P. interruptus* and *C. antennarius*, only two 20-min observation periods were taken daily. One was taken between 0800 and 1000 and the other between 1510 and 1700. The 1200-1400 observation period was omitted because of the low frequency of interactions shown by these species during initial observations. Table 1 summarizes the experimental paradigm used for this study.

Observations taken between 1510 and 1700 were made using two 100-W red lights with a spectral distribution between 550 and 720 nm. Most of the red light (75%) fell within 600-650 nm. Spectral sensitivity of *H. americanus* ranges from 400 to 600 nm with peak sensitivity at 520-525 nm (Kennedy and Bruno, 1961). At present no information exists on the spectral sensitivity of *P. interruptus*, but the assumption was made that this species also is insensitive to light within this spectral range. During the study, we observed no evidence that movement and social behavior of either species was inhibited by the use of red lights.

TERMINOLOGY

The frequency and type of behavioral interactions between *P. interruptus* and *H. americanus* or *C. antennarius* were recorded on a data sheet which was partitioned into 1-min intervals. The behavior of the actor (the individual presenting the stimuli or initiating the interaction) and the subsequent response of the reactor (the individual

TABLE 1.—Experimental paradigm for social interaction study between *Homarus americanus*, *Panulirus interruptus*, and *Cancer antennarius*

Experimental condition	Precontrol			Experimental			Postcontrol		
	Number of days	Length of observation periods (min)	Time of observations	Number of days	Length of observation periods (min)	Time of observations	Number of days	Length of observation periods (min)	Time of observations
H. americanus vs. *P. interruptus* No shelter	5	30	0800-1000 1200-1400 1510-1700	10	30	0800-1000 1200-1400 1510-1700	5	30	0800-1000 1200-1400 1510-1700
H. americanus vs. *P. interruptus* Shelter	5	30	0800-1000 1200-1400 1510-1700	10	30	0800-1000 1200-1400 1510-1700	5	30	0800-1000 1200-1400 1510-1700
P. interruptus vs. *C. antennarius* No shelter	5	20	0800-1000 1510-1700	5	20	0800-1000 1510-1700	5	20	0800-1000 1510-1700

responding to the stimuli) were both recorded in the predetermined categories described below. In addition, the amount of locomotion displayed by subjects, their location in the tank with respect to the wall, and the number of individuals in shelters, when present, were recorded. The behavioral action patterns of *P. interruptus, H. americanus,* and *C. antennarius* described by previous workers were employed in this study where possible.

I. The following categories were employed for the actor: A) Approach, B) Threat, C) Attack, and D) Social contact. These terms are defined, in most cases, separately for each of the three species considered.

A) Approach—Movement of the actor directly toward a moving or stationary heterospecific. During approach, the actor compensates for changes in the direction of movement of a moving heterospecific so that the actor is always moving directly toward the heterospecific. No implication of function is intended in our use of the term approach.

B) Threat

1) *Homarus americanus*

Meral spread—In this study only the display described by Schrivener (1971) as meral spread was recorded as threat. Schrivener's description of this behavior is as follows: "During meral spread, the lobster stands on its walking legs with its body raised from 4 to 5 cm off the bottom. The abdomen is usually fully extended, with the cephalothorax angled slightly upwards from the horizontal. The chelae are held about 5 cm off the bottom spread wide apart with their long axes pointing directly at the opponent. Some animals hold the claws fully extended, wide apart, and as high off the bottom as possible."

2) *Cancer antennarius*

Lateral Merus Display—The merus of the chelipeds is extended laterally, with the distal end of the meri raised and extended somewhat anteriorad. The higher the intensity of the display, the greater is the lateral spreading of the chelipeds (Schone, 1968; Wright, 1968). Wright (1968) subdivides the Lateral Merus Display into three subtypes based on the position of the chelae. These are: 1) the High-Intensity Merus Display in which the chelae are unflexed (maximum adduction) with the tips held laterally; 2) the Mid-Intensity Merus Display in which the chelae are half flexed so that the tips point forward; and 3) the Low-Intensity Merus Display in which the chelae are flexed, with their tips medial. All intensities of the meral spread were observed, but these were simply recorded together as threat in our study.

3) *Panulirus interruptus*
Two of the aggressive postures described by Roth (1972) were used in this study. These aggressive postures are body raise and rear-up. We observed that these are the most common and morphologically distinct aggressive postures exhibited by *P. interruptus*.
   a) Body raise—Raising the body off the substrate by partial extension of the walking legs. This corresponds to Roth's term Rise Up (R_1).
   b) Rear-up—Raising the body off the substrate by full extension of the third, fourth, and fifth walking legs. The anterior part of the body is raised much higher than the posterior part of the body. This was also called Rise Up by Roth (R_2 and R_3). However, we have combined his R_2 and R_3 into a separate category, rear-up, because they appear to be different intensities of the same behavior action pattern, which is distinct from R_1.

C) Attack
1) *Homarus americanus* and *Cancer antennarius*
Four actions were included under attack. These were pinch, push, scissoring, and chase.
   a) Pinch—Rapid gripping and release of any part of a California spiny lobster's body with one or both chelipeds.
   b) Push—Contact between the chelipeds and any part of a California spiny lobster's body when the chelipeds are thrust forward while the body remains stationary or the chelipeds are extended or in a meral spread in a stationary position during locomotion.
   c) Scissoring—As described by Schrivener (1971) for *H. americanus*, "This occurs when one lobster faces its opponent, with the chelae in the meral spread posture (spread wide apart, long axes of the palms pointing at the adversary). The chelae are then rapidly brought together in a scissoring motion. As a result, they either strike or pass rapidly in front of the other animal."
   d) Chase—During chase the actor moves rapidly toward a heterospecific that in turn is usually moving rapidly and is obviously trying to remove itself from the vicinity of the lobster following it. Chase was recorded only after the actor and reactor had been within 30 cm from one another. Frequently, chase precedes a push or pinch and follows an initial lunge by an actor towards the reactor. During chase *H. americanus* usually displays meral spread.
2) *Panulirus interruptus*
Two actions were included under attack. These were physical contact and chase.
   a) Physical contact—This involves colliding with some part of a heterospecific's body; in some cases clasping of the opponent with the first three pairs of walking legs or a bite may occur. This includes Roth's (1972) low intensity attack (A_1), high intensity attack (A_2), and clasp (CL).
   b) Chase—Rapid locomotion toward a reactor while it is removing itself from the vicinity of the lobster following it.

D) Social contact—Two heterospecifics were recorded as having social contact when one of the following events occurred.
1) Two or more heterospecifics came within 30 cm of one another during movement about the tank without aggressive interaction occurring. This category was recorded

whether one or both animals were moving, and in some cases direct physical contact was made.

2) Two or more heterospecifics were touching or within 30 cm of one another, were not moving, and exhibited no aggressive interaction. Social contact during movement was distinguished from approach by the absence of direct movement of heterospecifics toward one another. That is, the animals were not on a collision course.

II. The following categories were employed for the reactor: A) No response, B) Walk away, C) Abdomen flex, D) Threat, and E) Attack.

A) No response—No change in the overt behavior of the reactor.

B) Walk away—Movement away from an approaching, threatening, or attacking heterospecific, using the walking legs.

C) Abdomen flex—Movement away from an approaching, threatening, or attacking heterospecific, using rapid flexion of the abdomen.

D) Threat—The description(s) of threat used for *H. americanus, P. interruptus,* and *C. antennarius* provided above for actors (I-B) was also used for the reactor.

E) Attack—The description(s) of attack used for *H. americanus, P. interruptus,* and *C. antennarius* provided above for actors (I-C) was also used here for the reactor.

III. Additional categories used on the data sheet and their definitions were as follows:

A) Roaming—Slow or moderate walking about the tank. During roaming, direct interaction between heterospecifics or conspecifics does not occur. For *P. interruptus,* roaming by an individual was recorded only if it occurred for 31 s or more during a 1-min interval. For *H. americanus* and *C. antennarius,* the amount of time they were observed roaming during each 1-min interval was recorded.

