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SEASONAL DEPTH DISTRIBUTION OF FISH IN SOUTHEASTERN LAKE MICHIGAN

By LaRue Wells, *Fishery Biologist*

Bureau of Commercial Fisheries Biological Laboratory
Ann Arbor, Michigan 48107

ABSTRACT

This study is based on systematic seasonal bottom trawling between 3 and 50 fathoms (5.5 and 91.5 m.) from February to November 1964 and supplementary information from other experimental fishing at additional depths and with other gear. The seasonal depth distribution of eight common species is described, and temperature relations are discussed. Catch records for less common species are mentioned briefly.

Alewives are mostly pelagic during their first 2 years, but many young of the year are on the bottom in the fall, and yearlings occasionally descend to the bottom in substantial numbers in the spring and fall. Adults are mostly on the bottom in the winter and spring, but a significant portion of the population may be at mid-levels in the summer and fall. Bloaters are in midwater during their first 2 years, but usually on the bottom thereafter. Young-of-the-year American smelt are in midwater except in the fall, yearlings are in midwater or on the bottom, and adults are mostly on the bottom.

Alewives, bloaters, smelt, spottail shiners, trout-perch, and yellow perch on the bottom moved into shallower water in the spring and into deeper water in the fall, in response to temperature changes. Slimy sculpins abandoned inshore areas as water warmed in the spring. Fourhorn sculpins showed a slight movement shoreward in the spring, but changed their depth distribution little thereafter to the end of the trawling season.

Alewives showed the greatest seasonal change in distribution. Large concentrations at 40 to perhaps 70 fathoms (73.2–128.0 m.) in mid-March had migrated to water of less than 15 fathoms (27.4 m.) by mid-April. They were in shallow water along shore or in rivers until early summer; then they began a postspawning movement back into deeper water which continued into the fall. Depth ranges in which greatest numbers of other common species occurred, considering all seasons as a whole, were as follows: bloater, 12 to 50 fathoms (21.9–91.5 m.); American smelt, 5 to 17 fathoms (9.1–31.1 m.); spottail shiners, 3 to 15 fathoms (5.5–27.4 m.); trout-perch, 5 to 17 fathoms (9.1–31.1 m.); yellow perch, 3 to 15 fathoms (5.5–27.4 m.); slimy sculpins, 15 to 40 fathoms (27.4–73.2 m.); fourhorn sculpins, 45 to 70 fathoms (82.2–128.0 m.).

Water temperature ranges (° C.) in which the various species were most abundant in summer were: alewife, 8 to 22; bloater, 6 to 10; smelt, 6 to 14; spottail shiner, 13 to at least 22; trout-perch, 10 to 16; yellow perch, 11 to at least 22; slimy sculpin, 4 to 6; fourhorn sculpin, 4 to 4.5. Fluctuations in inshore water temperatures in the summer caused short-term changes in depth distribution.

Published records of depth distribution of fish in the Great Lakes have been limited largely to general information included as part of other studies. Data on seasonal aspects of distribution are especially scarce, although Dryer (1966) gave considerable information on seasonal changes in bathymetric distribution of fish in the Apostle Islands region of Lake Superior. His review of current literature on the depth distribution of Great Lakes fish need not be repeated here. The present paper describes the seasonal depth distribution of eight of the most abundant species in Lake Michigan and gives information on the effect of temperature on depth distribution, especially during the summer.

METHODS AND MATERIALS

Data were obtained from bottom tows with a semiballoon trawl in 1964 off Saugatuck, Mich. This net had a 39-foot (11.9 m.) headrope, 51-foot (15.5 m.) footrope, and a cod end of ½-inch (1.3

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cm.) mesh, extension measure. Series of tows (one haul at each of 14 depths) were made from the R/V *Kaho* in mid-February and mid-March, and from the R/V *Cisco* at about 3-week intervals from April 11 to August 21, in mid-October, and in early November. A "standard" series of tows consisted of bottom tows along the contour at 3, 5, 7, 10, 12, 15, and 17 fathoms (5.5, 9.1, 12.8, 18.3, 21.9, 27.4, and 31.1 m.) and at 5-fathom (9.1 m.) intervals from 20 to 50 fathoms (36.6 to 91.5 m.). Distances from shore of the sampling depths ranged from 0.4 to 16.7 nautical miles (0.7–31.0 km.) (table 1). Ice prevented the collection of samples at 3 fathoms (5.5 m.) in February and March. All tows lasted 10 minutes except those at 3 fathoms (5.5 m.) which lasted only 5 minutes, due to limited areas of suitable trawling bottom. The catches at 3 fathoms (5.5 m.) were adjusted to 10 minutes in all tabulations. All 14 tows of each standard series were made on the same day, with two exceptions (February 13 and 14; July 7 and 9), when tows at 45 and 50 fathoms (82.3 and 91.5 m.) were made 1 or 2 days after shallower tows. The dates "February 13" and "July 7" are used here in all further references to these series.

Engine speed was the same for all tows, and the trawling speed was about 2.6 knots. Variation in speed of tows during periods of significant wind was minimized by making all tows (which, to follow the bottom contours, were always either north or south) with the wind on a stern quadrant. Currents along the shore in the study area are highly responsive to wind and ordinarily flow north or south according to the wind. We did not trawl during periods of high winds.

Bathythermograph casts were made at the beginning of each tow, and the surface water temperature was recorded continuously with a thermograph.

The catch was sorted by species and by age groups when possible. Usually total catches of all species were retained, but occasionally large catches of individual species were subsampled. Discarded fish of a species were weighed as a group and counted or, rarely, their number was estimated on the basis of their average weight in the subsample. Data were taken from some fish on the date of collection, but most specimens were stored in plastic bags in an ice chest and examined on the following day. The data for each tow included counts and total weights of each species and individual total lengths and weights of certain species.

Although this study is based primarily on catches of the "standard" series of bottom trawl tows, information has been used from other bottom trawling, midwater trawls, gill nets, and underwater television. These supplementary data, which were gathered in Lake Michigan (mostly by the R/V *Cisco*) in 1954, 1955, and 1960–67, serve primarily to extend observations into midlevels, into

TABLE 1.—*Bottom temperatures at all sampling depths during all standard series of trawl tows in southeastern Lake Michigan*

Depth	Distance from shore		Date (1964)										
			Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms	*Nautical miles*	*Km.*	°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.
3	0.4	0.7	-----	-----	6.7	9.4	14.8	7.9	12.9	22.3	16.5	12.2	11.9
5	.6	1.1	0.1	0.4	6.0	9.4	13.8	5.9	10.3	22.1	14.8	12.4	11.9
7	.9	1.7	.1	.5	4.0	8.8	13.3	5.4	8.4	16.1	13.4	12.2	11.8
10	2.0	3.7	.1	1.2	3.6	6.7	11.9	4.6	5.2	13.5	10.0	12.2	11.7
12	2.4	4.5	.2	1.4	3.7	4.3	11.5	4.3	5.0	8.4	7.9	12.2	11.7
15	3.3	6.1	.3	1.3	3.3	4.0	8.1	3.9	4.7	6.5	5.7	12.3	11.2
17	3.6	6.7	.5	2.0	3.0	3.9	7.8	3.8	4.6	6.4	5.5	11.7	11.0
20	4.0	7.4	.7	2.1	2.9	3.5	6.1	3.8	4.3	4.8	4.7	11.7	10.8
25	4.9	9.1	1.0	2.1	2.4	3.6	5.1	3.8	4.1	4.8	4.4	11.5	6.1
30	5.9	11.0	2.3	2.2	2.2	3.5	4.5	3.5	4.3	4.7	4.4	6.0	5.7
35	7.2	13.4	2.2	2.5	2.0	3.2	4.3	3.9	4.1	4.3	4.1	5.0	4.9
40	8.9	16.5	2.8	2.7	2.1	3.2	3.9	3.8	3.9	4.2	4.1	4.8	4.8
45	13.5	25.1	2.9	2.9	2.2	3.2	3.9	3.9	3.9	4.2	3.9	4.5	4.3
50	16.7	31.0	3.1	2.9	2.3	3.0	3.8	3.8	3.9	4.1	4.2	4.5	4.3

bottom areas deeper than those of the standard series, and (to a limited extent) to other portions of the Lake.

Common and scientific names of the species mentioned in the text, listed below, follow the list published by the American Fisheries Society (1960).

Common name	*Scientific name*
Alewife	*Alosa pseudoharengus*
Gizzard shad	*Dorosoma cepedianum*
Bloater	*Coregonus hoyi*
Shortnose cisco	*Coregonus reighardi*
Longjaw cisco	*Coregonus alpenae*
Kiyi	*Coregonus kiyi*
Lake herring	*Coregonus artedii*
Lake whitefish	*Coregonus clupeaformis*
Lake trout	*Salvelinus namaycush*
American smelt	*Osmerus mordax*
Spottail shiner	*Notropis hudsonius*
Emerald shiner	*Notropis atherinoides*
Carp	*Cyprinus carpio*
Quillback	*Carpiodes cyprinus*
White sucker	*Catostomus commersoni*
Burbot	*Lota lota*
Ninespine stickleback	*Pungitius pungitius*
Trout-perch	*Percopsis omiscomaycus*
Yellow perch	*Perca flavescens*
Johnny darter	*Etheostoma nigrum*
Logperch	*Percina caprodes*
Slimy sculpin	*Cottus cognatus*
Spoonhead sculpin	*Cottus ricei*
Fourhorn sculpin	*Myoxocephalus quadricornis*

THERMAL CHANGES

The Lake was vertically homothermous at all sampling stations on February 13 and March 11. Bottom temperatures close to shore were near freezing (0.1° C.) and increased with depth to near 3.0° C. at 50 fathoms (table 1). Homothermous conditions continued through early May except near shore. On May 26 bottom temperatures had risen to 14.8 and 11.5° C. at 3 and 12 fathoms, respectively, and some thermal stratification had developed at depths greater than 12 fathoms. From mid-June until late August bottom temperatures of water 15 fathoms and deeper remained cold (3.9–6.5° C.), and thermal stratification became more pronounced. In water shallower than 15 fathoms (and especially at depths less than 12 fathoms) bottom temperatures in summer fluctuated and varied widely (7.9–22.3° C. at 3 fathoms). By October 15 the epilimnion had cooled and thickened so that the water was near 12° C. from surface to bottom at all stations out to 25 fathoms. Cooling progressed little from October 15 to November 4 because of unseasonably warm weather. A detailed account of seasonal thermal changes in Lake Michigan has been published by Church (1942, 1945).

DEPTH DISTRIBUTION

ALEWIFE

Alewives are the most widely distributed of any species in Lake Michigan. Depending on the time of year and life stage, they occupy all depths along the bottom and all waters above the bottom. Vertical distribution is discussed first, in general terms, then bottom distribution is described in more detail.

Young-of-the-year alewives, which hatch mostly in June and July, live at midlevels until late summer or early fall. They have been observed near the surface in early September in midlake and probably occur from shore to shore. They are always caught on the bottom in large numbers by October and have been taken in bottom trawls off Saugatuck as early as August 31. Many, however, are probably at midlevels even in the fall. Nearly all of the young on the bottom, regardless of date of capture, have been 1.5 to 3.5 inches (3.8–8.9 cm.) long, compared with an average calculated 1st-year growth of 3.7 inches (9.4 cm.). Thus, it appears that young alewives are on the bottom only at a certain size, and because the spawning season is rather long, all are not on the bottom at the same time. Possibly some alewives, particularly those which move into midlake in their earlier stages, may not go to the bottom at all in their first year. High winds and resultant turbulent conditions in the fall apparently cause most of the young on the bottom to ascend to midlevels temporarily.

Alewives after their first year tend more strongly toward a bottom existence as they grow older. Yearling alewives (age-group I) are essentially pelagic, but occasionally substantial numbers are on the bottom in the spring and fall, and a few

are usually there in the summer.[1] Alewives move to the bottom in increasing numbers throughout their third year (age-group II) and make up a sizable portion of the bottom catch by late summer. Fish older than 3 years may be found on the bottom at all times, but usually are also at midlevels in varying proportions, depending on the season.

The midwater distribution of alewives, especially when the Lake is homothermous, is poorly known. When the Lake is stratified, young of the year apparently are confined to the epilimnion except in the fall. Concentrations of older fish have been found in the thermocline. Many, especially those older than yearlings, are also regularly above the thermocline and at times are probably present in large numbers a few fathoms off the bottom in areas where the bottom water is warm. In mid-August 1965, alewives older than 1 year were found in midwater from shore to shore in southern Lake Michigan.

The following discussion of bottom distribution is based almost entirely on alewives caught in standard series. Young of the year are referred to as "young" and older fish arbitrarily as "adults."

Young

Young alewives were first caught in the standard series on October 14 (table 2). At that time they were at all bottom depths to 25 fathoms at temperatures of 11.5 to 12.4° C. The temperature at the shallowest depth at which they were absent (30 fathoms) was 6.0° C. On November 4, when the cold bottom water (6.1° C.) had moved shoreward to 25 fathoms, young alewives were taken only at depths of 20 fathoms and less in bottom temperatures of 10.8 to 11.9° C. Largest catches, however, were deeper in November than in October; apparently a movement away from shore was in progress, but fish in the deepest water had moved shoreward to avoid cold water.

Young alewives in the November series were larger in deeper water. The average length ranged from 2.0 to 2.2 inches (5.1 to 5.6 cm.) in the tows at 3 to 10 fathoms and 2.6 to 2.9 inches (6.6 to 7.4 cm.) at 12 to 20 fathoms. This size-depth relation was not apparent in the October series, but was pronounced in sampling off several ports in southeastern Lake Michigan in 1967.

TABLE 2.—*Numbers of young-of-the-year (0 group) alewives and young-of-the-year smelt taken in 10-minute trawl tows at various depths, October 14 and November 4, 1964*

[No young-of-the-year alewives or smelt were caught at 30, 35, 40, 45, and 50 fathoms on either date; none were taken in standard series on Feb. 13, Mar. 11, Apr. 15, May 5, May 26, June 16, July 7, July 28, and Aug. 21]

Depth	Alewives		American smelt	
	Oct. 14	Nov. 4	Oct. 14	Nov. 4
Fathoms	*Number*	*Number*	*Number*	*Number*
3	6,658	1,714	0	0
5	2,985	1,478	0	0
7	1,701	2,599	10	0
10	312	107	313	564
12	780	319	673	247
15	525	1,591	145	89
17	75	1,989	85	37
20	602	5,863	47	3
25	302	0	14	0

Adults

Adult alewives showed a more striking seasonal migration than any other species. In February they were concentrated in deep water (table 3). They were taken at 30 to 50 fathoms in the standard series of February 13. The catches increased sharply with depth; 74 were caught at 30 fathoms and 11,267 at 50 fathoms. (Other catches by the R/V *Kaho* and reports from commercial fishermen indicate that concentrations in winter may extend at least to 70 fathoms.) By March 11 the beginning of a shoreward movement was evident. A few alewives were as shallow as 15 fathoms, but concentrations were still at the greatest depths. Movement toward shore was rapid after March 11; by April 15 the largest concentration was at 10 fathoms, and relatively few were taken at depths greater than 17 fathoms. The shoreward movement was probably greatest in the latter portion of the March 11 to April 15 period. Commercial fishermen reported heavy concentrations of alewives at 35 fathoms on April 7; on April 11 the R/V *Cisco* took few at 35 fathoms but large numbers at 20 fathoms. Adult alewives were present in large numbers at 3 fathoms on May 5 and 26. Concentrations probably extended into still shallower water. Catches also were large at 12 and 15 fathoms on May 5 and at 15 to 20 fathoms on May 26. Most alewives on the bottom remained in shallow water throughout the

[1] Large numbers of yearling alewives were concentrated between the breakwalls at the mouth of the Kalamazoo River at Saugatuck in early July 1967. Commercial fishermen, who trawl for adult alewives between breakwalls in the spring and early summer, reported that such large numbers of small ones had not appeared before.

TABLE 3.—*Number of adult alewives (I group and older) taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964*

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
3	(1)	(1)	938	3, 172	3, 506	466	736	0	90	88	9
5	0	0	594	652	917	107	126	11	63	144	176
7	0	0	1, 589	531	234	10	505	296	209	36	28
10	0	0	4, 201	372	998	38	0	358	208	104	198
12	0	0	1, 841	1, 113	708	57	0	162	188	115	238
15	0	5	1, 330	1, 019	1, 089	49	1	18	17	346	308
17	0	9	636	173	1, 125	40	1	7	8	327	204
20	0	28	192	74	1, 416	61	0	0	1	164	396
25	0	42	13	26	686	40	0	5	0	224	106
30	74	88	13	56	12	6	0	0	0	32	34
35	614	824	42	5	2	4	0	0	0	67	52
40	3, 326	5, 083	15	0	0	5	0	1	0	8	56
45	6, 201	9, 524	85	1	4	0	0	0	0	42	49
50	11, 267	7, 494	12	1	0	0	0	0	0	25	28

[1] No data.

summer. Some shift away from shore was evident in late July and August, however, and adult alewives were taken at all sampling depths on October 14 and November 4. Greatest numbers in the fall were at 5 to 25 fathoms.

Catches were considerably smaller in summer and fall than those made earlier. Several factors could account for this decline. In early summer large numbers had moved into the rivers for spawning and many others probably were along the Lake shore in water shallower than 3 fathoms. A substantial die-off in late spring and summer may have reduced the population enough to affect the trawl catches. It is possible also that the larger alewives at midlevels in summer represented a major segment of those which had moved back out into the Lake after spawning. These fish might well have remained at midlevels in the fall.

The size-depth relation of adult alewives changed with the seasons. Larger fish led the migration to shore during late winter and early spring. In February the average lengths at 30, 40, and 50 fathoms were 6.9, 6.6, and 5.5 inches (17.5, 16.8, and 14.0 cm.), respectively; in March at 20, 30, 40, and 50 fathoms the lengths were 7.0, 7.0, 6.6, and 5.9 (17.8, 17.8, 16.8, and 14.0 cm.). Size did not change with depth in April and early May, but after that the average size increased with depth (except in early July, when alewives were concentrated close to shore). The unweighted average length of alewives caught in the shallowest and deepest tows of the seven standard series after May 5 was 6.0 inches in the shallowest tows and 6.8 inches in the deepest (only tows that took 10 or more alewives were included).

The seasonal migration of adult alewives observed by Graham (1956) in the Port Credit and Bay of Quinte areas of Lake Ontario closely resembled that in Lake Michigan. Adults began to move from deep water toward shore in April, and numbers were greatest inshore in about middle or late June. Soon after spawning (mostly mid-June to early July) they began to move into deeper water. They appeared in numbers in deep water (25–50 fathoms) about mid-September and were abundant there from December through March.

BLOATER

Bloaters live at midlevels in Lake Michigan until their third year. Few less than 7 inches (17.8 cm.) long are on the bottom. The larvae are in the hypolimnion in deep water (Wells, 1966), but the exact distribution of juveniles at middepths is unknown. The few that have been caught were taken in the thermocline or in upper levels when the water was cool. A few adult bloaters (2 years old or older) are frequently taken at midlevels, almost invariably in or below the thermocline, but the propor-

tion off the bottom is usually small (largest catches in gill nets set obliquely from the surface to the bottom are characteristically near the bottom).

Bloaters on the bottom inhabit intermediate and deep areas, but are sometimes in shallow water. In February, March, and April the largest numbers taken in the standard series were at 25 fathoms and deeper; few were caught during this period at depths less than 20 fathoms, and none were taken in less than 12 fathoms (table 4). A shoreward movement began in May, and by July the greatest numbers were at depths shallower than 20 fathoms. Bloaters avoided warm inshore water, but in the July 7 series, when the inshore water was cooled during an upwelling, the largest catches were at 5 to 12 fathoms and two bloaters were taken at 3 fathoms. Movement into deeper water was pronounced in the fall. On October 14 and November 4 few bloaters were shallower than 17 and 20 fathoms, respectively, and the largest catches were at 35 fathoms.

The above discussion based on the catches of the standard series is, of course, limited to seasonal distribution at depths of 50 fathoms and less. Other experimental fishing indicates that the number of bloaters decreases progressively at depths beyond 50 fathoms. Numbers are occasionally substantial at 60 fathoms but not often at 70 fathoms or deeper. A few bloaters, however, are present in the deepest portion of the southern basin (90 fathoms) and at depths of at least 140 fathoms in the northern basin. (One bloater was taken at 200 fathoms in a gill net fished from the R/V *Cisco* in Lake Superior in 1953.)

The length of bloaters varied little with depth and season. Bloaters in the three shallowest depths at which they were caught in each series, however, usually averaged about 0.2 to 0.4 inch (0.5–1.0 cm.) longer than those in deeper tows. The average length of all bloaters was 8.4 inches (21.3 cm.); 97.1 percent were between 7.0 and 9.9 inches (17.8–25.1 cm.).

Jobes (1949) reported the greatest abundance of bloaters in Lake Michigan at 20 to 59 fathoms. He suspected a movement toward shore in summer and a return to deeper water in fall.

Distribution of bloaters in southeastern Lake Michigan is shallower than in the Apostle Islands region of Lake Superior where largest numbers were usually taken at 40 to 59 fathoms (Dryer, 1966). The shoreward movement in summer and fall in Lake Superior was later and less pronounced than that in Lake Michigan. None were taken at depths less than 10 fathoms, and catches at 10–29 fathoms were never greater than at 40–49 fathoms.

AMERICAN SMELT

American smelt in Lake Michigan move in increasing numbers from a pelagic to a bottom exist-

TABLE 4.—*Number of bloaters taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964*

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
3	(1)	(1)	0	0	0	0	2	0	0	0	0
5	0	0	0	1	0	8	177	0	0	0	0
7	0	0	0	1	0	59	301	1	3	0	0
10	0	0	0	4	0	198	164	14	188	1	1
12	0	0	1	12	3	170	119	178	146	4	1
15	0	6	0	23	53	144	80	172	137	8	11
17	2	9	5	31	95	134	57	207	226	95	12
20	13	25	31	39	80	124	59	72	162	75	47
25	58	94	71	74	16	102	53	62	98	95	33
30	158	63	57	77	30	39	59	66	148	208	94
35	145	165	172	63	36	87	47	65	169	391	131
40	92	483	300	150	62	148	64	39	89	121	68
45	35	132	77	71	46	38	67	58	56	84	77
50	98	126	151	103	81	66	53	27	12	33	68

[1] No data.

ence as they grow older. First-year fish (0 group) live in the upper levels until the fall (or very late summer) when at least some move to the bottom. In their second year (I group) they may be either at midlevels (commonly in the thermocline) or on the bottom. After their second year (II group and older) they are mostly on the bottom. Ferguson (1965) reported a diurnal vertical migration of adult smelt in eastern Lake Erie. In the discussion below "young" refers to young of the year and "adults" (arbitrarily) to older fish.

Young

Appreciable numbers of young smelt were caught in the trawls on October 14 and November 4, mostly at 10 to 15 fathoms (table 2). No change in distribution appeared between the two periods. None had been taken prior to October 14, but the nearly 2-month span since the immediately preceding series on August 21 precludes a statement of the exact time they first appear on the bottom. Most young smelt in the Apostle Islands region of Lake Superior were caught at less than 10 fathoms and seldom were deeper than 19 fathoms (Dryer, 1966). In eastern Lake Erie they frequented the shallow epilimnial waters and at times were highly concentrated near shore (Ferguson, 1965).

Adults

Adult smelt on the bottom occupy shallow and intermediate depths in southeastern Lake Michigan. They were caught consistently during standard series but never in large numbers (table 5). They were widely scattered from 7 to 35 fathoms on February 13, but most had abandoned the deeper water by March 11, when greatest numbers were at 10 to 17 fathoms. Most older smelt had moved into very shallow spawning areas by April 15, when few were caught. Smelt reappeared in the catches on May 5, at depths of 3 to 10 fathoms. They had extended their range to 20 fathoms by May 26. Thereafter none were taken deeper than 20 fathoms but they avoided warm water near shore.

The length of smelt varied with depth. In spring and summer (except during the spawning season) those in shallow water were largely yearlings (which averaged 3.2 inches or 8.1 cm.) and those in deeper water were mainly older fish (average 5.3 inches or 13.5 cm.). In the fall, yearlings and older fish could not be separated readily by size, but the larger fish still preferred deeper water. The average length on November 4 was 5.4 inches (13.7 cm.) at 5 to 7 fathoms and 6.8 inches (17.3 cm.) at 10 to 20 fathoms.

Adult smelt in northern Lake Michigan, where they are far more abundant than in the southeastern portion of the Lake, extend their summer range into deeper water than in southeastern Lake Michigan. They were commonly taken in the northern area by the R/V *Cisco* in 1961 at 25 to 35 fathoms and occasionally in small numbers at 50 fathoms. The largest catches were at 15 fathoms (usually the shallowest water fished).

TABLE 5.—*Number of adult American smelt taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964*

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms[1]	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
3	[2]	[2]	0	2	0	10	0	0	0	0	0
5	0	0	2	54	0	7	33	0	0	0	3
7	2	1	0	44	4	7	12	0	17	0	8
10	1	6	0	16	6	11	4	11	0	3	5
12	2	6	0	0	14	7	0	2	2	8	1
15	1	10	0	0	17	2	0	4	3	6	6
17	1	9	0	0	11	1	1	0	1	5	6
20	1	0	0	0	1	0	1	1	0	0	5
25	5	1	0	0	0	0	0	0	0	0	0
30	3	0	0	0	0	0	0	0	0	0	0
35	1	0	0	0	0	0	0	0	0	0	0

[1] No adult smelt were caught deeper than 35 fathoms.

[2] No data.

Most yearling (I group) smelt in the Apostle Islands region of Lake Superior were caught at less than 10 fathoms, and older ones were most common at 10 to 39 fathoms (Dryer, 1966).

SPOTTAIL SHINER

The spottail shiner was more strongly limited to shallow water than other common species; it was the only species caught in the shallowest tows of every series (table 6). The range was extended into intermediate depths, however, in winter and fall. Shiners were irregularly distributed from the shallowest depths to 20 or 25 fathoms in February–April; numbers were greatest at 3 to 17 fathoms. A definite shoreward movement was evident by May 5. None were caught deeper than 7 fathoms from May 26 to August 21. For each of the six series in May to August the average percentages of the total catch that were taken at 3, 5, and 7 fathoms were 42.5, 48.2, and 9.3 percent, respectively. In other years, however, spottail shiners have occurred in appreciable numbers as deep as 12 fathoms in summer, when very warm water extended on the bottom to that depth. Catches in shore seines near the trawling area indicated that they also may be common at depths less than 3 fathoms. By October 14 spottail shiners had scattered into water as deep as 17 fathoms; largest catches were at 12 and 15 fathoms. They were caught at depths of 3 to 15 fathoms on November 4, except for one taken at 25 fathoms; largest numbers were at 5 fathoms, but all catches were small.

Larger spottail shiners tended to be at the deeper end of the distribution throughout the year. The average weight from tows which contained at least 10 individuals was 0.37 ounce (10.5 g.) in the shallowest tow and 0.51 ounce (14.5 g.) from the deepest (unweighted mean of average for each series). Spottail shiners taken on October 14 averaged 4.0, 4.4, and 4.7 inches (10.2, 11.2, and 11.9 cm.) at 10, 12, and 17 fathoms, respectively.

TROUT-PERCH

Trout-perch were restricted to shallow and intermediate depths. Most fish in the small catches of February-April were at 12 to 17 fathoms, but they were scattered from 5 to 30 fathoms (table 7). Trout-perch were concentrated nearer shore in May, when most were at 5 and 7 fathoms, and none were caught deeper than 17 fathoms. The depth of greatest abundance of trout-perch continued to be 5 to 7 fathoms in summer, and the maximum depth at which they were taken was only 10 fathoms. In the summer of other years, however, they have been caught in appreciable numbers as deep as 15 fathoms when epilimnial waters reached the bottom at that depth. Trout-perch had moved back into deeper water by October 14, when they were at 10 to 20 fathoms, and largest numbers were at 12 fathoms. On November 4 a few trout-perch were caught at 3 and 5 fathoms, but most were at 10 to 20 fathoms.

Average weights of trout-perch in each catch suggest some segregation by size, but no clear-cut size-depth relation.

TABLE 6.—*Number of spottail shiners taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964*

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms [1]	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
3	(2)	(2)	16	88	44	70	626	2	62	4	18
5	11	45	16	1,046	299	11	15	80	421	5	24
7	12	11	5	158	178	0	0	10	25	0	1
10	21	28	22	3	0	0	0	0	0	12	1
12	33	39	39	0	0	0	0	0	0	75	2
15	82	19	24	0	0	0	0	0	0	74	3
17	13	30	4	3	0	0	0	0	0	7	0
20	1	8	1	0	0	0	0	0	0	0	0
25	0	1	0	0	0	0	0	0	0	0	1

[1] No spottail shiners were caught deeper than 25 fathoms.

[2] No data.

TABLE 7.—*Number of trout-perch taken in 10-minute trawl tows at various depths, February 13 to November 4, 1964*

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms [1]	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
3	(2)	(2)	0	6	0	46	16	0	18	0	2
5	1	0	1	134	117	74	186	0	648	0	1
7	0	0	3	31	185	39	2	11	18	0	0
10	4	5	5	2	8	1	0	22	1	12	7
12	3	15	6	1	28	0	0	0	0	44	3
15	12	15	10	1	2	0	0	0	0	4	2
17	12	9	9	2	2	0	0	0	0	3	14
20	9	3	2	0	0	0	0	0	0	2	6
25	2	1	4	0	0	0	0	0	0	0	0
30	1	1	1	0	0	0	0	0	0	0	0

[1] No trout-perch were caught deeper than 30 fathoms.

[2] No data.

Dryer (1966) reported that trout-perch in the Apostle Islands region of Lake Superior were widely distributed down to 49 fathoms, were most abundant at 10 to 19 and 30 to 39 fathoms, and exhibited no seasonal changes in distribution.

YELLOW PERCH

Yellow perch in their first 2 years of life in southeastern Lake Michigan are in water shallower than 3 fathoms, as indicated by their presence in shore seines and scarcity in trawls fished as shallow as 3 fathoms. No young-of-the-year (O group) yellow perch and only 23 yearlings (I group), distinguished by size, were caught in the 11 standard series. Extensive trawling off Grand Haven, Mich. (23 nautical miles north of Saugatuck), in 1954 and 1960 produced only one large catch of young-of-the-year perch (4 fathoms, November 20, 1954) and two of yearlings (5 and 7 fathoms, June 20, 1960). The yearlings were caught during a mild upwelling. The depth distribution of small yellow perch in southeastern Lake Michigan contrasts strikingly with that in Lake Erie, where research vessels of the Bureau of Commercial Fisheries regularly have found large numbers of young of the year (as small as 1.2 inches or 3.0 cm.) in depths to 6 fathoms and yearlings commonly to 17 fathoms. Young-of-the-year perch in Saginaw Bay (Lake Huron) strongly preferred water shallower than 2 fathoms in summer, but many moved several fathoms deeper in October (R/V *Cisco* trawling and shore-seining records, 1956). Yearlings were distributed at least as deep as 7 fathoms in summer.

Adult yellow perch (defined here as those older than 2 years) in southeastern Lake Michigan inhabit shallow and intermediate depths. Most are on the bottom, but appreciable numbers may be at midlevels in summer. Greatest numbers in February to early May were at 10 to 12 fathoms, and the extreme depth range was 5 to 25 fathoms (table 8). A movement into shallower water was in progress by May 26. Yellow perch congregate in middle and late May for spawning at depths less than 8 fathoms on rocky bottom about 2 miles south of the trawling area. Most adult yellow perch were at 7 fathoms or less during summer. Substantial numbers probably were often shallower than 3 fathoms; the maximum depth was 10 to 12 fathoms. Perch have been abundant as deep as 12 to 17 fathoms during occasional periods in August of other years when warm water reached unusual depths. Adult yellow perch moved into deeper water in fall. None were taken at depths shallower than 10 fathoms in the October 14 and November 4 standard series. The largest catch on November 4 was at 20 fathoms, but no fish were caught deeper. The fall movement of yellow perch into greater depths in Lake Michigan can be more pronounced than the catches of the standard series indicate. An extremely heavy catch was made off Charlevoix, Mich., on October 17, 1955 in a gill net at 25 fathoms (bottom temperature 15.1° C.), where none had been taken in several sets in spring and summer.

TABLE 8.—*Number of yellow perch, II group and older, taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964*

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms [1]	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
3	(2)	(2)	0	0	24	138	1,082	240	108	0	0
5	18	76	0	28	48	114	46	978	157	0	0
7	14	9	8	23	85	240	110	6	72	0	0
10	70	28	55	422	22	7	2	25	1	7	3
12	42	194	35	46	16	0	0	22	0	27	23
15	29	26	16	5	2	0	0	0	0	35	9
17	4	12	0	1	0	0	0	0	0	5	3
20	0	4	0	0	1	0	0	0	0	2	53
25	0	0	0	1	0	0	0	0	0	1	0

[1] No yellow perch caught deeper than 25 fathoms.

[2] No data.

In the summer, appreciable numbers of yellow perch follow warm upper strata farther out into the Lake than their normal range on the bottom. They have been taken on several occasions from the upper portions of gill nets set obliquely from top to bottom at a bottom depth of 26.7 fathoms along the eastern shore of Lake Michigan. About 90 percent were from the epilimnion (usually about the upper 10 fathoms); all were from the upper 17 fathoms.

Yellow perch, usually in poor condition, occasionally have been taken on the bottom at great depths in Lake Michigan. The deepest recorded by the R/V *Cisco* was a fish taken at 140 fathoms off Frankfort, Mich. (June 29, 1955); another was caught at 100 fathoms in Grand Traverse Bay (June 3, 1955).

Size of adult yellow perch varied somewhat with depth. Larger ones were inclined to be in shallower water in February, March, and April; among tows in which at least 10 perch were taken the average length was 8.8 inches (22.4 cm.) for the shallowest tow and 7.7 inches (19.6 cm.) for the deepest (unweighted means of averages for each of the three series). The size-depth relation was reversed in May to August when average lengths for fish from the shallowest and deepest tows were 7.2 and 8.0 inches (18.3 and 20.3 cm.), respectively. Size did not change with depth in the fall.

SLIMY SCULPIN

Larval slimy sculpins are at midlevels, mostly in the hypolimnion. Little else is known of the O group, except that some apparently appear on the bottom in the fall. Most slimy sculpins caught in the standard series were between 2 and 4 inches (5.1 and 10.2 cm.) long and probably included yearlings and older fish. In the series of November 4, however, the catches at 25 and 30 fathoms contained 72 and 5 individuals, respectively, between 1.0 and 1.5 inches (2.5 and 3.8 cm.) long. Studies of age and growth by Rottiers [2] suggest that these fish were young of the year. They are not included in the following discussion.

The depth range of slimy sculpins extends beyond the maximum depth of the present standard series of collections. Limited trawling data for greater depths indicate that in summer slimy sculpins are present in small numbers at least to 71 fathoms but are rare or absent at 85 fathoms. Deason (1939) found them in stomachs of lake trout and burbot caught in Lake Michigan as deep as 70 fathoms, but concluded that they were usually between the shore and 50 fathoms.

The slimy sculpin is distributed over a wide depth range in winter, but abandons shallow areas in spring as soon as warming is significant and continues a gradual movement away from shore through summer and fall. Greatest numbers of slimy sculpins on February 13 were at 10 to 35 fathoms (table 9). They were in all catches except at 45 and 50 fathoms (where an occasional specimen might have been overlooked because of the

[2] Rottiers, Donald V. Some aspects of the life history of *Cottus cognatus* in Lake Michigan. Master's thesis, University of Michigan, 1965. 49 pp.

TABLE 9.—*Number of slimy sculpins taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964*

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
3	(1)	(1)	14	0	0	0	0	0	0	0	0
5	10	2	15	4	0	0	0	0	0	0	0
7	5	10	43	8	0	1	0	0	0	0	0
10	51	22	97	4	0	5	0	0	0	0	0
12	109	61	90	6	2	4	0	0	0	0	0
15	117	118	115	44	2	29	37	1	0	1	2
17	107	121	91	161	19	36	72	0	4	0	1
20	117	97	122	48	54	101	100	41	44	3	1
25	106	146	35	32	187	122	133	132	124	58	68
30	171	293	42	11	138	170	100	88	97	73	139
35	74	126	14	60	75	65	86	75	86	81	97
40	9	43	9	38	41	46	139	79	119	105	140
45	0	28	29	41	46	31	42	36	66	14	36
50	0	6	8	46	38	21	29	31	12	15	15

[1] No data.

great quantities of alewives). Small numbers appeared in the catches at 45 and 50 fathoms on March 15, but distribution had not changed significantly. In every later series, slimy sculpins were found at all depths greater than 17 fathoms. A slight shift shoreward was evident on April 15, when greatest numbers were at 7 to 30 fathoms. They had started to move away from shallow water by May 5, when relatively few were at 12 fathoms or shallower, and none were at 3 fathoms. A general trend away from shore continued thereafter until fall. On May 26 the shallowest depth of capture was 12 fathoms, and on August 21 it was 17 fathoms; largest numbers in the period May 26–August 21 were at 20 to 40 fathoms. On October 14 and November 4 most were at 25 to 40 fathoms, and few were at 20 fathoms or shallower.

Slimy sculpins beyond the earlier growth stages ordinarily are considered strict bottom dwellers, but at times larger ones may ascend several fathoms above the bottom in Lake Michigan. On May 20, 1955, 20 (probably slimy sculpins, but possibly spoonhead sculpins) were caught at night (about 2000 e.s.t.) in a trawl fished by the R/V *Cisco* 6 fathoms above the bottom where total depth was 23 fathoms; another was taken at night on November 18, 1954, 27 fathoms above the bottom at a 40-fathom depth. On June 20, 1967, 31 slimy sculpins were caught during daytime by the Bureau's R/V *Siscowet* 3 to 9 fathoms above the bottom in turbid water 13 to 14 fathoms deep in western Lake Superior (Merryll Bailey, personal communication).

Slimy sculpins were concentrated in deeper water in the Apostle Islands region of Lake Superior than in southeastern Lake Michigan; they were most common in the Apostle Islands at depths greater than 40 fathoms, and probably the greatest numbers were at 50 to 59 fathoms (Dryer, 1966).

The depth distribution of slimy sculpins in southeastern Lake Michigan varied noticeably with size in winter and early spring, but not thereafter. Sculpins at intermediate depths were smaller than at other depths in February to May. In the five series of February 13 to May 26, the average weights of sculpins taken at depths less than 30 fathoms were 0.36, 0.34, 0.32, 0.24, and 0.23 ounce (10.2, 9.6, 9.1, 6.8, and 6.5 g.) respectively; at 30 to 40 fathoms the averages were 0.27, 0.27, 0.14, 0.12, and 0.16 ounce (7.7, 7.7, 4.0, 3.4, and 4.5 g.); and at 45 and 50 fathoms (no data for February 13 and March 11) the weights were 0.30, 0.21, and 0.25 ounce (8.5, 6.0, and 7.1 g.). No obvious size-depth relation existed after May, but some tendency existed for the larger fish to be in intermediate depths in August–November—the opposite of the situation in early season.

FOURHORN SCULPIN

Fourhorn sculpins (also called deepwater sculpins) are confined to deep water much more than

any of the other species. They were uncommon in the catches shallower than 40 fathoms in the standard series. Data from additional trawling of the R/V's *Cisco* and *Kaho* indicate that fourhorn sculpins are present in the deepest part of the southern basin (90 fathoms) and are abundant to at least 70 fathoms. They are found at least as deep as 140 fathoms in northern Lake Michigan, where their range does not appear to extend into as shallow water as in the southern basin. Deason (1939) estimated the depth of greatest abundance of fourhorn sculpins in Lake Michigan as 40 to 75 fathoms on the basis of their occurrence in stomachs of lake trout and burbot. Fourhorn sculpins in the Apostle Islands region of Lake Superior were seldom shallower than 50 fathoms (Dryer, 1966); they were fairly abundant in R/V *Cisco* trawl catches at 200 fathoms in eastern Lake Superior in 1953.

Larval fourhorn sculpins are in the hypolimnion in deep areas. No other information is available on distribution in the first year.

Although the standard series did not cover a large enough portion of the depth range of fourhorn sculpins to give a good indication of seasonal distribution, certain features are evident from the data. The species was always abundant at 45 and 50 fathoms, but was never numerous at other depths (table 10). It extended its range slightly shoreward in spring. None were shallower than 45 fathoms on February 13, but a few were as shallow as 35 fathoms on March 11 and 17 fathoms on April 15. Numbers which had been considerably larger at 50 fathoms than at 45 fathoms in February–May were usually larger at 45 fathoms afterwards. Distribution showed no obvious change in summer and fall.

The shallowest water in which a fourhorn sculpin was caught in the standard series was 7 fathoms (May 26), but one specimen, seemingly in good condition, was taken at 4 fathoms off Saugatuck in August 1965.

The segment of the depth range of fourhorn sculpins sampled in the standard series was too small for an evaluation of the size-depth relation. The average individual weight in most catches was 0.8 to 1.0 ounce (22.7–28.3 g.). Fourhorn sculpins in the standard series were not measured, but 80 percent of those from identical trawling off Saugatuck in 1965 were 4.5 to 5.5 inches (11.4–14.0 cm.) long, and few fell outside the length range 4.0 to 6.0 inches (10.2–15.2 cm.).

OTHER SPECIES

Several species were caught in such small numbers in the standard series that their depth distribution could not be determined accurately. The limited data available are discussed briefly.

Shortnose ciscoes (18 collected) were taken at 5 to 50 fathoms, mostly 40 to 50 fathoms. One longjaw cisco was caught at 15 and another at 50 fathoms, and individual kiyis were taken at 45 and 50 fathoms. Lake herring (62 collected) were taken at 5 to 50 fathoms; they were most common at 15 to 25 fathoms, especially on February 13 and March 11. In the mid-1950's, when this species was more abundant in Lake Michigan, it was frequently caught in nets of the R/V *Cisco* at mid-levels, occasionally near the surface. Studies by Smith (1956) and Dryer (1966) indicated that lake herring in the Great Lakes are essentially pelagic during the warm months, but may be

TABLE 10.—*Number of fourhorn sculpins taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964*

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms[1]	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
17	0	0	1	0	0	0	0	0	0	0	0
20	0	0	1	0	0	0	1	0	1	0	0
25	0	0	1	0	0	0	1	0	0	0	0
30	0	0	2	2	1	2	1	0	1	1	1
35	0	7	2	3	4	3	3	3	4	3	0
40	0	22	13	35	25	13	22	12	30	38	25
45	105	85	235	303	356	324	494	264	732	454	228
50	279	876	580	508	500	289	425	381	275	286	250

[1] No fourhorn sculpins caught at depths shallower than 17 fathoms, except for one at 7 fathoms on May 26.

abundant on the bottom at other times. The ranges of all the ciscoes mentioned here, especially the kiyi, extend into water deeper than 50 fathoms in southeastern Lake Michigan.

Lake whitefish (5 collected) were taken at 3 to 20 fathoms. Seven carp were caught at 5 to 7 fathoms. Ninespine sticklebacks (3 collected) were at depths of 20 to 50 fathoms. This species is more common in bottom catches in most other parts of the Lake and is occasionally taken at midlevels. Johnny darters (19) were collected at 7 to 35 fathoms (mostly 12–17) and logperch (12) at 5 to 12 fathoms. Single individuals of gizzard shad, white sucker, and quillback were caught at 3, 5, and 15 fathoms, respectively.

EFFECTS OF TEMPERATURE ON DISTRIBUTION

Temperature was the most obvious factor in the depth distribution of fish in this study. Even in winter, temperature influenced the distribution of some of the species. Alewives and bloaters, for example, congregate in the deeper areas to avoid the colder inshore waters. Numbers of both species increased significantly at 15 to 20 fathoms between February 13 and March 11 as bottom temperatures rose from 0.3–0.7° C. to 1.3–2.1° C. The movement toward shore in the spring of all species except the sculpins is closely correlated with a warming of inshore waters. The shift of all species except the fourhorn sculpin into deeper water in the fall also is obviously related to temperature. As warm water steadily encroaches on deeper bottom areas warm-water species spread with it, and cold-water forms move deeper to avoid it. The control of temperature over depth distribution is best seen in summer when thermal changes are most pronounced.

After thermal stratification, bottom temperatures in water shallower than 12 or 15 fathoms in southeastern Lake Michigan are seldom stable for any length of time. Direction and speed of wind influence water temperatures strongly. Onshore winds thicken the epilimnion near shore and increase the depth to which warm water extends on the bottom; offshore winds have the opposite effect. Exceptionally strong, persistent northeast or north winds cause extensive upwellings along a large portion of the east shore of the Lake and hypolimnial water of 5 to 6° C. may replace water of 20° C. in 1 or 2 days. At such times cold water from surface to bottom may extend from shore several miles out into the Lake, and no warm bottom water is available to the fish.

Catches of the standard series illustrate the influence of thermal conditions on the depth distribution of fish in summer. A comparison may be made between the catches of July 7, when epilimnial waters near shore were relatively cool and the hypolimnion extended into shallow water, and July 28, when epilimnial waters were much warmer and reached the bottom to greater depths. The thermal conditions of July 28 were more common for summer; those of July 7, though less frequent, were by no means unusual. Species in the shallowest water had a deeper distribution on July 28. Bloaters and slimy sculpins showed changes only in the shallow extremity of their depth range because the temperature in the remainder of their range was unchanged. The fourhorn sculpin was too deep to be affected.

The standard series were too infrequent to show the rapidity of movement in response to temperature change; however, evidence from other trawling indicates that appreciable movement may occur in a few hours, and that major redistribution may take place in 2 or 3 days. On August 24, 1963, tows were made in the morning (0807–1001 e.s.t.) and afternoon (1344–1541 e.s.t.) at 7, 10, and 12 fathoms off Saugatuck during a period of rather rapidly changing bottom temperatures. The temperature remained steady at 16.5° C. at 7 fathoms but rose from 12.6 to 14.0° C. at 10 fathoms and from 12.4 to 13.3° C. at 12 fathoms (table 11). At the same time several species moved into deeper water. Spottail shiners decreased drastically at 7 fathoms and increased greatly at 10; several appeared in the afternoon catch at 12 fathoms where none had been taken in the morning. Catches of yellow perch decreased slightly at 7 fathoms and strongly at 10 fathoms and increased drastically at 12. No other species were present in significant numbers at 7 fathoms in either period. Trout-perch decreased appreciably at 10 fathoms and increased correspondingly at 12. Bloaters decreased at both 10 and 12 fathoms. Smelt showed only a slight change at 10 fathoms and none at 12. Alewives did not change significantly. Sculpins were not caught in any of the tows. These changes do not necessarily indicate that individual fish

TABLE 11.—*Trawl catches in identical morning (0807–1001 e.s.t.) and afternoon (1344–1541 e.s.t.) tows at various depths off Saugatuck, Mich., August 24, 1963*

[Bottom temperatures (° C.) with each tow are in parentheses]

Species	7 fathoms		10 fathoms		12 fathoms	
	a.m. (16.5)	p.m. (16.5)	a.m. (12.6)	p.m. (14.0)	a.m. (12.4)	p.m. (13.3)
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Alewife	12	3	39	51	39	34
Bloater	0	1	49	23	184	65
American smelt	1	3	193	246	92	87
Spottail shiner	36	1	5	113	0	5
Trout-perch	9	3	254	146	5	92
Yellow perch	97	76	233	113	34	246

traveled a great distance (e.g., the 0.5 nautical mile from 10 to 12 fathoms), but may reflect a more modest shift of the entire populations of various species.

A pronounced shift in depth distribution of fish during a few days occurred between August 14 and 17, 1962, when trawl tows were made at 7, 10, 12, and 15 fathoms off Saugatuck. Bottom temperatures in this period rose from 7.9 to 17.7° C. at 7 fathoms and from 5.9 to 11.2° C. at 15 fathoms. Spottail shiners were rare as deep as 7 fathoms at the cooler temperatures on the earlier date, but were common out to 12 fathoms when the water warmed. Trout-perch were caught only at 7 fathoms on August 14, but were concentrated at 15 fathoms on the 17th. Yellow perch, bloaters, and smelt moved similarly. Alewives, which characteristically responded less to sudden temperature changes than other species, showed little movement. Sculpins were not in the catches.

Shifts in the depth distribution of fish in shallow water in summer, although not usually as abrupt as the examples cited, are frequent if not almost continuous in southeastern Lake Michigan (and probably along other exposed shorelines of the Lake as well) as bottom temperatures fluctuate. During upwellings, however, warm-water species may suddenly be exposed to temperatures much colder than those preferred from which they cannot escape. Such conditions can occur at crucial times, such as the spawning season or during hatching. It would seem then that temperatures for these species would be much more suitable in terms of growth rates and spawning success in smaller bodies of water or protected bays, where thermal stability is greater.

TEMPERATURE PREFERENCES

Certain generalities regarding temperature preferences of the various species are possible from the standard series and other trawling at Saugatuck, although unstable thermal conditions and other factors prevented any determination of either exact temperature preferences or "final preferenda" (see Fry, 1947). These observations apply to adult fish during periods when the range of temperatures on the bottom was wide.

All species except fourhorn sculpins were in water with a temperature range of several degrees. Alewives apparently had the least temperature specificity. At times they were simultaneously in water from 5° C. or less to 20° C. or more, but most were in water warmer than 8° C. Evidence suggests that they tend to shun temperatures greater than 22° C., although in some spawning streams they must occasionally endure temperatures of 25° C. or more. Bloaters generally inhabited water from 4 to 11° C., although a few usually were present at temperatures several degrees higher; greatest concentrations often were at 6 to 10° C. Smelt were mostly in water of intermediate temperatures, about 6 to 14° C. Spottail shiners with few exceptions were in water from 13° C. to the warmest available. Trout-perch were mainly in water of 10 to 16° C. Yellow perch were usually in water above 11° C. and were occasionally abundant in water as warm as 22° C.; substantial numbers, however, were found at temperatures as low as 8° C. Slimy sculpins were seldom taken in water above 10° C., and most were at 4 to 6° C. Occasionally in fall overturns, however, when moderately warm water reached bottom at greater depths,

large numbers of slimy sculpins were taken from water as warm as 13° C. Fourhorn sculpins with rare exceptions were restricted to water colder than 4.5° C. Factors other than temperature must exert a strong influence on the depth distribution of fourhorn sculpins because they did not move into shallow water in numbers even where temperatures were under 4.5° C.

ACKNOWLEDGMENT

E. H. Brown furnished age data for Lake Michigan alewives and bloaters.

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BIOLOGY OF THE BLUE CRAB, *CALLINECTES SAPIDUS* RATHBUN, IN THE ST. JOHNS RIVER, FLORIDA

By Marlin E. Tagatz, *Fishery Biologist*

Bureau of Commercial Fisheries Biological Laboratory
Beaufort, N.C. 28516

ABSTRACT

Blue crabs commonly mated from March to July and from October to December in the St. Johns River; the proportion of males and females that matured at a small size was larger in salt water than in fresh water.

Blue crabs spawned in the first 30 km. of river above the mouth, and the eggs hatched in the ocean within 6 km. of shore. Spawning began as early as February and continued through October.

Some blue crabs of both sexes migrated from the St. Johns River to the Intracoastal Waterway, to four other rivers, and to the ocean. Among crabs tagged 40 to 195 km. above the mouth of the St. Johns River and recovered at a distance from the tagging site, 89 percent of the males and 96 percent of the females were recaptured downstream from the point of release. Many females tagged in the ocean were recaptured in inland waters throughout the year. During the spawning season some reentered the St. Johns River for a second spawning within 15 days after their eggs hatched.

First- and second-stage zoeae and megalops of crabs of the genus *Callinectes* were collected as far as 40 km. upstream. Of 22 kinds of crab zoeae collected near the mouth, *Callinectes* ranked third in abundance in 1961 and second in 1962.

Small blue crabs (2–9 mm. wide) entered the river in waves and moved as far as 135 km. upstream. Nearly all of the upstream migrants were beyond the first postlarval stages except during early winter.

Blue crabs 5 to 200 mm. wide fed principally on mollusks (primarily clams and mussels), fish, and crustaceans (primarily amphipods and crabs). Generally, they ate the same type of food regardless of crab size, area, and season.

This report presents the results of studies in 1961–63, on the biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River. Detailed information on their biology is necessary to learn which factors affect the harvestable population.

The blue crab supports important fisheries along the Atlantic and Gulf coasts of the United States. Landings in 1950–65 averaged about 58 million kg. per year. The 1965 catch was 71 million kg., worth slightly more than $12 million to the fishermen. In the St. Johns River, 109 fishermen, using pots and 52 fishing trawls, caught 1,465,840 kg. of blue crabs during 1962 (Tagatz, 1965).

The biology of the blue crab has been investigated extensively in Chesapeake Bay (Hay, 1905; Churchill, 1919; Truitt, 1939; Pearson, 1948; and Van Engel, 1958), and to a lesser degree in Delaware (Porter, 1956), Louisiana (Darnell, 1959), and Texas (Daugherty, 1952; Pounds, 1961). No investigation has been reported, however, of the biology of the blue crab in the St. Johns River or in other Florida waters.

Blue crabs occur far upstream in the St. Johns River, at least as far as Lake Harney, 305 km. above the mouth (Moody, 1963). Their widespread distribution in the fresh-water portion of the river is thought to be largely due to the abundance of calcium chloride in the water and to the presence of the salt springs that drain into the river (Odum, 1953). In other estuaries, blue crabs seldom penetrate far into fresh water (Williams, 1965). Our studies on the St. Johns River extended 215 km. upstream to Astor, the terminus of the commercial fishery for crabs (fig. 1).

MATERIALS AND METHODS

Sampling and tagging were conducted to determine the size, sex composition, sexual maturity, distribution, and movements of adult blue crabs.

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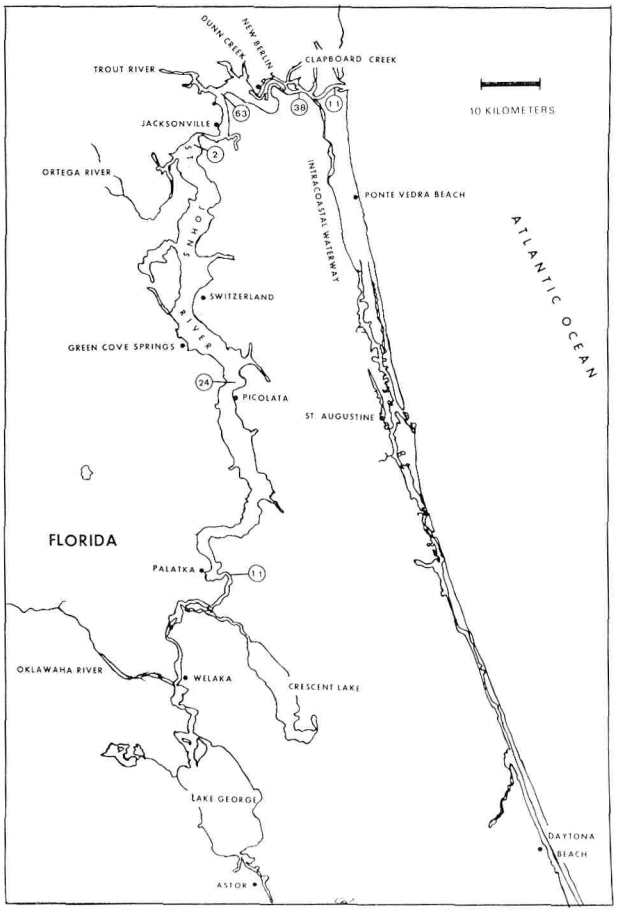

FIGURE 1.—St. Johns River, Fla., from mouth to Astor. (Circled numerals indicate buoys referred to in text.)

In 1961 and 1962, 92 samples of about 150 crabs each were obtained from the unculled commercial catches of crabs in the river, and on 1 or 2 days each month, crabs were observed in catches of shrimp trawlers fishing 1 to 8 km. offshore between Fernandina Beach and Ponte Vedra Beach. Samples were taken monthly with a 3-m.-wide trawl at selected stations in the river to supplement data from the fishery. Size, recorded as width, is the distance between the tips of the large lateral spines of the carapace.

I examined females and every fifth male crab in samples from commercial catches for sexual maturity, which is more obvious in the female blue crab than in the male—the apron (abdomen) is semicircular in mature females and triangular in immature females. I also examined every fifth mature female to determine stage of ova development. The shape of the apron of the male does not change at maturity; I based maturity in males on the development of the anterior and middle vasa deferentia. In the mature male the vasa deferentia are large prominent ducts and the middle vas deferens is bright pink. In the immature male the vasa deferentia are small and the middle vas deferens is white.

From April 1961 to April 1963, 8,927 blue crabs (6,383 males, 2,544 females) were tagged in the St. Johns River and 2,595 (58 males, 2,537 females) in the ocean off the mouth of the river, 1.5 to 5 km. offshore and 1.5 km. north to 11 km. south of the jetties. I obtained these crabs from commercial fishermen. Only mature females and males wider than 135 mm. were tagged; maturity of males could not be determined by external observation. Each tag was plastic, bore a number, and was fastened by stainless steel wire between the large lateral spines of the carapace (fig. 2). Cronin (1949) reported that this method of tagging was more effective than others he tested.

I collected larval crabs in the St. Johns River in 1961 and 1962, using Clarke-Bumpus samplers for simultaneous collections at the surface (0.3-m. depth) and bottom (10 m.). Collections, water temperatures, and salinities (surface and bottom) were obtained hourly over any selected 4- to 11-hour period. Captured plankton was placed in jars which were then filled to capacity (135 ml.) by addition of water. Crab larvae were identified and counted in three 4-ml. subsamples removed from each jar.

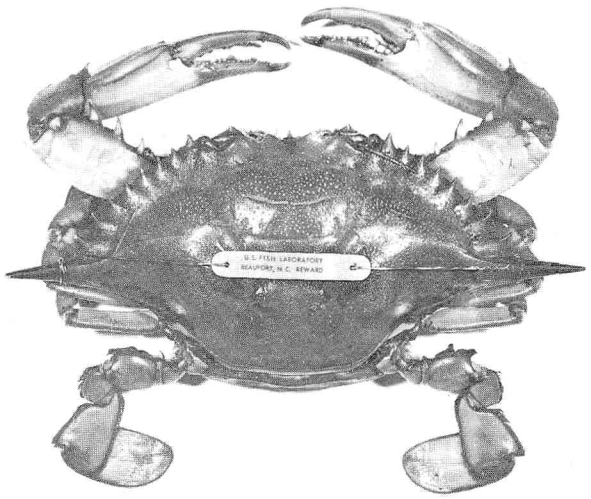

FIGURE 2.—Blue crab with carapace tag attached.

Reliable separation of the larvae of *Callinectes sapidus* from those of other species of *Callinectes* is not yet possible. Because *C. similis* and *C. ornatus* are common in the lower 40 km. of the river and in the ocean off the river's mouth (Williams, 1966), and their spawning seasons coincide with that of *C. sapidus*, larvae of *Callinectes* were designated by genus only.

A 21-m.-long seine with a funnel-shaped bag (4-mm. stretched mesh) and a 2.5-m.-wide trawl (tail bag was 6-mm. stretched mesh) were used to determine the distribution of juvenile blue crabs in the St. Johns River. In addition to extensive random sampling (1961–63), certain areas were sampled at 2-week intervals (1962–63).

The stomachs of 695 blue crabs 5 to 200 mm. wide were obtained from December 1962 to August 1963 for the food study. Crabs were selected from samples taken during scheduled collecting with a seine and trawl. The percentage frequency of each class of organism was determined. For each stomach, the percentage of each food type in the total volume of food was estimated.

Aquatic plants, fish, and invertebrates obtained in the nets and with a Petersen dredge were counted to indicate natural abundance of foods selected by crabs, and representative specimens were preserved for comparison with stomach contents.

THE ST. JOHNS RIVER

The St. Johns River lies entirely within Florida. It rises from headwater marshes 80 km. north of Lake Okeechobee and 24 km. inland from Florida's east coast, flows north for 420 km. to Jacksonville, and continues east 40 km. to the Atlantic Ocean. North and south jetties extend from the mouth of the river about 1.5 km. into the ocean. Along its course the river receives the flow of many tributaries and often expands into lakes. Its largest tributary is the 200-km.-long Oklawaha River (172 km. upstream); its largest lake is 9.5-km. wide and 19-km. long Lake George (185 km. upstream). The Intracoastal Waterway intersects the river 8 km. from the mouth. The St. Johns River is less than 1.5 km. wide from the jetties to 11 km. upstream, 1.5 to 5 km. wide from this point 125 km. upstream to Palatka (except for a narrow section at Jacksonville), and 1.5 km. wide from Palatka upstream 145 km. to Sanford. Upstream from Sanford, the greatest width is less than 1 km. The depth of the river channel is 10 m. from the mouth to Jacksonville, 4 m. to Palatka, and 3.5 m. to Sanford.

Characteristics of the St. Johns River are low gradient, extensive tidal influence, and varying salinity and temperature. The river drops only about 6 m. in the 460 km. from its source to the ocean and has a slow current. The usual head of tidal influence is Lake George, 185 km. upstream. Salinity readings 15 km. from the mouth of the river ranged from 2.5 to 33.4 p.p.t. (parts per thousand) during 1961–62. They varied with depth, direction of the tide, and season (salinity was lowest in late summer and highest in late spring). South of Jacksonville, 40 km. from the mouth, salinity is normally less than 1 p.p.t. Water temperature between the mouth and Jacksonville ranged from a winter low of 8.2° C. to a summer high of 34.1° C.

ADULT CRABS

SEX COMPOSITION

Most of the blue crabs of commercial size (larger than 120 mm.) caught during most of the year in the lower river were females, but males were always dominant in the upper river. Among crabs caught in the first 24 km. of the lower river, 60 to 90 percent were females in January to September and 10 to 25 percent in October to December. In the next 24 km. of river, extending to 8 km. south of Jacksonville, females made up 75 percent of the catch in December to February and 15 to 55 percent in March to November. From a point about 8 km. above Jacksonville to Palatka the percentage of females ranged during the year from 10 to 35 percent; and above Palatka, from 5 to 35 percent.

Except in the fall when large numbers of males occasionally were captured very close to the jetties, nearly all of the adult blue crabs caught in the ocean were females.

MATING AND SIZE AT SEXUAL MATURITY

Female blue crabs mate once, after the last in a series of molts, but males may mate during each of their last three growth stages (Truitt, 1939). Before mating, the male carries the female beneath him, often for more than 2 days, until she sheds her immature shell. Sperm from the male is then

transferred to the spermathecae of the female where it remains viable a year or more and is used for repeated spawnings.

Mating blue crabs were commonly observed from 11 to 215 km. above the mouth of the river. Primary mating areas were the shallower near shore waters of the main river and tributary streams. Mating occurred sparingly in January and February, was common in March to July, decreased sharply in late summer, and was common again in October to December. Among 25 randomly collected mating pairs that I measured, the smallest male was 121 mm. and the smallest female was 71 mm.

Maturity of blue crabs is attained at varying widths. The proportion of male and female crabs that matured at a small size was larger in salt water (from the mouth of the river to Jacksonville) than in fresh water (south of Jacksonville, table 1). The smallest mature female measured in the St. Johns River was 99 mm. and the largest immature female was 177 mm. Mature females believed to be *Callinectes sapidus* have been captured in North Carolina as small as 52 mm. (Fischler, 1959), but to my knowledge no immature female as large as 177 mm. has been reported for any other area. Overlap in the size ranges of immature and mature females in the St. Johns River was considerably greater than reported by Tyler and Cargo (1963) for Chesapeake Bay; their smallest mature female was 118 mm. wide and the largest immature female was 135 mm.

TABLE 1.—*Percentage of mature male and female blue crabs in samples of commercial catches from the lower St. Johns River (salt water) and from the upper river (fresh water), 1961–62*

Carapace width	Males				Females			
	Lower river		Upper river		Lower river		Upper river	
	Number examined	Mature	Number examined	Mature	Number examined	Mature	Number examined	Mature
Mm.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
120–24	16	44	28	0	64	31	182	2
125–29	22	50	51	8	56	52	150	6
130–34	23	52	55	14	93	83	155	15
135–39	23	70	54	18	121	90	121	27
140–44	32	66	76	33	199	96	121	46
145–49	43	84	103	42	258	98	90	66
150–54	42	88	105	50	371	99	110	80
155–59	44	95	132	66	425	100	131	90
160–64	65	88	127	72	473	100	148	96
165–69	49	98	95	76	422	100	139	99

SPAWNING

Intervals between mating and spawning of blue crabs, or migrations preparatory to spawning, vary with season. Spawning usually takes place within 1 to 2 months after mating in spring and summer. If crabs mate during fall or winter, spawning is delayed until warmer temperatures the following spring. Most mature females of the upper river migrate downstream to near Jacksonville (about 30 to 55 km. above the mouth) for maturation of the ovaries. In spring and fall, almost all females make the migration soon after mating and during early development of the ovaries. In summer and winter, however, more mature females delay migration downstream, and 20 to 50 percent of those in the upper river have large ovaries with well-developed eggs.

Most blue crabs spawn in the lower 32 km. of the river. Relatively few females spawn near Jacksonville, and I observed no spawning south of there. The eggs, numbering between 1 and 2 million and known as a sponge, are deposited on the abdominal appendages and carried by the female until they hatch. They are initially yellow-orange, but as the larvae develop and absorb the yolk during the 2 weeks required for hatching, the eggs become brown and finally black.

Spawning occurs in the St. Johns River 8 or 9 months of the year; only the very coldest winter months are excluded. In 1962, sponge crabs first appeared in the lower 32 km. of the river in February, were most abundant from March to September (when 40 to 82 percent of the mature females collected were with sponge), and were present through October. In 1963, sponges did not appear until March, probably because of the colder water in February. Water temperature in 1962 increased from an average of 13.2° C. in January to 18.4° C. in February. In 1963, water temperature decreased from 12.9° C. in January to 11.4° C. in February; in March it rose to 20.4° C.

As the eggs develop, the females move from the river into the ocean where the eggs hatch. Almost all of the sponges of river females are yellow-orange, whereas most sponges on blue crabs in the ocean are dark brown or black. Sponge crabs were first common in the ocean in March or April but only within 1 km. of shore at the river mouth. As the spawning season progressed, egg-bearing females were found over a wider and wider ocean

area. In June they were common out to 2.5 km., and from July through September, when they were most abundant, large numbers were 5 to 6 km. offshore between Fernandina Beach and Ponte Vedra Beach. The number of females offshore dropped sharply in October, but 62 percent were in sponge compared with 4 percent in the lower 32 km. of river. From November to February, female crabs were least common in the sampling area off the mouth of the St. Johns. During this period only one sponge crab was taken (in January) but the well-developed ova of most of the females indicated that they would spawn in the spring.

Many if not all female blue crabs spawn twice—in the same season or over two seasons—and they often return to inland waters to develop their second sponge. Throughout the spawning season, some females reentered the lower 40 km. of the river from the ocean and developed another sponge. These repeat spawners could be distinguished by the appearance of their shells. Crabs which have not left the river have shiny, clean, bright-colored shells. Crabs which have spent time in the ocean have dull-colored shells with an encrustation of fouling organisms—especially the turtle barnacle, *Chelonibia patula*. Blue crabs which had previously had sponges also could be distinguished by the ragged appearance of their abdominal appendages and the presence of eggshell remnants.

TAGGING AND RECOVERY

The few tagging studies that have been made to determine movements of adult blue crabs have been confined largely to bays and to lower parts of estuaries. Fiedler (1930) found that tagged females released in the northern part of Chesapeake Bay migrated to the southern portion and tended to remain there. The direction of movement for males was random. Cronin (1954) detected no clear pattern for movements of crabs in Delaware Bay. Some males and females moved up Delaware Bay after wintering near the mouth; none of the tagged crabs was returned from other coastal regions. Cargo (1958), who tagged only females in Chincoteague Bay, Va., found they moved southward to the lower bay even if released in areas where high-salinity water was to the north. Only two crabs were captured outside Chincoteague Bay—one at Oyster, Va., the other in Delaware Bay. Fischler and Walburg (1962) released 4,353 tagged blue crabs in three estuaries and two offshore locations in South Carolina. Both male and female crabs moved considerably between the lower estuaries and adjoining coastal waters. Only seven males and six females were recaptured in estuaries other than those in which the crabs were released. Crabs that entered estuaries were almost always from the adjacent ocean tagging site. All but two crabs were recaptured within 80 km. of the release area. The authors concluded that, in South Carolina at least, adult blue crabs do not migrate between estuaries but limit their movements to the estuary or adjacent marine area.

Of the 11,522 blue crabs tagged in the St. Johns River and in the ocean off its mouth, 4,059 (35 percent) were recovered. Ninety-seven percent of the recoveries were by commercial gear, which was fished every month of the year; 3 percent of the recoveries were by sport fishermen.

Return of tags from 2,839 males and 830 females recaptured after release in the river indicated some movement of both sexes throughout the year. Migrations within the river were principally downstream (table 2). Among crabs tagged from Jacksonville to Lake George and recovered at a distance from the tagging site, 89 percent of the males and 96 percent of the females were recaptured north or downstream from the point of release. Some males moved randomly between New Berlin and Picolata, but nearly all of those tagged south of Picolata were recaptured downstream. Females tagged at all sites during spring and summer usually migrated into the ocean within 1 month, but those tagged in late fall and early winter entered the ocean after 3 or more months. Only three females were recaptured more than 25 km. upriver from any tagging site. Many females from the upper river congregated near Jacksonville in late fall. They moved downstream to New Berlin as early as January but in greater numbers during March. Early in the spawning season (February–May) females were slower to spawn and lingered longer at New Berlin before entering the ocean than those of later months (May–September).

Two hundred thirty-five blue crabs (52 males and 183 females) tagged in the St. Johns River were recovered from other waters (fig. 3). Males entered the Intracoastal Waterway north of the

TABLE 2.—*Number of tagged adult male blue crabs recovered after release at different localities in the St. Johns River*

Locality of release [1]	Crabs tagged	Area of recovery (kilometers upstream from mouth of river) [2]									Total recoveries
		215	195	170	135	95	70	40	15	0	
Km.	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Percent*
195	1,287	5	481	74	19	36	7	1	2	2	49
170	790	1	18	274	53	58	6	2	3	0	53
135	717	0	0	2	151	109	12	5	6	1	40
95	1,474	0	0	1	2	575	41	43	16	6	46
70	738	0	0	0	0	35	219	32	11	3	41
40	599	0	0	0	0	1	5	203	22	10	40
15	778	0	0	0	0	2	2	32	220	30	37

[1] Kilometers upstream from mouth of St. Johns River.
[2] Approximate areas of recovery corresponding to kilometers upstream are: 215 km.—Astor; 195—Lake George; 170—Welaka; 135—Palatka; 95—Picolata; 70—Switzerland; 40—Jacksonville; 15—New Berlin; and 0—outside river.

St. Johns River and the Nassau River during all seasons of the year and migrated to the waterway south of the St. Johns River, to the Ft. George River, and to the ocean (from Fernandina Beach to Cocoa Beach) primarily during fall and early winter. Females migrated into the ocean from April through October. Most returns were from the vicinity of the mouth of the river, but others ranged from Jekyll Island, Ga., to New Smyrna Beach, Fla. Sixty-six females recaptured in inland waters north of the St. Johns River were taken in the Intracoastal Waterway, the Ft. George, Nassau, St. Marys, and Crooked Rivers, and Kings Bay. Eight returns were from the waterway south of the St. Johns. Two of these crabs, which were tagged during late fall 1962, were recaptured dur-

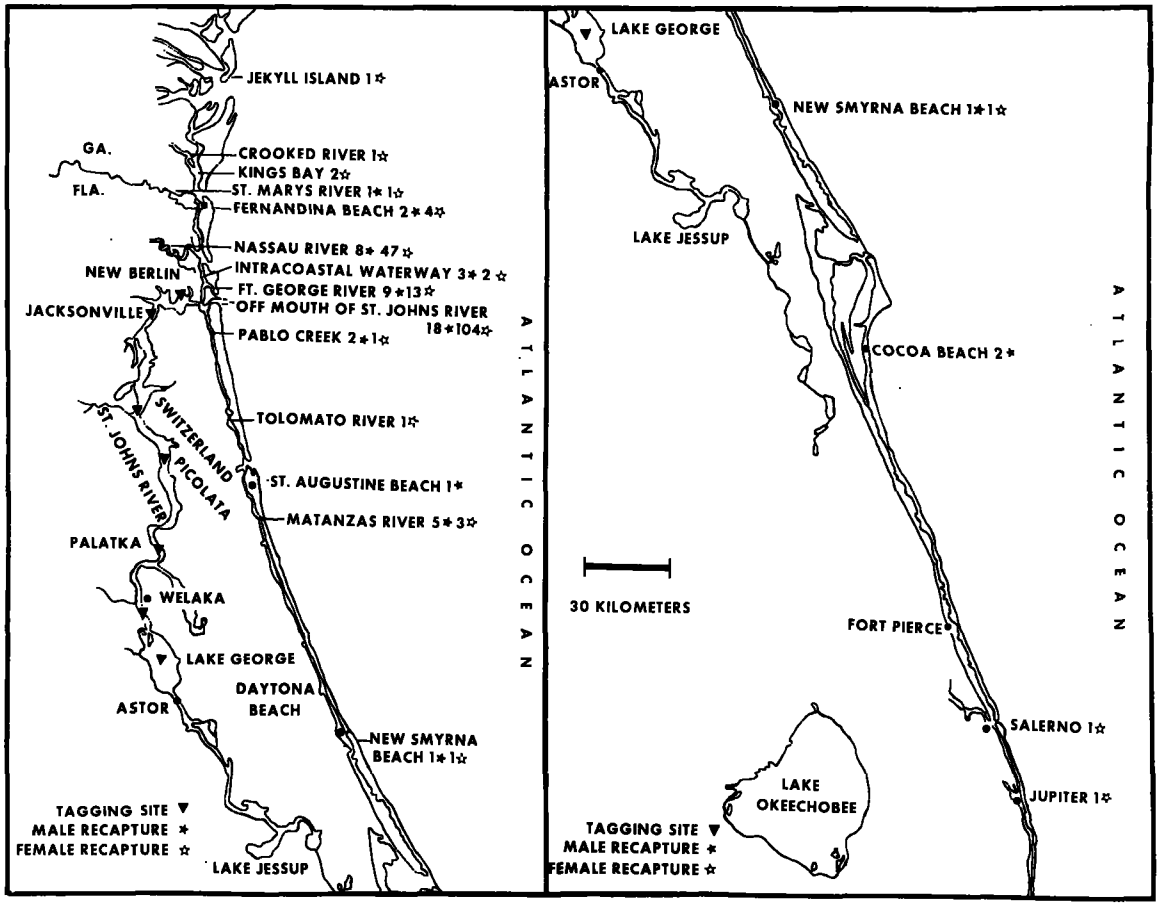

FIGURE 3.—Localities of recapture of blue crabs tagged in the St. Johns River that were recovered outside the river.

ing the succeeding winter near Salerno and Jupiter, about 460 and 540 km. from the point of release. The female recovered at Salerno traveled an average of at least 7.9 km. per day.

Some sponge female blue crabs migrated from New Berlin directly into the Intracoastal Waterway (north) and apparently entered the ocean by way of other rivers. Ten sponge females tagged at New Berlin (from April to September) were recaptured in the waterway and the Ft. George and Nassau Rivers within 3 to 14 days and before hatching in the ocean and return to inland waters were possible.

The migration of female blue crabs toward spawning grounds in high-salinity waters resembles that in other areas. The similar migration of at least some males, often parallel to females in time and distance, is unlike that reported elsewhere. In Chesapeake Bay, Van Engel (1958) reported that when females migrated downstream to the lower bay, adult males remained in brackish waters and many moved farther upstream.

Of the 381 tags recovered from female blue crabs tagged in the ocean off the mouth of the St. Johns River, 107 were from inland waters (fig. 4). Of these, 59 were recovered in the St. Johns River, 38 in the Nassau River, and the remainder in Cumberland Sound, Intracoastal Waterway, Crooked River, St. Marys River, and Ft. George River. Sixteen of the crabs that had been tagged off the mouth between May and January were recaptured in the St. Johns River during January, February, and March. These returns indicated, as did the composition of the commercial catches, that some crabs which spawned the previous season and others which matured and left the river in winter reentered the river before and during the earliest part of the spawning season. After their eggs hatched, females continued to enter the St. Johns and Nassau Rivers during summer and fall. Nearly all of the returns in the St. Johns River were between New Berlin and Jacksonville; a tag from Picolata was the only return upstream from Jacksonville. Returns from the Nassau River were mostly more than 11 km. from the mouth and extended upstream as far as 32 km.

Some female blue crabs reenter rivers very soon after their eggs hatch. From May through September, the majority of the returns in the St. Johns and Nassau Rivers of females tagged in the ocean

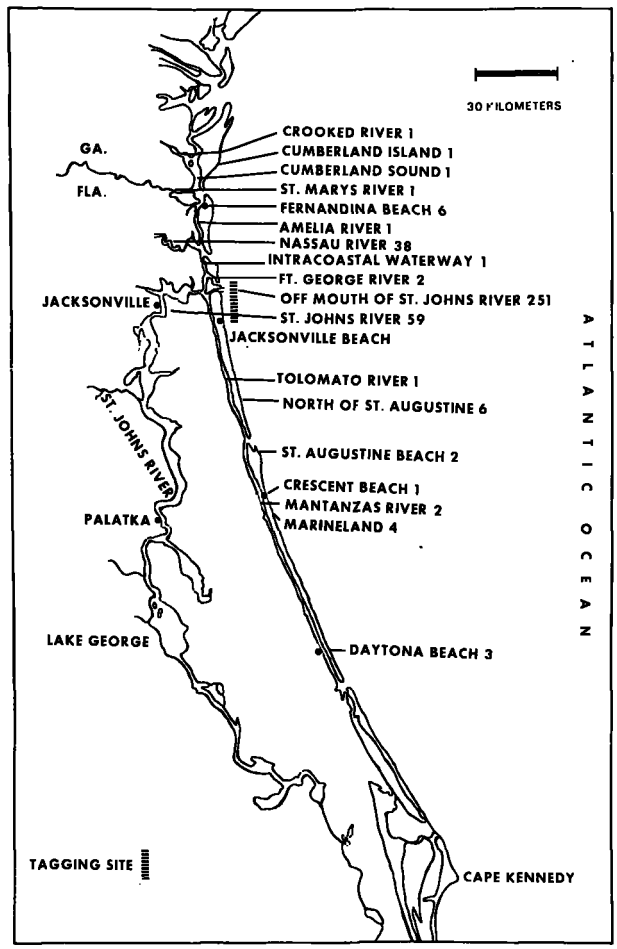

FIGURE 4.—Recovery locations of female blue crabs tagged in the ocean off the mouth of the St. Johns River.

(almost all in sponge or recently in sponge) came within 30 days, and most came within 15 days. Fifty-four of the sponge females tagged at New Berlin were recovered in the St. Johns and Nassau Rivers after more than 15 days, and, therefore, after hatching of the eggs. Of these, 40 were recovered in the rivers as soon as 16 to 45 days after release.

Eight of nine returns of male blue crabs tagged in the ocean off the mouth of the river were recaptured in that vicinity within 2 months. One male tagged in August was recovered in the Ft. George River in November.

LONGEVITY

In the St. Johns River, relatively few blue crabs survive more than 1 year after reaching maturity. We recovered only 13 tagged crabs more than 12

months after release. Three females were recaptured during the third spawning season, 20 to 24 months after they were tagged; and two males were recaptured after 33 and 36 months. If these periods are added to the approximately 12 months required to attain adult size, the maximum age of St. Johns crabs is estimated at little more than 4 years.

LARVAL STAGES

Newly hatched blue crabs pass through two larval forms, zoea and megalops. Rearing of larvae in the laboratory has shown that crabs have seven zoeal stages over a period of 31 to 49 days and a subsequent megalops stage of 6 to 20 days (Costlow and Bookhout, 1959).

Callinectes zoeae were found from April through October in samples taken between buoys 11 and 38, 3 to 11 km. above the mouth of the river. Peak abundance occurred earlier in 1962 than in 1961 (table 3). The number of zoeae per cubic meter of water ranged from 0 to 460.9. More *Callinectes* zoeae were collected near the surface than at the bottom regardless of tidal direction. No evidence appeared of retention of *Callinectes* zoeae within the estuary, as more were obtained during outgoing tides than during incoming tides.

Most of the larval *Callinectes* captured were first-stage zoeae, but some second-stage zoeae and some megalops also were caught. The proportion of second-stage to first-stage zoeae was 1 to 323. The second-stage form occurred in one surface sample in May (1.5 per 1 m.^{3}) and in four surface and four bottom samples in August (0.6–2.6 per 1 m.^{3}). The proportion of megalops to zoeae was 1 to 164. Megalops were found in three July samples (0.5–1.1 per 1 m.^{3}), two August samples (1.1–18.6 per 1 m.^{3}), and two September samples (0.4 and 0.5 per 1 m.^{3}). Ninety-six percent of the megalops were taken in bottom collections.

Zoeae of 22 kinds of crabs and megalops of 5 genera were collected between buoys 11 and 38. In 1961, *Callinectes* zoeae ranked third in abundance after *Uca* and *Sesarma* (table 4), and in 1962 *Callinectes* ranked second to *Uca* (table 5). Megalops of four other genera were collected from May through October. Sixteen samples contained *Uca*

TABLE 3.—*Number of* Callinectes *zoeae collected per cubic meter of water in the St. Johns River between buoys 11 and 38 (3–11 km. above mouth of river)*

Month and depth (meters)	1961			1962		
	Samples	Zoeae per 1 m.^{3}		Samples	Zoeae per 1 m.^{3}	
		Average	Range		Average	Range
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
January:						
0.3				8	0	0
10.0				8	0	0
February:						
0.3				7	0	0
10.0				7	0	0
March:						
0.3				8	0	0
10.0				8	0	0
April:						
0.3				4	5.4	2.3– 8.2
10.0				4	1.5	0 – 4.2
May:						
0.3	12	0.3	0 – 3.7	8	51.4	0 –157.3
10.0	12	.7	0 – 7.6	8	18.2	1.1– 52.4
June:						
0.3	11	6.2	0 – 24.0	16	53.8	0 –460.9
10.0	11	2.0	0 – 8.3	16	24.2	0 –129.0
July:						
0.3				8	6.2	0 – 23.7
10.0				8	6.9	0.5– 22.3
August:						
0.3	8	119.5	16.9–358.0	23	4.0	0 – 25.2
10.0	8	82.8	12.1–221.8	23	1.7	0 – 9.0
September:						
0.3	8	.2	0 – 1.3	15	.9	0 – 4.1
10.0	8	.4	0 – .9	15	.3	0 – 2.0
October:						
0.3	16	.1	0 – 1.4	14	.1	0 – .8
10.0	16	.1	0 – 1.2	14	0	0
November:						
0.3	8	0	0	14	0	0
10.0	8	0	0	14	0	0
December:						
0.3	8	0	0			
10.0	8	0	0			

TABLE 4.—*Estimated average number of crab zoeae per cubic meter of water, between buoys 11 and 38 (3–11 km. above mouth of St. Johns River) in May, June, and August–December, 1961*

[Number of samples each month in parentheses]

Species	May (24)	June (22)	Aug. (16)	Sept. (16)	Oct. (32)	Nov. (16)	Dec. (16)	Total (142)	Rank in abundance
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	
Callinectes sp.	0.5	4.1	101.2	0.3	0.1	0.0	0.0	106.2	3
Emerita sp.	[1].0	.1	.0	.2	.0	.0	.0	.3	16
Eurypanopeus sp.	3.2	1.7	28.2	3.5	.9	.0	.0	37.5	5
Hepatus sp.	.0	.0	.8	2.4	.0	.0	.0	3.2	9
Leucosiidae	.0	.0	.2	1.0	.0	.0	.0	1.2	14
Menippe sp.	[1].0	.6	1.5	3.1	.0	.0	.0	5.2	7
Neopanope sp.	.6	.0	2.5	.9	.1	.0	.0	4.1	8
Pachygrapsus sp.	.0	.0	.0	.0	[1].0	.1	.0	.1	18
Panopeus sp.	.7	1.4	51.8	19.9	.1	.0	[1].0	73.9	4
Pilumnus sp.	.0	.0	.0	.1	.0	.0	.0	.1	18
Pinnixa sp.	.4	.3	.7	10.2	.5	.2	.3	12.6	6
Pinnotheres maculatus	.0	.4	.8	.7	[1].0	.1	.0	2.0	12
Pinnotheres ostreum	[1].0	[1].0	2.1	.2	.1	.0	.0	2.4	11
Polyonyx sp.	.2	.0	.2	2.5	[1].0	.0	.0	2.9	10
Portunus gibbesii	.0	.1	1.0	.8	.0	.0	.0	1.9	13
Portunus sayi	.2	.0	.0	.0	.0	.0	.0	.2	17
Rithropanopeus sp.	.8	.0	.1	.1	[1].0	.0	.0	1.0	15
Sesarma sp.	2.5	6.3	104.4	6.6	.2	.0	.0	120.0	2
Uca sp.	4.4	29.3	742.5	18.5	.4	.0	.0	795.1	1
Unknown A	.0	.0	[1].0	.1	[1].0	.0	.0	.1	18
Unknown D	.0	.0	.0	.0	.0	.1	.0	.1	18

[1] Less than 0.06.

(0.6–59.6 per 1 m.^{3}), 12 contained *Sesarma* (0.6–19.8 per 1 m.^{3}), 10 contained *Neopanope* (0.5–9.7 per 1 m.^{3}), and 9 contained *Panopeus* (0.5–2.3 per 1 m.^{3}). Megalops of *Uca* and *Sesarma* were more abundant than *Callinectes*. As for *Callinectes*, 96 percent of the megalops of the other genera were from bottom collections.

Plankton collections were made also at buoy 63, 40 km. from the mouth of the river, during May and October 1961 and August 1961 and 1962 (table 6). *Callinectes* zoeae occurred in three May samples (1.2–4.7 per 1 m.^{3}) and 10 August samples (0.9–6.1 per 1 m.^{3}); 10 of these 13 samples were taken near the bottom. One bottom sample in May contained second-stage zoeae (2.4 per 1 m.^{3}), and two bottom collections in August had megalops (both 1.2 per 1 m.^{3}). *Rithropanopeus*, *Sesarma*, and *Uca* were the most abundant genera in the collections. Megalops collected in May were, in decreasing order of abundance, *Sesarma*, *Uca*, *Rithropanopeus*, and *Panopeus*. August samples contained megalops of only *Uca* and *Callinectes*.

Most of the larval *Callinectes* collected in the St. Johns River occurred at salinities and temperatures favorable to larvae reared in the laboratory. Laboratory-reared larvae of *C. sapidus* had a uniform rate of growth in salinities between 20.1 and 31.1 p.p.t. at 25° C. (Costlow and Bookhout, 1959). Even though almost all *Callinectes* larvae captured near the mouth of the St. Johns River (buoys 11–38) both at the surface and near the bottom were in favorable salinities, some of those captured upriver (buoy 63) were in salinities which probably would be too low to sustain them over extended periods. Salinity near the mouth (surface and bottom) was between 25 and 35 p.p.t. from April to July and between 12 and 36 p.p.t. from August to October. Bottom salinity was nearly always greater than that at the surface, particularly during ebb tide. At buoy 63, larval *Callinectes* were captured in salinities from 9 to 27 p.p.t. Water temperature (April to October) in the lower 40 km. of river ranged from lows of 20° C. in April and October to a high of 31° C. in August. Temperature at the surface and bottom usually differed less than 1° C.

Plankton was collected between buoys 2 and 3 in south Jacksonville (48 km. above mouth of river) during August and October 1961. No *Callinectes* larvae were obtained. Zoeae and megalops of *Rithropanopeus* were predominant and present in almost all of the collections (zoeae: 0.7–61.7 per 1 m.^{3}). Zoeae of *Uca* and *Sesarma*, many of them dead, were the only other larvae collected. Surface salinities in these months ranged from 0 to 10 p.p.t. and bottom salinities from 5 to 11 p.p.t.

Plankton collections made in the South Atlantic by the *Theodore N. Gill* in 1953–54 have been analyzed for the occurrence of *Callinectes* larvae (Nichols and Keney, 1963). Six stations were sampled off the mouth of the St. Johns River—one at the mouth, and five others, 32 km. apart, extending due east. Stages of zoeae found at the inshore station were the same as in the river—primarily

TABLE 5.—*Estimated average number of crab zoeae per cubic meter of water, between buoys 11 and 38 (3–11 km. above mouth of St. Johns River) in January–November, 1962*

[Number of samples each month in parentheses]

Species	Jan. (16)	Feb. (14)	Mar. (16)	Apr. (8)	May (16)	June (32)	July (16)	Aug. (46)	Sept. (30)	Oct. (28)	Nov. (28)	Total (250)	Rank in abundance
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	
Callinectes sp.	0.0	0.0	0.0	3.4	34.8	39.0	6.5	2.8	0.6	[1]0.0	0.0	87.1	3
Dissodactylus sp.	.0	.0	.0	.0	.2	.0	.0	.0	.0	.0	.0	.2	17
Eurypanopeus sp.	.0	.0	.2	1.0	11.1	5.4	.7	.9	1.6	.6	.0	21.5	5
Hepatus sp.	.0	.0	.0	.0	4.9	.3	[1].0	.1	.4	.1	.0	5.8	9
Leucosiidae	.0	.0	.0	.0	1.4	.1	[1].0	.2	.1	.0	.0	1.8	12
Menippe sp.	.0	.0	.0	.0	.1	.1	.4	.5	1.3	.2	.0	2.6	11
Neopanope sp.	.0	.0	[1].0	2.4	4.8	1.2	.2	.3	.3	.1	[1].0	9.3	6
Pachygrapsus sp.	.0	.0	.0	.0	.0	.0	.0	.0	[1].0	.0	[1].0	[1].0	19
Panopeus sp.	.0	.0	.0	3.9	26.3	5.2	.9	1.2	.2	.1	.0	37.8	4
Pilumnus sp.	.0	.0	.0	.0	[1].0	.0	.0	[1].0	[1].0	[1].0	.0	[1].0	19
Pinnixa sp.	.3	.2	[1].0	.4	3.6	1.0	.3	.3	.7	.4	.3	7.5	7
Pinnotheres maculatus	.0	.0	.0	.0	.1	.8	.0	.2	.2	.1	.1	1.5	14
Pinnotheres ostreum	.0	.0	.0	2.3	2.4	1.3	.2	[1].0	[1].0	.1	[1].0	6.3	8
Polyonyx sp.	.4	.0	.2	.4	.3	.1	[1].0	[1].0	.2	.1	[1].0	1.7	13
Portunus gibbesii	.0	.0	.0	.3	.5	.0	.0	[1].0	.0	.0	.0	.8	15
Portunus sayi	.0	.0	.1	.0	2.1	.6	[1].0	.0	.0	.0	.0	2.8	10
Rithropanopeus sp.	.0	.0	.0	.1	[1].0	.2	.0	[1].0	.2	[1].0	[1].0	.5	16
Sesarma sp.	.0	.0	.0	8.6	33.6	3.4	3.7	6.6	4.3	1.1	.0	61.3	3
Uca sp.	.0	.0	.0	63.5	137.6	17.2	7.0	5.5	4.2	2.5	.0	237.5	1
Unknown A	.0	.0	.0	.0	.0	.0	.0	.0	.0	.1	.0	.1	18
Unknown D	.0	.0	.0	.0	.0	.0	.0	.0	.0	[1].0	.0	[1].0	19

[1] Less than 0.06.