B) Wall—Like many decapods, *P. interruptus* exhibits thigmotactic behavior. When shelter is absent individuals are found with their bodies in contact with a solid object. In our no shelter condition, the tank wall was the only solid object present. A lobster that had some part of its body, excluding the antennae, within 30 cm of the side of the tank for 31 s or more of each 1-min interval was recorded as wall. The location of a lobster within the tank that was greater than 30 cm from the side of the tank for 31 s or more of each 1-min interval was recorded as no wall.

C) Group—A congregation of two or more subjects, each within 30 cm of one another. Thus, in a group of five *P. interruptus,* a maximum distance of 120 cm would separate lobsters at opposite ends of a group.

RESULTS AND DISCUSSION

Agonistic Behavior

The frequency and outcome of agonistic behavioral interactions between *H. americanus* and *P. interruptus* for conditions involving shelter and no shelter are shown in Table 2. Similar data also are presented in this table for interactions between *P. interruptus* and *C. antennarius*.

Homarus vs. *Panulirus* with No Shelter

There were a total of 2,515 *Homarus*-initiated behavioral interactions by actors for the five replicate *H. americanus-P. interruptus* no shelter experiments. Twenty percent of the behavioral interactions were classed as social contact, 40% as *Homarus* approach, 24% as *Homarus* threat, and 15% as *Homarus* attack (Table 2). Sixty-eight percent (1,700) of the *Homarus*-initiated behavioral interactions occurred during the 1510-1700 h observation period (lights off).

There were a total of 1,683 responses by reactors to *Homarus*-initiated interactions. Thirty seven percent of these were classed as no response, 49% *Panulirus* walk away, and 14% *Panulirus* abdomen flex (Table 2). Thus, *P. interruptus* was displaced a total of 63% of the time when *H. americanus* initiated a behavioral interaction. *Panulirus interruptus* was never observed to threaten or attack *H. americanus* in *Homarus*-initiated behavioral interactions.

A total of 227 *Panulirus*-initiated behavioral interactions were recorded in the five replicate

TABLE 2.—The total number of behavioral interactions between *Homarus americanus* and *Panulirus interruptus* during 10-day experimental periods for the shelter (n = 5 groups) and no shelter (n = 5 groups) conditions, and between *P. interruptus* and *Cancer antennarius* during 5-day periods for a no shelter condition (n = 5 groups). Social contact (SC) and no response (NR) for *Homarus*-initiated interactions include both *Homarus* and *Panulirus* actions where only social contact occurred. HA = *Homarus* approach; HT = *Homarus* threat; HAT = *Homarus* attack; PWA = *Panulirus* walk away; PAF = *Panulirus* abdomen flex; PA = *Panulirus* approach; PT = *Panulirus* threat; PAT = *Panulirus* attack; HWA = *Homarus* walk away; HAF = *Homarus* abdomen flex; CA = *Cancer* approach; CT = *Cancer* threat; CAT = *Cancer* attack; CWA = *Cancer* walk away.

		Homarus-initiated interactions								
		Actor					Reactor			
P.s.t.	Experimental condition	SC	HA	HT	HAT		NR	PWA	PAF	
0800	No shelter	177	172	106	56		207	156	24	
	Shelter	7	6	1	2		8	5	1	
1200	No shelter	97	97	63	47		128	92	43	
	Shelter	6	2	1	1		7	3	1	
1510	No shelter	238	748	438	276	Σ = 1,700 (68%)	299	572	162	Σ = 1,033 (61%)
	Shelter	24	104	74	41	Σ = 243 (90%)	53	72	27	Σ = 152 (86%)
Totals	No shelter	512	1,017	607	379	Σ = 2,515	634	820	229	Σ = 1,683
	Percent	20	40	24	15		37	49	14	
	Shelter	37	112	76	44	Σ = 269	68	80	29	Σ = 177
	Percent	14	42	28	16		38	45	16	

		Panulirus-initiated interactions							
		Actor			Reactor				
P.s.t.	Experimental condition	PA	PT	PAT	NR	HWA	HAF	HT	HAT
0800	No shelter	36	0	0	3	1	0	29	16
	Shelter	3	0	0	0	0	0	3	0
1200	No shelter	83.	1	0	7	3	1	65	26
	Shelter	3	0	0	1	0	0	2	1
1510	No shelter	107	0	0	6	41	4	54	21
	Shelter	22	0	0	0	2	0	20	5
Totals	No shelter	226	1	0	16	45	5	148	63
	Percent	100	0	0	6	16	2	53	23
	Shelter	28	0	0	1	2	0	25	6
	Percent	100	0	0	3	6	0	74	18

		Cancer-Panulirus interactions													
		Actor							Reactor							
P.s.t.	Experimental condition	SC	CA	PA	CT	PT	CAT		NR	CWA	PWA	PAF	CT	PT	CAT	
0800		130	4	16	2	0	5		145	0	6	0	2	0	2	
1510		37	8	20	2	3	2		49	0	15	0	9	0	3	
Total	No shelter	167	12	36	4	3	7	Σ = 229	194	0	21	0	11	0	5	Σ = 231
	Percent	73	5	16	2	1	3		84	0	9	0	5	0	2	

experiments. Of these, 226 were *Panulirus* approach while only 1 was *Panulirus* threat (Table 2). There was a total of 277 responses by the reactors (*Homarus*). Sixteen (6%) of these were classed as no response, 45 (16%) as *Homarus* walk away, 5 (2%) as *Homarus* abdomen flex, 148 (53%) as *Homarus* threat, and 63 (23%) as *Homarus* attack (Table 2). Thus, 76% of *H. americanus* responses to *P. interruptus* approach were threat and attack. These threats and attacks by *H. americanus* subsequently resulted in displacement of *P. interruptus* from the immediate area.

The number of behavioral actions by both the actor (primarily *Homarus*) and reactor (primarily *Panulirus*) decreased with time, as shown in Table

3. There was a significant reduction in *Homarus*-initiated actions with time as indicated by the results of a Spearman Rank Correlation Analysis ($r_s = -0.66$, $P < 0.05$; Siegel, 1956). Social contact was excluded from the statistical analysis of actor actions because it included and did not differentiate *H. americanus* and *P. interruptus*-initiated interactions. Most social contact, however, was initiated by *H. americanus*. There also was a significant decrease in behavioral actions with time for *P. interruptus* responses ($r_s = -0.82$, $P < 0.01$). Only *Panulirus* walk away and abdomen flex were considered. No response was excluded from the statistical analysis of reactor actions because it included both *H. americanus* and *P. interruptus* responses.

In the absence of shelter, some *H. americanus* excavated a depression in the sand where they remained when they were not roaming. When a *P. interruptus* approached an *H. americanus* in its sand depression, the likelihood of attack increased, and the attacks appeared to last longer and involve more pinching.

Homarus vs. *Panulirus* with Shelter

The addition of seven shelters reduced the number of *Homarus*-initiated interactions as compared with the no shelter condition. A comparison of all *Homarus*-initiated interactions (both actor and reactor) between the shelter and no shelter conditions indicated that *Homarus*-initiated interactions for the shelter condition were significantly reduced ($P = 0.01$, Wilcoxon matched-pairs test; Siegel, 1956). There were a total of 269 behavioral actions by actors and 177 by reactors (Table 2). Ninety percent (243) of the behavioral actions by actors and 86% (152) of behavioral actions by the reactors occurred in the 1510-1700 h observation period.

Fourteen percent of the *Homarus*-initiated interactions of actors were classed as social contact, 42% as *Homarus* approach, 28% as *Homarus* threat, and 16% as *Homarus* attack. The behavioral actions of the reactors were 38% no response, 45% *Panulirus* walk away, and 16% *Panulirus* abdomen flex.

There was a total of 28 *Panulirus*-initiated behavioral actions for the five replicate experiments. All were classed as *Panulirus* approach. Thirty-four behavioral actions by *H. americanus* (reactor) resulted. Of these, 1 was classed no response, 2 *Homarus* walk away, 25 *Homarus* threat, and 6 *Homarus* attack. Thus, 92% of these responses of *H. americanus* to *Panulirus* approach involved threat and attack.

Most of the behavioral interactions that occurred in the *Homarus-Panulirus* shelter condition took place when the lobsters were out of their shelters. On some occasions, however, *H. americanus* attacked *P. interruptus* while they were in shelters. When this occurred *H. americanus* entered the shelter through the front entrance, the attack ensued, and *P. interruptus* fled through the back entrance which was nearly flush against the side of the tank. The amount of time *H. americanus* remained in the shelter of the displaced *P. interruptus* varied greatly. Some *H. americanus* left the shelter within 1 min and either roamed or displaced another *P. interruptus* from its shelter. Others remained in the shelter longer, and some for the duration of the observation period. *Panulirus interruptus* that approached *H. americanus* in a shelter were usually

TABLE 3.—The total number of *Homarus americanus*-initiated behavioral interactions with *Panulirus interruptus* by day for the no shelter condition ($n = 5$ groups). These totals include data from morning, noon, and evening observations. Social contact (SC) and no response (NR) totals include both *H. americanus* and *P. interruptus* actions. However, the great majority of SC is *Homarus* initiated, and the great majority of NR is derived from *Panulirus*. HA = *Homarus* approach; HT = *Homarus* threat; HAT = *Homarus* attack; PWA = *Panulirus* walk away; PAF = *Panulirus* abdomen flex.

	Actor						Reactor				
Day	SC	HA	HT	HAT	Total	Total[1]	NR	PWA	PAF	Total	Total[2]
1	113	234	116	65	528	415	146	185	38	369	223
2	48	112	93	61	314	266	59	92	22	173	114
3	25	85	56	37	203	178	32	78	29	139	107
4	32	85	73	55	245	213	42	72	28	142	100
5	49	79	18	15	161	112	53	68	12	133	80
6	40	92	51	26	209	169	45	84	16	145	100
7	37	108	59	36	240	203	54	72	29	155	101
8	93	109	72	48	322	229	105	75	32	212	107
9	53	75	46	19	193	140	66	65	10	141	75
10	22	38	23	17	100	78	34	29	13	76	42

[1]These totals exclude SC.
[2]These totals exclude NR.

quickly threatened or attacked. However, this event was rare.

When *H. americanus* pinched *P. interruptus*, in both the shelter and no shelter condition, the pincer claw appeared to be the only one used. *Panulirus interruptus* that had been attacked, and especially those pinched by *H. americanus*, appeared to move away from an approaching *Homarus* in subsequent encounters at greater distances than they did initially before they had been attacked.

Panulirus vs. *Cancer* with No Shelter

There was little aggression shown in behavioral interactions between *P. interruptus* and *C. antennarius*, species which commonly occur together in nature. A total of 229 behavioral actions were initiated by actors. Of these, 73% (167) were classed as social contact, 5% (12) as *Cancer* approach, 16% (36) as *Panulirus* approach, 2% (4) as *Cancer* threat, 1% (3) as *Panulirus* threat and 3% (7) as *Cancer* attack (Table 2). There was a total of 231 responses by the reactors. Eighty-four percent (194) of these were classed as no response, 9% (21) were classed as *Panulirus* walk away, 5% (11) as *Cancer* threat, and 2% (5) as *Cancer* attack.

One of us (Krekorian) observed *P. interruptus* walk over *C. antennarius* 21 times with no response from the latter species. This was never observed between *P. interruptus* and *H. americanus*. In addition, on 63 occasions noninteracting groups were observed composed of two or more *P. interruptus* and *C. antennarius* within 30 cm of one another, and on 50 other occasions similar groups were observed consisting of *C. antennarius* and one *P. interruptus*. In contrast, we never observed groups composed of *H. americanus* and *P. interruptus*.

Discussion of Agonistic Behavior

These results show that a large percentage of *Homarus*-initiated behavioral interactions in the shelter (44%) and no shelter (39%) conditions involved aggressive behavior (*Homarus* threat + *Homarus* attack, Table 2). The response of *P. interruptus* to *Homarus* approach and aggressive acts was usually defensive. In the shelter condition *P. interruptus* was displaced by *H. americanus* 61% of the time. *Panulirus* either walked away or used an abdomen flex to remove itself from the area occupied by *Homarus*. In the no shelter condition *P. interruptus* was displaced 63% of the time. Although shelter reduced the total number of behavioral interactions initiated by *H. americanus*, the percentages for aggressive and defensive acts remained about the same (Table 2).

The number of *Panulirus*-initiated behavioral interactions was far less than the number of behavioral interactions initiated by *Homarus*. However, the result of the interactions which followed were qualitatively the same. That is, *P. interruptus* was ultimately displaced by threatening and attacking *H. americanus* in the shelter (92% of the time) and no shelter (76% of the time) conditions.

Grasping of one *H. americanus* by another was rarely involved in the agonistic encounters observed by Schrivener (1971). In contrast to this, we frequently observed *H. americanus* pinching *P. interruptus*. Pinching by *H. americanus* is typical of its predation behavior. At no time in our study did we observe *P. interruptus* attack *H. americanus* or *C. antennarius*.

Studies by other members of our group have shown that the laboratory activity rhythms of *P. interruptus* and *H. americanus* over a 24-h period are very similar, both species exhibiting their highest levels of activity during the first 4 h of darkness (Van Olst and Carlberg, pers. commun.). This similarity in the timing of activity probably would intensify interactions between the two species in the field. Such interactions could result in *P. interruptus* being displaced from areas occupied or frequented by *H. americanus*, and/or being placed under considerable stress due to possible competition for food, suitable refuges, or other aspects of space within the habitat. In the laboratory, *H. americanus* displaced *P. interruptus* when there was only one shelter for two lobsters (Lester, pers. commun.) and inhibited *P. interruptus* from feeding when food was limited (Needham, pers. commun.).

Assuming that the behavior displayed by the two lobster species in the laboratory would be similar to that occurring in the field, one would expect considerable agonistic interaction between the two species if they were to occupy the same habitat. Although there have been few studies that have thoroughly compared the behavior of animals in the laboratory with their behavior in the field, there are some data that suggest the

two are very similar, at least where species other than primates are involved. For example, a recent study by Myrberg (1972b), involving such a direct comparison, showed that the agonistic and other social behavior of the bicolor damselfish, *Eupomacentrus partitus*, in the laboratory was very similar to its field behavior both qualitatively and quantitatively. In another study, Hazlett and Bossert (1965) similarly detected no qualitative differences between the laboratory and field behavior of some pagurid and diogenid crabs. As a result of this, they chose to study the behavior of these crabs in the laboratory where conditions were more uniform and controllable.

There have been surprisingly few studies concerned with interspecific aggression. This is especially true of many decapod crustaceans for which most of the studies have been rather superficial (Reese, 1964). It is rapidly becoming apparent from the few studies that have been made, however, that interspecific aggression may be very important in regulating the distribution and abundance of many marine animal populations. Myrberg (1972a) has found that in the bicolor damselfish interspecific chases accounted for approximately 40% or more of the chases carried out by territorial males. Interspecific aggression was displayed by both sexes and occurred throughout the year.

In laboratory experiments, Teal (1958) found that the fiddler crab, *Uca pugnax*, reduced the number of burrows dug by *U. pugilator* and *U. minax*. In field studies, described by Aspey (1971), it was found that where *U. pugnax* and *U. pugilator* existed in overlapping areas, the number of burrows per square meter was significantly less than in areas inhabited only by *U. pugilator*. The reduction in the number of burrows dug by other species of *Uca* when paired with *U. pugnax* appears to be due to the greater frequency of agonistic display exhibited by *U. pugnax* (Aspey, 1971).