TABLE 6.—*Estimated average number of crab zoeae per cubic meter of water at buoy 63 (40 km. above mouth of St. Johns River) for certain months, 1961–62*

[Number of samples each month in parentheses]

Species	May (16)	Aug. (38)	Oct. (16)	Range
	Number	*Number*	*Number*	*Number*
Callinectes sp.	0.6	0.5	0.0	0– 6.1
Eurypanopeus sp.	5.9	.2	.2	0– 21.5
Menippe sp.	.0	[1].0	.0	0– .7
Neopanope sp.	1.9	.1	.0	0– 7.2
Panopeus sp.	.4	.2	.0	0– 2.2
Pinnixa sp.	.2	[1].0	.1	0– 1.6
Pinnotheres maculatus	.2	.0	.0	0– 1.9
Pinnotheres ostreum	.1	[1].0	.0	0– 2.1
Portunus gibbesii	.1	.0	.0	0– 1.1
Portunus sayi	.0	[1].0	.0	0– .9
Rithropanopeus sp.	25.2	22.4	.2	0–184.7
Sesarma sp.	28.8	2.6	.0	0–132.6
Uca sp.	112.3	6.5	.0	0–294.0

[1] Less than 0.06.

first but some second stage. All stages occurred at 32, 64, and 96 km. offshore. A few zoeae were obtained about 160 km. from shore. The relatively few megalops collected were at 64 and 128 km. offshore. *Callinectes* megalops were collected directly off the jetties in July, however, during limited sampling offshore in our study.

In brief, sampling for larval crabs in the St. Johns indicated that *Callinectes* was one of the most abundant forms in the region near the mouth. First- and second-stage zoeae entered and left the lower 40 km. of river from April to October. They were transported by surface and bottom currents; megalops usually were confined to the bottom. Early development occurs in the ocean within a few kilometers of shore, and growth after the second zoeal stage takes place farther offshore. Some larvae return to inshore waters as megalops.

JUVENILE CRABS

Although juvenile blue crabs were found in many localities from the mouth of the river to Astor, they usually occurred in small numbers or in larger numbers for short periods of time. Preferred habitats of those less than 40 mm. wide were in shallow water where the bottom consisted of either muck covered with dead plant material or firmer mud covered with dense growths of coontail (*Ceratophyllum*) and eelgrass (*Vallisneria*). Certain areas, where relatively large numbers of crabs congregated the year round, were selected for sampling at regular intervals in 1962 and 1963. These areas, and distances from the mouth of the St. Johns, were: Clapboard Creek (15 km.); Dunn Creek (30 km.); Trout River (40 km.); buoy 24, Picolata (95 km.); and buoy 11, Palatka (135 km.).

Postlarval stages of crabs continue to molt periodically until full size is attained. The megalops molts directly into the first crab stage (2–3 mm. wide), which has the general appearance of the adult. Growth ceases after about 20 postlarval molts. Full size is attained in about 1 year; crabs shed every few days at the earliest stages and at intervals of 1 month or more at later preadult stages.

Early stages of blue crabs (2–9 mm. wide) entered the sampling areas in the lower 40 km. of river primarily as waves, beginning 5 or more months after spawning began and continuing to the end of the year. A few early crab stages appeared before this time, but only the occurrence of large numbers was considered a wave. The waves, except in early winter, were made up of crabs predominantly 6 to 9 mm. wide and beyond the initial crab stages. I collected few crabs 2 to 3 mm. wide during summer and fall. Escape of an appreciable number of first crab stages through the nets was unlikely as the catch in the stations of the lower river was always mixed with a great amount of mud and debris.

The area of metamorphosis of the megalops to the first crab stage has not been determined, but transformation probably takes place most frequently in the ocean. In the south Atlantic, most *Callinectes* megalops were found 64 or more kilometers offshore (Nichols and Keney, 1963). It is not surprising that we collected relatively few first and second crab stages in the river if transformation to the first crab stage also happens beyond 64 km. Some megalops may enter the first crab stage within the estuary, because megalops do appear in the river and directly off its mouth. Two megalops were collected along with early crab stages in Trout River.

The first waves of early crab stages in Dunn Creek and Trout River were in July 1962 and September 1963. With the early waves each year, abundance of individuals less than 20 mm. wide increase markedly (fig. 5). Like the initial spawning run, the first appreciable occurrence of young crabs was later in 1963 than in 1962.

First and second crab stages (2–4 mm. wide) predominated among early stages (2–9 mm. wide)

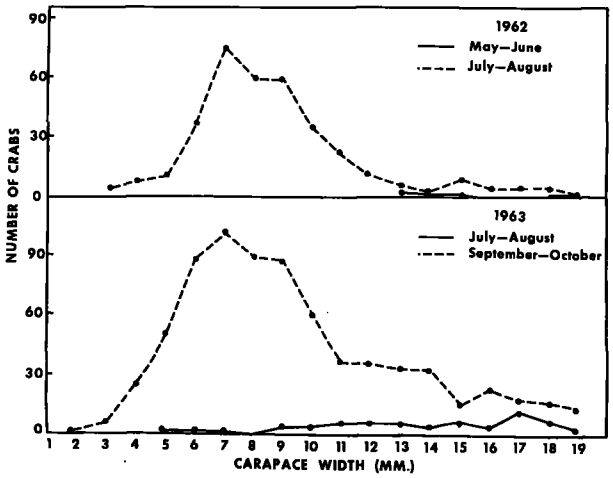

FIGURE 5.—Width distribution of blue crabs less than 20 mm. wide collected before and after the initial wave in Dunn Creek and Trout River.

in Dunn Creek and Trout River during December and January (fig. 6). These crabs were hatched in October and November, and subsequent winter temperatures probably inhibited postlarval growth. They shed throughout the winter but less frequently than in other seasons.

Waves of early blue crab stages also entered Clapboard Creek in 1962, but no appreciable influx was observed during 1963. Small numbers, including a few first crab stages, occurred among much larger numbers of *Callinectes similis* or *C. ornatus* from July to October 1963. No congregations of blue crabs developed, possibly because of competition for food and space from small juveniles of these other species, which were established in Clapboard Creek as early as May (Tagatz, 1967).

The influx of early crab stages was not confined to the lower river but extended 95 km. and more upstream. Early crab stages over 5 mm. wide first appeared at Picolata (buoy 24) during the same month as the initial waves in the lower river—July 1962 and September 1963. In 1962, most early crab stages were widely scattered in shallow areas adjacent to buoy 24; in 1963, waves and subsequent growth were clearly evident at this station (fig. 7). Crabs that made up the waves were larger than those entering lower river areas, and no crabs less than 6 mm. wide were caught. A few early crab stages 8 to 9 mm. wide were collected at Palatka (buoy 11).

In the St. Johns River, some juvenile blue crabs grew to maturity (or a harvestable size of at least 120 mm.) between the mouth and Jacksonville, but most females attained maturity between Jacksonville and Palatka; most males matured upstream of Palatka. Juvenile males were less abundant than juvenile females in the lower river, and the percentage of males increased with distance upstream (table 7). I found the largest concentrations of juvenile crabs 20 to 119 mm. wide at Picolata (buoy 24). Because of variation in growth rate and a long spawning season, significant numbers of crabs were one or more molts away from harvestable size during all seasons (table 8). Juveniles 20 to 39 mm. wide were most common in spring and fall. They were more widely distributed in the shallows along shore than larger crabs which remained in the channel. Juveniles 20 to 119 mm. wide also concentrated at Palatka (buoy 11). Upstream of Palatka, juveniles were nearly

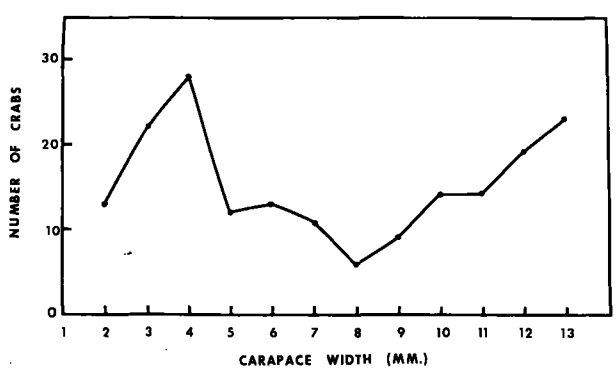

FIGURE. 6.—Width distribution of blue crabs less than 14 mm. wide collected in Dunn Creek and Trout River during December 1962 and January 1963.

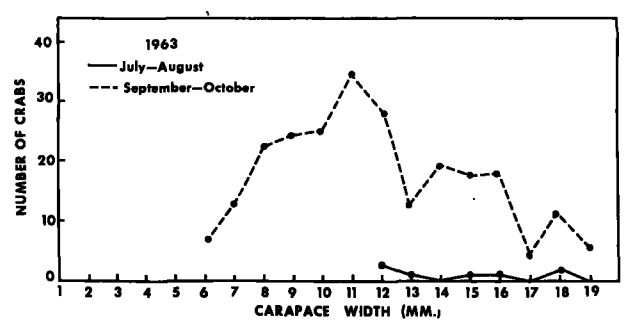

FIGURE 7.—Width distribution of blue crabs less than 20 mm. wide collected before and after the initial wave at Picolata (buoy 24).

TABLE 7.—*Percentage of males among juvenile blue crabs collected at selected stations in the St. Johns River. Distance upstream in kilometers is shown in parentheses*

Width	Trout River (40)		Buoy 24 Picolata (95)		Buoy 11 Palatka (135)	
	Crabs collected	Males	Crabs collected	Males	Crabs collected	Males
Mm.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
20- 39	231	47	211	52	56	79
40- 59	167	43	376	50	121	68
60- 79	118	47	481	50	162	76
80- 99	118	32	502	47	161	61
100-119	103	27	639	41	114	68
Total	737	41	2,209	47	614	69

all males and generally were larger than 100 mm. wide (relatively few mates are available to the mature males that remain above Palatka). Juvenile blue crabs under 100 mm. and usually over 30 mm. occurred irregularly between Palatka and Welaka. Nearly all juveniles above Welaka were over 100 mm. wide; the smallest blue crab I caught was 25 mm.

In summary, juveniles, primarily beyond the initial crab stages, enter the St. Johns in waves during the latter part of the spawning season. The time of the first wave appeared to depend on the time of initial spawning. Many first and second crab stages entered in early winter. Individuals as small as 8 mm. wide moved at least 135 km. upstream. Juvenile blue crabs were widely distributed but concentrated the year around in certain localities. Those less than 40 mm. wide were most common in shallower waters; those more than 40 mm., in deeper areas. Females predominated in the lower river and males in the upper river.

FOOD OF BLUE CRABS

Blue crabs eat a great variety of foods. Fish, alive and dead, are eaten regularly (dead fish are used as bait in the commercial fishery). The diet of blue crabs includes many types of aquatic vegetation (Truitt, 1939), and they have been reported to eat oysters (Lunz, 1947) and other bivalves (Carriker, 1951). Darnell (1958) found that blue crabs of Lake Pontchartrain, La., fed principally on mollusks (clams, mussels, and snails), crustaceans (mostly crabs but also barnacles and undetermined forms), and to a lesser degree on insects, hydroids, annelid worms, fish, algae, and vascular plants.

Little is known of the foods that sustain larval crabs. Most successful foods for growth of zoeae in the laboratory are yellow dinoflagellates (Sandoz and Rogers, 1944) and *Artemia* nauplii and *Arbacia* eggs (Costlow and Bookhout, 1959). The megalops is omnivorous and will eat pieces of fish, shellfish, and aquatic plants (Van Engel, 1958).

Of the 695 blue crab stomachs collected at four localities—Clapboard Creek (15 km. upstream from mouth of St. Johns River), Dunn Creek (30 km. upstream), Trout River (40 km. upstream), and buoy 24, Picolata (95 km. upstream)—668 contained food. Classes of food as percentage frequency of occurrence were:

Food item	*Percent*
Mollusks	32.4
Crustaceans	19.4
Organic debris	17.0
Fish	15.6
Plants	8.5
Annelids	5.0
Insects	1.4
Bryozoans	.6

Classes of food as percentage of the total volume of food per stomach were:

Food item	*Percent*
Mollusks	39.0
Organic debris	19.8
Fish	19.4
Crustaceans	15.0
Plants	3.9
Annelids	1.8
Insects	.9
Bryozoans	.1

TABLE 8.—*Monthly size distribution of juvenile blue crabs collected at buoy 24, Picolata, St. Johns River, Fla., 1962*

Width	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mm.	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
20- 39	5	9	13	2	7	1	2	14	21	21	14	22
40- 59	21	16	25	12	12	12	3	10	35	23	15	15
60- 79	29	19	21	22	30	30	11	9	20	22	19	19
80- 99	28	19	23	27	30	27	20	17	12	14	23	22
100-119	17	37	18	36	21	30	64	50	12	19	29	22
Total number of crabs	187	104	381	313	186	246	142	174	113	188	143	32

A large percentage of stomach contents consisted of organic material in advanced stages of digestion which could not be identified. Sand, mud, wood, charcoal, and similar debris (not recorded) were often taken by crabs incidentally in feeding. Sand, ranging from a single grain to several hundred grains, occurred in all gastric mills. A greater proportion of sand, relative to food content, was present in smaller crabs (less than 50 mm. wide) than in larger ones.

Generally all sizes of blue crabs ate the same types of foods (table 9) at all four stations sampled (table 10). Most of the mollusks eaten were mussels and clams. No mussels were found in crabs less than 21 mm. wide. Mussels eaten in the lower river stations (Clapboard Creek, Dunn Creek, and Trout River) were almost all *Modiolus demissus* but included a few *Musculus niger*. The only species present and eaten at Picolata was *Mytilopsis leucopheata*. Mussels were strongly predominant in crabs from Picolata where clams played a relatively minor role in the diet. Small numbers of *M. leucopheata* were present in Trout River, but none appeared in stomach samples. Mussels selected were less than an estimated 15 mm. long, and usually the shell in the stomach was fragmented. Very small mussels, 1.5 to 5.0 mm., were preferred; the gastric mill of adults often contained 25 to 50. Of the clams, Sphaerridae, *Rangia cuneata*, and *Mulinia lateralis* were consumed, and probably other clams common to the lower river—*Tellina alternata*, *T. syharitica*, *Tagelus gibbus*, and *Mactra fragilis*. Crabs less than 21 mm. wide selected clams less than 2 mm., and even adults usually took clams under 10 mm. The stomachs of small crabs most often contained 5 to 10 clams, whereas those of larger crabs usually had 20 to 35 individuals. A few of the mollusks eaten were oyster spat, *Crassostrea virginica*, and snails, *Nassarius obsoletus* and possibly *Nassarius vibex* and *Neritina reclivata*.

Amphipods and crabs were the dominant Crustacea eaten. *Gammarus fasciatus* was taken at all stations, and *Corophium* sp. was a particularly important food of all sizes of blue crabs at Picolata. *Carinogammarus mucronatus* and *Talorchestia longicornis*, present in the lower river, probably were among other amphipods eaten. Crabs less than 31 mm. wide commonly had 10 to 15 amphipods in their stomachs. Of the crabs eaten, about one-half of those that could be identified were blue crabs and the remainder mud crabs—*Rithropanopeus harrisi* and probably *Panopeus herbstii* and *Eurypanopeus depressus*. No more than four individuals were in any food tract, and none appeared to have exceeded 20 mm. The mysid, *Neomysis americana* (listed as a shrimplike form), was taken fairly frequently, particularly in Clapboard Creek. Shrimplike forms as large as an estimated 30 mm. provided food but were too fragmented for positive identification. The most common shrimp at all stations were *Palaemonetes pugio* and *P. vulgaris*, and at Picolata, also *Macrobrachium ohione*. Ostracods

TABLE 9.—*Food of the blue crab, by crab size, in the St. Johns River as percentage frequency of occurrence and (in parentheses) as percentage of total volume per stomach*

[Number of stomachs with food in parentheses below designation of size group of crabs]

Food item	Width in mm.							
	5–10 (32)	11–20 (94)	21–30 (82)	31–40 (56)	41–50 (42)	51–100 (139)	101–200 (223)	Total (668)
Bryozoans		[1] 1(0)			[1] 2(0)	[1] 1(0)	[1] 2(0)	[1] 1(0)
Mussels			5(1)	9(4)	10(3)	34(25)	46(36)	24(18)
Clams	9(4)	31(19)	49(26)	38(18)	33(17)	34(21)	32(17)	34(19)
Oysters						1(1)	4(2)	2(1)
Snails			13(3)	9(4)	5(3)	4(1)	[1] 1(0)	4(1)
Nereis pelagica	[1] 6(0)	7(1)	21(4)	18(5)	24(7)	10(1)	[1] 2(0)	10(2)
Other annelids						[1] 1(0)		[1] 0(0)
Amphipods	6(6)	3(2)	18(6)	12(8)	17(9)	27(12)	10(2)	14(6)
Barnacles		[1] 1(0)	[1] 1(0)			[1] 1(0)	[1] 2(0)	[1] 1(0)
Ostracods	9(5)	[1] 2(0)					[1] 1(0)	[1] 1(0)
Shrimplike forms			4(2)	4(2)	5(5)	4(1)	[1] 1(0)	2(1)
Crabs		[1] 1(0)	10(4)	12(7)	12(2)	19(7)	13(3)	12(4)
Other crustaceans	28(22)	23(14)	8(5)	11(4)	7(1)	5(1)	[1] 1(0)	8(4)
Insects		6(4)	5(2)	7(1)	[1] 2(0)	[1] 1(0)	[1] 1(0)	3(1)
Fish		16(9)	39(19)	27(16)	38(26)	32(19)	38(26)	31(19)
Algae	12(4)	16(6)	11(3)	14(5)	14(2)	4(1)	[1] 3(0)	8(2)
Vascular plants		[1] 3(0)	7(1)	7(1)	21(6)	12(1)	8(2)	8(2)
Organic debris	72(59)	66(43)	43(24)	50(24)	36(17)	16(8)	18(10)	34(20)

[1] Less than 0.6 percent.

TABLE 10.—*Food of the blue crab, by crab size and by station, in the St. Johns River as percentage frequency of occurrence and (in parentheses) as percentage of total volume per stomach*

[Stations and distance from mouth: 1–Clapboard Creek 15 km., 2–Dunn Creek 30 km., 3–Trout River 40 km., 4–Picolata 95 km. Number of stomachs with food in parentheses below designation of station]

Food item	Width in mm., station number, and number of stomachs with food											
	5–50				51–100				101–200			
	1 (55)	2 (120)	3 (100)	4 (31)	1 (31)	2 (15)	3 (37)	4 (56)	1 (67)	2 (34)	3 (46)	4 (76)
Bryozoans		[1] 1(0)	[1] 1(0)				[1] 3(0)			[1] 3(0)	[1] 2(0)	[1] 4(0)
Mussels			9(3)	13(5)	[1] 6(0)	7(3)	30(23)	61(44)	12(5)	15(11)	65(45)	79(68)
Clams	73(47)	27(13)	35(15)		58(31)	67(50)	43(28)	7(3)	43(31)	59(24)	35(20)	8(1)
Oysters					6(4)				12(7)	3(1)	[1] 2(0)	
Snails		[1] 1(0)	17(6)		3(1)		11(4)	[1] 2(0)	[1] 1(0)			[1] 1(0)
Nereis pelagica	5(2)	[1] 10(0)	31(9)		16(1)	[1] 7(0)	22(4)		[1] 3(0)	[1] 9(0)		
Other annelids							[1] 3(0)	[1] 2(0)				
Amphipods	[1] 2(0)	2(1)	16(5)	48(30)	3(1)	[1] 13(7)		62(28)		[1] 3(0)		29(6)
Barnacles			[1] 2(0)			7(0)					2(1)	4(1)
Ostracods	5(3)		[1] 1(0)	3(2)								[1] 3(0)
Shrimplike forms	11(8)		[1] 1(0)		6(2)	7(1)	8(1)			[1] 3(0)	2(1)	
Crabs	[1] 2(0)	4(2)	12(5)	10(4)	10(5)	20(8)	32(14)	14(3)	12(2)	15(3)	11(3)	16(3)
Other crustaceans	16(8)	12(7)	15(8)	29(22)	[1] 3(0)		8(1)	5(2)				[1] 3(0)
Insects		9(4)	2(1)	6(1)			[1] 3(0)	[1] 2(0)		[1] 3(0)		[1] 1(0)
Fish	27(15)	28(16)	27(12)	10(10)	48(37)	40(25)	32(15)	20(11)	52(42)	62(39)	35(26)	17(8)
Algae	9(1)	9(5)	19(5)	22(4)	10(1)		3(2)	[1] 4(0)	[1] 3(0)	[1] 3(0)		5(1)
Vascular plants	5(2)	[1] 2(0)	13(2)	10(2)	[1] 10(0)	20(1)	16(2)	9(2)	4(2)	15(2)	[1] 2(0)	12(4)
Organic debris	38(13)	64(49)	51(28)	45(21)	19(16)	7(5)	16(6)	16(6)	18(11)	24(19)	9(3)	21(9)

[1] Less than 0.6 percent.

were an important food of 5- to 10-mm. crabs. Barnacles were infrequent foods but as many as 50 small *Balanus eburneus* were eaten by a 124-mm. crab at Picolata. Many crustaceans were too decomposed or fragmented to classify—particularly microcrustacea in crabs less than 21 mm. Some of the larger fragments closely resembled isopods.

Fish was a major food, especially of larger crabs. Ingested fish could not be identified, but distinguishable parts indicated that small and large fish of many species were eaten. No fish was observed in crabs less than 11 mm. wide.

Algae and vascular plants were frequent in the stomachs of blue crabs. Algae with the exception of *Ulva* were not identified but most often occurred as many filaments. Crabs ate the leaves, stems, roots, and seeds of various species of higher plants (only *Ceratophyllum* and *Vallisneria* were identified). Occasionally 20 to 30 small uniform-sized pieces of *Vallisneria* leaves in a stomach appeared to have been eaten from the plant.

Among lesser food items, *Nereis pelagica* was regularly consumed by all sizes of crabs at the lower river stations. Other annelids were taken infrequently at Trout River and Picolata. Insects were eaten at all stations except Clapboard Creek. Each stomach always contained several individuals. Gastric mill contents included adults of Coleoptera, Diptera, Hemiptera, and Hymenoptera, and young of Diptera and Odonata. Bryozoa occurred only as occasional fragments.

Blue crabs often ate the same food items during each of the three seasons of sampling (table 11), and they usually consumed the most available foods. The largest numbers of mussels were eaten in spring and summer when young mussels (less than 5 mm.) were first abundant. We found clams of all sizes common in the lower river during all seasons. Because small clams were uncommon at Picolata the abundant mussel population probably was utilized to a greater degree. Oysters and snails (particularly *Nassarius obsoletus*) were common in the lower river but provided only limited amounts of food. Amphipods were most abundant at Picolata, where they were consumed most extensively. Young blue crabs and mud crabs were common in all months of sampling, but relatively few occurred in the food tracts in winter. Shrimplike forms were not eaten in proportion to the large number generally present at all stations. We collected many fish of all sizes the year around. The percentage eaten was smaller at Picolata than at the lower river stations, which served as nursery areas for a greater variety of abundant species. Consumption of fish was high during winter before recruitment of young mussels. Although aquatic plants grew most profusely at Picolata, they were not a preferred food.

TABLE 11.—*Food of the blue crab, by crab size and by season, in the St. Johns River as percentage frequency of occurrence and (in parentheses) as percentage of total volume per stomach*

[Number of stomachs with food in parentheses below designation of season]

Food item	Width in mm., season, and number of stomachs with food								
	5–50			51–100			101–200		
	Dec.–Feb. (61)	Mar.–May (160)	June–Aug. (85)	Dec.–Feb. (21)	Mar.–May (74)	June–Aug. (44)	Dec.–Feb. (25)	Mar.–May (143)	June–Aug. (55)
Bryozoans		[1] 1(0)			[1] 1(0)			[1] 2(0)	[1] 4(0)
Mussels		4(2)	7(2)	14(9)	44(35)	27(15)	20(14)	52(42)	42(29)
Clams	26(13)	34(20)	44(20)	24(15)	28(20)	50(26)	40(31)	28(13)	38(22)
Oysters						4(3)		6(2)	4(2)
Snails		2(2)	16(4)		[1] 3(0)	9(3)		[1] 1(0)	[1] 2(0)
Nereis pelagica	[1] 6(0)	17(4)	18(4)		9(1)	16(2)		[1] 3(0)	
Other annelids				[1] 5(0)	[1] 1(0)				
Amphipods	5(3)	11(5)	16(7)	28(14)	24(11)	32(13)	12(1)	[1] 6(0)	22(6)
Barnacles		[1] 1(0)	[1] 1(0)			[1] 2(0)			7(2)
Ostracods	2(1)	1(1)	[1] 2(0)					[1] 1(0)	[1] 2(0)
Shrimplike forms	6(5)	1(1)	[1] 2(0)	10(2)	[1] 3(0)	[1] 4(0)		[1] 1(0)	[1] 2(0)
Crabs	3(2)	7(4)	9(2)		22(8)	23(8)		11(2)	25(7)
Other crustaceans	18(14)	13(6)	18(12)	5(1)	[1] 3(0)	9(3)		[1] 1(0)	
Insects	[1] 2(0)	6(3)	6(2)		[1] 1(0)	[1] 2(0)		[1] 1(0)	[1] 2(0)
Fish	30(23)	20(11)	33(13)	57(44)	24(14)	32(16)	48(42)	41(27)	25(17)
Algae	23(10)	17(5)	[1] 1(0)	24(3)	1(1)		24(3)	[1] 1(0)	
Vascular plants	5(1)	8(1)	7(2)	[1] 5(0)	14(2)	14(1)	[1] 8(0)	9(3)	5(1)
Organic debris	38(28)	56(36)	60(31)	14(10)	15(6)	18(10)	12(9)	17(9)	24(12)

[1] Less than 0.6 percent.

The year-round abundance of preferred food items undoubtedly is a major cause for the large concentrations of juvenile blue crabs near Picolata. Random sampling with trawl and dredge below Picolata (between buoys 18 and 22) in summer indicated relatively less plant cover and less food, particularly amphipods and mussels. Juvenile crabs that fed on mollusks in the lower river conceivably are attracted to an accustomed food, such as mussels, at Picolata. Crabs also benefit from an interesting food chain transition at buoy 24. Young mussels occur most commonly within large clam valves. When the mussels are chewed off, chironomid larvae build algal tunnels on which amphipods feed and provide a second feeding for crabs.

In brief, blue crabs 5 to 200 mm. wide fed principally on mollusks, fish, and crustaceans and to a lesser degree on plants, annelids, insects, and bryozoans. Crabs generally ate the same type of food regardless of crab size, area, and season. They usually consumed the most available foods.

SUMMARY

Studies on the biology of the blue crab in the St. Johns River were made to obtain information necessary to determine factors which affect the harvestable population.

Females made up the majority of adult crabs during most of the year in the lower St. Johns River, but males were dominant in the upper river.

Blue crabs commonly mated from March to July and from October to December. The proportion of males and females that matured at a small size was larger in salt water than in fresh water. Size at maturity varied widely as evidenced by a 177-mm. wide immature female and a 99-mm. mature female; some of this variation can be attributed to individual differences in growth rate.

Spawning occurred in the first 30 km. of river above the mouth, and the eggs hatched in the ocean within 6 km. of shore. Spawning began in February 1962 and in March 1963 and continued to October in both years. An appreciable number of ovigerous females from the St. Johns River apparently entered the ocean by way of the Intracoastal Waterway and other rivers. Some females entered the river from the ocean before the spawning season. Many others returned to the St. Johns River or entered other rivers, often within 15 days after their eggs hatched, to spawn a second time in the same season.

Of crabs tagged 40 to 195 km. above the mouth and recovered at a distance from the tagging site, 89 percent of the males and 96 percent of the females were recaptured downstream from the point of release. In fall and early winter, females from the upper river congregated 30 to 55 km. above the mouth. During the same period aggregations of males appeared nearer the mouth and in the ocean directly off the mouth. Crabs of both sexes mi-

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grated from the St. Johns River to the Intracoastal Waterway, to four other rivers, and to the ocean.

Females tagged in the ocean off the mouth of the river were recaptured in the St. Johns River and other inland waters; in addition widespread recoveries were made in the ocean.

Time between tagging and recoveries indicated that relatively few blue crabs live longer than 1 year after becoming adults. Maximum age is about 4 years.

Zoeae—primarily first stage but some second—and megalops of crabs of the genus *Callinectes* were collected in the river as far as 40 km. from the mouth. Zoeae were present in April to October. Of 22 kinds of crab zoeae collected near the mouth, *Callinectes* ranked third in abundance in 1961 and second in 1962.

Early crab stages (2–9 mm. wide) entered lower river areas primarily in waves which started 5 or more months after spawning began and continued to the end of the year. Most individuals in these waves were beyond the initial crab stages except during early winter. The time of the first waves was later in 1963 than in 1962, probably because of the later spawning season in 1963. Influx of early crab stages was not confined to the lower river but extended 95 km. and more upstream.

Juvenile crabs of many sizes were widely distributed but were concentrated the year around in certain localities. Those less than 40 mm. wide were most common in shallower waters. Juvenile females outnumbered juvenile males in the lower river, but the percentage of males increased with distance upstream.

Crabs 5 to 200 mm. wide fed principally on mollusks (primarily clams and mussels), fish, and crustaceans (mostly amphipods and crabs). Lesser amounts of plants, annelids (almost all *Nereis pelagica*), insects, and bryozoans were eaten. Usually the same types of foods were taken by all sizes of crabs and at all areas sampled. Crabs often ate the same foods during different seasons and generally consumed the most available foods.

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PASSAGE OF ADULT CHINOOK SALMON THROUGH BROWNLEE RESERVOIR, 1960-62

BY PARKER S. TREFETHEN AND DOYLE F. SUTHERLAND, *Fishery Biologists*

BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY

SEATTLE, WASHINGTON 98102

ABSTRACT

Adult chinook salmon (*Oncorhynchus tshawytscha*) were tagged and released in Brownlee Reservoir and upstream in the Snake River to determine if adults could pass through the reservoir and reach spawning grounds. Experiments with Petersen disk tags were performed by the Idaho Fish and Game Department in 1960–61 and by the Department and the Bureau of Commercial Fisheries in 1962. In addition, the Bureau marked salmon with sonic tags in 1961–62 to trace orientation and movement. Information was also obtained on the use of tributary streams for spawning and success of spawning.

Fish marked with Petersen disk tags and released in the 92.5-km.-long reservoir reached their spawning area as successfully as those transported above the impoundment and released in the river. Fish released during periods of constantly high water temperature in 1961–62 suffered losses, which may have been caused by stress during tagging. Some salmon with sonic tags were initially disoriented when released in the reservoir; those released in the river above the impoundment quickly oriented to the flow and resumed migration upstream.

Subpopulations of spring- and fall-run chinook salmon continued to use ancestral spawning areas in streams tributary to the impoundment after it was formed in 1958. No differences were noted between percentages of totally spent fall-run fish on the spawning grounds in the years before and after Brownlee Reservoir was filled.

Knowledge of the effect of impoundments on upstream migration is needed to plan the passage of adult salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) at high dams. If mortality is high in the reservoir, or if delays or other factors associated with passage impair the ability of survivors to spawn, the fish may have to be transported around the impoundment. Transportation could prove difficult if spawners bound for several tributaries were intermingled below the dam. Subpopulations would then have to be separated before their release into respective tributaries—a difficult or impossible task. On the other hand, if anadromous fish can migrate up through the impoundment and spawn successfully, they can be passed directly to the forebay of the dam to continue their natural migration upstream.

Neither Brownlee Dam nor Oxbow Dam, which is 19.3 km. downriver from Brownlee, has a fishway leading up to its impoundment. Migrating adults enter a collection facility at Oxbow Dam where they are trapped and transferred to a tank truck; they are then transported 23.3 km., to a point 4.0 km. above Brownlee Dam, and released into Brownlee Reservoir to resume their migration. Release of fish in the reservoir was discontinued after these studies were completed; all fish were transported to hatcheries for artificial propa-

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gation. A small hatchery for fall chinook salmon (*O. tshawytscha*), 1 km. downstream from the trapping site, has been operated at Oxbow Dam from 1960 to the present by the Idaho Fish and Game Department.

Fishery agencies recognized that Brownlee Reservoir posed a number of problems. The impoundment is 92.5 km. long; it has almost no current except during periods of high river discharge and extreme drawdown; water temperatures are high and oxygen concentrations are low during summer and early fall when spawning migrations occur.

To learn if adults could pass successfully through Brownlee Reservoir and reach the spawning grounds, the Idaho Fish and Game Department tagged fall chinook salmon (with Petersen disk tags) in 1960–61. The Bureau of Commercial Fisheries, in cooperation with Idaho, continued the investigations in 1962. Petersen disk tags were used in all years; the Bureau also used sonic tags in 1961–62 to trace the orientation and movement of fish.

This report summarizes the results of the 1960–62 studies. It also contains information on (1) orientation and migratory behavior of sonic-tagged salmon, (2) observations of totally spent fish in the Snake River above Brownlee Reservoir, and (3) use of tributary spawning streams after completion of Brownlee Reservoir.

METHODS AND MATERIALS

The general plan was to capture adult chinook salmon in a trap at Oxbow Dam and transport them upstream for release either in Brownlee Reservoir or in the Snake River above the reservoir (fig. 1). Some of the fish released in the reservoir were either tagged or fin clipped; others were caught and released unmarked without additional handling. The relative numbers recovered on ancestral spawning grounds below Swan Falls provided data that enabled us to measure the ability of migrants to pass through Brownlee Reservoir. Sonic tags were applied to 59 fish in 1961–62 to obtain information on orientation and migratory behavior in and above the impoundment. A summary of data on tagging and release is shown in table 1.

CAPTURE AND HANDLING

Adult chinook salmon used in the experiments were taken at different stages of the spawning run in the different years. In 1960 and 1961 the fish were obtained after the peak of the run. Hauck (1961)[1], describing the work in 1960, mentioned ". . . that the selection of fish for tagging was not on a random basis; that some selection was made for better fish on the basis of appearance and physical vigor."

[1] Hauck, Forrest. 1961. Fall chinook salmon tagging studies, Snake River, 1960. Idaho Fish and Game Dept., 7 pp. [Processed.]

TABLE 1.—*Summary of data on tagging and release during tests on passage of fall-run chinook salmon through Brownlee Reservoir, 1960–62*

[Unmarked fish were released in the reservoir during normal transport to maintain run; all fish were taken from trap at Oxbow Dam (fig. 1)]

Year and kind of mark	Released in reservoir			Released in river		
	Date	Number	Anesthetized[1]	Date	Number	Anesthetized[1]
1960						
Petersen tag	Sept. 30–31	108	No	Sept. 23–30	267	No
Do	Oct. 4–7	253	No	----------	----	----
None	Aug. 4–Dec. 12	4,282	No	----------	----	----
1961						
Petersen tag	Sept. 18–Oct. 31	686	Yes	Sept. 18–Oct. 31	688	Yes
None	Aug. 9–Dec. 10	3,272	No	----------	----	----
Sonic tag	Sept. 20–Oct. 21	15	No	----------	----	----
1962						
Petersen tag	Aug. 27–Oct. 21	444	Yes	Aug. 27–Oct. 21	340	Yes
None	Aug. 20–Dec. 11	342	No	----------	----	----
Fin clip	Aug. 27–Oct. 21	365	Yes	----------	----	----
Sonic tag	----------	----	----	Sept. 24–Oct. 8	44	Yes

[1] Anesthetized for tagging, but not during transport to release site.

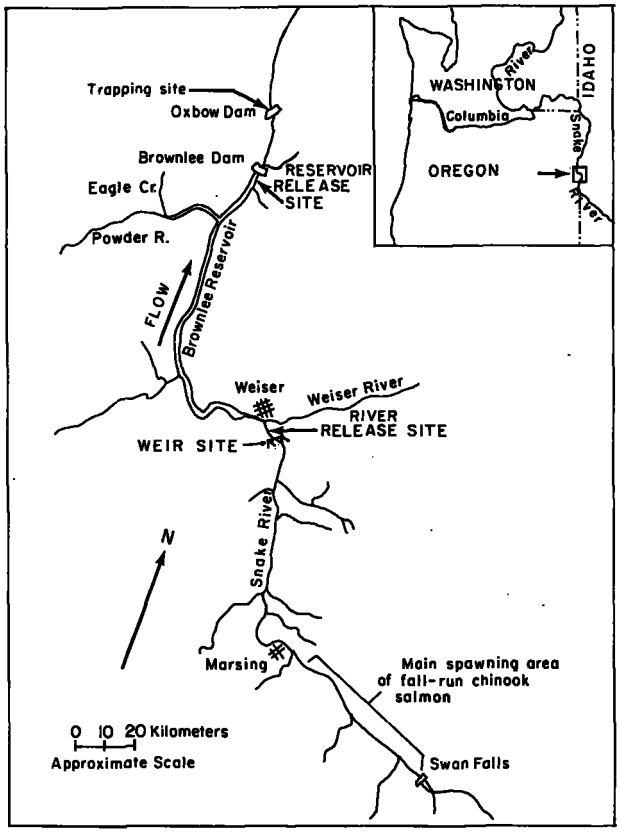

FIGURE 1.—Map showing trapping site below Oxbow Dam, release sites in and above Brownlee Reservoir, weir site, and main spawning area of fall-run chinook salmon in the Snake River, 1960-62.

In 1961, fish were collected in the trap until numbers were sufficient for tagging. The trapping time ranged from a few hours, soon after the peak of the run (when the tests started), to 1 day in the later stages of the run. In 1962, the trapping to obtain fish for tagging and release was scheduled by stage of migration. In the early and late stages (August 20 to September 23 and October 15–21) fish were collected for 24 hours before they were removed to the tagging area, and during the peak of migration (September 24 to October 14) fish were removed from the trap for tagging after about 30 had accumulated.

Fish were transported in a tank truck (3,785-liter capacity); water was recirculated and, except for a few hauls in 1960, oxygenated. Ice was used to control water temperatures during the 3½-hour drive to the release site at the river, but not during the 1-hour drive to the release site at the reservoir.

All salmon were anesthetized (with tricaine methane sulfonate) for tagging in 1961–62, but not in 1960; none were anesthetized during transportation.

Prophylactic treatments, supervised by the Fish Commission of Oregon, were used in 1962 to attempt to minimize the transmission of disease among fish during tagging and close confinement in the tank trucks. Prophylactics included tincture of iodine, roccal, ethanol, and malachite green. Tagging equipment was sterilized in a 70 percent solution of ethanol; the tagging area on the fish was treated with iodine. Wounds, abrasions, and infected areas were treated by topical application of a 15 percent solution of malachite green. In addition, all fish were treated for 1 hour with 1 p.p.m. (parts per million) of malachite green while being transported to the release sites. At the end of a day's operation, fish tanks on the hauling trucks were sterilized with roccal.

Skin discoloration and formation of blisters early in the experiment indicated that the iodine treatment might be affecting the fish adversely. As a precautionary measure, a 15 percent solution of malachite green was used in lieu of the iodine after the third week of tagging. On one occasion the fish tank was inadequately rinsed and the remaining roccal killed a load of fish. Thereafter malachite green at a concentration of 2 p.p.m. was used instead of roccal for sterilization.

TAGGING AND RELEASE

Petersen disk tags, sonic tags, and adipose fin-clips were used to mark adult chinook salmon before they were released. Personnel of the Idaho Fish and Game Department applied all disk tags (fig. 2), which were numbered or multicolored for identifying individual fish. The Bureau of Commercial Fisheries attached all sonic tags; only fish over 61 cm. were tagged. The Bureau also excised the adipose fins.

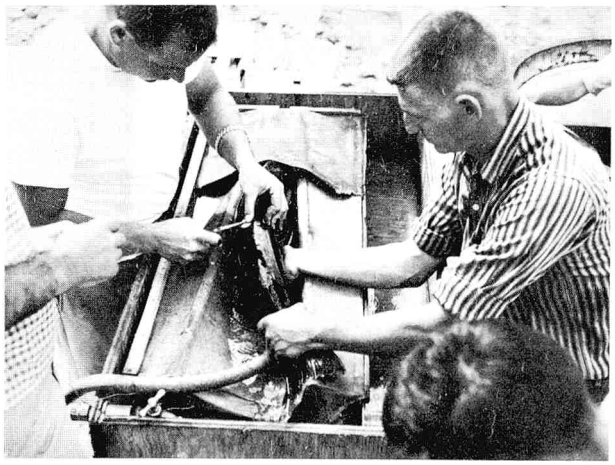

FIGURE 2.—Personnel of the Idaho Fish and Game Department attaching disk tag to chinook salmon. Fish is partially submerged in water supplied by hose in left foreground. Canvas cover over head of salmon helps quiet it during tagging.

Petersen Disk Tag

Tagging and release of disk-tagged fish differed in certain details during the 3 years of the study. In 1960, fish were tagged at the Oxbow trap and transported directly to release sites in the river or the reservoir. In 1961, untagged fish were transported to the release site and discharged into a holding pen; individual fish were then removed, anesthetized, tagged, and released at the site. In 1962, fish were taken from the Oxbow trap in groups of as many as 30, anesthetized en masse, tagged, put in a tank truck with fresh water to recover, hauled to the river or reservoir release site, and discharged into an open-ended holding pen. They swam over a submerged weir at the open end of the pen to resume migration. Individuals that did not leave the pen in 24 hours were eliminated from the experiment.

Releases of tagged and untagged fish in 1962 varied between migration periods. During the early and late stages of migration, fish were released daily for 6 successive days at a single site. For example, tagged fish were released in the Snake River on the first day of a week and in the reservoir on the next day. On the third day of the series, only untagged fish were released in the reservoir. This sequence was repeated over the next 3 days. No tagging was done on the seventh day, but fish captured in the trap at Oxbow Dam were transported and released in the reservoir by the Idaho Power Company as part of their usual fish-passage work. At the peak of migration (September 24 to October 14), tagged fish were released daily at both sites for 5 days a week. No more than 30 fish with Petersen tags were released at either site on any day. (In this same period, fin-clipped fish were released in the reservoir along with untagged fish that were excess to the tagging needs.) On the other 2 days of the week, only untagged fish were released in the reservoir.

Fin Clip

Fish marked by an adipose fin clip were released at the reservoir site only in 1962. These fish had been anesthetized and inspected during selection for spawn taking at the Oxbow hatchery but were not retained for that purpose. They were fin clipped to differentiate them from untagged fish that were released during the early stage of the 1962 experiment (September 10–16), but most were released during the peak stage of migration (September 24 to October 14).

Sonic Tag

Each sonic tag, used in 1961–62, was fastened by a metal clip or hog-ring which was crimped into the flesh behind the dorsal fin. The battery-powered tags emitted 132-kc. signals, detectable by receiving equipment within a range of about 1 km.; the operational life was about 5 days.

Salmon bearing sonic tags were released only in the reservoir in 1961 and only in the Snake River in 1962. In 1961, they were tagged at the reservoir release site and allowed to resume their migration from an open-ended holding pen. In 1962, the fish were tagged in groups of 6 to 14 at the Oxbow trap, coincident with the Petersen-disk tagging, and transported with the other tagged fish to an open-ended holding pen at the Snake River release site.

The sonic tags enabled us to obtain detailed

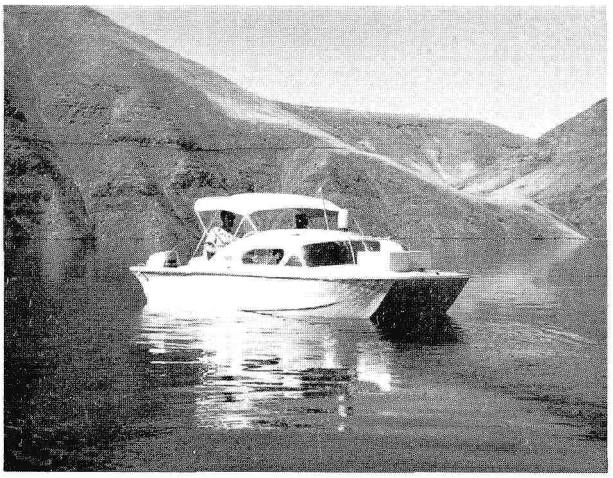

FIGURE 3.—Boat following chinook salmon with sonic tag in Brownlee Reservoir. Electronic tracking equipment provided precise data on day and night movements of tagged fish.

information on movements of individual fish in the reservoir by tracking them in a boat equipped with receiving equipment and plotting their positions on a chart at about 5-minute intervals (fig. 3). In the Snake River, the date and time of passage of fish with sonic tags past specific points was automatically recorded on time-event charts connected to fixed monitors [2] placed along the shoreline (fig. 4). Information on movement of individuals and groups of tagged fish between monitoring stations was obtained with portable hydrophones on a skiff propelled by an outboard motor.

RECOVERY

Marked and unmarked chinook salmon were recovered from the spawning area in periodic surveys from October to mid-January. The surveys were made monthly for the 1960 spawning run by the Idaho Fish and Game Department and weekly for the 1961 and 1962 runs, when the Bureau of Commercial Fisheries assisted the Department.

During the surveys, observers drifted downstream in a small boat or waded through shallow areas to search the entire known spawning area for carcasses. The dead salmon were examined for tags, fin clips, and spawning stages and then marked with spaghetti-type tags to identify them on future surveys. SCUBA diving was added in 1962 for investigation of deep pools where the spent fish might accumulate and remain unobserved. The greater recovery effort in 1962—plus experience gained in searching for fish in 1960–61—may have led to higher rates of recovery of untagged fish in 1962 (24.9 percent) than in 1960 (5.1 percent) or 1961 (14.3 percent). Water level and clarity appeared to be about the same for the 3 years.

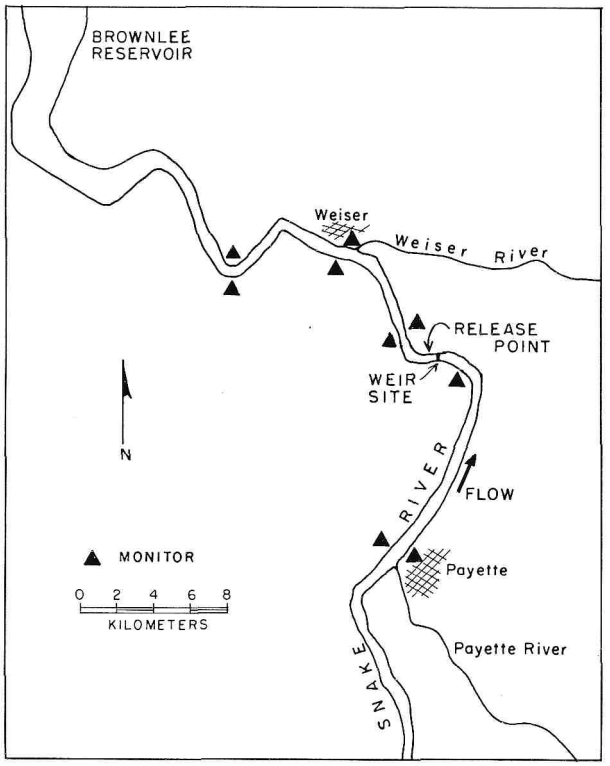

FIGURE 4.—Locations along Snake River between Brownlee Reservoir and the mouth of Payette River where fixed monitors recorded the passage of upstream-migrating chinook salmon carrying sonic tags.

PROPORTIONS OF FISH REACHING SPAWNING GROUNDS

In evaluating recoveries from both release sites, we considered the possible effect of differences in hauling time and post-release environment on the eventual passage of chinook salmon to the spawning grounds. Differences in haul-

[2] Johnson, James H. 1963. Development and use of sonic tracking as an aid to Pacific salmon conservation studies, 13 pp. [Processed.]

ing time, however, did not appear to be an important factor in survival. Although fish transported to the Snake River were confined in a tank truck about 2½ hours longer than those transported to the reservoir, they appeared to be in excellent condition at release. Other investigators have also indicated that prolonged transportation is not detrimental to adult chinook salmon. Parker and Hanson (1944) successfully transported adult salmon for 2 hours, and Fish and Hanavan (1948) reported hauls of about 4 hours without adverse effects. Groves (personal communication[3]) transported adult chinook salmon for about 5 hours to a test area in 1961 and followed this at a later date by a 5-hour return haul to a hatchery. He reported no mortalities directly attributable to the prolonged transportation.

Differences in postrelease environment also had no apparent effect on survival in the present experiments. Differences between recoveries of tagged fish released in the reservoir and of those released in the river were not significant in any year (table 2).

TABLE 2.—*Numbers of marked and unmarked fall-run chinook salmon released in Brownlee Reservoir and the Snake River and numbers recovered on the spawning grounds, 1960–62*

Year and release site	Mark[1]	Fish released	Fish recovered on spawning grounds	
		Number	*Number*	*Percent*
1960[2]				
Reservoir	Tag	361	23	6.4
	None	4,282	218	5.1
River	Tag	267	16	6.0
1961[2]				
Reservoir	Tag	686	70	10.2
	None	3,272	467	14.3
River	Tag	688	83	12.1
1962				
Reservoir	Tag	444	13	2.9
	Fin clip	365	31	8.5
	None	342	85	24.9
River	Tag	340	11	3.2

[1] Tag indicates Petersen disk; none of the 59 fish tagged with sonic tags were recovered.
[2] Hauck, Forrest. 1961. Fall chinook salmon tagging studies, Snake River, 1960. Idaho Fish and Game Department, 7 pp. [Processed.]
[3] Graban, James R. 1964. Evaluation of fish facilities, Brownlee and Oxbow Dams, Snake River. Idaho Fish and Game Dept. 60 pp. [Processed.]

The effect of tagging on survival of fish released in the reservoir apparently varied in different years. In 1960, the percentages of tagged and untagged fish recovered in the spawning areas were closely similar; in 1961, more untagged than tagged fish were recovered; and in 1962 the percentage recovery was higher for untagged fish than for either fin-clipped or tagged fish, and higher for fin-clipped than for tagged fish (table 2).

A high mortality of tagged fish was apparent in the early phase of the 1962 experiment. No recoveries were made of tagged fish released in the reservoir or in the Snake River during the first 4 weeks of tagging, August 27 to September 23 (table 3), and only one recovery was made from fish released in the first 5 days of the following week of tagging. This lack of tag recoveries coincided with a period of sustained high water temperature at both release sites. The average temperature of surface water was 22.1° C. (range, 21.1° to 23.9°) in Brownlee Reservoir and 18.4° C. (range, 16.6° to 20.6°) in the Snake River.

TABLE 3.—*Numbers of tagged fall-run chinook salmon recovered on the spawning grounds after release above Brownlee Dam in 1962, by week of release*

Week of release	Fish released in reservoir	Fish recovered on spawning grounds	Fish released in river	Fish recovered on spawning grounds
	Number	*Number*	*Number*	*Number*
Aug. 27–Sept. 2	11	0	7	0
Sept. 3–9	30	0	29	0
Sept. 10–16	33	0	31	0
Sept. 17–23	96	0	85	0
Sept. 24–30	74	2	46	3
Oct. 1–7	158	7	80	5
Oct. 8–14	34	3	41	2
Oct. 15–21	8	1	21	1

The high temperature, however, apparently was not the direct cause of mortality. The good recovery of untagged fish in 1962 (highest of the 3 years) suggests that a fair number of untagged fish from the early releases must have survived and reached the spawning grounds in spite of the high water temperatures. Possibly the additional stress on fish during handling, anesthetizing, and tagging produced the mortalities.

Mortality from tagging was also indicated in 1961 by the differences in percentage recov-

[3] Alan B. Groves. 1963. Fishery Biologist, Biological Laboratory, Bureau of Commercial Fisheries, Seattle, Wash.

ery of tagged and untagged fish released in the reservoir. Graban (1964)[4] observed that tagging mortality approached 30 percent. Although total recoveries of tagged and untagged fish in the 1960 experiments did not differ appreciably—possibly because of the selection of large, healthy fish for tagging—Hauck (see footnote 1) reported, "A decrease in survival (recovery) rates is indicated with increasing water temperatures at release site. . . ."

Recoveries of fish from the fin-clipped group in 1962 also give evidence of stress from handling: the percentage of returns was only about one-third that of returns from untagged salmon (table 2). The percentage of recoveries was higher from fin-clipped fish than from tagged fish (even though handling procedures were about the same for both lots), but most of the fin-clipped fish were released when water temperatures were declining and, hence, becoming more favorable for survival.

SPAWNING SUCCESS

Annual surveys by Richards [5] and Pirtle and Keating (1955) [6] provided percentages of totally spent fish on the spawning grounds from inspection of gonads and counts of eggs retained before and after the filling of Brownlee Reservoir in 1958 (fig. 5). These observations showed that passage through the reservoir did not affect the ability of fall-run chinook salmon to spawn successfully. The difference between percentages of totally spent fish in the preimpoundment and postimpoundment years was not significant.

Information on the use of specific areas for spawning by various salmonids was obtained from surveys before and after the impoundment was formed and from discussions with personnel of the Oregon State Game Commission, who annually surveyed spawning fish in the Powder River and its major tributary—

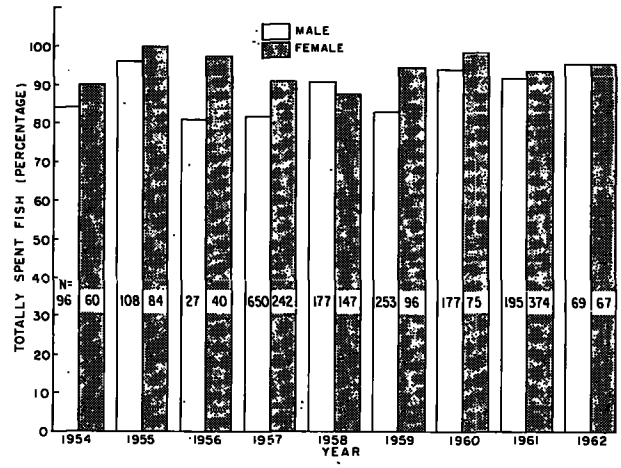

FIGURE 5.—Percentage of totally spent fall-run chinook salmon recovered on spawning ground surveys in the Swan Falls area, Snake River, 1954–62. Numerals in each bar indicate number of fish. Brownlee Reservoir was filled in 1958.

Eagle Creek; the Idaho Fish and Game Department carried out similar spawning surveys upstream from the impoundment in the Snake and Weiser Rivers. Records of State fishery agencies and of the Bureau of Commercial Fisheries on the capture of juveniles migrating from these various spawning areas also verified previous spawning.

The formation of Brownlee Reservoir apparently did not affect the ability of anadromous salmonids to use specific spawning areas. Fall-run chinook salmon passed through the impoundment after construction of Brownlee Dam and spawned in their accustomed area near Swan Falls. Because no tagged fall-run chinook salmon were observed in other spawning streams in 1960–62, straying evidently was slight or nil. Spring-run chinook salmon and steelhead trout, as evidenced by surveys on spawning grounds and by catches of their progeny in sampling traps, continued to use widely separated spawning areas after the reservoir was filled. Some spring-run populations entered the Powder River about 32 km. above Brownlee Reservoir and migrated into Eagle Creek to spawn (fig. 1), whereas others passed through the entire length of the impoundment and continued into spawning grounds in the Weiser River system.

[4] Graban, James R. 1964. Evaluation of fish facilities, Brownlee and Oxbow Dams, Snake River. Idaho Fish and Game Department, 60 pp. [Processed.]

[5] Richards, Monte. 1956–62. Snake River fall-chinook spawning ground surveys. Idaho Fish and Game Department. Various pagination. [Processed.]

[6] Pirtle, Ralph B., and James Keating. 1955. Annual report: The size and timing of runs of anadromous species of fish in the Columbia and Snake Rivers and their tributaries above the confluence of the Snake River, 1954. Idaho Fish Game Dept., Contract DA 35-026-eng-20608, for U.S. Army, Corps Engrs., 30 pp. [Processed.]

RATES OF MIGRATION OF FISH MARKED WITH PETERSEN TAGS

The rate of movement of chinook salmon in Brownlee Reservoir in 1960 was estimated by Hauck (see footnote 1) from tagged fish that sport fishermen recovered on the spawning grounds. Eight fish released in the reservoir and five released in the river were recovered; the elapsed time from release to recovery averaged 32.0 days (range, 17 to 42) for fish released in the reservoir and 25.8 days (range, 18 to 30) for those released in the river 16 km. above the reservoir. On the basis of the difference between the averages (6.2 days) and the distance between the reservoir and the river release sites (104.5 km.), he estimated the average rate of movement in the reservoir as 16.8 km. per day.

Rates of migration were not studied in 1961, but in 1962 the rate of movement through the reservoir was estimated from data on five tagged fish that were identified as they migrated through a gate in a weir in the Snake River (fig. 6). The weir was 20 km. above the reservoir and 1 km. above the river release site, which was 19 km. above the reservoir in 1962. (Midway through the experiment, it became evident that the weir was delaying upstream migration; the structure was removed at the end of September to allow free passage of adult migrants.) The total elapsed time between release of the five fish above Brownlee Dam and recapture at the weir (108.5 km. upstream) ranged from 3.2 to 9.9 days and averaged 6.7 days. Thus, the average rate of upstream movement from release to passage through the weir was 16.1 km. per day. The true rate of movement may have been somewhat faster than indicated because the calculation does not take into account any possible delays at the weir.

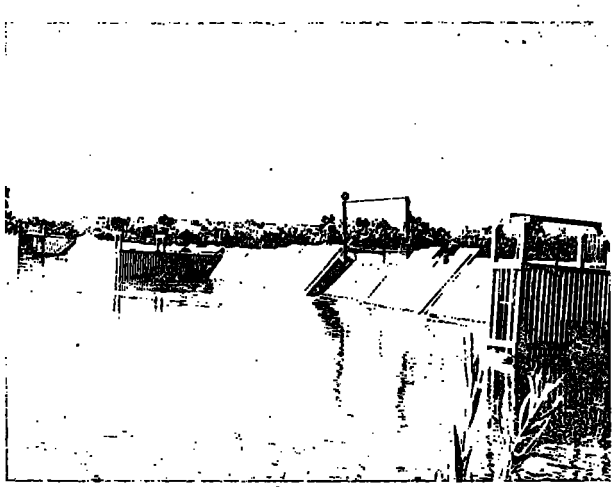

FIGURE 6.—Snake River weir (upstream view) with fish traps for identification and release of migrating salmon. Site is about 20 km. above Brownlee Reservoir.

Thirteen tagged salmon released in the Snake River in 1962 were observed passing through the weir, 1 km. upstream, in elapsed time that ranged from 2.2 hours to 6.6 days and averaged 2.8 days (or about 0.36 km. per day). The delaying effect of the weir undoubtedly accounted for the low rate of movement in this stretch of river. As is shown in the next section, more than half of the sonic-tagged fish reached the weir in less than 1 hour; hence, they moved up this short section of stream at about 19 km. per day.

ORIENTATION AND MOVEMENT OF SONIC-TAGGED FISH

Because the sonic tags we used transmitted identifiable signals for only about 5 days, our experiments were limited to a study of initial behavior after release. In such a study, it is essential that the attachment of the tag not affect the behavior of the fish. We were unable to detect any immediate effect of the tag from visual observations of tagged and untagged fish released in the same area. Although the long-term effect on behavior is unknown, previous work by the Bureau of Commercial Fisheries during the past 10 years suggests that the effect may be slight (Johnson, 1957).

BROWNLEE RESERVOIR

Most of the chinook salmon with sonic tags released in Brownlee Reservoir in 1961 were initially disoriented and spent considerable time in the lower end of the reservoir before resuming migration upstream. The movement

of an obviously disoriented fish is shown in figure 7. A track of one fish that resumed migration upstream soon after release is shown in figure 8.

The initial aimless wandering of most of the sonic-tagged fish may also have been characteristic of untagged fish released in the reservoir; if so, they eventually recovered because a high percentage of fish arrived on the spawning grounds from releases in the reservoir. In 1962, for example, nearly 25 percent of the untagged fish released in the reservoir were recovered in the spawning areas. In view of the size of the Snake River (flow more than 365 c.m.s.) and the extent of spawning grounds (over 25 river km.), we can be certain the percentage of fish that reached the spawning grounds was far greater than the percentage recovered.

SNAKE RIVER

More than half of the 44 fish with sonic tags that were released in the Snake River covered the 1.0 km. stretch to the weir in less than an hour. Other fish moved more slowly. A few fish remained in the release area up to 24 hours, and one stayed 4 days before moving upstream. Only one fish moved downstream; this salmon drifted 2.4 km. below the release site, lingered about 2 hours, and then resumed its migration upstream. Distributions that show the delaying effect of the weir are given in figure 9.

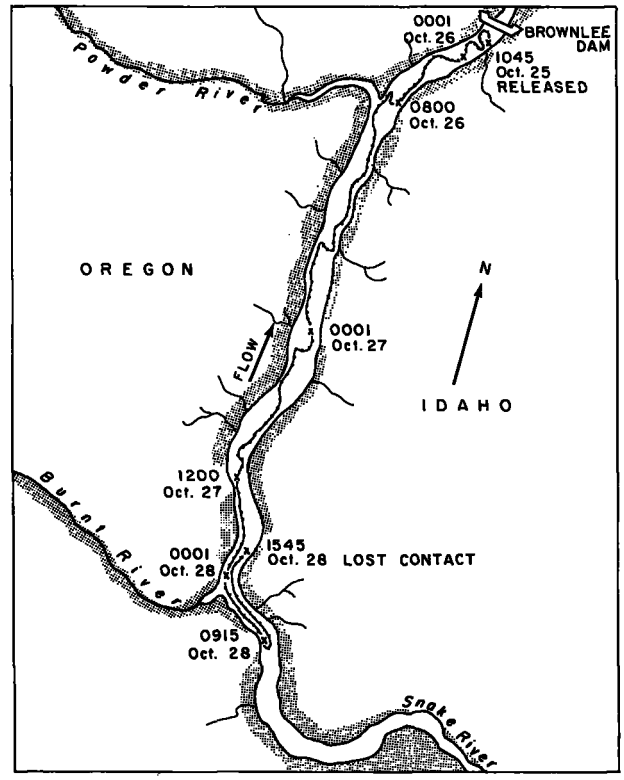

FIGURE 8.—Chronological record (diagrammatic) of a 77-hour track of well-oriented adult chinook salmon moving 81 km. upstream in Brownlee Reservoir. Fish carried a sonic tag.

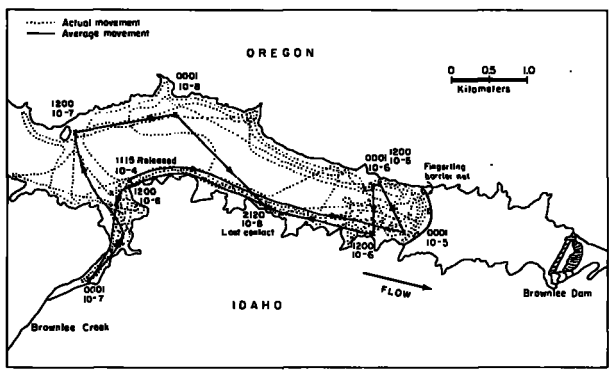

FIGURE 7.—Disoriented movement of an adult chinook salmon tagged with a sonic tag and released in Brownlee Reservoir. This fish, tracked for 106 hours, moved almost continuously day and night and traveled about 81 km. Travel was confined to area within 3.2 km. of the release point.

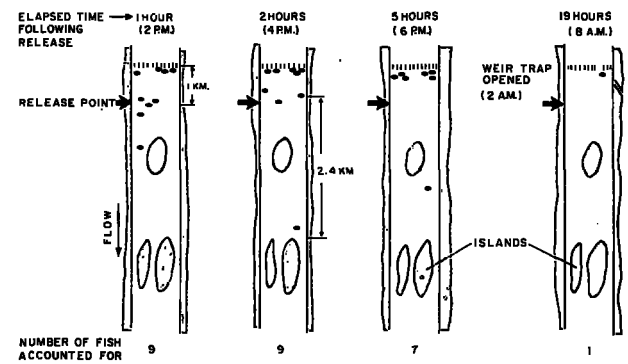

FIGURE 9.—Diagram of the changing distribution of a group of nine chinook salmon tagged with sonic tags and released in the Snake River above Brownlee Reservoir. Two fish presumably passed through the weir between 4 and 6 p.m. No fish were found farther than 2.4 km. downstream from the weir.

In a similar, earlier release from the same site, all but one of seven fish moved up to the weir during the afternoon. Some fish then dropped downstream about 1 km. after dark but returned to the weir in the morning, at which time only two were counted through the gates. In three releases (total of 25 fish) after the weir was removed, the fish moved past the vacated site without hesitation.

Sonic tags provided additional information on rates of movement in the river. Fish took from 26 to 120 hours to move upstream from the release point to the monitor at the Payette River mouth, which was 24 km. upstream. The maximum rate of movement for the distance was, therefore, slightly more than 0.8 km. per hour, or 19 km. per day. The slowest fish recorded by the monitor moved 13 km. upstream in 6 days; this was the same fish mentioned earlier, which had spent 4 days in the release area before resuming migration.

EXAMPLES OF PASSAGE THROUGH LARGE NATURAL LAKES

Because Brownlee Reservoir provides the only evidence of chinook salmon passage through a long, deep impoundment, we searched for other examples of their passage capabilities under comparable conditions. Passage of chinook salmon through large, shallow impoundments, such as those formed by low-head dams on the Columbia River, has long been established. These impoundments pass tremendous volumes of water and normally provide strong directional currents that are usually absent in large, deep reservoirs, such as Brownlee. What was needed were examples of passage through large bodies of water having low or no directional currents. Although large lakes with inlets and outlets may differ from reservoirs, the flow of water and limnological conditions can be similar to those in large, deep impoundments.

We discussed the passage of adult chinook salmon through large, natural bodies of water with biologists familiar with chinook salmon runs in Alaska, British Columbia, and the Yukon Territory. They estimated the sizes of sustained runs and provided data on the sizes of lakes through which the species migrates to reach spawning areas.

We concluded that the size of a body of water may not influence greatly the upstream migration of this species. In Bristol Bay, Alaska, chinook (king) salmon have been observed in the upper Wood River Lakes (Burgner, personal communication[7]). To reach this area, the fish migrate through three connecting lakes—about 30 km. through Aleknagik Lake, about 56 km. through Lake Nerka, and about 24 km. through Lake Beverly. An average of 5,000 adults entered in 1957–62 and spawned in tributaries to Naknek Lake (about 64 km. long) (Jaenicke, personal communication[8]). Some of these fish were observed at the Brooks Lake weir in a tributary stream about 48 km. above the outlet of Naknek Lake.

In British Columbia (Fraser River system), researchers[9] estimated that 500 to 1,000 adult chinook salmon pass through Harrison Lake (80 km.) into the Birkenhead River; about 5,000 migrate through Kamloops Lake (24 km.) and continue for 72 km. through Shuswap, Eagle, and Mara Lakes to spawn. Some chinook salmon pass 72 km. through Quesnel Lake into the Mitchell River. Before Coulee Dam was constructed on the Columbia River, large runs of chinook salmon were reported by local residents (Bryant and Parkhurst, 1950) to have migrated through the lower Arrow Lake (72 km.) and upper Arrow Lake (56 km.) to spawn below Windermere Lake, 128 km. farther upriver.

More than 3,600 chinook salmon are estimated by Elliott (personal communication[10]) to enter LaBerge Lake on the Yukon River, Yukon Territory. A small number enter a tributary about halfway through the 56-km. lake, but most continue through the lake to the Takhini and McKlintock Rivers. Another run

[7] Robert L. Burgner. 1963. Fisheries Research Institute, University of Washington, Seattle, Wash.

[8] Herbert W. Jaenicke. 1964. Fishery Biologist, Bureau of Commercial Fisheries, Auke Bay, Alaska.

[9] J. R. Brett, Fishery Research Board of Canada, Nanaimo, B. C.; and W. R. Hourston, D. McKinnon, and B. M. Chatwin, Department of Fisheries, Canada, Vancouver, B. C.

[10] W. K. Elliot. 1964. Fishery Officer, Department of Fisheries, Canada, Whitehorse, Yukon Territory.

of 2,000 fish migrate up the Teslin River, tributary to the Yukon River below LaBerge Lake, and continue 72 km. into Teslin Lake before entering the Nisutlin River; from here the fish continue for another 153 km. to a spawning area at the outlet of Nisutlin Lake.

IMPLICATIONS OF PRESENT RESEARCH

Our experiments indicated that adult fall-run chinook salmon can migrate through large impoundments. This ability apparently does not require previous reservoir experience in the juvenile stage; adult salmon returning upstream through Brownlee Reservoir in 1958–60 had passed downstream through this area as juveniles when it was still a river. The results point to the feasibility of passing adult chinook salmon directly through large storage reservoirs, thus eliminating the need for extended transport around impoundments.

The successful passage of fall chinook salmon through Brownlee Reservoir has special significance because the environment for the survival of upstream migrants is perhaps as poor as any found in the present freshwater range of this species. Surface temperatures over 21° C. are common in the reservoir until mid-September, and oxygen concentrations in the deeper, cooler water generally are 4 p.p.m. or less [11] during the fall migration. Despite the marginal environment for survival of salmonids in the reservoir, adult migrants apparently suffered no greater losses than the fish bypassed upstream to the river, where water temperatures and oxygen concentrations were much more favorable.

[11] Ebel, Wesley J., and Charles H. Koski. Physical and chemical limnology of Brownlee Reservoir. Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash. Manuscript in preparation.

CONCLUSIONS

The studies on chinook salmon in the Brownlee Reservoir area support the following conclusions:

1. Evidence of successful passage by chinook salmon through Brownlee Reservoir and of their sustained migration through large lakes in Alaska, British Columbia, and Yukon Territory suggests that the large size of an impoundment may not be detrimental to upstream migration of this species.

2. Despite initial disorientation, chinook salmon released in the reservoir were able to reach spawning areas as successfully as those transported and released in the river above the impoundment. In the river, fish resumed migration shortly after release.

3. The ability of fish to spawn successfully was not affected by passage through the reservoir.

4. Ancestral spawning grounds in the Snake River above the reservoir continued to be used after the impoundment was formed.

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DISTRIBUTION, APPARENT ABUNDANCE, AND SIZE COMPOSITION OF ALBACORE (*THUNNUS ALALUNGA*) TAKEN IN THE LONGLINE FISHERY BASED IN AMERICAN SAMOA, 1954–65

BY TAMIO OTSU, *Fishery Biologist*, AND RAY F. SUMIDA, *Biological Technician*
BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY
HONOLULU, HAWAII 96812

ABSTRACT

This fishery began in 1954 when tuna canning began in Pago Pago, American Samoa, with fish delivered by seven Japanese longline vessels. The size of the fishing fleet grew rapidly. In 1963, a second cannery began operating in Pago Pago. The 105-vessel fleet fishing during the last quarter of 1965 had 62 vessels from Japan, 30 from the Republic of Korea, and 13 from the Republic of China. The fishery was close to the Samoa Islands in the early years but expanded rapidly to the east and south; in 1965 it covered an area of about 23 million square kilometers (6.7 million square nautical miles) in the central and eastern South Pacific Ocean.

Albacore is fished selectively by the fleet because it commands the highest prices at the canneries. Data from the American Samoa-based fishery are complete, therefore, only for the albacore catches. Data on the other tuna species are not analyzed. The landings of albacore in American Samoa have increased from 338 metric tons in 1954 to 15,588 metric tons in 1965. In general, the annual landings have tended to be directly proportional to the total amount of fishing effort.

Various indices of apparent abundance of albacore (catch per trip, catch per day, and catch per 100 hooks fished) are examined. The catch per unit of effort in 1954–65 showed relatively little change in terms of numbers of fish, but a rather marked downward trend in terms of weight. This decline was due largely to a decrease in the average size of the albacore. Among the possible causes for the decrease in fish size are (1) fishing ground selection, (2) decrease of older, larger fish in the stock due to fishing and natural mortalities, (3) entry into the fishery of an abundant year class, and (4) change in sex ratio of the albacore taken.

Before World War II there was almost no longline fishing for tuna in the South Pacific Ocean. After the ratification of the Peace Treaty in April 1952, the South Pacific Ocean became accessible to the Japanese. They started fishing in the western South Pacific near the Solomon Islands, principally for yellowfin tuna (*Thunnus albacares*). The Japanese sent fishing expeditions to waters as far south as lat. 15° S. in late 1952 and extended fishing to lat. 25° S. in the western South Pacific Ocean in 1953 and 1954 (personal communications, Nankai Regional Fisheries Research Laboratory, Kochi, Japan).

In 1954, the tuna fishery based in American Samoa began with a small fleet of Japanese longline vessels. A base was also established by the Japanese at Espiritu Santo in the New Hebrides in 1958 and in the Fiji Islands in 1963. Many independently operated vessels, without the support of foreign land bases or of mother ships, are fishing in the South Pacific and landing their catches of tunas and billfishes directly in Japanese ports. Unquestionably, fishing effort in the South Pacific Ocean has increased substantially over the last decade.

The fishery was conducted exclusively by the Japanese in the early years, but, beginning about 1958, more and more vessels from the Republic of Korea and the Republic of China have been participating. The Japanese early discovered the value of albacore (*T. alalunga*) as a high-quality export product. Since 1956 most of the fishing effort of the American Samoa-based fleet has been concentrated on albacore rather than yellowfin tuna.

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This paper describes the American Samoa-based fishery, gives biological data (size and sex) on albacore, and presents results of some preliminary analyses of the catch rates (catch per unit of effort) of albacore as a measure of apparent abundance. The exact amount of fishing effort expended by the American Samoa-based vessels relative to the total longline fishing effort in the South Pacific Ocean is not known. Although no reliable estimates are available, it is apparent that the relative effort changes from year to year. Apparently, the American Samoa effort decreased progressively in relation to the total South Pacific fishing effort from 1954 at least through 1962. Because of this, we have incorporated data from Japan-based longline vessels fishing in the same general area, wherever possible, to supplement the data collected from American Samoa.

In late 1962 the BCF (Bureau of Commercial Fisheries) Biological Laboratory, Honolulu, began to record the size and sex of albacore landed in American Samoa. Because of the rapid growth of the longline fishery we decided to attempt to follow the effects of the fishery on the resource by also collecting catch and effort statistics. In April 1963 a field station, manned by personnel from the BCF Biological Laboratory in Honolulu, was established in Pago Pago, American Samoa, to conduct intensive sampling of the fishery.

Data are collected both on the biology of the albacore landed at the canneries and on fishing operations as recorded by the vessel operators. The length, weight, and sex of 50 albacore, randomly chosen, are being obtained from each trip landing. Detailed catch and effort data are provided voluntarily by fishing vessel operators. The cooperation of vessel operators has been gratifying; data are returned from about 85 percent of the fishing trips. These data provide information on the daily fishing effort (number of hooks fished per set) as well as the catch in numbers of the various species.

THE AMERICAN SAMOA-BASED FISHERY

The past two decades have seen the establishment of two tuna canneries in American Samoa. In 1949, a small tuna cannery was installed on the north shore of Pago Pago Bay on Tutuila Island, American Samoa, by Island Packers, Inc. Attempts to supply this cannery with tuna by live-bait fishing and purse seining in Samoan waters failed, and the plant never operated. The Government of American Samoa, owner of the land and the buildings, purchased the cannery equipment to prevent its being dismantled and sold abroad. In 1953, the Van Camp Sea Food Company obtained a lease with a renewal option (Van Campen, 1954). Today, the tuna cannery, much improved by the installation of new equipment and modernized facilities, is being operated by the Van Camp Sea Food Company-Samoa. In the latter part of 1963, Star-Kist Samoa, Inc. began operating a new cannery adjacent to the Van Camp plant.

The two canneries depend entirely upon foreign flag vessels and fishermen for their catch. Vessels from Japan, the Republic of Korea, and the Republic of China are placed under contract for specified periods, either directly with vessel owners or more generally through fishing companies, to deliver their catches to these American tuna canneries.

The fish are caught by longlines in the South Pacific in an extensive area covering 23 million square kilometers; the 1965 fleet of 154 vessels landed 15,588 metric tons of albacore and lesser quantities of other pelagic species. The following sections give details on the fishing method, fishing grounds, the fleet, and the fish landings.

FISHING METHOD

The American Samoa-based vessels fish with longlines (fig. 1). The basic unit of longline gear ("basket") consists of a length of mainline 200 to 400 m. long, from which are suspended branch lines (usually five or six) with baited hooks. The mainlines are buoyed to the surface by float lines. About 300 baskets of gear are joined in a series. The gear, thus, extends about 100 km. in a single fishing operation. In 1965, the vessels from American Samoa fished an average of 1,400 hooks in a single set. A fishing operation requires upward of 20 to 22 hours from the time the gear is set (about 0400 hours) until it is completely retrieved (about 0100 the following morning).

FISHING GROUNDS

The geographical expansion of the fishery is illustrated in figure 2. In the early years the fishery was confined largely to the vicinity of the Samoa Islands, but the vessels have gradually extended their operations to more distant waters. By 1956,

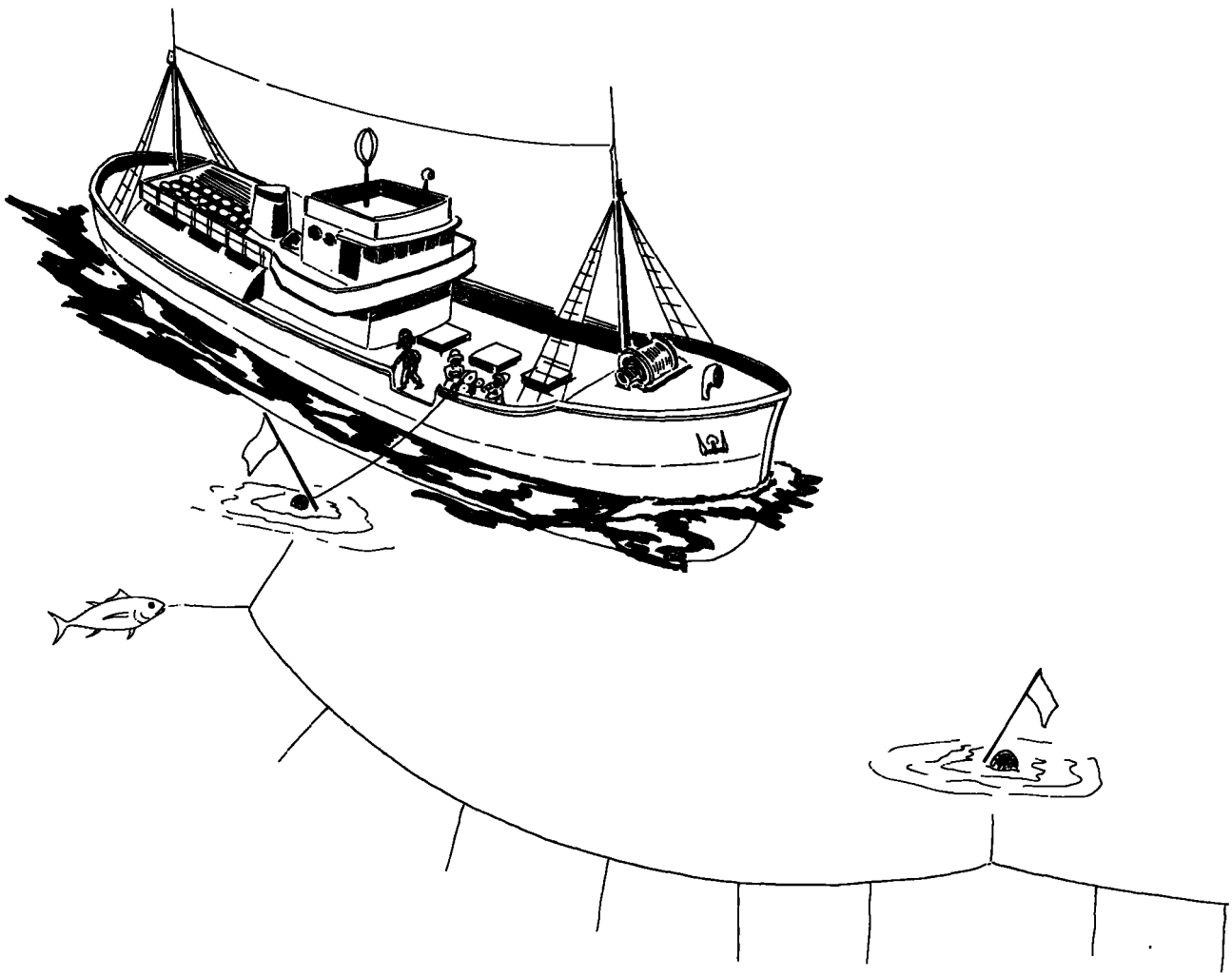


FIGURE 1.—Schematic representation of the longline fishing method used in the American Samoa-based fishery.

considerable fishing had already taken place as far south as lat. 28° S., in waters southeast of the Tonga Islands. The greatest expansion of grounds was in 1958, however, when vessels extended fishing eastward to the Marquesas Islands. In 1965, the vessels fished in an extensive area from the Equator to lat. 30° S. and from about long. 175° E. to about long. 120° W., an area of about 23 million square kilometers (6.7 million square nautical miles). Vessels have fished as far as 5,500 km. (3,000 nautical miles) from their base.

FISHING FLEET

Beginning in 1954 with 7 fishing boats contracted from Japan (a total of 16 different vessels participated in the fishery for varying periods during the year), the fleet in American Samoa has continued to increase over the years (fig. 3). Despite year-to-year fluctuations, the trend has been one of rapid increase; in 1965, 154 different vessels fished from American Samoa. The tremendous increase in fleet size in 1963 reflects the start of operations that year of the Star-Kist tuna cannery.

The composition of the fishing fleet, in terms of the country of origin of the vessels, has changed over the years. In the early years of the fishery, the entire fleet was Japanese. Vessels from the Republic of Korea began operating in the area in 1958 and vessels from the Republic of China in

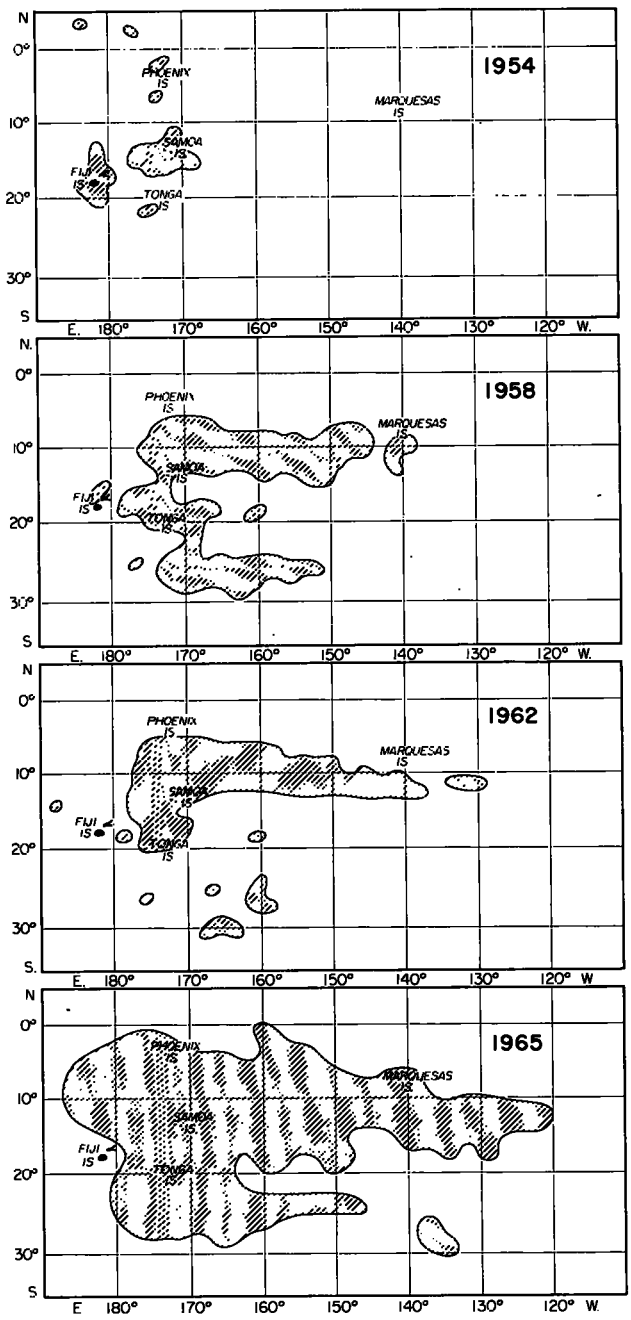


FIGURE 2.—Geographic expansion of fishing grounds of American Samoa-based vessels, 1954–65.

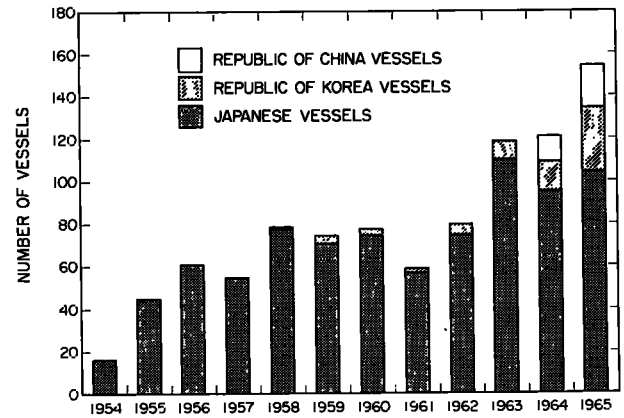


FIGURE 3.—Number of vessels in the American Samoa-based longline fishery, 1954–65.

1964 (fig. 3). The 105-vessel fleet operating during the last quarter in 1965 had 62 vessels from Japan, 30 from the Republic of Korea, and 13 from the Republic of China.

SPECIES COMPOSITION OF THE LANDINGS

Albacore commands the highest price at the cannery and is, consequently, fished for selectively by the fleet. This selection occurs both by the choosing of areas in which albacore are most plentiful instead of areas with the greatest combined species catch and (on occasion) by the discarding of other species caught to conserve storage room for more albacore. Thus, the albacore catch alone is delivered in its entirety to the cannery.

Yellowfin tuna constitutes the second most important species delivered to the canneries, but makes up only about 15 percent of the weight of fish landed. Other species taken by the fishery include the bigeye tuna (*T. obesus*), southern bluefin tuna (*T. maccoyii*), skipjack tuna (*Katsuwonus pelamis*), wahoo (*Acanthocybium solandri*), and various billfishes, sharks, and other pelagic species. Because catches that are not kept for delivery are often not recorded, no reliable data are available on the apparent abundance of species other than the albacore.

ANNUAL AND SEASONAL LANDINGS OF ALBACORE [1]

The albacore landings by the American Samoa-based fleet have gradually increased from 338 metric tons in 1954 to 15,588 metric tons in 1965 (fig. 4). The upward trend was broken in 1961 and 1964, when landings smaller than those of the pre-

[1] Catch statistics in this report are based on dates of capture and may not agree with figures previously reported from this fishery, which were based on dates of delivery.

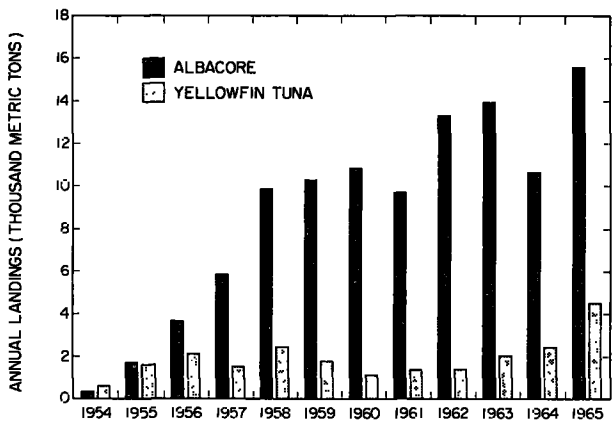


FIGURE 4.—Total annual albacore and yellowfin tuna landings in American Samoa, 1954–65.

ceding year were registered. Although yellowfin tuna was the dominant species landed in 1954 and in parts of 1955 and 1956, the albacore has dominated the catch since 1957.

Albacore are taken throughout the year (fig. 5). In most years for which we have data, slightly better landings have been made during the latter half of the year. In some years (e.g., 1961, 1963, 1964), however, no seasonal trend is evident.

APPARENT ABUNDANCE OF ALBACORE

Various indices of apparent abundance of albacore are examined in the following sections. These include catch per trip, catch per day, and catch per 100 hooks fished.

CATCH PER TRIP AS A MEASURE OF APPARENT ABUNDANCE

The apparent abundance of tunas taken by a longline fishery is generally measured by the catch per 100 hooks fished. We did not, however, begin to collect information on the number of days fished per trip until 1959 and did not begin to collect data on the number of hooks fished per day until 1963. We were compelled, therefore, to use the fishing trip itself as the unit of effort to indicate trends in apparent abundance of albacore for the entire period of existence of the American Samoa-based fishery.

Admittedly, the catch per trip is an inexact measure of apparent abundance because it is greatly influenced by changes in number of days fished

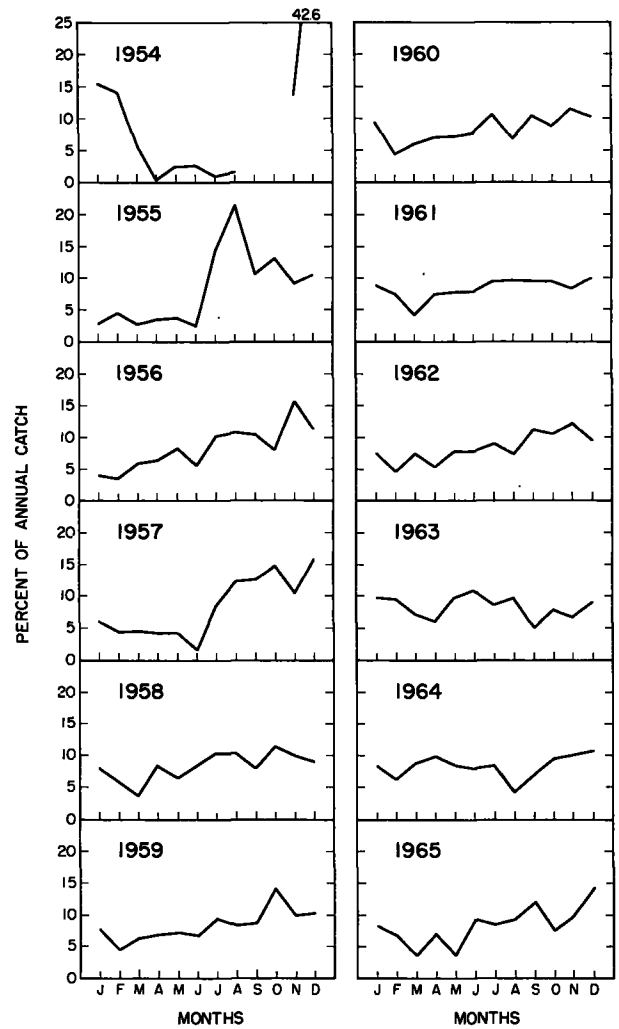


FIGURE 5.—The monthly catch of albacore, in percentages of annual total, by American Samoa-based vessels, 1954–65.

per trip and by size composition of vessels in the fleet. The average number of days fished per trip by the American Samoa-based vessels has, however, remained relatively steady from year to year, at least between 1959 and 1964 (fig. 6). As we show later, size composition of vessels also changed little during the entire 1954–65 period. Furthermore, the close relation between the monthly average catch per trip and the monthly average catch per day fished, assuming that catch per day is a more reliable index (fig. 7), indicates that the catch per trip is a satisfactory measure of apparent abundance.

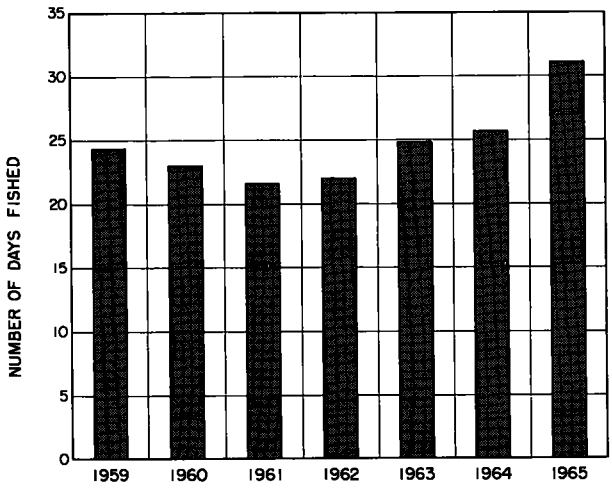


FIGURE 6.—Average number of days fished per trip by vessels based in American Samoa, 1959–65.

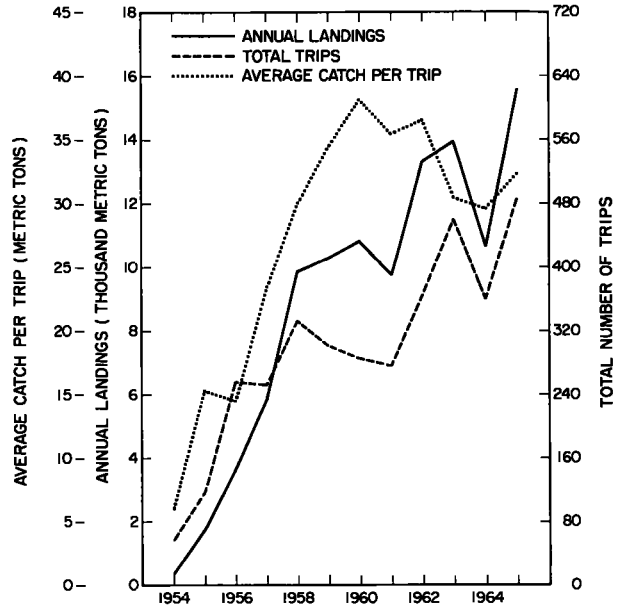


FIGURE 8.—Total annual number of fishing trips, average catch of albacore per trip, and annual albacore landings, by American Samoa-based vessels, 1954–65.

In figure 8 are shown the total number of fishing trips and the average catch of albacore per fishing trip, along with the annual landings of albacore, for 1954–65. Annual landings have fluctuated with fishing effort. Between 1958 and 1960, however, landings increased despite a decrease in fishing effort. This increase was due to increased average catch of albacore per trip during the period. The rather sharp decline in landings in 1964 resulted from the combined effects of a decrease in average catch per fishing trip and a drop in fishing effort.

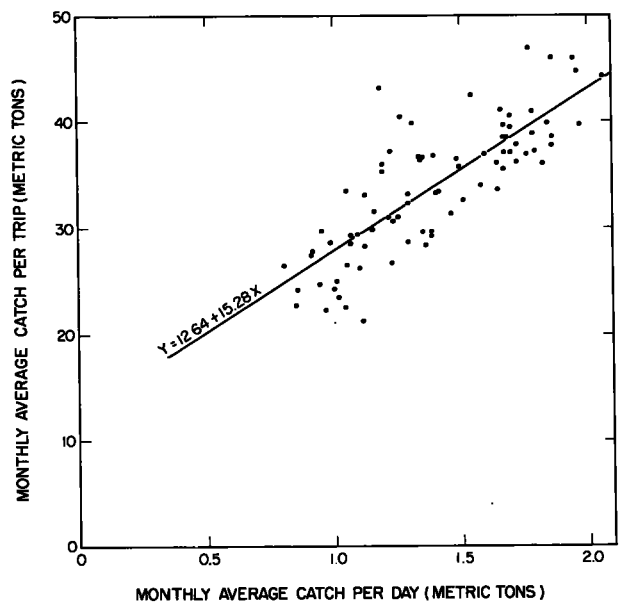


FIGURE 7.—Relation between monthly average catch of albacore per trip and monthly average catch per day by American Samoa-based vessels, 1959–65.

From 1954 through 1960 the catch per trip increased, then tapered off and stabilized at a lower level in 1963–64, and finally increased slightly in 1965. The upward trend in 1965 was attributable primarily to the increased length of the average trip (fig. 6). The catch per trip, in metric tons, averaged 35.7 in 1961–62, 30 in 1963–64, and 31.6 in 1965.

The total annual landings declined in 1964 although the size of the fleet had increased since 1963. The number of fishing trips, however, declined sharply, from 451 to 359, and the average number of days fished per trip increased only slightly, from 24.9 to 25.7 days.

The Japan Fisheries Agency (1966), in its publication of the 1963 Japanese tuna longline data, pointed to a rather marked decline in albacore catch rates throughout the South Pacific Ocean during 1963, with the possible exception of the "newer" grounds east of long. 130° W. (table 1). It noted that although fishing effort had increased 16 percent, from 58.2 million hooks fished in 1962

to 67.7 million in 1963, the catch of albacore had decreased 14 percent, from 2.1 million fish to 1.8 million. For example, in the western South Pacific between long. 150° E. and 180°, the catch rates decreased from 3.1 albacore per 100 hooks in 1962 to 1.9 in 1963, and in the central South Pacific (between 180° and 130° W., corresponding to the fishing grounds of the American Samoa-based vessels) the decrease was from 4.6 to 3.1 albacore per 100 hooks. Unlike the relatively low catch rate of 3.1 reported by the Japanese for 1963, our data from American Samoa-based vessels show an average of 4.9 albacore per 100 hooks for the year (fig. 9). This difference may possibly be attributable to a greater degree of selectivity for albacore on the part of the American Samoa-based vessels. The decrease in 1963, pointed out by the Japanese, is, however, paralleled by a similar decrease in our data on catch per trip beginning early in 1963.

TABLE 1.—*Japanese data on catch and effort for albacore in the South Pacific Ocean, 1962 and 1963*

[This table is based on table 10, Japan Fisheries Agency, 1966]

Fishing area	Number of hooks		Number of albacore		Catch per 100 hooks	
	1962	1963	1962	1963	1962	1963
	Millions	*Millions*	*Thousands*	*Thousands*	*Number of fish*	*Number of fish*
Long. 150° E.–180° Lat. 10°–30° S.	27.7	17.9	846.2	333.1	3.1	1.9
Long. 180°–130° W. Lat. 5°–30° S.	25.6	32.0	1,167.3	997.3	4.6	3.1
Long. east of 130° W. Lat. 10°–30° S.	4.9	17.8	122.3	437.7	2.5	2.5
Totals	58.2	67.7	2,135.8	1,768.1	3.7	2.6

Catch per 100 hooks is an index of apparent abundance in terms of numbers of fish, whereas catch per trip is measured in terms of weight of albacore taken. The decrease in the latter index in 1963, 1964, and part of 1965 was caused in large part by a decrease in the average size of albacore.

Though fluctuating greatly, the catch in numbers per 100 hooks from 1963 to 1965 did not show a marked downward trend. On the other hand, the same data, converted into catch in weight per 100 hooks (by using the monthly mean weight of albacore sampled from the fishery), showed a decreasing trend through 1965 (fig. 9). Several possible causes for the observed decrease in the size of the fish are discussed later.

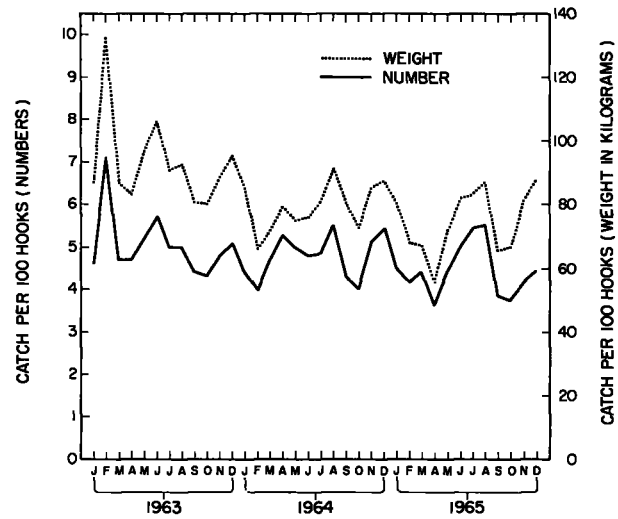


FIGURE 9.—Catch of albacore per 100 hooks, in numbers and in weight, by the American Samoa-based vessels, 1963–65.

RELATION BETWEEN CATCH AND EFFORT

The relation between annual total landings of albacore and total fishing effort (number of fishing trips) shown in figure 10, though seemingly linear, needs to be interpreted with caution, be-

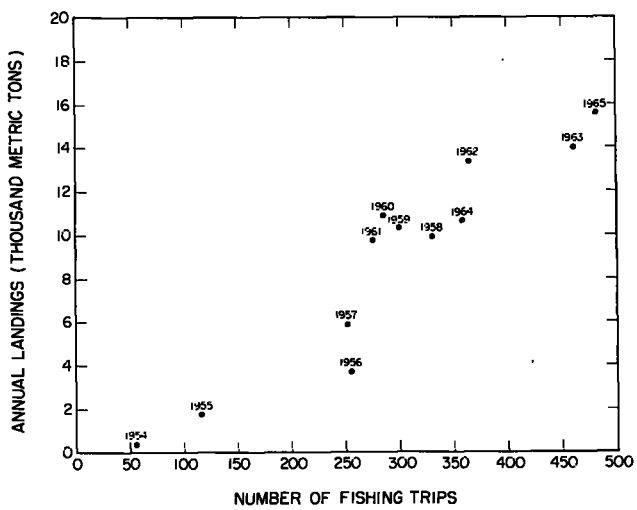


FIGURE 10.—Relation between annual total landings of albacore and total fishing trips of American Samoa-based vessels, 1954–65.

cause the data for the earlier years—particularly 1954 and 1955—are not strictly comparable with those of later years. As we already stated, fishing in the early stages of the fishery was aimed primarily at taking yellowfin tuna rather than albacore; thus, the catch of albacore per fishing trip was relatively small as compared with later years.

It is clear, however, that the annual landings of albacore have tended to increase with increasing fishing effort. Generally, it would be expected that the total catch would increase as fishing effort increases, until a point of maximum yield (not necessarily the point of optimum yield) is reached. After this point is reached, the catch would generally decrease despite further increase in effort. From the data presented in figure 10, it does not seem that the point of maximum yield of albacore has yet been reached in the American Samoa-based fishery. The extent of the growth potential, however, is a subject of another study—one which will require the analysis of all available South Pacific data, not merely those collected from the American Samoa-based vessels.

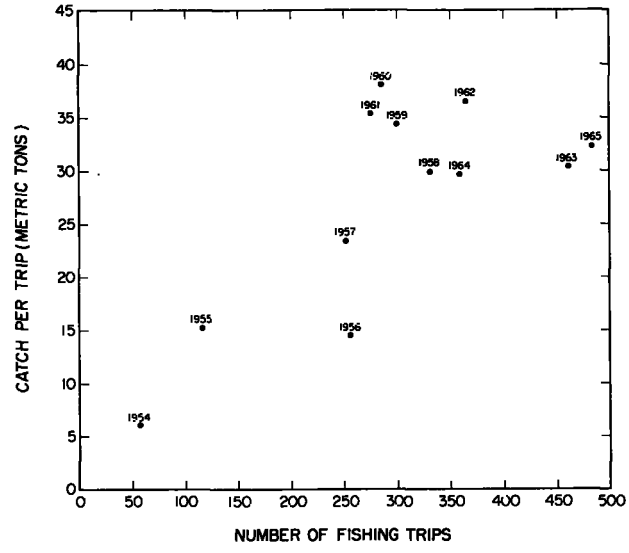


FIGURE 11.—Relation between average catch of albacore per trip and total fishing trips, of American Samoa-based vessels, 1954–65.

RELATION BETWEEN CATCH PER UNIT OF EFFORT AND EFFORT

The annual average catch per trip shows an apparent increase with increase in fishing effort (fig. 11). The catch per trip in 1963, 1964, and 1965, however, failed to increase at the rate seen before 1962. The data are far too few, however, to be conclusive.

VALIDITY OF CATCH PER 100 HOOKS AS MEASURE OF APPARENT ABUNDANCE

Under the assumption that the catch per 100 hooks is the better measure of apparent abundance of a species taken by the longline method, such data have been collected continuously since 1963. Estimates of abundance of fish based on catch per day or catch per trip might be influenced by the size of the fishing vessel. Although there seems to be no reason for believing that catch per 100 hooks would also be affected by vessel size, this question was examined inasmuch as it is conceivable that the larger vessels may be more attractive to fishermen than smaller vessels and, thus, may have a better choice of fishermen and fishing masters who would have the skill to catch more fish. If so, some efficiency factors would need to be incorporated in the use of catch per 100 hooks to adjust for differences among vessels.

A tabulation of albacore catch per 100 hooks by vessel sizes (gross tonnage) revealed a tendency for larger vessels to obtain higher catch rates than smaller vessels (table 2). In 1963, the smallest vessels (under 80 gross tons) averaged 4.6 albacore per 100 hooks, but catches trended upward to 5.8 albacore per 100 hooks for the vessels of 121 to 140 tons. The average catch rate was lower (5.1) for the largest vessels (those over 141 gross tons). In 1964, the trend, if any existed, was less obvious. To examine this apparent relation between vessel size and catch rate, the catch rate for each trip was plotted against vessel size for each of the 24 months. The scatter of points about the regression lines, fitted by the least squares method, was considerable; only the data for June and November 1963 and September 1964 showed statistically significant regressions ($P<0.01$). The data for these 3 months, however, were very heavily influenced by the results of a disproportionately small number of both the smallest and largest vessels in the fleet.

TABLE 2.—*Catch rates and fishing effort of American Samoa-based vessels*[1] *by vessel size groups, 1963 and 1964*

Item	Vessel size (tons)				
	<80	81–100	101–120	121–140	>141
Catch of albacore per 100 hooks:					
1963	4.6	4.9	5.1	5.8	5.1
1964	4.9	4.7	4.8	5.4	4.4
Number of fishing trips:					
1963	68	266	44	24	21
1964	23	171	59	27	36
Percentage of fishing trips:					
1963	16.1	62.9	10.4	5.7	5.0
1964	7.3	54.1	18.7	8.5	11.4

[1] Vessel-size data were not available for all vessels.

The higher average catch rates achieved by the larger vessels (121–140 gross tons) in 1963 and 1964, were probably due to the skill of the fishing master in selecting productive fishing grounds, or to subtle differences in fishing techniques rather than to vessel size alone. For example, the high average catch rate of 5.8 albacore per 100 hooks in 1963 was achieved by only six vessels, which rather consistently made good catches. One large vessel fished 2 months in 1963 with poorer than average results, but this vessel apparently left the American Samoa fishery soon thereafter.

Furthermore, the excellent performance of some of the smaller vessels also argues strongly against dependence of catch rates upon vessel size. A 60-ton vessel, for example, attained higher than average catch rates in 6 of the 9 months during 1963; its annual mean catch rate was 5.3 albacore per 100 hooks as compared with the average of 4.6 achieved by all vessels smaller than 80 gross tons.

It is, therefore, reasonable to conclude that catch rates (catch per 100 hooks) are not influenced by vessel size, and that they are valid indices of the apparent abundance of albacore.

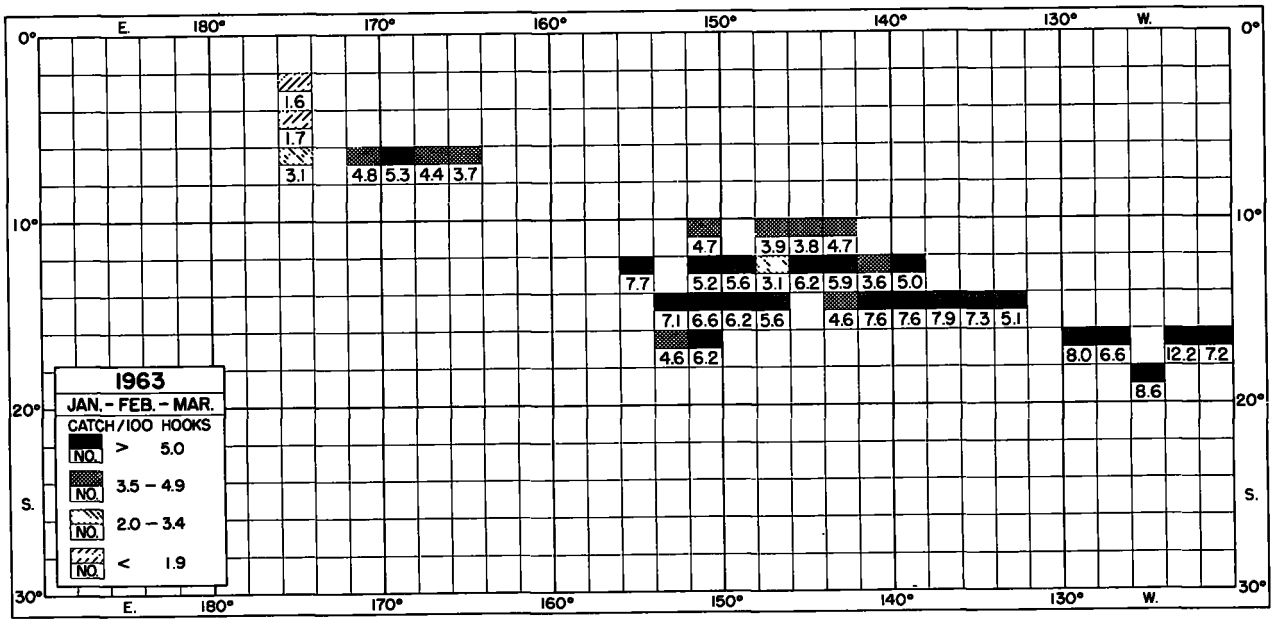
Although catch per day's fishing and catch per trip tend to increase with size of vessel, the fact that relatively few vessels in the fleet were larger than 120 tons or smaller than 80 tons enabled us to use average catch per trip as a gross index of apparent abundance for years in which data on catch per 100 hooks are not available. Fortunately, a very large proportion of the vessels in the American Samoa fleet has been those of about 100 tons during the period of this study.

SEASONAL AND GEOGRAPHIC VARIATIONS IN CATCH PER 100 HOOKS

The Nankai Regional Fisheries Research Laboratory (1959) has published charts of the average monthly albacore catch rate in each 1-degree square area fished in the Pacific and Indian Oceans by using all data available through March 1956. These charts are widely used today as representative of catch rates under average conditions. Koto (1966) published the average year's catch rates of albacore in the South Pacific Ocean by summarizing data obtained from the Japanese tuna longline fishery between January 1950 and December 1961. Many of the data from the American Samoa-based fishery are missing from both the above publications. For this reason and to make possible examination of the data for any time trends in catch per unit of effort, more recent data collected from the American Samoa-based vessels are presented in figures 12–14. The catch rates (catch of albacore per 100 hooks) have been averaged by quarterly periods for 1963, 1964, and 1965 and plotted by 2-degree square areas.

These charts depict the shifting of the fishing grounds during the year. The vessels from Samoa tend to fish north of lat. 20° S. during the first and second quarters, although a few vessels venture farther south to about lat. 28° S. Vessels tend to scatter widely beginning about June or July, and many boats fish between lat. 25° and 30° S. The southern grounds are heavily fished during the latter part of the year. In general, the fishing grounds are in the north during the first half of the year, and both north and south during the second half. This situation probably holds true in most years and may reflect the movements of albacore in the South Pacific Ocean. Interviews with fishermen indicate that catch rates in northern waters are more favorable during the early months of the year. Suzuki (1961), in recording his observations on the Samoa fishing operations in 1956, attributed the seasonal shifts in fishing grounds to movements of fish. He observed that most of the vessels fished in the vicinity of lat. 27° S. in August and September and then followed the northward movement of the fish.

Seasonal and geographical differences in catch rates are not readily evident from these charts. High catch rates (more than five albacore per 100



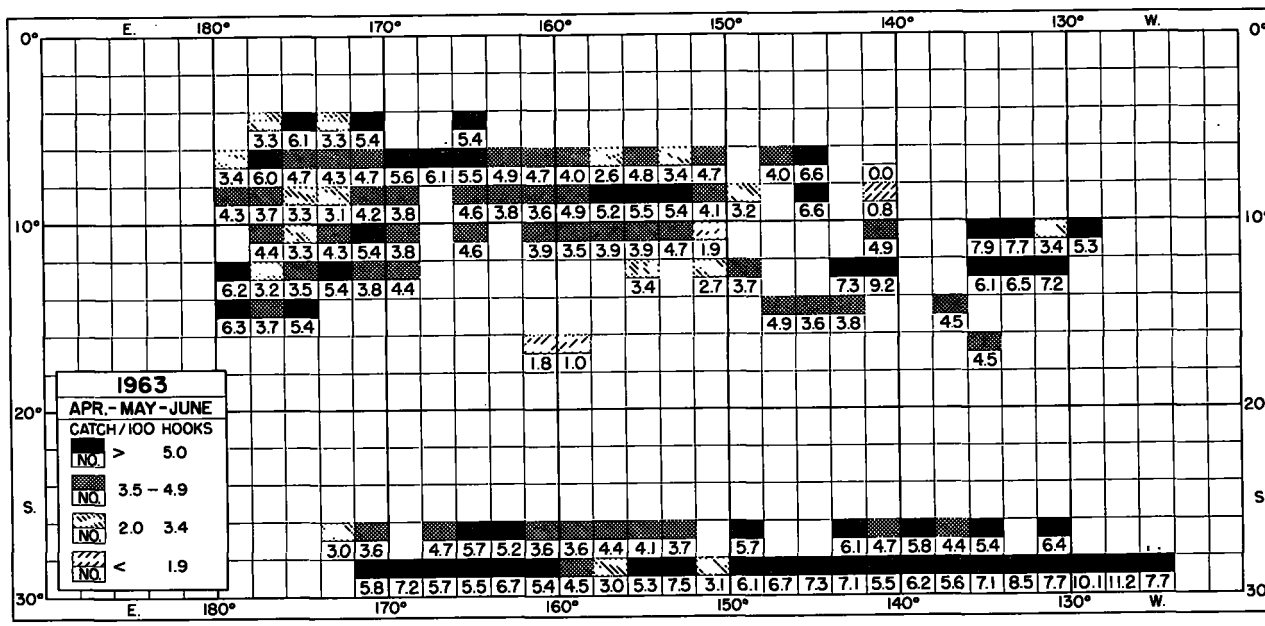
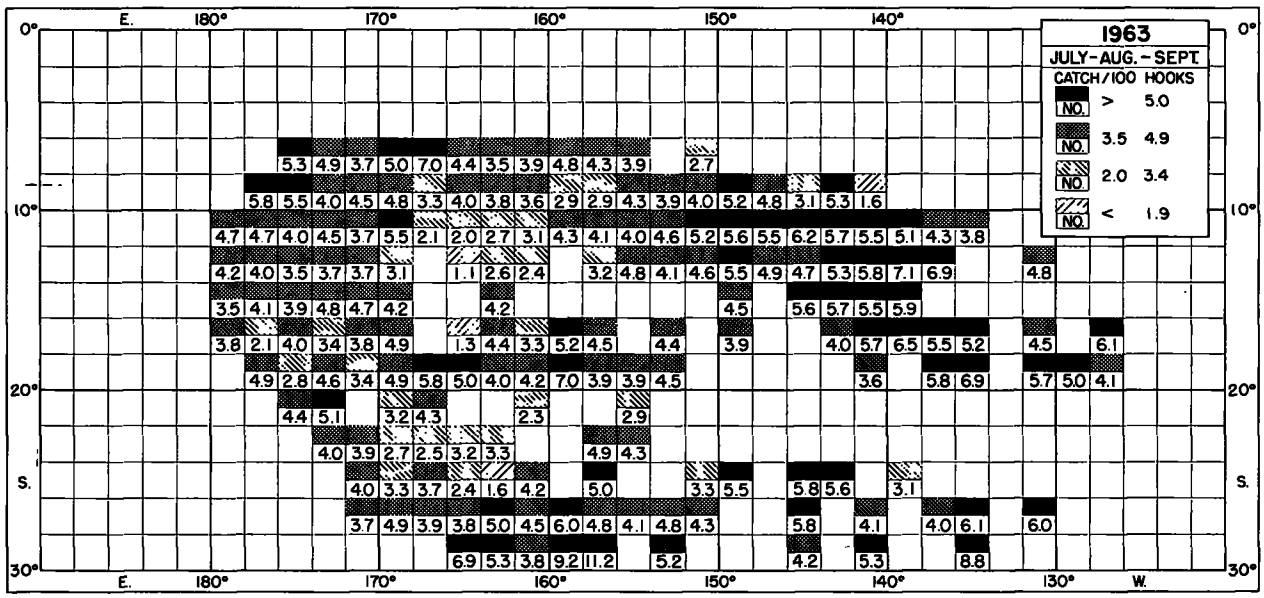
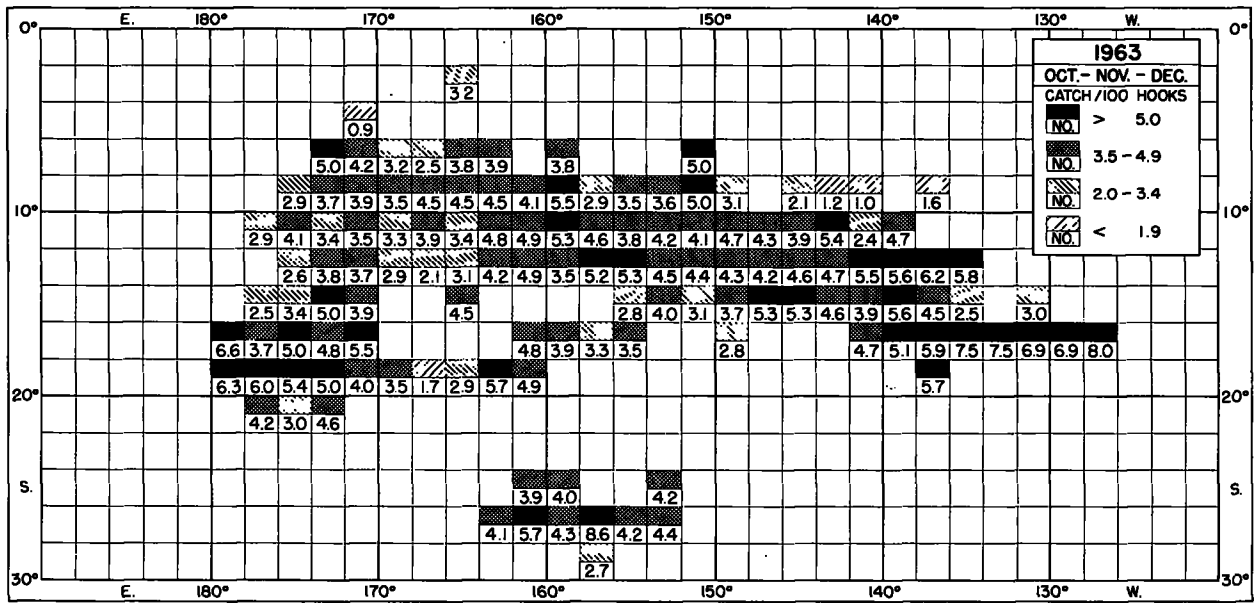


FIGURE 12.—The average catch rate (catch of albacore per 100 hooks) of American Samoa-based vessels shown by quarters of the year, 1963.


1963
JULY-AUG.-SEPT.
CATCH/100 HOOKS
NO. > 5.0
NO. 3.5 4.9
NO. 2.0 3.4
NO. < 1.9
0°
10°
20°
S.
30°
E.
180°
170°
160°
150°
140°
130°
W.


1963
OCT.-NOV.-DEC.
CATCH/100 HOOKS
NO. > 5.0
NO. 3.5-4.9
NO. 2.0-3.4
NO. < 1.9
0°
10°
20°
S.
30°
E.
180°
170°
160°
150°
140°
130°
W.

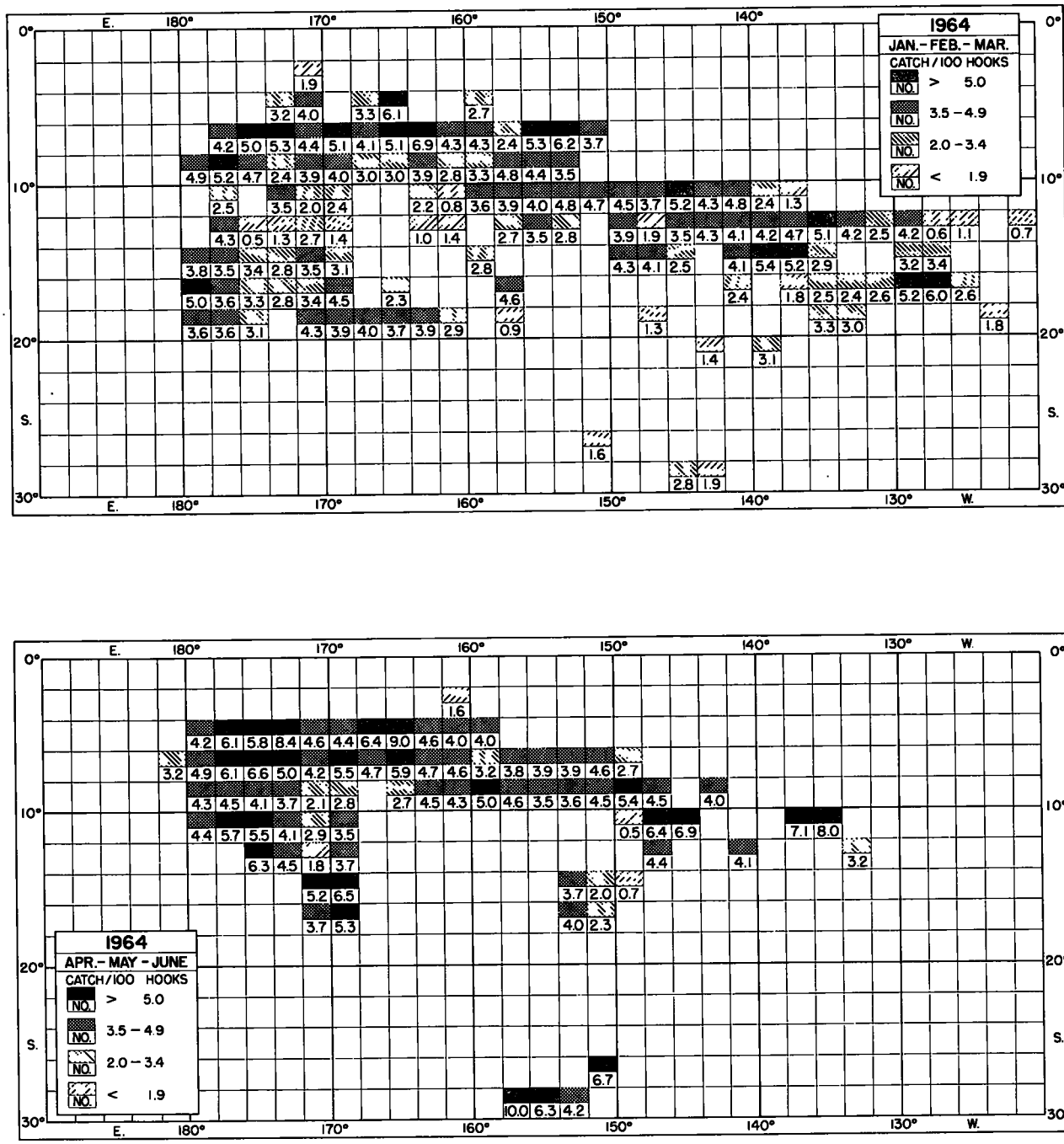
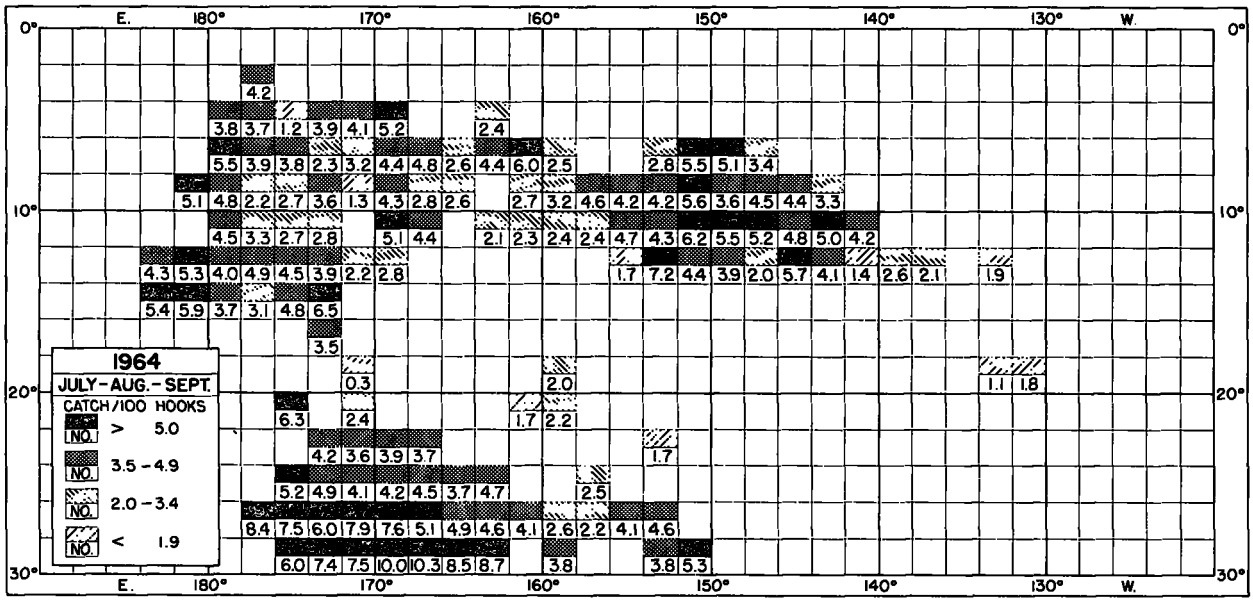
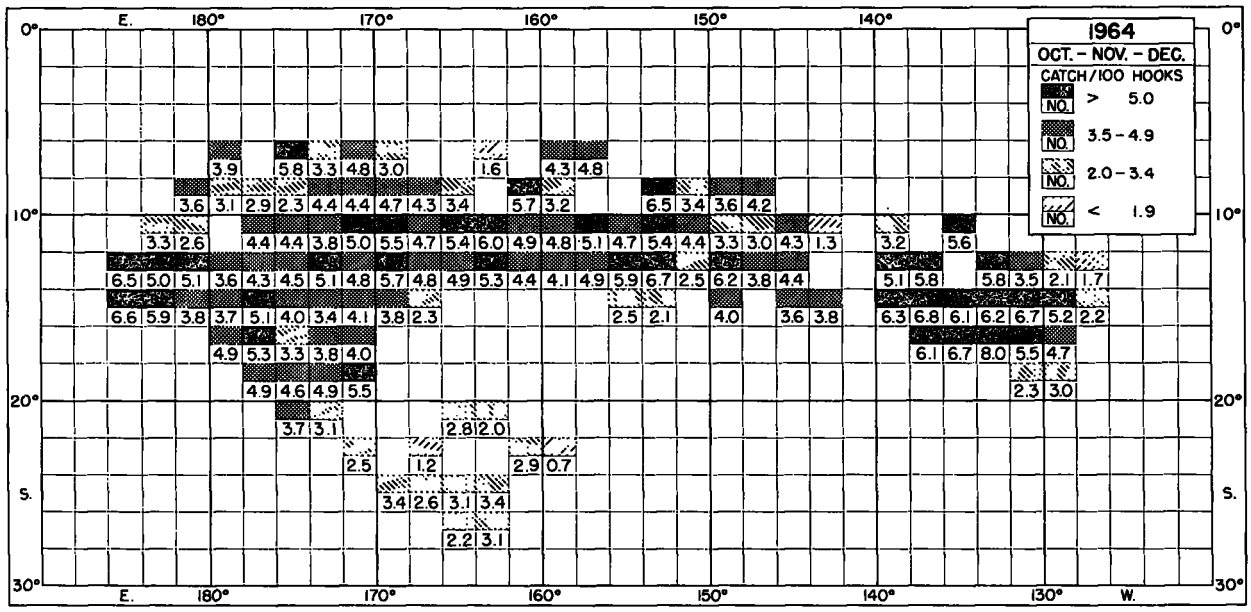


FIGURE 13.—The average catch rate (catch of albacore per 100 hooks) of American Samoa-based vessels shown by quarters of the year, 1964.


1964
JULY-AUG.-SEPT.
CATCH/100 HOOKS
NO. > 5.0
NO. 3.5-4.9
NO. 2.0-3.4
NO. < 1.9
0°
10°
20°
30°
E.
180°
170°
160°
150°
140°
130°
W.


1964
OCT.-NOV.-DEC.
CATCH/100 HOOKS
NO. > 5.0
NO. 3.5-4.9
NO. 2.0-3.4
NO. < 1.9
0°
10°
20°
S.
30°
E.
180°
170°
160°
150°
140°
130°
W.

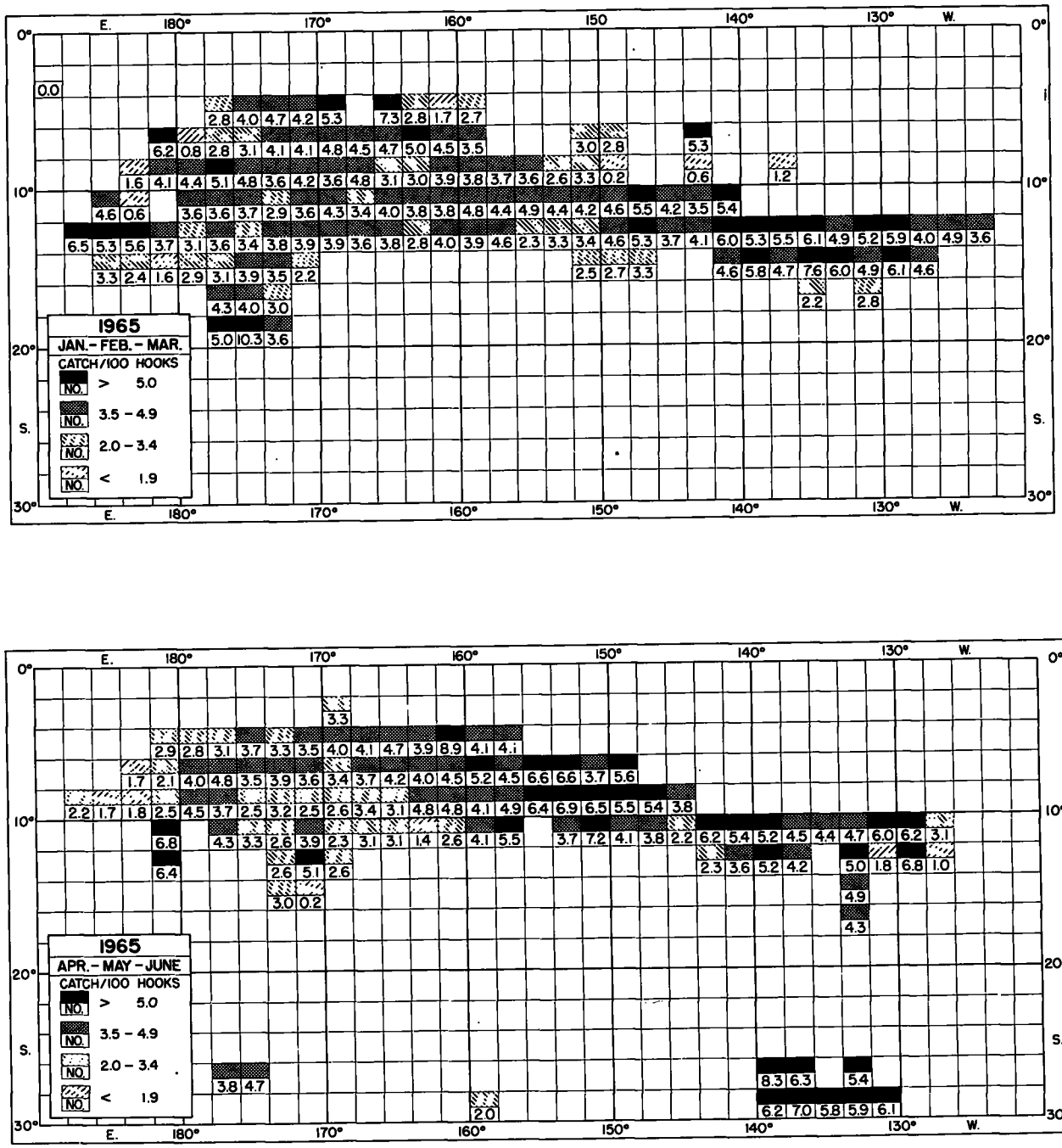
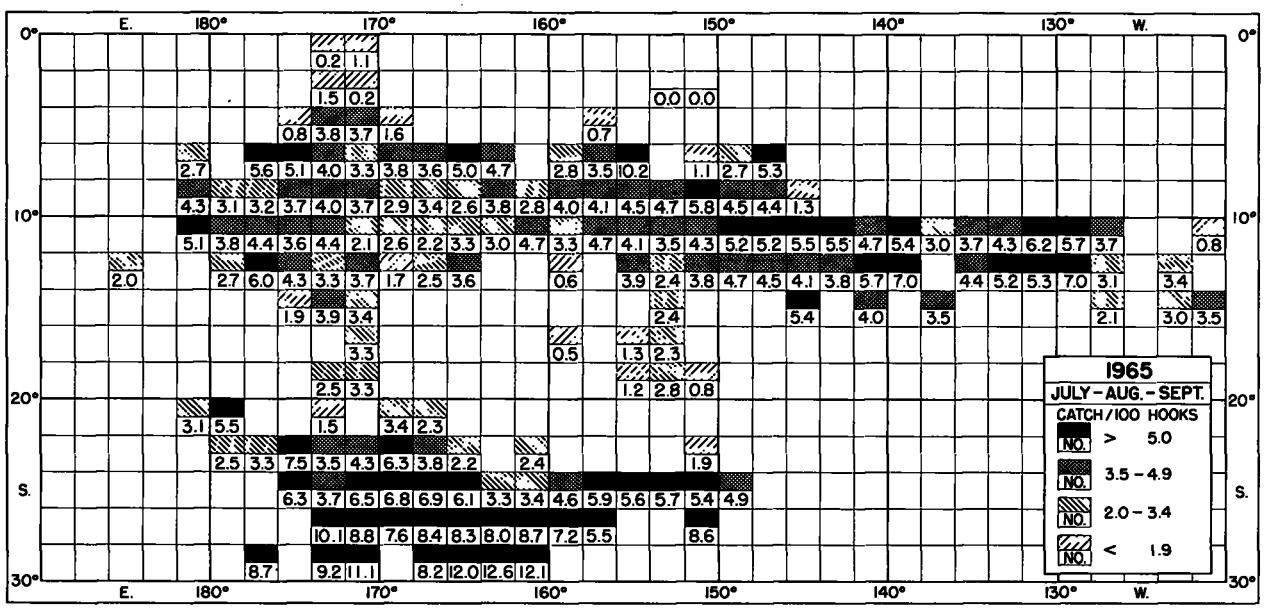
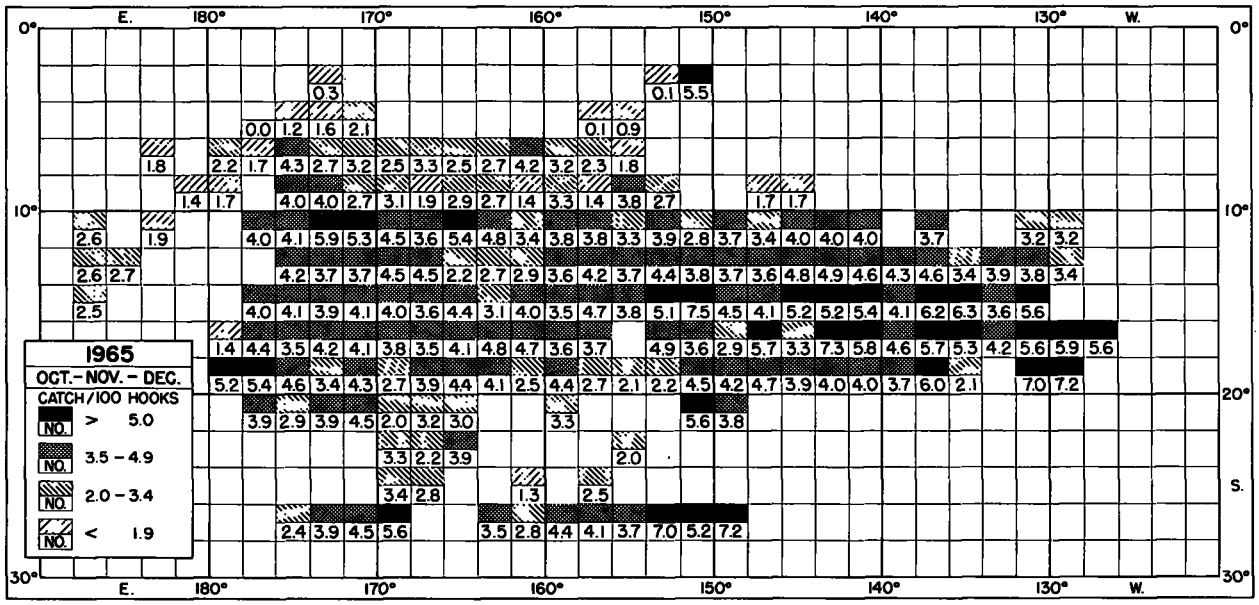


FIGURE 14.—The average catch rate (catch of albacore per 100 hooks) of American Samoa-based vessels shown by quarters of the year, 1965.


E.
180°
170°
160°
150°
140°
130°
W.
0°
10°
20°
30°
S.
1965
JULY - AUG. - SEPT.
CATCH / 100 HOOKS
NO. > 5.0
NO. 3.5 - 4.9
NO. 2.0 - 3.4
NO. < 1.9


E.
180°
170°
160°
150°
140°
130°
W.
0°
10°
20°
30°
S.
1965
OCT. - NOV. - DEC.
CATCH / 100 HOOKS
NO. > 5.0
NO. 3.5 - 4.9
NO. 2.0 - 3.4
NO. < 1.9

hooks) are scattered throughout the areas fished in all quarters of the year. A tabulation of the data by 5 degrees of latitude (table 3) indicates no well-defined seasonal and geographical differences. Average catch rates declined slightly, however, in 1965 as compared with 1963.

TABLE 3.—*Quarterly mean catch rates (number of fish per 100 hooks) of albacore and (in parentheses) the fishing effort (number of hooks) in the central and eastern South Pacific Ocean (long. 170° E. to 120° W.)*

[From data of American Samoa-based vessels]

Item	Latitudes (S.), west of long. 150° W.								Latitudes (S.), east of long. 150° W.						
	0°–5°	6°–10°	11°–15°	16°–20°	21°–25°	26°–30°	31°–35°	Mean	5°–10°	11°–15°	16°–20°	21°–25°	26°–30°	31°–35°	Mean
1963:															
Jan.–Mar.	3.5 (22,456)		6.0 (14,390)	5.4 (2,600)				5.0		5.8 (85,455)	7.6 (31,260)				6.7
Apr.–June		5.0 (1,019,395)	3.8 (151,765)	1.4 (3,080)		4.9 (263,370)	5.9 (9,000)	4.2	3.5 (22,786)	6.3 (86,780)	4.3 (7,935)		7.9 (295,362)		5.5
July–Sept.		4.3 (758,552)	4.4 (766,280)	4.4 (280,592)	4.1 (103,045)	5.2 (212,192)		4.5	5.2 (48,836)	5.7 (909,246)	4.1 (195,783)	5.5 (15,575)	5.2 (30,140)		5.1
Oct.–Dec.	1.1 (8,750)	4.3 (581,867)	4.5 (838,114)	4.4 (363,583)	4.4 (19,420)	4.4 (89,752)		3.9	1.7 (22,385)	5.2 (670,923)	5.7 (230,335)				4.2
Mean	2.3	4.5	4.7	3.9	4.3	4.8	5.9		3.5	5.8	5.4	5.5	6.6		
1964:															
Jan.–Mar.	1.5 (8,268)	4.4 (862,704)	3.4 (253,000)	3.3 (285,409)		1.6 (1,338)		2.8		4.3 (306,511)	4.1 (109,120)	.6 (3,838)	2.4 (4,296)	1.0 (6,000)	2.5
Apr.–June	2.3 (6,100)	5.0 (1,902,756)	4.6 (97,870)	4.7 (27,030)		7.0 (12,650)		4.7	4.6 (78,958)	4.6 (63,780)					4.6
July–Sept.	3.4 (15,158)	4.2 (347,279)	4.4 (299,406)	1.9 (3,830)	3.1 (111,030)	6.7 (536,836)		4.0	4.1 (73,908)	4.8 (164,804)	1.3 (9,120)				3.4
Oct.–Dec.		4.4 (167,910)	4.9 (1,706,235)	5.3 (141,804)	2.9 (47,896)	3.1 (20,172)		4.1	3.6 (43,866)	4.4 (191,028)	5.6 (279,708)				4.5
Mean	2.4	4.5	4.3	3.8	3.0	4.6			4.1	4.5	3.7	.6	2.4	1.0	
1965:															
Jan.–Mar.	3.9 (296,751)	4.2 (1,421,053)	3.8 (568,327)	4.2 (74,584)				4.0	2.0 (3,120)	5.0 (836,168)	2.4 (24,930)				3.1
Apr.–June	2.6 (74,692)	4.3 (2,708,555)	4.7 (137,720)			3.1 (6,420)	1.7 (1,620)	3.3	5.5 (124,124)	5.6 (242,129)	4.3 (3,120)		6.6 (172,690)	7.7 (13,836)	5.9
July–Sept.	2.7 (63,400)	4.0 (970,613)	3.8 (447,249)	2.6 (38,976)	4.5 (249,438)	8.0 (739,899)		4.3	3.3 (109,834)	4.8 (566,903)	2.0 (5,894)	4.9 (5,170)	5.0 (3,600)		4.0
Oct.–Dec.	.2 (22,420)	3.0 (380,594)	4.1 (910,555)	4.0 (1,327,684)	3.7 (100,038)	3.7 (111,977)		3.1	1.7 (1,458)	5.4 (699,574)	4.7 (518,535)	3.8 (2,700)	7.2 (11,230)		4.6
Mean	2.4	3.9	4.1	3.6	4.1	4.9	1.7		3.1	5.2	3.4	4.4	6.3	7.7	

To gage the abundance of albacore in areas not fished by the American Samoa-based vessels, some Japanese data were tabulated (table 4). Data for 1958–63 indicate that albacore are not as abundant in the western South Pacific Ocean, between long. 140° E. and 180°, as in areas fished by vessels from American Samoa. The catch rates, averaging less than two albacore per 100 hooks, are lower than those in more eastern waters. Perhaps some of the difference may be due to the selective fishing for albacore by American Samoa-based vessels, whereas in more western areas, the vessels from Japan may be fishing primarily for other species. Subtle differences in the fishing gear, such as in the lengths of the various lines, are known to affect the catch rates of albacore. It is probable, however, that these catch rates reflect the actual abundance of albacore in these areas.

Seasonally, the best catch rates in the western South Pacific are obtained in May through September. Latitudinally, the mean catch rates increase southward from the Equator, and the best catches are generally made between lat. 15° and 30° S. Koto (1966) found the best catch rates in the South Pacific during 1950–61 between lat. 10° and 30° S. and reported peaks of abundance along lat. 20° S. The catch rates south of lat. 30° S. were lower. In the areas fished by the American Samoa fleet, the catch rates are also low near the Equator but do not change as markedly from north to south. Generally, catch rates are also higher in the southernmost areas fished, between lat. 25° and 30° S.

TABLE 4.—*Pooled monthly mean catch rates of albacore (catch per 100 hooks) in the western South Pacific Ocean (long. 140° E. to 180°), 1958–63*

[From data provided by the Nankai Regional Fisheries Research Laboratory, Kochi, Japan, and those published by the Japan Fisheries Agency (1965, 1966)]

S. latitude	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
0°–5°	<0.1	0.1	1.2	0.2	0.2	0.3	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	0.2
6°–10°	.3	.4	.5	.6	.8	1.7	1.5	1.3	.7	.5	.4	.2	.7
11°–15°	1.7	1.6	1.5	2.3	2.1	2.5	2.9	2.4	2.2	1.6	1.3	1.0	.9
16°–20°	2.3	1.3	1.1	2.5	3.0	2.2	2.8	3.0	2.7	2.7	1.9	2.2	1.3
21°–25°	1.0	.8	.0	1.1	1.3	3.8	4.2	4.1	2.8	1.6	1.2	1.4	2.9
26°–30°	.2	------	.0	1.0	3.5	4.5	4.6	4.0	3.1	1.9	1.3	.8	1.3
31°–35°	1.4	------	------	1.6	2.7	3.8	.9	.8	.9	1.2	2.3	2.6	1.8
36°–40°	.6	------	------	------	1.3	1.2	.8	.6	.7	.8	1.1	2.3	1.0
41°–45°	------	------	.3	1.2	1.2	.8	.7	------	------	.2	1.2	1.6	.9
46°–50°	------	------	------	.6	.2	.2	------	------	------	------	------	------	.3
Mean	.9	.8	.7	1.2	1.6	2.1	2.1	2.0	1.6	1.2	1.2	1.3	------

In general, the distribution of albacore is continuous from west to east, at least between long. 140° E. and 120° W. in the South Pacific Ocean. A difference between the eastern and western South Pacific Ocean is in the apparent abundance of albacore; catch rates are lower in the western South Pacific Ocean.

SIZE OF ALBACORE

The albacore taken by the American Samoa-based fishery generally range from about 70 to 110 cm. long; 95 percent of the fish fall between 80 and 105 cm. (fig. 15). Among fish longer than 90 cm., males greatly outnumber females. The average length of albacore in 1965 was 88 cm. for females and 93 cm. for males.

CHANGES IN SIZE OF ALBACORE

In 2 of the 3 years during which length data were obtained, the mean length of fish declined sharply during February-April (fig. 16). This decrease could have resulted from shifts in fishing grounds, seasonal variation in fish sizes on the fishing grounds, or both. The trend toward a decrease in length from February 1964 to August 1965 may have been caused by the entry into the

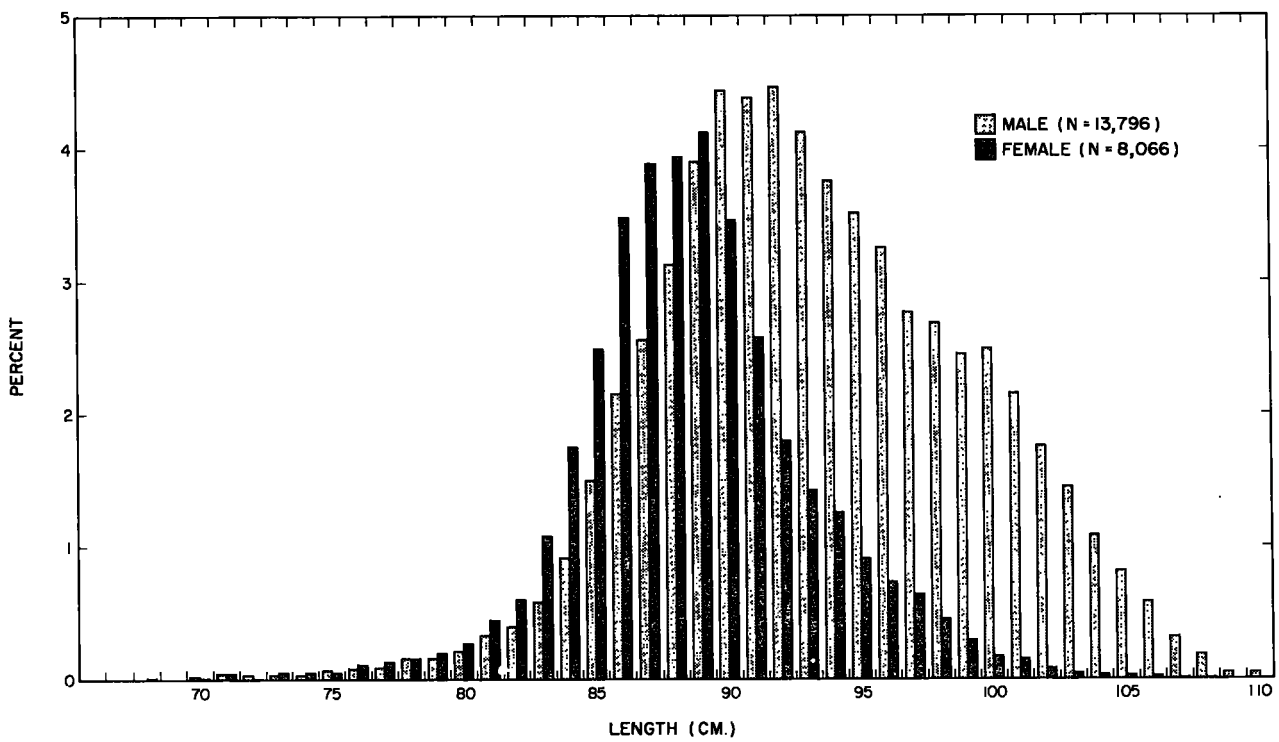


FIGURE 15.—Composite length-frequency distribution of albacore landed by the American Samoa-based longline vessels during 1965.

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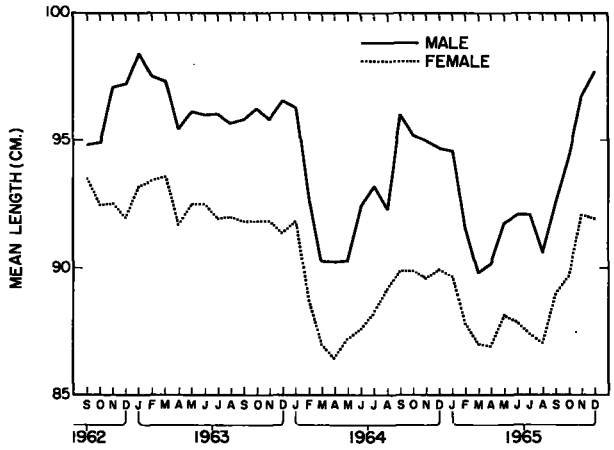

FIGURE 16.—Monthly mean lengths of albacore landed at American Samoa, September 1962 to December 1965.

fishery of an abundant year class or by a general decrease in the abundance of the older, larger fish in the stock. To determine if either of these factors might contribute to the decrease in mean length during February–April, we shall examine the size data in more detail.

DIFFERENCES IN FISH SIZE BY LATITUDE AND LONGITUDE

The mean length of albacore taken within 5-degree latitudinal bands (fig. 17) tends to increase from north to south. The fish are smallest near the Equator and largest at lat. 20° to 25° S. Albacore tend to be small again south of 25° S. These results are in general agreement with the findings of Honma and Kamimura (1957), although in contrast to these workers, we did not observe any significant increase in the size of albacore to the north of lat. 10° S. with the exception of 1963.

No longitudinal trend is noticeable. Honma and Kamimura found a general tendency for the size of albacore to increase from west to east. These authors, however, examined data from the western South Pacific between long. 140° E. and 170° W.,

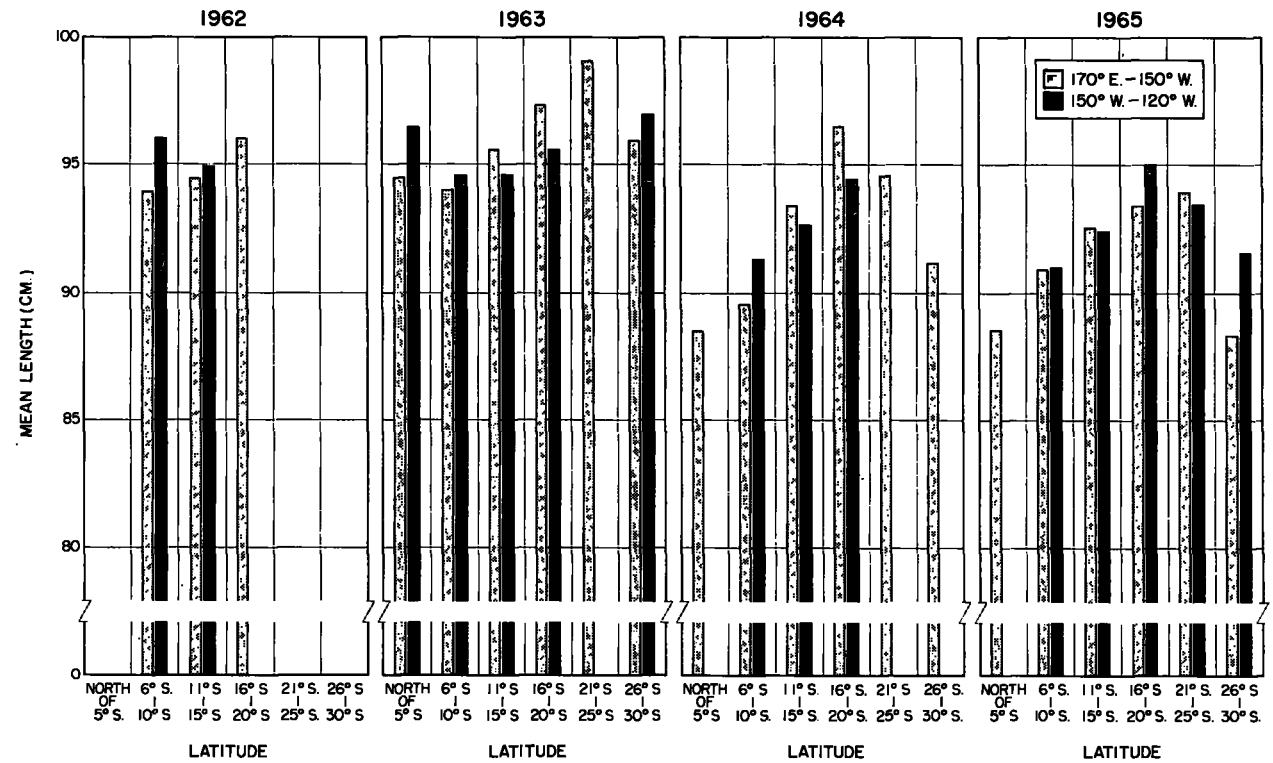

FIGURE 17.—Annual mean lengths of albacore (sexes combined) taken by the American Samoa-based vessels, by latitudes, 1962–65.

whereas our data cover a different segment of the ocean, from long. 170° E. to 120° W.

SIZE CHANGES DUE TO SHIFTS IN FISHING GROUNDS

Since average fish size is known for each area, it is possible to determine to what extent selection of fishing ground is responsible for changes in fish sizes in the landings. The shifting of the fishing effort from one area to another is readily seen (table 5). The regular shift of fishing grounds in 1964 and 1965 accounted for a large measure of the size changes in the landings. The average size of albacore decreased in March and April of both years when nearly all of the catches came from the area north of lat. 10° S. where the fish are smaller. For example, when the average size first began to decrease in February 1964, 68.7 percent of the catch was made between 6° and 10° S., where the albacore are small. During March, April, and May, when the average sizes were smallest of the entire year, 84.8, 93.5, and 93.0 percent, respectively, of the landings came from this area. The sizes gradually increased as fishing shifted to other areas. The same situation was repeated in 1965. In contrast, fishing was less concentrated in these northernmost waters during the early months of 1963. In March, April, and May, for example, only 20.0, 73.0, and 70.3 percent, respectively, of the landings came from lat. 6° to 10° S.

TABLE 5.—*The monthly mean length of albacore, and (in parentheses) the estimated percentage of the total catch from each locality by American Samoa-based vessels, shown by 5 degrees of latitude in the central South Pacific*

Item	Latitudes (S.), west of long. 150° W.						Latitudes (S.), east of long. 150° W.					
	North of 5°	6°–10°	11°–15°	16°–20°	21°–25°	26°–30°	North of 5°	6°–10°	11°–15°	16°–20°	21°–25°	26°–30°
1963:												
January		96.1	95.9	95.8					95.8	94.7	92.1	93.0
		(10.7)	(38.4)	(14.3)					(25.0)	(8.3)	(1.5)	(1.7)
February		96.5	95.9	96.4					96.7			
		(25.0)	(32.1)	(25.0)					(17.9)			
March	96.0	96.8	96.3	96.3			96.4	95.0		96.4		
	(5.0)	(20.0)	(20.0)	(25.0)			(5.0)	(10.0)		(15.0)		
April	92.9	93.8	95.2					94.9	94.4			100.1
	(2.5)	(73.0)	(2.5)					(14.3)	(5.1)			(2.5)
May		94.0	95.3					94.5	94.5			97.8
		(70.5)	(3.1)					(2.0)	(3.1)			(21.5)
June		93.4	95.5			96.4		92.3				95.4
		(40.7)	(14.9)			(20.3)		(4.0)				(2.2)
July		93.6	96.5	99.7					94.9	97.1		94.8
		(50.0)	(3.6)	(10.7)					(21.4)	(10.7)		(3.6)
August		93.7	95.8	100.2	98.9	96.0		94.2	94.2	95.4		
		(19.5)	(34.1)	(2.4)	(2.4)	(2.4)		(2.4)	(29.2)	(7.3)		
September		94.5	94.2	98.5	97.8	95.6		94.4	93.8			
		(31.0)	(6.9)	(10.3)	(6.9)	(3.4)		(3.4)	(37.9)			
October		94.9	95.1	96.8	101.8	94.6		95.1	94.5	96.2		
		(19.3)	(19.3)	(9.7)	(3.2)	(6.5)		(6.5)	(32.3)	(3.2)		
November		93.2	95.7	98.0					96.4	94.7		
		(31.5)	(19.6)	(4.6)					(31.7)	(12.5)		
December		92.6	92.9	97.7					93.9	95.0		
		(35.4)	(5.6)	(30.9)					(8.4)	(19.6)		
1964:												
January		92.5	94.9	96.8					93.8			
		(22.4)	(14.5)	(42.7)					(20.4)			
February		90.3	94.9	96.5					92.9			
		(68.7)	(3.5)	(10.4)					(17.4)			
March	89.2	88.7						87.8	92.5	95.2		
	(6.1)	(84.8)						(3.0)	(3.0)	(3.0)		
April		88.9	94.1						88.9			
		(93.5)	(3.2)						(3.2)			
May		88.7				90.6		90.0				
		(93.0)				(3.5)		(3.5)				
June	87.8	90.2	90.4	95.5				91.5	91.2			
	(3.3)	(70.0)	(3.3)	(3.3)				(10.0)	(10.0)			
July		90.7	96.0	97.7		87.9		91.9	92.3			
		(35.7)	(19.5)	(1.9)		(23.4)		(11.7)	(7.8)			
August		89.6	94.2		89.3	91.0		92.3	93.6			
		(27.6)	(13.8)		(6.9)	(34.5)		(13.8)	(3.4)			
September		91.8	95.2		95.1	94.4		92.9	91.3			
		(5.1)	(30.8)		(28.2)	(25.6)		(5.1)	(5.1)			
October		92.2	92.9	98.2	97.0	95.8		91.0	91.0	93.7		
		(15.4)	(57.7)	(3.8)	(3.8)	(3.8)		(3.8)	(3.8)	(7.7)		
November		91.0	92.6	95.4					94.0	95.1		
		(9.9)	(71.6)	(8.6)					(3.3)	(6.6)		
December		90.7	92.9	95.0					93.9	93.5		
		(7.6)	(73.5)	(7.6)					(7.6)	(3.8)		
1965:												
January		91.1	94.3	93.1				92.1	93.2			
		(16.8)	(23.5)	(16.8)				(2.8)	(40.1)			
February		89.6	87.4					90.0	92.1			
		(63.3)	(3.3)					(3.3)	(30.0)			
March		87.7							92.1			
		(88.9)							(11.1)			

TABLE 5.—*The monthly mean length of albacore, and (in parentheses) the estimated percentage of the total catch from each locality by American Samoa-based vessels, shown by 5 degrees of latitude in the central South Pacific*—Continued

Item	Latitudes (S.), west of long. 150° W.						Latitudes (S.), east of long. 150° W.					
	North of 5°	6°–10°	11°–15°	16°–20°	21°–25°	26°–30°	North of 5°	6°–10°	11°–15°	16°–20°	21°–25°	26°–30°
1965—Continued												
April	87.6	88.9										
	(22.0)	(78.0)										
May	89.8	89.9	91.7					90.5				92.9
	(8.0)	(60.0)	(4.0)					(24.0)				(4.0)
June		90.0	94.6			88.4		91.2	90.8			90.2
		(60.5)	(4.9)			(7.4)		(4.9)	(17.3)			(4.9)
July	89.0	91.2	97.2	83.6		84.5		91.4	91.3			
	(3.1)	(37.5)	(6.3)	(3.1)		(15.6)		(18.7)	(15.6)			
August	87.1	90.0	87.3	90.3	89.5	85.8			91.9			
	(3.0)	(33.3)	(6.1)	(3.0)	(21.2)	(18.2)			(15.2)			
September	89.5	89.9	93.3	94.7	91.5	89.6		90.6	91.2	90.4	92.4	
	(6.8)	(13.7)	(11.0)	(2.0)	(33.3)	(13.7)		(2.0)	(9.8)	(3.9)	(3.9)	
October		91.0	91.5	97.6	96.7	89.0			92.5		94.5	
		(40.5)	(13.5)	(13.5)	(8.1)	(2.7)			(18.9)		(2.7)	
November		93.3	94.5	97.1	98.0	92.6			93.8	98.1		
		(11.4)	(25.0)	(38.6)	(2.3)	(2.3)			(18.1)	(2.3)		
December		97.9	94.0	97.5					94.6	96.5		
		(2.1)	(25.0)	(43.7)					(10.4)	(18.8)		

In spite of the widespread knowledge among fishermen that fish are smaller in the more northern waters (north of lat. 15° S.), they persist in fishing these waters during February–May because of their belief that the higher catch rates will more than compensate for the smaller sizes of fish. Fishing effort was concentrated in these waters during the early months of both 1964 and 1965. This type of selection has undoubtedly contributed to the general size decrease of albacore in the landings in those two years.

SEASONAL VARIATION IN FISH SIZES

Although we can generalize that sizes of albacore change with latitude, seasonal variation in sizes within the same areas is also considerable. For example, the average sizes of albacore taken from the area between lat. 6° and 10° S. were smallest during February–May in both 1964 and 1965, as compared with the rest of the year (fig. 18). The decrease in size may be explainable to a large extent by the fact that the vessels concentrate their fishing north of 10° S. where the fish are smaller; this effect on fish size is further aggravated by the coincidental presence of smaller fish in the area at that particular time of the year.

DECREASE OF OLDER FISH IN STOCK

Albacore taken in 1964 and 1965 were shorter on the average than those caught in 1963 and perhaps earlier (figs. 16 and 17 and table 5). This decrease in size may be attributable, at least in part, to an actual decrease of older, larger fish in the stock. A decrease of this magnitude might be expected when a stock undergoes exploitation, because increasing fishing mortality over the years increases total mortality. As total mortality increases, the average age and, thus, the average size of the stock must decline.

EFFECT OF ABUNDANT YEAR CLASS ON SIZE COMPOSITION

Numbers of larger fish of both sexes decreased from September 1962 to about May 1965, while smaller fish (<90 cm.) tended to increase (figs. 19 and 20). Superimposed on this general increase of smaller fish was an abrupt, exceedingly large increase beginning around February 1964. This rise of apparent abundance of smaller fish suggests the possibility of the entry into the fishery of an abun-

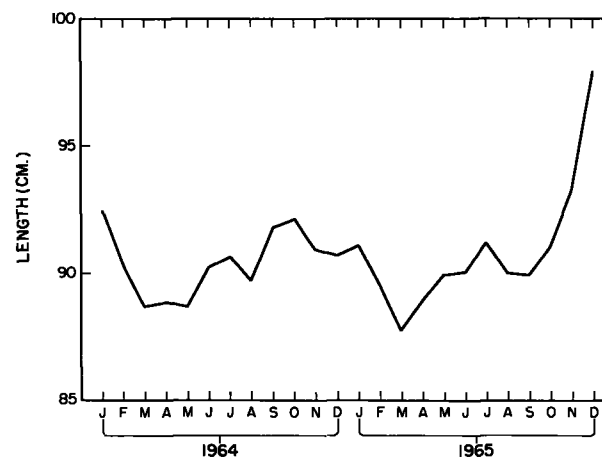

FIGURE 18.—The monthly mean length of albacore (sexes combined) taken by American Samoa-based vessels in the area 6° to 10° S., 170° E. to 150° W., in 1964 and 1965.

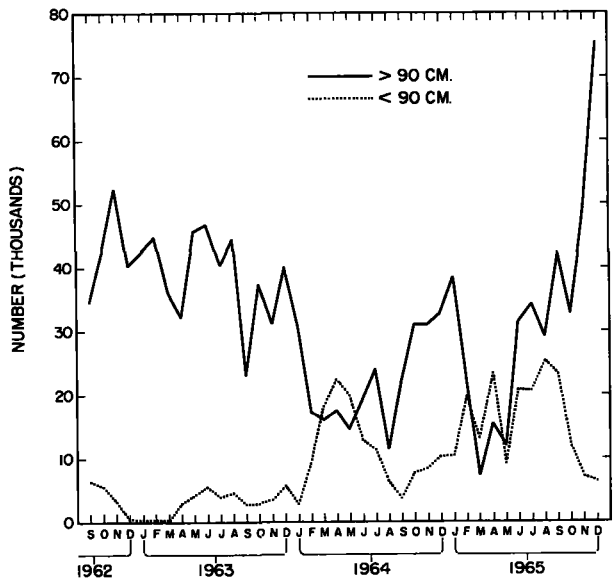

FIGURE 19.— Estimated numbers of two size categories of male albacore landed by the American Samoa-based fishery, September 1962 to December 1965.

dant year class. If so, we would expect that the numbers of larger fish—those longer than 90 cm.—would increase as this large year class moved through the fishery. Such an increase is indicated by the data. The abrupt increase in small fish in February 1964 was followed by an increase in larger fish toward the latter part of 1964. Near the end of 1964 and in early 1965, an increase in the number of small fish of both sexes was followed by an increase in longer fish a few months later.

A large part of this change in size composition is attributable to shifts of fishing grounds, as discussed previously. Year-class strength, however, is probably also an important contributor to the apparent changeover in size composition during the 3-year period. Analysis of data from a few more years would clarify this question.

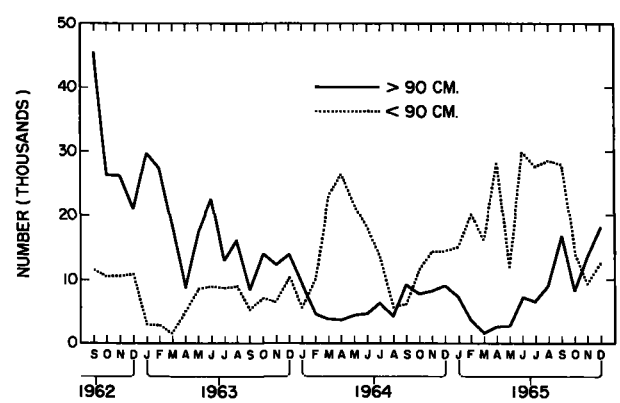

FIGURE 20.—Estimated numbers of two size categories of female albacore landed by the American Samoa-based fishery, September 1962 to December 1965.

SEX RATIO OF ALBACORE

Changes in sex ratio could also affect the size composition of the landings since the monthly mean lengths of male albacore are from 1 to 6 cm. greater than those of females.

The proportion of males in the total landings (fig. 21) has fluctuated greatly without noticeable trend over the years. On the other hand, the proportion of males among the larger fish (>90 cm.) increased through September 1964, after which it tended to level out.

Although males averaged around 62 percent of the monthly landings between September 1962 and December 1965, their percentage did decrease in 1964 and 1965 during periods corresponding to months of reduced mean sizes (i.e., February–June 1964, February–August 1965). Though the mean lengths of both sexes decreased simultaneously during these months (fig. 16), the coincidental re-

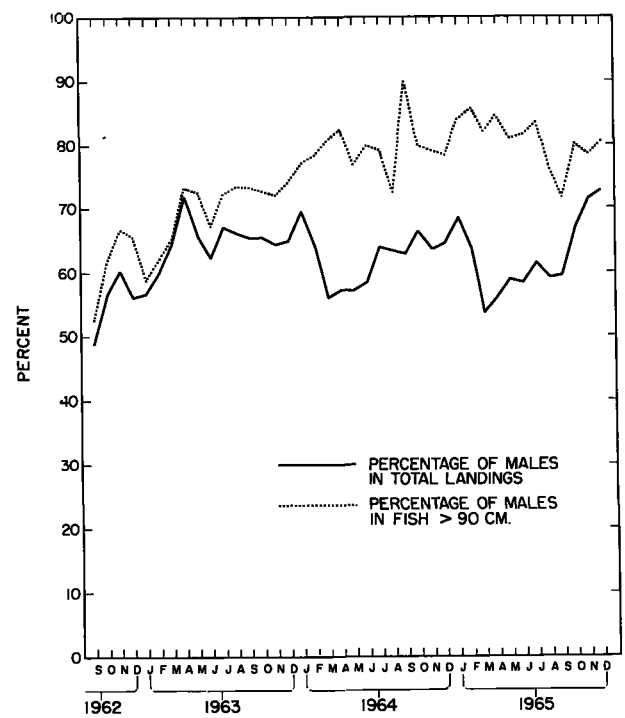

FIGURE 21.—Monthly sex ratio of albacore landed by the American Samoa-based vessels.

duction in the proportion of males has acted to amplify the general size decrease. This influence was reflected in the decreased catch per 100 hooks (by weight) during these months (fig. 9).

SUMMARY

1. This report is based on (a) data on landings provided by the two tuna packing firms operating in American Samoa, (b) catch and effort data provided by the operators of American Samoa-based fishing vessels, (c) size and sex data on albacore sampled at the tuna canneries in American Samoa, and (d) Japanese data made available to us by the Japan Fisheries Agency.

2. The tuna fishery based in American Samoa began in 1954 with a fleet of seven Japanese longline vessels. The fleet grew rapidly and in 1965, 154 vessels fished out of American Samoa. The composition of the fishing fleet, in terms of country of origin of the vessels, has changed. In the early years of the fishery, the fleet was composed entirely of longliners from Japan. The 105-vessel fleet operating during the last quarter of 1965 was composed of 62 vessels from Japan, 30 from the Republic of Korea, and 13 from the Republic of China.

3. The fishery was confined to the immediate vicinity of the Samoa Islands in the early years, but has expanded rapidly to the east and south. In 1965, the fishery area was bounded on the north by the Equator, on the south by lat. 30° S., on the west by long. 175° E., and on the east by about long. 120° W. These boundaries enclose an area of about 23 million square kilometers.

4. Though a variety of pelagic fishes is taken by the longline fishery, albacore command the highest price at the canneries and are, for this reason, fished for selectively. Data provided by the fishermen are complete only with respect to the albacore catches, the major species taken. Consequently, no attempt was made in this report to analyze the data on the other tuna species.

5. The annual landings of albacore in American Samoa have gradually increased from 338 metric tons in 1954 to 15,588 metric tons in 1965.

6. The occurrence of albacore in the South Pacific Ocean exhibits no clear seasonality although in most years landings have been slightly better during the latter half of the year.

7. The catch of albacore per fishing trip was used as the measure of apparent abundance for the entire period of the fishery's existence. No other unit of effort was available before 1959 when data first were recorded on number of days fished per trip and 1963 when we began to collect data on number of hooks fished per day. This index proved to be reasonably satisfactory, however, because neither the average number of days fished per trip nor the size composition of the vessels has varied appreciably over the years covered by our study.

8. The catch per trip (in terms of weight of fish) tends to increase with size of vessel, mainly because (1) larger vessels generally fish more gear than smaller vessels, and (2) their trips tend to be longer. However, the fact that relatively few vessels in the American Samoa fleet were larger than 120 tons or smaller than 80 tons permits the use of catch per trip as an index of apparent abundance.

9. The catch per trip tended to increase steadily through 1960, tapered off, and stabilized at a lower level in 1963 and 1964. There was again a slight increase in 1965.

10. Annual landings have tended to be directly proportional to the total amount of fishing effort.

11. The size of the vessel does not significantly affect the catch rate in terms of catch per 100 hooks fished.

12. The distribution of albacore is continuous from west to east in the South Pacific Ocean, at least between long. 140° E. and 90° W. The fish have their greatest abundance, however, in the central and eastern South Pacific Ocean between 180° and 120° W.

13. During the first half of the year, the American Samoa-based vessels generally fish north of lat. 20° S., where catches are most favorable. In later months, beginning about June or July, the albacore longline fishery moves southward to as far as lat. 30° S.

14. The number of albacore caught per 100 hooks did not vary appreciably in 1963–65. But owing to the decrease in average size of albacore caught, the weight of fish landed per 100 hooks declined significantly in 1964 and early 1965.

15. The mean lengths of albacore landed in American Samoa did not change significantly from September 1962 to January 1964, but suddenly became smaller in February 1964. Although the mean length increased slightly after May, the fish remained smaller than in 1962–63. The average

length again decreased in February 1965, but by the end of the year the albacore landed in Samoa were even larger than in 1962–63.

16. Several factors are responsible for changes in mean lengths of albacore. One of the primary causes is change of fishing grounds; fishing is confined during the early months of the year to more northern waters, north of lat. 15° S., where the albacore tend to be small. As some of the fishing shifts southward beginning about June or July, the lengths of albacore gradually increase since the largest fish occur near lat. 20°–25° S. Albacore are smaller to the south of lat. 25° S.

17. We found no longitudinal differences in average fish sizes.

18. The general decrease in average lengths of albacore taken in 1964 as compared to 1962–63, may have been due in part to an abundant year class of small albacore that entered the fishery early in 1964. As this year class moved through the fishery, average size increased slightly toward the latter part of 1964. The data suggest that another large year class of small albacore entered the fishery early in 1965.

19. Although albacore are generally smallest in areas north of 15° S., sizes also vary seasonally within the same areas. The fish are smallest during February-May when coincidentally the vessels tend to concentrate their fishing in this northern area.

20. Males average 1 to 6 cm. longer than females each month; therefore, any change in the sex ratio affects the average size of fish in the catch. Indeed, during the periods of reduced mean sizes in 1964 and 1965, the percentage of males decreased, permitting the smaller females to have an unusually depressing effect on the average size of the albacore. The smaller catch (in weight) per unit of effort could be attributed partly to the change in sex ratio.

ACKNOWLEDGMENTS

The early stages of the sampling (September 1962–April 1963) were supervised by Thomas Annastas, then Supervisor of Fisheries for the Department of Agriculture, Government of American Samoa. Our sampling field station in Pago Pago was established through the cooperation of Governor H. Rex Lee, of the Government of American Samoa, and the management of the Van Camp Sea Food Company in Samoa. The continued success of the field station in providing data from the fishery is due to the cooperation of the management and staff of the Van Camp Sea Food Company-Samoa and the recently established (1963) Star-Kist Samoa, Inc., who allow our personnel to sample the landings at their canneries. The fishing vessel operators from Japan, the Republic of Korea, and the Republic of China provided us with detailed information on their fishing operations.

The fishery technicians from the BCF Laboratory in Honolulu who have served and continue to serve at the field station have collected the data used in this study. Andrew Scanlan of Samoa assisted our personnel at the field station.

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MICRONEKTON OF THE EASTERN TROPICAL PACIFIC OCEAN: FAMILY COMPOSITION, DISTRIBUTION, ABUNDANCE, AND RELATIONS TO TUNA [1] [2]

BY MAURICE BLACKBURN, *Research Biologist*
INSTITUTE OF MARINE RESOURCES, SCRIPPS INSTITUTION OF OCEANOGRAPHY
UNIVERSITY OF CALIFORNIA, SAN DIEGO, CALIF. 92037

ABSTRACT

The taxonomic composition and distribution of micronekton (fishes, crustaceans, and cephalopods about 1 to 10 cm. in largest dimension) were studied from catches of night net hauls in the upper 90 m. in most parts of the eastern tropical Pacific Ocean. One type of haul (net 1.5 m. square at mouth, uniform mesh size throughout, hauled obliquely at ship speed of 5 knots) contributed most of the data and is considered to be superior to any other existing type of haul with a net or trawl of comparable size for quantitative work on micronekton.

Ten families (Myctophidae, Gonostomatidae, Galatheidae, Euphausiidae, Penaeidae, Squillidae, Portunidae, Sergestidae, Enoploteuthidae, and Cranchiidae) and one suborder (Apodes: leptocephali) contributed 93.4 percent of the volume of the total catch. Some of these groups are localized, and others are widely distributed geographically; abundance varies according to the distribution of physical phenomena which are responsible for eutrophic conditions. Agreement in family composition was poor for fishes between the net catches and the stomach contents of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Euthynnus pelamis*) from the same areas; agreement between catches and stomach samples was fair for crustaceans. The reasons for the differences are discussed. The commonly held opinion, that tunas are opportunistic feeders, within their sensory limitations, remains tenable.

To the extent that the net hauls sample kinds of micronekton which are important as food for tunas, they can be used to compare quantities of tuna prey in different areas. This comparison shows that the richest tuna forage is off western Baja California and that an area west of Ecuador and northern Peru with practically no surface fishing probably has about as much forage as some areas which support commercial surface fishing.

Comprehensive biological-oceanographic investigations in the eastern tropical Pacific Ocean began with expeditions Eastropic (1955) and Scope (1956). Much attention was given on these expeditions to distributions of primary productivity, standing crop of chlorophyll *a*, and standing crop of zooplankton (Holmes, Schaefer, and Shimada, 1957; Holmes and others, 1958); these observations were intended to contribute to the understanding of the ecology of the tunas of the region and to oceanographic knowledge. Much of this work was done by the Scripps Institution of Oceanography, University of California. In 1957 the Institution's work in this field was put on a continuing basis in the STOR Program, with support from the Bureau of Commercial Fisheries. As a result, several more cruises were made in the eastern tropical Pacific, which differed from Eastropic and Scope in that measurements of an additional biological property, namely standing crop of micronekton, were made routinely.

Micronekton, a term occasionally found in marine biological literature (e.g., Marshall, 1954), is here defined as the assemblage of actively swimming fishes, crustaceans, and cephalopods, ranging from about 1 cm. to 10 cm. in greatest dimension. In this paper it means all fishes, crustaceans, and cephalopods caught by a net designed to sample

[1] Contribution from the Scripps Institution of Oceanography, University of California, San Diego.

[2] This work was financed by the Bureau of Commercial Fisheries under Contract Nos. 14-19-008-9354, 14-17-0007-1, 14-17-0007-28, 14-17-0007-70, 14-17-0007-139, and 14-17-0007-221, with funds made available under the Act of July 1, 1954 (68 Stat. 376), commonly known as the Saltonstall-Kennedy Act. It was also supported by the Atomic Energy Commission through contract AT(11-1)-34, Project 99, with the Institute of Marine Resources, University of California. It was part of the research of the STOR (Scripps Tuna Oceanography Research) Program.

Some preliminary results of this research were given in a symposium at the Tenth Pacific Science Congress of the Pacific Science Association, held at the University of Hawaii in August and September 1961. The symposium was entitled "Factors affecting the behavior of predaceous marine fishes, especially sharks."

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the animals mentioned above. The catches included some animals smaller than 1 cm. or larger than 10 cm., but they probably contributed less than 5 percent of the total volume. Micronekton and zooplankton overlap in catches in plankton nets—for instance, euphausiids occur in both.

The reasons for measuring the standing crop of micronekton and each of its main components were as follows:

(1) Because tunas feed on micronekton, a knowledge of its distribution might help to explain the variable distribution of tunas in the eastern tropical Pacific.

(2) Comparisons of net-caught and tuna-caught micronekton (the latter from tuna stomachs) might be of value in the study of feeding behavior of tunas, especially in the matter of possible selection of organisms.

(3) Food-chain relations in the ocean have had much physiological and statistical study between the producer and herbivore trophic levels, but comparatively little study has been made between those levels and the carnivore levels. This deficiency seems to reflect a shortage of data on standing crops of oceanic carnivores, especially primary carnivores such as small fish and cephalopods which are eaten by secondary carnivores; where such data are available, they generally refer to a few species for which there are commercial fisheries (e.g., herring, *Clupea harengus*). Because good programs of measurement of phytoplankton and zooplankton were already operating in the eastern tropical Pacific, it seemed worthwhile to measure micronekton as well.

This paper presents a summary of most of the micronekton data obtained before 1964 in the eastern tropical Pacific and analyzes them in reference to distribution and relation to contents of stomachs of tuna. Statistical analysis in reference to food-chain relations has been made, in part, elsewhere (Blackburn, 1966a).

MATERIAL AND METHODS

The net-caught micronekton obtained in the eastern tropical Pacific and adjacent waters was taken in the following three ways:

(1) In standard (identically made) night hauls of a net called the 1.5–m. (or 5-foot) net (described below), at a ship speed of 5 knots.

(2) In nonstandard night or day hauls of the same net.

(3) In hauls of a net called the high-speed net, described below, made at the ordinary cruising speed of the vessel (which ranged from about 9 to 12 knots, for the different vessels used).

The most useful quantitative data are those from standard night hauls, and this paper is concerned almost entirely with them. They were obtained on the following cruises: TO–58–1 (or SCOT), April–June 1958; TO–59–1, January–February 1959; TO–59–2, August–September 1959; TO–60–1; May 1960; TO–60–2 (or STEP–1), September–December 1960; and TO–61–1, March–April 1961 (see figs. 1 and 2 for areas covered). The total number of standard night hauls from all these cruises was 131 (see table 1). In addition, brief mention is made of 38 standard hauls (19 night, 19 day) made on cruise TO–62–1 (or TEMPO), August 1962, off Acapulco, Mexico. The hauls in this series (see table 2) are separated from the main data because they were made close together in space and time; they were not comparable with the other 131 hauls which were much more widely distributed in space and time in the eastern tropical Pacific.

Nonstandard hauls, occasionally made by day or night, are not discussed. The high-speed hauling method, and some data from it, are briefly described and evaluated.

1.5–M. NET: DESCRIPTION, OPERATION, AND PERFORMANCE

Figure 3 shows the 1.5–m. net. It is in the form of an elongated pyramid; the base (the mouth of the net) is 1.5 m. square, and the measurement from the center of the base to the apex is 5.8 m. The base or mouth is surrounded by a narrow selvage laced to a square frame of galvanized iron, to which the towing bridles and depressors are attached. The apex is open and the opening contains a brass fitting set in canvas, by which a cod end (not included in the 5.8–m. length) can be attached. The material and mesh of the net (excluding selvage and cod end) are uniform throughout: Marion Textiles 467-pattern nylon netting,[3] with meshes approximately oblong and measuring about 5.5 mm. by 2.5 mm. The long

[3] Mention of manufacturer does not imply endorsement of the product.