In contrast to the results of the *Panulirus-Homarus* experiments, very little behavioral interaction or aggression occurred between *C. antennarius* and *P. interruptus*. Seventy-three percent of actor behavior involved nonaggressive actions (social contact), and 84% of the reactor responses involved no change in behavior (no response). In addition, *C. antennarius* frequently remained in close proximity to *P. interruptus*, and *P. interruptus* frequently walked over *C. antennarius* when moving from one area in the tank to another area. These events were never observed in *Homarus-Panulirus* experiments. The laboratory observations on *Panulirus-Cancer* interactions agree with observations made in the field where *C. antennarius* is sometimes found sharing the same refuges with *P. interruptus*.

Our data also show that even though the number of *Homarus-Panulirus* interactions decreased with time, there was still a large number of behavioral interactions between *P. interruptus* and *H. americanus* on day 10 in the no shelter condition. This is most clearly seen when the number of interactions on day 10 are compared with the total number of *Cancer-Panulirus* interactions. The percentage of aggression shown by *Homarus* (*Homarus* threat + *Homarus* attack) on day 10 (40%) was very similar to the total percentage of aggression (39%). Likewise, the amount of fleeing (*Panulirus* walk away + *Panulirus* abdomen flex) shown by *Panulirus* on day 10 (55%) was similar to the total percentage of fleeing (63%). Thus, although the absolute number of behavioral interactions decreased with time, the relative amounts of *Homarus* aggression and *Panulirus* fleeing remained the same as the total percentages. These data suggest that, even if the number of encounters in the field between introduced *H. americanus* and *P. interruptus* were small, the behavioral actions by *H. americanus* would be largely aggressive and the responses by *P. interruptus* defensive.

Locomotion

Homarus vs. *Panulirus* with No Shelter

The total numbers of *P. interruptus* observed roaming during the three observation periods, precontrol 1,277, experimental 1,271, and postcontrol 1,171, were not significantly different (Table 4; $P < 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). A comparison of the three observation periods showed that the majority of this roaming by both *P. interruptus* and *H. americanus* occurred during the 1510-1700 h observation period. In *P. interruptus*, 62% of the roaming occurred during this period. In *H. americanus*, 81% of the roaming occurred during the 1510-1700 h observation period.

The relationship between the amount of time spent roaming by *H. americanus* and the number of *Homarus*-initiated behavioral actions is shown

TABLE 4.—The total number of *Panulirus interruptus* roaming during precontrol (*Homarus* absent), experimental (*Homarus* present), and postcontrol (*Homarus* absent) periods for shelter and no shelter conditions. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable. The maximum number of roaming lobsters possible for each group, during each period and for each condition (shelter or no shelter) was 2,250.

	Precontrol		Experimental		Postcontrol	
Group	Shelter	No shelter	Shelter	No shelter	Shelter	No shelter
1	27	214	97	197	30	308
2	99	361	56	252	12	125
3	168	55	132	213	106	358
4	282	89	156	207	63	62
5	129	558	125	402	154	318
Totals	705	1,277	566	1,271	365	1,171

in Table 5. There was a significant correlation ($r_s = +0.90, P = 0.05$) between the total roaming time of each *H. americanus* ($N = 5$) and the number of *Homarus*-initiated behavioral actions. That is, the greater the total roaming time, the greater was the number of behavioral actions.

TABLE 5.—Total *Homarus*-initiated behavioral actions and roaming time for shelter and no shelter conditions. *Homarus*-initiated behavioral actions include social contact, *Homarus* approach, *Homarus* threat, and *Homarus* attack. Social contact includes some *Panulirus*-initiated actions; however, the great majority of the total is due to *Homarus*-initiated actions.

	Shelter				No shelter			
Group	Sex	Size (g)	Roaming (s)	Behavioral actions	Sex	Size (g)	Roaming (s)	Behavioral actions
1	♂	419	6,435	72	♀	480	15,665	442
2	♀	469	2,785	84	♀	635	33,590	541
3	♂	457	1,650	55	♂	467	20,005	514
4	♂	471	1,735	26	♂	457	23,125	725
5	♀	430	2,025	32	♀	417	9,435	293

Homarus vs. *Panulirus* with Shelter

The numbers of *P. interruptus* roaming during the three observation periods were: precontrol 705, experimental 566, and postcontrol 365 (Table 4). The differences between the three test periods were not significant ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

The majority of roaming that occurred in both *P. interruptus* and *H. americanus* took place during the 1510-1700 h observation period as in the no shelter condition. Seventy-seven percent of *P. interruptus* roaming and 78% of *H. americanus* roaming occurred during this period. The amount of roaming done by *H. americanus* in the shelter condition was not significantly correlated with the number of *Homarus*-initiated behavioral actions (Table 5; $r_s = +0.60, P > 0.05$).

The amount of *P. interruptus* roaming without shelter was significantly greater than the amount of roaming with shelter (Table 4; $P = 0.028$, Mann-Whitney U test). Similarly, the amount of *H. americanus* roaming without shelter was also significantly greater than the amount of roaming with shelter (Table 5; $P = 0.004$, Mann-Whitney U test).

Panulirus vs. *Cancer* with No Shelter

The number of *P. interruptus* roaming during the three observation periods was: precontrol 532, experimental 534, and postcontrol 549 (Table 6). There were no significant differences in the amount of roaming during the three observation periods ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

TABLE 6.—The total number of *Panulirus interruptus* roaming and within 30 cm of the wall during the precontrol (*Cancer* absent), experimental (*Cancer* present), and postcontrol (*Cancer* absent) periods for the *Panulirus* vs. *Cancer* no shelter condition. The maximum number of roaming lobsters for each group during each period was 1,000. The maximum number of wall + no wall positions for each group during each period was also 1,000.

	Precontrol		Experimental		Postcontrol	
Group	Wall	Roaming	Wall	Roaming	Wall	Roaming
1	967	11	956	44	997	20
2	873	168	828	169	748	196
3	925	127	952	112	901	104
4	922	160	913	118	909	76
5	953	66	865	91	810	153
Totals	4,640	532	4,514	534	4,365	549

Distribution of *Panulirus*

Homarus vs. *Panulirus* with No Shelter

The displacement effect *H. americanus* had on *P. interruptus* is clearly shown in Table 7. During the precontrol observation period (*Homarus* absent) *P. interruptus* was most frequently found within 30 cm of the wall. In all five replicate experiments the subjects spent the majority of their time near the wall. Group 5 was observed within 30 cm of the wall three times more frequently than it was observed away from the wall. The other groups exhibited even greater wall—no wall differences. For example, Group 3 was

observed within 30 cm of the wall 13 times more frequently than it was observed away from the wall (Table 7).

TABLE 7.—The total number of *Panulirus interruptus* within 30 cm of the wall during the precontrol (*Homarus* absent), experimental (*Homarus* present), and postcontrol (*Homarus* absent) periods for the no shelter condition. The maximum number of positions (wall + no wall) for each group during each period was 2,250. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable.

	Precontrol		Experimental		Postcontrol	
Group	Wall	No wall	Wall	No wall	Wall	No wall
1	1,998	252	360	1,890	1,959	291
2	1,967	283	500	1,750	713	1,537
3	2,094	156	723	1,527	1,592	658
4	2,011	239	964	1,286	2,162	88
5	1,684	566	1,496	754	1,432	818

During the experimental observation period (*Homarus* present) *P. interruptus* was usually found in the center of the tank (no wall). Four of the five groups were observed more frequently in the center of the tank than within 30 cm from the wall. Only Group 5 was observed near the wall more frequently than in the center. However, Group 5 spent less time near the wall during the experimental period than in the precontrol period.

During the postcontrol period, four out of five groups were observed within 30 cm of the wall more frequently than in the center (Table 7). Group 2 spent approximately twice as much time in the center than within 30 cm of the wall.

The wall-no wall distribution of *P. interruptus* during the three observation periods was significantly different ($P = 0.009$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). The sums of ranks for the three observation periods were: precontrol 59, experimental 19, and postcontrol 42. These sums of ranks indicate that the differences are between the experimental and control periods. There were no significant differences between the precontrol and postcontrol periods ($P > 0.05$, Mann-Whitney U test; Siegel, 1956).