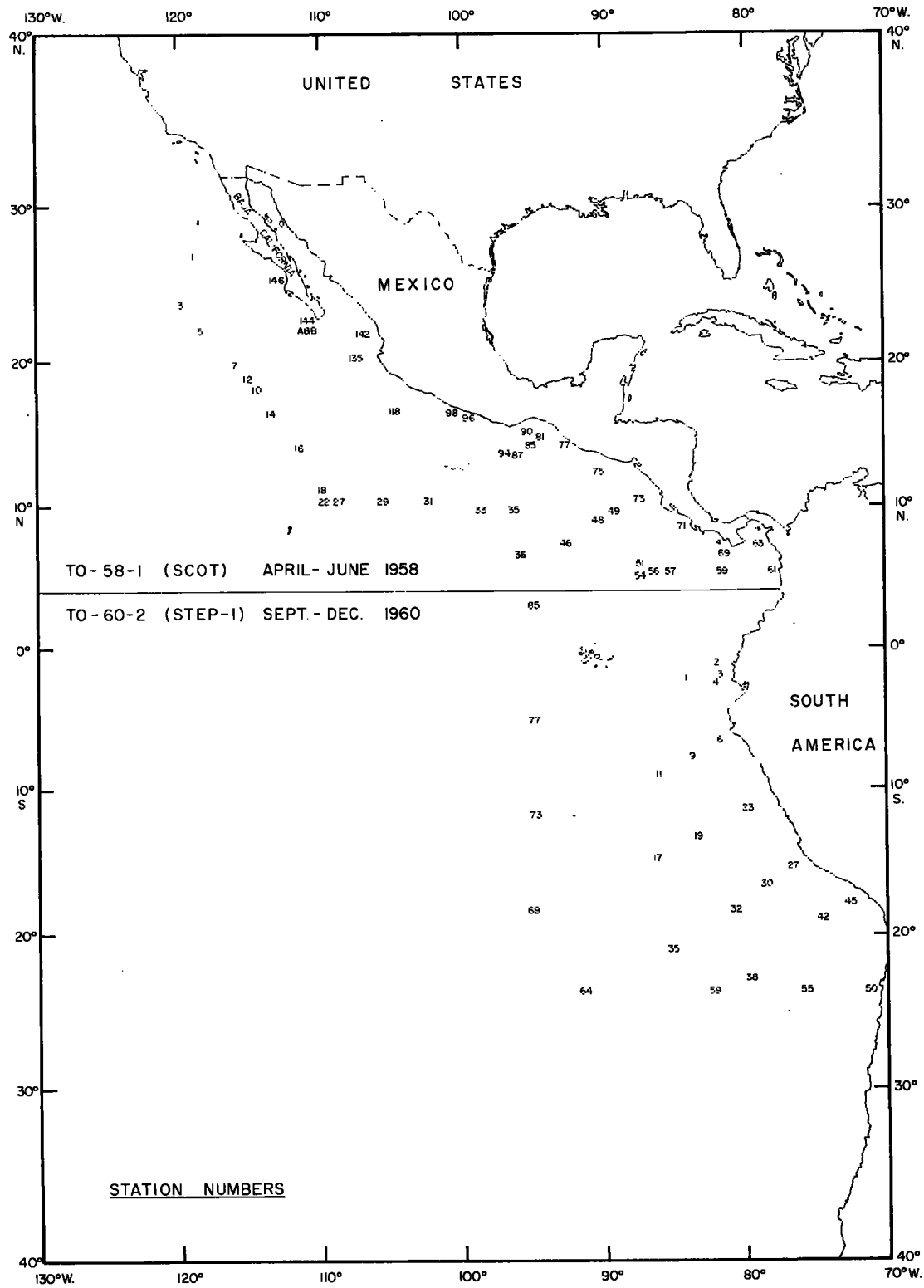

FIGURE 1.—Serial numbers and positions of stations at which standard night micronekton hauls were made on cruises TO–58–1 and TO–60–2.

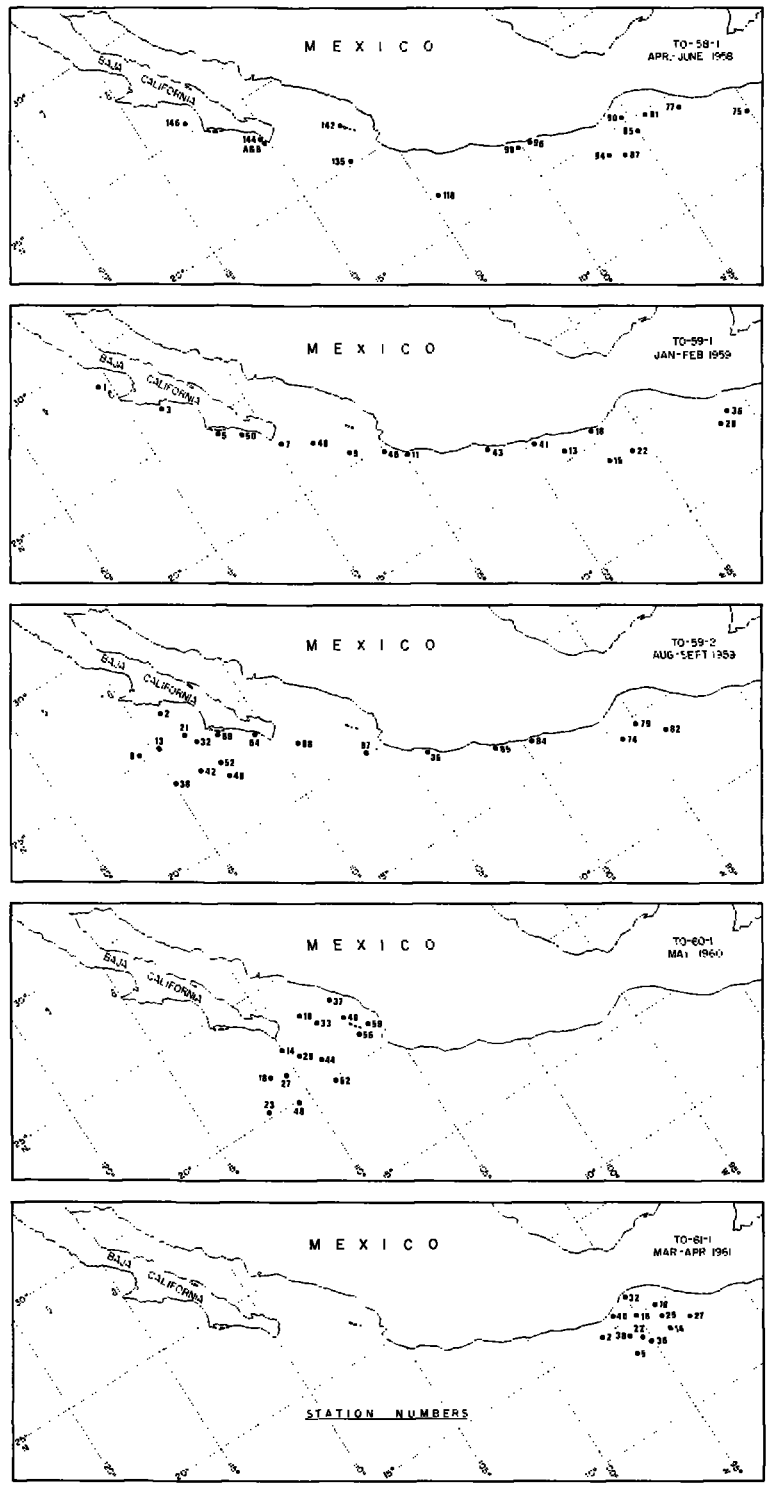

FIGURE 2.—Serial numbers and positions of stations at which standard night micronekton hauls were made in waters adjacent to Mexico and Guatemala, on cruises prior to 1962.

TABLE 1.—*Actual volumes and standardized volumes for fishes, crustaceans, cephalopods, and total micronekton from 131 standard night hauls of a 1.5–m. net*

[Asterisk means that the station did not fall within the area stated, but has been included in it]

Station [1] number	Date	Area [2]	Time [3]	Depth [4]	Actual volumes				Standardized volumes			
					Fishes	Crustaceans	Cephalopods	Total	Fishes	Crustaceans	Cephalopods	Total
A. Cruise TO-58-1 (SCOT): April-June 1958												
		Number	*Minutes*	*M.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml./10³m.³*	*Ml./10³m.³*	*Ml./10³m.³*	*Ml./10³m.³*
1	Apr. 25	15	65		26	67	3	96	1.5	3.8	0.2	5.5
3	26	15	65		44	104	<1	148	2.5	5.9	<.1	8.4
5	27	15	64		17	35		52	1.0	2.0		3.0
7	28	*02	64		55	28		83	3.2	1.6		4.8
10	28	02	65		47	13	<1	60	2.7	.7	<.1	3.4
12	29	02	75		2	471		473	.1	23.2		23.3
14	30	02	64		109	5	3	117	6.3	.3	.2	6.8
16	May 1	*02	72		45	4	3	52	2.3	.2	.2	2.7
18	2	*09	65		18	13	2	33	1.0	.7	.1	1.8
22	2	09	65		1	9	2	12	.1	.5	.1	.7
27	3	09	65		14	10	2	26	.8	.6	.1	1.5
29	5	16	64		64	10	9	83	3.7	.6	.5	4.8
31	6	16	64		63	18	8	89	3.6	1.0	.5	5.1
33	7	16	65		131	63	10	204	7.4	3.6	.6	11.6
35	8	16	65		57	44	9	110	3.2	2.5	.5	6.2
36	9	16	64		147	56	19	222	8.5	3.2	1.1	12.8
46	12	16	64		152	69	7	228	8.8	4.0	.4	13.2
48	13	05	63		189	70	43	302	11.1	4.1	2.5	17.7
49	13	05	64		189	62	130	381	10.9	3.6	7.5	22.0
51	15	11	69		59	52	11	122	3.1	2.8	.6	6.5
54	15	11	65		87	58	3	148	4.9	3.3	.2	8.4
56	16	11	64		93	82	15	190	5.4	4.7	.9	11.0
57	17	11	63		60	58	9	127	3.5	3.4	.5	7.4
59	18	12	62		106	126	19	271	6.3	8.7	1.2	16.2
61	19	10	65		91	143	7	241	5.2	8.1	.4	13.7
63	20	10	67		398	113	72	583	22.0	6.2	4.0	32.2
69	24	*12	64	90	147	113	20	280	8.5	6.5	1.2	16.2
71	25	05	66	105	110	68	21	199	6.2	3.8	1.2	11.2
73	26	05	64	80	183	68	95	346	10.6	3.9	5.5	20.0
75	27	05	63	83	196	111	62	369	11.5	6.5	3.7	21.7
77	28	04	60	100	319	58	90	467	19.7	3.6	5.5	28.8
81	29	04	71		533	72	124	729	27.8	3.7	6.5	38.0
85	30	04	66	110	168	88	88	344	9.4	4.9	4.9	19.2
87	30	04	68		109	28	18	155	5.9	1.5	1.0	8.4
90	31	04	66	72	150	17	62	229	8.4	.9	3.5	12.8
94	June 1	04	65	72	147	11	20	178	8.4	.6	1.1	10.1
96	2	04	65	115	221	36	10	267	12.6	2.0	.6	15.2
98	6	04	65	100	248	23	30	301	14.1	1.3	1.7	17.1
118	11	04	64	83	211	18	19	248	12.2	1.0	1.1	14.3
135	14	03	65	72	201	31	41	273	11.4	1.8	2.3	15.5
142	16	03	64		329	62	35	426	19.0	3.6	2.0	24.6
144A	17	01	65		266	67	6	339	15.2	3.8	.3	19.3
144B	17	01	65		206	1,605	3	1,814	11.7	91.3	.2	103.2
146	18	01	63		7	1,924	<1	1,931	.4	112.9	<.1	113.3
B. Cruise TO-59-1: January–February 1959												
1	Jan. 17	01	48	99	161	379		540	12.4	29.2		41.6
3	17	01	47	90		102		102		8.0		8.0
5	18	01	40	81	<1	358	<1	358	<.1	33.1	<.1	33.1
7	20	03	48	86	150	11	1	162	11.6	.8	.1	12.5
9	21	03	49	88	73	12	9	94	5.5	.9	.7	7.1
11	22	03	44	90	93	6	8	107	7.8	.5	.7	9.0
13	26	04	50	75	97	90	8	195	7.2	6.6	.6	14.4
15	27	04	53	80	125	66	8	199	8.7	4.6	.6	13.9
18	28	04	40	77	97	258	17	372	9.0	23.8	1.6	34.4
22	30	04	34	92	60	79	<1	139	6.5	8.6	<.1	15.1
28	Feb. 8	05	47	78	120	54	29	203	9.4	4.3	2.3	16.0
36	14	05	49	82	90	53	61	204	6.8	4.0	4.6	15.4
41	16	04	48	81	50	269	19	338	3.9	20.7	1.5	26.1
43	17	04	45	79	101	39	20	160	8.3	3.2	1.6	13.1
46	20	03	52	73	68	15	16	99	4.8	1.1	1.1	7.0
48	20	03	46	83	66	22	11	99	5.3	1.8	.9	8.0
50	21	01	50	94	20	807		827	1.5	59.7		61.2

See footnotes at end of table.

TABLE 1.—*Actual volumes and standardized volumes for fishes, crustaceans, cephalopods, and total micronekton from 131 standard night hauls of a 1.5–m. net*—Continued

Station [1] number	Date	Area [2]	Time [3]	Depth [4]	Actual volumes				Standardized volumes			
					Fishes	Crustaceans	Cephalopods	Total	Fishes	Crustaceans	Cephalopods	Total
C. Cruise TO–59–2: August–September 1959												
2	Aug. 15	01	52		60	1,187		1,247	4.3	84.5		88.8
8	16	*01	48		60	2,262	<1	2,322	4.6	174.4	<.1	179.0
13	17	01	49	115	18	779		797	1.4	58.8		60.2
21	19	01	49	85	42	907	1	950	3.1	68.5	.1	71.7
32	22	01	36	84	306	2,500	<1	2,806	31.5	257.0	<.1	288.5
38	24	01	44	82	92	637	3	732	7.7	53.6	.3	61.6
42	24	01	43	80	59	1,585		1,644	5.1	136.3		141.4
52	26	01	49	99	81	1,552	<1	1,633	6.1	117.2	<.1	123.3
58	27	01	46	93	149	530	9	688	12.0	42.6	.7	55.3
64	28	01	58	85	3	19	5	27	.2	1.2	.3	1.7
74	Sept. 8	04	44	85	85	11	10	106	7.2	.9	.8	8.9
79	10	04	46	81	100	18	19	137	8.1	1.4	1.5	11.0
82	11	05	49	91	81	37	25	143	6.1	2.8	1.9	10.8
84	13	04	47	90	267	82	16	365	21.0	6.4	1.3	28.7
85	15	04	51	84	203	34	14	251	14.7	2.5	1.0	18.2
86	16	03	49	91	98	8	39	145	7.4	.6	2.9	10.9
87	17	03	42	77	44	14	6	64	3.9	1.2	.5	5.6
88	18	03	48	80	122	250	8	380	9.4	19.3	.6	29.3
89	19	01	42	89	1	13	2	16	.1	1.1	.2	1.4
D. Cruise TO–60–1: May 1960												
10	May 6	08	52	160	26	110		136	1.9	7.8		9.7
14	7	03	36	150	7	5	<1	12	.7	.5	<.1	1.2
18	8	01	30	145	9	72		81	1.1	8.9		10.0
23	9	01	35	91	21	6		27	2.2	.6		2.8
27	10	01	25	114	34	56	<1	90	5.0	8.3	<.1	13.3
29	11	03	39	93	9	5		14	.8	.5		1.3
33	12	03	45	91	67	11		78	5.5	.9		6.4
37	13	08	44	122	338	14	11	363	28.4	1.2	.9	30.5
40	15	03	44	95	70	32		102	5.9	2.7		8.6
44	16	03	45	114	40	26	9	75	3.3	2.1	.7	6.1
48	17	02	43	109	29	10	3	42	2.5	.9	.2	3.6
52	18	03	43	110	77	8	2	87	6.6	.7	.2	7.5
56	19	03	37	120	14	9		23	1.4	.9		2.3
59	20	03	43	150	60	1,532	4	1,596	5.2	131.8	.3	137.3
E. Cruise TO–60–2 (STEP–1): September–December 1960												
1	Sept. 27	17	36		29	20	2	51	3.0	2.0	.2	5.2
2	30	06	52		148	34	11	193	10.5	2.4	.8	13.7
3	Oct. 1	06	62		126	53	8	187	7.5	3.2	.5	11.2
4	2	06	53		151	29	3	183	10.5	2.0	.2	12.7
6	8	06	50		166	449	2	617	12.3	33.2	.1	45.6
9	10	*06	45		113	50	22	185	9.3	4.1	1.8	15.2
11	11	11	48		83	15	3	101	6.4	1.2	.2	7.8
17	15	17	51		26	27	6	59	1.9	2.0	.4	4.3
19	16	17	51		52	11	8	71	3.7	.8	.6	5.1
23	17	17	49		94	40	4	138	7.1	3.0	.3	10.4
27	29	14	52		19	124	1	144	1.4	8.8	.1	10.3
30	30	*14	47		28	55	<1	83	2.2	4.3	<.1	6.5
32	31	18	51		20	4	3	27	1.5	.3	.2	2.0
35	Nov. 1	18	51		6	21	2	29	.4	1.5	.2	2.1
38	3	18	57		10	60	4	74	.6	3.9	.3	4.8
42	5	14	49		29	3	7	39	2.2	.2	.5	2.9
45	7	14	52		86	16	28	130	6.1	1.1	2.0	9.2
50	18	18	54		56	34	<1	90	3.8	2.3	<.1	6.1
55	19	18	49		26	170	<1	196	2.0	12.8	<.1	14.8
59	22	18	50		37	19		56	2.7	1.4		4.1
64	24	18	49		16	1	2	19	1.2	.1	.1	1.4
69	27	18	45		17	13	2	32	1.4	1.1	.1	2.6
73	29	17	49		64	2	<1	66	4.8	.2	<.1	5.0
77	Dec. 2	17	49		78	7	3	88	5.9	.5	.2	6.6
85	4	16	49		68	11	8	87	5.1	.8	.6	6.5

See footnotes at end of table.

TABLE 1.—*Actual volumes and standardized volumes for fishes, crustaceans, cephalopods, and total micronekton from 131 standard night hauls of a 1.5–m. net*—Continued

Station [1] number	Date	Area [2]	Time [3]	Depth [4]	Actual volumes				Standardized volumes			
					Fishes	Crustaceans	Cephalopods	Total	Fishes	Crustaceans	Cephalopods	Total
F. Cruise TO–61–1: March–April 1961												
2	Mar. 17	04	53		83	30	8	121	5.8	2.1	.5	8.4
5	19	04	50		177	59	96	332	13.1	4.4	7.1	24.6
14	22	05	51		142	48	32	222	10.3	3.5	2.3	16.1
16	23	04	50		94	432	5	531	6.9	32.0	.4	39.3
18	24	04	49		116	50	22	188	8.7	3.8	1.7	14.2
22	29	04	49		138	20	40	198	10.4	1.5	3.0	14.9
27	Apr. 1	05	49		43	43	15	101	3.2	3.2	1.2	7.6
29	2	04	51		69	55	26	150	5.0	4.0	1.9	10.9
32	3	04	49		84	32	4	120	6.3	2.4	.3	9.0
36	4	04	49		81	30	54	165	6.1	2.3	4.1	12.5
38	6	04	49		87	22	18	127	6.6	1.7	1.3	9.6
40	7	04	49		36	7	36	79	2.7	.5	2.7	5.9
Total, all cruises					12,756	25,240	2,008	40,004				

[1] See figure 1 for location of stations.
[2] See figure 5 for location of areas.
[3] Duration of haul.
[4] Maximum depth of haul measured by bathythermograph.

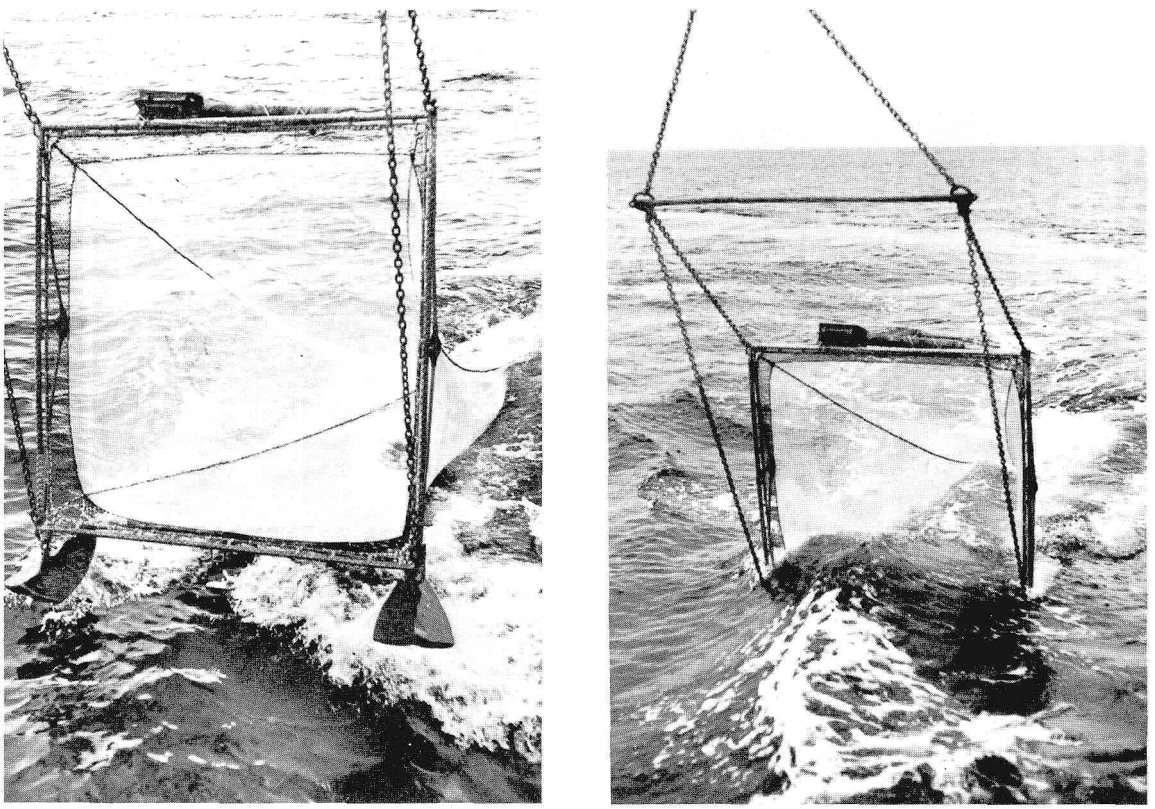

FIGURE 3.—Views of the 1.5–m. net, showing attachment of towing bridles, depressors, and bathythermograph (along upper side of square frame).

axis of the mesh is parallel to the long axis of the net. The ratio of total filtering area to area of mouth aperture (area of nylon thread included in the filtering area) is about 7.6:1. The detachable cod end is made of 56XXX nylon or silk grit gauze, with mesh apertures 0.31 mm. wide; the choice of this material was dictated purely by convenience (the same type of cod end was routinely used on the same cruises for collecting zooplankton). A larger mesh might have served equally well. Lengths of 6-mm. galvanized-iron welded-link chain are attached at one end to the four corners of the square frame and at the other end (in pairs, right side and left side) to the ends of a 1.5-m. galvanized-iron bar of 25-mm. diameter. Two similar chain bridles from the ends of the bar are attached to a swivel at the end of the 10-mm. towing wire rope. The arrangement and approximate lengths of the chain bridles are shown in figure 3. One sinker was attached to each bottom corner of the square frame; two 45-kg. cylindrical iron weights were used during cruise TO-58-1, but these were replaced by two 20-kg. bronze streamlined depressors during the other cruises.

When the 45-kg. weights were used, the hauling operation was as follows: 450 m. of the 10-mm. wire rope were paid out at 25 m./min. and then immediately retrieved at 10 m./min., all at a ship speed of 5 knots. The haul, thus, took about 63 min. (in practice there was some variation from the desired winching speeds—see table 1). It was found, by attaching a bathythermograph to the frame of the net, that the maximum depth ranged from 72 to 115 m. and averaged 90.2 m. (12 hauls). When the 20-kg. depressors were used, 350 m. of wire were paid out and retrieved at the same winch and ship speeds, for a total hauling time of about 49 min.; the maximum depth ranged from 73 to 160 m. and averaged 95.5 m. (48 hauls). Because the difference between the means is small, the two types of operation have been considered comparable except for the time; the second type has been continued routinely, and the catches from both types of hauls have been considered to represent broadly the quantity and quality of micronekton present at night that can be caught by the net in the upper 90 to 95 m. of ocean. The actual depths, where obtained by bathythermograph, are listed in table 1. The depressors were, as expected, more effective in sinking the net than the much heavier cylindrical weights. A sampling depth of 90 to 95 m. would be expected with the Isaacs-Kidd midwater trawl also, if used on 350 m. of cable at a towing speed of 5 knots, according to tests made by Aron, Ahlstrom, Bary, Bé, and Clarke (1965).

No attempt was made to use a flowmeter in the net routinely, because it was thought that it might prevent the entry of some of the micronekton. Flowmeters were used twice to estimate the filtration coefficient of the net by making successive tows in a precisely identical manner, and of precisely the same duration, first with a flowmeter in the mouth of a fully rigged net, and then with the net removed and only flowmeter, frame, bridles, and depressors remaining. The ratio of flowmeter readings was 0.757 on the first trial and 0.738 on the second trial (3 years later). The net, used as described, apparently filters 74 to 76 percent of the water available (product of net-mouth area in square meters and distance towed in meters). Because the two estimates of the filtration coefficient are so close, the one first obtained, which had already been used to calculate volume of water strained on many of the hauls, was used for all. Water was available for filtration at the rate of 1,000 $m.^3$ every 2.79 min. at a speed of 5 knots; the rate of actual filtration was estimated by the coefficient 0.757 to be 1,000 $m.^3$ every 3.69 min. By dividing the measured volume by the total number of minutes for the haul and multiplying by 3.7, the micronekton was standardized to volume per 1,000 $m.^3$ of water strained (see table 1).

The most important feature of this net is the mesh size, which retains most of the micronekton and releases most of the zooplankton, and, more importantly, is uniform throughout the net. This uniformity gives the standardized volumes a much more precise biological meaning than would be possible for similar measurements with a mixed-mesh net; some parts of a mixed-mesh net permit more escapement of organisms than other parts. Aron (1959, 1962a, 1962b) admitted this problem in relation to the Isaacs-Kidd midwater trawl, which has larger meshes near the mouth than near the cod end (as do most other nets and trawls hitherto used for catching micronekton and zooplankton). King and Iversen (1962), who used the Isaacs-Kidd and other trawls, observed that

"The nature of the trawling gear * * * did not permit or justify an exact quantitative evaluation of the catch." The Isaacs-Kidd and similar mixed-mesh midwater trawls seem to be much more useful for qualitative than for quantitative sampling. Pearcy and Laurs (1966) used an Isaacs-Kidd trawl lined with material of uniform small mesh size (5 mm. square).

The main difficulty with the 1.5–m. net is that some organisms, presumably the larger and more mobile ones—e.g., flying fish (Exocoetidae)—probably avoid the net or escape through the mouth after entry; doubtless similar escapement also occurs from the Isaacs-Kidd trawl and others of similar size. Apart from such unknown losses, standardized volumes from the 1.5–m. net estimate real concentrations of micronekton in the water.

The 1.5–m. net has proved to be easy to operate; it can be fished by two men, plus a winchman, except in rough weather or heavy swells, when it is prudent to employ a third man. Specimens caught generally are in good condition.

The standard 1.5–m. net hauls were made at night—usually about midnight—because most kinds of micronekton are more readily caught in near-surface waters by night than by day (Aron, 1959, 1962a; King and Iversen, 1962; Pearcy, 1964; and table 2 of this paper). It would be necessary to lower the net to greater depths, at appreciably greater cost in ship time, to obtain similar samples in the daytime. Pearcy (1964) found no obvious difference in numbers of mesopelagic fishes caught with the Isaacs-Kidd midwater trawl at different times of night at the same station, and I assume that time of night is equally unimportant for the other animals sampled.

HIGH–SPEED NET: DESCRIPTION, OPERATION, AND PERFORMANCE

The high-speed net is an elongated cone with a base (the mouth of the net) 70 cm. in diameter and measures 2.6 m. from the center of the base to the apex (fig. 4). The base or mouth is surrounded by a narrow selvage laced to a circular frame of galvanized iron. The opening at the apex

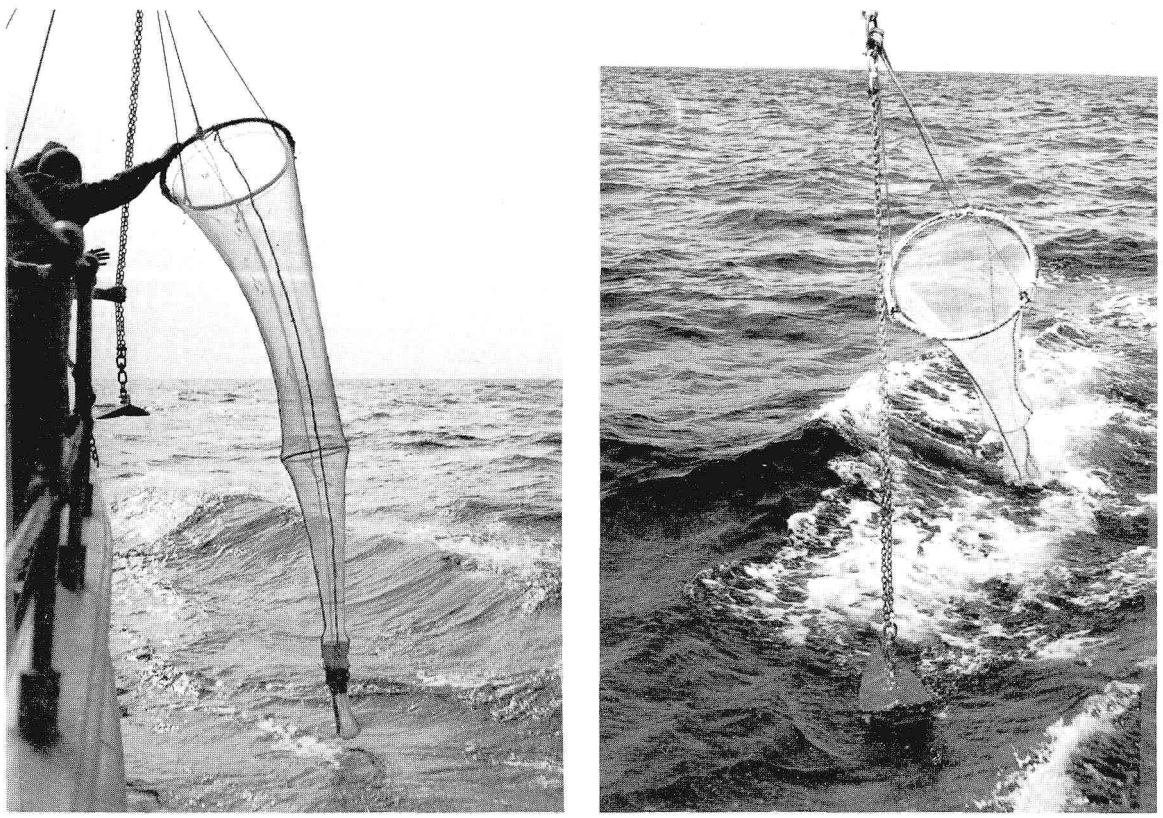

FIGURE 4.—Views of the high-speed net, showing attachment of towing bridles and depressor.

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contains a brass fitting set in canvas, by which a cod end (the same cod end as for the 1.5–m. net; length not included in the 2.6–m. length of net) can be attached. The material and mesh of the net are the same as for the 1.5–m. net and uniform throughout. The ratio, total filtering area to mouth-aperture area (area of nylon thread included in the filtering area), is about 7.5 :1. Three plastic cord bridles extend from the circular frame to the swivel at the end of the towing wire (the same as for the 1.5–m. net); one 20–kg. bronze streamlined depressor is also attached to this swivel on a 2.4–m. length of 6–mm. welded-link chain so that it is below the net when both are in the water.

This net has been used only for horizontal hauls at cruising speeds of 9 to 12 knots, with 50 m. of towing wire out. Under these conditions it is about 10 m. below the surface (as determined with an attached bathythermograph). Most hauls with the high-speed net were made at night, because daytime hauls caught little. Generally, only one man and a winchman were required to operate the net; when other operations were compatible, the normal routine was to tow the net about 2 or 3 hours, haul it up to change the cod ends, and put it out again for a similar tow, all without stopping or slowing the ship. The main difficulties (in order of magnitude) were that (a) other operations often did not permit a reasonably uniform time for each tow, (b) the organisms caught were generally in poor condition (with much flesh lost) when removed from the cod end, and (c) wear generally forced replacement of the net after about 1,000 to 1,500 nautical miles (1,850 to 2,780 km.) of towing (sooner, if catches were heavy).

The filtration coefficient (at 9 knots), estimated twice in 3 years in the same way as described for the 1.5–m. net, was 0.938 for the first trial and 0.811 for the second. This coefficient shows that the high-speed net filters more efficiently at 9 knots than the 1.5–m. net does at 5 knots; the two estimates do not agree as well as the two for the 1.5–m. net.

The value of 0.938 for the coefficient had been used to standardize the volumes of catches from two cruises before the 0.811 value was determined; these standardized volumes have been retained for the present, since there is no reason to prefer the second value of the coefficient to the first. Volumes were standardized by dividing actual volumes by the number of minutes for the haul and multiplying by 10.0, since I calculated (from the 0.938 coefficient) that the net actually strained 1,000 $m.^3$ of water every 9.96 minutes. The standardized volumes are not tabulated in this paper, but the actual volumes for cruises TO–59–2 and TO–60–2 have been listed elsewhere (Blackburn, Griffiths, Holmes, and Thomas, 1962; Scripps Institution of Oceanography, 1961), and some of the standardized volumes for those cruises are summarized here in figures 18 and 19.

TREATMENT OF COLLECTED MATERIAL

The net catches were preserved in 10 percent buffered formalin (4 percent formaldehyde). All organisms except sea snakes, which are dangerous to handle, were included. Later I sorted the material (a few days later for the major cruises TO–58–1 and TO–60–2; up to 3 years later for other cruises) into four components—fish, crustaceans, cephalopods, and others—and measured the displacement volume of each of the first three components. I also noted the taxonomic composition of each component, by volume or number of individuals, as far as I was able. The fourth component consisted of tunicates, medusae, siphonophores, chaetognaths, heteropods, and pteropods, which are not considered to be micronekton and are not significant in the diets of tropical tunas.

Subsequently, the fish, crustaceans, and cephalopods were sorted, generally to family or, for cephalopods, to genus and species. Displacement volumes of these groups for each haul were then measured (for large samples of fish and crustaceans) or estimated from the number and size of the organisms (for cephalopods, and small samples of fish and crustaceans), and these measurements were reconciled with the original measurements of the three main groups. Occasionally the reconciliation was impossible as a result of unauthorized removal of specimens between the first and the second sorting; the taxonomic composition of the catch by volume was then estimated from the notes made at the first sorting and, rarely, from the catch at another station adjacent in space and time. I realize that the measurements of minor groups are not entirely free from error, but the errors are small and scattered and mostly affect the scarcer groups. The sorted material from these hauls has been catalogued and stored at the Scripps Institution of Oceanography.

CHANGES IN MICRONEKTON FROM DAY TO NIGHT ON SUCCESSIVE DAYS IN THE SAME AREA

Table 2 gives the standardized volumes from standard hauls made alternately about local noon and midnight during a 20-day period of tracking a drifting surface-current drogue off the coast of southern Mexico (cruise TO–62–1 or TEMPO, August 1962). The hauls were encompassed by a rectangle bounded by lat. 14°58.0′ N. and 15°17.8′ N. and long. 99°49.7′ W. and 100°48.0′ W.; the same body of surface water was sampled throughout the period. Table 2 shows the expected striking difference between noon and midnight volumes of total micronekton, which have ranges of 0.4 to 2.1 and 4.3 to 14.3 ml. per 1,000 m.³ respectively. The main reason for this difference is that several families of mesopelagic fishes—Myctophidae, Gonostomatidae, Stomiatidae, Bathylagidae, and Melamphaidae—occurred frequently in midnight catches although they were practically unrepresented in noon catches. Bregmacerotidae also occurred exclusively in the midnight catches, and Carangidae and Leptocephali were taken in larger numbers at midnight than at noon. The principal crustacean groups in this series of micronekton samples were hyperiid amphipods and stomatopod (squillid) larvae, both of which tended to be more abundant in the noon catch than in the midnight catch on any particular day. These groups were the most abundant in the noon samples, which contained comparatively few fishes. Cephalopods occurred in small, broadly similar, amounts in both noon and night samples.

The noon and night series are, thus, greatly different quantitatively and qualitatively; on the other hand, the hauls in each of these series have a great deal of similarity, especially between those made on consecutive days. Consecutive night hauls seldom differed in total volume by a factor of >2 and consecutive noon hauls seldom differed by a factor of >3. Consecutive samples in either series

TABLE 2.—*Micronekton from standard 1.5-m. net hauls made alternately about local noon (D) and local midnight (N) during a 20-day drogue-tracking experiment on cruise TO–62–1 (TEMPO), August 11 to 30, 1962*

[Asterisk means <0.1 ml. per 1,000 m.³]

Haul No.	D or N	Time (minutes)	Group (Ml./10³m.³)													
			Myctophids	Gonostomatids	Leptocephali	Carangids	Stomiatids	Bathylagids	Melamphaids	Bregmacerotids	Other fishes	Hyperiids	Squillid larvae	Other crustaceans	Cephalopods	Total micronekton
1	D	55									0.3	0.3	(*)		0.1	0.7
2	N	50	2.8	1.1	0.3			1.0	0.6	0.3	.3	.6		0.3	.3	7.6
3	D	50	.1	.2							.1	1.4	(*)		.3	2.1
4	N	50	8.9	.4	.2	2.0						.2	0.2	.1	.2	12.2
5	D	50									.1	.3	.1			.4
6	N	50	6.1	.7	.2				.1		.1	.2	(*)		.1	7.5
7	D	49			.2						.1	.4	.1	(*)	.1	.9
8	N	50	5.8	.2	1.5	(*)					.1	.1	(*)	.1	.1	7.9
9	D	49			(*)						(*)	.4	.2	.1	.1	.8
10	N	49	2.9	.3	1.7	(*)					(*)	.3	.1	.1		5.4
11	D	49									.2	.2	(*)	.1	.6	1.1
12	N	50	6.6	.6	.2						.1	.2	(*)	.1	.2	8.0
13	D	49									.2	.7	.1	(*)	.2	1.2
14	N	50	5.9	.5	2.0	.4					(*)	.2	(*)	.1	.1	9.2
15	D	49		(*)	.1						.1	.7	.1	.1	.2	1.3
16	N	47	7.3	2.2	2.2	1.6					.1	(*)	(*)	.1		13.5
17	D	48			.1						(*)	.2	.1	.1	.1	.6
18	N	50	6.3	.9	.8		0.4				.1	.2	(*)	.2	.4	9.3
19	D	48										1.0	.1		.1	1.2
20	N	49	.8	12.8	.1	(*)	.4			(*)	.1	(*)		.1	(*)	14.3
21	D	49										.2	.2			.4
22	N	49	2.9	1.3	.5	.8	.4		.1	(*)	.2	.1	(*)	.1	.1	6.5
23	D	50			.1	.2					.1	.3	.1		.3	1.1
24	N	50	3.2	.9	.4		.7	.2	.8	.1		(*)	(*)	.1	(*)	6.4
25	D	50			(*)	.4					.4	.2	.2	.1		1.3
26	N	50	3.9	.3	.2		.3	.4	.7	.1	.1			.1	(*)	6.1
27	D	49			(*)						(*)	.4	.2		.2	.8
28	N	50	4.7	1.0	(*)	(*)	.3	.1			.1	(*)			.2	6.4
29	D	48									.1	.8	.5			1.4
30	N	50	2.8	.9			.2	.4	.2	(*)	.1			.1		4.7
31	D	49									.2	.5	.7	.1	.1	1.6
32	N	55	3.3	.5	.1		.2	.6	.1	(*)	.1	(*)	(*)	.1	(*)	5.0
33	D	49										.4	.3	.1	.1	.9
34	N	50	5.7	1.0	.4		(*)	.3	(*)	.3	.1	(*)	(*)	.1	(*)	7.9
35	D	49									(*)	.3	.2		(*)	.5
36	N	50	3.3	.4	.2	(*)	.1	.2	.3	(*)	.1		(*)	(*)	.2	4.8
37	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
38	N	50	1.3	.7	.2		.8	.5	.4	.2	(*)	(*)		.2	(*)	4.3
39	D	49											.2		.2	.4

[1] Haul omitted.

also did not differ greatly in taxonomic composition (table 2). These results were expected because all the catches were made in the same body of surface water. They suggest that the catches of the other, more isolated, single hauls listed in this paper are reasonably representative, both qualitatively and quantitatively, of the micronekton population sampled.

AREAL DISTRIBUTION OF MICRONEKTON BY TAXA

Table 1 gives the actual and standardized volumes of fish, crustaceans, and cephalopods for each of the 131 standard night hauls of the 1.5-m. net, excluding the special series mentioned in the previous section. It also gives the number, date, and area (see below) of each of the stations at which each haul was made.

The approximate position of each station is shown in figure 1 or figure 2. The actual positions of the stations are available from the following sources: cruise TO–58–1, Holmes and Blackburn, 1960; TO–59–1 and TO–59–2, Blackburn et al., 1962; TO–60–1, Scripps Institution of Oceanography, 1967; TO–60–2, Scripps Institution of Oceanography, 1961; TO–61–1, Blackburn, unpublished.

The stations were assigned to areas which are shown in figure 5. Areas 1 to 14 are those recognized by Alverson (1963a) in a study of the food of tropical tunas taken in the U.S. surface tuna fishery. Areas 15 to 18 enclose stations occupied farther offshore. No stations with micronekton hauls were occupied in areas 7 and 13; areas 11 and 12 have been combined in this paper; a few stations close to the boundaries of certain areas have been assigned to those areas for convenience.

For the 131 hauls, the actual total volumes were: 12,756 ml. of fish; 25,240 ml. of crustaceans; and 2,008 ml. of cephalopods; grand total, 40,004 ml. These numbers are given by taxa (including some species) and areas in table 3, which is the most convenient way of presenting the composition of the whole material. Some of these data are used in later sections (tables 8–15).

Although many families are listed in table 3, only 10, together with the Leptocephali of the suborder Apodes (Pisces) which have not been classified to family, contributed more than 1 percent of the grand total; these 11 groups combined accounted for 93.4 percent (table 4). The Euphausiacea of table 3 are all members of the family Euphausiidae.

Table 5 gives standardized volumes of the principal fish and crustacean components of the micronekton as listed in table 4, for each station. The sum of volumes equals the standardized volumes for total fish and total crustaceans in table 1.

Figures 6 to 13 show distributions of standardized group volumes for the two most extensive cruises, TO–58–1 (SCOT) and TO–60–2 (STEP–1); figure 1 identifies the stations; the data are from tables 1 and 5. These cruises were made in the Northern Hemisphere in the northern spring and the Southern Hemisphere in the southern spring, respectively. The two space-time situations were comparable climatically; trade winds were declining in average strength from their seasonal maximum about late winter or early spring. A general similarity should, therefore, exist between the two situations in certain wind-connected upper-ocean features which affect the production and distribution of organisms. For instance, amount of coastal upwelling, mean depth of mixed layer, and mean velocity of westerly surface currents would all be expected to be declining, as a result of the decrease in the trade winds, in each situation. Because the two cruises were comparable in range of latitude from the Equator, and range of distance offshore, it is reasonable to combine biological data from both in the way that has been done in figures 6 to 13. These figures, then, give the best available picture of regional distribution of the standing crops of various kinds of micronekton over a large part of the eastern tropical Pacific, under comparable physical conditions.

Figures 6, 7, and 8 chart the distribution of fish, crustaceans, and cephalopods, respectively (data from table 1). They show clearly that the standing crop of each of these three components of the micronekton declines from onshore to offshore. Table 6 shows the magnitude of these changes.

This distribution is rather similar to that of standing crops of chlorophyll *a* and zooplankton in the same region (Brandhorst, 1958; Bennett, 1963; Forsbergh and Joseph, 1964; Blackburn, 1966b). Each of the three standing crops—chloro-

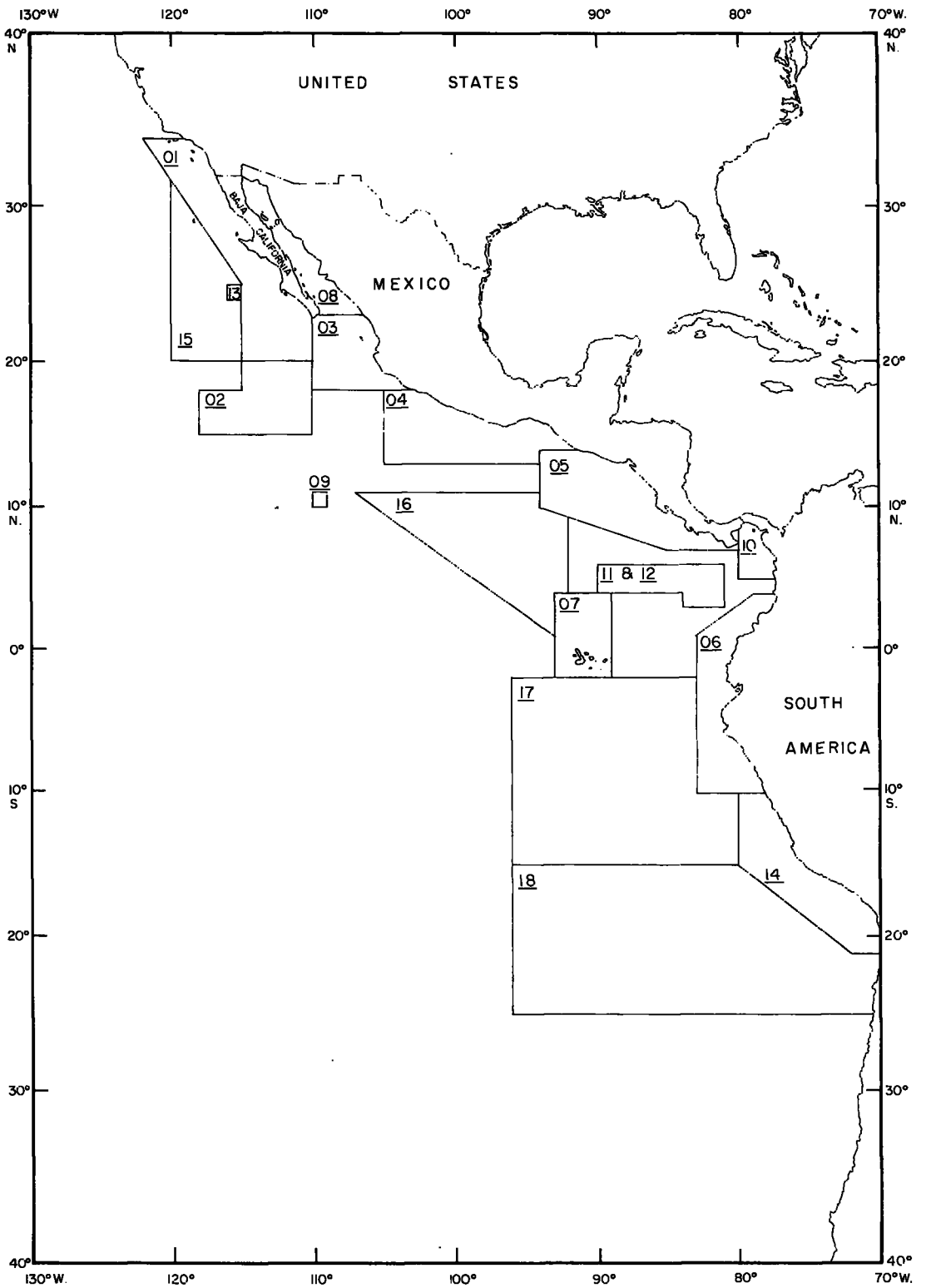

FIGURE 5.—Areas to which standard night hauls were assigned in table 1.

Table 3.—*Actual volumes of micronekton from table 1, classified by taxa and areas*

[Groups with <1 ml. for the combined areas are unlisted; asterisk means <1 ml. for a particular area. Abbreviations in the left-hand column signify: a.—adult, j.—juvenile, l.—larva, m.—megalops, ph.—phyllosoma, po.—postlarva, pu.—puerulus, r.—remains, unid.—unidentified, z.—zooea; if no ontogenetic stage is specified, the adult stage, or a mixture of adults and younger stages is meant.]

Animals	Area Number															
	01	02	03	04	05	06	08	09	10	11, 12	14	15	16	17	18	Total
CEPHALOPODA																
Decapoda																
Enoploteuthidae:	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	
Pterygioteuthis giardi	7					6			15	8			4	6	3	49
Do. j	(*)								1				1	4	2	8
Pterygioteuthis sp. j			1													1
Abraliopsis morisi	9	7	116	434	305	18	9		55	45	6	3	15	7		1,029
Do. j			5	24	7	4	2		3	5			1			51
Do. l			1		1											2
Abraliopsis sp			2	9	3						2				1	17
Do. j															1	1
Abralia sp			2	13	5			1								21
Do. j													1			1
Onychoteuthidae:																
Onychoteuthis banksi				7	5											12
Do. j				11	1											12
Onychoteuthis sp. j					1											1
Unid. Onychoteuthidae					1											1
Do. j				1	1									1		3
Cranchiidae:																
Leachia eschscholtzi	2	1	35	342	88	12		5		11	23		40	5	3	567
Do. j		(*)	8	15	7			(*)	(*)	2	2		3		2	39
Do. l					1										(*)	1
Leachia sp				2												2
Do. j			1	1												2
Pyrgopsis sp	(*)		1	3	4						1				1	10
Do. j	1		12	7	1						1					22
Liocranchia reinhardti									5							5
Do. j			1			1							1			3
Teuthowenia sp										2						2
Do. l					(*)	1										1
Unid. Cranchiidae j	(*)		1													1
Do. l				(*)	1								1			2
Bathyteuthidae:																
Ctenopteryx sicula					1					3						4
Ctenopteryx sp						2								1		3
Octopodoteuthidae:																
Octopodoteuthis sp													1			1
Ommastrephidae unid	5															5
Histioteuthidae unid				2	2											4
Unid. squid r	2		3	20	72					1	(*)			1		99
Do. j					1	1					1					3
Do. l	(*)	(*)	(*)	2	1	1		(*)	(*)	(*)		(*)	2	1	(*)	7
Octopoda																
Tremoctopodidae:																
Tremoctopus sp. j	2															2
Argonautidae:																
Argonauta sp		1														1
Do. j	1				2											3
Amphitretidae:																
Amphitretus sp				5						(*)						5
Do j				2												2
Do. l			(*)	1	2	(*)					(*)			(*)		3
Total Cephalopoda	29	9	189	901	513	46	11	6	79	77	36	3	70	26	13	2,008
CRUSTACEA																
Isopoda	(*)	1	(*)	(*)	(*)											1
Amphipoda																
Gammaridea		(*)	(*)	(*)	(*)			2	(*)				3			5
Hyperiidea:																
Phronimidae	4	2	13	33	24	5	2	2	1	13	2	(*)	8	6	6	121
Phrosinidae	(*)	(*)	3	7	7	4		1	2	7			5	1	7	44
Oxycephalidae	2	1	9	23	12	5	(*)	3	1	5	2		7	5	5	80
Platyscelidae			2	7	7	4		(*)	(*)	1			7	(*)	(*)	28
Paraphronimidae				3	5	(*)		(*)	1	5	2		3	3	2	24
Vibiliidae	3	4	4	9	6	(*)	(*)	1	1	3	2		(*)	3	4	40
Scinidae	(*)	2	(*)	(*)	(*)	3		(*)	(*)	(*)				(*)	3	8
Unid. Hyperiidea	1	(*)	6	17	6	5		2	1	5	5		4	4	4	60
Euphausiacea	1,528	38	265	91	101	438	104	6	23	163	170	6	71	29	250	3,283
Decapoda																
Sergestidae	8	1	17	82	181	40	2	2	49	138	2	4	92	27	10	655
Do. po			2	(*)	5	(*)		1	(*)	(*)			3	2	2	15
Penaeidae	1		1,516	(*)	20	46	4		(*)	8	3	1	8	28	16	1,651
Do. z	2	(*)	8	27	10	5	2		1	(*)			(*)	(*)		55
Pasiphaeidae	277												4			281
Oplophoridae				(*)		2									2	4
Pandalidae	1					2							3	(*)	(*)	6
Amphionidae l	(*)		2	(*)	5	3		2	1	(*)			4	(*)	3	20
Unid. Caridea				2												2
Palinuridae ph	2	1	4	13	10	(*)		1	(*)	7			8			46
Do. pu			2	8	(*)				1	1			(*)			12
Galatheidae:																
Pleuroncodes planipes	15,474	470	2									191				16,137
Unid. Galatheidae z & j	(*)		1	15	(*)	3	1						(*)	(*)		20
Porcellanidae z	1	2	5	19	5	3		1	1	5	1		1	(*)	(*)	44
Paguridae m	(*)		6	17	6	(*)			1	5			(*)			35
Hippidae z	(*)		2	11	(*)						(*)		(*)	(*)	(*)	13

Table 3.—*Actual volumes of micronekton from table 1, classified by taxa and areas*—Continued

Animals	Area Number															
	01	02	03	04	05	06	08	09	10	11, 12	14	15	16	17	18	Total
CRUSTACEA—Continued	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Ml.*	
Albuneidae z	(*)		3	23	5	(*)	(*)		(*)	(*)			3			34
Portunidae:																
Portunus affinis				830	37				130	65						1,062
Euphylax dovii									1							1
Unid. Portunidae					4											4
Do. j				1						(*)						1
Dorippidae z	(*)		4	18	7	5	1		2	(*)			(*)	1		38
Unid. crab m	3		8	36	8	5	1	2	1	6	2		1	2	(*)	75
Unid. decapod l	4	1	9	25	8	5	2	2	1	6	5		4	3	4	79
Do. r	(*)		2	(*)	(*)	(*)								(*)		2
Stomatopoda																
Squillidae 1	33	8	164	228	109	32	5	4	31	45	2	3	32	5	(*)	701
Do. po. & a	(*)		(*)	477	15											492
Unid. crustacea r	3			12	11	(*)			6	21		1		3	4	61
Total Crustacea	17,347	531	2,059	2,034	614	615	124	32	256	509	198	206	271	122	322	25,240
PISCES																
Albulidae 1				2		2										4
Gonostomatidae:																
Vinciguerria spp	125	62	272	322	84	33	14	6	60	28	17	19	48	69	22	1,181
Unid. Gonostomatidae	4	7	24	(*)	3							4	4	1	19	66
Stomiatidae	16		20	42	46	10		2	53	31	(*)	5	18	27		270
Melanostomiatidae				14	8								3			25
Astronesthidae 1									1	(*)						1
Sternoptychidae	(*)			2	1	46		(*)	1	(*)			3	1	21	75
Idiacanthidae		3		55	45			1	6	34						144
Myctophidae	1,342	134	523	1,557	403	452	304	21	240	225	125	52	278	311	115	6,082
Bathylagidae	8		3	27	39	13			5	1	2		11	5	(*)	114
Paralepididae	1		2	13	6	4		(*)	8	1		(*)	1		1	37
Scopelarchidae	1		2	13	9	7	(*)	(*)						2	(*)	34
Synodontidae 1					1											1
Nemichthyidae	3			22	60	21				5			4			115
Apodes: leptocephali	89	78	651	2,030	558	96	30	2	97	199	2	7	294	(*)	6	4,139
Belonidae 1			1													1
Scomberesocidae j											6					6
Hemirhamphidae 1						1										1
Exocoetidae j			7													7
Gadidae 1			(*)			2								(*)		2
Bregmacerotidae	5	2	50	36	6				7	18			11			135
Trachypteridae 1													1			1
Regalecidae 1										2			2			4
Heterosomata po	(*)			45	28	4	(*)						1			78
Holocentridae 1			1													1
Melamphaidae			5	20	4	4	16				1			1		51
Syngnathidae 1				2												2
Thunnidae po	(*)		(*)	(*)	2				(*)							2
Trichiuridae po						6			5							11
Gempylidae po														3	(*)	3
Coryphaenidae l			(*)	2						(*)			(*)			2
Bramidae l				(*)									1			1
Stromateidae	(*)		7	8	23		(*)			2			1	2	2	45
Carangidae	(*)			5	1	2			2		9			4	2	25
Serranidae j			2	4	3				1	(*)						10
Priacanthidae l				1	1											2
Callionymidae l										1						1
Scorpaenidae po	(*)		3	15	5				3	1						27
Labridae po	(*)		4	2	4			(*)		1			(*)			11
Blennidae l			1							1						2
Ophididae l			5	2	2	1				1						11
Balistidae l	1															1
Ostracidae j		1														1
Tetraodontidae j			1					1		1						3
Diodontidae j				2												2
Unid. pisces			4	13	1								1			19
Total Pisces	1,595	287	1,588	4,256	1,343	704	364	33	489	552	162	87	682	426	188	12,756

TABLE 4.—*Major components of the micronekton; actual volumes from table 3, for all areas combined*

Family or suborder	Actual volume	Percentage of total volume
	Ml.	*Percent*
Enoploteuthidae	1,180	2.95
Cranchiidae	657	1.64
Euphausiidae	3,283	8.21
Sergestidae	670	1.68
Penaeidae	1,706	4.26
Galatheidae	16,157	40.39
Portunidae	1,068	2.67
Squillidae (larvae)	701	1.75
Squillidae (postlarvae and adults)	492	1.23
Gonostomatidae	1,247	3.12
Myctophidae	6,082	15.20
Apodes (Leptocephali)	4,139	10.35
All others	2,622	6.55
Total micronekton	40,004	100.00

phyll *a*, zooplankton, and micronekton—is positively correlated with the others in the area of cruise TO–58–1 (Blackburn, 1966a). The distributions reflect the fact that physical situations which lead to high production of organisms, namely upwelling and vertical mixing by wind over shoal pycnoclines, are better developed along the eastern sides than in other parts of tropical oceans, except along the Equator (Wooster and Reid, 1963; Wyrtki, 1966). Crops of chlorophyll *a* and zooplankton are fairly high in offshore waters along the Equator (Forsbergh and Joseph, 1964; Blackburn, 1966b); this paper presents no data on micronekton for those waters, but King and Iversen (1962) found more micronekton near the Equator than elsewhere in the central tropical Pacific. In nonequatorial offshore waters the pycnoclines lie deeper and mixed layers are thicker (Wyrtki, 1964b); the likelihood of chemical enrichment from below is diminished, and, if there is such enrichment, part of the resulting plant crop will be carried by mixing below the compensation depth.

The standing crop of micronekton is not uniformly high in the coastal region. It tends to be higher in some parts of the region than in others. The standardized volumes of total micronekton for the 40 onshore stations (table 6) range from 113.3 to 2.9 ml. per 1,000 m.[3], and this group can be divided into an upper two deciles (8 stations) and a lower eight deciles (32 stations). Table 7 shows that the eight stations with the higher total volumes also had the higher mean volumes for each of three main components of the micronekton.

The eight stations with high volumes are numbers 49, 63, 77, 81, 142, 144B, and 146 of cruise TO–58–1, and number 6 of cruise TO–60–2. With the possible exception of station 142, they all occur in localities which are known to be especially productive of organisms, as a result of physical processes which operate at or a few months prior to the season at which the micronekton was collected. Stations 144B and 146 occur in the coastal upwelling region off Baja California (Reid, Roden, and Wyllie, 1958; Blackburn, 1966b); stations 77 and 81 are in the Gulf of Tehuantepec where vertical mixing occurs over a shoal thermocline (Blackburn, 1962); station 49 lies in the "Costa Rica Dome" region where upwelling, from cyclonic flow, takes place (Wyrtki, 1964a; Holmes, MS.[4]); station 63 occurs in the coastal upwelling region of the Gulf of Panama (Forsbergh, 1963); and station 6 is in the coastal upwelling region off Peru (Wyrtki, 1963; Forsbergh and Joseph, 1964).

Station 142 is in the mouth of the Gulf of California, which is not known to be as biologically productive as the other areas just mentioned. The mixed layer is <20 m. thick in an average June, however (Wyrtki, 1964b) and was so when the station was occupied in June 1958; the possibility of chemical and biological enrichment, as a result of vertical mixing, therefore, exists. On the other hand, this station is very close to an island; the high volume of micronekton (mainly fishes, see table 1), therefore, may represent an "island effect."

The standing crop of cephalopod micronekton appears to diminish polewards from the tropics (fig. 8) even along the coast, but this trend does not hold with the fish and crustaceans.

Figures 9 to 13 show similar data, from table 5, for some of the major groups of fish and crustaceans. The distribution of myctophids (fig. 9), the largest group by volume among the fishes, is broadly similar to that of all fish (fig. 6). Standing crops decline from onshore to offshore, although not as markedly as crops of some of the other groups (table 6). Myctophids are also well represented in the micronekton off the west coast of the United States (Aron, 1962a; Pearcy, 1964) and in the central Pacific (King and Iversen, 1962); it is impossible to make close quantitative comparisons of standing crops from those regions with crops

[4] Holmes, Robert W. A contribution to the physical, chemical, and biological oceanography of the northeastern tropical Pacific (Scripps Institution of Oceanography, University of California. 357 pp.).

TABLE 5.—*Standardized volumes of the principal components of fish and crustacean micronekton in the hauls listed in table 1*

[Asterisk means <0.1 ml. per 1,000 m.³; see table 1 for standardized volumes of total fish and total crustaceans]

Station number	Fish components				Crustacean components							
	Mycto-phids	Leptoce-phali	Gonosto-matids	Others	Gala-theids	Euphau-siids	Penaeids	Portunids	Sergestids	Squillid larvae	Squillid adults	Others
	Ml./10³m.³											
A. Cruise TO-58-1 (SCOT): April to June, 1958												
1	1.1	0.1	0.3	(*)	3.4	0.2	(*)		0.1	0.1		
3	1.4		.8	0.3	5.7	.1	(*)		.1	(*)		(*)
5	.4	.3	.2	.1	1.8	.1			(*)	(*)		0.1
7	1.6	.7	.9			1.4				(*)		.2
10	1.0	1.2	.5			.5			(*)	.1		.1
12		(*)	(*)		23.2							(*)
14	3.8	1.4	1.0	.1		.2			(*)	.1		(*)
16	.8	.8	.5	.2		(*)				(*)		.2
18	.9	(*)	.1	(*)		.2			(*)	(*)		.5
22		.1	(*)	(*)		.1			(*)	(*)		.4
27	.3	.1	.2	.2		.1			(*)	.1		.4
29	1.4	1.3	.7	.3		.1			(*)	.1		.4
31	1.3	1.8	.3	.2		.2			.1	.2		.5
33	2.8	4.0	.4	.2		.3			2.3	.3		.7
35	2.0	.6	.3	.3		.7			1.3	.1		.4
36	4.3	3.3	.5	.4		1.6	0.3		.3	.4		.6
46	2.9	3.5	.6	1.8		.9	.2		1.3	.6		1.0
48	3.8	4.4	.5	2.4		.8	.1	0.2	1.5	.8		.7
49	3.5	2.3	1.7	3.4		.5	.2		.9	.8		1.2
51	1.1	1.1	.2	.7		.8	(*)		.9	.2		.9
54	2.0	2.1	(*)	.8		.7	.1		1.4	.4		.7
56	1.7	2.8	(*)	.9		1.8	(*)		1.4	.5		1.0
57	1.5	1.4	(*)	.6		.6	(*)	.7	.8	.4		.9
59	2.7	2.3	.6	.7		3.5	(*)	.8	2.1	1.0		1.3
61	1.7	.1	1.4	2.0		.3	(*)	6.3	.8	.4		.3
63	11.6	5.2	1.9	3.3		1.0	(*)	1.1	1.9	1.3		.9
69	4.0	1.8	.9	1.8		2.1	.1	2.3	1.0	.2		.8
71	1.9	1.8	.3	2.2		.7	.8	.4	1.0	.2		.7
73	2.6	4.9	.7	2.4		1.4	(*)	.4	.8	.6		.7
75	1.8	7.0	.9	1.8		.8	(*)		3.5	.8		1.4
77	2.2	14.4	2.2	.9		.7	(*)		.9	.8	(*)	1.2
81	7.0	16.4	2.1	2.3	(*)	.5	.1		.3	1.6		1.2
85	3.8	3.5	.5	1.6		.5	(*)		1.3	.6	1.5	1.0
87	.5	4.9	.3	.2		.3	(*)		.2	.3		.7
90	5.2	2.4	.7	.1		(*)	(*)		(*)	.2		.7
94	1.8	5.5	.9	.2		(*)	(*)			.1	(*)	.5
96	1.1	10.8	.2	.5		(*)	(*)	.4	(*)	.5	.1	1.0
98	6.4	4.6	2.2	.9		.1	(*)		.1	.3		.8
118	2.4	3.8	3.2	2.8		.1	(*)		(*)	.2		.7
135	3.7	4.0	2.2	1.5		.7			(*)	.5		.6
142	1.0	12.7	3.1	2.2		.3	(*)		.2	2.3	(*)	.8
144A	10.2	4.0	.6	.4	.2	2.5	(*)		(*)	.7		.4
144B	9.4	.3	.9	1.1	89.9	1.1	(*)		(*)	.2		.1
146	.2	.1		.1	100.7	(*)				(*)	(*)	12.2
B. Cruise TO-59-1: January to February, 1959												
1	12.1		.2	.1	26.4	2.8			(*)	(*)		
3					8.0	(*)	(*)					
5			(*)		32.7	.3				(*)		.1
7	3.5	7.2	.8	.1	.2	(*)	(*)			.5		.1
9	1.9	2.3	.7	.6		.1	(*)		(*)	.5		.3
11	5.0	2.6	.2	(*)		(*)	(*)			.2		.3
13	4.8	2.3	.1	(*)		(*)	(*)			.1		.5
15	4.3	3.5	.1	.8		.3	(*)	5.7	.3	.1		.7
18	6.1	2.4	.1	.4		.2	(*)	3.5	(*)	.1		1.1
22	1.4	4.4	.2	.5	1.6	.4	(*)	21.6		.9		.9
28	2.9	4.7	.1	1.7	(*)	.4	(*)	3.5	(*)	2.2		2.0
36	2.3	2.3	.2	2.0		.7	(*)	.3	.3	1.3		1.0
41	1.8	1.7	.2	.2	(*)	.1			.7	1.6	(*)	(*)
43	4.0	4.1	.1	.1		.1		20.0	.5	.1		
46	2.1	1.8	.3	.6	(*)	.1	(*)	1.7	(*)	.5		.9
48	.6	4.0	.5	.2		(*)	(*)		(*)	.4		.6
50	.8	.4	.3	(*)	55.1	3.6			(*)	1.0		.8
										(*)		1.0

TABLE 5.—*Standardized volumes of the principal components of fish and crustacean micronekton in the hauls listed in table 1*—Continued

Station number	Fish components				Crustacean components							
	Mycto-phids	Leptoce-phali	Gonosto-matids	Others	Gala-theids	Euphau-siids	Penaeids	Portunids	Sergestids	Squillid larvae	Squillid adults	Others
C. Cruise TO-59-2: August to September, 1959												
2	4.3		(*)	(*)	81.5	(*)						3.0
8	4.6		(*)		165.3	9.0			(*)	(*)		.1
13	1.2		.2		46.5	12.3			(*)			
21	3.1		(*)		65.3	2.6			(*)	(*)		.6
32	31.5		(*)		222.6	34.2				.1		.1
38	7.0		.7	(*)	40.6	13.0			(*)	(*)		(*)
42	4.4	(*)	.7		132.5	3.8			(*)	(*)		(*)
52	5.9		.2	(*)	107.6	9.4			(*)	.2		(*)
58	7.2	(*)	4.7	.1	20.0	22.0			(*)	(*)		.6
64	.1	(*)		.1	(*)	.4	(*)		(*)	.1		.7
74	4.0	2.0	.2	1.0		.1	(*)			.2		.6
79	2.3	4.8	.2	.8		(*)	(*)		.1	.7		.6
82	3.4	1.5	.2	1.0		.2	(*)	1.1	.2	.5		.8
84	9.4	10.6	(*)	1.0		(*)	(*)	4.9	.1	.2		1.2
85	10.2	3.3	(*)	1.2		.1	(*)	1.4	.1	.7		.2
86	4.9	2.0	(*)	.5		(*)	(*)		.1	.4		.1
87	3.6	.3	(*)	(*)		(*)	(*)		(*)	.7		.5
88	3.9	1.1	4.2	.2		18.1			(*)	.4		.8
89	(*)	.1	(*)	(*)		.3	(*)			.4		.4
D. Cruise TO-60-1: May 1960												
10	.4	.2	.1	1.2	.1	7.3	.3		(*)	.1		(*)
14	.2	.1	.1	.3	(*)	.2	.1		(*)	.1		.1
18	.5		.5	.1		8.3	(*)		.1	(*)		.5
23	1.4	.3	.5	(*)		.4				.1		.1
27	3.4	.3	1.3	(*)		7.7			(*)	(*)		.6
29	.5	.1	.2			.1				(*)		.4
33	3.5	.8	1.1	.1		(*)			(*)	.3		.6
37	25.1	2.2	1.1	(*)		.1	(*)		.2	.3		.6
40	1.8	3.9	.2	(*)		.1	(*)		.1	1.9		.6
44	2.4	.4	.4	.1		.2	(*)		.2	1.2		.5
48	.7	.3	1.5	(*)		(*)	(*)		(*)	.3		.6
52	1.4	.8	4.4	(*)		(*)			(*)	.3		.4
56	(*)	.6	.8	(*)		(*)	(*)			.4		.5
59	(*)	.7	2.9	1.6		(*)	130.1			1.3	(*)	.4
E. Cruise TO-60-2 (STEP-1): September to December, 1960												
1	.9		1.4	.7	(*)	.2	.2		.2	.2		1.2
2	7.1	1.1	1.1	1.2		.4	.4		.1	.7		.8
3	5.7	.4	.6	.8	(*)	.1	1.2		.5	.5		.9
4	9.6	.3	.2	.4	(*)	.1	(*)		.3	.5		1.1
6	5.6	5.0	.3	1.4		29.0	1.5		1.6	.4		.7
9	3.7	.2	.1	5.8	(*)	3.0	.1		.2	.1		.7
11	4.3		.6	1.5		.6			.1	.1		.4
17	1.6		.3			.3	.4		1.0			.3
19	2.3		.9	.5		.1			.3	(*)		.4
23	4.3		1.9	.9		.8	1.6		.2	(*)		.4
27	1.0		.3	.1		8.2	(*)		(*)	(*)		.6
30	.8		.7	.7		3.8	(*)			.1		.4
32	1.2		.2	.1		.1				.1		.1
35	.3	.1	(*)	(*)		.5				.1		.9
38	.5		.1			3.5			(*)			.4
42	1.6	.2	.1	.3		.1			(*)	(*)		.1
45	5.7		.2	.2	(*)	.4			(*)	(*)		.7
50	1.6		.8	1.4		1.1	.5		.2	(*)		.5
55	.7		1.1	.2		11.9	.5		.1			.3
59	1.8		.6	.3		.8	.1		.1			.4
64	1.0	.2	(*)						(*)			.1
69	1.0	.2	.2			.2			.2	(*)		.7
73	4.5	(*)	.4			(*)			(*)			.2
77	5.7		.2						.2	(*)		(*)
85	1.6	3.2	.3		(*)	.5			(*)	.2		.1
F. Cruise TO-61-1: March to April, 1961												
2	3.9	1.3	.1	.5		.1	(*)	.9		.4	.1	.6
5	3.9	2.1	4.2	2.9		1.6	.1	.6	.3	.5	.1	1.2
14	2.8	5.8	.4	1.3	(*)	.5	.1	.3	.1	.6	1.0	.9
16	4.4	2.1	.2	.2	(*)	.1	(*)			.5	31.0	.4
18	3.4	3.4	.2	1.7	(*)	.4	(*)		(*)	.7	2.1	.6
22	3.1	6.8	.1	.4		(*)	(*)	.1	.2	.6		.6
27	1.4	1.4	.3	.1	(*)	.5	.1		2.0	.2	.1	.3
29	.9	2.8	1.0	.3		.1	.2	1.5	.1	1.5		.6
32	3.9	1.7	.3	.4		(*)	(*)	.9	(*)	.7		.8
36	.8	4.6	.1	.6	(*)	(*)	(*)	.6	.2	.8		.7
38	4.5	1.1	.9	.1		.2	(*)	.6	(*)	.2		.7
40	.8	1.9		(*)		(*)	(*)		(*)	.2		.3

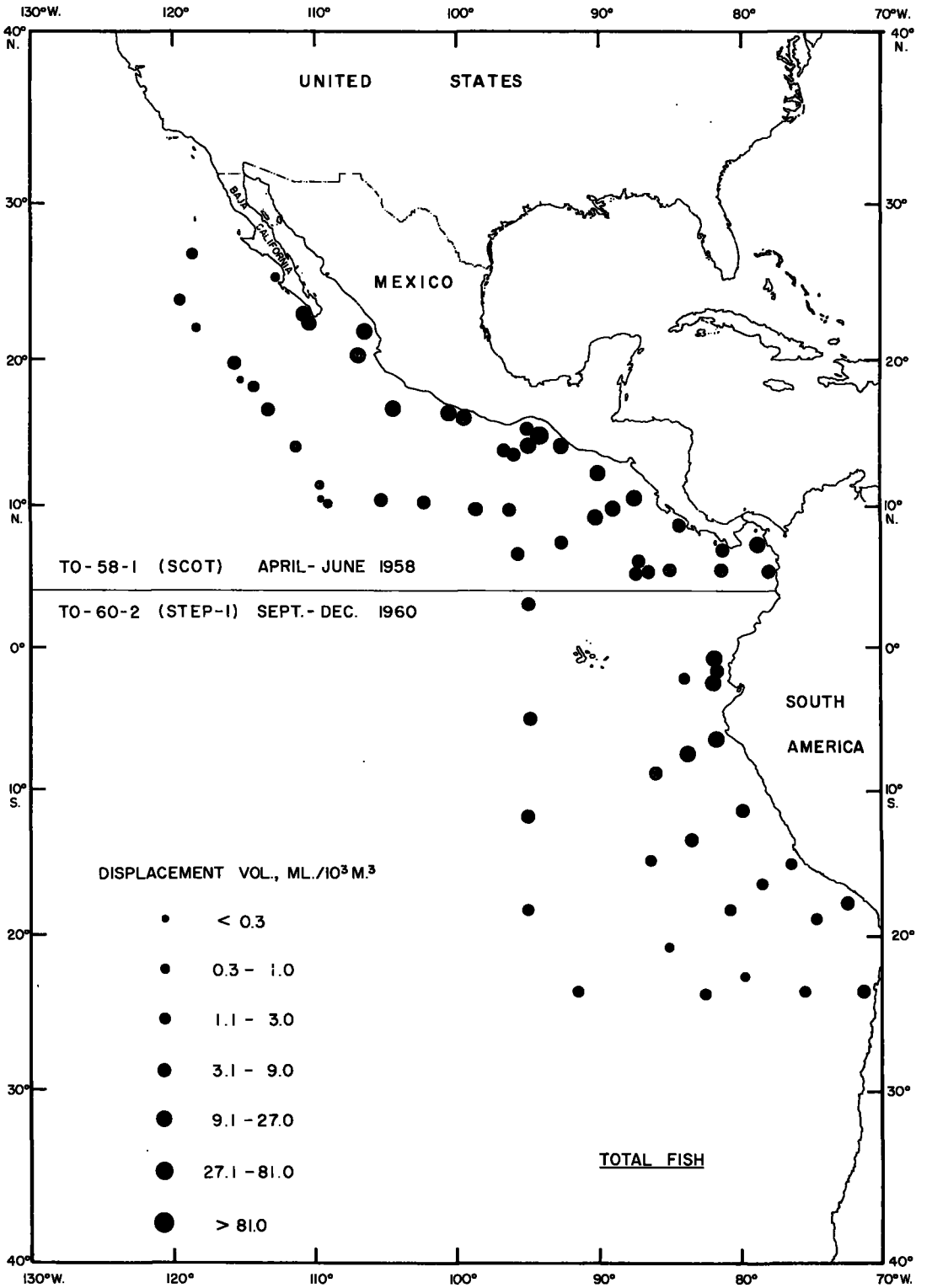

FIGURE 6.—Distribution of standing crop (standardized volume) of total fish taken in night micronekton hauls on cruises TO–58–1 and TO–60–2.

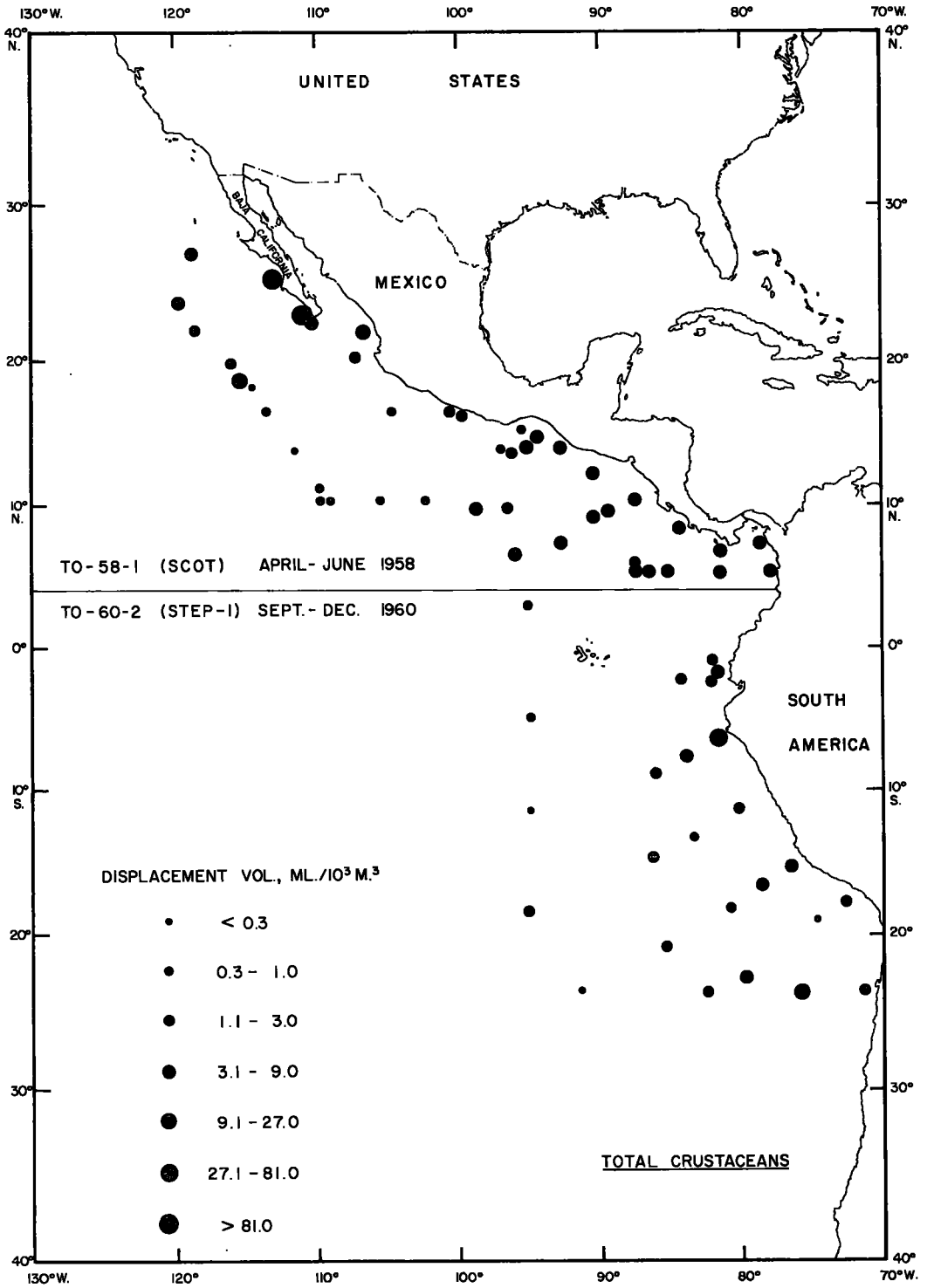

FIGURE 7.—Distribution of standing crop (standardized volume) of total crustaceans taken in night micronekton hauls on cruises TO–58–1 and TO–60–2.

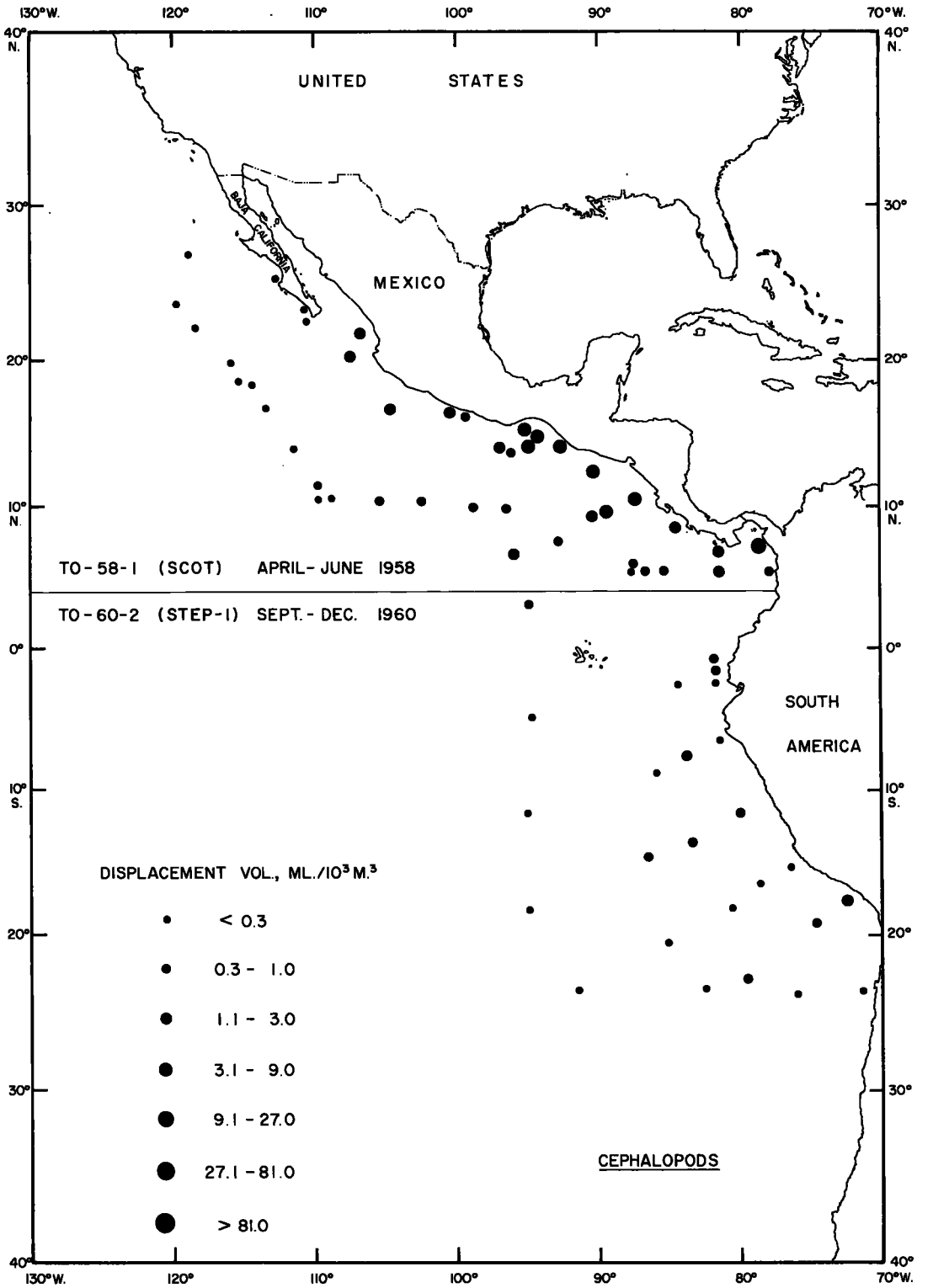

FIGURE 8.—Distribution of standing crop (standardized volume) of total cephalopods taken in night micronekton hauls on cruises TO–58–1 and TO–60–2.

TABLE 6.—*Means and medians of standardized micronekton volumes (milliliters per 1,000 m.³) from stations shown in figures 1, 6, 7, and 8, grouped by distance in miles from the mainland coast*

[Data from tables 1 and 5; n means number of stations]

Micronekton components	<300 miles [1] (n=40)		300 to 600 miles [2] (n=19)		>600 miles [3] (n=10)	
	Mean	Median	Mean	Median	Mean	Median
			Ml./10³ m.³			
Myctophids	3.59	2.50	1.80	1.40	1.71	1.00
Leptocephali	3.30	2.20	1.00	.60	.39	.10
Gonostomatids	.90	.65	.52	.50	.20	.20
Total fishes	9.07	8.40	3.65	3.20	2.34	1.30
Euphausiids	1.73	.55	1.03	.30	.27	.20
Stomatopod (squillid) larvae	.46	.40	.10	<.10	.03	<.10
Sergestids	.66	.25	.31	.10	.06	<.10
Total crustaceans	9.22	3.60	3.67	2.00	.74	.65
Total cephalopods	1.67	.95	.30	.20	.15	.10
Total micronekton	19.96	14.00	7.62	5.10	3.23	2.35

[1] TO-58-1 stations 1, 48 to 146; TO-60-2 stations 1 to 9, 23 to 30, 42 to 50.
[2] TO-58-1 stations 3 to 16, 29 to 46; TO-60-2 stations 11 to 19, 32, 38, 55.
[3] TO-58-1 stations 18 to 27; TO-60-2 stations 35, 59 to 85.

TABLE 7.—*Means of standardized micronekton volumes from two groups of the 40 onshore stations of table 6*

[Data from table 1]

Micronekton component	8 stations with total micronekton volumes each ≥22.0 ml./ 10³m.³ [1]	32 stations with total micronekton volumes each <22.0 ml./10³m.³ [2]
	Ml./10³m.³	*Ml./10³m.³*
Fishes	15.48	7.47
Crustaceans	32.26	3.46
Cephalopods	3.22	1.28
Total	50.96	12.21

[1] TO-58-1 stations 49, 63, 77, 81, 142, 144B, 146: TO-60-2 station 6.
[2] Stations in table 6, footnote 1, except those in footnote above.

from the eastern tropical Pacific because of the differences in sampling gear.

The distribution of leptocephali, the second largest group by volume among the fishes, is shown in figure 10. Standardized volumes are again higher near the coast than offshore (table 6), but they decline toward the south (table 5) and possibly also to the north. On a cruise made in June 1964, the mean standardized volume of leptocephali recorded at seven stations along the west coast of Baja California was < 0.1 ml. per 1,000 m.³ Leptocephali have been recorded in micronekton catches off the United States west coast and in the central Pacific, but apparently in much smaller quantities than in the coastal waters of the eastern tropical Pacific (Aron, 1959, 1962a; Pearcy, 1964; King and Iversen, 1962).

The distribution of gonostomatids—mainly *Vinciguerria* spp., as shown in table 3—is similar in its general features to the distribution of total fishes (fig. 6) and is, therefore, not shown. Volumes decline from onshore to offshore (table 6), and the volumes in table 5 show no obvious change with latitude for stations located at similar distances from the coast.

Similar data for two of the more common crustaceans, euphausiids and stomatopod (squillid) larvae, are given in figures 11 and 12. Euphausiids (fig. 11) are more abundant onshore than offshore (table 6) and may increase in biomass toward the poles. Figure 11 and table 5 show higher concentrations south of the Equator than elsewhere, and similar concentrations occurred on a cruise made in June 1964 along the west coast of Baja California (mean standardized volume for seven stations, 14.6 ml. per 1,000 m.³). Euphausiids are well represented in the material from Pacific regions farther north and west (Aron, 1959, 1962a; King and Iversen, 1962), although, again, the nature of the collecting gear used in those regions prevents quantitative comparisons with the eastern tropical Pacific.

The distribution of volumes of stomatopod larvae (fig. 12) is similar to that of leptocephali: higher onshore than offshore (table 6), and diminishing polewards. Figure 12 and table 5 show low concentration south of lat. 10° S., and similar concentrations occurred on a cruise made in June 1964 along the west coast of Baja California (mean standardized volume for seven stations, 0.1 ml. per 1,000 m.³). Stomatopod larvae were not mentioned by Aron (1959, 1962a) in his reports on micronekton collections west of the United States. King and Iversen (1962) obtained them fairly regularly in central Pacific waters between about lat. 19° S. (the southern limit of their sampling) and lat. 35° N.; they were not taken north of lat. 35° N.

The distribution of sergestids is similar in its general features to the distribution of stomatopod larvae and is, therefore, not shown. Volumes decline from onshore to offshore (table 6), and from the tropics toward the poles; all volumes ≧ 1.0 ml. per 1,000 m.³ in table 5 are from stations located between lat. 15° N. and 15° S.

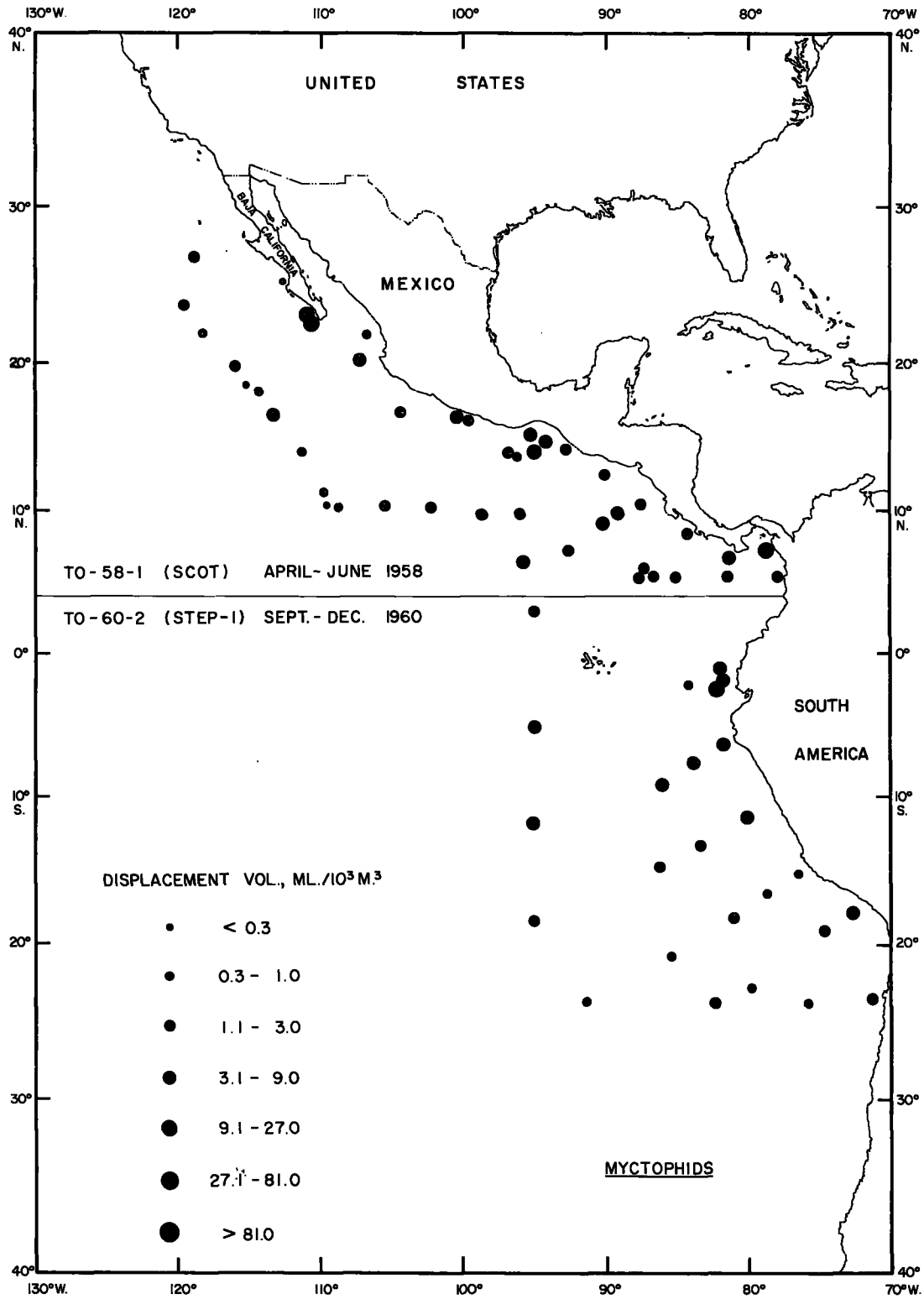

FIGURE 9.—Distribution of standing crop (standardized volume) of myctophids taken in night micronekton hauls on cruises TO–58–1 and TO–60–2.

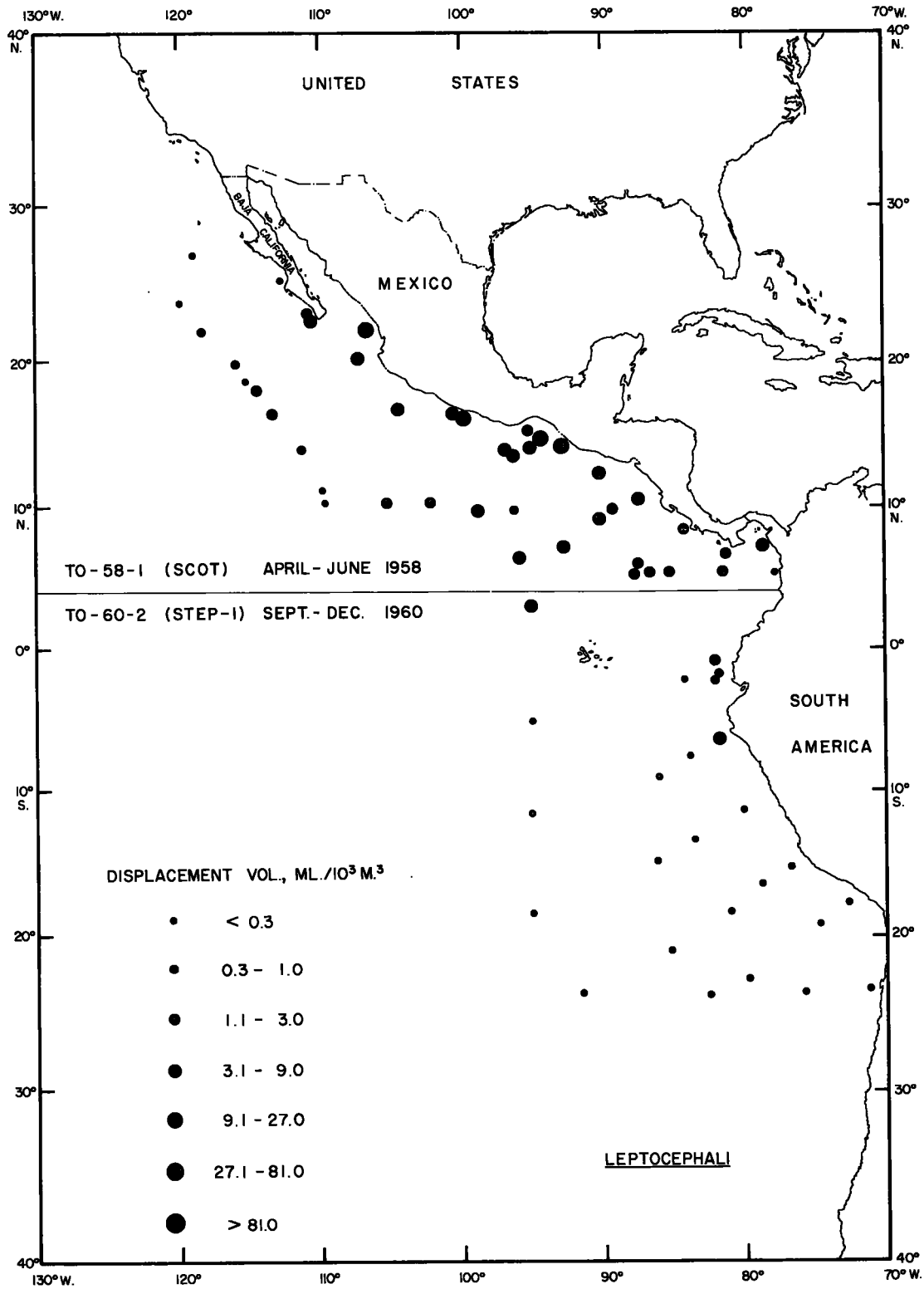

FIGURE 10.—Distribution of standing crop (standardized volume) of leptocephali taken in night micronekton hauls on cruises TO–58–1 and TO–60–2.

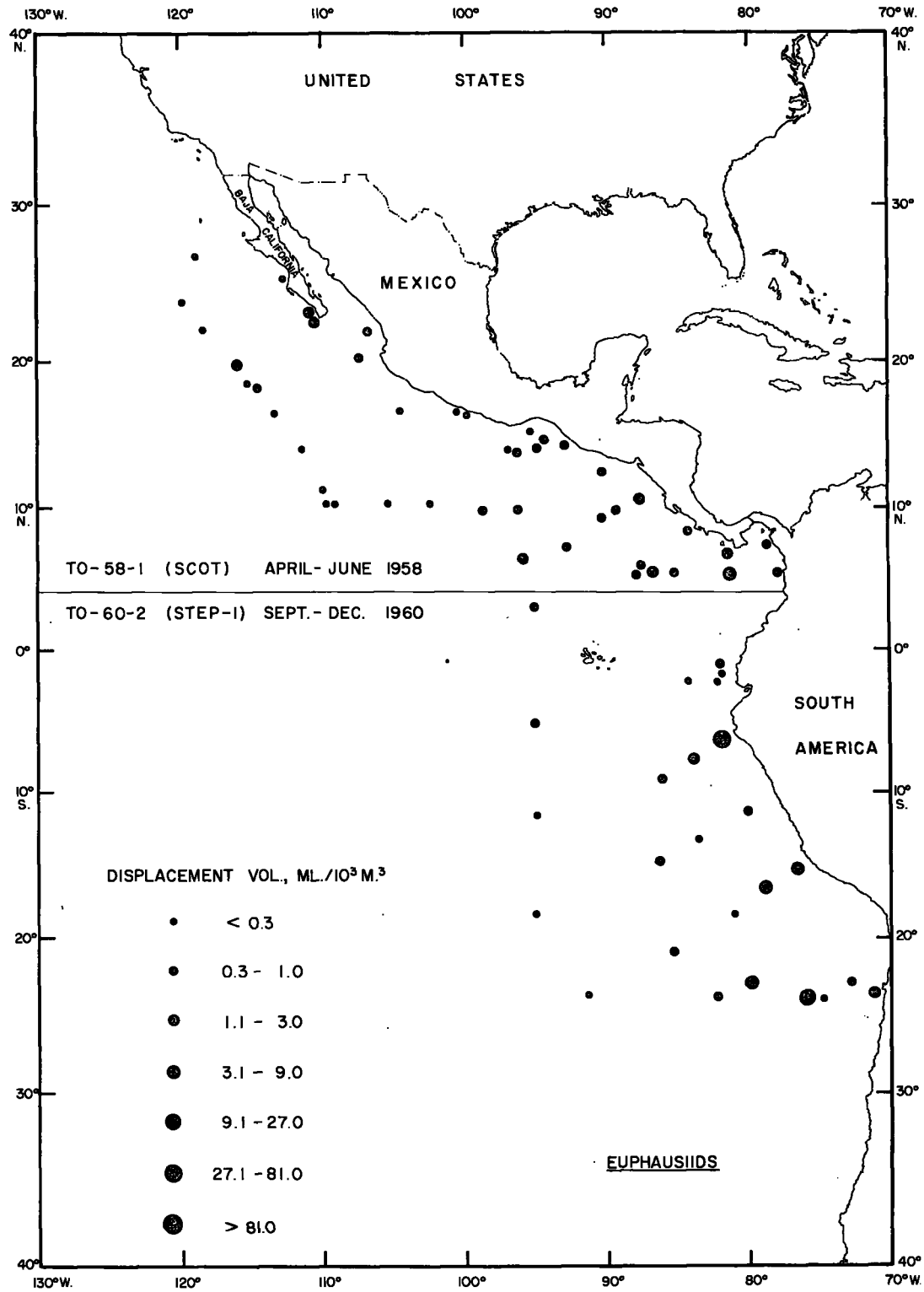

FIGURE 11.—Distribution of standing crop (standardized volume) of euphausiids taken in night micronekton hauls on cruises TO–58–1 and TO–60–2.

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Figure 13 gives similar data for three other important crustacean components of the micronekton, namely galatheids, portunids, and adult stomatopods (squillids). These forms were not taken during cruise TO–60–2 and occurred at only 17 stations on cruise TO–58–1, generally only one kind to a station (although both portunids and stomatopods were collected at station 96, in a 4:1 ratio by volume, see table 5). Their distribution is much more localized than the distribution of the other components previously discussed.

The galatheids were all adult *Pleuroncodes planipes* ("red crab"); a few small samples of galatheid juveniles, which could not be identified to species, are listed in tables 3 and 5 but are not shown in figure 13. This family was by far the largest in volume for the total micronekton of all the cruises (tables 3 and 4), but it was taken only in a small part of the region covered, where it was generally very abundant. The area of occurrence shown in figure 13 (and in fig. 15, which gives data for other cruises) is the west coast of Baja California and offshore in the California Current Extension as far west as long. 120° W. and as far south as lat. 18°30′ N. (Clarion Island); table 5 gives the data on which figures 13 and 15 are based. These western and southern limits are approximately the same as reported by Alverson (1963a) and Longhurst (1967); according to these authors, *P. planipes* also occurs farther east (across the Gulf of California) and farther north (to Monterey in central California). It did not occur in the material of Aron (1959, 1962a) or King and Iversen (1962). Because of the generally high standing crops of this animal encountered in area 1, this area yielded 47.4 percent of all the total micronekton collected in the 18 areas (table 3), although only 21 hauls (16.0 percent of the total for all areas) were made there (table 1); mean standardized volume of *P. planipes* for the hauls was 56.9 ml. per 1,000 m.^{3} (table 5). Area 1 includes several localities where coastal upwelling occurs seasonally, as noted earlier.

The portunid material of figures 13 and 15 was 99.4 percent *Portunus affinis* (table 3). Portunids were taken in the 1.5-m. net only along the coast from southeastern Mexico to northern Colombia, to about 200 nautical miles (370 km.) offshore. Alverson (1963a) charted a distribution of *P. affinis* which has a greater range in latitude (about 23° N. to 10° S.) and a wider range offshore (to about 700 nautical miles—1,300 km.—from the continent). Aron (1959, 1962a) did not mention portunids; King and Iversen (1962) recorded only two individuals from the central Pacific, both from tropical latitudes.

The stomatopod adults (or near-adults—our specimens were pelagic, whereas adults are generally regarded as benthic) were even more localized than the galatheids and portunids. They were taken only along the coast of southeastern Mexico, especially in the Gulf of Tehuantepec (figs. 13 and 15). Alverson (1963a) noted that they occurred in tuna stomachs only in areas 4 and 5, which include the Gulf of Tehuantepec. Their abundance in that region may be associated in some way with the fact that the Continental Shelf is wider in the eastern part of the Gulf of Tehuantepec and in the western part of area 5 than it is along most parts of the eastern side of the eastern tropical Pacific.

Figures 14 to 16 give information for total fish, crustacean, and cephalopod micronekton taken in night hauls on four other cruises (TO–59–1, TO–59–2, TO–60–1, and TO–61–1), which were made only along the Pacific coasts of Mexico and Guatemala; to the extent that cruise TO–58–1 was concerned with that area, the information about it (the same as in figs. 6 to 8) has been included to facilitate comparison between seasons (see below). Figure 2 identifies the stations (see also table 1).

The main features of distribution by area which these figures show have already been mentioned. In figure 15, code letters indicate the kind of crustaceans which accounted for half or more of the volume of Crustacea at a particular station. Included were penaeids at station 59 of cruise TO–60–1, which contributed practically all the material of this family for all the cruises, as well as the groups listed above. Many of the stations had a heterogeneous crustacean fauna, of which no one group made up half or more of the volume (table 5); the number of these stations increased toward the tropics.

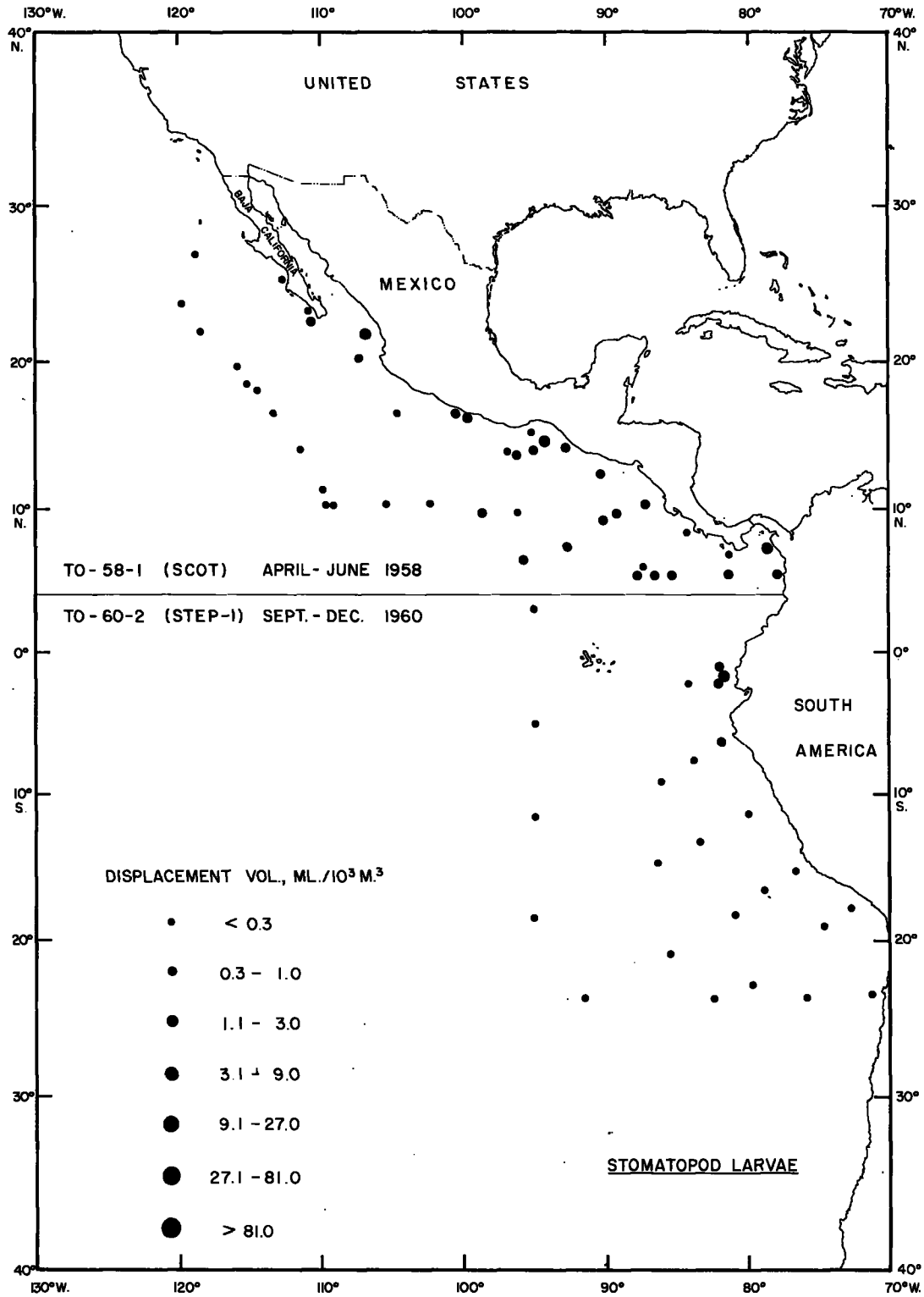

FIGURE 12.—Distribution of standing crop (standardized volume) of stomatopod (squillid) larvae taken in night micronekton hauls on cruises TO–58–1 and TO–60–2.

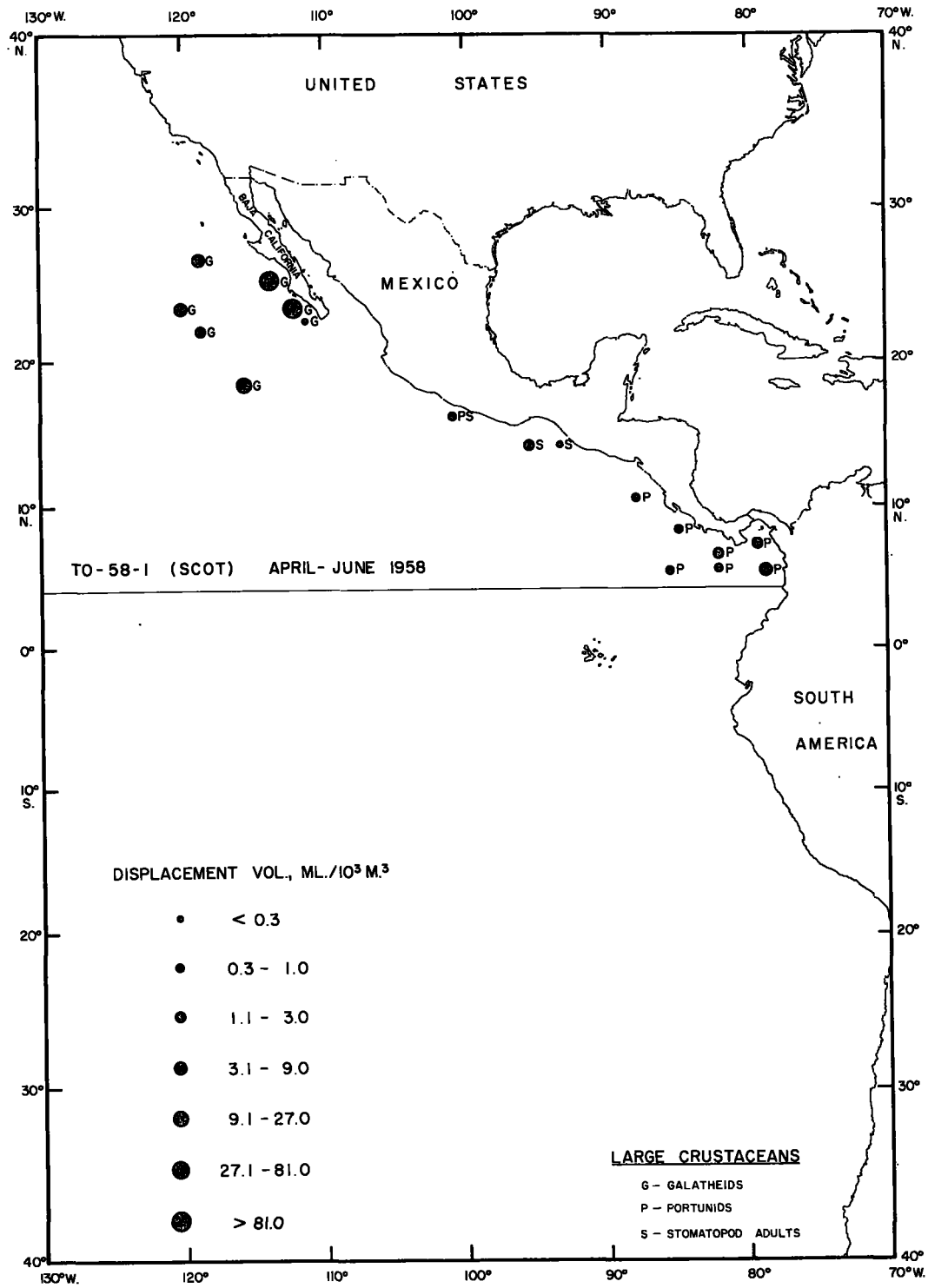

FIGURE 13.—Distribution of standing crop (standardized volume) of large crustaceans, namely galatheids, portunids, and adult stomatopods (squillids), taken in night micronekton hauls on cruises TO–58–1 and TO–60–2.

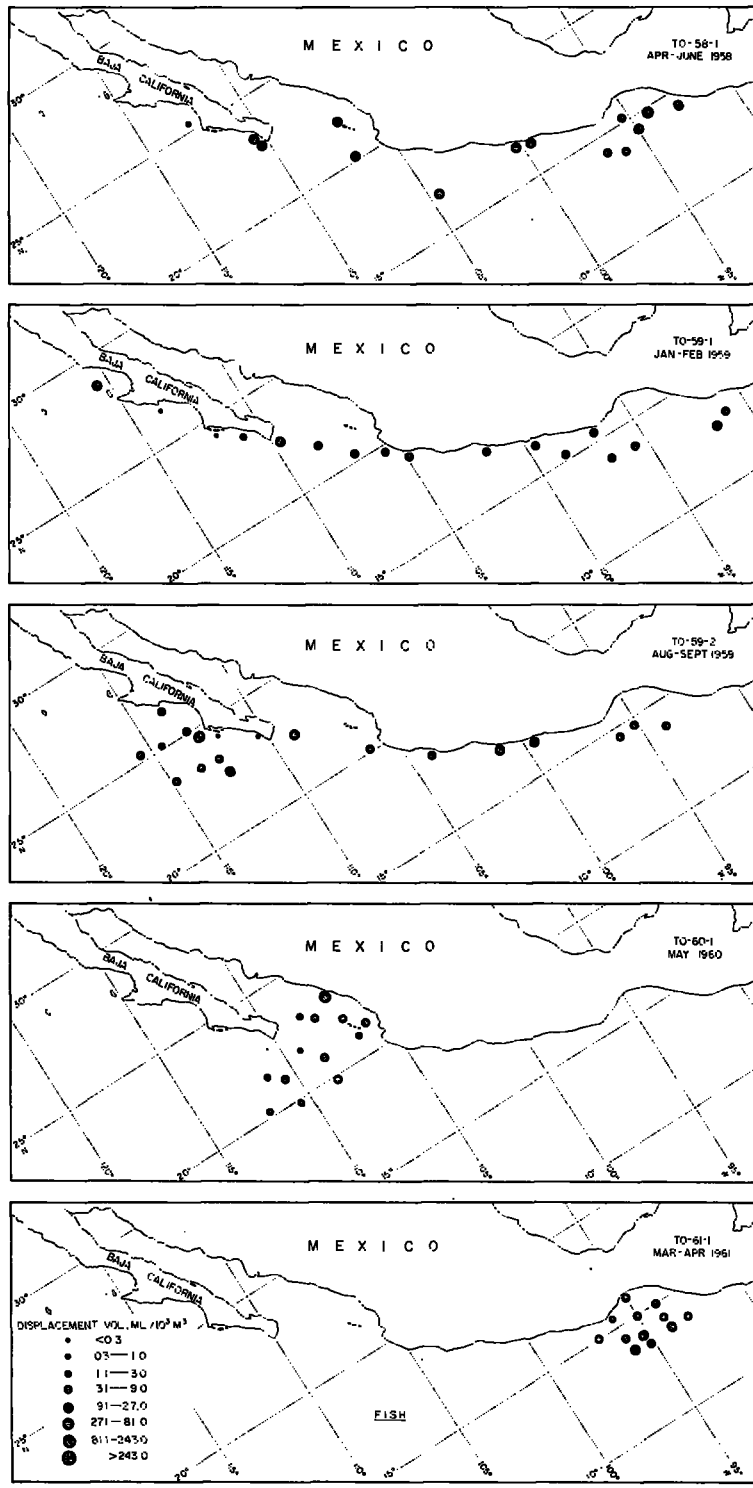

FIGURE 14.—Distribution of standing crop (standardized volume) of total fish taken in night micronekton hauls on cruises made along the Pacific coasts of Mexico and Guatemala.

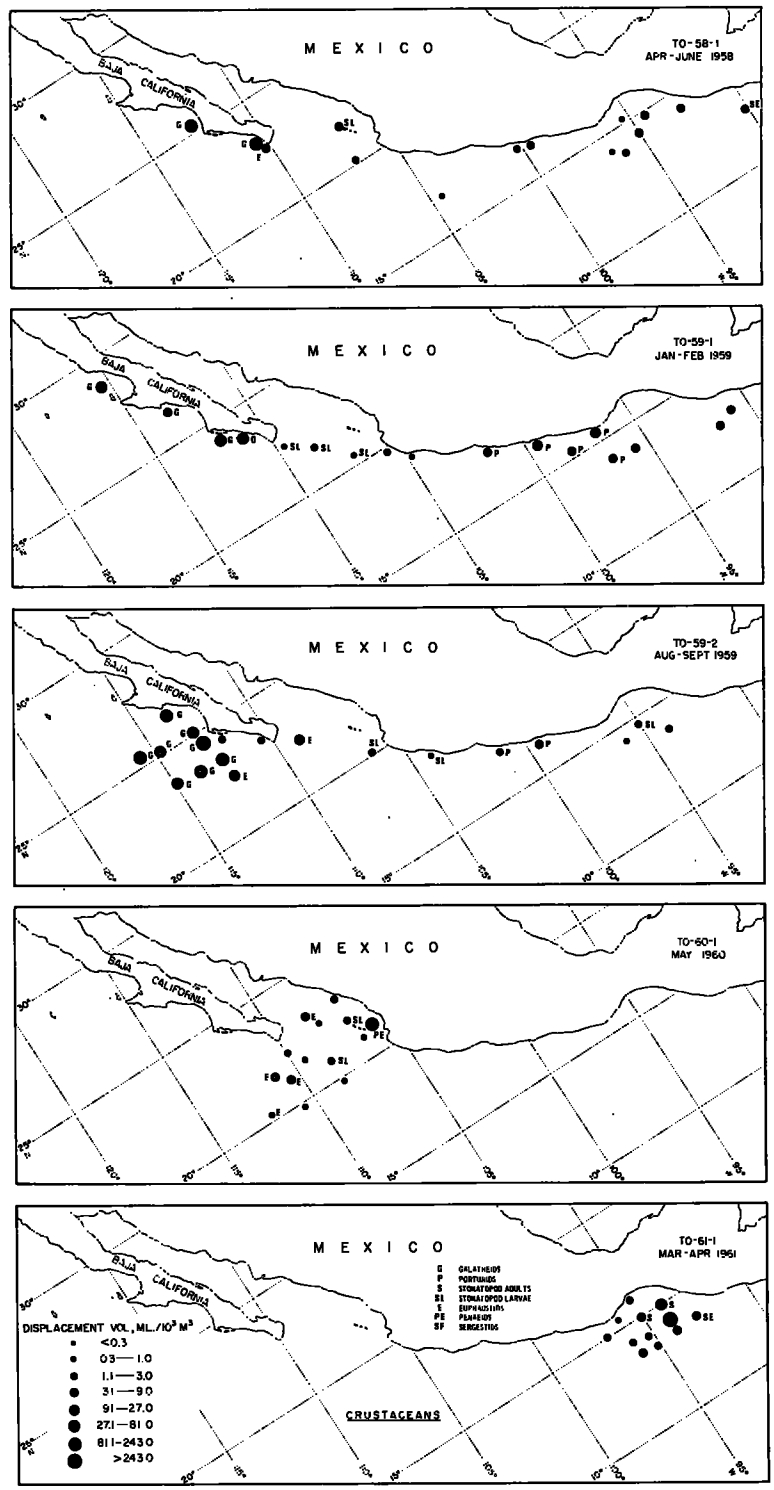

FIGURE 15.—Distribution of standing crop (standardized volume) of total crustaceans taken in night micronekton hauls on cruises made along the Pacific coasts of Mexico and Guatemala. Code letters, explained in the bottom panel, indicate the group, if any, which represented half or more by volume of the catch of crustaceans.

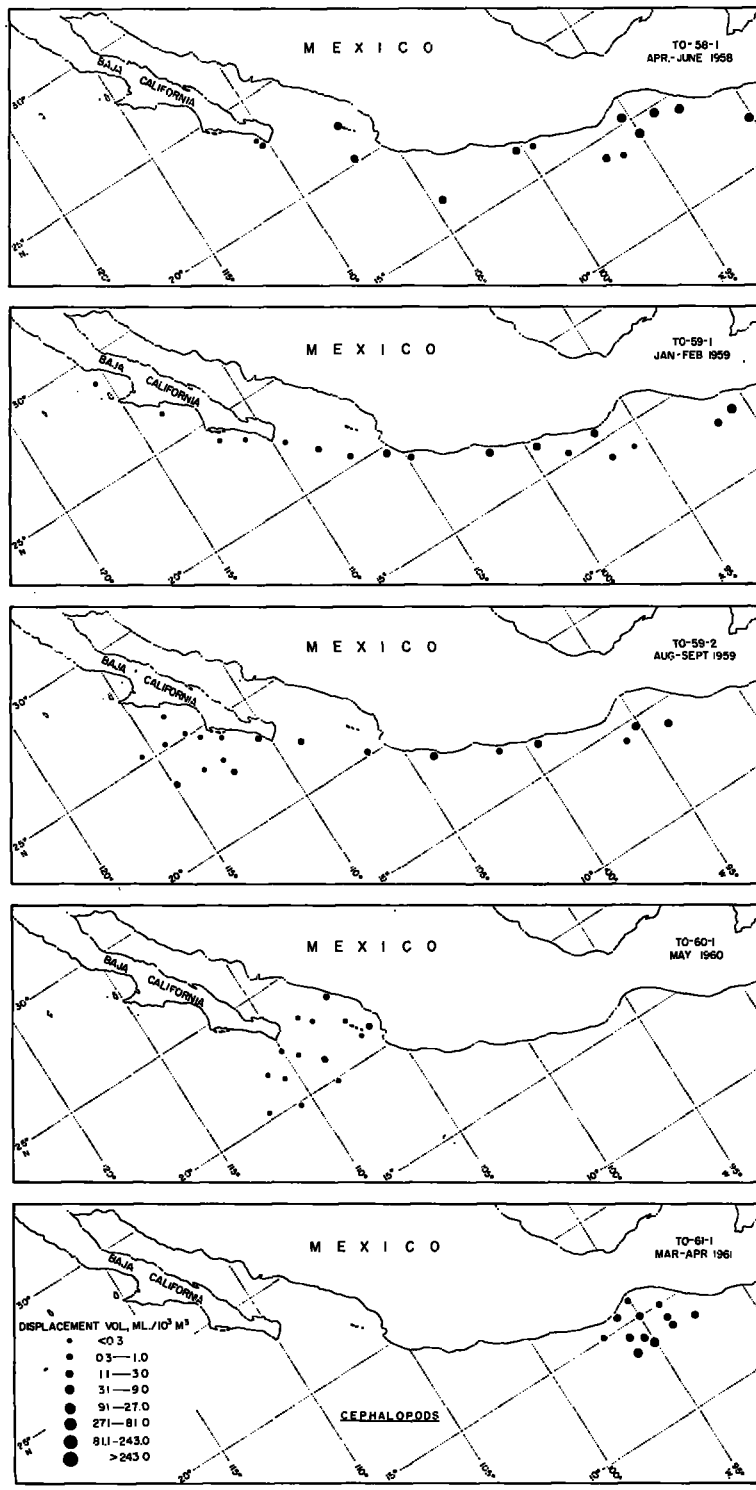

FIGURE 16.—Distribution of standing crop (standardized volume) of total cephalopods taken in night micronekton hauls on cruises made along the Pacific coasts of Mexico and Guatemala.

DISTRIBUTION OF MICRONEKTON BY SEASONS

The only series of cruises which could possibly reveal seasonal changes in the micronekton of standard night hauls is the series for the Pacific coasts of Mexico and Guatemala —cruise TO–58–1 in part, and cruises TO–59–1, TO–59–2, TO–60–1, and TO–61–1 —for which results are summarized in figures 14 to 16.

Except for TO–60–1, these cruises were planned to determine certain seasonal changes in the standing crop of micronekton, and other ocean properties, in the Gulf of Tehuantepec (long. 95° W.). Comparisons for this area are available for the months January–February (TO–59–1; no data for the center of the Gulf, because of bad weather), March–April (TO–61–1), May–June (TO–58–1), and August–September (TO–59–2). The data in figures 14 to 16 show that all three main components of the micronekton were scarcer by volume in this area in August–September than in March–June (possibly January–June). This difference is to be expected from the study by Blackburn (1962, 1963) of seasonal changes in the physical, chemical, and biological oceanography of the Gulf. The physical processes that cause shoaling of the pycnocline in certain areas and intermittent vertical mixing in parts of these areas are well developed in winter, and nutrient-rich water brought to the surface could be expected to result in a high crop of micronekton by spring. On the other hand, the eutrophic conditions decline through the spring, and the micronekton crop of late summer should be low. The time required for a crop of micronekton to grow has been discussed by Blackburn (1966a).

Off the west coast of Baja California, eutrophic conditions (coastal upwelling) are generally most pronounced in spring (Reid et al., 1958). If a lag of a few months is assumed between the appearance of a physical eutrophic process and the appearance of the resulting crop of micronekton (see previous paragraph), an increase in micronekton volume from winter through spring to late summer might be expected. The data for fish and cephalopods (figs. 14 and 16) are not inconsistent with this hypothesis, but they are generally scanty (except for August–September). For crustaceans (mainly *Pleuroncodes planipes*) the data in figure 15 suggest a rather high abundance throughout the whole period mentioned above. Longhurst (1967), who analyzed occurrences of *P. planipes* in zooplankton net hauls, drew a similar conclusion. Practically no quantitative data are yet available from micronekton hauls on occurrences of *P. planipes* in October through December, although it was abundant in hauls made with the high-speed net in December 1960. Data on *P. planipes* from zooplankton net hauls also are scanty at this period, and it is possible that the species is then less abundant than during the rest of the year, although the evidence is inconclusive (Longhurst, 1967). The distribution and ecology of this animal are being further studied in the Scripps Tuna Oceanography Research Program.

Elsewhere along the Mexican coast, namely across the mouth of the Gulf of California and thence southwards along the coast to the Gulf of Tehuantepec, no hypothesis about seasonal distribution of micronekton has been developed to test, and the scanty data in figures 14 to 16 do not suggest any particular seasonal change.

COMPARISON OF MICRONEKTON CAUGHT BY NETS AND TUNAS

Alverson (1963a), who sorted stomach contents of 2,846 yellowfin tuna [5] and 1,010 skipjack tuna [5] from the eastern tropical Pacific, published tables showing the percentage composition by volume of this material by taxa (including some species) for each of the areas 1 to 14 of figure 5.

Alverson's specimens of tuna were obtained from commercial catches made by surface hooking (bait-and-pole) or surface netting (purse seine). Yellowfin tuna are caught also by subsurface hooking (pelagic long-line) in parts of the eastern tropical Pacific, but few data on stomach contents are available for fish from that region (Juhl, 1955; Blunt, 1960).

Tables 8 to 14 compare the percentage composition of actual volumes of micronekton from standard night hauls with the actual volumes of stomach contents of yellowfin and skipjack tuna, for areas in which at least five hauls were available (namely areas 1, 2, 3, 4, 5, 6, and areas 11 and 12

[5] These two species of tuna were called, respectively, *Neothunnus macropterus* and *Katsuwonus pelamis*, by Alverson; according to Collette and Gibbs (1963), they should be known as *Thunnus albacares* (Bonnaterre) and *Euthynnus pelamis* (Linnaeus).

combined). The source of data for the net hauls is table 3 of this paper; the sources for the tuna stomach contents are various tables by Alverson (1963a).

Each of the tables 8 to 14 shows the percentage composition of fish, crustaceans, and cephalopods in material caught by the 1.5–m. net, by yellowfin tuna, and by skipjack tuna, respectively, for a particular area. Each of the three main categories is then further divided into components (generally families), of which each accounted for at least 0.5 percent by volume of the total material (from 1.5–m. net, yellowfin tuna, or skipjack tuna), for the area; other components (including material not identified to family) were lumped. The percentages in tables 12 and 14 for skipjack tuna differ slightly from the corresponding percentages in Alverson's tables, because he included small amounts of materials from stomachs of skipjack tuna (1.5 percent in area 5; 0.3 percent in areas 11 and 12) which are not regarded as micronekton. Alverson separated Thunnidae from Katsuwonidae in the fish families represented in his material, but they are here combined as Thunnidae, and have been so entered in table 3 and tables 8 to 14. Volumes for groups of animals in tables 8 to 14 include all ontogenetic stages unless otherwise stated.

TABLE 8.—*Percentage taxonomic composition of micronekton in area 1 of figure 5, from net hauls and tuna stomachs*

[21 standard night net hauls of 1.5-m. net (18,971 ml.); 567 stomachs of yellowfin tuna (37,489 ml.); 151 stomachs of skipjack tuna (4,661 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	*Percent*	*Percent*
Myctophidae	7.1		
Leptocephali	.5		
Gonostomatidae (*Vinciguerria*)	.7		
Engraulidae		9.6	28.3
Scomberesocidae			9.5
Scombridae		2.0	
Other fish	.1	7.8	5.6
Total fish	8.4	19.4	43.4
Galatheidae	81.5	78.1	36.8
Euphausiidae	8.1		19.2
Pasiphaeidae	1.5		
Other crustaceans	.3	.3	(*)
Total crustaceans	91.4	78.4	56.0
Cephalopods	.2	2.2	.6
Grand total	100.0	100.0	100.0

TABLE 9.—*Percentage taxonomic composition of micronekton in area 2 of figure 5, from net hauls and tuna stomachs*

[6 standard night net hauls of 1.5-m. net (827 ml.); 328 stomachs of yellowfin tuna (62,225 ml.); 48 stomachs of skipjack tuna (1,862 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	*Percent*	*Percent*
Myctophidae	16.2		
Leptocephali	9.4		
Gonostomatidae (*Vinciguerria*)	7.5	(*)	5.3
Gonostomatidae (others)	.8		
Ostracidae	(*)	21.1	.5
Thunnidae		19.9	
Tetraodontidae		15.6	
Serranidae		4.7	5.0
Exocoetidae		1.9	
Balistidae		.6	
Carangidae		.5	
Other fish	.8	3.7	10.1
Total fish	34.7	68.0	20.9
Galatheidae	56.8	31.1	78.3
Euphausiidae	4.6	(*)	.1
Squillidae (larvae)	1.0	(*)	(*)
Other crustaceans	1.8	.1	.2
Total crustaceans	64.2	31.2	78.6
Enoploteuthidae	.9		
Other cephalopods	.2	.8	.5
Total cephalopods	1.1	.8	.5
Grand total	100.0	100.0	100.0

TABLE 10.—*Percentage taxonomic composition of micronekton in area 3 of figure 5, from net hauls and tuna stomachs*

[18 standard night net hauls of 1.5-m. net (3,836 ml.); 155 stomachs of yellowfin tuna (12,062 ml.); 5 stomachs of skipjack tuna (247 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	*Percent*	*Percent*
Leptocephali	17.0		
Myctophidae	13.6	0.1	
Gonostomatidae (*Vinciguerria*)	7.0	.5	27.2
Gonostomatidae (others)	.7		
Bregmacerotidae	1.3	(*)	
Stomiatidae	.5		
Thunnidae	(*)	12.2	23.9
Coryphaenidae	(*)	7.0	
Polynemidae		1.6	34.1
Carangidae		1.5	
Balistidae		.7	
Exocoetidae	.2	.6	
Other fish	1.1	10.9	14.0
Total fish	41.4	35.1	99.2
Penaeidae	39.8		
Euphausiidae	6.9		
Squillidae (larvae)	4.3	.7	.8
Galatheidae	(*)	41.0	
Other crustaceans	2.7	.2	
Total crustaceans	53.7	41.9	.8
Enoploteuthidae	3.3		
Cranchiidae	1.5		
Onychoteuthidae		4.7	
Other cephalopods	.1	18.3	(*)
Total cephalopods	4.9	23.0	(*)
Grand total	100.0	100.0	100.0

TABLE 11.—*Percentage taxonomic composition of micronekton in area 4 of figure 5, from net hauls and tuna stomachs*

[29 standard night net hauls of 1.5-m. net (7,191 ml.); 247 stomachs of yellowfin tuna (14,839 ml.); 1 stomach of skipjack tuna (97 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	*Percent*	*Percent*
Leptocephali	28.3		
Myctophidae	21.7	1.8	
Gonostomatidae (*Vinciguerria*)	4.5	(*)	
Idiacanthidae	.8		
Heterosomata	.6		
Stomiatidae	.6		
Bregmacerotidae	.5		
Thunnidae	(*)	10.8	
Carangidae	(*)	10.4	
Exocoetidae		8.8	93.8
Balistidae		.8	
Other fish	2.2	8.0	6.2
Total fish	59.2	40.6	100.0
Portunidae	11.6	40.6	
Squillidae (adults)	6.6	13.5	
Squillidae (larvae)	3.2	.3	
Euphausiidae	1.3		
Sergestidae	1.3		
Unid. crab megalopa	.5		
Galatheidae	.2	1.0	
Other crustaceans	3.6		
Total crustaceans	28.3	55.4	
Enoploteuthidae	6.7		
Cranchiidae	5.1		
Ommastrephidae		.7	
Other cephalopods	.7	3.3	
Total cephalopods	12.5	4.0	
Grand total	100.0	100.0	100.0

TABLE 12.—*Percentage taxonomic composition of micronekton in area 5 of figure 5, from net hauls and tuna stomachs*

[10 standard night net hauls of 1.5-m. net (2,470 ml.); 319 stomachs of yellowfin tuna (16,256 ml.); 42 stomachs of skipjack tuna (661 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	*Percent*	*Percent*
Leptocephali	22.6		
Myctophidae	16.3	21.6	
Gonostomatidae (*Vinciguerria*)	3.4	.7	
Nemichthyidae	2.4		
Stomiatidae	1.9		
Idiacanthidae	1.9		
Bathylagidae	1.6		
Heterosomata	1.1	(*)	
Stromateidae	.9		
Exocoetidae		17.4	
Thunnidae	(*)	1.5	
Balistidae		.8	0.7
Sternoptychidae	(*)		1.0
Other fish	2.3	11.8	61.4
Total fish	54.4	53.8	63.1
Sergestidae	7.5		
Squillidae (larvae)	4.4	2.2	7.1
Euphausiidae	4.1	(*)	(*)
Portunidae	1.7	27.2	2.7
Penaeidae	1.2		
Phronimidae	1.0		
Squillidae (adults)	.6	1.1	
Oxycephalidae	.5		
Unid. crab megalopa	.3	.3	12.4
Galatheidae	(*)	1.8	
Other crustaceans	3.5	.2	.6
Total crustaceans	24.8	32.8	22.8
Enoploteuthidae	13.0		
Cranchiidae	4.1		
Argonautidae	(*)	.9	3.7
Other cephalopods	3.7	12.5	10.4
Total cephalopods	20.8	13.4	14.1
Grand total	100.0	100.0	100.0

Differences between micronekton from nets and tuna stomachs were rather marked as far as percentages of fish families are concerned. Myctophidae was the largest fish component of net material in most areas, but in tuna stomachs it was generally a small component, where it occurred at all. Only in area 5 (yellowfin tuna) and possibly area 6 (skipjack tuna) were the percentages for tuna comparable with those for nets. Leptocephali, a large item in net catches in most areas, were represented in tuna stomachs only as a negligible percentage in area 6 (yellowfin tuna). The occurrence of the gonostomatid fish *Vinciguerria* (which is shown separately from other members of the family because it is the only one recorded from tuna stomachs) was reasonably similar in the three kinds of material in tables 8 to 14 considered as a whole. Sternoptychidae, Bregmacerotidae, Nemichthyidae, Stomiatidae, Idiacanthidae, and Bathylagidae were significant components of net micronekton in some areas, but never of tuna stomach contents (unless they occurred in the unidentifiable fish remains, which have been included in "other fish"). Most of the families mentioned in this paragraph are generally regarded as mesopelagic.

On the other hand, some significant fish components of tuna stomach contents were absent or scarce in net catches—Engraulidae, Scombridae, Scomberesocidae, Ostracidae, Tetraodontidae, Thunnidae, Serranidae, Exocoetidae, Coryphaenidae, Polynemidae, Carangidae, Gadidae, and Trichiuridae. These families are generally regarded as epipelagic. Engraulidae occurred in tuna stomachs only in area 1, and their absence in net catches for that area may reflect the fact that they occur mainly in the northern half of the area, whereas the net hauls were made principally in the southern half; the 1.5-m. net has some capacity for catching engraulids, because a specimen of *Engraulis mordax* was caught in area 1 in June 1964, after the tables in this paper were compiled. The absence or scarcity of Ostracidae, Tetraodontidae, Serranidae, Gadidae, and Trichiuridae in

TABLE 13.—*Percentage taxonomic composition of micronekton in area 6 of figure 5, from net hauls and tuna stomachs*

[5 standard night net hauls of 1.5-m. net (1,365 ml.); 204 stomachs of yellowfin tuna (15,698 ml.); 517 stomachs of skipjack tuna (26,583 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	*Percent*	*Percent*
Myctophidae	33.2	1.4	5.7
Leptocephali	7.0	(*)	
Sternoptychidae	3.4		(*)
Gonostomatidae (*Vinciguerria*)	2.4	4.7	13.4
Nemichthyidae	1.5	(*)	
Bathylagidae	1.0		
Stomiatidae	.7		
Scopelarchidae	.5		
Scombridae		25.0	
Thunnidae		16.0	
Gadidae	.1	4.7	.3
Exocoetidae		.7	4.9
Carangidae	.1	3.2	.2
Trichiuridae	.4	1.2	6.4
Other fish	1.3	20.1	4.1
Total fish	51.6	77.0	35.0
Euphausiidae	32.0	(*)	59.9
Penaeidae	3.7		
Sergestidae	2.9		
Squillidae (larvae)	2.3	.4	.2
Portunidae		10.2	
Other crustaceans	4.0	.5	.7
Total crustaceans	44.9	11.1	60.8
Enoploteuthidae	2.0		1.6
Cranchiidae	1.0		.2
Ommastrephidae		1.4	
Other cephalopods	.5	10.5	2.4
Total cephalopods	3.5	11.9	4.2
Grand total	100.0	100.0	100.0

TABLE 14.—*Percentage taxonomic composition of micronekton in areas 11 and 12 of figure 5, from net hauls and tuna stomachs*

[6 standard night net hauls of 1.5-m. net (1,138 ml.); 72 stomachs of yellowfin tuna (4,880 ml.); 37 stomachs of skipjack tuna (2,321 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	*Percent*	*Percent*
Myctophidae	19.8	1.0	
Leptocephali	17.5		
Idiacanthidae	3.0		
Stomiatidae	2.7		
Gonostomatidae (*Vinciguerria*)	2.5	(*)	
Bregmacerotidae	1.6		
Carangidae		9.8	2.8
Exocoetidae		1.5	89.8
Paralepididae	(*)	.5	
Other fish	1.4	6.6	6.8
Total fish	48.5	19.4	99.4
Euphausiidae	14.3	.1	
Sergestidae	12.1	1.4	
Portunidae	5.7	71.7	(*)
Squillidae (larvae)	4.0	(*)	(*)
Phronimidae	1.1	(*)	
Penaeidae	.7		
Palinuridae	.7		
Phrosinidae	.6		
Unid. crab megalopa	.5		(*)
Other crustaceans	5.0	1.2	
Total crustaceans	44.7	74.4	0.1
Enoploteuthidae	5.1	(*)	
Cranchiidae	1.3		
Loliginidae		(*)	
Other cephalopods	.4	6.2	.5
Total cephalopods	6.8	6.2	.5
Grand total	100.0	100.0	100.0

net catches, in areas where they were significant in tuna stomachs, may reflect the fact that only five or six net hauls were made in each of those areas. The other major differences in representation of families in net catches and tuna stomach contents probably indicate real differences between the catching performance of the net and of the tunas, discussed below. Carangidae are possibly underrepresented in the net material of area 4; some hauls taken in that area on cruise TO–62–1, which are neglected in most parts of this paper for reasons given elsewhere, were moderately rich in carangids (table 2).

A similar situation is suggested by the cephalopod data of tables 8 to 14, which show the main families in net catches little represented in tuna stomachs and vice versa; but the component "other cephalopods" (which is mainly material that was too much digested for identification) was relatively large in the tuna stomach contents, and the principal components of the net catches (Enoploteuthidae and Cranchiidae) might have occurred in it.

The crustacean components were much more alike than the fish and cephalopod components, qualitatively and quantitatively, in the micronekton from nets and in the stomachs of yellowfin and skipjack tunas. The galatheids were represented by large and somewhat comparable percentages in all three series in areas 1 and 2, where the material was mostly *Pleuroncodes planipes*. Percentages of similar material were very different in area 3 (very low in net catches, high in stomachs of yellowfin tuna, nil in the scanty material from skipjack tuna), but the percentage in net catches would have been higher if a special group of hauls from the Cape San Lucas front had been included (see Griffiths, 1965). Percentages of galatheids in areas 4 and 5 were small and similar for net catches and yellowfin tuna, and this material consists mainly of juveniles. Percentages of euphausiids in net micronekton were comparable with those in stomachs of skipjack tuna in some areas (especially 1 and 6) but the percentages were uniformly very low, or nil, in yellowfin tuna. Squillid larvae occurred in net

catches and in stomachs of both tuna species in most areas in somewhat similar percentages, although those in net micronekton were generally higher than those in tuna stomachs. Adult squillids were a significant item only in areas 4 and 5. There they occurred comparably in net catches and stomachs of yellowfin tuna; the skipjack material, in which they did not occur, was scanty for those areas.

Percentages of portunids were less similar; they were generally much higher for yellowfin tuna stomachs than for net catches or skipjack tuna stomachs. Percentages of unidentified crab megalopa were variable, but generally low except in stomachs of skipjack tuna from area 5. Sergestids occurred in the net micronekton of some areas, sparsely in the yellowfin tuna stomachs of areas 11 and 12, and not at all in skipjack tuna. Other crustacean families and groups in tables 8 to 14 (Pasiphaeidae, Penaeidae, Phronimidae, Oxycephalidae, Phrosinidae, and Palinuridae) appeared in the net catches only and on the whole sparsely, in the areas to which the tables refer.

Possible reasons for the differences in percentage composition of the micronekton as caught by nets and by tunas are given in the following paragraphs. These reasons are in addition to the sparse and probably unrepresentative sampling for net micronekton and skipjack tuna stomachs in some areas, to which reference has already been made. It is also possible that tuna concentrate for feeding upon aggregations of certain species of prey; such species might, therefore, be better represented in tuna stomachs than in net catches.

(1) The nets were used at night, but most tunas from the surface-hook and surface-net fisheries are caught in the daytime. Because diurnal vertical movement causes many kinds of micronekton to be more plentiful in near-surface waters by night than by day, the nets and tunas probably sample different assemblages of micronekton. This point was discussed by King and Iversen (1962), who found some of the same differences between net-caught and tuna-caught micronekton as those described above.

(2) The nets fish through a layer of water some 90 to 95 m. thick, but the range of depth at which surface-caught yellowfin tuna and skipjack tuna feed is unknown. If, as seems likely, the tuna feed closer to the surface than the average depth of the net, epipelagic organisms would probably be better represented in tuna stomachs than in net catches.

(3) Tuna may fail to catch organisms which are available for capture, for lack of stimuli which release feeding behavior. Such stimuli can be visual or chemical (Magnuson, 1963, and references there). Visual stimuli could be lacking in the presence of suitable prey by night, or by day if the organisms are translucent.

(4) Nets, even at a speed of 5 knots, may fail to catch certain kinds of alert or strong micronekton that could be captured by tunas, which are credited with swimming speeds up to 40 knots in short bursts (Walters and Fierstine, 1964).

(5) Tuna stomachs frequently contain a significant proportion of semidigested material which is not identifiable to family. This was so in Alverson's material. Some families of micronekton might, therefore, be eaten by tunas despite their absence in the appropriate columns of tables 8 to 14.

A combination of the first and third points (netting by night, but tuna feeding by day) could explain the much better representation of myctophids, sternoptychids, nemichthyids, stomiatids, idiacanthids (and perhaps other mesopelagic fish families mentioned above, and sergestids), in the net-caught than in the tuna-caught micronekton. These groups are known to move closer to the sea surface by night (when tunas probably cannot see them well) than by day (when they are probably too deep, generally, for the tunas to catch). Alverson (1961) showed that tunas will catch the myctophid *Benthosema pterota* when it is available at the surface in daylight. It is not clear that this explanation could apply to leptocephali, but these animals might not be taken by tunas because of their translucence; the same might apply to the phronimids, oxycephalids, phrosinids, and palinurids (the last is represented in the net catches only as translucent larvae).

The second and fourth points (the net catching at greater depth and slower speed than the tunas) could explain the greater occurrence of active epipelagic fish (scombrids, scomberesocids, thunnids, exocoetids, coryphaenids, polynemids, carangids, and perhaps others) in tuna-caught than in net-caught micronekton. The Exocoetidae (flyingfishes) are a good example: only one small speci-

men was taken in the 131 hauls of the 1.5-m. net, but several, including large ones, have been taken at various times in hauls of the high-speed net. Under the circumstances in which we have used these nets, the high-speed net is obviously the more efficient (behaving more like a tuna) for catching exocoetids, in spite of its smaller mouth. This greater efficiency arises from the greater speed of hauling or because we have towed it only in the upper 10 m., where exocoetids are probably most abundant.

The apparent scarcity of enoploteuthid and cranchiid cephalopods in tuna stomachs might not be real, because of their inclusion in unidentifiable material, as noted in the fifth point above. This explanation might also apply to leptocephali.

For some of these reasons, it is perhaps surprising that the percentages for some other groups (Galatheidae, Euphausiidae, Squillidae, and *Vinciguerria*) agree as well as they do in the net-caught and tuna-caught micronekton; euphausiids certainly, and probably *Pleuroncodes planipes* (Longhurst, 1967), and *Vinciguerria* (Ahlstrom, personal communication), are more abundant near the surface by night than by day. These kinds of micronekton sometimes occur at the sea surface in full daylight, however, and possibly their daytime submergence is not so great or so regular as to make them entirely unavailable to tunas.

It is possible that records of the percentages of individual species of Crustacea, which are mostly not available at present, would remove some of the similarities which appear to exist between net catches and contents of tuna stomachs—for example, in the euphausiids. Such records would not affect the galatheids greatly, however, since nearly all were *Pleuroncodes planipes* in both the net catches and the contents of tuna stomachs. *Vinciguerria* would not be seriously affected either, because all of Alverson's specimens and most of mine were *V. lucetia*, although my material included a few *V. nimbraria*, and several specimens that were doubtful (see Ahlstrom and Counts, 1958, concerning *Vinciguerria* in the eastern Pacific).

These considerations give insufficient reason to doubt the commonly held opinion that yellowfin and skipjack tuna feed on most kinds of micronekton which occur in their habitat, with the qualification that the prey must occur under conditions in which the tuna could perceive them visually. The tunas are opportunistic feeders, within their sensory limitations. The only important exception to this generalization is the apparent failure of yellowfin tuna to eat euphausiids, which are much used by skipjack tuna. Efficient capture of euphausiids by large pelagic fish may require special behavior, however (see Blackburn, 1957, on the gempylid scombriform *Thyrsites atun*), and it is possible that these behavior patterns have not evolved in yellowfin tuna.

COMPARATIVE ABUNDANCE OF POTENTIAL TUNA PREY BY AREAS

From tables 8 to 14, and the tables of Alverson (1963a) which show percentage composition of tuna stomach contents for other areas, a list was made of families and other groups which made up 5 percent or more by volume of stomach contents of yellowfin and skipjack tunas in any one of the areas 1 to 14.[6] These groups were considered potential tuna prey in all areas where they occur. Groups which were not represented in the net hauls—the Engraulidae and Polynemidae—were disregarded. This omission left the following groups, which represent kinds of potential tuna prey which the net is capable of catching to some extent in standard night hauls:

Yellowfin tuna prey	*Skipjack tuna prey*
Fish:	Fish:
Gonostomatidae	Gonostomatidae
Myctophidae	Myctophidae
Exocoetidae	Exocoetidae
Thunnidae	Thunnidae
Carangidae	Serranidae
Stromateidae	Scomberesocidae
Coryphaenidae	Trichiuridae
Ostracidae	
Tetraodontidae	
Crustaceans:	Crustaceans:
Galatheidae	Galatheidae
Portunidae	Portunidae
Sergestidae	Euphausiidae
Squillidae (adults)	Squillidae (larvae)
	Phrosinidae
Cephalopods:	Unidentified crab megalopa
Ommastrephidae	

The total volume of net-caught potential prey for yellowfin tuna and for skipjack tuna was standardized (as explained above) for each area (1 to

[6] Stromateidae (table 3, and below) are equivalent to Nomeidae as listed by Alverson.

18). Although it cannot be assumed that each of the prey groups was captured by the net or by the tunas with the same degree of efficiency in each area, the standardized volumes may be compared from area to area (for the prey of each tuna species separately), to indicate broad quantitative differences and similarities among areas in the extent to which they support standing crops of potential tuna prey. Obviously, these volumes do not represent absolute concentrations of tuna prey.

Standardized volumes of skipjack tuna prey were higher than those of yellowfin tuna prey (table 15) for most areas, because they included euphausiids and squillid larvae. Volumes in area 1 were by far the highest, because of the great abundance of *Pleuroncodes planipes;* they are further discussed below. The next highest volumes were in areas 8 and 10, but they are based on only two hauls per area and may, therefore, not be representative; volumes for areas 9, 14, and 15 are likewise ignored because only three or four hauls were made per area.

TABLE 15.—*Standardized volumes (ml./10³m.³) of total potential prey of yellowfin and skipjack tuna as taken in standard night hauls of the 1.5–m. net, for the areas shown in figure 5*

[Actual volumes (ml.) from table 3, other data from table 1; for further explanation see text]

Area	Hauls	Total time	Prey of yellowfin tuna		Prey of skipjack tuna	
			Actual	Standardized	Actual	Standardized
	Number	*Minutes*	*Ml.*	*Ml./10³m.³*	*Ml.*	*Ml./10³m.³*
1	21	984	16,951	63.7	18,497	69.5
2	6	383	674	6.5	716	6.9
3	18	839	845	3.7	1,255	5.5
4	29	1,546	3,277	7.8	3,039	7.3
5	10	565	747	4.9	748	4.9
6	5	262	527	7.5	961	13.5
8	2	96	318	12.2	428	16.5
9	3	195	28	.5	35	.7
10	2	132	481	13.4	501	13.9
11 and 12	6	387	455	4.3	528	5.0
14	4	200	152	2.8	318	5.8
15	3	194	270	5.1	274	5.2
16	7	435	418	3.5	437	3.7
17	7	333	414	4.6	414	4.6
18	8	406	170	1.6	410	3.7
Total	131					

Comparisons may now be made between volumes for areas 1, 2, 3, 4, 5, 6, and 11–12, which have a significant commercial surface fishing for yellowfin and skipjack tunas and volumes for areas 16, 17, and 18, in which there is no significant fishery (see Alverson, 1960, 1963b, for distribution of the surface fishery). The lowest volume of yellowfin tuna prey in an area which supports a fishery was 3.7 ml. per 1,000 m.³, in area 3; the lowest for skipjack tuna prey was 4.9 ml. per 1,000 m.³, in area 5. Volumes for area 16 were slightly below, and those for area 18 well below, these figures; but in area 17 the volume was higher than 3.7 for prey of yellowfin tuna and only slightly lower than 4.9 for prey of skipjack tuna.

Such small differences among areas should be interpreted very cautiously, for reasons given above. It could be argued, however, that area 17 has a sufficiently high standing crop of tuna prey to support a standing crop of yellowfin tuna, and possibly one of skipjack tuna, which might profitably be fished. Of course, the presence of an adequate crop of tuna food does not guarantee the presence of tuna, as is shown by the general scarcity of skipjack tuna in areas 3 and 4 in the years in which the micronekton was collected (Alverson, 1960, 1963b); high sea temperatures may have been limiting in those years, however (Blackburn and associates, 1962; Blackburn, 1963). A more conservative conclusion from the data of table 15 is that some areas west of the existing surface fishery might support commercial surface-fishing operations and should be further explored; and that area 17 is likely to be the best and area 18 the poorest of the three areas considered, as far as abundance of yellowfin and skipjack tunas are concerned.

A Japanese commercial subsurface hook fishery for yellowfin tuna exists at about the same latitudes as area 17; it is located west of area 17 but seems to be extending into that area. Similar fishing is carried on west of, and to some extent in, area 16, but the catch per unit of fishing is lower than in area 17. No longline fishery exists in or near area 18 (Suda and Schaefer, 1965). Skipjack tuna are not commonly taken by subsurface hooking.

The high standardized volumes of potential tuna prey in area 1 warrant comment. Although area 1 is eutrophic, its mean rate of primary production appears to be comparable with that of some other areas, such as 5 and 6, in which tuna prey are much scarcer (Holmes, 1958; Hela and Laevastu, 1962; Blackburn, 1966b). The special feature of area 1, as far as trophic relationships of yellowfin and skipjack tunas are concerned, appears to be the presence of an abundant herbivore, *Pleuroncodes planipes*, which is large enough to release

feeding behavior in tunas. By feeding on this animal, yellowfin and skipjack tunas probably consume a much greater fraction of the organic material produced by photosynthesis in this area than they do in other areas where herbivores are small and carnivores make up most of the tuna diet (see King and Iversen, 1962, table 15, for probable trophic levels of several groups of tuna prey listed above).

QUANTITATIVE COMPARISON OF CATCHES BY 1.5-M. AND HIGH-SPEED NETS

Reference was made previously to qualitative differences between the catches of the 1.5-m. net and the high-speed net; the example given was the greater representation of flyingfish in catches of the high-speed net. The high-speed net was hauled much faster and much closer to the sea surface, on the average, than the 1.5-m. net. It is of interest to compare quantitatively certain areal distributions of micronekton as measured by the two nets for the cruises (TO-59-2 and TO-60-2) for which both sets of material have been fully worked up. The volumes were standardized, as explained earlier, so that all volumes for both nets are comparable in ml. of micronekton per 1,000 m.^{3} of water strained.

Figure 17 summarizes the distribution of total micronekton (fish, crustaceans, and cephalopods combined) in standard night hauls of the 1.5-m. net on cruise TO-60-2; the volumes are the sum of the volumes shown for the same stations in figures 6, 7, and 8. Figure 18 gives similar information for night hauls of the high-speed net (only hauls lasting between 2½ and 3½ hours) on the same cruise.

As far as they are comparable, figures 17 and 18 show similar trends in distribution of micronekton from place to place within the area, especially from onshore (high volumes) to offshore (low volumes) for the area as a whole. Standardized volumes for the 1.5-m. net, however, tend to be about 9 or 10 times higher than those of the high-speed net, in the same area on the same night.

Figure 19 shows a similar comparison, for part of cruise TO-59-2 for catches of red crab (*Pleuroncodes planipes*) only. As far as the 1.5-m. net and high-speed net catches occur in the same areas, they are broadly comparable in general distribution—particularly as between the area east of long. 112° W., where the crabs were scarce, and the rest of the region, where they were abundant. It is again evident that the volumes from the 1.5-m. net were generally much higher than volumes from the high-speed net when both were available at the same time and place.

The reason for the difference between the volumes is uncertain. Possible reasons that have been advanced are: (1) the catches in the high-speed net tend to get shredded by the fast towing so that much material is lost through the meshes; (2) micronekton is actually scarcer at 10 m., where the high-speed net fishes, than it is over the whole water column 0–90 m., where the 1.5-m. net fishes; and (3) the micronekton at 10 m. is disturbed by the ship, and some of it submerges or escapes laterally before the net reaches it. Inspection of catches shows that the first point probably does not apply to the extent that would be required to explain the observed difference, although it does apply to some extent; for instance, it is common to find fish reduced to skeletons in the high-speed net. There is no information on which to base a judgment on the other points. Aron (1962b) noted that catches of the Isaacs-Kidd midwater trawl were invariably low when the net was towed at the surface and attributed this effect to disturbance by the ship.

SUMMARY

Micronekton (fishes, crustaceans, and cephalopods about 1 to 10 cm. long) was collected on oceanographic cruises in most parts of the eastern tropical Pacific Ocean, mainly from 1958 to 1961. The most commonly used collecting method was to haul a large net (mouth 1.5 m. square; length about 5.8 m.) of uniform mesh size obliquely through the upper 90 m. of water at night, at a ship speed of 5 knots. Catches (total micronekton and its family components) were measured by displacement volume; these volumes were then standardized to 1,000 m.^{3} of water strained, by using data on the length of the haul and an empirical filtration coefficient of 76 percent. These measurements of standing crop of micronekton are superior to those that can be obtained with mixed-mesh nets or trawls of the same general size.

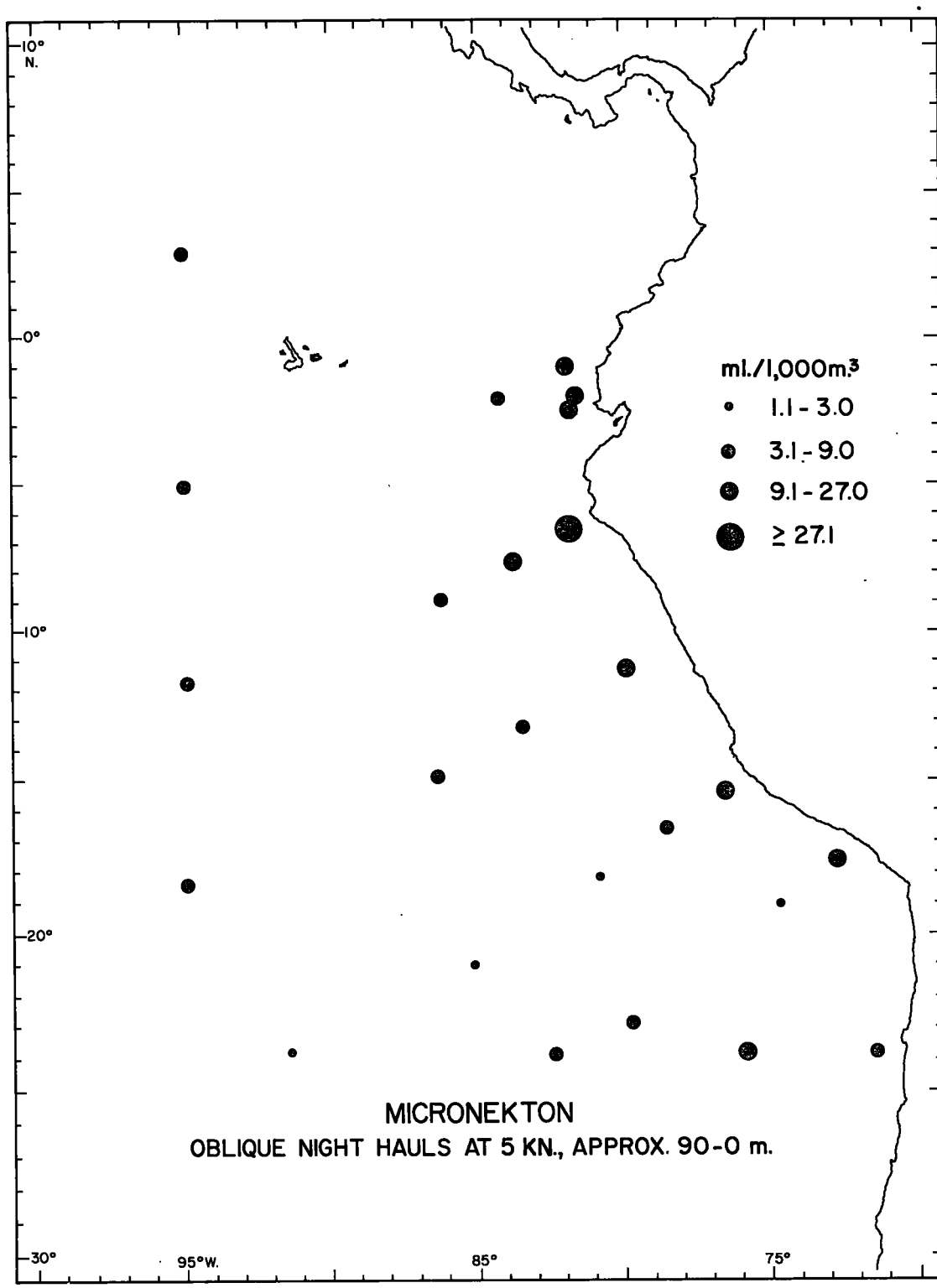

FIGURE 17.—Distribution of standing crop (standardized volume) of total micronekton taken in standard night hauls of the 1.5-m. net on cruise TO-60-2.

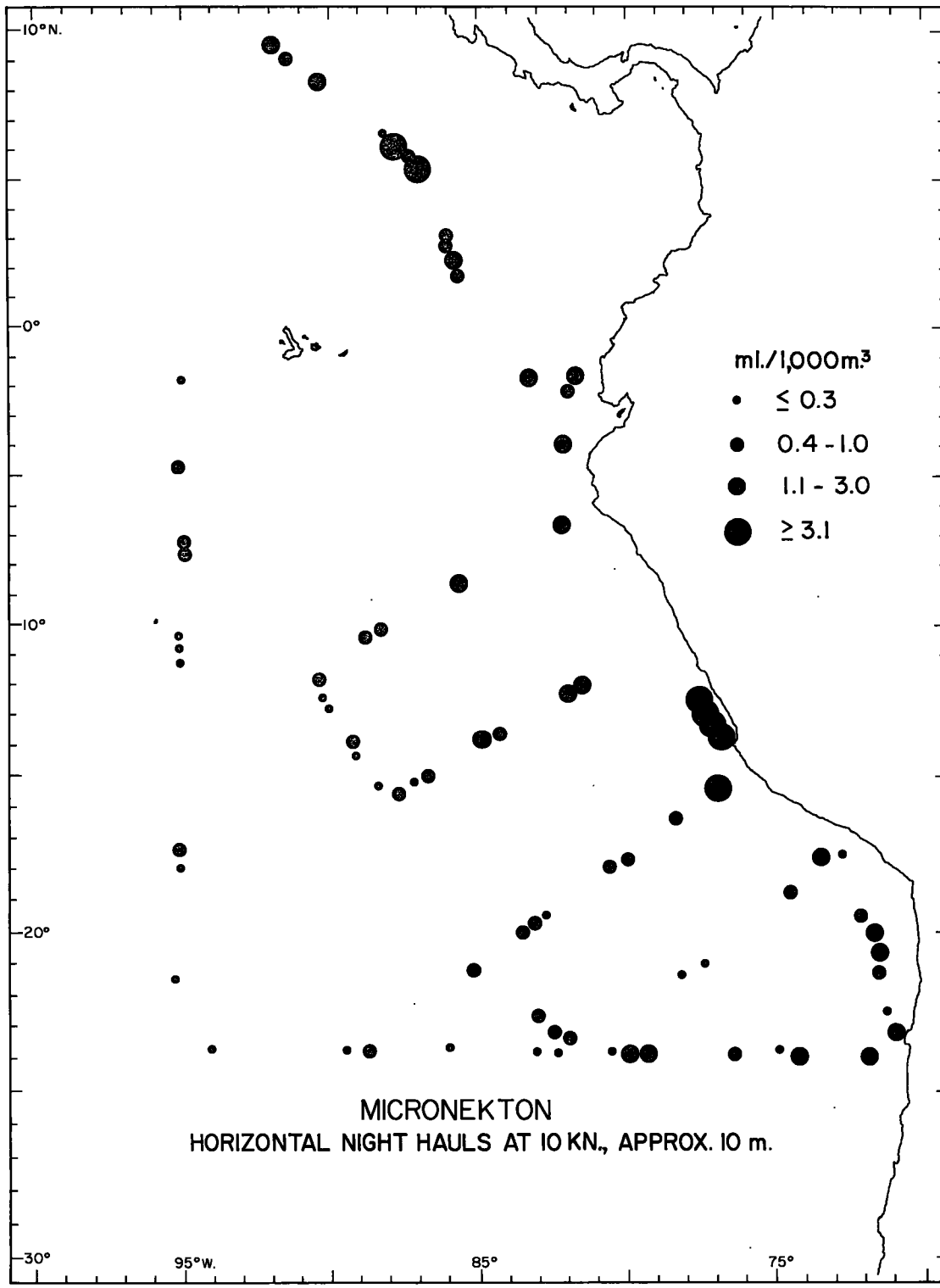

FIGURE 18.—Distribution of standing crop (standardized volume) of total micronekton in night hauls of 2½ to 3½ hours' duration with the high-speed net on cruise TO-60-2.

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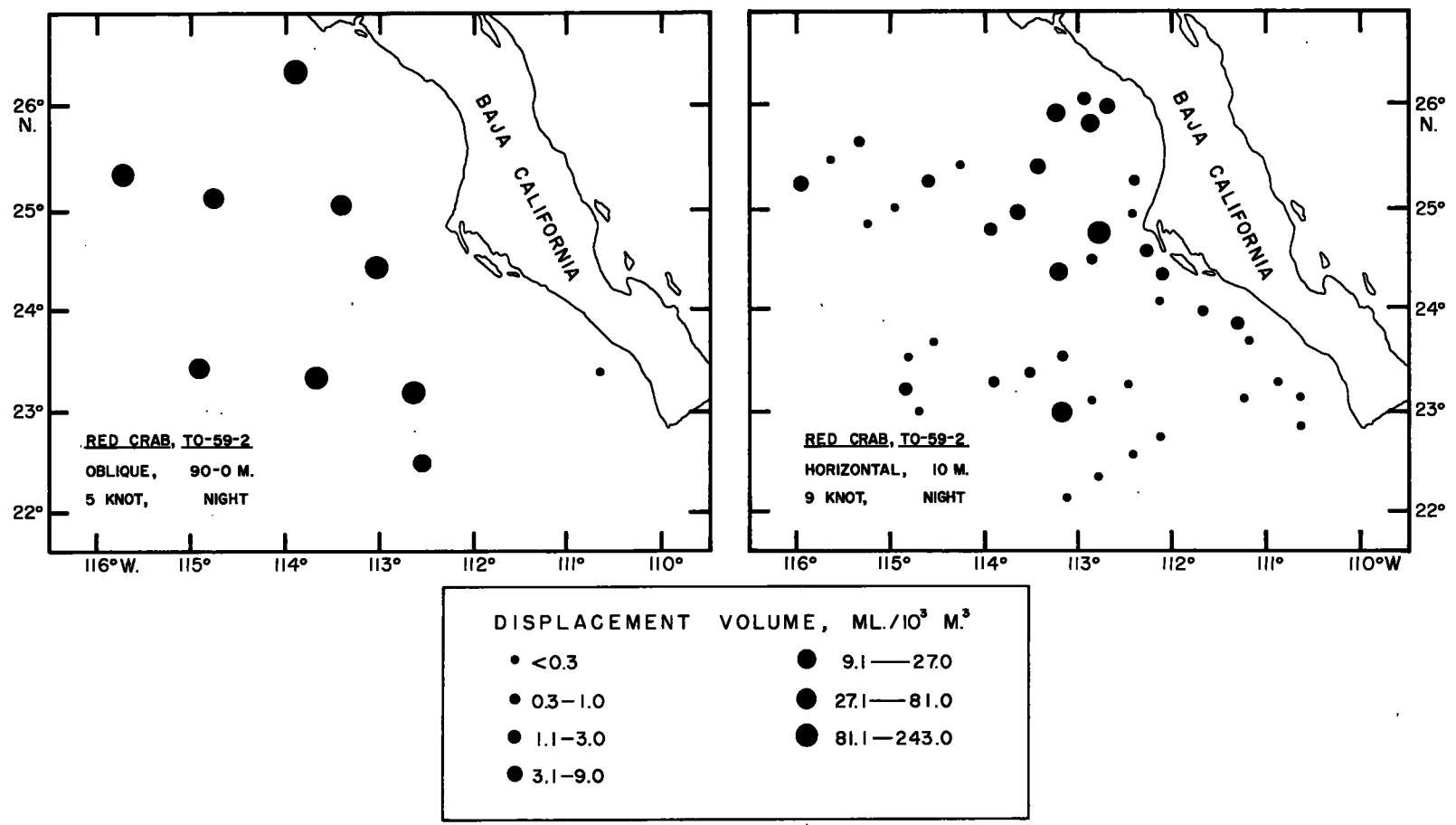

FIGURE 19.—Distribution of standing crop (standardized volume) of *Pleuroncodes planipes* taken in standard night hauls of the 1.5-m. net (left) and in night hauls of the high-speed net (right), on part of cruise TO–59–2. Duration of hauls of the high-speed net ranged from 2 to 3 hours.

Ten families (Myctophidae, Gonostomatidae, Galatheidae, Euphausiidae, Penaeidae, Squillidae, Portunidae, Sergestidae, Enoploteuthidae, and Cranchiidae), and one suborder (Apodes; leptocephali only), which was not sorted to family, made up 93.4 percent of the total volume of micronekton collected in 131 standard night hauls. The areal distribution of standing crop was broadly the same for most of the groups; crops were higher onshore than offshore and highest in onshore areas where physical processes that enrich the upper water layer are known to operate. Three groups of crustaceans (Galatheidae, Portunidae, and adult Squillidae) were confined to relatively small, mainly onshore, areas. The data were insufficient for comparison of standing crops at different seasons, except in the Gulf of Tehuantepec, where the crops appear to fall a few months after enriching physical processes decline.

The composition of the net-caught micronekton was compared with the composition of stomach contents of yellowfin and skipjack tunas as published elsewhere, for certain areas of the eastern tropical Pacific. As compared with tuna, the nets caught different fishes, but broadly similar crustaceans. The differences are attributed to: the fact that the nets catch large quantities of night-rising mesopelagic fishes which do not occur in the tunas' habitat by day, and are probably not seen by the tunas at night; leptocephali are probably not perceptible to tunas in the daylight, since they are translucent; and the more active epipelagic fishes are more efficiently caught by tunas than by nets.

Families which made up at least 5 percent of the stomach contents of yellowfin or of skipjack tuna in any area were considered to be potential prey for the species. To the extent that the net sampled these families, comparisons could be made of potential tuna prey in ml. per 1,000 m.^{3} in different areas (with and without a commercial fishery), for which net data were available. The comparisons suggested that one virtually unfished area supports a crop of potential prey of yellowfin tuna which is higher than that in one of the well-fished yellowfin tuna areas; and also a crop of potential skipjack tuna prey which is nearly as high as that in one of the well-fished skipjack tuna areas. This area, which lies west of the existing fishery area for surface tuna along the coasts of Ecuador and northern Peru, might, therefore, contain yellowfin or skipjack tuna in commercial quantities. Crops of potential tuna prey are much higher off western Baja California than elsewhere; the principal prey species there is the galatheid pelagic crab *Pleuroncodes planipes*, which is in part a herbivore (giving the tunas a more efficient food chain than in most other areas) and extremely abundant.

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SUPERSATURATION OF ATMOSPHERIC GASES IN THE COASTAL WATERS OF THE GULF OF MAINE

By Alden P. Stickney, *Fishery Biologist*

Bureau of Commercial Fisheries Biological Laboratory

West Boothbay Harbor, Maine 04575

ABSTRACT

Year round observations of dissolved oxygen in 1964–67 regularly revealed supersaturation of 120 to 150 percent during the spring and summer. Seasonal variations took the form of a sinusoidal cycle that showed definite phase relations to temperature. Comparisons with data for offshore dissolved oxygen showed that in general the coastal waters were more highly supersaturated.

Nitrogen measurements made in conjunction with those of oxygen led to the conclusion that oxygen supersaturation was usually due to photosynthesis, but occasionally supersaturation of both gases indicated some physical cause.

Supersaturation of oxygen in marine waters, particularly in coastal areas, is not uncommon, and references to it are numerous in the literature. Its effect on marine life has apparently not been investigated, nor are there adequate records for comparison with observed fluctuations in distribution or abundance of organisms.

The coastal waters of the Gulf of Maine support several fisheries, chief among which are those for lobsters (*Homarus americanus* M. Edw.) and for Atlantic herring (*Clupea harengus harengus* L.). The herring fishery in particular suffers from irregular periods of poor catches due to unfavorable distribution (hence, lack of availability) as well as to low abundance. The causes for these irregularities in availability are not known.

To seek possible relations between herring distribution and hydrography, the Bureau of Commercial Fisheries Biological Laboratory in Boothbay Harbor, Maine, is investigating several aspects of the hydrography of coastal waters. Interest in dissolved oxygen stemmed primarily from an outbreak of gas disease in the laboratory aquaria in June 1964. At that time the sea water in these aquaria effervesced with tiny bubbles; several herring died from gas disease and many more showed the typical symptoms—disorientation, exophthalmia (popeye), and bubbles in the fins and lateral line organs. This disease is frequently a result of supersaturation caused by defects in the water pumping system. Careful inspection of our system, however, revealed no defects. Furthermore, Winkler tests of water taken directly from the harbor as well as that supplied through the pumping system showed substantial supersaturation of oxygen. Whether the supersaturation was due to excessive dissolved air, or to oxygen only, was not determined at the time as no equipment was then available at the laboratory for measuring nitrogen. Routine measurements of dissolved oxygen began in the early summer of 1964, but nitrogen measurements were not undertaken until 1965.

Although some data on dissolved oxygen have been published for the Gulf of Maine (Gran and Braarud, 1935; Rakestraw, 1933; Colton, Marak, Nickerson, and Stoddard, 1968), these records are limited to short periods during a few years and cover mainly the open waters of the Gulf rather than the inshore regions. Only occasional measurements have heretofore been made in the coastal waters.

METHODS

Water samples for oxygen analysis were not taken according to a regular schedule, but were spaced to provide a fair coverage of each month. Samples were taken three to five times per week in spring and summer and about once a week in fall and winter. The most conveniently and frequently sampled source was the water pumped into the laboratory from a depth which varied accord-

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ing to tide from about 3 to 6 m. The harbor water was sampled directly with a dissolved oxygen sampling bottle[1] at a depth of 2 m. at the same time the pumped water was sampled, except that during the first winter only one sample was taken each month.

For the first 6 months, samples were analyzed with a polarographic dissolved oxygen meter, but this method proved somewhat unreliable at low temperatures. After the first winter, all determinations were made by the unmodified Winkler procedure. Because the Winkler method has several sources of error, the routine technique was periodically checked on standards of water saturated with air under controlled conditions. The errors averaged about ±0.1 p.p.m.; I did not consider them serious for the purpose of this study. Solubility data for oxygen were obtained from the tables of Green (1965).

Measurements of dissolved nitrogen were not made during the first year (1964). In 1965 a few determinations were made with a manometric Van Slyke apparatus, and in 1966 and 1967 periodic nitrogen determinations were made according to the micro-gasometric method of Scholander, Van Dam, Claff, and Kanwisher (1955). Solubility data for nitrogen were obtained from the tables of Rakestraw and Emmel (1938).

The amount of dissolved oxygen sometimes varied considerably during the day. This fluctuation reflects in part the diurnal cycle of oxygen sometimes called the "oxygen pulse." To obtain comparable measurements from day to day, samples were taken in the afternoon, when concentrations of dissolved oxygen were approaching their maximum. Tides also caused some variation that was reflected as irregularities in the seasonal trends.

OBSERVATIONS IN 1964

The highest oxygen concentration in the laboratory water during 1964 was 12.7 p.p.m. on June 23; the saturation was 153 percent. At the same time, the oxygen in the surface water at Boothbay Harbor was 10.8 p.p.m. and the saturation was 131 percent. Daily maxima of 130 to 140 percent saturation were frequent during June, but thereafter during the summer the levels decreased and fluctuated between 110 and 120 percent saturation.

[1] Type recommended by A.P.H.A. Standard Methods of Water Analysis.

Samples taken elsewhere along the coast in July ranged from 107 to 115 percent saturation in Casco Bay, 100 to 104 percent saturation in Penobscot Bay, and 102 to 112 percent saturation along the eastern Maine coast. Unfortunately, these measurements were not made until after the extremely high values of dissolved oxygen at Boothbay Harbor had diminished; hence, they may be lower than would have been observed earlier in the year.

OBSERVATIONS IN 1965

Oxygen measurements were discontinued toward the end of 1964, but were resumed in January 1965. The water remained close to 100 percent saturation during the winter, but in mid-March the first of a series of peaks in both concentration and saturation appeared; concentration reached 13.5 p.p.m. and saturation 120 percent. The second major peak was in early May when the concentration was 13.5 p.p.m. and saturation over 130 percent. At that time dissolved nitrogen was also high (in excess of 120 percent saturation) for a few days. Thereafter, the concentration of dissolved oxygen decreased slowly and irregularly until the end of July, but because of rising temperature the saturation remained between 120 and 130 percent. Except for a few days in May, dissolved nitrogen, whenever measured, was close to 100 percent saturation.

Winds can sometimes produce dramatic changes in the amounts of dissolved oxygen. A precipitous decrease in dissolved oxygen took place after a strong northwest wind on August 28 and 29; the concentration dropped to 7.3 p.p.m. and saturation to less than 90 percent, but rose shortly to levels as high as before. A second northwest wind-storm on September 26 again dropped the oxygen to below 100 percent saturation where, except for a slight rise during October, it remained for the rest of the year.

For localities other than Boothbay Harbor, saturations in June were 114 to 119 percent in Casco Bay and 117 to 127 percent along the eastern Maine coast.

OBSERVATIONS IN 1966

Saturation of oxygen began to rise above 100 percent late in January. Three major peaks occurred during the spring. In the laboratory water supply these reached 128 percent in late March, 128 percent again in mid-April and 137 percent in

mid-May. The May peak was the highest for the year (13.6 p.p.m., 137 percent saturation) in the laboratory supply water, but the harbor surface did not reach its annual maximum until June 8 (12.3 p.p.m., 133 percent saturation). Thereafter the dissolved oxygen in both water sources decreased irregularly throughout the summer, although the highest average for August was in 1966. Throughout the fall and winter, saturation was usually between 90 and 100 percent.

OBSERVATIONS IN 1967

The dissolved oxygen remained near or below saturation through February, but the concentration reached a record high for the period of study: 14.8 p.p.m. on March 27. Despite the relatively low temperature, saturation reached 130 percent at this time. The next major peak appeared during the third week in May, when the concentration reached 13.5 p.p.m. and saturation 135 percent. Values for pumped water and harbor surface water differed only slightly. As in the 2 preceding years, dissolved nitrogen rose to about 120 percent saturation for a few days in May.

By the end of June the supersaturation of oxygen declined markedly, and the July average was the lowest for that month in the 4-year period. In general, oxygen supersaturation was lower during the whole summer of 1967 than in the 3 preceding years. This drop may have indicated a long-term downward trend, or could have been due to an unusual amount of cloudy or foggy weather.

ANNUAL TRENDS AND COMPARISON WITH OFFSHORE WATERS

The seasonal and annual trends in temperature and in oxygen concentration, percentage saturation of oxygen, and temperature are shown in figure 1. The values shown are averages of all afternoon measurements made each month. They can be considered to be the monthly means of daily maxima.

A study of the figure reveals several points of interest. Both concentration and saturation show a cyclic pattern that bears some relation to temperature. Oxygen concentration tends to be highest when the water temperature is low, but the peaks lag the temperature minima by about a month. Percentage saturation is highest during periods of rising temperatures. The probable reasons for these phase relations are that oxygen is more soluble at low temperatures but the peak of oxygen production by photosynthesis occurs later than the time of minimum temperatures. Maximum concentrations, therefore, occur when the interaction of high solubility and maximum production is optimal. Maximum saturation is similarly the result of optimal interaction between high production and low solubility. Saturation is further increased when the rate of warming outpaces the rate at which the dissolved gas can come into equilibrium with the atmosphere.

The supersaturation of oxygen appeared to be somewhat higher at Boothbay Harbor that at other localities along the coast, although the number of samples taken elsewhere may not have been sufficient to provide a fair comparison. Values for coastal waters were generally higher in 1965 and 1966 than those observed for comparable periods in offshore waters during the *Albatross IV* cruises (Colton et al., 1968). In 1965 no offshore samples exceeded 120 percent saturation in May and June, and in 1966 only 3 percent of all samples from the top 20 m. in the open Gulf of Maine were greater than 120 percent. At Boothbay Harbor during the comparable period of both years, 78 percent of the samples in 1965 and 82 percent in 1966 exceeded 120 percent saturation. Elsewhere along the coast during a comparable period, 14 percent of the samples in 1965 and 43 percent of those in 1966 showed over 120 percent saturation.

CAUSATIVE FACTORS

Oxygen supersaturation in the sea can result from several processes, of which two have major significance. The most important is probably the actual increase in oxygen concentration resulting from photosynthesis; the other is a change in the physical properties of the water which affects the solubility of gases. Air that diffuses into water from the atmosphere at the sea surface can produce 100 percent saturation of oxygen and nitrogen at the ambient temperature, salinity and barometric pressure; if these physical properties change rapidly, the water can become at least temporarily supersaturated. Rapid warming of saturated water, or the mixing of warm and cold saturated water results in supersaturation until the gases are able to once again achieve equilibrium with the atmosphere.