Homarus vs. *Panulirus* with Shelter

In the shelter condition individuals of all five groups spent most of their time in the shelters (Table 8). There were no significant differences between the precontrol, experimental, and postcontrol observation periods for the number of *P. interruptus* observed in shelters ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

TABLE 8.—The total number of *Panulirus interruptus* in shelters or within 30 cm of the wall during the precontrol (*Homarus* absent), experimental (*Homarus* present) and postcontrol (*Homarus* absent) periods for the shelter condition. The maximum number of positions (shelter + wall + no wall) for each group during each period was 2,250. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable.

	Precontrol		Experimental		Postcontrol	
Group	Shelter	Wall	Shelter	Wall	Shelter	Wall
1	2,217	23	2,036	166	2,163	86
2	2,076	110	1,635	434	2,160	66
3	1,372	694	1,449	643	1,982	255
4	1,639	490	1,714	427	1,780	298
5	1,862	356	1,893	285	1,966	252

The wall-no wall distribution of *P. interruptus* for the three observation periods also was not significantly different (Table 8; $P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). The greatest number of *P. interruptus* found outside the shelters (wall and no wall condition) occurred during the 1510-1700 h observation period.

Panulirus vs. *Cancer* with No Shelter

During the precontrol, experimental, and postcontrol periods, individuals of all five groups of *P. interruptus* were observed within 30 cm of the wall much more frequently than in positions 30 cm away from the wall (Table 6). The groups were observed near the wall from approximately 3 (Group 2 postcontrol) to 332 (Group 1, postcontrol) times more frequently than away from the wall. Group 1 spent nearly all its time near the wall during the postcontrol period. There were no significant differences in the number of lobsters found near the wall for the three periods ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

Discussion of Lobster Distribution and Locomotion

The effect of the presence of *H. americanus* on the distribution of *P. interruptus* in a tank without shelter is quite evident. *Homarus americanus* displaced *P. interruptus* from its preferred

areas (areas within 30 cm of the wall). There was a reversal of the precontrol wall position of four out of five *P. interruptus* groups during the experimental period (Table 7). When *H. americanus* was removed for the postcontrol period, three of the four groups which had reversed their precontrol position during the experimental period moved back to the wall position. Group 2 remained in the no wall position during the postcontrol. The exact reason for this is unknown, but perhaps this group's encounters with *H. americanus* were somehow more intense and thus the enounters had a more lasting effect on the behavior of Group 2. The individual used in this group was by far the most active *H. americanus* tested for both the shelter and no shelter condition and initiated the second highest number of behavioral actions (Table 5).

Group 5 remained in the wall position more than the no wall position during all three test periods. Thus, the *H. americanus* introduced to this group had little effect on its distribution within the tank. The reason for this is probably the low level of activity and aggression shown by this individual. It showed the least amount of roaming (approximately one-half the value shown by the next least active individual) and the lowest number of behavioral actions of any lobster in the no shelter condition. It directed only 16 attacks at *P. interruptus*, less than one-half of those shown by the next least aggressive *H. americanus*.

In contrast to the above, *C. antennarius* had no effect on the distribution of *P. interruptus* in the absence of shelter. All five groups of *P. interruptus* spent nearly all their time near the wall during each of the three test periods (Table 6). That is, *P. interruptus* groups were never observed spending more time in the no wall position than in the wall position when paired with *C. antennarius*.

Douglis (1946) found that when *H. americanus* was present in a large aquarium tank with one or more blue crab, *Callinectes sapidus*, spider crab, *Libinia emarginata*, or hermit crab, *Pagurus polycarus*, "it tended by pushing and fighting to keep the crabs on the opposite side of the tank from itself." Thus, although details were not given, it appears that *H. americanus* displaced crabs that, by virtue of their claws, would seem to be much better prepared to cope with *H. americanus* than is *P. interruptus*.

The presence of more shelter than was necessary for the number of lobsters in a tank substantially decreased the number of *P. interruptus* displaced from the wall position. This was primarily due to the fact that when shelter was present, all lobsters spent the majority of their time in the shelter. This interpretation is supported by comparing data on the roaming time for the shelter and no shelter conditions. The presence of shelter significantly reduced the amount of roaming in both *P. interruptus* and *H. americanus*.

The greater frequency of agonistic interactions observed between *H. americanus* and *P. interruptus* during the 1510-1700 h observation period, as compared with the 0800-1000 and 1200-1400 h observation periods, was also no doubt due to the higher level of locomotion during this period.

A great amount of variability in the activity and aggression of individual *H. americanus* was also observed in our study. Some individuals were very active and aggressive, while others were neither. In our study these variables were not related to the sex or size of *H. americanus*. In the shelter condition, a female exhibited the greatest number of behavioral actions, while in the no shelter condition, it was a male. Of the 10 *H. americanus* tested, these lobsters ranked fourth and seventh in size (Table 5).

CONCLUSIONS

Although we cannot predict with certainty the effect a large introduced population of *H. americanus* would have on *P. interruptus* and other decapod crustaceans native to southern California, our data suggest that an adverse outcome from such an introduction could occur. The types of behavioral interactions we observed in the laboratory between *H. americanus* and *P. interruptus* would most likely also occur in the field. This conclusion is strengthened by the studies and observations of other workers who have compared and found close agreement between the laboratory and field behavior. Our data show that a large percentage of the behavioral actions of *H. americanus* toward *P. interruptus* probably would involve aggressive actions. Assuming that individuals of these two species came in contact with one another in nature, these aggressive actions could have direct or indirect effects on the distribution and abundance of *P. interruptus*. Thus, our evidence suggests that it would

be inadvisable to introduce *H. americanus* into southern California waters.

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MERCENARIA MERCENARIA (MOLLUSCA: BIVALVIA): TEMPERATURE-TIME RELATIONSHIPS FOR SURVIVAL OF EMBRYOS AND LARVAE[1]

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ABSTRACT

To estimate the effects of entrainment of *Mercenaria mercenaria* embryos and larvae in the cooling-water systems of steam-electric power plants, we used a thermal gradient apparatus. Cleavage stages, trochophore larvae and straight-hinge veliger larvae were subjected to 11 different temperatures for 8 different time periods. There was a direct relationship of mortality with temperature increase and, at higher temperatures, with increase in time exposure. As the clams aged, temperature tolerance increased, with cleavage stages most sensitive to higher temperature and straight-hinge larvae least sensitive. Multiple regression analyses of percentage mortality on temperature and time produced estimating equations that allow prediction of percentage mortality under different conditions of temperature and time exposure. Entrainment of *M. mercenaria* embryos and larvae in cooling systems of power plants should be as short as possible if mortality is to be held to a minimum.

Passage of plankton through the cooling system of steam-electric power plants is a matter of concern (Coutant, 1970). Mortality caused by such entrainment (e.g. Marcy, 1971) might lead to loss of species from the vicinity of a power plant, with various ecological and economic consequences. It is estimated that increased demand for cooling water may necessitate the location of power plants in estuarine and marine environments (Tarzwell, 1972). Thermal tolerances of planktonic organisms in these environments must be determined to allow estimation of lengths of entrainment and increases in temperature that are least harmful to entrained organisms.

The hard clam, *Mercenaria mercenaria* (L.), is an abundant and commercially important bivalve found in shallow inshore waters of the east coast of North America. It is easily spawned in the laboratory and has been the subject of numerous investigations on the influence of various factors on its larval biology (see Loosanoff and Davis, 1963; Calabrese and Davis, 1970 for appropriate references). We used an aluminum thermal gradient apparatus (Thomas, Scotten, and Bradshaw, 1963) to determine thermal tolerances of hard clam embryos and larvae at different combinations of temperature and time exposure. This simulated exposure of these organisms to heat for varying time periods in power plant cooling systems. The research was undertaken in the summer of 1972 and spring of 1973 at the Eastern Shore Laboratory, Virginia Institute of Marine Science, Wachapreague, Va. Similar experiments have been made on embryos and larvae of the coot clam, *Mulinia lateralis* (Say) (Kennedy et al., 1974). Reference should be made to that paper for fuller details of experimental apparatus and techniques.

MATERIALS AND METHODS

Mercenaria mercenaria were stimulated to spawn by fluctuating water temperatures (Loosanoff and Davis, 1963) over the range of 22° to 30°C. Gametes from 3 to 32 females and 2 to 30 males were pooled in each experiment to provide genetic diversity (Calabrese and Davis, 1970). We used three developmental stages: early cleavage stages (2 h old); trochophore larvae (10-11 h); straight-hinge veliger larvae (32-50 h).

Wild stock collected as needed in the summer near Wachapreague provided the gametes. After the experiments ended in 1972, the preservative

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TABLE 1.—Percentage mortality of cleavage stages of *Mercenaria mercenaria* under different temperature-time combinations. Values in parentheses are temperatures corrected for the influence of injection water.

Time (min)	Temperature °C										
	17.5	20.2	22.7	25.1	27.6	30.0	32.5	34.9	37.4	39.7	42.4
1	0	39	14	12	12	35	0	0	3	26	85
	(18.8)	(21.5)	(23.3)				(31.6)	(34.0)	(35.8)	(37.7)	(39.4)
5	26	0	24	11	21	0	0	12	64	99	100
	(18.4)	(21.1)	(22.7)				(31.9)	(34.3)	(36.4)	(38.5)	(40.3)
10	22	0	12	0	16	0	0	78	98	100	100
	(18.3)	(21.0)						(34.1)	(36.4)	(38.5)	(40.8)
30	0	16	1	0	8	40	63	100	100	100	100
60	11	0	12	0	22	46	88	100	100	100	100
120	0	0	10	0	16	0	91	100	100	100	100
180	0	7	0	28	0	54	72	100	100	100	100
360	21	0	0	0	0	0	98	100	100	100	100

TABLE 2.—Percentage mortality of trochophore larvae of *Mercenaria mercenaria* under different temperature-time combinations. Values in parentheses are temperatures corrected for the influence of injection water.

Time (min)	Temperature °C										
	17.6	20.1	22.6	25.0	27.5	29.9	32.4	34.8	37.3	39.7	42.3
1	29	19	14	0	0	2	11	0	0	14	20
	(18.9)	(21.4)	(23.2)				(31.5)	(33.9)	(35.7)	(37.7)	(39.3)
5	25	30	19	14	0	0	0	0	0	41	93
	(18.5)	(21.0)	(22.6)				(31.8)	(34.2)	(36.3)	(38.5)	(40.2)
10	25	21	2	3	1	0	0	0	2	86	100
	(18.4)	(21.1)						(34.1)	(36.3)	(38.5)	(40.7)
30	20	13	0	17	8	1	2	10	55	100	100
60	20	0	5	7	6	0	0	0	100	100	100
120	17	0	0	0	0	0	0	63	100	100	100
180	18	1	0	0	0	0	0	100	100	100	100
360	11	8	7	10	0	3	47	100	100	100	100

TABLE 3.—Percentage mortality of straight-hinge larvae of *Mercenaria mercenaria* under different temperature-time combinations. Values in parentheses are temperatures corrected for the influence of injection water.

Time (min)	Temperature °C										
	18.3	21.0	23.5	26.1	28.5	30.9	33.4	35.8	38.2	40.7	43.1
1	3	2	3	2	2	3	4	4	3	5	4
	(19.6)	(21.6)				(30.0)	(32.5)	(34.2)	(36.4)	(38.4)	(40.1)
5	3	3	3	5	5	4	6	4	4	4	5
	(19.2)					(30.3)	(32.8)	(34.8)	(37.0)	(39.2)	(41.0)
10	3	3	3	4	3	4	3	5	5	5	7
	(19.1)							(35.0)	(37.2)	(39.5)	(41.5)
30	3	2	3	3	4	3	5	5	8	5	29
60	5	4	2	4	4	4	5	7	5	47	76
120	3	3	5	2	5	4	5	3	9	13	99
180	5	4	4	4	6	3	3	11	6	12	96
360	4	4	4	5	5	6	4	8	9	97	98

in most of the vials containing the cleavage stages and trochophores was found to have developed a precipitate that hindered microscopic analysis of the results. Consequently, in March 1973 we spawned 2-yr-old individuals of the F_2 generation produced in the hatchery in 1971 from the same local wild stock. These clams had been held in beds near the hatchery. They were conditioned for 6 wk in warm water before being spawned (Loosanoff and Davis, 1963) and provided us with replacement cleavage stages and trochophore larvae. Results of experiments using these replacements did not appear to differ from preliminary results of the 1972 experiments.

Embryos and larvae not used immediately in experiments were held at ambient temperatures in 60-liter plastic containers at a density of about 33/ml (cleavage stages, trochophores) or about 17/ml (straight-hinge) with the seawater changed daily. Development appeared normal with no high mortalities observed. Larvae not used in our experiments were successfully carried through to metamorphosis.

We used clarified, ultraviolet irradiated seawater (28-31‰) in the experiments. The cast aluminum block, bored to hold 88 test tubes (25 mm) in an 8 + 11 matrix (see Figure 1, Kennedy et al., 1974) provided a thermal gradient

that was approximately linear, varying by 2.3° to 2.7°C from one column of test tubes to the next. Each of the 11 columns in the block represented a different temperature level (Tables 1-3). Temperatures rarely varied more than ± 0.3°C either within a test tube or from one test tube to another in a column. The eight rows represented different time exposures (1, 5, 10, 30, 60, 120, 180, 360 min). There were a total of 88 different temperature-time combinations or treatments.

Twenty-six milliliters of water placed in each test tube were brought to stable temperature levels. Four milliliters of water containing the appropriate developmental stages were injected into each test tube to give a concentration of about 9 to 12 animals/ml. We inoculated the 11 test tubes in any row simultaneously, using an apparatus holding 11 syringes whose plungers were depressed together (see Figure 1, Kennedy et al., 1974).

Eighty-eight plastic beakers, each holding about 340 ml of seawater, were placed in an 8 × 11 matrix in a water bath at 25° to 26°C. When a time period in the block ended, we removed the appropriate row of 11 test tubes at once and washed the contents of each test tube into its corresponding beaker. Survivors were incubated in the beakers for 19 h (trochophores) or 23 h (cleavage stages, straight-hinge) after the experiments ended. Preliminary experiments indicated that this allowed surviving cleavage stages and trochophores to develop to the straight-hinge stage and bacteria to decompose dead individuals. It also allowed bacteria to decompose the meat of dead straight-hinge larvae.

At the end of the incubation period, the animals in each beaker were preserved in 1% buffered Formalin.[4] Numbers of straight-hinge larvae that were alive or dead at the end of an experiment were counted for each treatment. Indications of death included an empty shell or decomposing meats within a shell. For each experiment, we used 10 control test tubes held at room temperature, with the experimental animals treated to all handling described except exposure in the block. Three experiments were made on each of the three developmental stages.

Temperature of the injected water was about 23° to 25°C. This altered the temperature in the test tubes at the cold and warm ends of the block for a short period of time after injection. We made approximate corrections for these changes (Kennedy et al., 1974), and the corrected temperatures are noted in Tables 1 to 3. No corrections were made for periods longer than 10 min.

In a separate experiment, we measured oxygen levels in the test tubes over a 6-h period using straight-hinge larvae of *M. mercenaria*. Numbers of larvae were similar to numbers used in temperature-time experiments. Over the temperature range of 18° to 43°C, dissolved oxygen levels remained near saturation, with almost no change during the 6 h. We concluded that there would be no stress from low oxygen levels (Morrison, 1971) so we did not aerate during the experiments.