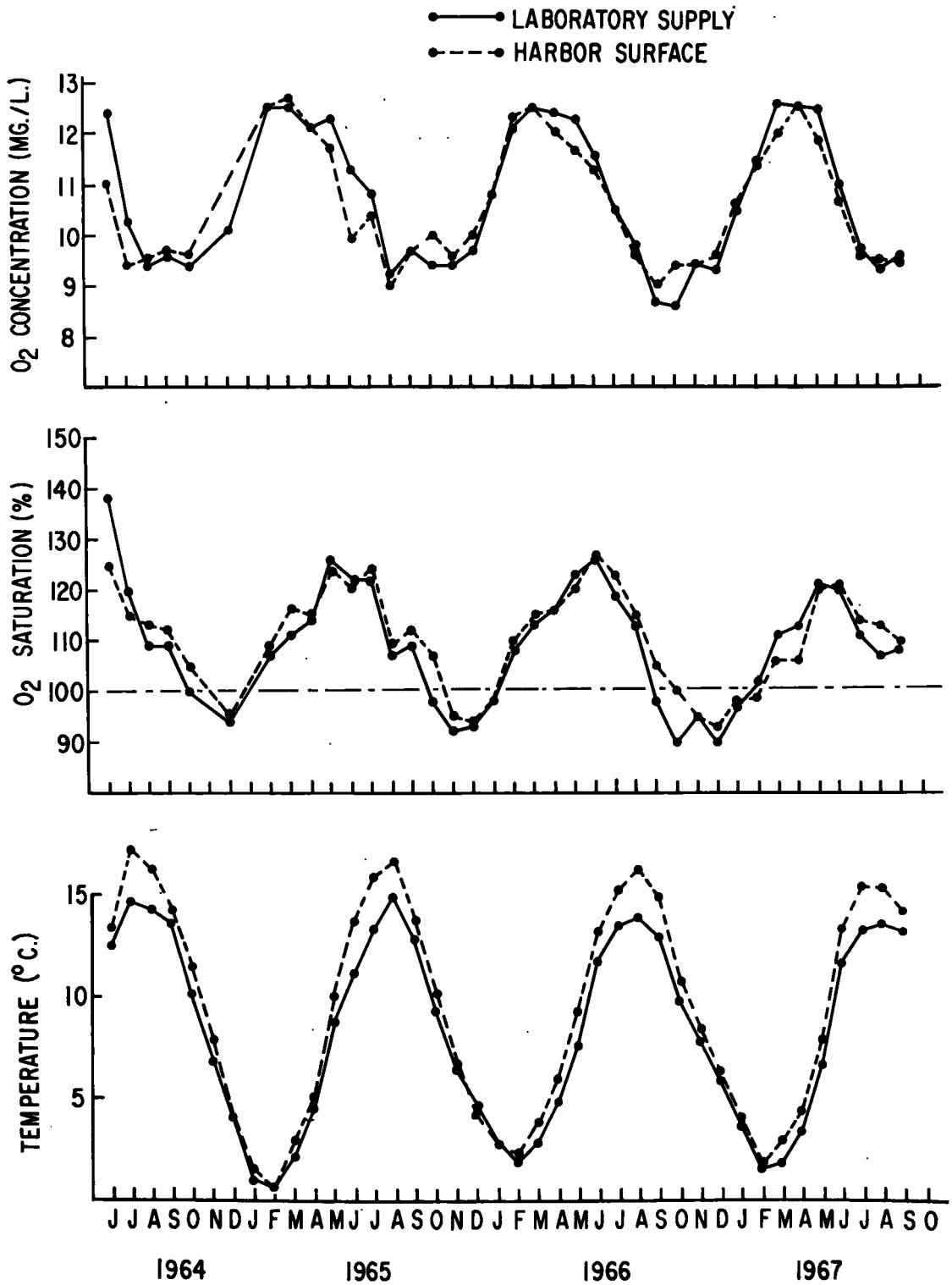

FIGURE 1.—Monthly means of daily maximum concentration and percentage saturation of dissolved oxygen and corresponding mean water temperatures at Boothbay Harbor, Maine, 1964–67.

TABLE 1.—*Percentage saturation of nitrogen and concentrations of oxygen in excess of saturation according to source, calculated from observed nitrogen and oxygen concentrations. P: photosynthetic oxygen, A: atmospheric oxygen. Entries for each month are given chronologically but the dates for each entry do not correspond exactly from year to year; approximate time of month is indicated by the position of each entry in a column.*

Year	1965			1966			1967		
Month	N_2 saturation	Excess O_2		N_2 saturation	Excess O_2		N_2 saturation	Excess O_2	
		P	A		P	A		P	A
	Percent	*Ml./l.*		*Percent*	*Ml./l.*		*Percent*	*Ml./l.*	
March				102	0.15	0.15			
				98	.75	None	109	0.10	0.75
April	98	None	None						
	104	0.80	0.30						
	113	None	.65				104	None	.27
	109	.55	.70	100	1.75	None	113	None	.70
	105	.25	.30	108	None	.45	110	.55	.80
				113	None	.60			
May	106	1.20	.30	106	1.50	.45			
	127	None	1.80	109	1.75	.50			
	127	.60	1.90	116	1.60	1.15			
				116	.95	1.20	117	1.05	1.25
				112	1.30	.80			
				114	1.20	.95	121	None	1.45
	103	2.05	.15	110	.90	.70			
				109	.70	.70	106	1.05	.50
June	85	1.25	None	107	.40	.50			
	104	.35	.25	107	1.30	.50			
	96	1.35	None	100	1.10	.10			
	97	1.45	None	104	.40	.35	107	None	.55
	101	1.40	.10	101	.90	.10	105	.25	.50
	98	1.35	None	102	.50	.20			
	94	1.00	None	101	.30	.10			
July	92	1.15	None	109	.35	.65			
				108	.35	.60			
				109	None	.75			
				108	.05	.60	106	None	None
				111	.05	.75	108	None	.25
				110	None	.55			
				112	None	.50			
				115	.20	.95	111	None	None
August	109	.60	.60	110	None	.40	111	None	.30
				117	None	.60	107	None	None
	98	.55	None	111	None	None	111	None	None
				113	None	None	106	None	.30
				108	None	.35			
September	104	1.25	.30	112	None	None			
				108	None	.40			

Supersaturation arising from these two processes can be distinguished if the concentration of nitrogen is known. Nitrogen and oxygen which enter solution from the atmosphere bear a nearly constant ratio to one another, expressed by the equation $O_2 = .577\ N_2 - .22$ (Rakestraw and Emmel, 1938). This equation indicates the amount of oxygen which ought to be in solution for any given concentration of nitrogen. Oxygen in excess of this amount represents that added by photosynthesis; the difference between the calculated oxygen concentration and the oxygen concentration at saturation represents the excess or deficit of atmospheric oxygen.

Nitrogen observations were made only intermittently in the present study; the observations, however, together with source composition of excess oxygen are given in table 1. As can be seen, the greatest nonphotosynthetic oxygen supersaturation and supersaturation of nitrogen occurred usually in April or May or occasionally in midsummer.

The physical causes of supersaturation could be intensified by the coastal topography. Numerous protected and shallow embayments permit rapid warming of the water; tidal movement is strong and conducive to the mixing of warm and cold saturated water, producing supersaturation of the mixture; warming of subsurface waters is a possible result of the flooding of sunheated tidal flats. I have no evidence that these particular processes are, in fact, the cause of nonphotosynthetic oxygen supersaturation, but they are theoretically possible.

ECOLOGICAL SIGNIFICANCE

The immediate question posed when the first indications of supersaturation were noticed was whether this situation was unusual or a regular annual occurrence. On the basis of 4 years of observations, the answer seems to be that it is a regular occurrence, although annual variations in the seasonal cycle are marked. Longer term trends may also be indicated in the basic annual cycles.

The duration and degree of supersaturation declined with each passing year of the period studied.

Strong annual variations in the degree of supersaturation could very probably produce fluctuations in the abundance and distribution of marine organisms if these organisms can be affected by supersaturation. The most marked effect of supersaturation on fish and other organisms is gas bubble disease. This disease, however, does not appear unless certain conditions obtain. By convention, the percentage saturation of dissolved gases in the sea is the ratio between the observed concentration at some depth and the concentration which would exist at the sea surface in equilibrium with the atmosphere at the same temperature and salinity as the depth in question. Thus, water at moderate depths may be supersaturated according to this definition and yet because of the hydrostatic pressure actually be capable of holding much more gas in solution. Ricker (1934) has called the degree of saturation which is related not to a theoretical surface value, but to the absolute capacity of water at a given hydrostatic pressure, the "absolute saturation." "Gas disease" due to supersaturation alone can occur only in absolute supersaturation. Furthermore, this supersaturation must be extremely high if gas disease is to be caused by oxygen. Observations have been made of gas disease occurring in the natural environment at oxygen saturations of 250 percent (Renfro, 1963) and over 300 percent (Woodbury, 1942). I have experimentally induced gas disease in herring (*Clupea harengus harengus*) at saturations of pure oxygen of 300 percent, but could not produce the symptoms at less than 200 percent saturation. Nitrogen, however, seems to be dangerous to fish at saturations of 125 percent or more (Marsh and Gorham, 1905; Egusa, 1959). In air-supersaturated water, I have experimentally induced gas disease at saturations of 120 percent nitrogen and 130 percent oxygen. In my experiments, the herring showed a definite tendency to avoid the supersaturated water, but only when the saturation levels were high enough to produce gas disease.

Gas disease can occur, furthermore, only when the total gas pressure in the water exceeds the combined hydrostatic and atmospheric pressures. When the concentration of any gas is increased by the displacement of another gas, gas disease is unlikely as long as the total gas pressure is not increased. Fish have been exposed with little harm to oxygen saturations of up to 400 percent by bubbling this gas into the water at atmospheric pressure (Haempel, 1928; Bishai, 1960). Pathological symptoms occurred in some of Haempel's fish, but they seemed to be unrelated to gas disease.

The above evidence suggests very strongly that the levels of gas supersaturation along the Maine coast are not high enough to have a direct detrimental effect on fish in their natural environment. The situation under artificial conditions is much different, however. In aquaria, lobster pounds, and other similar installations where water is pumped from below the surface of the sea into relatively shallow tanks at sea level atmospheric pressure, any nominal supersaturation becomes absolute. This supersaturation, perhaps aggravated by elevations in temperature or by the pumping system itself could produce lethal conditions as it did in our laboratory in the summer of 1964. The most likely effect of supersaturation on fish populations, if there is any effect at all, would probably be indirect, but lack of evidence to demonstrate such effects precludes useful discussion of them at this time. The facts do show, however, that a condition does exist, and recurs annually in more or less cyclic fashion, which could conceivably play a definite role in the ecology of marine organisms.

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RELATION BETWEEN TAIL LENGTH AND TOTAL LENGTH FOR THREE COMMERCIALLY IMPORTANT SPECIES OF PENAEID SHRIMP[1]

By Clark T. Fontaine and Richard A. Neal, *Fishery Biologists*
Bureau of Commercial Fisheries Biological Laboratory
Galveston, Texas 77550

Length measurements of shrimp from commercial landings are an important source of biological information. Total length (tip of telson to tip of rostrum) is the measurement most commonly used, but it cannot be determined directly when fishermen separate shrimp "heads" (cephalothorax) and "tails" (abdomen) before they reach the docks. We determined the relations between tail length (anterior margin of first abdominal segment to tip of telson) and total length so that measurements obtained from headless shrimp could be converted to total lengths.

The relations were based on data from 1,581 brown shrimp, *Penaeus a. aztecus* Ives (86–225 mm., total length); 2,460 white shrimp, *P. setiferus* (Linnaeus) (74–213 mm.); and 1,909 pink shrimp, *P. d. duorarum* Burkenroad (82–194 mm.). The brown and white shrimp were caught off the Texas coast, and the pink shrimp were from the Tortugas grounds off Florida. Measurements were made to the nearest millimeter, and, when possible, equal numbers of shrimp were measured in each 5-mm. total length group.

The relation between tail length and total length appeared to be linear for the range of sizes examined; a straight line was fitted to data for each sex of each species by the method of least squares (figs. 1 and 2). Formulas for the lines are presented in table 1.

Table 1.—*Equations describing the relations between tail length and total length of pink, brown, and white shrimp*

[Y=total length, X=tail length]

Species and sex	Equation	Standard error of regression coefficient	Number measured
Pink:			
Male	$Y=8.762+1.547X$ $X=-4.041+.632Y$	0.008 .003	802
Female	$Y=4.506+1.628X$ $X=-1.923+.607Y$	.005 .002	1,107
Brown:			
Male	$Y=7.221+1.593X$ $X=-2.998+.616Y$	.009 .003	598
Female	$Y=-1.085+1.710X$ $X=2.029+.576Y$	.007 .002	983
White:			
Male	$Y=5.356+1.623X$ $X=-2.573+.611Y$	.004 .002	1,214
Female	$Y=2.882+1.672X$ $X=-1.154+.594Y$	.004 .001	1,246

[1] Contribution No. 262, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas 77550.
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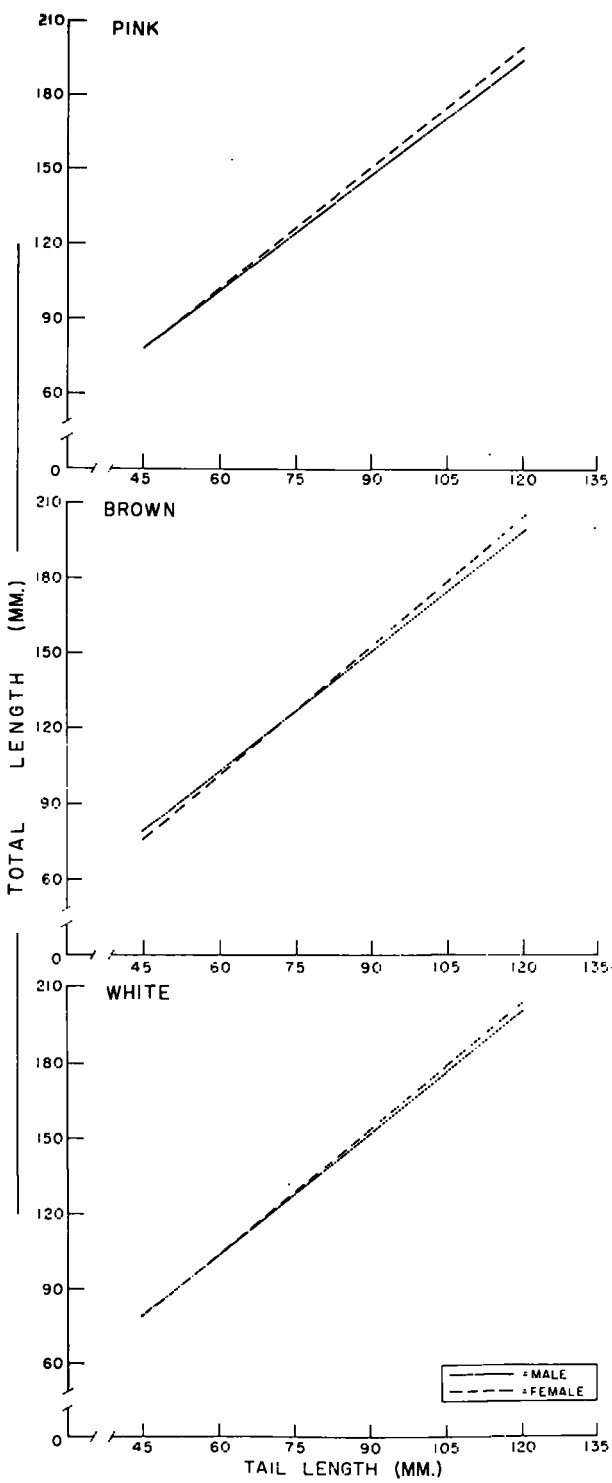

FIGURE 1.—The tail length-total length regression lines for pink, brown, and white shrimp.

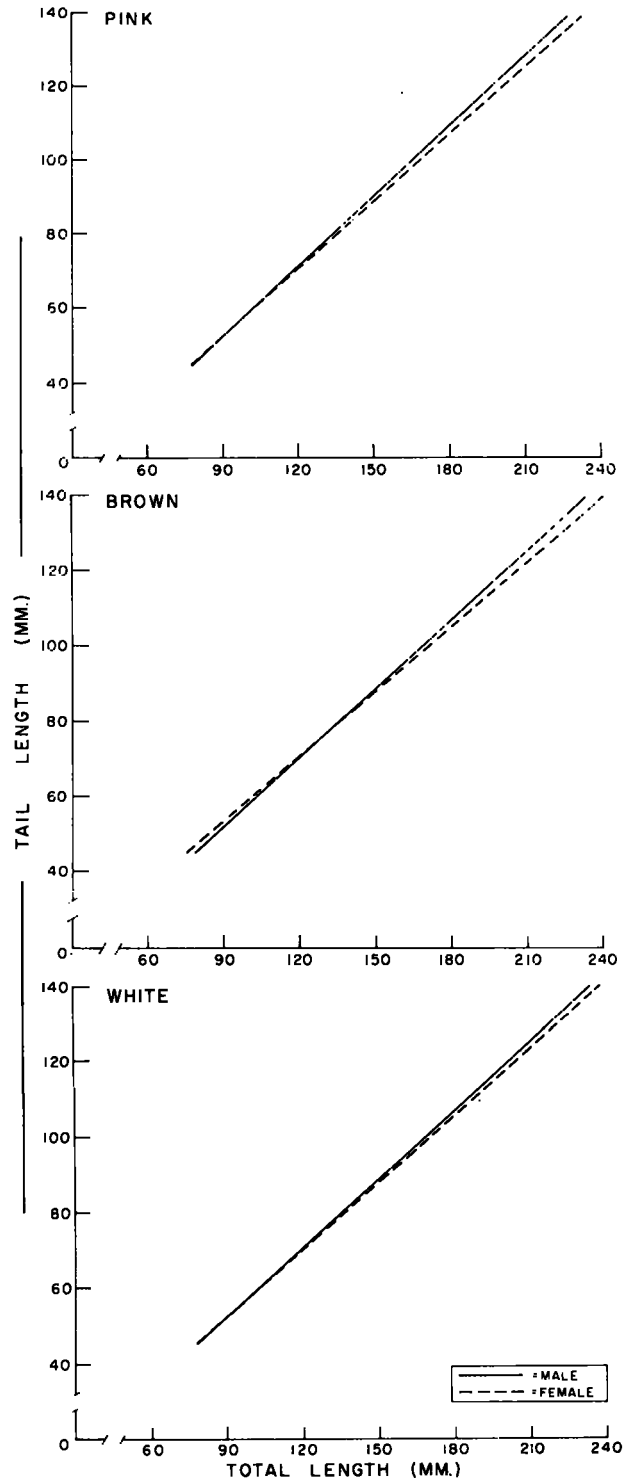

FIGURE 2.—The total length-tail length regression lines for pink, brown, and white shrimp.

SEA-STARS OF NORTH CAROLINA

BY I. E. GRAY,[1] MAUREEN E. DOWNEY,[2] AND M. J. CERAME-VIVAS[3]

ABSTRACT

Descriptions, keys to identification, and photographs are given for the 22 genera and 33 species of North Carolina asteroids. The starfish fauna is predominantly "southern." Eighteen species are distributed from North Carolina southward, nine range from North Carolina northward, and six occur both north and south of North Carolina. The affinities of the various species to the principal marine biotic provinces are discussed. Thirteen tropical and subtropical species occur only in an extension of the Caribbean Province along the outer shelf. Only four of the 33 species on the Continental Shelf can be considered abundant: *Astropecten articulatus, Luidia clathrata, Astropecten americanus,* and *Asterias forbesii.*

Although isolated records exist, no previous attempt appears to have been made to bring together a list, with workable keys for their identification, of the asteroids that occur in North Carolina waters. Only the inshore, shallow-water species are well known. Pearse and Williams (1951) in their study of reefs off New River Inlet added two species new to North Carolina records and Cerame-Vivas and Gray (1966) listed six others. Sampling has been extensive in recent years; at least 33 asteroids are now known from the North Carolina Continental Shelf, and probably many additional species occur in deeper waters off the shelf. The need for identification sources for starfishes in this area has become acute because of the marked increase of interest in marine biology, the expansion of opportunity for oceanographic training, and the greater frequency of research cruises and offshore collecting by university classes in marine ecology and invertebrate zoology.

The present discussion is limited to the Asteroidea of the Continental Shelf; deep-sea species, even though in the latitude of North Carolina, are not included. The 200-m. contour, near the edge of the shelf, makes a convenient seaward boundary of the area under consideration. Depth increases rapidly on the slope, and species of the continuously cold waters of the slope and beyond live in a different environment and more properly belong to the deep-sea benthos.

METHODS

SAMPLING PROCEDURES

Other than the fact that all starfishes are marine no single environmental condition is common to all species. Asteroids differ in habits, habitats, depths of water at which they occur, and in tolerance to adverse conditions. Consequently, no one sampling technique is adequate for all species. Hand-picking from jetties and the use of light dredges operated from small craft are satisfactory for collecting some species. Heavy gear is essential for dredging in deeper waters and on rocky ledges.

Especially useful to us, because they cut into the substrate, were the heavy Cerame-Vivas rock dredge (locally known as the C–V dredge) and the Cape Town dredge (also known as the Day dredge, because it was introduced by John Day of the University of Cape Town). The frame of the C–V dredge (Cerame-Vivas and Gray, 1966) was fashioned from scrap metal and, with lead shoes added, weighed over 200 kg. The leading edge consisted of a bulldozer blade estimated to cut into a substrate of hard-packed sand a minimum of 12

[1] Professor Emeritus, Duke University, Beaufort, N.C. 28516.
[2] Museum Specialist, Division of Echinoderms, Smithsonian Institution, Washington, D.C. 20560.
[3] Director, Department of Marine Sciences, University of Puerto Rico, Mayaguez, P.R. 00708.

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cm. The mouth opening was slightly over 1 m. in width. This rugged dredge was used on rocky ledges as well as on level bottoms. Use of the smaller, lighter, and less rugged Cape Town dredge was limited mainly to level bottoms. Chartered shrimp trawlers and Duke Marine Laboratory's RV *Eastward* were used in the dredging.

For such forms as *Astropecten* and *Luidia* that glide over the sandy substrate and feed by ingestion of numerous small surface organisms, commercial trawls proved very satisfactory. Diving on reefs in relatively shallow water and using SCUBA (Self Contained Underwater Breathing Apparatus) produced some species not taken by other means, but this excellent collecting method was not used beyond a depth of 30 m.

Bottom photographs have sometimes helped demonstrate relative abundance, but only rarely can these be used alone for positive identification of species. Also, many sea-stars cannot be satisfactorily photographed because they bury themselves beneath the substrate and leave only an imprint to indicate their presence.

Probably some species which appear to be scarce would prove to be more abundant if more suitable methods for their collection were used, especially on reefs, ledges, and rock outcroppings too deep for normal SCUBA diving.

Not all parts of the shelf have been sampled with equal intensity, and our list of asteroids is probably incomplete. The most frequent collections have been made between the latitude of Oregon Inlet, well north of Cape Hatteras, and New River Inlet, well south of Cape Lookout. Material is more scanty from the area off Cape Fear and Frying Pan Shoals. Nevertheless, we believe that the data presented justify the assumption that most of the species to be found in North Carolina are included, since the areas that have been extensively sampled cover the principal marine biotic provinces. The most serious potential source of error lies not in the range of latitude sampled but in the lack of adequate collections from reefs and hard bottoms.

PRESERVATION TECHNIQUES

Starfishes should preferably be relaxed before preservation, but this is not always possible on shipboard. Some species normally remain flat, but in others the arms tend to curl. They can be relaxed and preserved in sea water in a flat enamel pan large enough for the specimens to spread out without touching one another. The sea-stars flatten if magnesium sulphate (Epsom salt) is sprinkled on the water or if fresh water is added, a little at a time, until the sea water is replaced. Regardless of method, after relaxation is completed the water should be replaced by 70 percent alcohol or by 6 percent neutralized Formalin.[4] Echinoderms should never be kept permanently in Formalin, however, as it destroys their calcite plates. Unfortunately, and perhaps unavoidably, alcohol removes much of the color. Usually it is more satisfactory to dry specimens after they have been preserved; this solves many storage problems. If later there is need to examine soft parts (e.g., to determine whether or not the podia have suckers), the whole specimen, or better still, a single arm can be soaked for a few hours in ordinary detergent. To examine underlying plates or other hard parts, soft tissue can be removed by dipping the appropriate part of the animal in household bleach. Bleach must be used carefully; excessive amounts can easily remove all connective tissue holding the plates together. The action of bleach can be quickly ended by rinsing the specimen in running water. It is best to treat only one arm of a specimen, as it may be desirable later to check certain anatomical features of the soft tissues.

To examine pedicellariae, one or two can be removed under magnification with fine forceps and placed on a glass slide with a drop of dilute bleach. Bleach will not always be necessary, as the valves of the pedicellariae are sometimes clearly visible without further treatment.

BIOGEOGRAPHICAL AREAS

Analysis of the distribution of any major group of benthic species on any segment of the North Atlantic Continental Shelf holds more than local interest. This is especially true of the North Carolina section of the shelf, which in any discussion of north-south distribution of species occupies a position of marked biogeographic importance. Located about midway on the U.S. Atlantic coast between temperate New England and subtropical Florida, the North Carolina shelf has several marine climates and associated temperature barriers within relatively few kilometers. Several capes,

[4] Trade names referred to in this publication do not imply endorsement of commercial products.

especially Cape Hatteras, project onto the shelf and divert water masses. The southwesterly flowing Virginian Coastal Current brings cool water from Cape Cod to Cape Hatteras before it is shunted seaward, and the warm Florida Current flows northeasterly and overlaps the outer edge of the shelf to a point well north of Cape Hatteras. The Carolinian Coastal Current, varying greatly in intensity depending on wind regimes, flows southwesterly from Cape Hatteras. The width of the shelf varies from less than 32 km. off Cape Hatteras to more than 80 km. across Onslow Bay. As shown by Cerame-Vivas and Gray (1966), boreal animals from the north and subtropical species from the south are both able to maintain themselves in North Carolina waters. This does not imply that the Continental Shelf of North Carolina is necessarily a transition zone between northern and southern species, but rather that species with different geographic affinities may occur in ecologically different areas in North Carolina waters, even at the same latitude.

Three marine biotic areas (fig. 1) have been recognized on the North Carolina Continental Shelf (Cerame-Vivas and Gray, 1966):

A. The Virginian Province is a cold-water, wedge-shaped area that has its apex at Cape Hatteras and widens to the width of the shelf near the latitude of Oregon Inlet. This region is heavily influenced by the Virginian Coastal Current.

B. The Carolinian Province extends southward from Cape Hatteras and occupies the inner two-thirds to three-fourths of the shelf. In addition to its own fauna, this area receives contributions from the Virginian Province in winter and from the Caribbean Province in summer.

C. An extension of the Caribbean Province forms the outboundaries of both the Carolinian and Virginian Provinces and constitutes the outer shelf under the Florida Current. Northward it extends to the point where the Florida Current leaves the shelf. Because of the meanderings of the Florida Current over the edge of the shelf under different wind regimes (Bumpus, 1955; Bumpus and Pierce, 1955; Gray and Cerame-Vivas, 1963), neither the northern nor western limits of the Caribbean Province can be precisely defined.

The boundary between Virginian and Caribbean Provinces forms a much more formidable barrier to distribution than the barrier between Carolinian and Caribbean Provinces, which in summer is rather diffuse. The "Hatteras Barrier" between the Virginian and Carolinian Provinces is frequently broken in winter when persistent northeast winds (the prevailing winter winds) push Virginian coastal waters past Cape Hatteras and Diamond Shoals into Raleigh Bay and beyond (Bumpus and Pierce, 1955; Wells and Gray, 1960; Gray and Cerame-Vivas, 1963), creating favorable conditions for "northern" species to live in the Carolinian Province temporarily.

ABUNDANCE AND DISTRIBUTION

Although level bottoms of sand and mud predominate on the North Carolina shelf, scattered here and there are hard substrates: reefs of Trent Marl covered with calcareous tubes of mollusks, coquina formations, encrusted *Lithothamnion* algae, patches of coral, shelly areas, and wrecks that support a varied and abundant biota. The submerged reefs are well known to fishermen but, unfortunately, have been little studied by biologists. Pearse and Williams (1951) pioneered in describing the biota of the reefs off New River Inlet. More recently Menzies, Pilkey, Blackwelder, Dexter, Huling, and McCloskey (1966) made a comprehensive study of a *Lithothamnion* reef near the edge of the shelf off Onslow Bay. The fauna listed was predominantly tropical and subtropical. Pearse and Williams reported four sea-stars on their inshore reefs; Menzies et al. (1966) identified but one asteroid from their offshore reef. Granite substrates are limited to the inshore, shallow-water man-made jetties. Not all sea-stars require a hard substrate, but some that do (*Echinaster spinulosus* and *Thyraster serpentarius*, for example) are not abundant elsewhere. Grass beds (principally eelgrass *Zostera* and widgeon grass *Ruppia*), limited to soft bottoms of the estuaries, may be ignored as habitats for starfishes, although occasionally the very young of *Asterias forbesii* are found here.

The 33 species of sea-stars definitely known to occur on the North Carolina Continental Shelf fall into 22 genera. Of the four genera that have

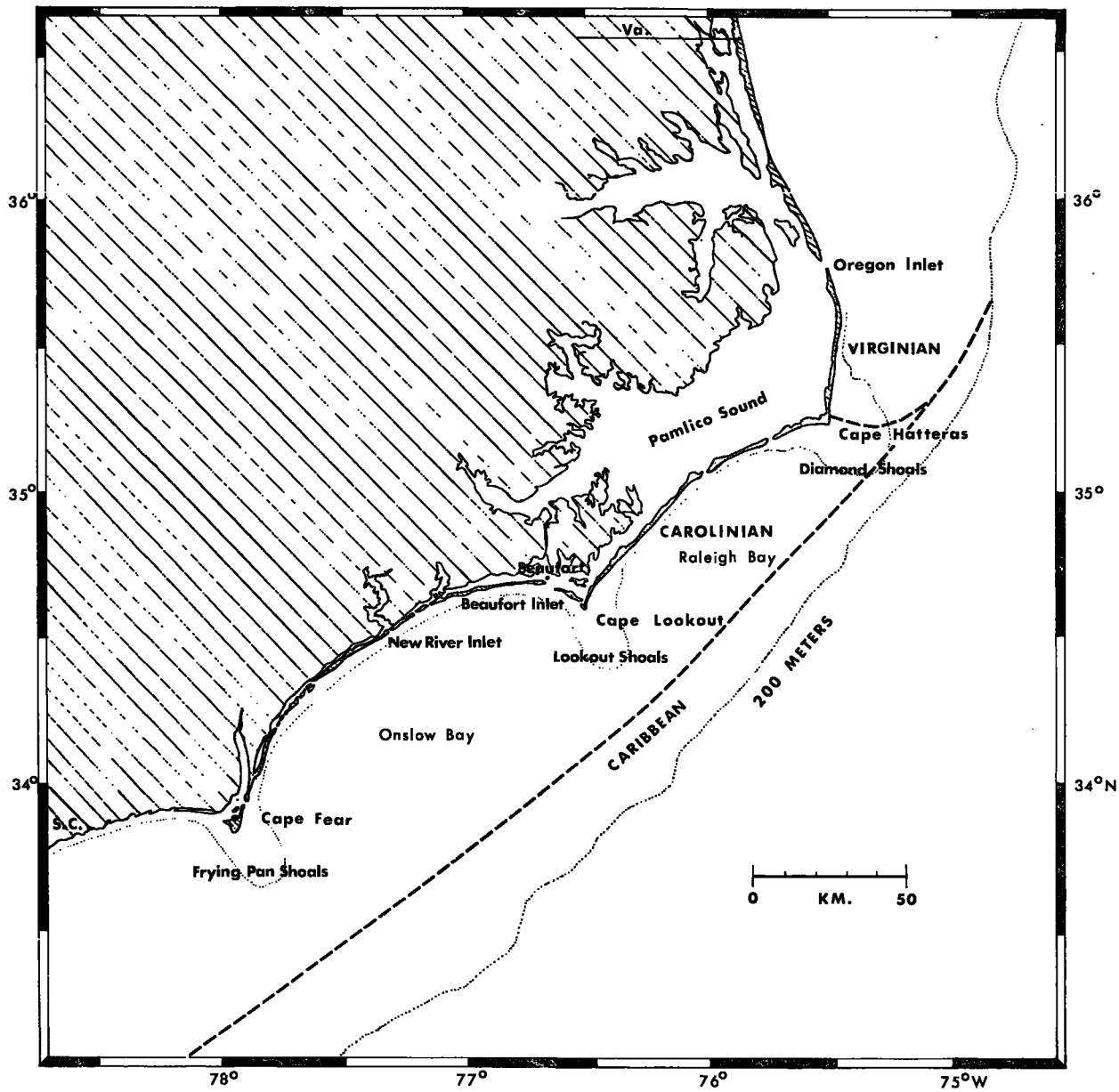

FIGURE 1.—Map of the North Carolina coast showing relation of the three major biotic provinces (Virginian, Carolinian, and Caribbean) to Cape Hatteras and the Continental Shelf. The heavy broken lines indicate the approximate boundaries between the provinces.

more than one species, three contain the four most common species. These are, in order of abundance: *Astropecten articulatus*, *Luidia clathrata*, *Astropecten americanus*, and *Asterias forbesii*. The first two occur in large numbers on level bottoms in 10 to 100 m. in Raleigh Bay and Onslow Bay, and commonly appear together in trawls of shrimp and scallop fishermen. Their numbers diminish north of Cape Hatteras and nearer the edge of the shelf. *Astropecten americanus*, on the other hand, is abundant north of Cape Hatteras but is rare south of the cape. *Asterias forbesii*, a shallow-water species, is the only sea-star that lives permanently within the estuaries. At times it is very abundant on the jetties. *Astropecten articulatus* and *L. clathrata* are sometimes discarded in the estuaries by shrimp fishermen when they clean their nets and boats, but these species seem to be unable to survive

here throughout the year—perhaps from lack of suitable substrate on which to feed, or because of their inability to withstand winter cold or occasional lowered salinity in the shallow estuaries.

The starfishes of North Carolina predominantly have a southern affinity. Eighteen species range from North Carolina southward and nine from North Carolina northward. Only six are found both north and south of North Carolina, and four of these are more southern than northern. One (*Coscinasterias*) extends only as far north as Virginia, and three as far as New Jersey. Comparison of figures 2 and 3 shows that strictly "northern" species—those that range northward from North Carolina—are rare south of Cape Hatteras. They appear in the cool south-flowing Virginian Coastal

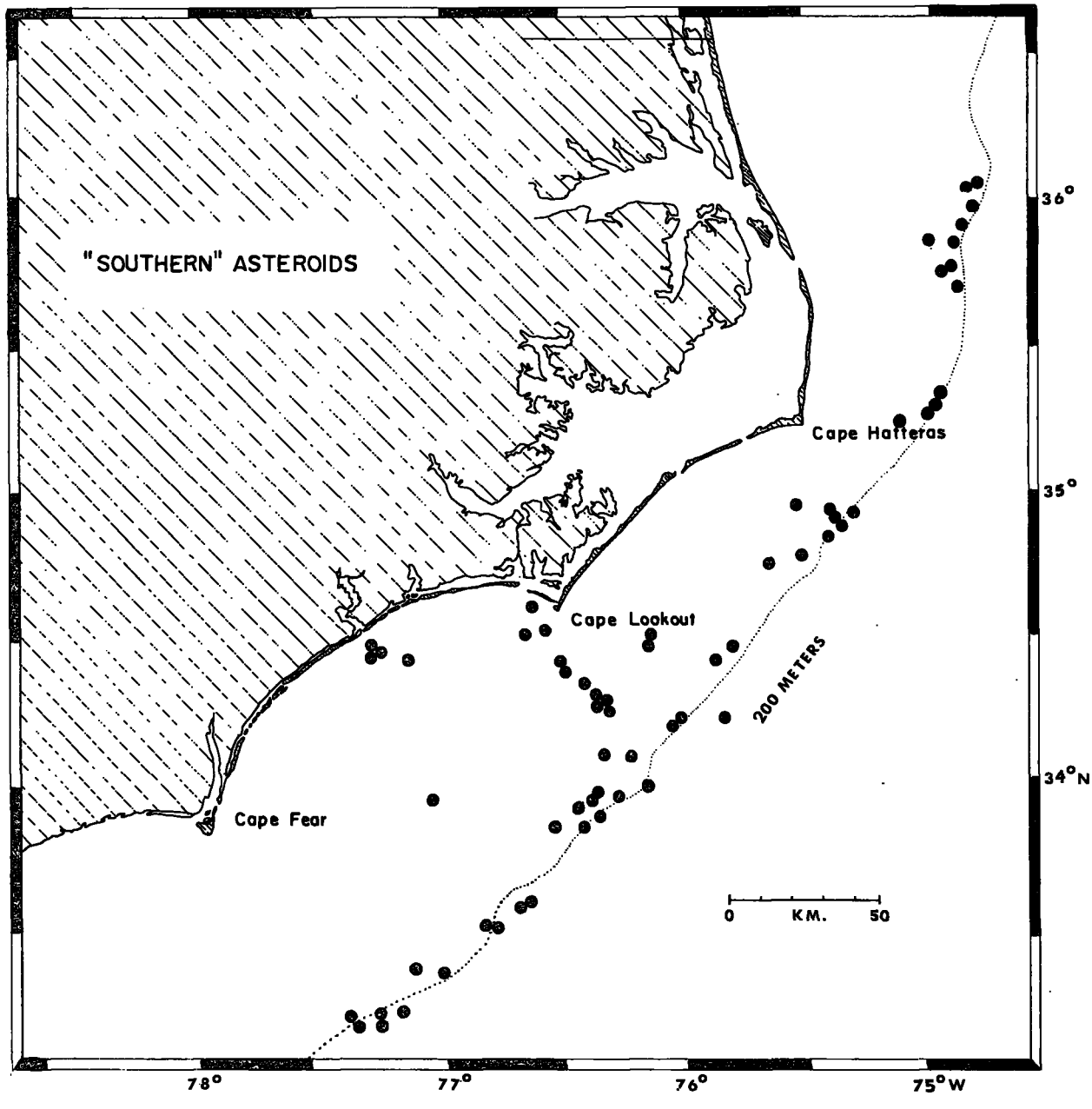

FIGURE 2.—Stations in North Carolina at which 16 of the 18 "southern" asteroids have been taken.

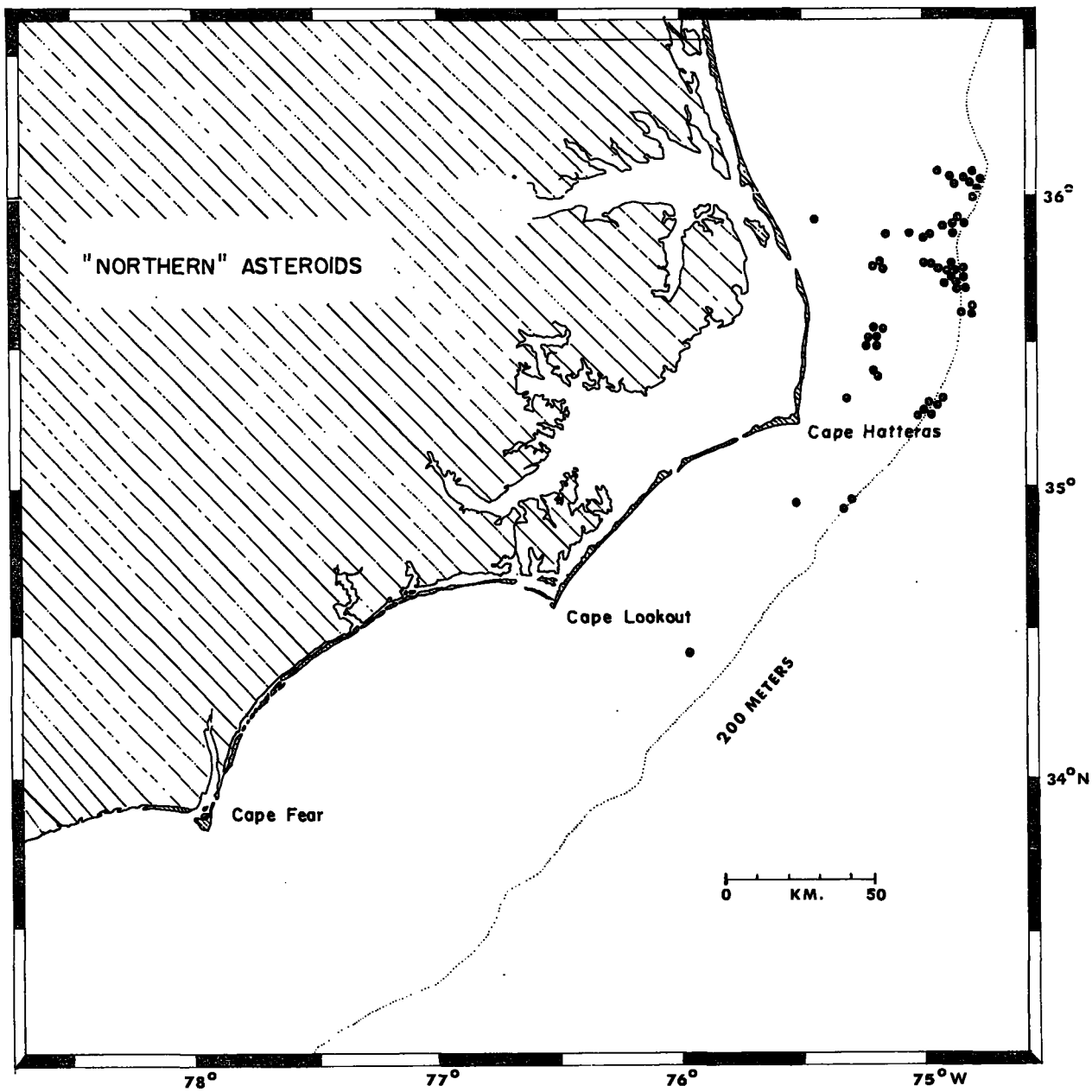

FIGURE 3.—Stations in North Carolina at which seven of the nine "northern" asteroids have been taken.

Current or in deeper waters near and off the edge of the shelf. On the other hand, "southern" species—those that are distributed from North Carolina southward—rarely are taken in stations north of Cape Hatteras except near the edge of the shelf under the Florida Current.

A greater number of species, but smaller populations, occur along the outer shelf (110–200 m.), whether in the Caribbean Province or north of it, than in either the Virginian or Carolinian Province. Either or both of two factors not easily separated may account for this distribution: depth and more uniform temperature. The range of bottom temperatures of the outer shelf is far less than that of either the middle or inner shelf. North of lat. 35°30′ N., northern and southern species ap-

pear to overlap somewhat. The few stations from which tropical species have been taken in this region may be under the Florida Current at some times but not at others, owing to the meanderings of the current. Also, the average bottom temperature is higher than it is nearer shore or in the deeper water of the slope.

Table 1 indicates the affinities of the various species in relation to their geographic ranges and to the biotic provinces of the shelf. The distribution of North Carolina asteroids largely follows the distribution pattern shown by Cerame-Vivas and Gray (1966) for other benthic species of the area.

TABLE 1.—*Asteroidea known to occur in North Carolina waters, their geographic affinities, and areas of distribution on the Continental Shelf*

Geographic affinity and species	Biotic Provinces		
	Virginian	Carolinian	Caribbean
Northern and Southern:			
Coronaster briareus	X		
Odontaster hispidus	X	X	
Asterias forbesii	X	X	
Astropecten articulatus	X	X	X
Luidia clathrata	X	X	X
Tethyaster vestitus			X
Northern:			
Asterias vulgaris	X		
Ctenodiscus crispatus	X		
Henricia sanguinolenta	X		
Leptasterias tenera	X		
Pellaster planus	X		
Porania insignis	X		
Astropecten americanus	X	X	X
Asterias tanneri	X		X
Mediaster bairdii			X
Southern:			
Echinaster sentus		X	
Echinaster spinulosus		X	
Thyraster serpentarius		X	
Astropecten duplicatus		X	X
Coscinasterias tenuispina		X	X
Luidia alternata		X	X
Astropecten nitidus			X
Astropecten nuttingi			X
Echinaster brasiliensis			X
Goniaster americanus			X
Linckia bouvieri			X
Luidia bernasconiae			X
Luidia elegans			X
Narcissia trigonaria			X
Oreaster reticulatus			X
Plinthaster dentatus			X
Solaster caribbaeus			X
Stephanasterias gracilis			X

The entire benthic fauna is largely "southern," that is, more species range southward from North Carolina than range northward. Fourteen of the 33 asteroids, all tropical or subtropical, occur only in the Caribbean Province. No strictly tropical species gets into the Virginian Province. On the other hand, some of the northern species do find their way into the Carolinian Province and sometimes into the Caribbean Province, especially at its northern end. Only three starfishes were found in all three biotic areas—but not in equal abundance in all of them. For example, *Luidia clathrata* and *Astropecten articulatus* are much more abundant in the Carolinian Province than in either the Virginian or Caribbean Province. The only "northern" species not collected in the Virginian Province is *Mediaster bairdii*. Thus far this species has been collected only from the edge of the shelf off Cape Lookout. Similarly, *Tethyaster*, a species that ranges both north and south of North Carolina, has been taken only in the Caribbean Province.

IDENTIFICATION OF SPECIES

Although the following keys cover the sea-stars now known to occur on the North Carolina shelf, it would not be surprising if additional species, especially Caribbean species, were collected from time to time. Technical terms are defined in the glossary and illustrated in figure 4. Additional details of morphology may be obtained from Hyman's (1955) volume on the Echinodermata, from which much of the terminology used here has been taken.

GLOSSARY

Abactinal: Upper or aboral surface opposite mouth and ambulacral grooves.

Aboral: See abactinal.

Actinal: Oral or lower surface on which mouth and ambulacral grooves are situated.

Adambulacrum: Ossicle in series bordering ambulacral groove adjacent to ambulacral ossicles.

Alveolar pedicellaria: Pedicellaria with two valves which are partly sunken into a depression on a plate.

Ambulacrum: Groove on the actinal surface of the arm, from mouth to arm tip, containing the tube feet. Also, a plate of the double series flooring the ambulacral groove.

Ampulla: Rounded (single) or bilobed (double) sac above each tube foot.

Bivalved pedicellaria: Pedicellaria having two valves.

Capitate: Enlarged at tip.

Carina: Distinct median row of plates on aboral surface of arm.

Clavate: Club-shaped.

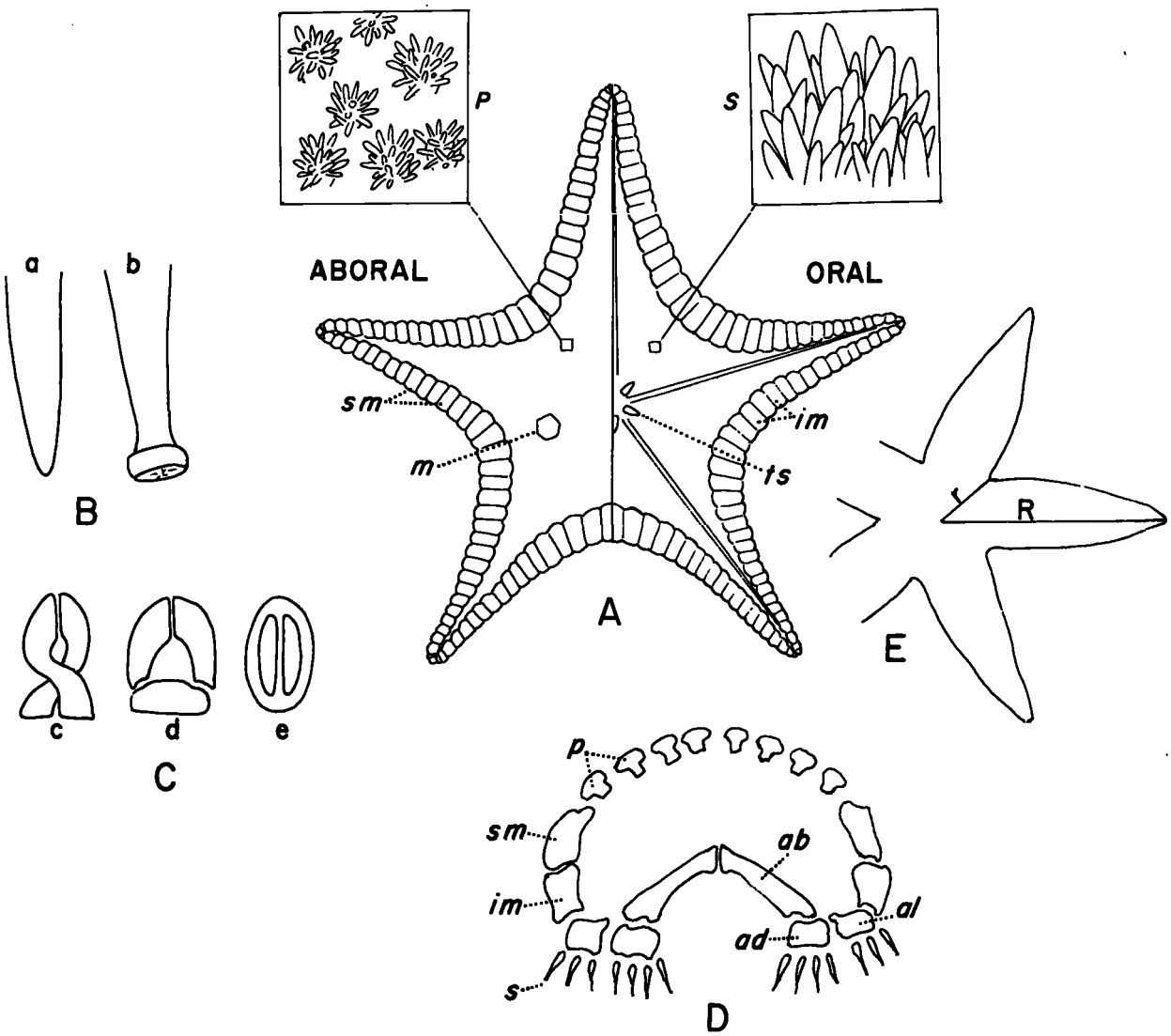

FIGURE 4.—Some morphological characteristics used in identification of asteroids (somewhat schematic). A. Aboral and oral sides of a starfish (*Odontaster hispidus*). B. Podia, without (a) and with (b) sucker. C. Pedicellaria, crossed (c); straight (d); and bivalve (e). D. Arm in cross section, showing ossicles. E. Radii. ab, ad, al—ambulacral, adambulacral, and actinolateral ossicles; im, inferomarginal plates; m, madreporite; p, paxillae; R, long radius; r, short radius; s, spines; sm, superomarginal plates; ts, tooth spine.

Cribriform organ: Vertical depression between adjacent marginals, lined with a series of thin vertical plates (lamellae).

Disc: Body of starfish, exclusive of arms.

Epiproctal cone: A sharp dermal elevation in the center of the aboral surface of certain starfish.

Fasciolated: Banded with small spinules, or ciliated.

Feliped pedicellaria: Straight pedicellaria with overlapping claws resembling a cat's forepaws when faced together.

Furrow: Groove running between adjacent series of plates.

Granule: Small grain.

Hyaline: Clear, glassy.

Imbricate: Overlapping.

Inferomarginal: Plate in lower marginal series.

Interradial: Between arms.

Lamella: Thin vertical platelet.

Lateral: Along sides, between actinal and abactinal.

Lateral furrow: Groove between superomarginals and inferomarginals.

Madreporite: Stony sieve-plate at terminus of water vascular system, on aboral surface, between margin and center of disc.

Mammilliform: Nipple-shaped.

Marginals: One or two series of plates bordering arms and disc, around periphery.

Mouth frame: Ossicles surrounding mouth opening.

Oral: Surface on which mouth is located.

Ossicle: Plate, or skeletal element.

Papilliform pedicellaria: Raised or elevated pedicellaria.

Papula: Thin respiratory evagination of the body wall which emerges between ossicles.

Papular pore: Pore through which papula projects.

Paxilla: Aboral plate drawn up into a column which is usually crowned with spinules.

Paxillate: Surface covered with paxillae.

Paxilliform: Shaped like a paxilla.

Pedicellaria: Small calcareous "pincher," of which there are various types, used mostly to remove particulate matter from surface of starfish.

Pentagonal: Five-sided, without distinction between disc and arms.

Podia: Tube feet.

Radial furrow: Furrow on actinal surface running from ambulacral groove to margin.

Radius: Long radius (R), distance from center of disc to tip of arm; short radius (r), radius of disc.

Reticulate: Netlike, a network.

Sessile pedicellaria: Pedicellaria resting directly on surface, not raised or sunken.

Spine: Sharp, calcareous projection resting on underlying plate.

Spinule: Very fine small spine.

Stellate: Radiating, starlike.

Sucker: Disc or flattened tip at end of tube foot.

Superomarginal: Plate of upper series of marginals.

Sutural groove: Groove between adjacent marginals.

Terete: Cylindrical, tapering.

Tessellate: Mosaic of small fairly regular plates.

Tridentate: With three teeth or valves.

Triseriate: In a series of three.

Tubercle: Calcareous projection shorter and thicker than spines.

Valvular pedicellaria: Pedicellaria with two valvelike pieces.

Wart: Calcareous projection larger than granule but smaller than tubercle.

KEY TO THE ORDERS OF NORTH CAROLINA ASTEROIDEA

1. Podia without suckers 2
   Podia with suckers 3
2. Superomarginals absent ..... Platyasterida (I)
   Superomarginals present ..... Paxillosida (II)
3. Marginals conspicuous ..... Valvatida (III)
   Marginals inconspicuous or absent 4
4. Pedicellariae absent ..... Spinulosida (IV)
   Pedicellariae present ..... Forcipulatida (V)

I. Key to the Species of Platyasterida

1. Arms with wide transverse bands or blotches of black or brown ..... *Luidia alternata*
   Arms without transverse color bands 2
2. Inferomarginals with three spines, upper one much larger than others (young specimens may have only two) ..... *Luidia elegans*
   Inferomarginals with two spines 3
3. Paxillae quadrangular, skeleton compact ..... *Luidia clathrata*
   Paxillae stellate, skeleton fragile ..... *Luidia bernasconiae*

II. Key to the Species of Paxillosida

1. Superomarginals separated by gap ..... *Ctenodiscus crispatus*
   Superomarginals broadly in contact 2
2. Marginal fringe of flattened, rectangular spines, usually not projecting much beyond margin; large size. *Tethyaster vestitus*
   Marginal fringe of acute spines forming conspicuous border; moderate size 3
3. Rays long, slender; superomarginals small, numerous 4
   Rays not very long, robust; superomarginals large, few 5

4. Paxillar spinules long, slender, movable; paxillae in irregular narrow transverse rows ---------- *Astropecten americanus*
   Paxillar spinules small, clavate, fixed; paxillae in regular wide transverse rows ---------- *Astropecten nuttingi*
5. All superomarginals without spines or tubercles ---------- *Astropecten nitidus*
   Some superomarginals with spines or tubercles ---------- 6
6. Stout acute spine on at least two interradial superomarginals. *Astropecten duplicatus*
   Small obtuse spine on distal half to three quarters of superomarginals. *Astropecten articulatus*

III. Key to the Species of Valvatida

1. Dorsal skeleton reticulate---------- 2
   Dorsal skeleton tabulate or paxillate---- 4
2. Disc large, arms short---- *Oreaster reticulatus*
   Disc small, arms long---------- 3
3. Arms triangular in cross section, tapering to acute ends------- *Narcissia trigonaria*
   Arms cylindrical, with rather blunt ends ---------- *Linckia bouvieri*
4. Dorsal skeleton paxillate-- *Odontaster hispidus*
   Dorsal skeleton tabulate---------- 5
5. Large heavy subacute spines on dorsal surface ---------- *Goniaster americanus*
   No spines on dorsal surface---------- 6
6. Rr more than three to one; arms long, acute ---------- *Mediaster bairdii*
   Rr less than two to one; arms short, blunt ---------- 7
7. Papulae few, in rows along each radius; marginals covered with granules. *Plinthaster dentatus*
   Papulae numerous, scattered among plates; marginals usually bare of granules, at least in center-- *Peltaster planus*

IV. Key to the Species of Spinulosida

1. Arms five---------- 2
   Arms six to eight------- *Solaster caribbaeus*
2. Disc broad, with broadly based arms---- *Porania insignis*
   Disc small, with long, cylindrical arms-- 3
3. Dorsal and marginal plates quadrangular, overlapping at corners, in longitudinal rows------- *Thyraster serpentarius*
   Dorsal and marginal plates not quadrangular, not overlapping at corners, not in regular rows---------- 4
4. Small spines in groups or along ridges; papulae on both surfaces---------- *Henricia sanguinolenta*
   One or few coarse spines at nodes; no papulae on oral surface---------- 5
5. Two adambulacral spines---------- *Echinaster spinulosus*
   Three adambulacral spines---------- 6
6. Aboral spines in about five irregular rows ---------- *Echinaster sentus*
   Aboral spines in 9 to 11 rows-------- *Echinaster brasiliensis*

V. Key to the Species of Forcipulatida

1. Aboral surface with short blunt spines (tubercles) ---------- 2
   Aboral surface with slender spines, at least along margins---------- 3
2. Arms somewhat flattened, sharply tapering, with distinct median row of aboral plates---------- *Asterias vulgaris*
   Arms inflated, blunt at tip, no distinct median row of aboral plates *Asterias forbesii*
3. Aboral spines with dense wreath of small pedicellariae ---------- 4
   Aboral spines without dense wreath of small pedicellariae---------- 5
4. With five arms---------- *Asterias tanneri*
   With ten to twelve arms-- *Coronaster briarius*
5. Aboral plates arranged in definite rows, one spine to each plate---------- *Coscinasterias tenuispina*
   Aboral plates not arranged in definite rows, more than one spine to each plate 6
6. Aboral surface with minute spines; arms seven to nine-- *Stephanasterias gracilis*
   Aboral surface with conspicuous spines; arms five---------- *Leptasterias tenera*

DESCRIPTION OF SPECIES

The following descriptions are given merely as supplements to the keys and additional aids to identification. It is not the purpose of this paper to give a complete systematic treatment of the North Carolina species of Asteroidea, and diag-

noses and descriptions of higher taxa have, therefore, not been included. The species descriptions have been kept as simple as possible for quick identification.

The preceding keys are strictly artificial, and their usefulness is, therefore, limited to the Continental Shelf off North Carolina.

PLATYASTERIDA

In North Carolina the Order Platyasterida is represented by one genus and four species. Three species have "southern" affinity and are not abundant. Distribution of *Luidia clathrata* is far wider than that of other species in this genus (fig. 5).

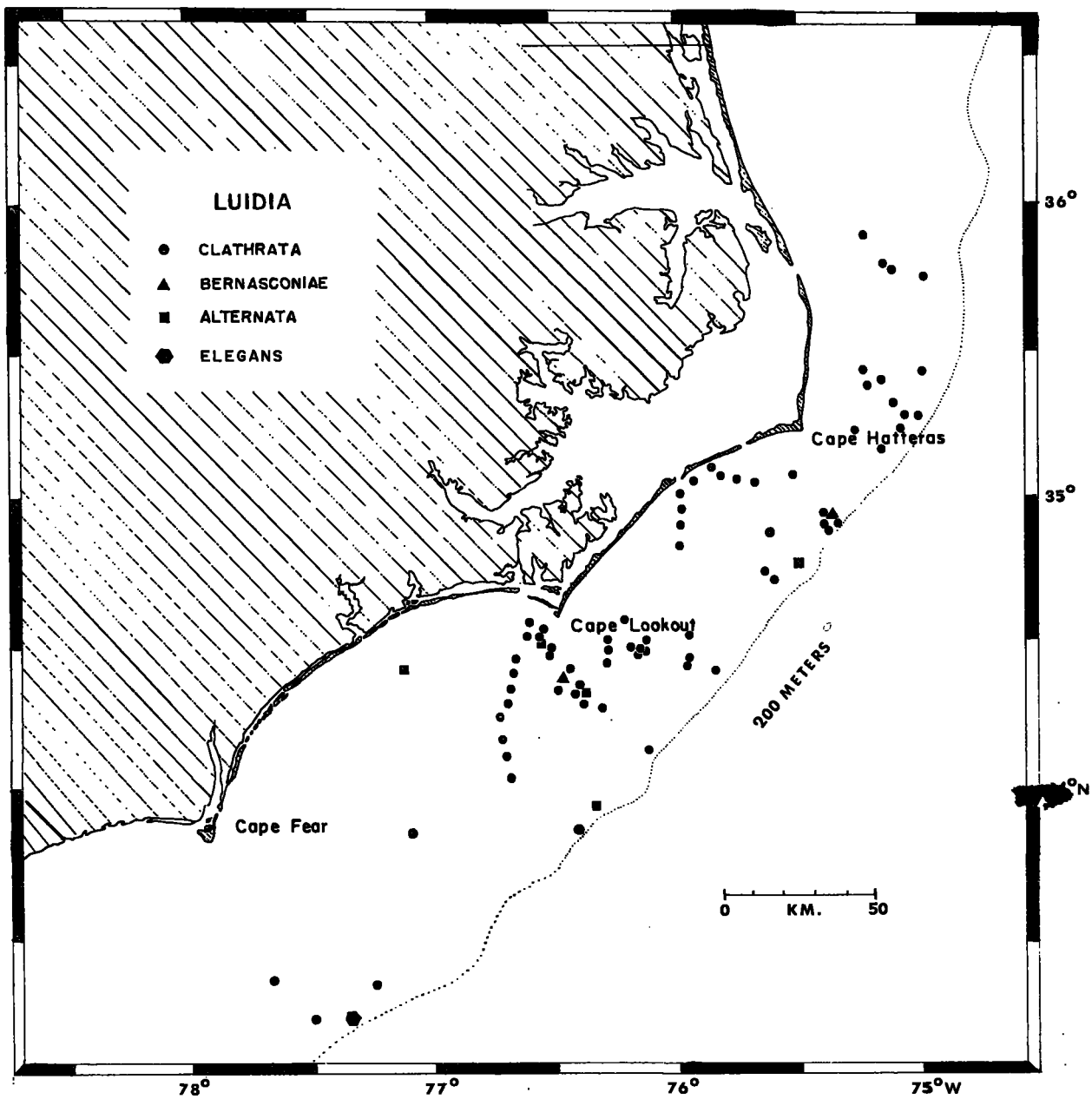

FIGURE 5.—Distribution and relative abundance of four species of *Luidia*. Many of the numerous stations at which *L. clathrata* was collected have been omitted.

***Luidia alternata* (Say)**

Synonymy:

Asterias alternata Say, 1825.

Luidia alternata: Lütken, 1859.

Luidia variegata Perrier, 1876.

Description:

Rays five, long and fragile. Aboral paxillae with 10 to 16 slender, acute spinules surrounding stouter central 1 or 2; some paxillae much larger than others, with large central spine, especially along margins of arms, and scattered on disc. Two to four lateral rows of paxillae larger than those on median portion of arm. Inferomarginals with two long acute upper spines and about three long spines and many small acute ones on lower side. Adambulacrals with three or four spines. Rr=8:1. Color gray or light brown with broad irregular bands of black or dark brown across arms; tube feet frequently bright orange.

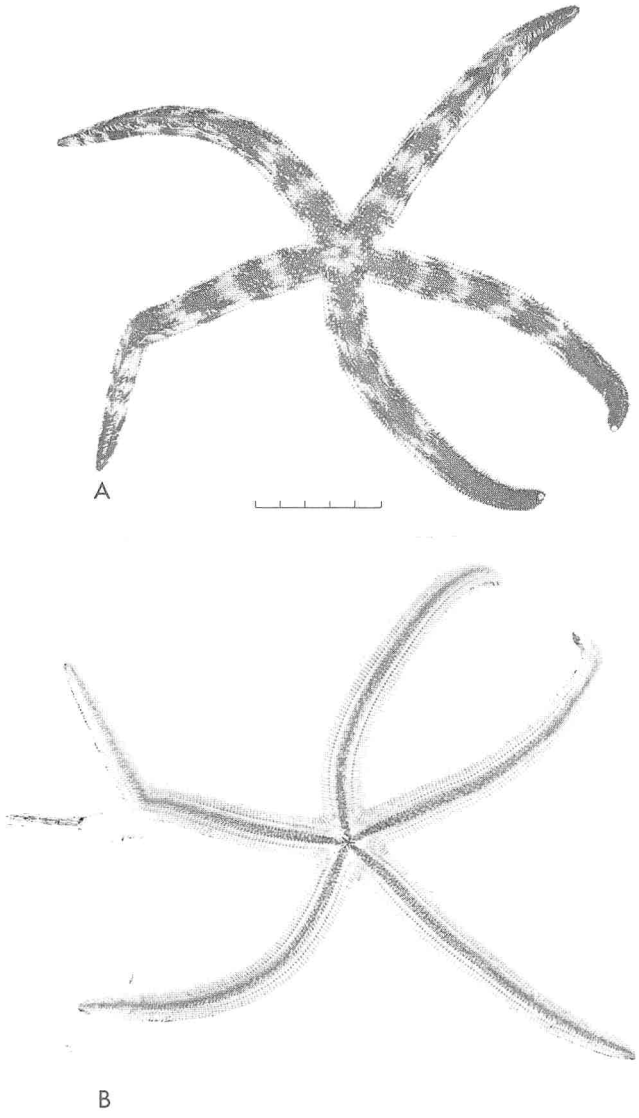

FIGURE 6.—*Luidia alternata.* A, aboral; B, oral. 5 cm. indicated.

Range:

Southeast coast of the United States to Brazil, 10 to 200 m. Although not abundant, *L. alternata* is occasionally taken in dredges and trawls. Pearse and Williams (1951) reported it in North Carolina waters from reefs off New River Inlet.

***Luidia bernasconiae* A. H. Clark, 1945**

Description:

Rays five, very long and narrow. Adambulacral spines two, inner one flattened laterally, recurved. One or two large, acute or subacute spines on outer rows of dorsal paxillae, colored brown and white. Two large, less acute white spines on inferomarginals; many small sharp spines on marginals and in grooves between marginals. Paxillae in center of rays crowded, irregular, small; single outer row of paxillae dark, next two rows large, light, often forming distinct band down each side of arm. These three rows of paxillae may bear short, stumpy tridentate sessile pedicellariae, and some bear a large central spine. Paxillae with 5 to 10 clavate spinules surrounding central paxillar boss with larger, thicker spinule. Large tridentate pedicellariae on columnar interactinals, between adambulacrals and inferomarginals, especially proximally (none distally). Marginal spines are long and erect, giving a thorny appearance. Rr=7:1. Color dark gray or brown above, white below.

Range:

Previously recorded only off Georgia (Clark, 1945). In North Carolina it has been taken several times, in depths of 20 to 110 m.

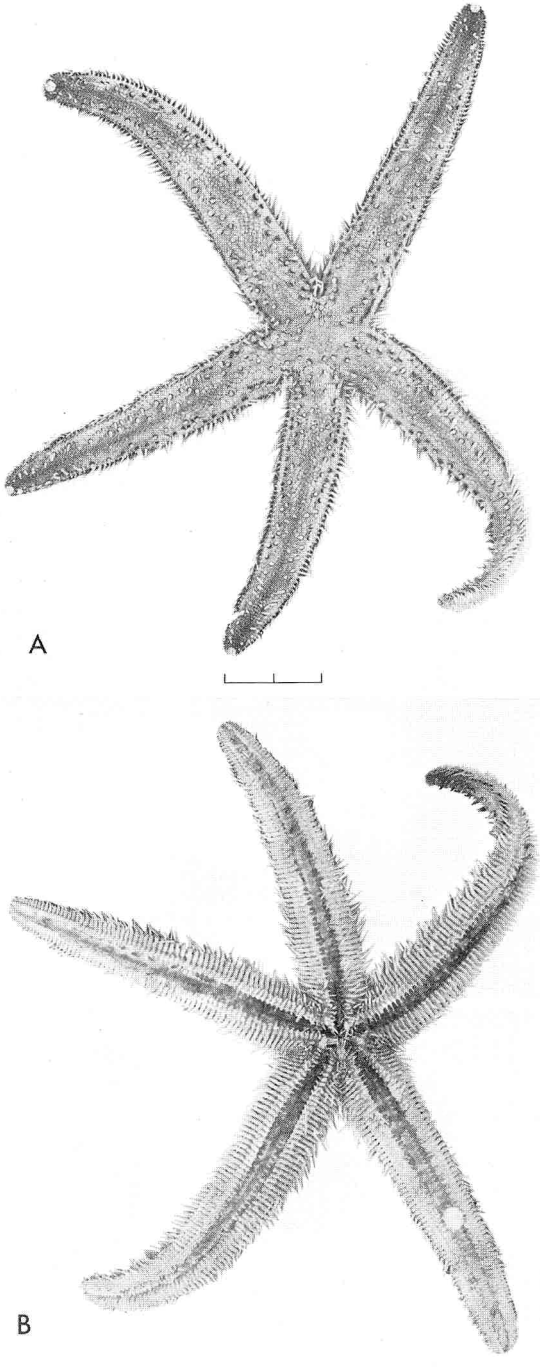

FIGURE 7.—*Luidia bernasconiae.* A, aboral; B, oral. 2 cm. indicated.

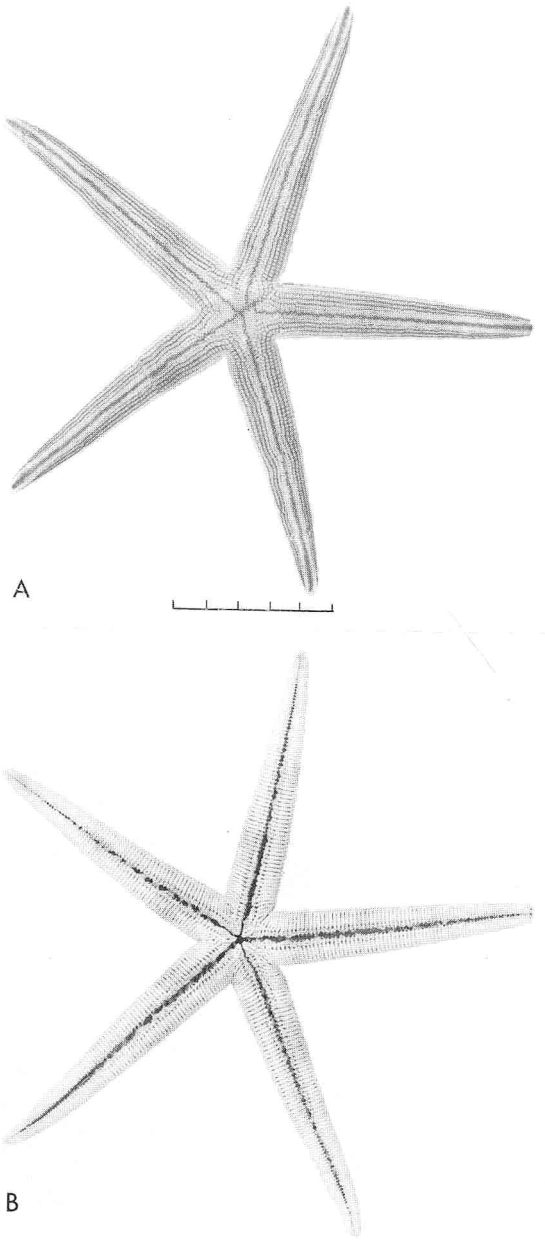

FIGURE 8.—*Luidia clathrata.* A, aboral; B, oral. 5 cm. indicated.

***Luidia clathrata* (Say)**

Synonymy:

Asterias clathrata Say, 1825.

Luidia clathrata: Lütken, 1859.

Description:

Rays five, long, straplike. Aboral surface flattened, regularly tessellated; paxillae quadrangular, 10 to 12 close, fairly regular rows, lateral rows distinctly larger than median rows. Paxillae covered with numerous short, coarse spinules. Inferomarginals with two

acute spines around bases. Rr=6:1. Color commonly gray or blue-gray, but may be salmon, rose, or light brown.

Range:

New Jersey to Brazil, 10 to 175 m. This species is the most common member of the genus in North Carolina and apparently the only one that is found north of Cape Hatteras. South of Cape Hatteras it is second only to *Astropecten articulatus* in abundance and is often taken with *Astropecten*. It is found in all three biotic provinces and in depths to 175 m., but is most abundant in the Carolinian Province in depths of 9 to 110 m.

***Luidia elegans* Perrier, 1876**

Description:

Rays five; aboral paxillae stellate, crowded, smallest in median portion of rays, larger near margins, with short central spinule and 6 to 10 marginal spinules not or scarcely enlarged at tip, giving very uniform appearance to paxillar area. Inferomarginals with two to three (three in fully grown specimens) large spines. Bivalved pedicellariae often present on actinal side. Rr=7:1. Color orange above, lighter below.

Range:

Cape Hatteras to Barbados, 95 to 267 m. Not common in North Carolina.

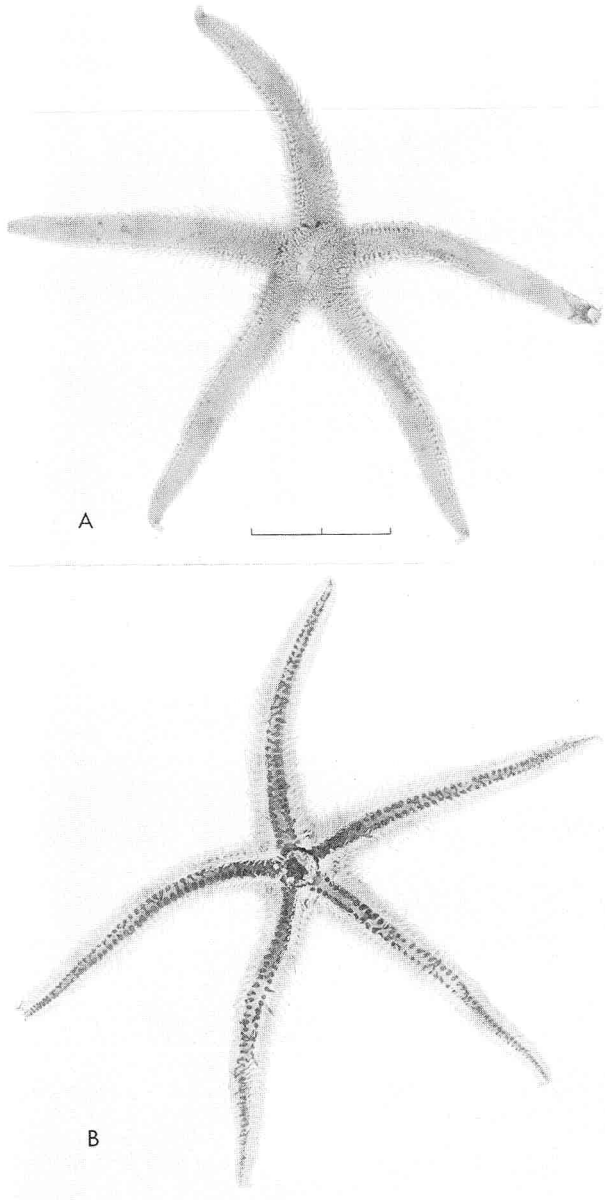

FIGURE 9.—*Luidia elegans*. A, aboral; B, oral. 2 cm. indicated.

PAXILLOSIDA

In North Carolina, *Astropecten*, with five species, is the most conspicuous of the three genera in the Order Paxillosida. *A. articulatus* and *A. americanus* are the most abundant species. The relative abundance and distribution of the various species of *Astropecten* are indicated in figure 10. Although *A. americanus* and *A. articulatus* are very abundant, they apparently are not competitors for the same space. The former occurs mainly in the deeper waters of the shelf north of Cape Hatteras, and the latter is most abundant south of the Cape. The two species have not been taken in the same dredge haul. *A. duplicatus* has occasionally been found at the same station with *A. articulatus*, however, and *A. nitidus* and *A. nuttingi* have been taken together near the edge of the shelf east of Frying Pan Shoals.

***Ctenodiscus crispatus* (Retzius)**

Synonymy:

Asterias crispata Retzius, 1805.
Ctenodiscus crispatus: Duben and Koren, 1846.
Ctenodiscus australis Lütken, 1871.
Ctenodiscus krausei Ludwig, 1886.
Ctenodiscus procurator Sladen, 1889.

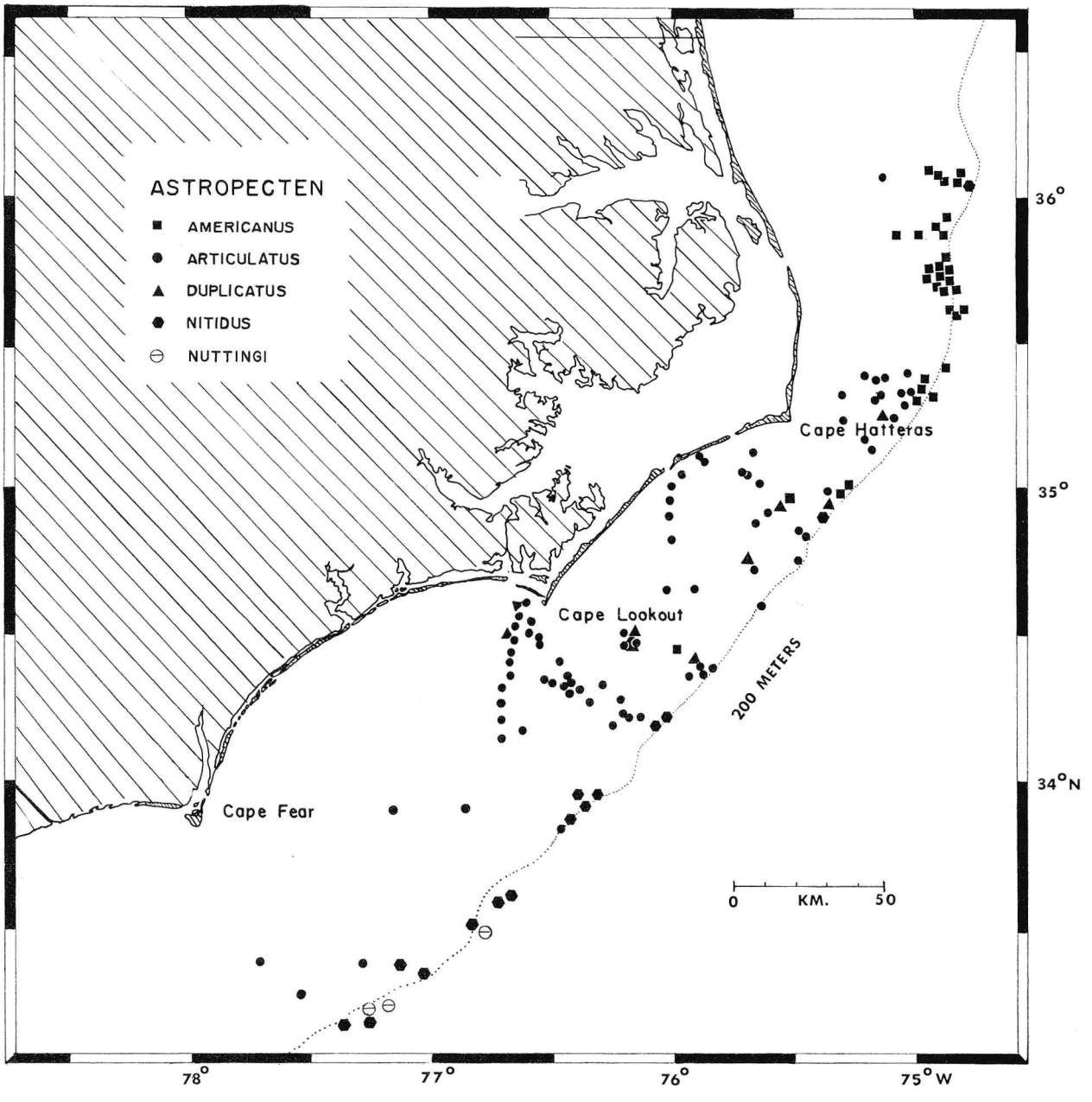

FIGURE 10.—Distribution and relative abundance of five species of *Astropecten*. Many of the numerous stations at which *A. articulatus* was collected have been omitted.

Description:

Five arms; body form variable, from almost pentagonal to nearly star-shaped. Aboral surface of typical paxillae; podia devoid of suckers. Conspicuous marginal plates, between each pair of which are simplified cribriform organs each in the form of a groove containing a few lamellae, which continue as simple channels between plates of oral side up to ambulacral grooves. Lacks intestine, intestinal caeca, and anus. Epiproctal cone present. Rr= 1.6–3.1 : 1. Color yellowish.

Range:

Circumboreal; in the Pacific, extends down to Chile; 55 to 1,800 m. Rare in North Carolina.

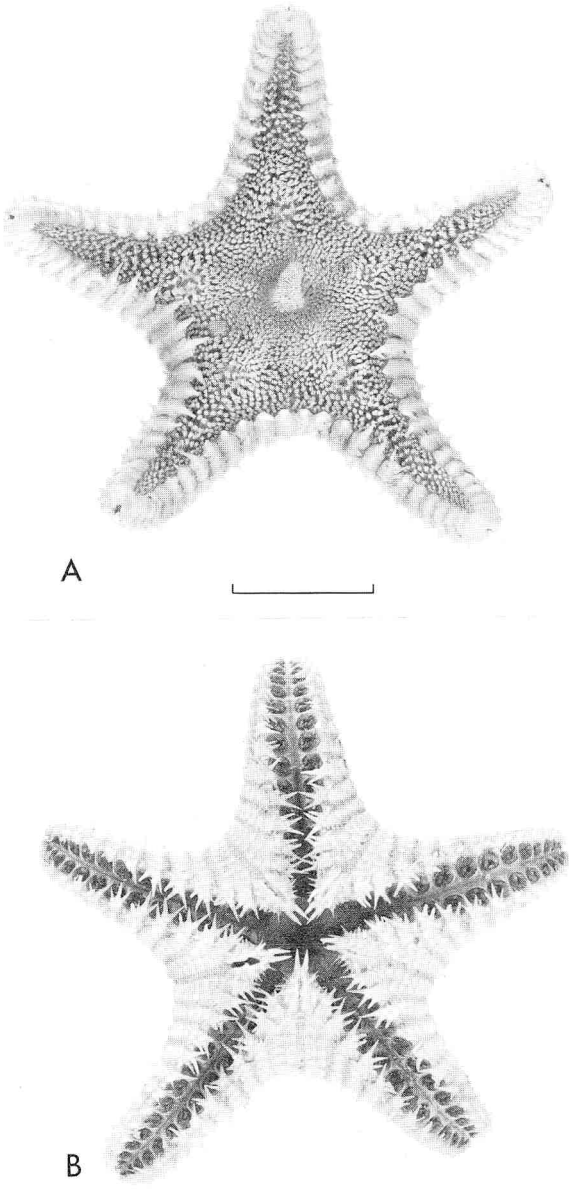

FIGURE 11.—*Ctenodiscus crispatus.* A, aboral; B, oral. 1 cm. indicated.

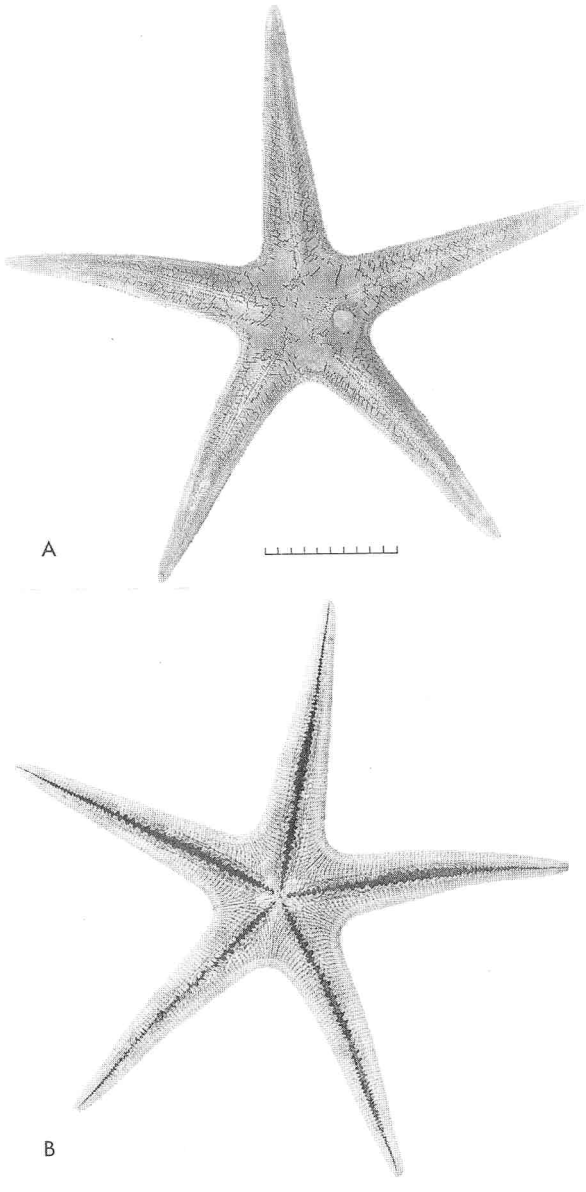

FIGURE 12.—*Tethyaster vestitus.* A, aboral; B, oral. 10 cm. indicated.

***Tethyaster vestitus* (Say)**

Synonymy:

Asterias vestita Say, 1825.

Astropecten vestitus: Lütken, 1859.

Sideriaster (?) *vestitus:* Verrill, 1914.

Description:

Form broadly stellate, with very large disc. Arms five. Aboral surface closely covered with uniform stellate paxillae. Upper marginals granulated, small, entirely lateral. Aboral interradial areas large, with numerous granulated plates. Madreporite very large, round, flat. Papular pores over entire aboral surface, about six around each plate. Adambulacrals with large median compressed spine, with two to three erect flattened spines on each side of furrow series; stout spines on actinal side,

with single or double row of shorter flat spines behind it. Rr=4:1. Color bright red or orange.

Range:

New Jersey to Venezuela, 37 to 293 m. North Carolina specimens were taken near the outer edge of the shelf.

***Astropecten americanus* Verrill**

Synonymy:

Archaster americanus Verrill, 1880.

Astropecten americanus: Verrell, 1894.

Description:

Body flat and thin; rays long, slender, tapering to acute tips. Aboral paxillar area about four times as wide as adjacent margin at base of ray. Paxillae small, with 6 to 10 elongate slender spinules surrounding central 1 or 2, in narrow transverse rows, rather openly spaced, so that papular pores are visible. Superomarginals small, numerous, usually broader than long, with deep, wide fasciolated grooves between; plates flat or concave. Inferomarginals project slightly beyond superomarginals, bear two slender, flattened, acute spines and sometimes a small papilliform pedicellaria; underside with small acute spines and spinules. Adambulacrals with three to five slender furrow spines. Rr=5.5:1. Color dark red or reddish brown.

Range:

East coast of the United States, 55 to 540 m. In North Carolina, *A. americanus* is limited largely to deeper waters of the outer edge of the shelf north of Cape Hatteras, where it appears to be the dominant asteroid. Bottom photographs show it to be abundant (fig. 14). Relatively few have been taken south of Cape Hatteras, where *A. articulatus* is the dominant *Astropecten.*

***Astropecten articulatus* (Say)**

Synonymy:

Asterias articulatus Say, 1825.

Astropecten articulatus: Mueller and Troschel, 1842.

Description:

Thick disc, five robust arms, with large stout superomarginals densely granulated. On distal half to three-quarters of rays, superomarginals sometimes bear a single small, obtuse spine on outer convex surface. Inferomarginals with two short, flattened marginal spines, side by side. Adambulacrals triseriate. Aboral paxillae stellate, crowded, with six to eight short clavate spinules surrounding central one

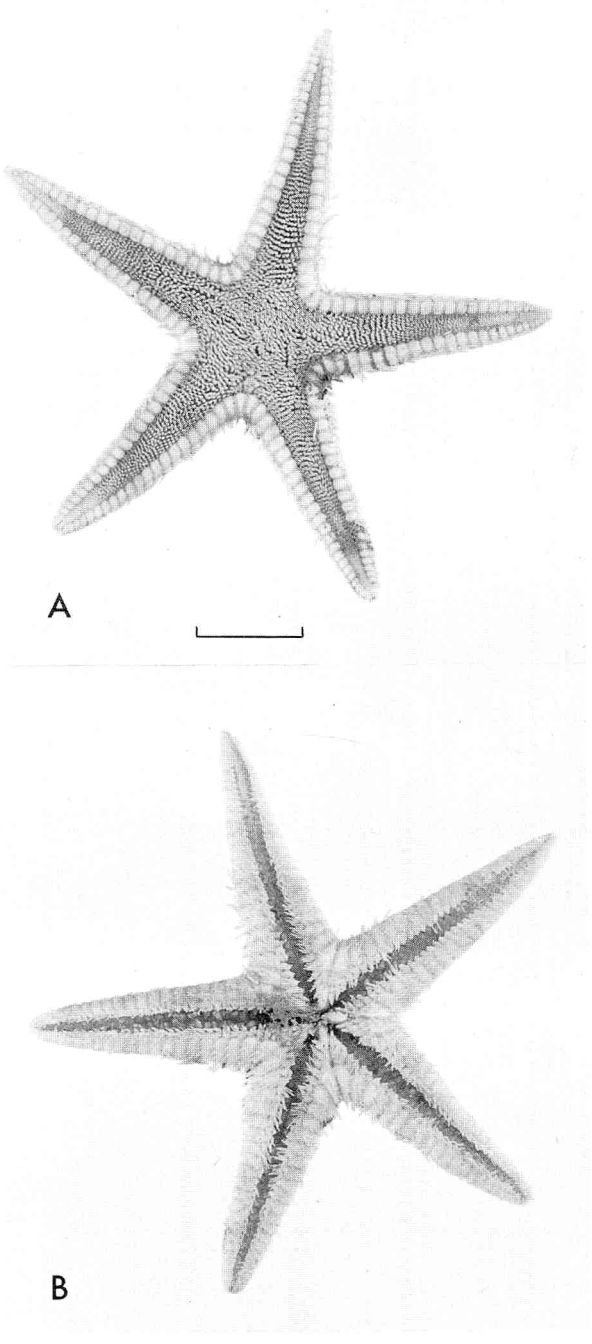

FIGURE 13.—*Astropecten americanus.* A, aboral; B, oral. 1 cm. indicated.

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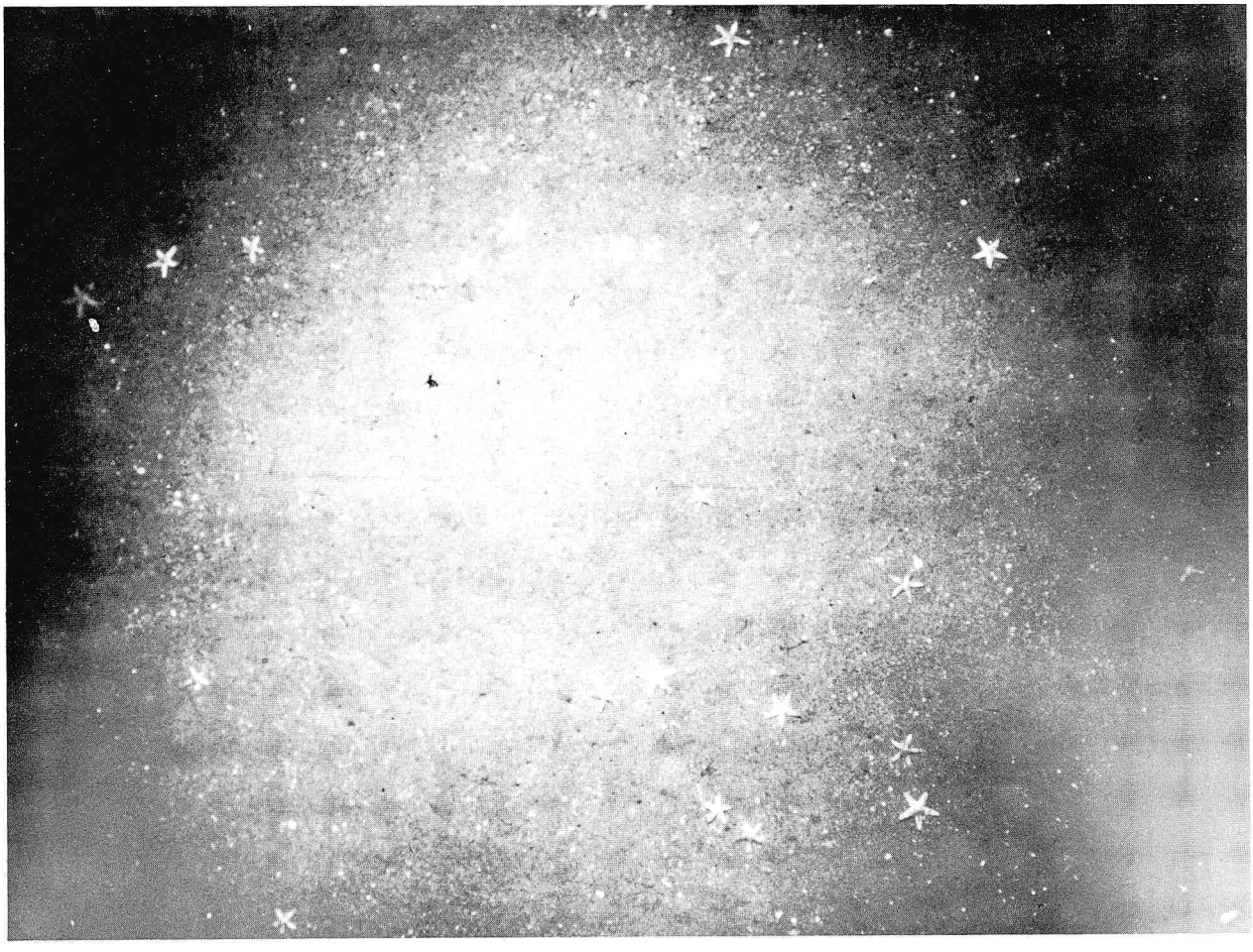


FIGURE 14.—Photograph of sea floor showing abundance of *Astropecten americanus* at 165 m., northeast of Cape Hatteras. The area shown is about 4 m.^{2}

to two. Rr=4–6.5:1. Color of paxillar area blue or purple, marginals white to orange.