Multiple regression analyses of percentage mortality on temperature and time were calculated by a UNIVAC 1108 using a BMD02R stepwise regression program, version of 2 May 1966, from the Health Sciences Computing Facility, University of California at Los Angeles.

Davis and Calabrese (1964) indicated that accuracy in experiments involving sampling and handling bivalve larvae is about ± 10%. Thus, differences of less than 20% in percentage mortality from one treatment to another may not be meaningful.

RESULTS

There was a direct relationship of mortality with temperature increase and, at higher temperatures, with increase in time exposure (Tables 1-3; Figures 1-3). As the animals aged, temperature tolerance increased, with cleavage stages most sensitive to higher temperature and straight-hinge larvae least sensitive (Tables 1-3; Figures 1-3).

The general mortality patterns for the triplicated experiments at each developmental stage were scrutinized and judged to be similar so the data were combined. Over the (approximately) 20° to 26°C interval (columns 2 to 4 in the block), survival was high at each temperature level. The average number of straight-hinge larvae found alive in each of these columns and in the controls were compared, with no significant differences found ($P > 0.05$). Therefore there was no unusual

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

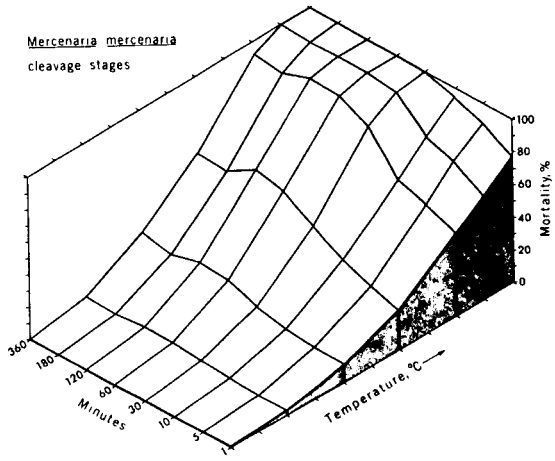

FIGURE 1.—*Mercenaria mercenaria* cleavage stages. Response surface generated from multiple regression analysis of percentage mortality on temperature and time. Refer to Table 1 for appropriate temperatures.

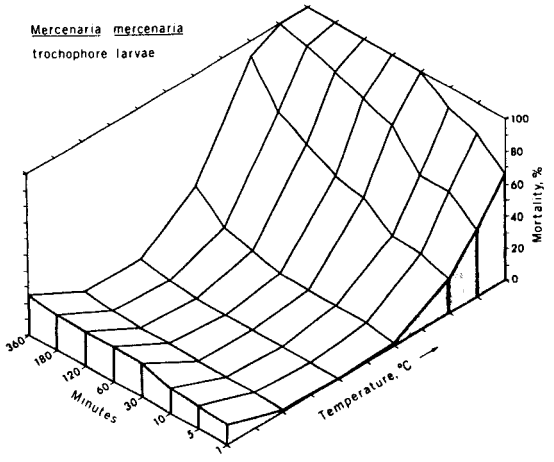

FIGURE 3.—*Mercenaria mercenaria* straight-hinge larvae. Response surface as in Figure 1. Refer to Table 3 for appropriate temperatures.

mortality associated with exposure in the block at normal temperatures (Kennedy et al., 1974). Percentage mortality data for each developmental stage were determined as for *Mulina lateralis* (Kennedy et al., 1974) and are presented in Tables 1 to 3. The stepwise multiple regression program transformed these data to arcsine square root of the percentage mortality to allow the distribution to approximate the normal. First, second, and third order terms for main effects (temperature, time) and all possible interactions were

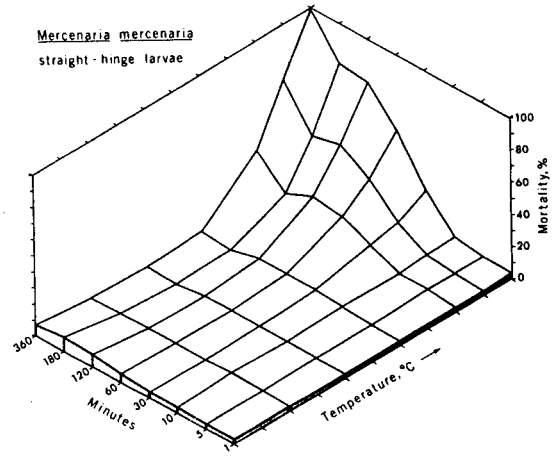

FIGURE 2.—*Mercenaria mercenaria* trochophore larvae. Response surface as in Figure 1. Refer to Table 2 for appropriate temperatures.

scrutinized. Only those terms (variables) with $F \geqslant 3.96$ ($P = 0.05$, *d.f.* 1, 80) were entered in the final equation. The program selected variables making greatest reduction in residual sum of squares until no further variables satisfied the acceptance criteria. The final empirical models appeared to be good predictive equations for all three stages (Table 4). The derived constant and variables selected for each stage are presented in Table 5, along with other statistics. The equations incorporating these constants and variables allow calculation of predicted percentage mortality for different combinations of temperature and time. The resulting estimates are in transformed form and must be converted to untransformed values (Sokal and Rohlf, 1969). Figures 1 to 3 were constructed using these equations and seven temperature levels to outline the basic pattern of the estimated response surface.

For each stage, the coefficient of determination ranged between 71% to 80% when all the variables were selected (Table 5), indicating that most of the variation in mortality can be explained by these variables (Steel and Torrie, 1960). For cleavage stages and trochophore larvae, T^3, by itself, was the best single predictor of percentage mortality. This was also true for straight-hinge larvae although T^3 was eventually eliminated by the program as new variables entered. In combination with the other variables in the final predictive equation, T^3 continued to be the most useful variable in estimating or predicting percentage mortality for trochophore larvae, as

TABLE 4.—Analysis of variance of multiple regression of percentage mortality on temperature and time for embryos and larvae of *Mercenaria mercenaria*. *** — significant at the 0.001 level; *d.f.* — degrees of freedom; *MS* — mean squares.

Source of variation	Cleavage stages		Trochophore		Straight-hinge	
	d.f.	*MS*	*d.f.*	*MS*	*d.f.*	*MS*
Regression	4	20557.780***	3	23484.304***	6	2903.295***
Residual	84	399.213	84	332.115	81	54.931

indicated by the values of the standard partial regression coefficients (Table 5). However, for cleavage stages, in the final predictive equation T^3 became relatively less important (Snedecor, 1956; Steel and Torrie, 1960).

The 88 residuals were tested for skewness (g_1) and kurtosis (g_2) (Sokal and Rohlf, 1969). Both statistics were normally distributed for cleavage stages ($g_1 = -1.02$; $g_2 = -1.78$). They were as follows for trochophore larvae: $g_1 = 2.02^*$; $g_2 = 0.90$ and for straight-hinge larvae: $g_1 = -0.12$; $g_2 = 5.92^{**}$ (* $P = 0.05$; ** $P = 0.01$).

We estimated temperature levels for 10%, 50%, and 90% mortality for each period of time exposure by plotting percentage mortality from Tables 1 to 3 against log temperature on probability paper. These values (Figure 4) allow us to estimate the possible effects of temperature elevation over time on the survival of the different stages.

DISCUSSION

Early cleavage stages of molluscs appear to have a narrower range of tolerable temperatures than older stages (Pelseneer, 1901; Loosanoff, Miller, and Smith, 1951; Loosanoff and Davis, 1963; Goodwin, 1970; Kennedy et al., 1974). Results for *Mercenaria mercenaria* indicate that increased temperature tolerance occurred as early as the trochophore stage. This is in agreement with our results for *Mulinia lateralis* (Kennedy et al., 1974).

Cleavage stages of *Mercenaria mercenaria* were generally more temperature sensitive than those of *Mulinia lateralis* (Kennedy et al., 1974). Trochophore larvae of both species were generally similar in their thermal tolerances. Straight-hinge larvae of the hard clam were more temperature tolerant.