Range:

New Jersey to Uruguay, 9 to 165 m. This is probably the most common sea-star in North Carolina, especially in Onslow and Raleigh Bays. Its abundance decreases north of Cape Hatteras. Trawlers take it in large numbers, frequently with *Luidia clathrata*. Although often found near the outer edge of the shelf, it is much more abundant in 18 to 110 m., where it glides over the sandy substrate and feeds on the numerous small organisms that abound there. Wells and Gray (1961) reported 93 species of small mollusks from the stomachs of 125 *A. articulatus*.

***Astropecten duplicatus* Gray**

Synonymy:

Astropecten duplicatus Gray, 1840.

Astropecten valenciennii Mueller and Troschel, 1842.

Astropecten variabilis Lütken, 1859.

Description:

Form stellate; rays five, angular, regularly tapered to narrow tips, high on sides at base. Superomarginals form thick border, elevated above paxillar area, with stout spine on first seven plates of each arm; spines on first two plates are largest. Inferomarginals project beyond superomarginals, forming lateral furrow felted with fine spinules. Surface of marginals granular. Inferomarginals with two to

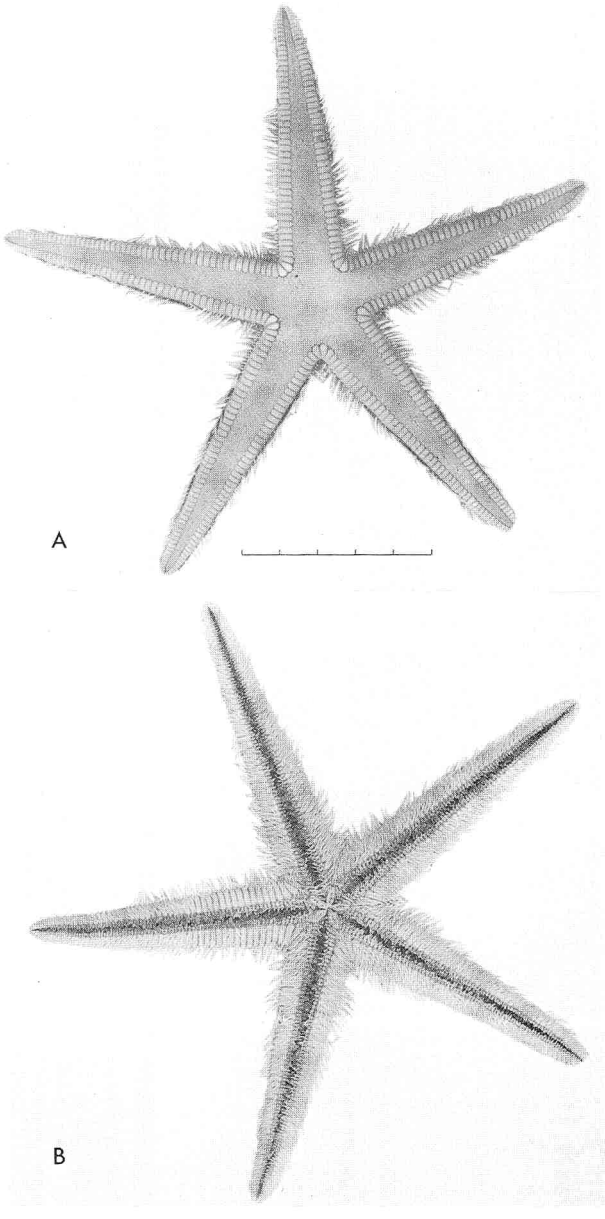


FIGURE 15.—*Astropecten articulatus*. A. aboral; B, oral. 5 cm. indicated.

three short, flattened, subacute spines. Aboral paxillae with 8 to 10 long clavate or capitate spinules surrounding 1 to 3 central ones. At base of rays, paxillae may have 12 to 16 spinules surrounding 4 to 8 central ones. Paxillae of generally uniform size and irregular arrangement. Rr=5.3:1. Color reddish brown or gray.

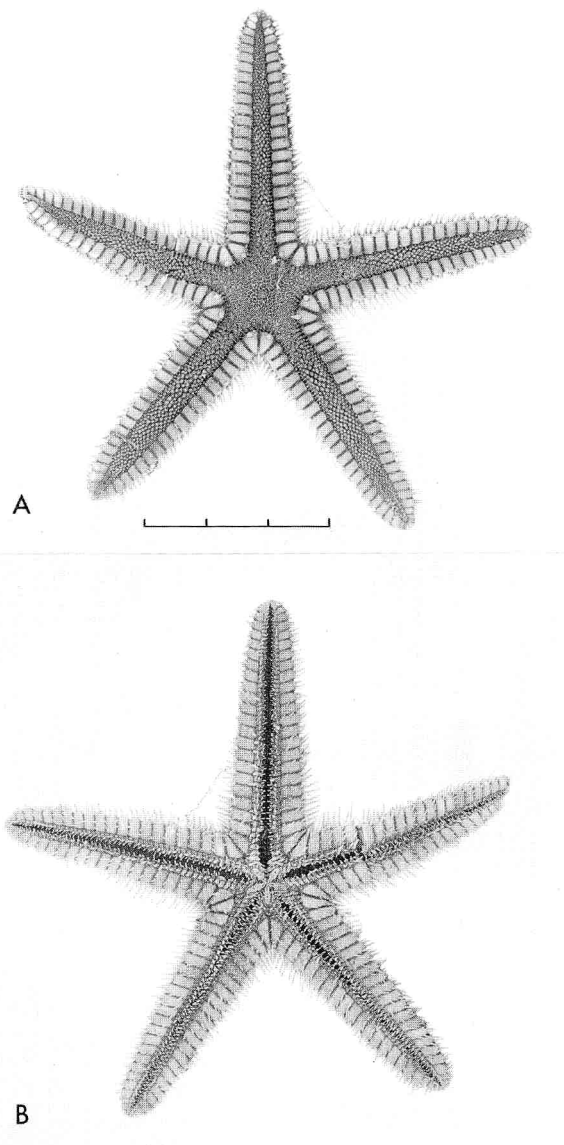


FIGURE 16.—*Astropecten duplicatus*. A, aboral; B, oral. 3 cm. indicated.

Range:

North Carolina to Brazil, 5 to 185 m. Although much less abundant, this species is sometimes collected with *A. articulatus*. It occurs mainly south of Cape Hatteras.

***Astropecten nitidus* Verrill, 1915**

Description:

Body thick, stellate, with five short, acute rays. Superomarginals wide, convex, with deep transverse sutural grooves forming wide

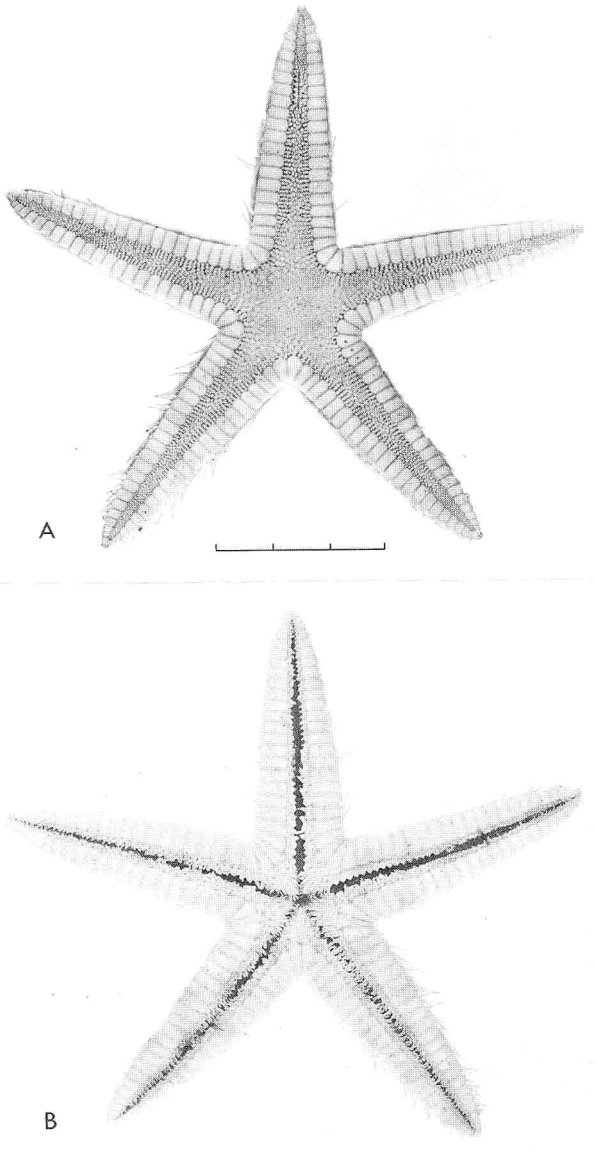


FIGURE 17.—*Astropecten nitidus*. A, aboral; B, oral. 3 cm. indicated.

prominent border, without spines or spinules, covered with granules. Aboral paxillar area narrow, less than twice width of adjacent marginals. Paxillae not very small, with 10 to 15 small, stellate, clavate spinules surrounding 1 to 2 central ones. Inferomarginals with two long, tapered, acute marginal spines, numerous fine, acute spinules, and two transverse rows of small acute spines on underside. Rr=3.7:1. Color light brown or cream, with blotches of rose pink.

Range:

North Carolina to Florida, 50 to 225 m. In North Carolina this species appears to be limited to the edge of the shelf, in 145 to 210 m. It is apparently more abundant between Cape Lookout and Cape Fear than between Cape Lookout and Cape Hatteras.

***Astropecten nuttingi* Verrill, 1915**

Description:

Rays five, shape regularly stellate, flat and thin. Epiproctal cone usually prominent. Marginals small, covered with tiny, fine spinules; may bear a short, tapered spine on upper side of superomarginal. Inferomarginals reach to adambulacrals and are covered with small acute spines, with two to three long somewhat compressed marginal fringe spines. Paxillae small, equal, even, arranged in obliquely transverse rows, with 0 to 10 short slender spinules around crown and 1 to 2 in center of crown. Adambulacrals with marginal row of three slender spines, central one slightly curved and compressed. Madreporite small, usually concealed by paxillae. Rr=5:1. Color reddish, with deep red median line on each arm.

Range:

North Carolina to Florida and the Bahamas, 165 to 412 m. Although the least abundant of the North Carolina *Astropectens*, it is not uncommon along the 180- to 200-m. contour east of Cape Fear.

VALVATIDA

None of the species in this group can be considered common in North Carolina. Some are taken only rarely.

***Oreaster reticulatus* (Linnaeus)**

Synonymy:

Asterias reticulatus Linnaeus, 1758.

Oreaster reticulatus: Mueller and Troschel, 1842.

Pentaceros reticulatus Agassiz, 1877.

Description:

Large, heavy stellate form, disc arched, inflated; arms four to six (normally five), short, acute. Skeleton reticulate, plates bar-shaped, with short, stout, conical spine at nodes. Marginals granular, covered with skin, each with a large conical spine. Papular areas conspicu-

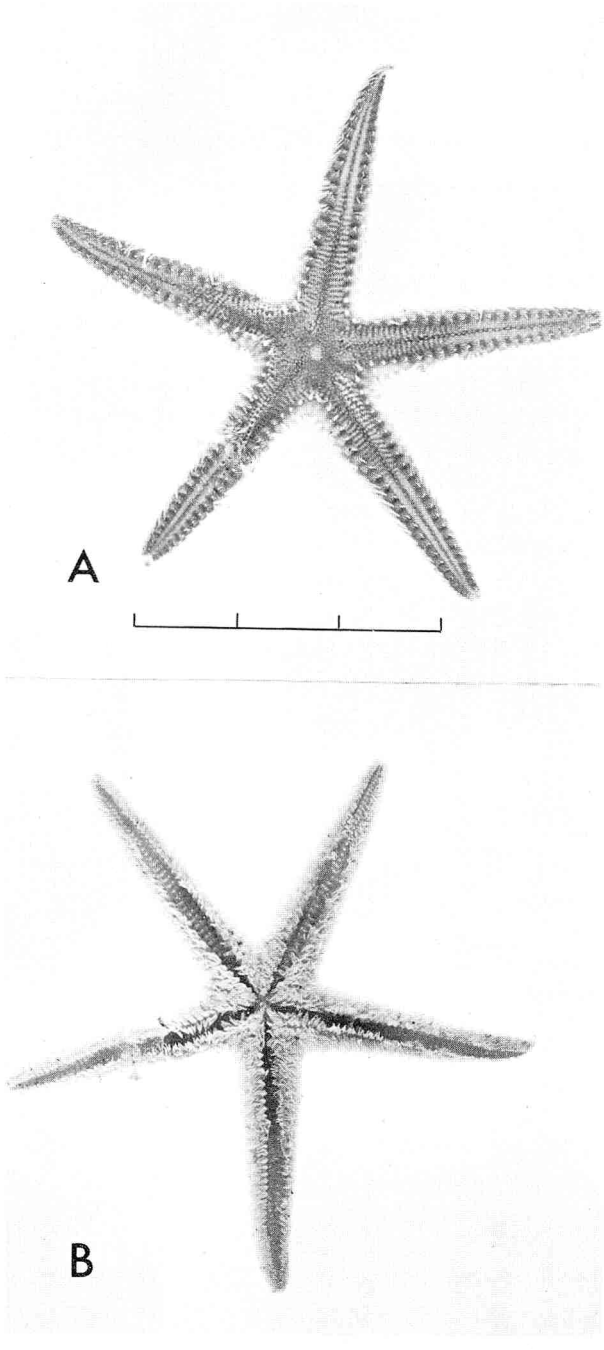


FIGURE 18.—*Astropecten nuttingi.* A, aboral; B, oral. 3 cm. indicated.

ous. Aboral surface covered by thick mosaic of plates with short stout central spine. Bivalved pedicellariae present. Rr=2:1. Color reddish brown, deep olive green, or yellowish orange.

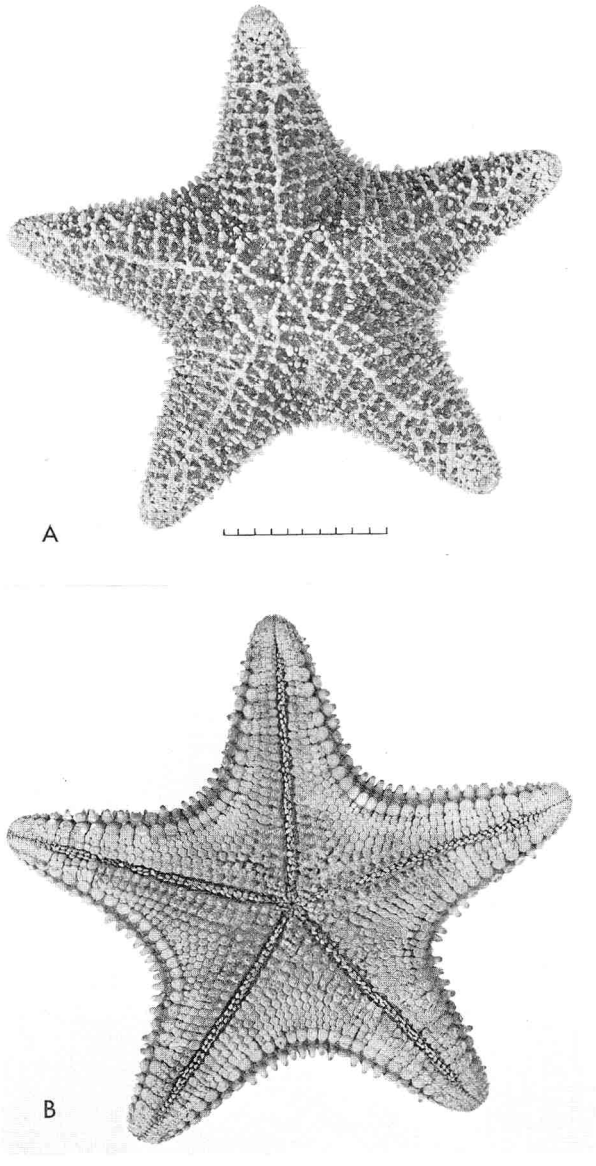


FIGURE 19.— *Oreaster reticulatus.* A, aboral; B, oral. 10 cm. indicated.

Range:

North Carolina to Brazil; Cape Verde Islands. Shallow water. A tropical species taken only rarely in North Carolina.

***Narcissia trigonaria* Sladen, 1889**

Description:

Rays five, elongate, tapering to sharp end, triangular in cross section, with distinct median keel. Marginal plates well defined. Disc small,

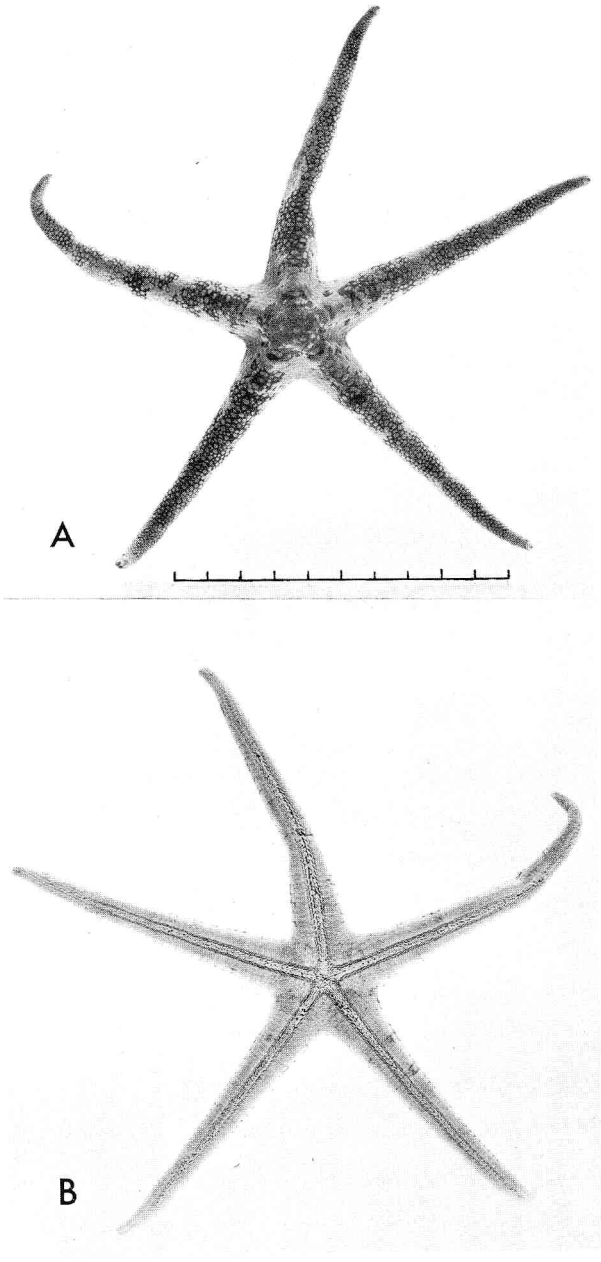


FIGURE 20.—*Narcissia trigonaria*. A, aboral; B, oral. 10 cm. indicated.

elevated. All plates covered with minute, uniform granules. Papulae single. Adambulacral spines in three series, broader at tip than at base, rather chisel shaped. Madreporite small, striated. Rr=6.7:1. Color creamy yellow with blotches of rusty red.

Range:

North Carolina to Gulf of Mexico. A single specimen taken at the edge of the shelf off Cape Lookout in 210 m. constitutes a new record for North Carolina.

***Linckia bouvieri* Perrier, 1875**

Description:

Disc small, rays five, long, slender, rounded. Primary plates of aboral surface large, irregular, rounded, tumid, five or more on disc. Plates become smaller, more numerous, and crowded distally. Papulae numerous, in clusters confined to aboral surface. Interactinal plates in two or more close rows. Inner adambulacral spines a close row of broad, somewhat flattened spines alternating with much smaller blunt, peglike spines; outer row of larger, stouter, more rounded spines arranged behind each small inner spine. Entire actinal and abactinal surface covered with fine granules. Rr=10:1. Color reddish fawn, primary plates and oral surface cream.

Range:

North Carolina to the West Indies, 73 to 360 m. Taken from near the edge of the shelf off Cape Lookout.

***Odontaster hispidus* Verrill, 1880**

Description:

Form depressed, stellate, with broad disc. Rays five. Single, hyaline, recurved spine at apex of each jaw. Marginals only moderately developed, convex, separated by wide sutural grooves. Aboral plates elevated, capitate, with dense cluster of slender, elongate spinules. Interactinals (between adambulacrals and marginals) with stout, elongate, acute or subacute spinules. Large papular pores over most of radial areas and center of disc. Rr=2.2:1. Color pale salmon or yellowish.

Range:

Cape Cod to Florida, 30 to 875 m. Most of the stations from which this species has been taken are north of Cape Hatteras.

***Goniaster americanus* Verrill**

Synonymy:

Goniaster americanus Verrill, 1871.
Pentagonaster semilunatus Perrier, 1876.

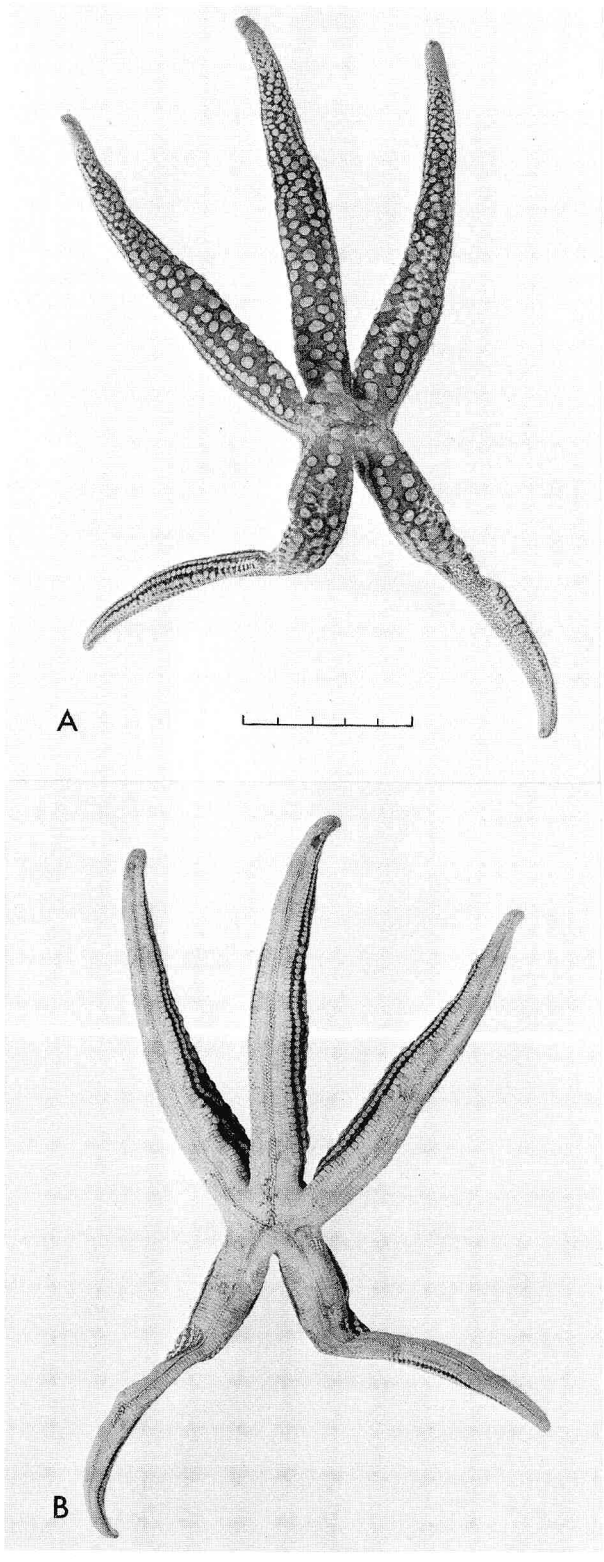


FIGURE 21.—*Linckia bouvieri.* A, aboral; B, oral. 5 cm. indicated.

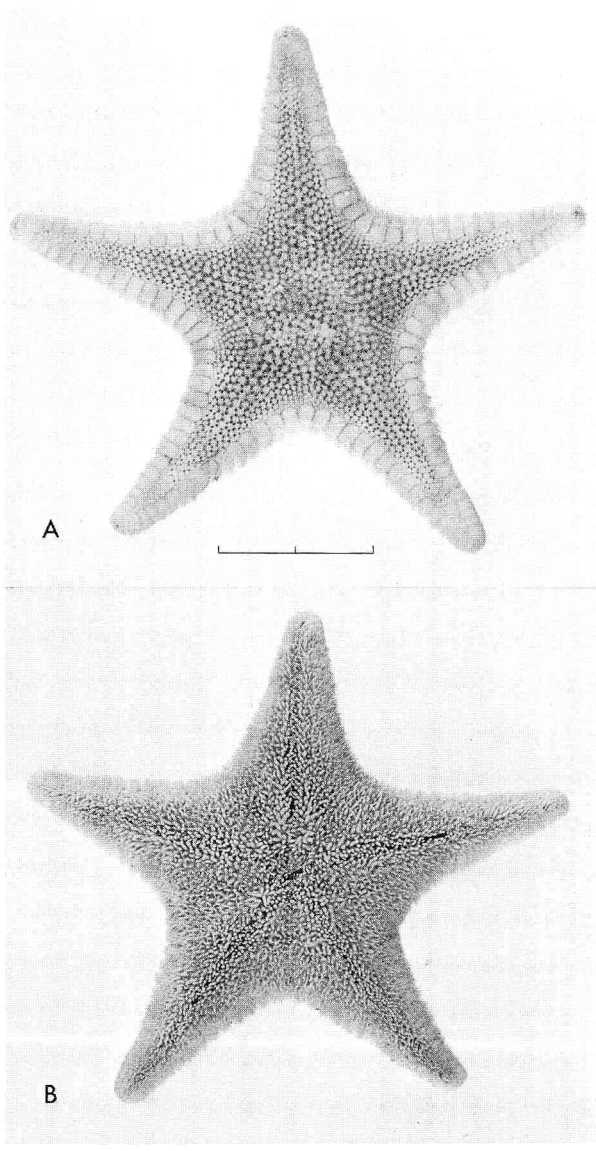


FIGURE 22.—*Odontaster hispidus.* A, aboral; B, oral. 2 cm. indicated.

Pentagonaster parvus Perrier, 1883.

Phaneraster semilunatus: Perrier, 1894.

Description:

Broadly pentagonal, with concave sides and short rays. Aboral plates large, polygonal or circular, covered with granules, many with a large, conical spine. Superomarginals and inferomarginals about equal, large, convex, quadrangular, with rounded inner sides, six to nine on each side of ray (number depends on age). Numerous alveolar pedicellariae with spatulate blades on oral and aboral surfaces,

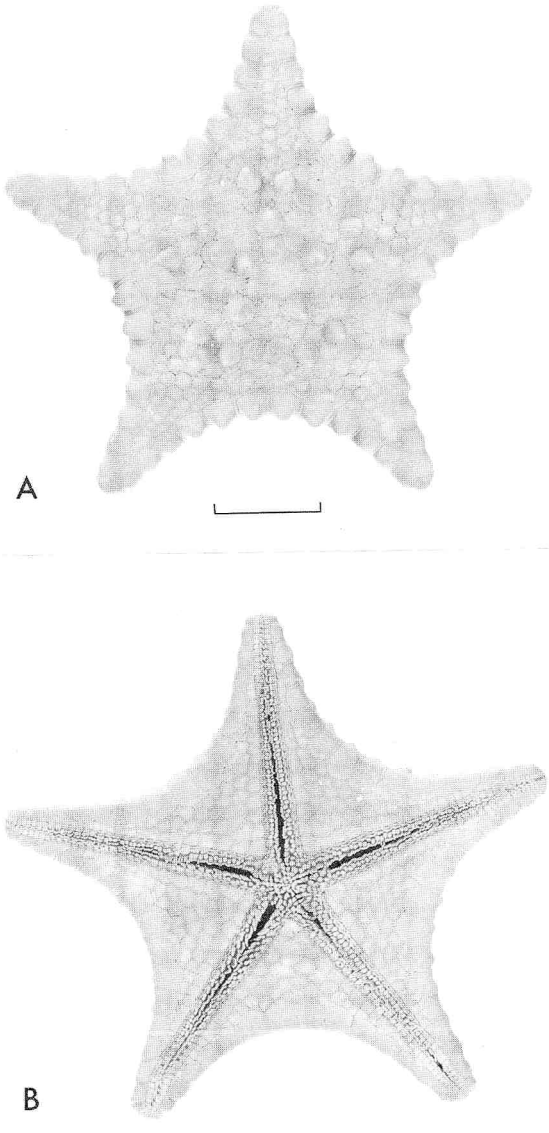


FIGURE 23.—*Goniaster americanus*. A, aboral; B, oral. 1 cm. indicated.

resting in depressions in plates. Adambulacrals with four stout, prismatic spinules in furrow series and, on distal adambulacrals, a single large obtuse spine outside the furrow series. Rr=1.8:1. Color dark brown on top, light brown underneath.

Range:

North Carolina to Florida and the West Indies, 55 to 235 m. Taken mainly from the edge of the shelf off Cape Lookout.

***Mediaster bairdii* Verrill**

Synonymy:

Archaster bairdii Verrill, 1882.
Mediaster stellatus Perrier, 1891.
Isaster bairdii: Verrill, 1895.
Mediaster bairdii: Verrill, 1899.

Description:

Form stellate, with broad flat disc and moderately long tapered rays. Marginals well devel-

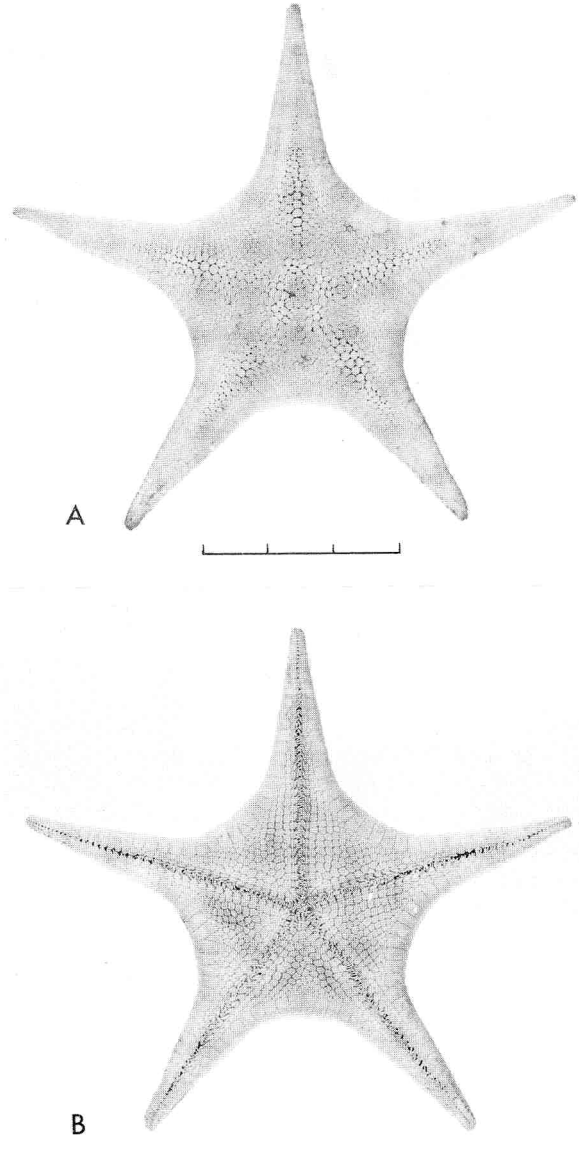


FIGURE 24.—*Mediaster bairdii*. A, aboral; B, oral. 3 cm. indicated.

oped, granulated, numerous, upper and lower series nearly equal. Aboral plates longitudinally arranged, roundish, moderate in size, covered with rosette of short, obtuse spinules, sometimes with a broad sessile valvular pedicellaria. Adambulacrals with marginal row of three to seven slender spinules, sometimes with two to three bladed clavate pedicellariae. Actinal plates angular, in rows parallel to ambulacral grooves, covered with rosette of granules. Rr=3.3:1. Color brilliant red abactinally, salmon orange actinally.

Range:

Northeast coast of the United States, 90 to 360 m. Our only record is from the edge of the shelf off Cape Lookout.

***Plinthaster* dentatus (Perrier)**

Synonymy:

Pentagonaster dentatus Perrier, 1883.
Pyrenaster dentatus (Perrier), Verrill, 1899.
Plinthaster dentatus (Perrier), Fisher, 1911.

Description:

Form flat, more or less pentagonal, rays short. Marginals rather large, both series similar and paired. The distal inferomarginal behind the ocular plate smaller than the others; ocular plate somewhat pointed. Marginals closely covered with granules in young specimens, but with scattered clumps of granules in older specimens. Pedicellariae on adambulacrals rare, similar to granules, with short chisel-shaped blades. Adambulacral plates large, squarish; furrow spinelets in regular series, well separated from granules of actinal surface. Actinal plates polygonal, flat, crowded. Abactinal plates rounded, convex, usually with a border of granules. Papular pores not numerous confined to median radial area. Rr=1.5:1. Color bright orange or yellow.

Range:

North Carolina to Gulf of Mexico, 360 to 915 m. Recovered from a *Lophelia* coral reef on the slope southeast of Cape Lookout.

***Peltaster planus* Verrill**

Synonymy:

Pentagonaster planus Verrill, 1885.
Peltaster planus: Verrill, 1899.

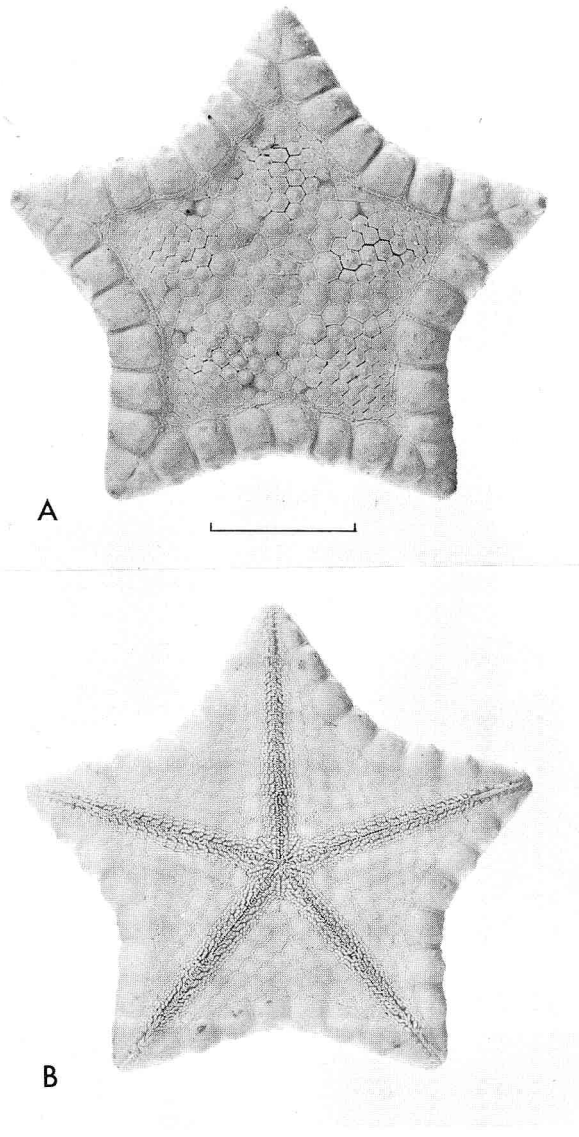


FIGURE 25.—*Plinthaster dentatus*. A, aboral; B, oral. 1 cm. indicated.

Description:

Body pentagonal, sides almost straight, rays five, triangular, obtuse. Marginals large, quadrangular, 14 in superomarginal series, 16 in inferomarginal series, covered with coarse granules (which easily rub off, sometimes leaving the superomarginals nearly bare). Aboral plates large, rounded or hexagonal, with many smaller secondary plates interspersed. All covered with rather uniform coat of granules. Actinal plates large,

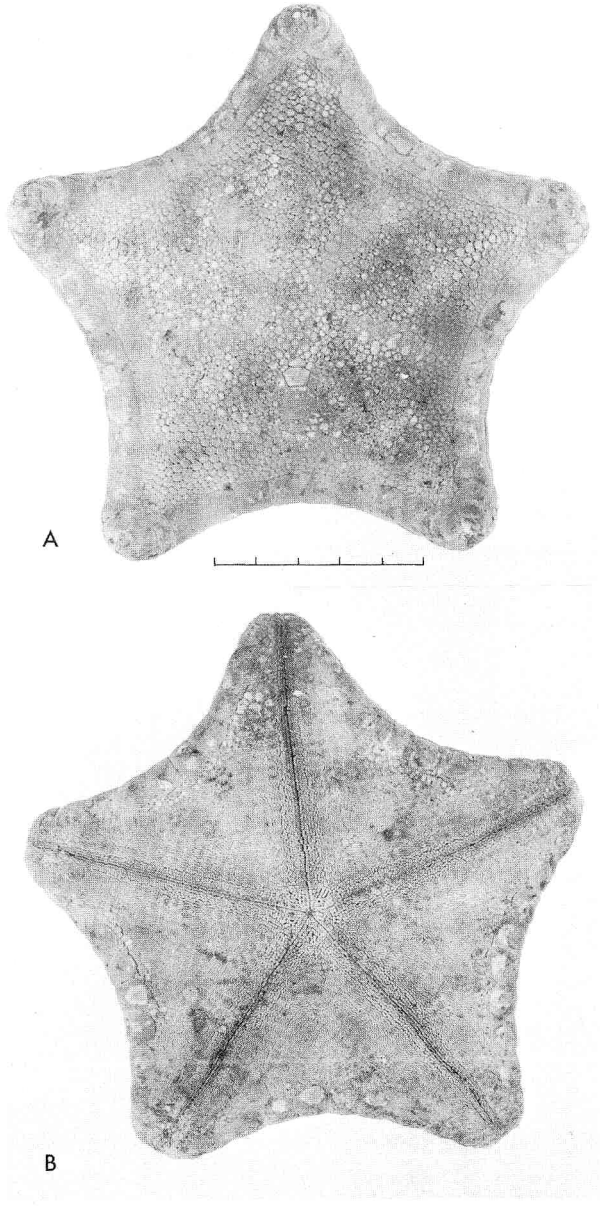


FIGURE 26.—*Peltaster planus.* A, aboral; B, oral. 5 cm. indicated.

rhombic, covered with granules. Adambulacrals numerous, crowded, with 3 to 4 marginal spines in row; outside of these are 9 to 12 thicker, obtuse spines in four irregular rows; all adambulacral spines resemble the actinal granules, which are large, angular. No pedicellariae. Rr=1.4:1. Color pale yellowish brown.

Range:

Cape Cod to Cape Hatteras, 180 to 365 m. North Carolina specimens have come mainly from north of Cape Hatteras.

SPINULOSIDA

None of the species of the Order Spinulosida are common in North Carolina. Although the two "northern" species are very abundant north of the State, they are rarely taken in North Carolina waters. The "southern" species have been taken only in Onslow Bay.

Solaster caribbaeus Verrill, 1915

Description:

Disc rather large, arms six to eight. Dorsal surface covered with numerous paxillae which are crowned with many long fine spinules. Papulae in rather regular rows from center out along arms. Inferomarginals conspicuous, forming distinct fringe around border; superomarginals not distinct from dorsals. Adambulacrals with inner furrow comb of three to four webbed spines and outer transverse comb of about four larger spines. Oral spines eight, with middle two largest and longest. Anus central, protected by spines of adjacent paxillae. Madreporite inconspicuous. Species known only from small, probably juvenile specimens. Rr=2.6:1. Color in life unknown, preserved, pale beige.

Range:

Known previously only from the West Indies, 30 to 230 m. A single specimen has been taken from a reef in Onslow Bay.

Porania insignis Verrill, 1885

Description:

Convex disc, five short rays. Dorsal surface smooth, covered with thick, leathery skin. Papulae elongate, in irregular bands from near center of disc out along either side of rays; single or double row between superomarginals and inferomarginals. Lower marginals with one to four sharp, conical, skin-covered spines, forming fringe around body. Adambulacrals with transverse row of two to three short stout spines, webbed at base, outer one stoutest. Two short, skin-covered oral spines on each jaw, and two to three on each side of jaw. Actinal radial furrows conspicu-

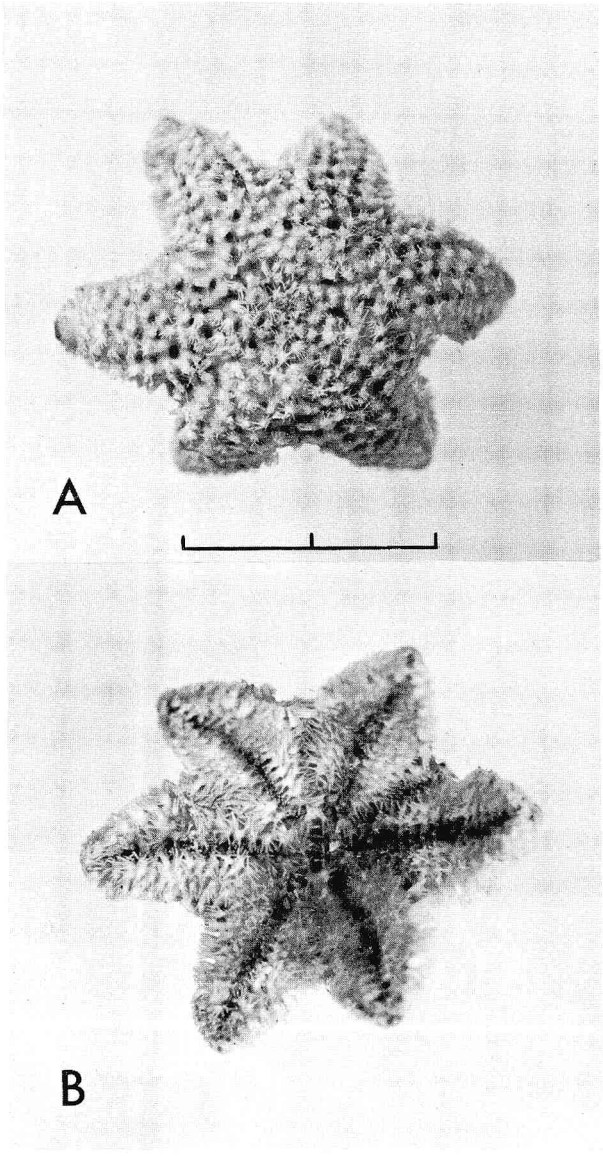


FIGURE 27.—*Solaster caribbaeus*. A, aboral; B, oral. 2 cm. indicated.

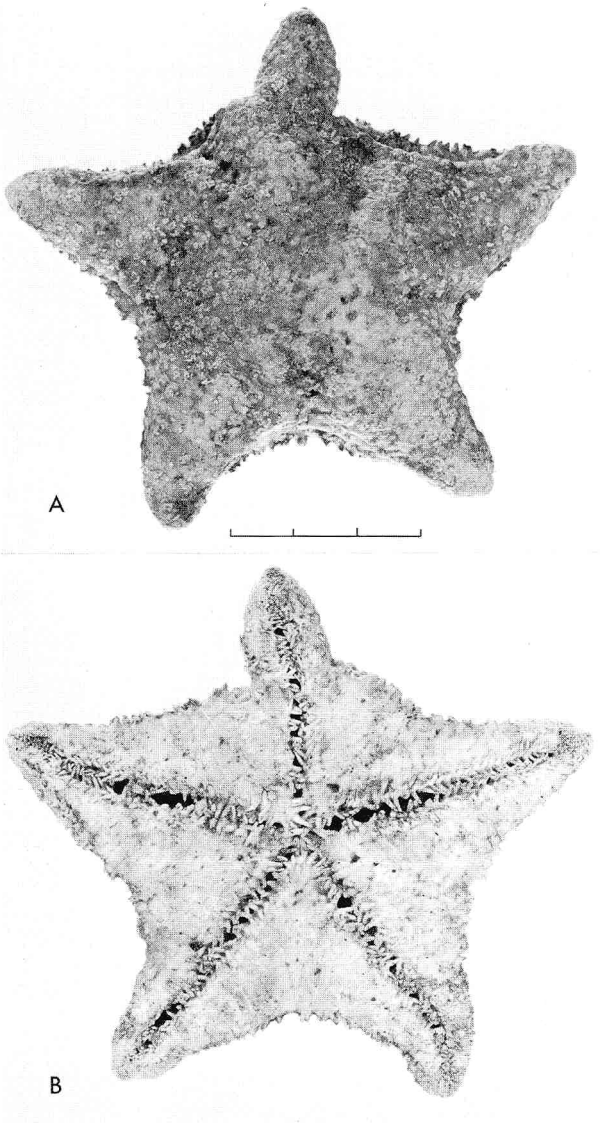


FIGURE 28.—*Porania insignis*. A, aboral; B, oral. 3 cm. indicated.

ous. Rr=1.6:1. Color red or reddish brown above, cream or white below.

Range:

Cape Cod to Cape Hatteras, 35 to 680 m. Seemingly limited in North Carolina to the area north of Cape Hatteras.

Thyraster serpentarius **(Mueller and Troschel)**

Synonymy:

Echinaster serpentarius Mueller and Troschel, 1842.

Thyraster serpentarius Ives, 1890.

Description:

Disc small, arms five, subcylindrical. Skeleton of quadrangular plates, overlapping at their corners, and arranged in very regular longitudinal series. Three to four small spines on distal edge of dorsal plates. Three to four spines on distal margin of adambulacral plates, with a small furrow spinelet. Tips of all spines thorny; plates minutely tuberculated. Papular areas rounded, regular, with

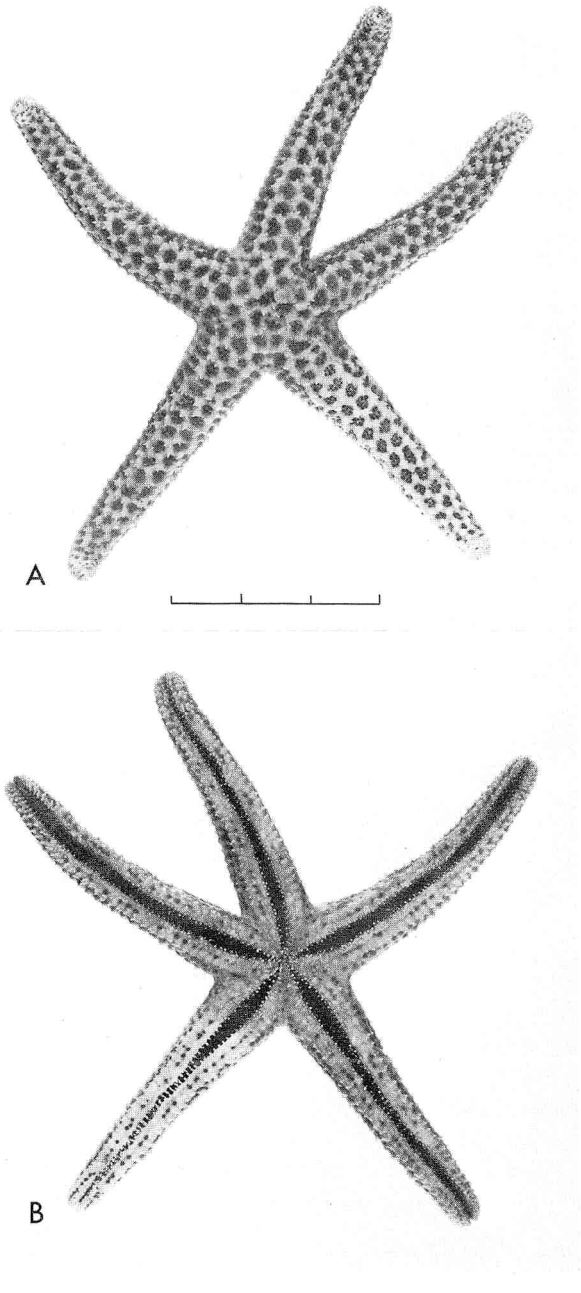


FIGURE 29.—*Thyraster serpentarius.* A, aboral; B, oral. 3 cm. indicated.

about 10 pores per area. Madreporite raised, channeled, warty. Rr=4:1. Color reddish brown.

Range:

North Carolina to Florida, Alabama, and Louisiana; Vera Cruz, Mexico, 9 to 75 m. In North Carolina mainly on reefs in Onslow Bay.

***Henricia sanguinolenta* (Sars)**

Synonymy:

Asterias sanguinolenta Müller, 1777.
Asterias pertusa Müller, 1777.
Asterias oculata Pennant, 1777.
Asterias spongiosa Fabricius, 1780.
Asterias seposita Retzius, 1783.
Linckia oculata: Forbes, 1839.
Henricia oculata: Gray, 1840.
Cribella oculata: Forbes, 1841.
Echinaster oculatus: Mueller and Troschel, 1842.
Echinaster sanguinolentus Sars, 1844.
Echinaster sarsii Mueller and Troschel, 1842.
Linckia pertusa: Stimpson, 1853.
Cribella sanguinolenta: Lütken, 1857.
Cribella oculata: Fischer, 1869.
Henricia sanguinolenta: Grieg, 1896.

Description:

Disc small, rays five, slender, pointed, cylindrical. Disc and arms evenly covered with small spinules on network of fine, closely reticulate plates. Papular pores numerous. Superomarginals small, indistinct, like aboral plates; inferomarginals larger. Adambulacrals transversely oblong. One to two furrow spines; actinal face of adambulacrals with numerous fine spinules. No pedicellariae. Rr=5–7:1. Color commonly bright red, but may be orange, green, purple, or brown.

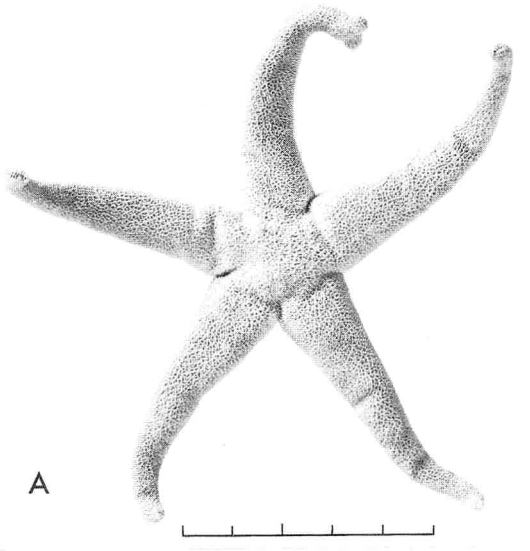
Range:

Circumboreal and south to about lat. 35° N., 55 to 2,400 m. Rare in North Carolina and limited to the cold waters north of Cape Hatteras.

***Echinaster spinulosus* Verrill, 1869**

Description:

Disc small, rays five, long, slender, tapered. Fifteen to 20 rows of 40 or more small, conical, subacute spines on aboral plates, often 2 or 3 to a plate. The two rows of marginals larger and more rounded than abactinal plates, and with a well defined patch of glassy granules. Each also bears one small conical spine. Most of the aboral plates also have a patch of glassy granules. Papular pores numerous, but none below inferomarginals. Adambulacrals with two small furrow spines and a stouter, conical



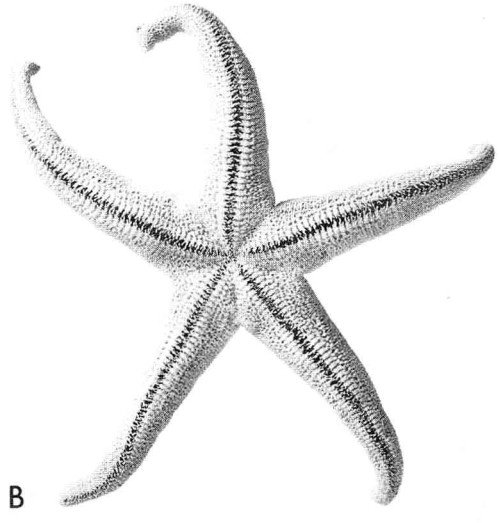
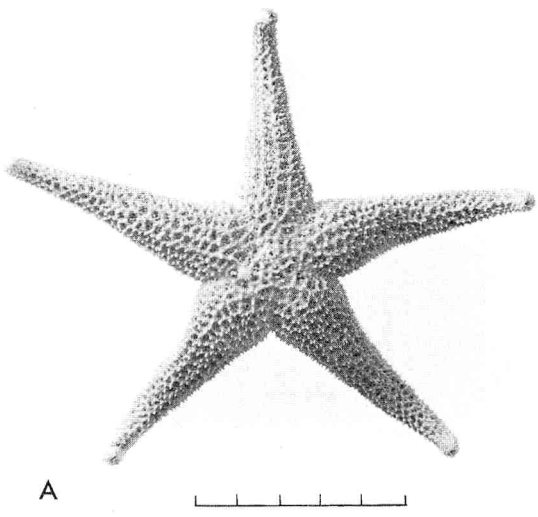


FIGURE 30.—*Henricia sanguinolenta.* A, aboral; B, oral. 5 cm. indicated.



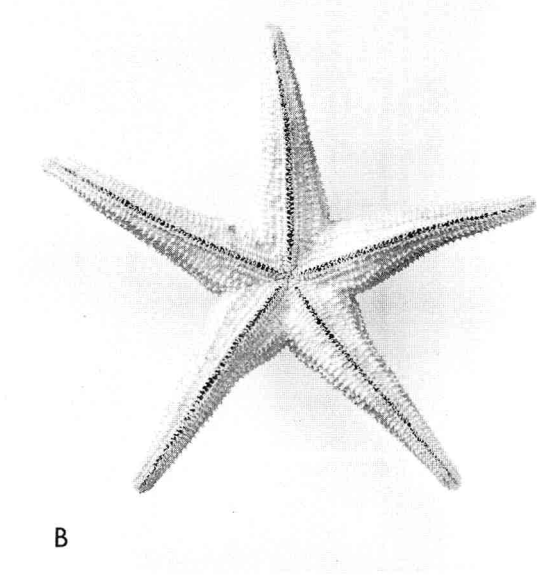


FIGURE 31.—*Echinaster spinulosus.* A, aboral; B, oral. 3 cm. indicated.

spine on the outer margin. Madreporite prominent, flattish, wartlike. The whole body invested in moderately thick dermis. Rr=4:1. Color dark red, purple, or reddish brown.

Range:

North Carolina to west coast of Florida and Gulf of Mexico, shore to 60 m. Found on reefs in Onslow Bay. Seemingly reported in North Carolina for the first time by Pearse and Williams (1951) from a reef off New River Inlet.

***Echinaster sentus* (Say)**

Synonymy:

Asterias sentus Say, 1825.

Echinaster sentus: Lütken, 1871.

Description:

Disc small, rays five, of moderate length, rounded. Aboral spines in five irregular rows, median row most distinct. Larger aboral plates sometimes have two to three spines, but usually one. Two marginal rows of plates

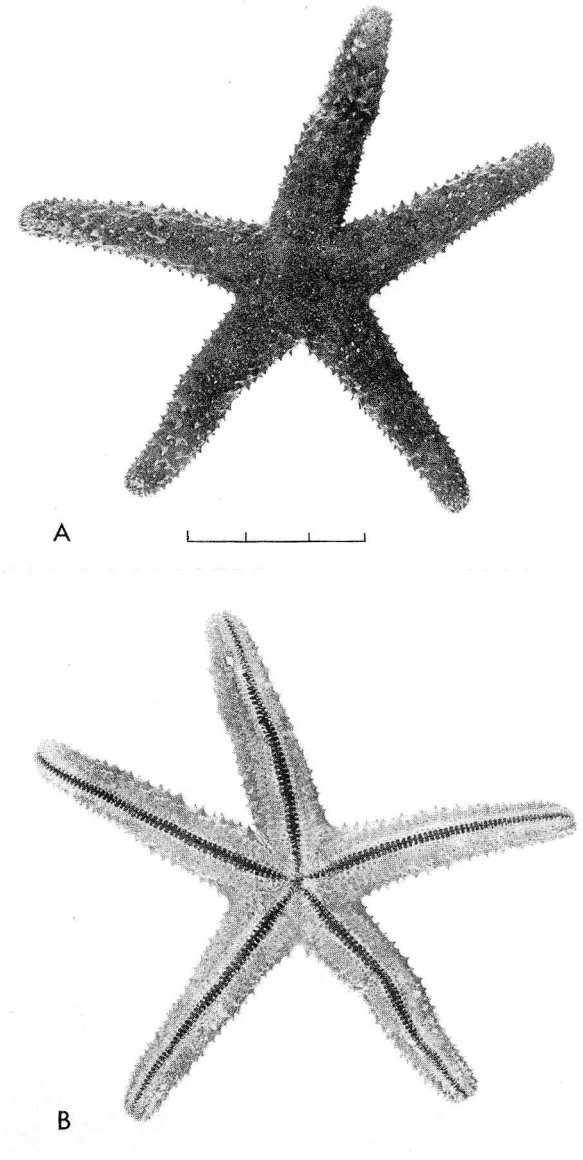


FIGURE 32.—*Echinaster sentus*. A, aboral; B, oral. 3 cm. indicated.

fairly regular, but do not differ from other plates in size or form. Superomarginals with one stout, conical spine, on mammiform base, on each plate. A single row of small oblong plates connects the inferomarginals with the adambulacrals. Adambulacral spines small, subacute, in oblique transverse series of three. Two webbed furrow spines, inner one much smaller. Papulae numerous, papular areas large, extending to adambulacrals. Madreporite raised, flat, covered with rough spinules. Rr=4:1. Color dark red or purple.

Range:

North Carolina to West Indies, shallow water. Found on reefs in Onslow Bay, often in association with *E. spinulosus*.

***Echinaster brasiliensis* Mueller and Troschel**

Synonymy:

(?) *Othilia braziliensis* A. Agassiz, 1869.
Echinaster brasiliensis Mueller and Troschel, 1842.

Description:

Disc small, rays five, slender, terete. Dorsal spines small, sturdy, acute-conical, in 9 to 11 rows. Marginals not distinct from aborals. Papular areas of moderate size, numerous on aboral surface, less numerous on oral surface. Three adambulacral spines: furrow spine small, curved, two outer spines sturdy, divergent, subequal. Madreporite small, warty, covered with rough spinules. Rr = 5:1. Color rust red above, paler below.

Range:

North Carolina to Florida and Brazil, shallow water. Our only locality record for this species is at the edge of the shelf northeast of Cape Hatteras.

FORCIPULATIDA

All North Carolina species in the Order Forcipulatida may be found north of Cape Hatteras, and a few also occur south of the Cape. The well-known and widespread shallow water *Asterias forbesii* is the most abundant. North of Cape Hatteras, the tropical species *Coscinasterias tenuispina* and *Stephanasterias gracilis* occur only near the outer edge of the shelf.

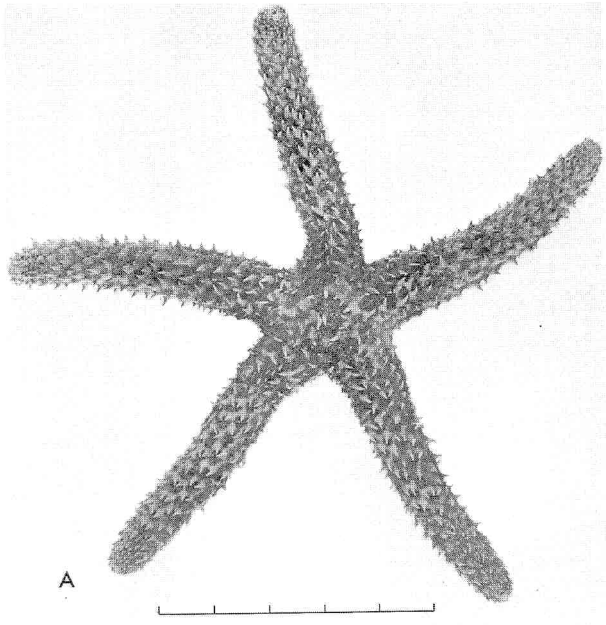
***Asterias forbesii* (Desor)**

Synonymy:

Asteracanthion forbesii Desor, 1848.
Asterias arenicola Stimpson, 1862.
Asterias forbesii: Verrill, 1866.

Description:

Disc moderate, often domed. Rays five, stout, cylindrical, blunt. Upper surface a firm mosaic of strong interlocking plates, each bearing a single large, blunt, rough-tipped spine encircled by a few smaller spines. Small pedicellariae encircle each spine, and larger pedicellariae are scattered over the surface. Ad-



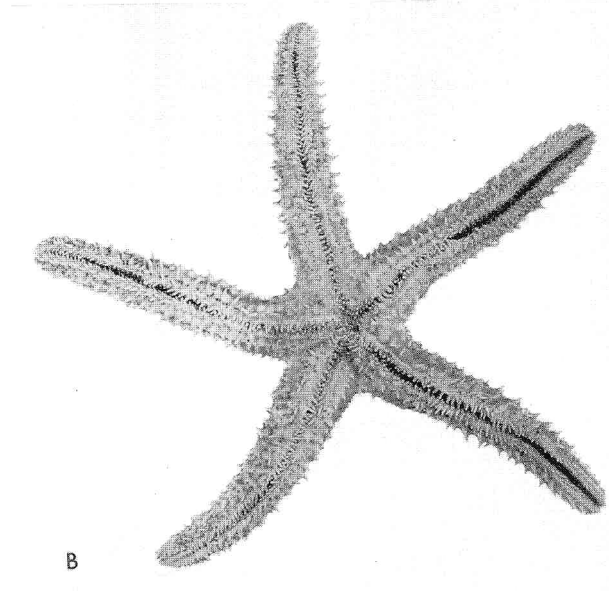
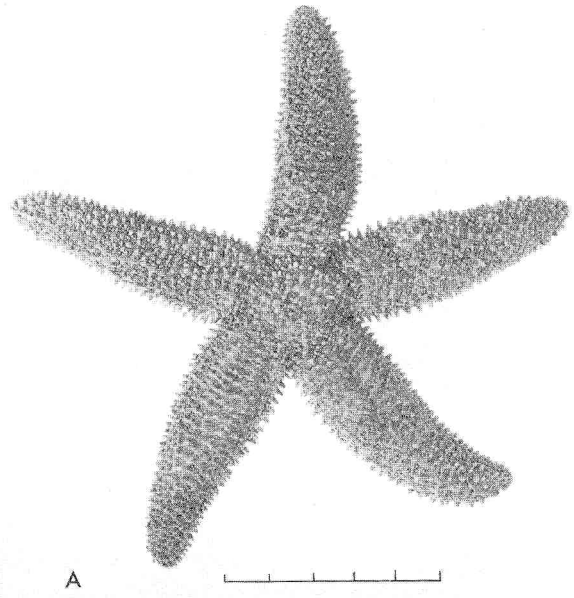


FIGURE 33.—*Echinaster brasiliensis*. A, aboral; B, oral. 5 cm. indicated.



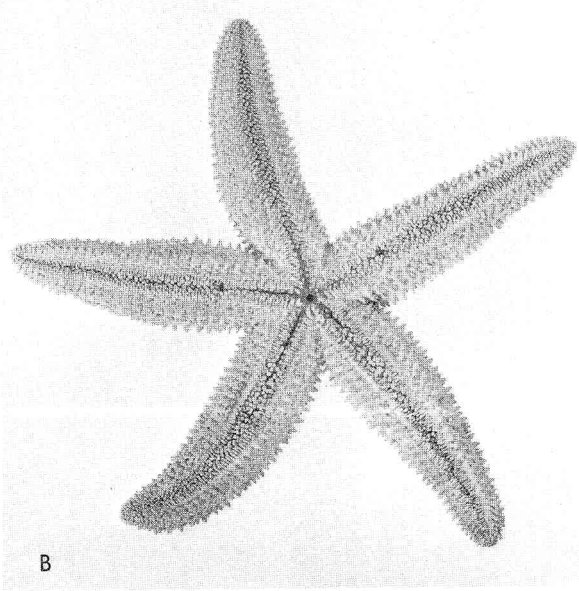


FIGURE 34.—*Asterias forbesii*. A, aboral; B, oral. 5 cm. indicated.

ambulacrals with one or two flattened, truncate, long, slender spines. Madreporite small, smooth, channeled, without warts, tubercles, or spinules. Rr=3:1. Color reddish brown, madreporite usually bright orange or red.

Range:

Maine to Gulf of Mexico, to 92 m. This shallow water species is the best known sea-star along the Atlantic coast and is the one most frequently used in biology classes. Large individuals, common in winter but less so in summer, inhabit hard substrates, such as jetties, pilings, shell bottoms, and wrecks, in shallow water along the North Carolina coast and

in the estuaries. In summer, the trawls of commercial fishermen take many small individuals.

***Asterias vulgaris* Verrill**

Synonymy:

Asterias vulgaris Packard, 1863 (nomen nudum).
Asterias stimpsoni Verrill, 1866.
Asterias vulgaris Verrill, 1866.
Asterias pallida: Perrier, 1875.
Asterias fabricii Perrier, 1875.

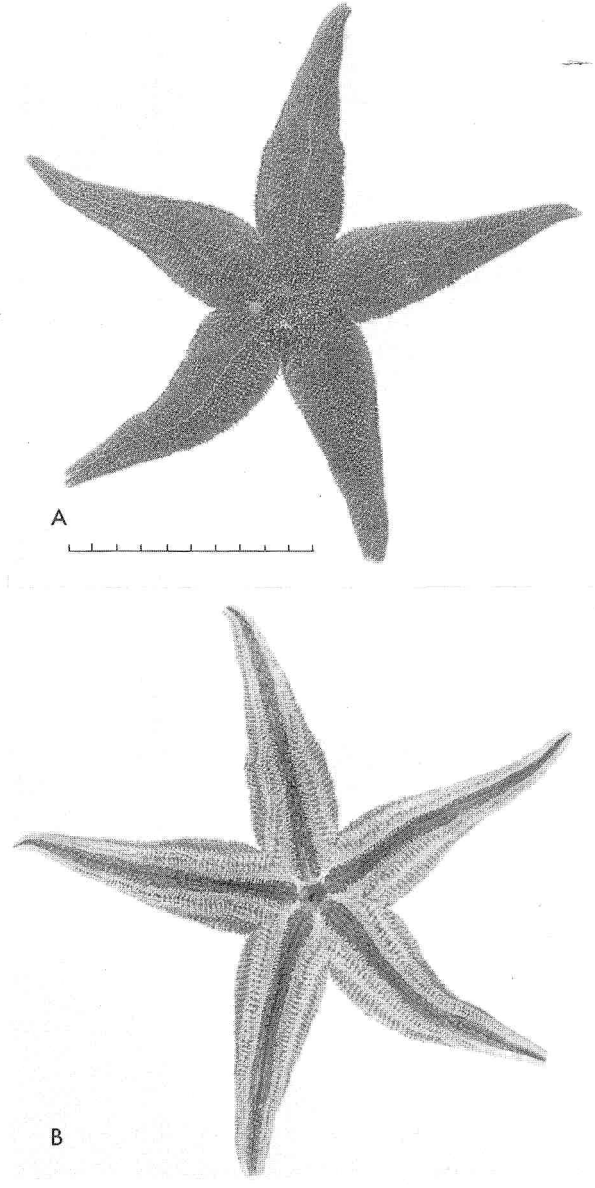


FIGURE 35.—*Asterias vulgaris*. A, aboral; B, oral. 10 cm. indicated.

Description:

Disc of moderate size, arms five, more flattened and pointed than in *A. forbesii*. Aboral surface a network of narrow barlike plates with large meshes, making a fairly weak skeleton. Clearly perceptible row of median plates. All plates with one or more blunt spines with rough tips, encircled by a wreath of blunt pedicellariae. Large acute pedicellariae along sides of arms, rising directly from dermis. Inferomarginals with conspicuous series of long, truncate spines. Adambulacrals with one or two long, flattened spines. Rr=3:1. Color reddish brown, madreporite usually yellow.

Range:

Labrador to Cape Hatteras, shore to 650 m. Uncommon in North Carolina, where it is limited to the cold waters north of Cape Hatteras.

***Asterias tanneri* Verrill, 1880**

Description:

Disc small, arms five, slender, terete. Aboral spines blunt, rather large and conspicuous, encircled with wreath of small pedicellariae about half way up the spine. Adambulacral spines long, slender. Jaw plates long, narrow, with two pairs of large, conspicuous spines. Madreporite very small. Rr=5.5:1. Color pale yellowish.

Range:

New Jersey to Cape Hatteras, 35 to 350 m. In North Carolina it has been taken at several stations north of Cape Hatteras.

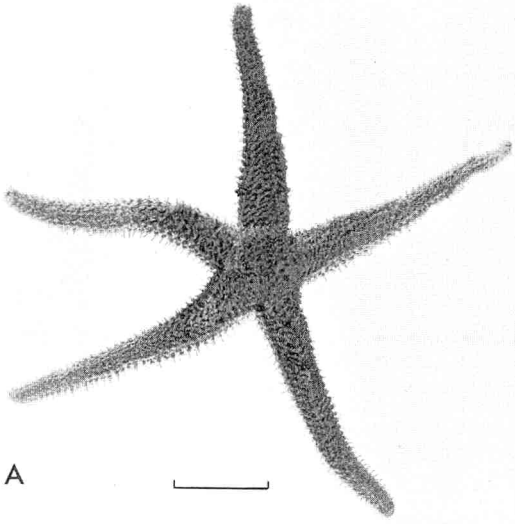
***Coronaster briareus* (Verrill)**

Synonymy:

Asterias briareus Verrill, 1882.
"near *Asterias volsellata*" Nutting, 1895.

Description:

Disc small, rays 10 to 12 slender, elongate. Aboral skeleton openly reticulate, with marked median carina. Marginal plates also form ridges. Aboral and marginal spines long, slender, acute, well separated. Large rectangular papular areas, with numerous papulae in clusters. Spines bear dense wreath of small pedicellariae. Large solitary feliped pedicellariae scattered on dermis above and below. Adambulacrals with two long, slender spines.



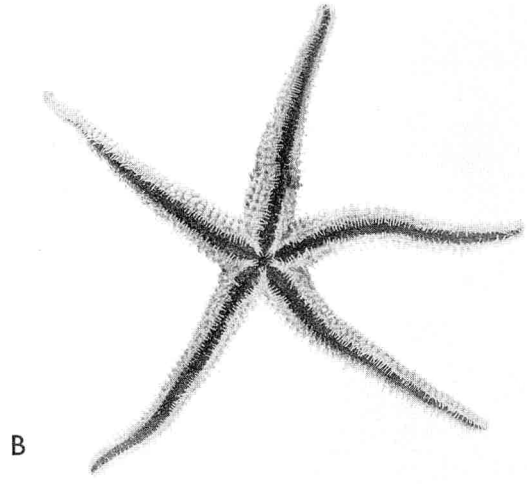


FIGURE 36.—*Asterias tanneri.* A, aboral; B, oral. 1 cm. indicated.

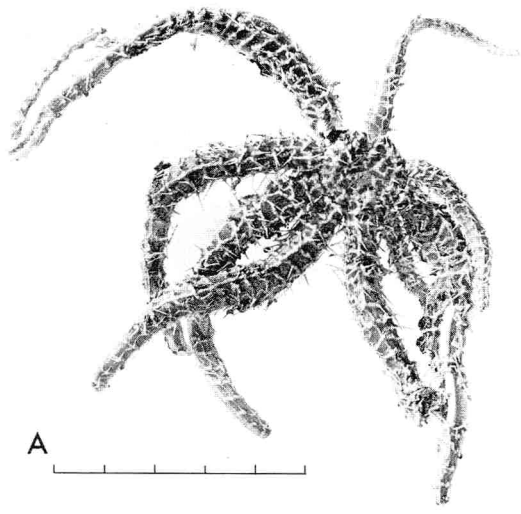


FIGURE 37.—*Coronaster briareus.* A, aboral; B, oral. 5 cm. indicated.

Rr=9.5:1. Color in life unknown; preserved, pale beige.

Range:

Virginia to Key West, Fla., 35 to 75 m. So far this species has been found at only one station—North of Cape Hatteras in about 40 m.

Coscinasterias tenuispina **(Lamarck)**

Synonymy:

Asterias tenuispina Lamarck, 1816.

Asteracanthion tenuispinus: Mueller and Troschel, 1842.

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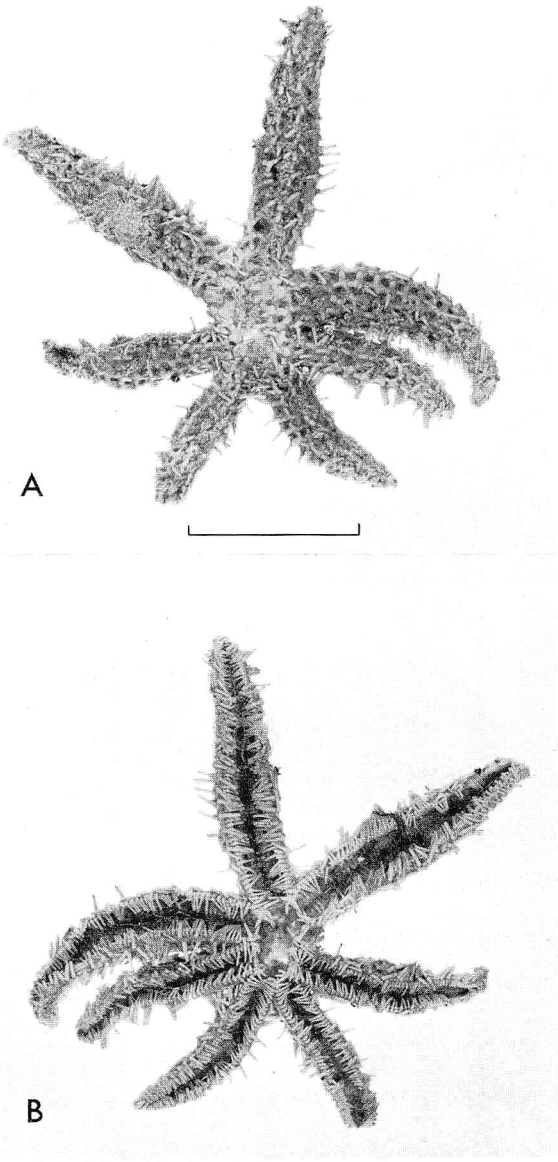

FIGURE 38.—*Coscinasterias tenuispina. A, aboral; B, oral.* 1 cm. indicated.

Asterias (*Stolasterias*) *tenuispina:* Sladen, 1889.

Coscinasterias tenuispina: Verrill, 1914.

Asterias atlantica (pars) Verrill, 1868.

Description:

Disc small, rays four to nine (most commonly seven), long, slender, angular. Aboral and marginal spines elongate and slender. Aboral plates form definite carinal row and one main dorso-lateral row on each side; each plate with one spine. Superomarginals and inferomarginals with one or two spines, longer than aboral spines. Adambulacrals with one long slender spine. Usually two or more madreporites present. Rr=10:1. Color yellowish brown, with darker markings.

Range:

Mediterranean, Madiera, Canary Islands, Cape Verde Islands, Brazil, Cuba, Bermuda, West Indies. In North Carolina, 20 to 165 m. South of Cape Hatteras it has been found on reefs off New River Inlet and Cape Lookout; north of Cape Hatteras it occurs along the edge of the shelf in 145 to 165 m.

***Stephanasterias gracilis* (Perrier)**

Synonymy:

Asterias gracilis Perrier, 1881.

Stephanasterias gracilis: Verrill, 1879.

Description:

Disc small, rays about six, often unequal, slender. Aboral surface closely covered with numerous minute slender spines, several to a plate. Marginal spines larger, flattened, and expanded at tip, which is blunt, thorny, and more or less hyaline. Adambulacrals with two short, slender, slightly clavate spines. Rr=4.5:1. Color in life unknown; preserved, white.

Range:

Lesser Antilles, Gulf of Mexico, Cuba, and Florida, 145 to 370 m. Although a southern species, it has been taken in North Carolina only north of Cape Hatteras—at several stations along the edge of the outer shelf.

***Leptasterias tenera* (Stimpson)**

Synonymy:

Asterias tenera Stimpson, 1862.

Asterias compta Stimpson, 1862.

Leptasterias compta: Verrill, 1866.

Description:

Disc moderate, rays five, slender, cylindrical, tapering to small blunt tip. Conspicuous slender spines rising from open network of aboral plates, no clear median row on arms. Wreath of pedicellariae around aboral spines. Adambulacral spines long, blunt-tipped. Madreporite inconspicuous. Rr = 5:1. Color

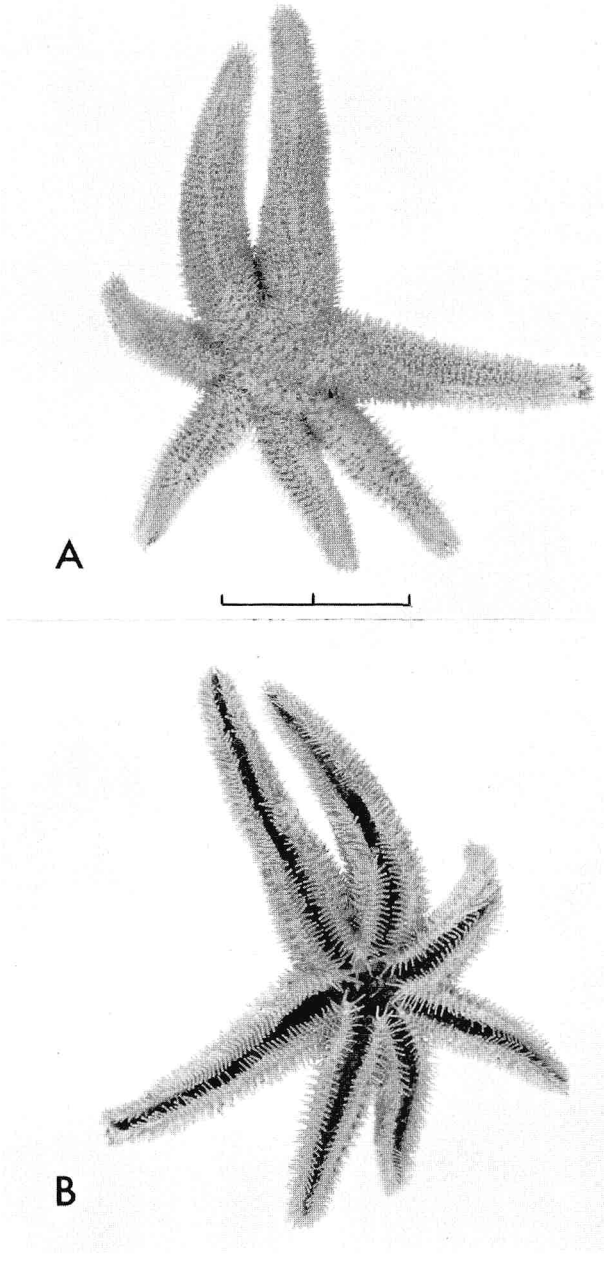

FIGURE 39.—*Stephanasterias gracilis.* A, aboral; B. oral. 1 cm. indicated.

pale purple or pink, red eyespot at tip of arm.

Range:

Nova Scotia to North Carolina, 18 to 150 m. A cold-water species limited, in North Carolina, to the area north of Cape Hatteras in 30 to 145 m.

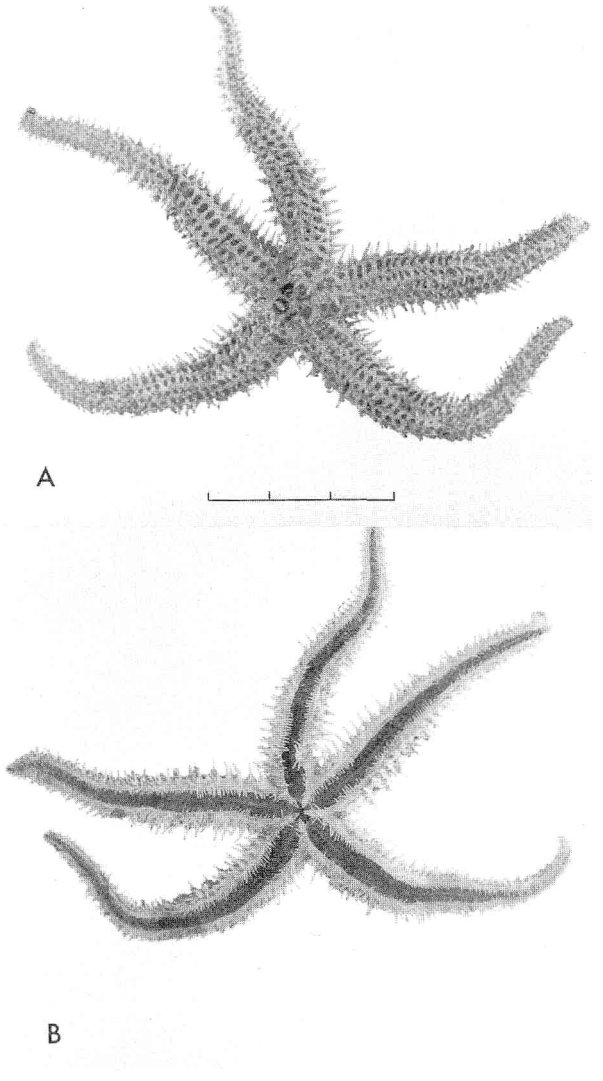

FIGURE 40.—*Leptasterias tenera.* A, aboral; B, oral. 3 cm. indicated.

ACKNOWLEDGMENTS

The National Science Foundation supported much of the work (Grant G–25,128) and made possible participation in several research cruises of the RV *Eastward* (Grant G–17,669 to Duke University). The U.S. Coast and Geodetic Survey permitted two assistants to work from the *Explorer* when the vessel was operating in North Carolina waters and allowed us to use underwater photographs taken on this cruise. Several graduate students from time to time participated in cruises of the *Eastward* and chartered trawlers and

helped in many other ways—particularly L. R. McCloskey and J. F. Grassle, who also served as research assistants.

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ABUNDANCE AND DISTRIBUTION OF THE LARVAE OF THE PINK SHRIMP (*PENAEUS DUORARUM*) ON THE TORTUGAS SHELF OF FLORIDA, AUGUST 1962–OCTOBER 1964 [1,2]

BY J. L. MUNRO[3] AND A. C. JONES,[4] *Fishery Biologists*, AND D. DIMITRIOU,[5] *Fishery Technician*

INSTITUTE OF MARINE SCIENCES, UNIVERSITY OF MIAMI
MIAMI, FLORIDA 33149

ABSTRACT

A 2-year study has shown that an estimated 870 x 10^{10} first protozoeae of pink shrimp are produced each year within the main part of the Tortugas spawning grounds. Survival rates are nearly constant and average 80.4 percent per day throughout larval life. Estimates of larval survival at specific sampling stations are influenced by the migration patterns of the larvae and vary considerably, depending on whether the sampling station receives older larvae from adjacent areas or loses larvae to other areas.

An investigation of bottom currents on the Tortugas grounds has shown that the prevailing westerly and southwesterly currents may carry the larvae into the Florida Current, which, in turn, may transport the larvae to the nursery grounds in the Everglades National Park.

Spawning, measured by the relative abundance of first protozoeae, is influenced by moon phase; most spawning occurs during the last half of the lunar month. Spawning activity reaches a maximum when bottom water temperatures are highest; the center of spawning shifts from shallow water into deeper water as the spawning season progresses.

The early life history of the pink shrimp, *Penaeus duorarum* Burkenroad, has received considerable attention in recent years. Dobkin (1961) described the early larval stages of *P. duorarum* hatched from eggs spawned in the laboratory, and Ewald (1965) succeeded in rearing all stages in the laboratory. These studies have provided evidence upon which identifications of the larvae in the plankton can be based. Eldred, Williams, Martin, and Joyce (1965) studied the inshore and offshore distribution and abundance of larval and postlarval *P. duorarum* in the Tampa Bay area. Jones, Dimitriou, Ewald, and Tweedy (unpublished manuscript)[6] described the distribution of pink shrimp larvae over a wide area of the Tortugas Shelf of Florida and located the main spawning grounds.

The purposes of the study reported here were to (1) define quantitatively the seasonal abundance of the planktonic shrimp larvae in the main spawning area on the Tortugas Shelf; (2) investigate the relation between spawning intensity and environmental factors; (3) estimate the mortality rates of various larval stages; and (4) describe how immigration and emigration of larvae affect mortality estimates pertaining to specific sampling stations.

Published September 1968.

PROCEDURES

The methods we have used covered four activities: selection of study stations, sampling procedures, laboratory techniques, and computer conversion of data.

STUDY AREA

We sampled on a grid system that covered the Tortugas Shelf area (fig. 1); stations were 18.5 km. apart. Ten stations were selected for regular sampling in the area considered by Jones et al. (footnote 6) to be the center of spawning. The stations are designated 50.100, 50.90, 50.80, 50.70, 40.90, 40.80, 40.70, 40.60, 32.70, and 30.58 and were located over depths between 10 and 36 m. (5.5 and 20.0 fathoms). (The latter two stations

[1] Contribution No. 235, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex. 77552.

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[3] Present address: Zoology Department, University of the West Indies, Kingston, Jamaica.

[4] Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Fla. 33149.

[5] Present address: 10045 Montego Bay Drive, Miami, Fla. 33157.

[6] "Distribution of early developmental stages of pink shrimp, *Penaeus duorarum*, in Florida waters," by A. C. Jones, D. Dimitriou, J. J. Ewald, and J. Tweedy, Institute of Marine Sciences, University of Miami, for Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex., 54 MS. pp., 13 figs.

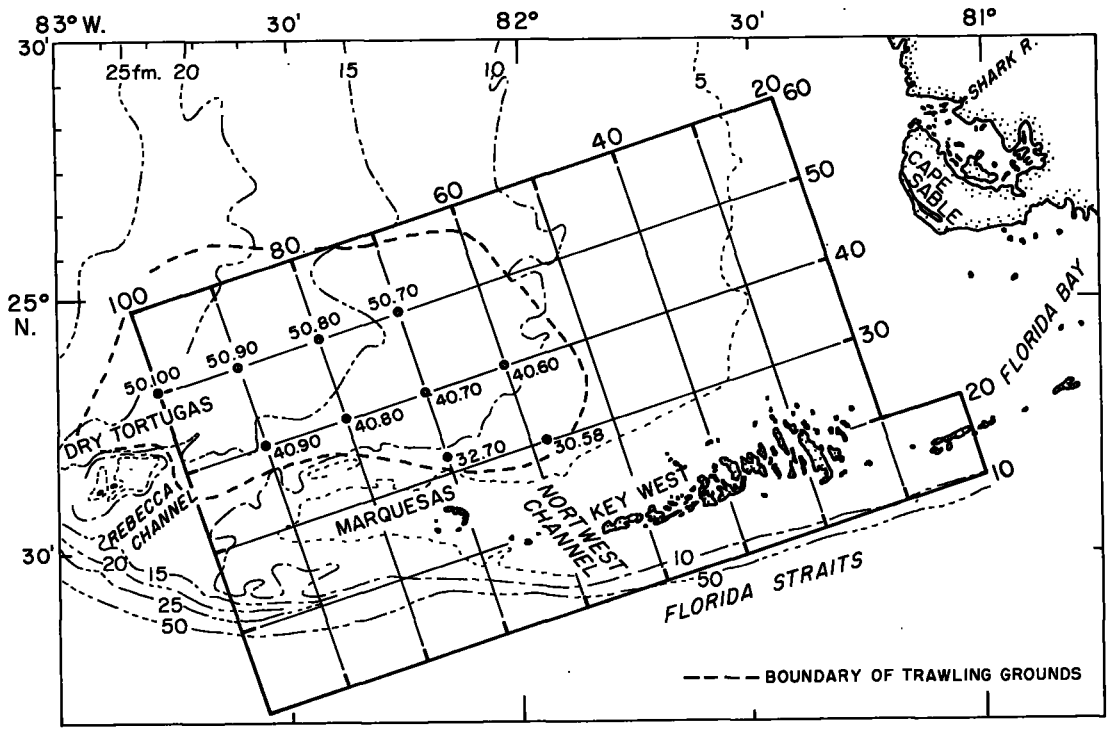

FIGURE 1.—Map of the Tortugas Shelf area showing the sampling grid, regular sampling stations, and place names mentioned in the text.

were slightly displaced from their theoretical grid coordinates because of shoal waters.)

SAMPLING

Throughout the study, we sampled about twice each month. A shrimp trawler 20 m. long overall, having an idling speed of 5.6 km. per hour (3 knots), towed the sampling apparatus. Towing speed varied according to wind velocity and at times was as low as 2.8 km. per hour (1.5 knots).

Gulf V plankton nets were used throughout the study. This net has been described by Arnold (1959) and consists of a metal frame in which is mounted a monel mesh net fitted with a brass bucket in which the plankters accumulate. The mouth diameter of the Gulf V net is 40 cm., and overall length is 100 cm. The mesh has an aperture size of 0.292 mm. Dobkin (1961) stated that first protozoeae have a maximum width of 0.35 to 0.44 mm., and all subsequent larval stages are of greater size. Nauplial stages are considerably smaller (maximum width of the fifth nauplius stage is 0.17 to 0.22 mm.) and were not retained by the mesh.

Flowmeters were mounted in the mouths of the nets. These meters were calibrated regularly and performed consistently over the entire period of operation.

Sampling procedures were rigidly controlled, and, in the event of gear failure or malfunction of timing equipment, the sample was discarded, and the tow was repeated. Replicate samples were taken at each station.

Step-oblique tows were made with the net towed for 3 minutes at each of 10 levels equally spaced between the bottom and surface. When the net was retrieved, the flowmeter reading was noted, and the bucket of plankton emptied. The net was then hosed down thoroughly, and the additional washings were added to the sample. Washing continued until no more plankton or debris appeared in the bucket. Samples were preserved with a 3-percent solution of buffered Formalin.[7] During the cruise of October 2–6, 1964, when 41 stations were occupied, each level was sampled for 1.5 minutes and tows were reduced to 15 minutes.