The sensitive cleavage stages of the hard clam are of primary importance in relation to the effects of entrainment and exposure to high temperature in cooling systems. If the cleavage stages are killed, obviously it does not matter that the next stages would be more temperature tolerant. The hard clam spawns during the summer throughout its geographical range (e.g. Loosanoff, 1937; Landers, 1954; Carriker, 1961; Porter, 1967; Chanley and Andrews, 1971). However, little precise information exists as to the temperature range for spawning. Carriker (1961) found that hard clams spawned between 22° and 30°C in Little Egg Harbor, N.J., with maximum frequency over the range of 24° to 26°C. This is in general agreement with the sparse

TABLE 5.—Statistics of multiple regression of percentage mortality on temperature and time. M = minutes; T = °C; b = regression coefficient; S_b = standard error of b; $100R^2$ = coefficient of determination (increases as each new variable is added); S_{rs} = standard error of the response surface (decreases as each new variable is added); b' = standard partial regression coefficient (absolute values).

Developmental stage	Constant	Variable	b	S_b	$100R^2$	S_{rs}	b'
Cleavage stages	−3.6	T^3	1.05×10^{-3}	1.40×10^{-4}	67.1	21.01	0.61
		MT^3	1.36×10^{-5}	4.90×10^{-6}	68.2	20.76	1.90
		M^2T^3	-9.24×10^{-8}	4.11×10^{-8}	69.9	20.34	4.40
		M^3T^3	1.61×10^{-10}	7.96×10^{-11}	71.3	19.98	2.74
Trochophore larvae	152.6	T^3	3.78×10^{-3}	4.40×10^{-4}	48.4	24.28	2.38
		T	−8.33	1.23	65.9	19.87	1.85
		MT^3	1.82×10^{-6}	4.40×10^{-7}	71.6	18.22	0.27
Straight-hinge larvae	8.7	MT^3	5.00×10^{-5}	5.87×10^{-6}	44.2	11.91	17.10
		MT^2	-2.48×10^{-3}	3.40×10^{-4}	61.7	9.92	21.74
		MT	3.43×10^{-2}	5.91×10^{-3}	69.7	8.88	8.20
		M^2T^3	-5.90×10^{-8}	1.10×10^{-8}	74.8	8.19	6.89
		M^3T^2	4.98×10^{-9}	1.11×10^{-9}	77.6	7.78	5.48
		M^3	-1.26×10^{-6}	4.33×10^{-7}	79.7	7.41	1.21

reports elsewhere (Nelson, 1928; Belding, 1931; Loosanoff, 1937; Porter, 1967). No temperatures have been published for spawning in Maryland or Virginia waters. We will assume conservatively that the range of 23° to 29°C would apply in these waters and that hard clam embryos and larvae would be present in the plankton under these conditions. Coutant (1970) estimated that the average temperature increase expected in cooling water carrying entrained organisms through a nuclear power plant would be 10.8°C. Therefore, entrained embryos and larvae of hard clams could be subjected to temperatures of 33.8° to 39.8°C while passing through such a facility. In spring (Figure 4), 90% of the cleavage stages could be eliminated if entrained for about 30 min. Fifty percent could be killed in about 13 min and 10% in about 6 min. For trochophores, 10% could be killed in about 25 min, perhaps longer. Straight-hinge larvae would appear to be unaffected by the temperature increase in spring. In late summer, 90% of the cleavage stages might be killed in 1 min or less, with 90% of the trochophores dying in less than 5 min. Over 180 min of exposure would be needed to kill 90% of the straight-hinge larvae.

The equations we have developed should allow predictive evaluations to be made concerning the effects of entrainment of hard clam embryos and larvae in Maryland and Virginia waters and elsewhere. Discharge canals of steam-electric power plants are usually located to avoid directing heated water over beds of commercial bivalves. It appears that it is also important to avoid taking in water that might come from the area of a bed of hard clams during spawning season. Should such water contain embryos and larvae of hard clams, long exposures in the cooling system of the plant (whether within the facility or in a discharge canal) could be lethal to the entrained

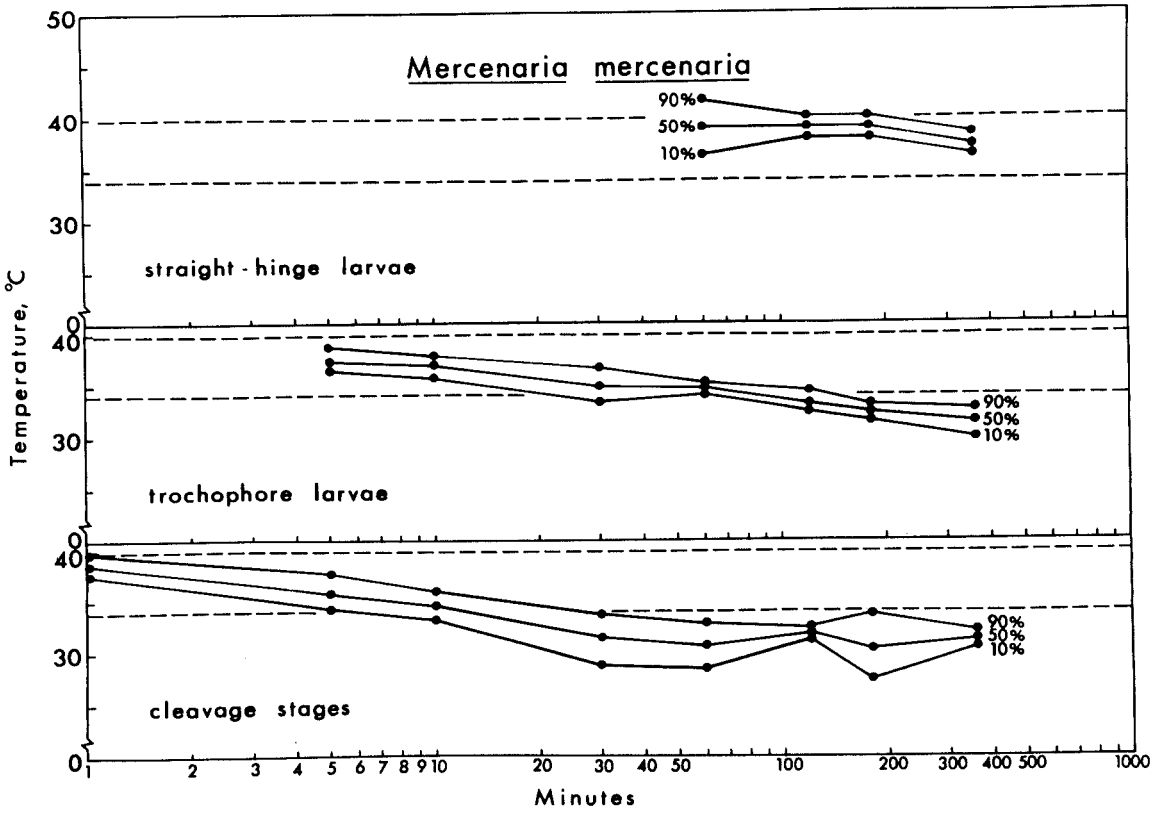

FIGURE 4.—Estimates of three percentage mortality levels for different exposure times. Percentage mortality for trochophore larvae and straight-hinge larvae was estimated to be less than 10% at 1 min and up to 30 min, respectively. For each stage, the dashed lines represent an increment of 10.8°C over estimated spawning temperature in spring (23°C - lower dashed line) and late summer (29°C - upper dashed line) in Maryland and Virginia waters.

organisms. Whether such mortality would affect the continued existence of the local hard clam resource depends upon local circumstances. Minimum destruction of the resource during use of cooling water from the vicinity of hard clam habitat requires that entrainment of embryos and larvae be as short as possible. The thermal discharge should be mixed with receiving water as quickly as possible to provide a rapid return to ambient temperature. In making evaluations it should be remembered that organisms passing through cooling systems are also subject to various stresses due to pressure changes, mechanical effects, and chlorination, in addition to temperature.

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