Water temperatures were recorded at each station. Surface temperatures were measured with a bucket thermometer, and a trace of the vertical

[7] Trade names referred to in this publication do not imply endorsement of commercial products.

temperature profile was obtained with a bathythermograph. Samples of the bottom waters were obtained with a Nansen bottle; the salinity of surface and bottom waters was determined on a conductivity bridge in the laboratory. Meteorological observations were recorded in World Meteorological Organization codes.

LABORATORY TECHNIQUES

Plankton sorting was carried out under wide-field, stereoscopic microscopes fitted with variable magnification.

All penaeid shrimp larvae were removed from the samples and identified to genus by using keys developed from descriptions by Pearson (1939), Gurney (1942, 1943), and Heldt (1938). Identification of different stages of *Penaeus* larvae was based on the work of Dobkin (1961). *P. duorarum* is the only member of this genus reported in the Tortugas area (Eldred, 1959); we found no larvae of other species of this genus.

Stages of other penaeid larvae also were identified. Genera encountered included *Trachypeneus*, *Sicyonia*, *Parapenaeus*, and *Penaeopsis*, as well as three unidentifiable species. Several species of *Trachypeneus* and *Sicyonia* occur in the Tortugas area (Eldred, 1959), but the specific identity of these larvae was not determined.

One-half of one of the two samples from each station was usually sorted. The second sample was retained for counting if ambiguities in the flowmeter readings or other data should be encountered. Samples were divided into equal parts by means of a two-compartment, rotating Plexiglas cylinder similar to that designed by Folsom (McEwan, Johnson, and Folsom, 1954).

COMPUTER CONVERSION OF DATA

On the basis of the methods of Ahlstrom (1954) and Sette and Ahlstrom (1948), we designed our data analysis to produce estimates of the abundance of *P. duorarum* larvae and to put the information in a form that could be reproduced easily. The plankton analyses were punched on computer data cards and processed at the Institute of Marine Sciences.

The original counts of the number of larvae in each stage were transformed in two ways. In the first, the numbers of each stage were divided by the volume of water filtered through the Gulf V sampler, giving an estimate of the number of larvae per cubic meter of water. In the second calculation the numbers of each stage under 10 m.^{2} surface area were estimated by multiplying 10 times the number per cubic meter by the depth of water (in meters) at the station. Unless otherwise specified, values in this report are based upon the numbers of each stage under 10 m.^{2} surface area. All physical and biological data gathered during this investigation were published by Munro and Dimitriou (1967).

VARIABILITY OF ESTIMATES OF LARVAL ABUNDANCE

Reproducibility of plankton hauls and confidence limits to be applied to plankton estimates based upon counts of one-half of a single sample were computed. For estimating this variability, we counted the protozoeae in 47 pairs of replicate samples. After reference to the records of flowmeter volume and water depth, counts were adjusted to give estimates of numbers of protozoeae present under 10 m.^{2} of surface area (table 1).

Following the methods of Winsor and Clarke (1940) and Silliman (1946), we carried out an analysis of variance to determine the variability of these estimates. Data were subjected to a logarithmic transformation, resulting in a moderately skewed normal distribution. The results of the single-classification analysis of variance are given in table 2.

The mean square between replicate estimates is $0.07319=\sigma E^2$. The standard deviation of a single estimate (σE) is $\sqrt{0.07319}$, or 0.27054 (a logarithmic value). The 95-percent confidence limits are the antilog of the $2\sigma_E$ value, viz, $2\times0.27054=0.54108$, and the antilog is 3.476. Percentage confidence limits for the estimates are $1/3.476\times100$ and 3.476×100, or 28.8 and 347.6 percent.

These confidence limits are wider than those obtained by Silliman (1946) and Strasburg (1960), who found that plankton counts at the 95-percent level should be considered significantly different if they were less than half or more than double the sample compared. In the present study, the "half-or-double" rule applies only at the 70-percent level of confidence.

The confidence limits dealt with here, however, include a greater number of sources of variation and error than those of the above-mentioned authors, because the present data were computed numbers of larvae under 10 m.^{2} surface area; thus,

TABLE 1.—*Replicate tow data for analysis of variance of catches of* Penaeus duorarum *protozoeae, Tortugas Shelf, Florida, August 1962 to October 1964*

Tow number	Station number	Month	Year	*P. duorarum* protozoeae	
				Sample 1	Sample 2
				Number per 10 m.²	
3091-92	40.80	9	1962	461	437
3108-09	40.70	9	1962	1,086	2,102
3110-11	40.70	9	1962	525	823
3112-13	40.70	9	1962	564	766
3116-17	40.70	9	1962	458	708
3124-25	40.80	10	1962	134	180
3209-10	40.60	3	1963	144	290
3211-12	40.70	3	1963	137	130
3213-14	40.80	3	1963	40	9
3233-34	40.80	3	1963	31	30
3306-07	50.70	5	1963	39	39
3348-49	40.70	6	1963	90	124
3381-82	40.60	7	1963	178	195
3383-84	40.70	7	1963	663	370
3385-86	40.80	7	1963	526	382
3387-88	40.90	7	1963	757	962
3389-90	51.00	7	1963	270	192
3391-92	50.90	7	1963	147	167
3395-96	50.70	7	1963	952	742
3401-02	40.60	7	1963	509	200
3405-06	40.80	7	1963	332	362
3419-20	40.70	8	1963	113	11
3421-22	40.70	8	1963	22	99
3425-26	40.70	8	1963	740	267
3427-28	40.70	8	1963	779	299
3393-94	50.80	7	1963	862	647
3432-33	40.60	8	1963	36	94
3434-35	40.70	8	1963	177	48
3446-47	50.70	8	1963	539	200
3452-53	40.60	8	1963	58	215
3466-67	50.70	8	1963	248	143
3520-21	51.00	10	1963	16	140
3638-39	51.00	4	1964	401	459
3640-41	50.90	4	1964	204	340
3642-43	50.80	4	1964	537	707
3652-53	40.70	4	1964	751	433
3694-95	40.80	5	1964	48	163
3811-12	40.80	8	1964	75	81
3813-14	40.80	8	1964	102	264
3815-16	40.80	8	1964	29	121
3817-18	40.80	8	1964	110	377
3819-20	40.80	8	1964	720	503
3823-24	40.80	8	1964	44	85
3831-32	50.80	8	1964	29	80
3835-36	40.70	8	1964	23	109
3847-48	40.80	9	1964	328	214
3821-22	40.80	8	1964	361	268

in addition to the normal sources of variation, such as patchiness of plankton, random variations in catch, and errors in the actual counting and subsampling procedures, the estimates incorporate variation in flowmeter performance and average depth over which the oblique tows were made. More important than these factors, however, is the fact that the analysis is based not upon paired hauls, but upon replicates. Replication was necessary because of the limitations of the winch used during the work. One sample was taken while the vessel traveled in a given direction and the other while the vessel moved over the station in the reverse direction. Such a sampling method must result in greater variability than would be obtained from simultaneous hauls.

Errors involved in integrating estimates over time and space have been discussed by a number of authors; the reader is referred to the works of Taft (1960), Saville (1964), and English (1964).

TABLE 2.—*Summary of analysis of variance of estimates of abundance of protozoeal* Penaeus duorarum *under 10 m.² surface area on the Tortugas Shelf, Florida, August 1962 to October 1964*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F [1]
Between stations	46	20.087	0.43667	5.97
Between replicate estimates	47	3.440	.07319	
Totals	93	23.527		

[1] The large value of F indicates that significantly more of the total variation is due to differences between stations than between replicates ($P < 0.01$).

On four occasions during this investigation, several sampling stations were occupied over 24-hour periods. No consistent differences were observed between night and daytime catches, and variability appeared to be within the margins expected according to the foregoing analysis. The oblique-tow method apparently sampled all layers of the water column and counteracted sampling problems caused by diurnal vertical migrations.

SEASONAL ABUNDANCE OF LARVAE

The equation developed for Pacific sardine by Sette and Ahlstrom (1948) and Ahlstrom (1954) has been applied to the counts of first protozoeae of *P. duorarum* to obtain estimates of larval production in the sampling area during the period covered by this survey.

The equation is $C=\sum(C_iW_it_i)$, in which

C = the total number of first protozoeae produced in the survey area during the period t_i

$C_i = L_i/D$

L_i = estimated number of first protozoeae per 10 m.² of surface area at the ith station

D = the duration of the first protozoeal stage (3 days)

W_i = the area represented by station i

t_i = the time weighting given to station i (equal to one-half the time elapsing since the preceding occupancy plus one-half the time elapsing before the succeeding occupancy)

The basic data for the analysis are given in tables 3 and 4. The area represented by each sampling station is 320 km.² (see Sette and Ahlstrom, 1948, for rationale regarding the area represented by a station) and the time weighting, t_i, is usually about 14 days.

The result of the application of the equation is a minimum estimate of total larval production, because the fraction of larvae surviving the period between spawning and metamorphosis to first protozoeae (about 3.5 days, according to Ewald, 1965) is unknown. Results of the analysis are given in table 5 and illustrated in figure 2.

The only complete year for which data are available is 1963. We estimated that $60{,}500 \times 10^8$ first protozoeae were produced. It is clear from figure 2, however, that 1963 was a poor year; fewer larvae appear to have been produced than in either 1962 or 1964. If equal weighting is allowed for all data, annual production is in the order of $87{,}000 \times 10^8$ first protozoeae.

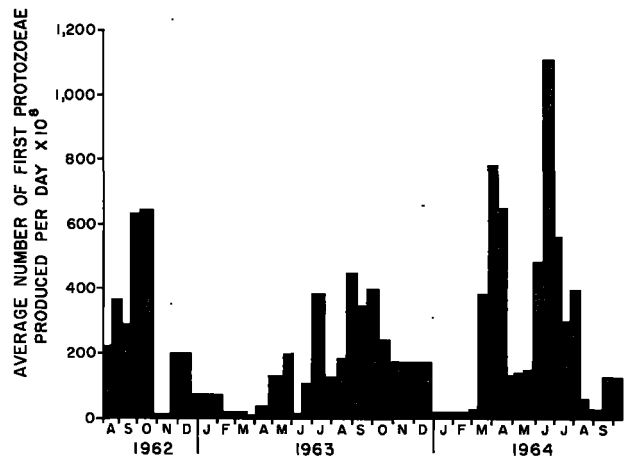

FIGURE 2.—Seasonal fluctuations in production of first protozoeae of *P. duorarum* in the Tortugas Shelf area, August 1962 to October 1964.

SEASONAL VARIATIONS IN SPAWNING INTENSITY

The percentage of the annual catch of protozoeae taken in each month from 1959 to 1964 is shown in figure 3. The data are for samples taken between 18.4 and 36.7 m. (10 and 20 fathoms). Data for 1959 through mid-1962 are taken from Jones et al. (footnote 6) and are for catches made with the Discovery net; the more recent data are derived from the use of the Gulf V sampler. Because of

TABLE 3.—*Summary of Tortugas tows: Cruise totals and physical data. All values are the sum of the computed numbers of* P. duorarum *larvae under 10 m.² surface area at 10 stations on the Tortugas Shelf, August 1962 to October 1964*

Cruise	Date	Subtotal by stage				Total	Percentage by stages				Average number of larvae/tow	Moon age	Average bottom temperature
		Protozoeae	Myses	Postlarvae			Protozoeae	Myses	Postlarvae				
				1-3 spines	4+ spines				1-3 spines	4+ spines			
	1962	*Number*	*Number*	*Number*	*Number*	*Number*	*Percent*	*Percent*	*Percent*	*Percent*	*Number*	*Days*	*° C.*
6201	8/14-16	3,146.1	136.8	129.4	0	3,412.3	92.2	4.1	3.7	0	379.1	16	--------
6202	8/28-30	5,342.3	151.2	106.6	5.3	5,605.4	95.3	2.7	1.9	.1	560.5	29	26.8
6203	9/11-12	6,408.5	612.3	308.8	5.8	7,335.4	87.4	8.3	4.2	.1	733.5	13	26.2
6204	9/25-28	7,448.2	510.7	124.8	3.0	8,086.7	92.1	6.3	1.5	.1	808.7	28	28.7
6205	10/9 -10	8,363.4	434.7	227.9	2.6	9,028.6	92.6	4.8	2.5	.1	902.9	12	28.7
6206	11/7 -8	103.6	3.9	19.5	16.1	143.1	72.4	2.7	13.6	11.3	17.8	11	24.6
6207	12/4 -5	1,923.8	52.0	0	0	1,975.8	97.4	2.6	.3	0	197.6	8	22.8
	1963												
6301	1/9 -10	834.2	36.0	28.4	1.7	900.3	92.7	4.0	3.2	.2	90.0	14	20.2
6303	3/11-12	339.8	3.9	0	0	343.7	98.9	1.1	0	0	34.4	16	20.7
6304	3/26-27	126.6	11.3	6.3	0	144.2	87.8	7.8	4.4	0	14.4	2	21.1
6305	4/8 -10	472.3	0	2.5	0	474.8	99.6	0	.4	0	47.5	16	20.9
6306	5/7 -9	1,692.4	104.9	24.9	0	1,822.2	92.8	5.8	1.4	0	182.2	16	23.2
6307	5/20-23	2,638.6	93.0	60.4	0	2,792.0	94.5	3.3	2.2	0	279.2	29	23.1
6308	6/4 -5	198.7	73.3	91.5	7.7	371.2	53.6	19.7	24.6	.1	41.2	13	22.6
6309	6/18-22	1,905.1	391.3	115.2	0	2,411.6	79.0	16.2	4.8	0	241.2	28	23.8
6310	7/1 -2	5,281.2	304.1	23.6	0	5,608.9	94.2	5.4	4.2	0	560.9	11	24.7
6311	7/30-8/1	2,823.2	935.8	1,188.4	28.0	4,975.4	56.7	18.8	23.9	.6	497.5	12	29.6
6313	8/13-14	2,868.4	221.5	411.7	0	3,501.6	81.9	6.3	11.8	0	350.2	25	29.9
6314	8/27-28	9,825.5	1,219.1	341.8	0	11,386.5	86.3	10.7	3.0	0	1,138.7	9	30.1
6315	9/10-11	5,929.8	927.7	314.3	0	7,171.8	82.7	12.9	4.4	0	717.2	23	30.2
6316	10/1 -2	1,380.9	1,793.6	612.7	0	9,787.2	75.4	18.3	6.3	0	978.7	15	28.9
6317	10/15-16	2,604.9	51.7	16.9	14.7	2,688.2	96.9	1.9	.6	.6	268.8	29	29.0
6318	11/5 -6	3,460.1	85.3	56.8	0	3,602.2	96.0	2.4	1.6	0	360.2	20	24.9
	1964												
6401	2/17-18	131.2	39.6	0	0	170.8	76.8	23.2	0	0	21.4	5	19.1
6402	3/3 -4	349.8	0	0	0	349.8	100.0	0	0	0	35.0	20	19.5
6403	3/17-18	6,389.1	277.1	6.4	0	6,672.6	95.8	4.2	.1	0	667.3	4	20.5
6404	4/1 -2	16,280.3	4,198.0	1,106.5	4.5	21,589.3	75.5	19.5	5.1	.1	2,158.9	19	22.1
6405	4/14-15	8,483.8	272.0	178.9	2.0	8,936.7	95.0	3.1	2.0	.1	893.7	3	23.4
6406	4/28-30	1,599.8	147.6	196.3	0	1,943.7	82.2	7.6	10.2	0	194.4	17	24.7
6407	5/12-14	1,721.2	137.9	79.9	8.5	1,947.5	88.4	7.1	4.1	.4	194.8	2	26.2
6408	5/26-28	2,242.8	324.8	149.0	0	2,716.6	82.6	12.0	5.5	0	273.6	16	26.9
6409	6/9 -11	7,225.6	409.6	89.9	0	7,725.1	93.5	5.3	1.2	0	772.5	1	27.6
6410	6/23-25	21,404.9	1,582.7	762.6	16.3	23,766.5	90.2	6.7	3.2	.1	2,376.7	14	27.1
6411	7/7 -9	9,739.7	444.0	360.9	0	10,544.6	92.4	4.2	3.4	0	1,054.5	28	28.3
6412	7/21-23	4,846.2	711.4	518.6	6.6	6,082.8	79.6	11.7	8.5	.1	608.3	13	28.3
6413	8/4 -5	5,887.0	406.5	304.2	4.8	6,602.7	89.2	6.2	4.6	.1	660.3	24	28.6
6414	8/18-21	1,207.9	146.8	38.6	0	1,393.3	86.7	10.5	2.8	0	139.3	12	25.5
6415	9/1 -2	343.0	7.6	50.3	0	400.9	85.5	1.9	12.5	0	40.0	22	22.9
6416	10/2 -6	1,725.8	38.9	9.3	0	1,774.0	97.3	2.2	.5	0	177.4	28	25.0

TABLE 4.—*Summary of Tortugas tows: Cruise totals by stage. All values are the sum of the computed numbers of each larval stage of* P. duorarum *under 10 m.² surface area at 10 stations on the Tortugas Shelf,[1] August 1962 to October 1964*

Year and cruise number	Stage										
	Protozoeae			Myses			Postlarvae				
	1	2	3	1	2	3	1	2	3	4	5
1962	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
6201	1,669.7	995.6	480.8	43.4	34.6	58.8	46.8	57.1	25.5	0	0
6202	3,201.8	1,384.3	756.2	75.5	19.0	56.7	48.1	36.3	22.2	5.3	0
6203	2,465.1	2,473.6	1,469.8	281.3	166.9	164.1	214.5	59.0	35.3	5.8	0
6204	5,508.0	1,575.7	364.5	288.4	83.4	138.9	50.4	41.5	32.9	3.0	0
6205	5,560.3	1,922.4	880.7	300.4	66.3	68.0	93.3	92.4	42.2	2.6	0
6206	64.0	39.6	0	0	0	3.9	16.2	0	7.0	16.1	0
6207	1,741.9	154.7	27.2	33.1	18.9	0	0	0	0	0	0
1963											
6301	628.3	132.3	73.6	15.6	12.6	7.8	20.2	4.1	4.1	1.7	0
6303	171.2	101.7	66.9	3.9	0	0	0	0	0	0	0
6304	63.7	37.2	25.7	11.3	0	0	2.1	2.1	2.1	0	0
6305	322.4	136.3	13.6	0	0	0	0	0	2.5	0	0
6306	1,119.1	418.0	155.3	41.7	0	63.2	24.9	0	0	0	0
6307	1,757.5	635.5	245.6	50.7	12.7	29.6	26.5	21.0	12.9	0	0
6308	93.3	46.0	59.4	23.5	6.6	43.2	21.2	52.3	18.0	5.1	2.6
6309	902.3	660.7	342.1	188.9	20.5	181.9	103.7	11.5	0	0	0
6310	3,346.6	1,501.9	432.7	210.4	46.4	47.3	11.8	6.8	5.0	0	0
6311	1,105.2	1,202.0	516.0	254.3	211.9	469.6	879.7	218.4	90.3	28.0	0
6313	1,633.3	614.4	620.7	138.8	24.1	58.6	44.5	267.3	99.9	0	0
6314	3,943.0	3,154.1	2,728.4	602.8	309.2	307.2	126.3	206.5	9.0	0	0
6315	2,976.5	1,682.8	1,270.5	631.6	120.8	175.3	208.1	82.6	23.6	0	0
6316	3,463.5	2,442.2	1,475.2	716.0	372.4	705.2	399.6	185.7	27.4	0	0
6317	2,126.2	244.0	234.7	40.4	11.3	0	5.7	5.6	5.6	14.7	0
6318	1,737.2	1,444.2	278.7	65.0	6.4	13.9	28.0	28.8	0	0	0
1964											
6401	126.9	4.3	0	12.8	6.6	20.2	0	0	0	0	0
6402	202.9	88.0	58.9	0	0	0	0	0	0	0	0
6403	3,348.6	2,190.4	850.1	185.2	53.4	38.5	6.4	0	0	0	0
6404	6,831.7	5,368.3	4,080.3	2,051.1	921.9	1,225.0	663.2	400.2	43.1	4.5	0
6405	5,662.2	2,146.4	675.2	90.4	66.3	115.3	55.3	96.7	26.9	2.0	0
6406	1,087.9	406.0	105.9	37.3	20.7	89.6	80.1	116.2	0	0	0
6407	1,219.6	361.0	140.6	69.8	38.3	29.8	11.3	32.6	36.0	8.5	0
6408	1,291.2	734.9	216.7	180.3	20.4	124.1	97.5	44.7	6.8	0	0
6409	4,210.7	1,882.9	1,132.0	228.4	103.1	78.1	38.7	51.2	0	0	0
6410	9,665.8	8,077.4	3,661.7	749.0	333.3	500.4	478.0	233.2	51.4	16.3	0
6411	4,885.3	3,195.6	1,658.8	232.2	105.4	106.4	222.1	95.4	43.4	0	0
6412	2,550.6	1,422.2	873.4	322.1	121.8	267.5	244.2	225.5	48.9	6.6	0
6413	3,447.4	1,801.0	638.6	138.8	126.2	141.5	197.0	75.4	31.8	4.8	0
6414	498.9	479.9	229.1	58.2	64.5	24.1	33.6	5.0	0	0	0
6415	206.4	72.7	63.9	3.8	3.8	0	0	50.3	0	0	0
6416	1,109.2	371.0	245.7	14.7	24.2	0	9.3	0	0	0	0

[1] The totals for cruises 6201, 6206, 6308, and 6401 are the sums of 9, 8, 9, and 8 stations, respectively.

the different sampling characteristics of the two nets, data for the first and second halves of 1962 cannot strictly be compared. The average catch of the Gulf V net per unit volume of water strained during the spawning seasons of 1963 and 1964 was about 10 times greater than the catch of the Discovery net during the spawning seasons of 1959–61. In the construction of the histograms for 1962, the numbers per 1,000 m.³ filtered by the Discovery net have been equated with the numbers per 100 m.³ filtered by the Gulf V net.

Spawning occurred throughout the annual temperature range of 19° C. to 30° C., but most spawning occurred when temperatures exceeded 25° C. and peaks were usually associated with the highest temperatures reached in each year. Highest temperatures were recorded as early as June and as late as the end of September, resulting in corresponding shifts from year to year in the main time of spawning.

SEASONAL RELATION BETWEEN DEPTH AND SPAWNING

In general, a seasonal shift was observed in the depth at which most spawning (as measured by the presence of first protozoea) occurred. The center of abundance of first protozoea was usually at the shallowest stations in early spring and then moved toward deeper water as the season progressed until in the fall it was at depths greater than 30 m. (16.7 fathoms). In 1962 the center of abundance of first protozoea moved from about 25 m. (13.8 fathoms) in August and September to about 32 m. (17.7 fathoms) by early November (fig. 4). In 1963 a steady movement of the center of spawning was again apparent from the shallow waters (20 to 25 m. or 11.1 to 13.8 fathoms) in early spring to a depth of 36 m. (20 fathoms) in early November. This movement was not as apparent in 1964, possibly because maximum spawning occurred earlier in the year.

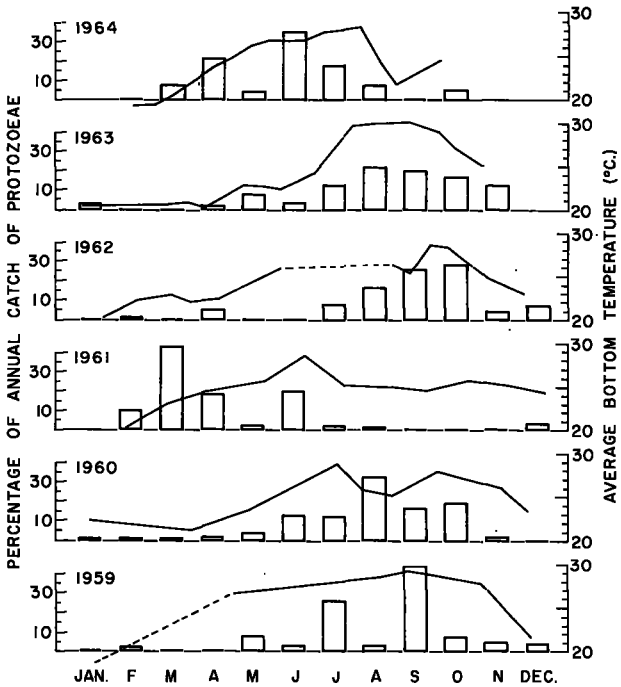

FIGURE 3.—Histograms showing the relation between the percentage of the annual catch of first protozoeae taken in each month, and (solid lines) the average bottom water temperature from the Tortugas Shelf area, 1959–64. Broken lines indicate no data.

An analysis of the distribution of bottom temperatures suggests that temperature plays no significant part in the movement of the center of spawning. During 1963, when the movement into deeper water was most marked, bottom temperatures appeared to be almost uniform at any given time throughout the sampling area. Shrimp landing data for 1963 (U.S. Fish and Wildlife Service, 1964) showed that small shrimp appeared in the shallow areas of the trawling grounds about April and again in October. Previous studies of adult shrimp (Iversen and Jones, 1961; Iversen, Jones, and Idyll, 1960; and Iversen and Idyll, 1959) have shown that the average size of shrimp increases with increasing depth. Shrimp tagging studies also have indicated a migration toward deeper water. Apparently the maturing shrimp entering the fishery in the early part of the summer begin spawning when they reach a suitable size and continue to spawn as they migrate to deeper water. This theory is compatible with data on maturation and growth provided by Eldred, Ingle, Woodburn, Hutton, and Jones (1961) and by Iversen (1962).

TABLE 5.—*Estimates of the production of first protozoeae of* P. duorarum *on the Tortugas Shelf, August 1962 to October 1964*

Cruise	Date	Length of intercruise period	First protozoeae produced during intercruise period	Average number of first protozoeae produced per day
	1962	*Days*	*Calculated number* $\times 10^3$	
6201	Aug. 14–16	14.0	2,993.0	213.8
6202	Aug. 28–30	13.8	5,091.9	369.0
6203	Sept. 11–12	14.3	4,062.2	284.1
6204	Sept. 25–28	14.0	8,886.2	634.7
6205	Oct. 9–10	21.0	13,455.5	640.7
6206	Nov. 7–8	28.0	258.5	9.2
6207	Dec. 4–5	32.0	6,423.0	200.7
	1963			
6301	Jan. 9–10	48.5	3,511.0	72.4
6303	Mar. 11–12	38.0	750.1	19.7
6304	Mar. 26–27	14.3	104.8	7.3
6305	Apr. 8–10	21.3	791.6	37.2
6306	May 7–9	21.3	2,746.6	129.0
6307	May 20–23	13.8	2,794.7	202.5
6308	June 4–5	14.8	177.0	12.0
6309	June 18–22	13.5	1,403.9	104.0
6310	July 1–2	20.8	8,021.3	385.6
6311	July 30–Aug. 1	21.5	2,738.2	127.4
6313	Aug. 13–14	13.5	2,540.8	188.2
6314	Aug. 27–28	13.5	6,134.0	454.4
6315	Sept. 9–10	17.5	6,002.7	343.0
6316	Oct. 1–2	18.0	7,184.2	399.1
6317	Oct. 15–16	17.5	4,287.6	245.0
6318	Nov. 5–6	64.5	11,352.1	176.0
	1964			
6401	Feb. 17–18	59.0	1,079.0	18.3
6402	Mar. 3–4	14.0	327.2	23.4
6403	Mar. 17–18	14.5	5,595.3	385.9
6404	Apr. 1–2	14.0	11,021.5	787.3
6405	Apr. 14–15	13.8	9,004.4	652.5
6406	Apr. 28–30	14.3	1,792.6	125.4
6407	May 12–14	14.0	1,967.4	140.5
6408	May 26–28	14.0	2,083.1	148.8
6409	June 9–11	14.0	6,793.4	485.2
6410	June 23–25	14.0	15,593.8	1,113.8
6411	July 7–9	14.0	7,881.4	563.0
6412	July 21–23	13.8	4,056.2	293.9
6413	Aug. 4–5	14.3	5,680.8	397.3
6414	Aug. 18–21	14.0	804.9	57.5
6415	Sept. 1–2	22.3	530.4	23.8
6416	Oct. 2–4	30.0	3,834.3	127.8

INTRAMONTHLY VARIATIONS IN SPAWNING—THE EFFECT OF MOON PHASE

The percentage of various larval stages in the total catch varied considerably on successive cruises. We analyzed these variations to determine whether they could in some way be related to the lunar phases.

The percentage which first protozoeae represented in the total catch of larvae and postlarvae taken on each cruise was calculated and plotted against moon age minus 5 days (table 6). The average age of first protozoeae is 5 days (Ewald, 1965), and subtracting 5 days backdates the observation of the relative abundance of protozoeae to the time of spawning. The average of the percentages of protozoeae in all catches was 50.6 percent; in 12 of 18 catches taken during the waxing moon (0–14.7 days) the relative abundance of first protozoeae was below average (fig. 5), whereas in 11 of 17 catches during the waning moon the relative abundance was above average.

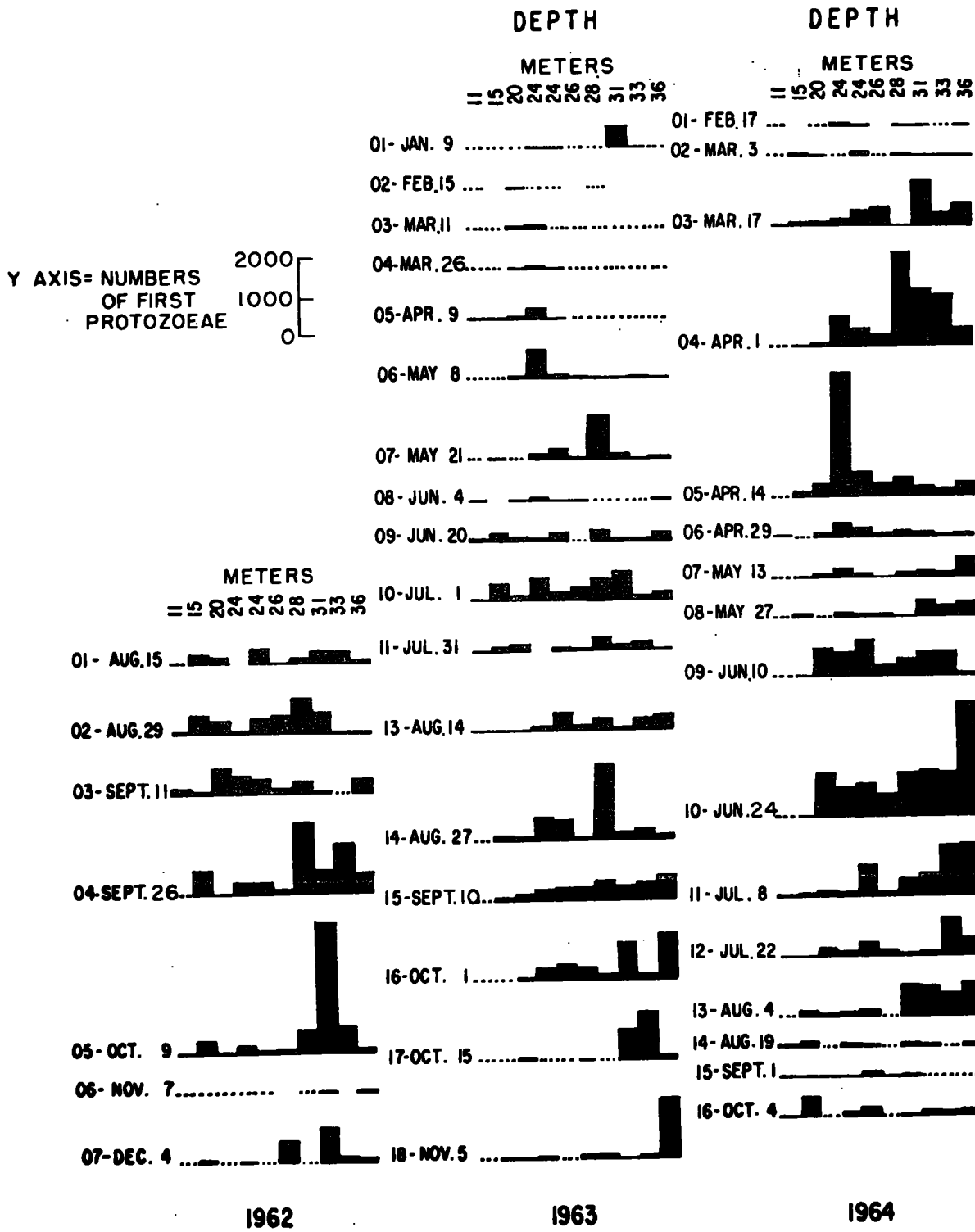

FIGURE 4.—Histograms showing the seasonal movement of the center of abundance of first protozoeae of *P. duorarum* from shallow-water stations toward deepwater stations, Tortugas Shelf, Fla., August 1962 to October 1964. Numbers preceding dates indicate cruise numbers.

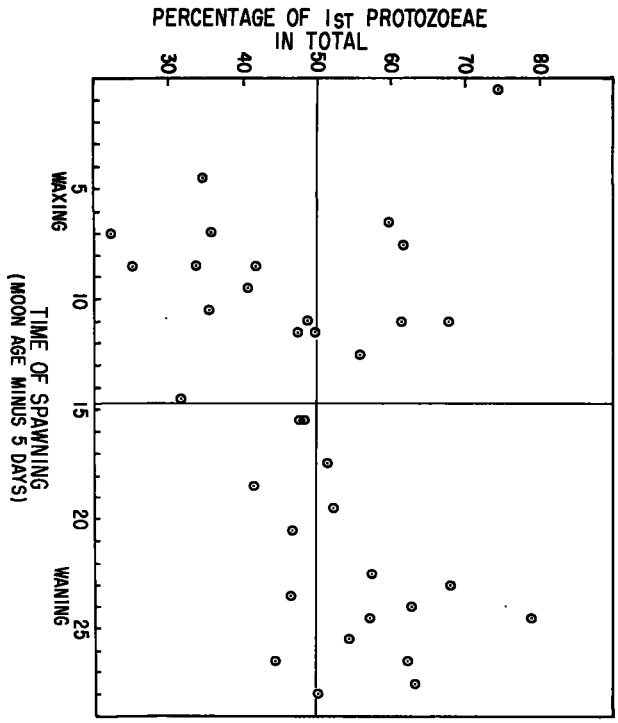

FIGURE 5.—The relation between moon phase and relative spawning intensity (as measured by the relative abundance of first protozoeae) in the Tortugas Shelf area, August 1962 to October 1964.

Using a chi-square test, we found that the probability of such a distribution arising by chance is slight (<0.02); we conclude, therefore, that spawning occurs mainly during the last half of the lunar month. That most spawning occurs in the last half of the lunar month agrees with the observations of Korringa (1957), who stated that in animals showing lunar periodicity in spawning, the spawning is often concentrated around the last lunar quarter. He suggested that this concentration is a result of a photoperiodic effect, the final stages of maturation of the gonads being triggered by the greater exposure to light during the full-moon period. This photoperiodic effect on maturation may also hold for *Penaeus*, but the advantages of lunar periodicity are obscure because copulation occurs in advance of spawning (Hudinaga, 1942, for *P. japonicus*), and all eggs are fertilized at extrusion. Alternating periods of high and low larval density may be advantageous in that they prevent a concentrating of major predators, thus reducing mortality caused by prolonged predation.

TABLE 6.—*Data for the analysis of the effect of moon phase on rate of spawning of* P. duorarum; *all data are in terms of estimated numbers of larvae under 10 m.² surface area at 10 stations on the Tortugas Shelf, August 1962 to October 1964.*

Year and cruise number	Date	First protozoeae	Total larvae	Percentage of first protozoeae in total catch	Time of spawning (moon age minus 5 days)
1962		*Number*	*Number*	*Percent*	*Days*
6201	Aug. 14-16	1,669.7	3,412.3	48.9	10-12
6202	Aug. 28-30	3,201.8	4,605.4	57.1	24-25
6203	Sept. 11-12	2,465.1	7,335.4	33.6	8-9
6204	Sept. 25-28	5,508.0	8,086.7	68.1	22-24
6205	Oct. 9-10	5,560.3	9,028.6	61.6	7-8
1963					
6303	Mar. 11-12	171.2	343.7	49.8	11-12
6304	Mar. 26-27	63.7	144.2	44.2	26-27
6305	Apr. 8-10	322.4	474.8	67.9	10-12
6306	May 5-7	1,119.1	1,822.2	61.4	10-12
6307	May 20-23	1,757.5	2,792.0	62.9	23-25
6308	June 4-5	93.3	371.2	25.1	8-9
6309	June 18-22	1,145.1	2,411.6	57.5	22-23
6310	July 1-2	3,346.6	5,608.9	59.7	6-7
6311	July 30-Aug. 1	1,105.2	4,975.4	22.2	6-8
6313	Aug. 13-14	1,633.3	3,501.6	46.6	20-21
6314	Aug. 27-28	3,943.0	11,386.5	34.6	4-5
6315	Sept. 10-11	2,976.5	7,171.8	41.5	18-19
6316	Oct. 1-2	3,463.5	9,787.2	35.4	10-11
6317	Oct. 15-16	2,126.2	2,688.2	79.1	24-25
6318	Nov. 5-6	1,737.2	3,602.2	48.2	15-16
1964					
6401	Feb. 17-18	126.9	170.8	74.2	0-1
6402	Mar. 3-4	202.9	349.8	58.0	15-16
6403	Mar. 17-18	3,348.6	6,672.6	50.2	27-29
6404	Apr. 1-2	6,831.7	21,589.3	31.6	14-15
6405	Apr. 14-15	5,662.2	8,936.7	63.3	27-28
6406	Apr. 28-30	1,087.9	1,943.7	55.9	12-13
6407	May 12-14	1,219.6	1,947.5	62.2	26-27
6408	May 26-28	1,291.2	2,716.6	47.5	11-12
6409	June 9-11	4,210.7	7,725.1	54.5	25-26
6410	June 23-25	9,665.8	23,766.5	40.7	9-10
6411	July 7-9	4,885.2	10,544.6	46.3	23-24
6412	July 21-23	2,550.6	6,082.8	41.9	8-9
6413	Aug. 4-5	3,447.4	6,602.7	52.2	19-20
6414	Aug. 18-21	498.9	1,393.3	35.8	5-9
6415	Sept. 1-2	206.4	400.9	51.5	17-18

MORTALITY AND MIGRATION

The two factors of larval mortality and migration toward the inshore nursery grounds are inseparable and will be dealt with concurrently. Sampling stations which lie on the migration route will always receive immigrant larvae, and, as a result, survival rates calculated from the catch of larvae at such stations will be higher than the true value; conversely, calculations of survival based upon the catch taken at stations from which larvae consistently emigrate will underestimate the true survival rates.

Totals are given in table 7 of the estimates of numbers of each larval stage under 10 m.² surface area for 37 cruises in the sampling area from August 1962 to July 1964. These estimates provide a measure of the relative abundance of each larval stage for 2 calendar years.

Calculation of survival rates on a temporal basis requires knowledge of the duration of the various larval stages. The following figures for the

average time spent in each larval stage have been derived from the information given by Ewald (1965) on the rate of development of larvae at 26° C.:

Stage	Days
Egg	1.5
Nauplius	2.0
1st protozoea	3.0
2d protozoea	2.4
3d protozoea	2.2
1st mysis	2.0
2d mysis	2.3
3d mysis	3.0
1-spine postlarva	2.0
2-spine postlarva	2.0
3-spine postlarva	3.0
4-spine postlarva	3.0
5-spine postlarva	6.0

Growth and development of larvae in the laboratory may differ considerably from that in the ocean; however, the relative duration of the instars may be expected to be nearly constant, and in the absence of better data the times given above have been used to plot catch curves for the larvae.

Catch curves, obtained by plotting the logarithm of the total "catch" of each stage against the estimated average age of the larval stage, are shown in figure 6. A feature common to all of the curves is that the catch of first and second myses appears to have been depressed. At all stations, the catch of second myses was less than the catch of third myses. Several possible explanations for this depression of the catch curve present themselves.

First, it is possible that the larvae are most active in the first and second mysis stages, and that the depressed catch of these stages reflects active avoidance of the Gulf V net. Heldt (1938) has stated that the myses appear to be the most active larval stages.

Secondly, third myses and older postlarvae spawned in another area (possibly to the north of the Tortugas) may drift into the Tortugas area, thus increasing the catch of the stages older than second mysis. Jones et al. (footnote 6), however, reported no evidence of any other center of spawning.

Finally, an error in the estimated time required for the shrimp to develop through the mysis stages may account for this discrepancy. Since mysis stages are rather ill-defined, allocation to first, second, or third mysis may be somewhat arbitrary, depending upon the degree of development of the pleopods and telson. More than three stages may exist at temperatures lower than 26° C. (Ewald, 1965). If average duration of mysis stages is less than the postulated 7.3 days, then the daily survival rate must decrease considerably after the third protozoeal stage and then increase again during the postlarval stages.

The first alternative—avoidance of the net—suggested above is considered to be most likely. An inspection of the catch curves shows that the slope of the curves during the protozoeal stages and during the stages subsequent to third mysis is fairly uniform; in a number of catch curves, the points describing the abundance of the third protozoeal stage and of the third mysis stage can be joined to produce an almost uniform slope throughout the catch curve (fig. 6). This view is also supported by the work of Jones et al. (footnote 6), who found that the numbers of larvae decline steadily between the third protozoeal stage and the third mysis stage. Jones et al. (footnote 6) used a Discovery net of 76-cm. mouth diameter and with larger mesh sizes than those of the Gulf V sampler. Such a net may capture a more representative proportion of the highly motile stages than the faster moving but smaller Gulf V sampler (Barkley, 1964).

The slopes of the catch curves shown in figure 6 appear to vary. For comparing these apparent variations in survival, we have calculated the gross survival between selected stages for each of the 10 stations. Distributions of gross survival values between first and third protozoeae, third protozoeae and third myses, and third myses and two-spine postlarvae are plotted in figure 7a, b, and c. Choice of these stages for the calculations was dictated by the anomalies that appeared

TABLE 7.—*Totals of the estimates of numbers of each larval stage of* P. duorarum *under 10 m.² surface area for 37 cruises in the Tortugas Shelf area, August 1962 to July 1964*

Station	Depth	Protozoeae			Myses			Postlarvae		
		1	2	3	1	2	3	1	2	3
	M.	*Number*								
50.100	36.5	*12,618*	5,420	2,307	591	241	452	*355*	43	17
50.90	33.0	*11,350*	*5,704*	*3,221*	*1,037*	283	*536*	209	150	0
50.80	31.0	*16,040*	*7,497*	*3,151*	*1,039*	*389*	*520*	*355*	146	6
40.90	27.5	*14,008*	*6,458*	*2,910*	*1,054*	272	451	182	195	17
50.70	25.5	5,020	2,841	2,145	972	*434*	477	*456*	*364*	*180*
40.80	24.0	8,572	*6,841*	*5,087*	*1,194*	*604*	*935*	*546*	*541*	37
40.70	24.0	*10,579*	*7,282*	*4,108*	949	*442*	*786*	*564*	*428*	*123*
40.60	20.0	5,112	4,824	1,848	*1,440*	*606*	*785*	*1,263*	*367*	*117*
32.70	14.5	3,324	1,474	783	345	127	150	159	193	*108*
30.58	11.0	279	472	438	215	60	152	204	*244*	*241*

NOTE. The five highest values in each column are in italic.

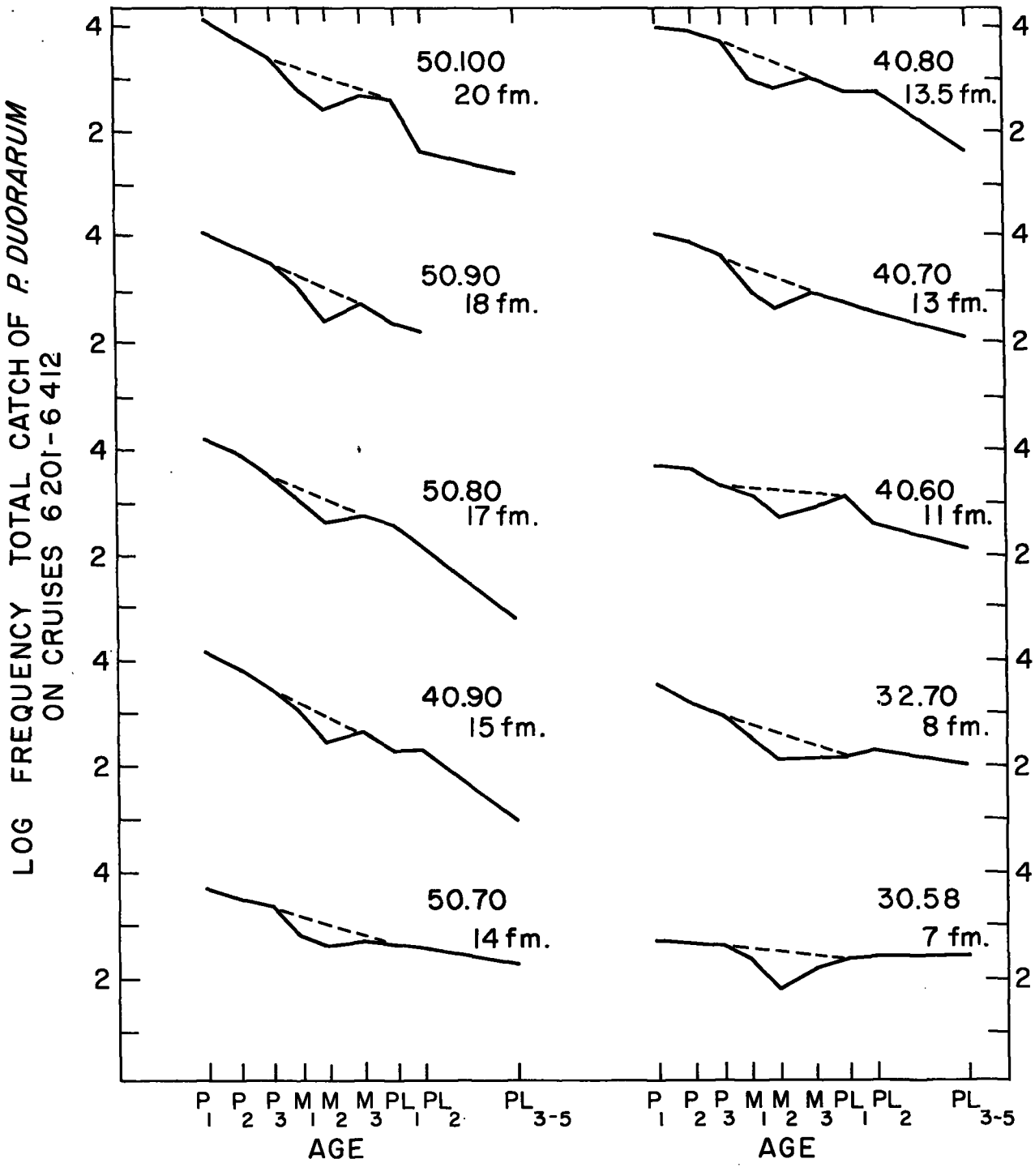

FIGURE 6.—Catch curves for larvae and postlarvae of *P. duorarum* based on the total catch at 10 stations on the Tortugas Shelf, August 1962 to October 1964. P_1, P_2, P_3= 1st, 2d, and 3d protozoeal stages; M_1, M_2, M_3= 1st, 2d, and 3d mysis stages; Pl_1, Pl_2, Pl_{3+5}=1-, 2-, and 3- to 5-spine postlarval stages. Stages are distributed along abscissa relative to the mean age of each larval stage.

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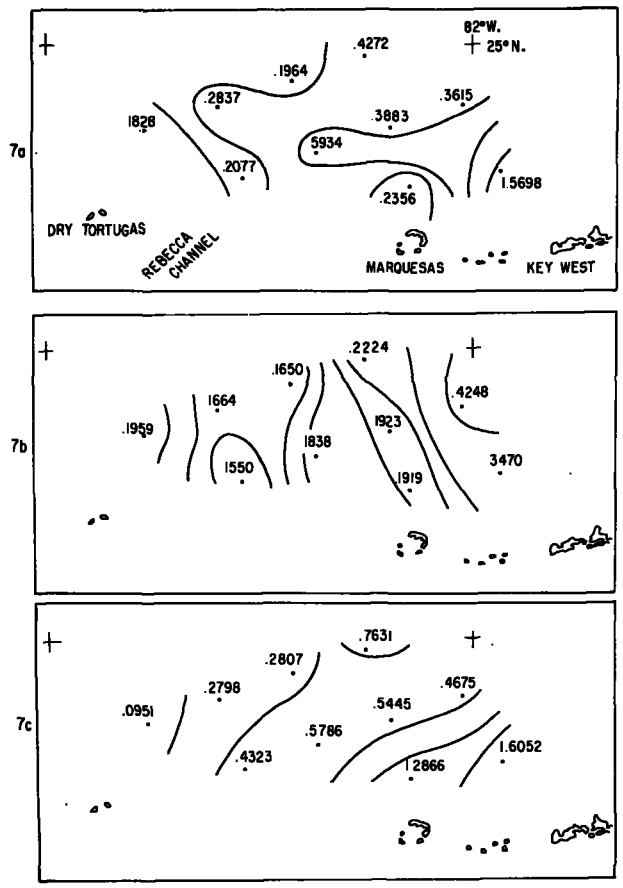

FIGURE 7a, b, and c.—Variations in apparent gross survival of larval and postlarval *P. duorarum* at 10 sampling stations on the Tortugas Shelf, August 1962 to October 1964: (a) 1st protozoeal to 3d protozoeal stage, (b) 3d protozoeal to 3d mysis stage, and (c) 3d mysis to 2-spine postlarval stages.

in the catch curves and which have been discussed above. Lowest apparent survival was consistently in the deepwater stations in the northwestern sector of the sampling area, and greatest apparent survival (in some cases exceeding 100 percent) was in the southeastern sector. It appears highly unlikely that the calculated values are real values and that survival of larvae is greater in the southeastern sector. These consistent differences are probably a result of the migration of larvae away from the center of spawning. Stations 40.90 and 50.80 are believed to represent the centers of spawning, and the larvae disperse from this center.

Calculated daily survival rates between successive larval stages at each of the 10 stations are given in table 8. Total survival between first protozoeal and one-spined postlarval stages also is given (right-hand column); the highest rate of survival between these stages is usually at the shallowest, more easterly stations (fig. 8).

Because the dispersal of larvae from the center of spawning appears to affect the survival estimates pertaining to specific stations, it is difficult to estimate the true survival rate. Calculations of survival rate based upon the total catch of successive stages in relation to the total catch of first protozoeae will have validity, however, provided it can be assumed that the main route of dispersal is over the area covered by the sampling stations (table 9).

If estimates of survival rates between first protozoea and first and second mysis are discarded, all remaining estimates are nearly constant and range from 78.6 to 82.0 percent (mean, 80.4 percent) per day.

Postlarvae enter the Everglades nursery grounds in the six-spine stage (Tabb, Dubrow, and Jones, 1962). On the basis of age data provided by Ewald (1965), these larvae are about 35 days old. At a survival rate of 80.4 percent per day, the fraction of the original population which survives to enter the nursery grounds can be estimated at 0.804^{35}, or 0.05 percent. The fraction of the original population of first protozoeae (average age 5 days)

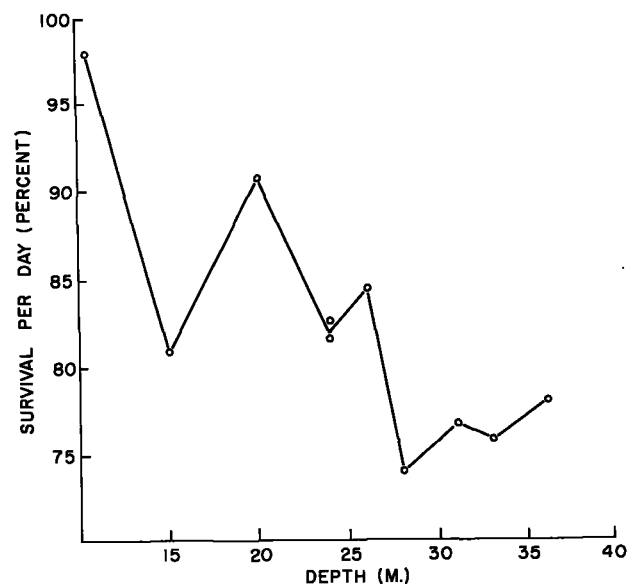

FIGURE 8.—The relation at 10 sampling stations on the Tortugas Shelf, August 1962 to October 1964, between depth and apparent survival rates of *P. duorarum* between 1st protozoeal and 1-spine postlarval stages.

TABLE 8.—*Calculated daily survival rates between successive larval and postlarval stages of* P. duorarum *at 10 sampling stations on the Tortugas Shelf*

Station	Depth	Stages[1]							
		P_1-P_2	P_2-P_3	P_3-M_1	M_1-M_2	M_2-M_3	M_3-Pl_1	Pl_1-Pl_2	Pl_2-Pl_{3+5}	P_1-Pl_1
	M.	*Fractional survival per day*								
50.100	36	.7311	.6898	.5228	.6585	1.2690	.9080	.3450	.8752	.7803
50.90	33	.7732	.7800	.5229	.5282	1.3090	.6858	.8468	----------	.7578
50.80	31	.7546	.6960	.5895	.6328	1.1160	.8582	.6409	.6384	.7678
40.90	28	.7496	.7081	.6166	.5330	1.2090	.6963	1.0350	.6884	.7396
50.70	26	.8098	.8849	.5508	.8513	1.0360	.9640	.9139	.9040	.8439
40.80	24	.9198	.8790	.5214	.7382	1.1800	.8067	.9965	.6814	.8269
40.70	24	.8708	.7796	.4977	.7008	1.2430	.8756	.8710	.8370	.8158
40.60	20	.9786	.6589	.8880	.6159	1.1790	1.2090	.5392	.8487	.9072
32.70	15	.7399	.7697	.6769	.6284	1.0650	1.0230	1.1000	.9137	.8098
30.58	11	1.2150	.9683	.7132	.5501	1.4230	1.1250	1.0950	.9979	.9786

[1] P_1, P_2, P_3=1st, 2d, and 3d protozoeal stages; M_1, M_2, M_3=1st, 2d, and 3d mysis stages; and Pl_1, Pl_2, Pl_{3+5}=1-, 2-, 3- to 5-spine postlarval stages.

TABLE 9.—*Estimated daily survival rates of larval* P. duorarum *over successively longer intervals on the Tortugas Shelf, August 1962 to October 1964*

Stages[1]	Duration between stages	Calculated daily survival rate
	Days	*Percent*
P_1-P_2	2.70	0.8074
P_1-P_3	5.00	.7856
P_1-M_1	7.10	[2].7247
P_1-M_2	9.25	[2].7031
P_1-M_3	11.90	.7898
P_1-Pl_1	14.40	.8112
P_1-Pl_2	16.40	.8087
P_1-Pl_{3+5}	23.40	.8202

[1] P_1, P_2, P_3=1st, 2d, and 3d protozoeal stages; M_1, M_2, and M_3=1st, 2d, and 3d mysis stages; and Pl_1, Pl_2, Pl_{3+5}=1-, 2-, and 3- to 5-spine postlarval stages.
[2] Estimates affected by sampling error.

would be 0.804^{30}, or 0.14 percent. In 1963, about $60{,}500\times10^8$ first protozoeae were produced within the sampling area; at the postulated rate of survival, about 85×10^8 six-spine postlarvae would enter the nursery grounds. The total commercial catch of *P. duorarum* adults in the Tortugas area during 1963 was about 500 million individuals (U.S. Fish and Wildlife Service, 1964), implying that about 6 percent of the postlarvae may survive to be captured when they move to the trawling grounds as juveniles and adults.

Owing to the lunar periodicity of spawning, the proportions of larval stages in the catch change constantly, and we cannot estimate the survival rate operating at a given time nor obtain any information on the effect of temperature on survival.

DIRECTION OF MIGRATION

The data on survival rate shown in figures 7 and 9 indicate that the migration pattern of the larvae radiates away from the centers of spawning and that the apparent drift is mainly in an easterly direction. Jones et al. (footnote 6) showed that few larvae are present north and west of our area of study. Koczy, Rinkel, and Niskin (1960) investigated the current system of the region and concluded that, although the water masses are subjected to a tidal movement of 9 to 11 km. per day, the resultant movement over a full tidal cycle is slight. Also, the small resultant drift is in a westerly direction and not in the required easterly direction. Additional evidence regarding the current system has been obtained recently through the release and recovery of seabed drifters. A vector analysis of the seabed drifter returns has indicated the presence of a slow southwest drift over the shrimp grounds. The detailed results have been reported by Rehrer, Jones, and Roessler (1967). The conclusions drawn from these results are that direct dispersal to the east seems improbable and that postlarvae reaching the nursery grounds of the Everglades are carried there by currents via some indirect route.

The most likely alternative means of larval transportation is by the Gulf Stream, passing through the Florida Straits. Biologists on cruises to the Tortugas region have on many occasions reported a strong southerly current flowing through Rebecca Channel and entering the Florida Straits. Current speed was measured on one occasion at 2.6 km. per hour (1.4 knots). Because Rebecca Channel is directly southwest of the centers of spawning (stations 40.90 and 50.80), considerable numbers of larvae must be swept through the channel and into the Florida Straits.

A survey cruise in October 1964 covered an area of some 10,789 km.^{2} between Cape Sable on the Florida mainland and the Tortugas shrimp fishing grounds (fig. 10). Additional stations were in the Florida Straits south of the Florida Keys.

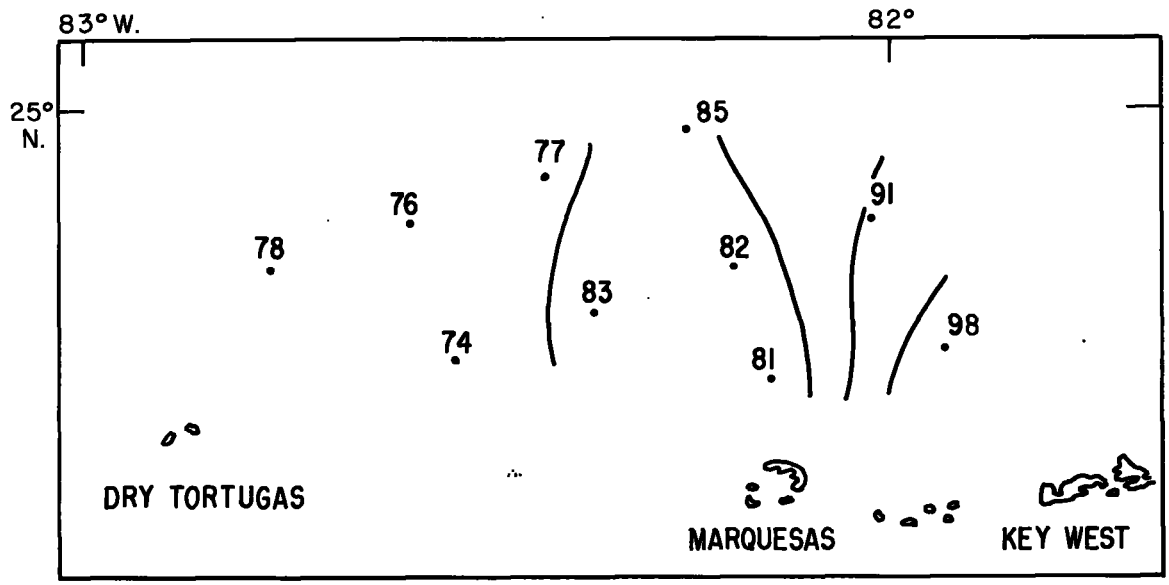

FIGURE 9.—Variations in the apparent daily survival rate between 1st protozoeal and 1-spine postlarval stages of *P. duorarum* on the Tortugas Shelf, August 1962 to October 1964.

The most striking feature of figure 10 was the capture of large numbers of *P. duorarum* larvae, mainly protozoeae, in the Florida Straits. These larvae were taken in the surface and midwaters of the Straits in water between 50 and 180 m. (28 and 98 fathoms) deep and at all the stations occupied. In contrast, few larvae or postlarvae were taken north of the Florida Keys.

We can, therefore, postulate that larvae are dispersed by transport out of Rebecca Channel and into the Florida Straits. The larvae would be carried eastward by the Florida Current and eddied back into the Florida Bay region by tidal currents moving through the inlets between the Florida Keys. If this transport does occur, the larvae would arrive at a point only about 37 to 56 km. from the Everglades nursery grounds, about 6 days after their exit from Rebecca Channel (calculated according to the velocity of the margins of the Florida Current given by Sverdrup, Johnson, and Fleming, 1942). The main part of the journey from the spawning grounds to the Everglades might take only a short time, leaving the bulk of the larval and postlarval life for the journey across Florida Bay, a distance of 37 to 56 km.

We have learned that postlarvae appear to react to tidal currents and ascend into the moving tide mainly during the nighttime flood tide. If this is so, movement across Florida Bay, where the tides flow roughly north and south, might be accomplished within a week. If this migration takes place, the estimates of survival given in the preceding section must be reconsidered. We have shown that the apparent survival rate increases steadily toward the eastern sector of the sampling grounds (fig. 9). If larvae are removed from Tortugas grounds via Rebecca Channel, then their greatest loss through the channel would occur at stations nearest to the channel (viz, the western stations), and the apparently low rates of survival in this area are caused by loss of older larvae and not by movement of larvae in an easterly direction. This loss might explain the anomalous catches at station 32.70 (directly north of the Marquesas) which yield estimates of survival that are not of the same order as those calculated for station 30.58 (fig. 7a), although the stations are only 18.5 km. apart and of similar depths (14.5 and 11 m. or 8 and 6.1 fathoms, respectively). If larvae have traveled from the spawning grounds via the Florida Current, and then have been eddied back into the vicinity of station 30.58 via tidal currents in the Northwest Channel, the high proportion of older larvae and postlarvae at this station could be explained. The position of station 32.70, directly north of the Marquesas and away from any tidal channels, would preclude it from receiving older larvae.

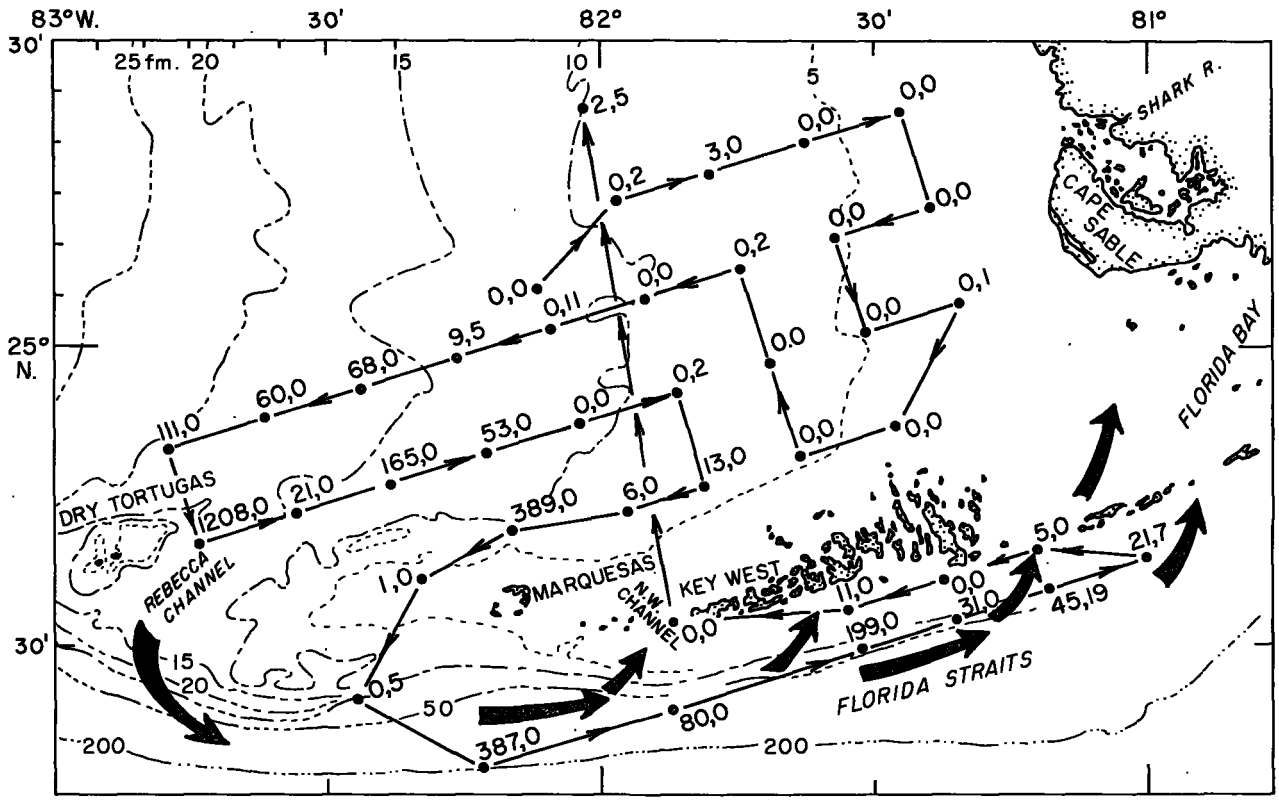

FIGURE 10.—Map of the Tortugas Shelf area showing track of Cruise 6416 (October 2 to 6, 1964) and the estimated abundance of *P. duorarum* larvae (first number) and postlarvae (second number) under 10 m.² surface area at each of the stations occupied. Probable migration route of larvae is indicated by wide dark arrows.

We, therefore, conclude that if the variations in survival at specific stations are a result of emigration in a southerly direction at the western stations and not the result of eastern stations receiving immigrants from the west, then the average rates of survival calculated from all catches may err in being slightly too low. They might be best represented by the survival at stations 40.70, 40.80, and 50.70, which are centrally located and farthest removed from the influence of Rebecca Channel and the Northwest Channel (fig. 8). Survival at these stations averages about 83 percent per day.

SUMMARY

1. The 95-percent confidence limits applicable to estimates of abundance of *P. duorarum* protozoeae are such that a single estimate cannot be considered significantly different unless it is less than 29 percent or greater than 348 percent of the sample with which it is compared. This variability is greater than that normally encountered in studies of this type, but part of the variability may be ascribed to the fact that the analysis was based upon replicate tows and not upon paired tows.

2. Gross annual production of first protozoeae of *P. duorarum* within the sampling area was in the order of 870×10^{10} individuals.

3. Spawning in each year usually reached a peak during the month of the highest bottom-water temperatures. The month in which the bottom water was warmest varied from year to year, and the months of maximum spawning activity varied accordingly.

4. The center of spawning tended to move toward deeper water as the season progressed, and the last heavy spawning was in depths of more than 30 m. (16.7 fathoms). This movement may be correlated with temperature decreases in shallow water, but the movement of adult shrimp into deeper water is the factor which is most directly responsible.

5. Intramonthly variations in abundance of larvae are related to moon phase. Most spawning occurred during the waning moon (15–29 days after new moon).

6. Survival rates are nearly constant throughout the postnauplial larval life, averaging about 80.4 percent per day. Differences in the apparent rate of survival at different sampling stations are caused by immigration and emigration of larvae between stations, by losses of larvae from stations in the path of currents which move into the Florida Straits, or by a combination of both.

7. Recoveries of seabed drifters confirm previous observations that currents in the sampling area are small (probably less than 1.8 km. per day), and that the movement of water is primarily toward the south and west. It is unlikely that larvae disperse directly toward the Everglades in the east. Available evidence indicates that dispersal may be effected primarily by the current which leaves the Tortugas area through Rebecca Channel, and enters the Florida Current in the Florida Straits. Entry into the Florida Current would result in rapid transport to the area adjacent to Florida Bay. If this migration route is the main method of dispersal and transport of larvae, then the average apparent rate of survival of 80.4 percent per day may be an underestimate, and the true rate of survival may be as high as 83 percent per day.

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E. Corcoran developed a method for fragmenting mucilaginous material taken in plankton hauls, thus shortening the task of sorting the plankton. T. J. Costello and D. M. Allen of the Bureau of Commercial Fisheries provided valuable assistance and advice.

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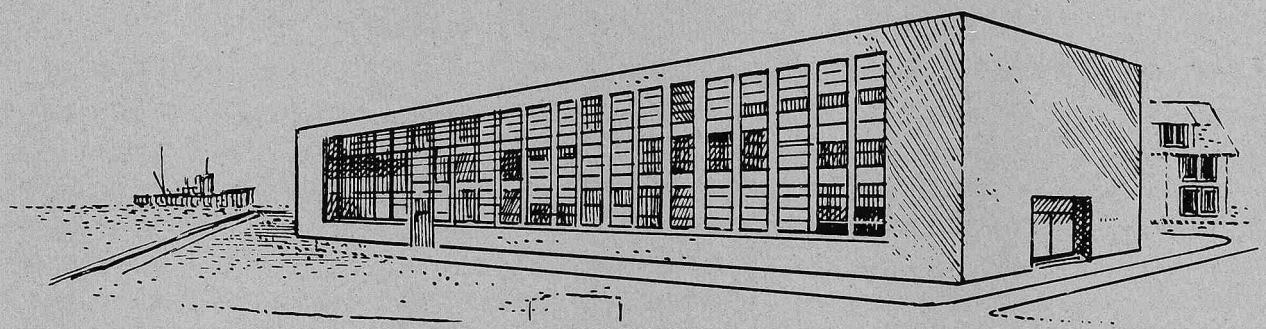

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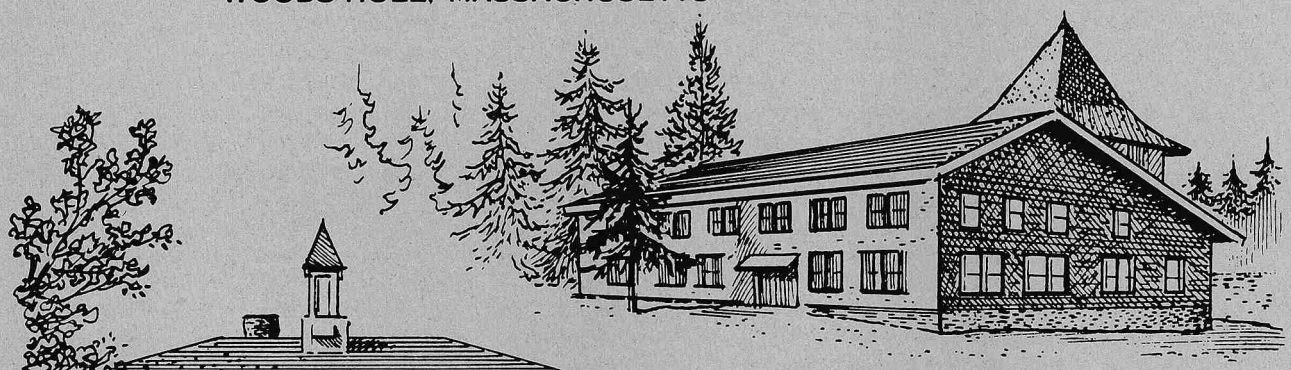

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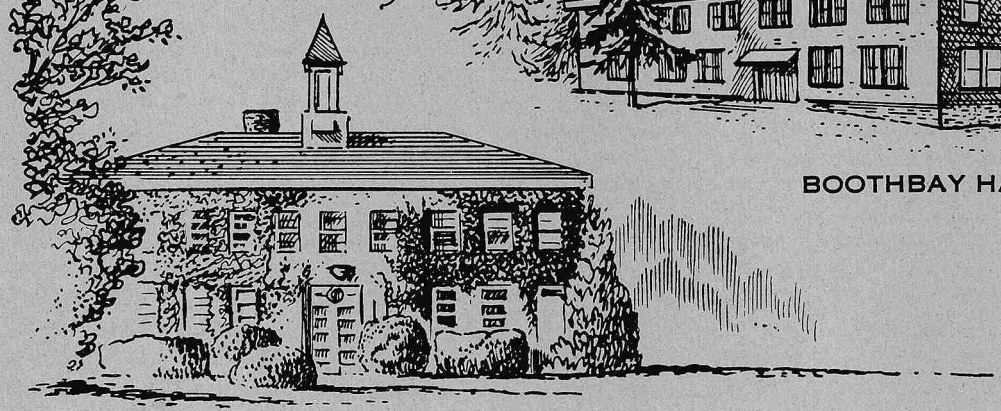

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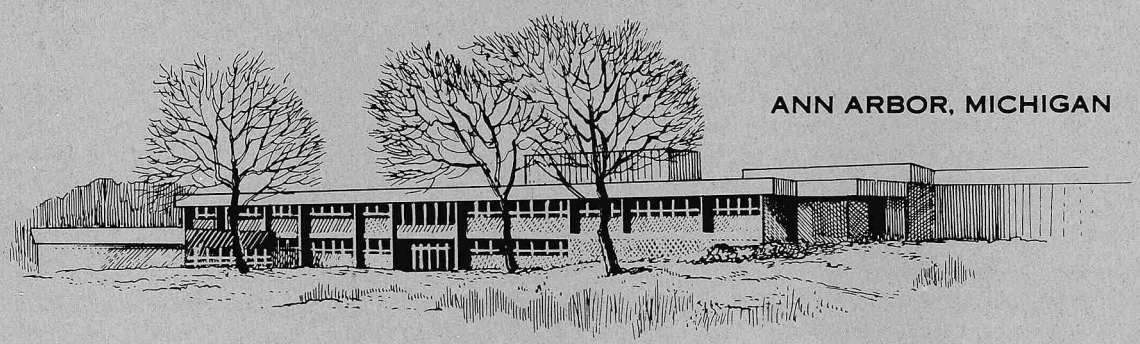

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As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

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THE FEEDING HABITS OF THE GREEN CRAB, *CARCINUS MAENAS* (L.)

BY JOHN W. ROPES, *Fishery Biologist*
BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY
OXFORD, MARYLAND 21654

ABSTRACT

Green crabs are believed to be the cause of a decline during the 1940's in the commercial landings of the soft-shell clam (*Mya arenaria* L.). Collections of 3,979 green crabs from Plum Island Sound, Mass., and vicinity in 1954–56 provided the stomachs for a study of their feeding habits. Laboratory and field observations were also made. The green crab is an omnivore, but usually contains pelecypods. It uses its claws for both digging and feeding. Accessory organs other than eyes aid in directing it to food. Feeding is influenced by the abundance, size, and kind of food. Although all sizes of green crabs contained essentially the same kinds of food, pelecypods were most frequent in crabs with carapace widths of 30 to 59 mm. Most crabs apparently feed during the night; crabs with food in their stomachs were most numerous in catches made just after sunrise. Water temperatures of 7° C. and below reduced activity and presumably feeding as well. Low salinities, however, apparently did not affect feeding. Because female crabs were relatively more numerous than males in the fall, the season when newly settled juvenile *Mya* occur in abundance, they probably were more destructive than males in Plum Island Sound.

The New England landings of soft-shell clams, *Mya arenaria* L., declined from a high of 14.7 million pounds in 1938 (Fiedler, 1940) to a low of 2.3 million pounds in 1959 (Power, 1961). The decline seriously affected the fishery and stimulated action to determine the cause. In 1948, Congress authorized the Bureau of Commercial Fisheries to study the resource (Glude, 1955).

The research of the Bureau has resulted in many publications on the biology of the soft-shell clam, with especial attention being paid to the predators of the clam. Some of the studies included observations on mortality (Smith, 1950), population size (Spear, 1953), activity (Baptist, 1955; Smith, 1955), and parasites (Uzmann, 1952; Uzmann and Stickney, 1954; Stunkard and Uzmann, 1958; Stunkard, 1960). The effects of man (Glud, 1951; Glude, 1954) and other predators (Smith and Chin, 1953) on the fishery were also observed. Animal predators were eventually identified as the most probable cause of the decline in clams; many species are known to feed on soft-shell clams. For example, soft-shell clams are sometimes included in the diet of rock crabs, *Cancer irroratus* (Mead and Barnes, 1904); lady crabs, *Ovalipes occelatus*, and blue crabs, *Callinectes sapidus* (Belding, 1930); horseshoe crabs, *Limulus polyphemus* (Belding, 1930; Turner, 1949; Smith and Chin, 1953); moon snails, *Polinices duplicatus* (Sawyer, 1950; Hanks, 1952, 1957); winter flounders, *Pseudopleuronectes americanus* (Medcof and MacPhail, 1952); herring gulls, *Larus argentatus* (Mendall, 1934; Medcof, 1949); and black ducks, *Anas rubripes* (Mendall, 1949). None of these animals, however, seemed to be responsible for the low abundance of clams. Neither blue crabs nor lady crabs are common north of Cape Cod, and none were found on the clam flats. The other predators either fed infrequently on clams or were found in only some of the areas where clams were not abundant.

One other possible predator, the green crab, *Carcinus maenas* (L.), was widespread, abundant, and apparently a species that had recently extended its range north of Cape Cod. Scattergood (1952) documented the spread of the green crabs from south

Published October 1968.

of Cape Cod during the late 1800's to northern New England in the 1940's and 1950's. By 1954, green crabs had extended their range northeastward to Wedgeport, Nova Scotia, Canada, and were also very numerous in Massachusetts, New Hampshire, and Maine. Glude (1955) and Taylor, Bigelow, and Graham (1957) considered an increase in air and surface sea-water temperatures north of Cape Cod to be an important factor in the increase in abundance and extension of the green crab's range.

The green crab was reported to be the most probable cause of the decline in soft-shell clams by Smith and Chin (1953), Glude (1955), Medcof and Dickie (1955), and Smith, Baptist, and Chin (1955). MacPhail, Lord, and Dickie (1955) and Dearborn [1] observed the feeding of green crabs in laboratories where they were restricted to certain foods, but only a few observations were available on the feeding of green crabs in nature. Smith and Chin (1953) first reported a green crab actually feeding on a soft-shell clam that it had apparently just dug out of the sediments. Hence, a study to determine feeding habits under natural conditions was needed for a broader understanding of the impact of this predator on its environment, and particularly on the soft-shell clam.

I studied the feeding habits of green crabs while at the field stations of the Bureau of Commercial Fisheries in Newburyport, Mass., and in the Narragansett Marine Laboratory, University of Rhode Island, Kingston, R.I., from 1954 through 1956. The stomach contents of green crabs collected from Plum Island Sound, Mass., and Hampton Harbor, N.H., were examined to determine the relative importance of their foods; I also made some observations on the relation of feeding behavior to the environment.

MATERIALS AND METHODS

Green crabs occurred and were collected in two distinct zones at low tide—the upper intertidal zone and the shallow subtidal zone. Crabs were caught at the edges of salt marshes in Plum Island Sound, Mass., and Hampton Harbor, N.H. (fig. 1), by opening caves in the banks of cordgrass (*Spartina*) and searching through seaweeds at the upper edges of the banks and beneath sods that had fallen onto the clam flats (table 1). Crabs were collected from the subtidal zone by dragging a scallop dredge at the edges of channels in Plum Island Sound, Mass. (table 2). The net was 76.2 cm. wide and 20.3 cm. high at the mouth and had a 51-mm. mesh (stretched measure) netting bag 76.2 cm. deep. A weighted line at the leading edge of the net scraped over the bottom; probably crabs buried in the sediments were missed, and active crabs were most likely to be captured. All dredge

TABLE 1.—*Number of green crabs dug from the banks at Plum Island Sound, Mass., and at Hampton Harbor, N.H., 1954–55*

Hales Cove		Bluff Creek		Hampton Harbor	
Date	Crabs	Date	Crabs	Date	Crabs
1954	*Number*	*1954*	*Number*	*1954*	*Number*
Sept. 23	51	Oct. 5	50	Sept. 16	35
Oct. 22	11	Nov. 2	93	Oct. 19	72
Nov. 5	96	Dec. 8	45	Nov. 18	113
Dec. 6	72			Dec. 22	155
1955		*1955*		*1955*	
Jan. 12	27	Apr. 18	83	Jan. 27	44
May 19	36	July 23	49	Feb. 16	83
Aug. 26	8	Oct. 21	137		
Oct. 21	13	Nov. 23	50		

TABLE 2.—*Number of green crabs dredged from the subtidal zone at Plum Island Sound, Mass., 1954–56*

Plum Island River		Lufkins Flat	
Date	Crabs	Date	Crabs
1954	*Number*	*1954*	*Number*
Oct. 5	[1] 24	Oct. 5	59
Oct. 28	10	Nov. 2	60
Nov. 5	62		
1955		*1955*	
Apr. 18	20	Apr. 18	20
May 26	47	May 18	33
June 13	54	June 13	37
July 18	55	July 18	57
Aug. 15	64	Aug. 15	51
Sept. 10	52	Sept. 10	128
Sept. 23	68	Sept. 23	44
Oct. 9	54	Oct. 9	67
Oct. 21	74	Oct. 21	44
Nov. 7	49	Nov. 7	69
Nov. 23	0	Nov. 23	0
1956		*1956*	
May 11	2	May 11	58
June 11	40	June 11	48
June 11	22	June 11	16
July 23	27	July 23	59
July 23	27	July 23	46
Aug. 6	25	Aug. 6	49
Aug. 6	27	Aug. 6	43
Sept. 4	10	Sept. 4	52
Sept. 5	67	Sept. 5	54
Sept. 21	26	Sept. 21	44
Sept. 22	51	Sept. 22	46
Oct. 5	62	Oct. 5	49
Oct. 19	57	Oct. 5	42
Oct. 20	61	Oct. 19	53
Nov. 5	24	Oct. 20	98
		Nov. 5	71

[1] Two crabs not used for stomach analysis.

[1] Dearborn, John H. 1957. A preliminary study of the food habits of the green crab, *Carcinides maenas* (L.) with particular reference to the soft-shell clam, *Mya arenaria* L. M.S. thesis, Mich. State Univ. Agr. Appl. Sci., 48 pp.

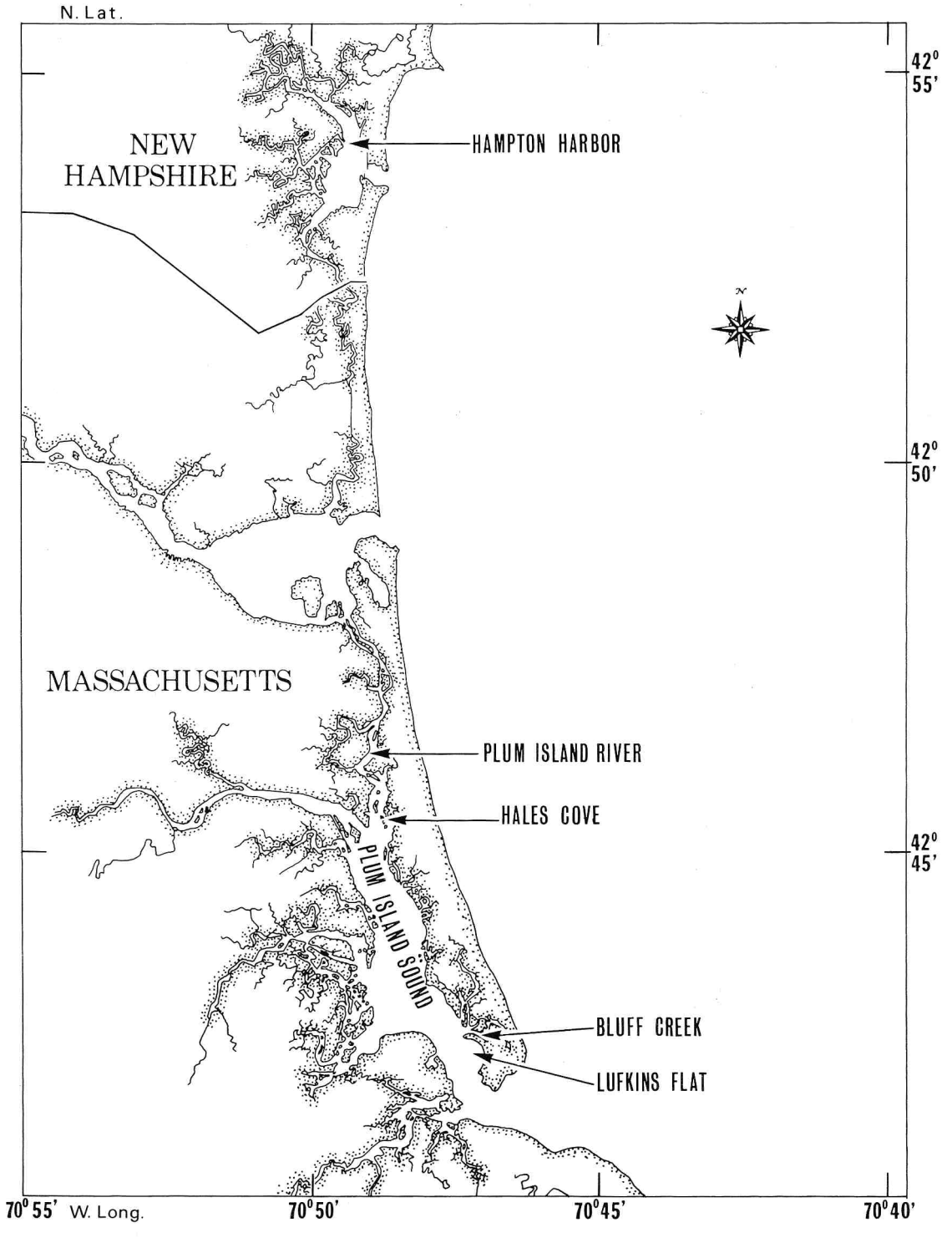


FIGURE 1.—Areas sampled for green crabs in Plum Island Sound, Mass., and Hampton Harbor, N.H.

collections were made during the ebb tide just before low water. Observations with a face plate indicated that during the ebb tide green crabs were actively moving from the intertidal zone into the channels. The crabs taken at nearly low tide had had an opportunity to feed in the intertidal zone during a complete tide before capture. The sample size was arbitrarily limited to about 50 crabs or eight drags. Occasionally more than 50 crabs were caught; all were retained for stomach analysis.

Tables of data on the stomach contents of the green crabs caught during this study are available in the U.S. Fish and Wildlife Service Data Report 29, which can be obtained from the Branch of Reports, Bureau of Commercial Fisheries, U.S. Department of the Interior, Washington, D.C. 20240. The tables and figures in the text are derived from these data.

Each crab stomach was removed at the laboratory and placed in a vial containing Formalin.[2] A record of the sex, molting stage, and carapace width, as well as the presence of eggs on female crabs, was included in each vial. Later each stomach was opened, the contents were flushed with water into a dish, and the food items were separated and identified under a dissecting microscope. The occurrence and, whenever possible, a count of each food item were recorded. For each collection of crabs, the total of these data and the number of stomachs containing food were used to obtain the percentage frequency of occurrence and average number of each food item per crab.

Estimates of the amount of food in the stomachs were separated into three categories: (1) stomachs containing tissues and hard parts of foods, (2) stomachs nearly empty, containing only hard parts of foods, and (3) stomachs with no food. The stomachs in the first category are tabulated here as a percentage of all crabs caught per collection, and those in the second category as a percentage of the stomachs containing food. Empty stomachs are omitted from all calculations.

Most food consisted of crushed or fragmented remains; so, I used various hard structures to identify the food organisms. Assigning a food to a definite species category was not always possible, but often enough of the food remained so that I could assign it to a general taxonomic group. As a consequence, not all major taxonomic groups are the sum of the specific items. Mollusk shells were the most readily identified food items (fig. 2). In particular, species of pelecypods could be recognized because their hinge structures usually were

[2] Trade names referred to in this publication do not imply endorsement of commercial products.

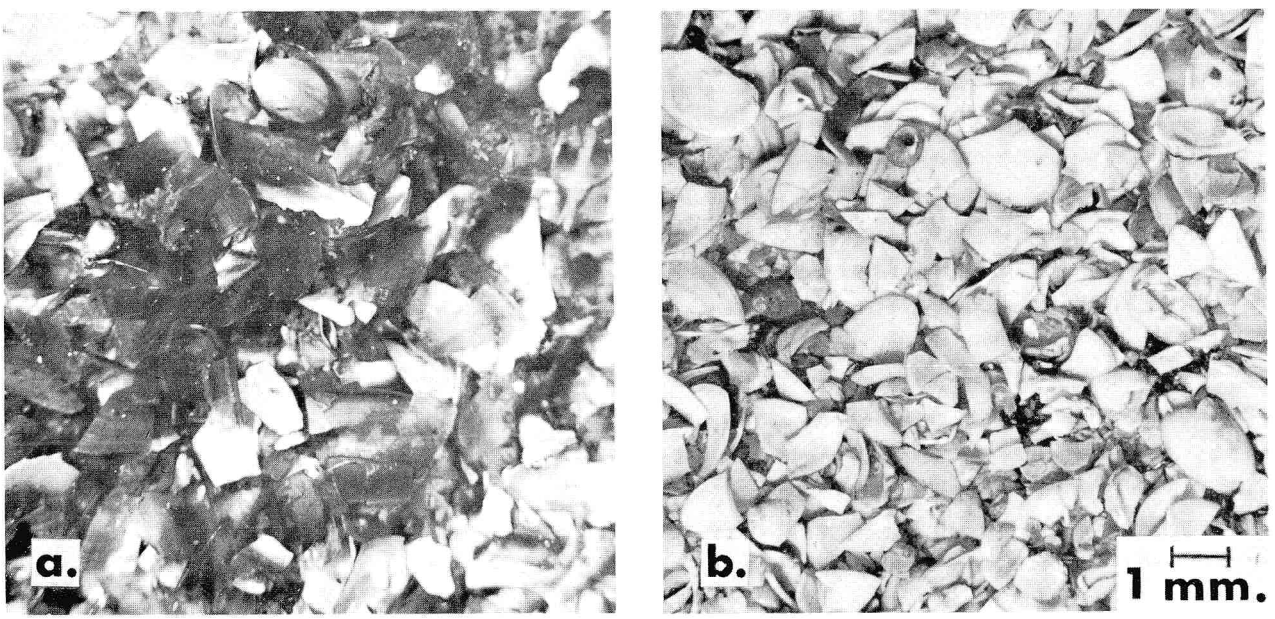


FIGURE 2.—Mollusk foods from the stomachs of green crabs: a. *Mytilus edulis*, and b. *Gemma gemma* and *Hydrobia minuta* (1-mm. scale near lower edge of figure).

intact. Because of their frequent occurrence in the stomachs, the species *Mya arenaria*, *Gemma gemma*, and *Mytilus edulis* were separated in the analyses; other species of pelecypods were combined. Gastropods were identified from the shells, operculi, and sometimes the radulae. Annelids were identified by their jaws (whole worms were rarely found). Arthropods could rarely be identified to species but were separated into three general groups: (1) crabs—the heavy, pigmented exoskeletons of green crabs, rock crabs, and horseshoe crabs; (2) small arthropods—the light, translucent exoskeletons of amphipods, isopods, and small shrimp; and (3) barnacles (shells and bodies). Insects, fish remains (mostly bones), Foraminifera, and colonial hydroids were also found. Only two plant foods, algae and cordgrass (*Spartina*), were identified. Many stomachs contained food remains that were classified as unidentified tissues.

THE RELATIVE FREQUENCY OF FOODS IN GREEN CRABS

Mya was only 1 of 31 kinds of food identified in the stomach contents during this study (table 3).

TABLE 3.—*List of organisms in the stomachs of 3,979 green crabs collected in 1954–56*

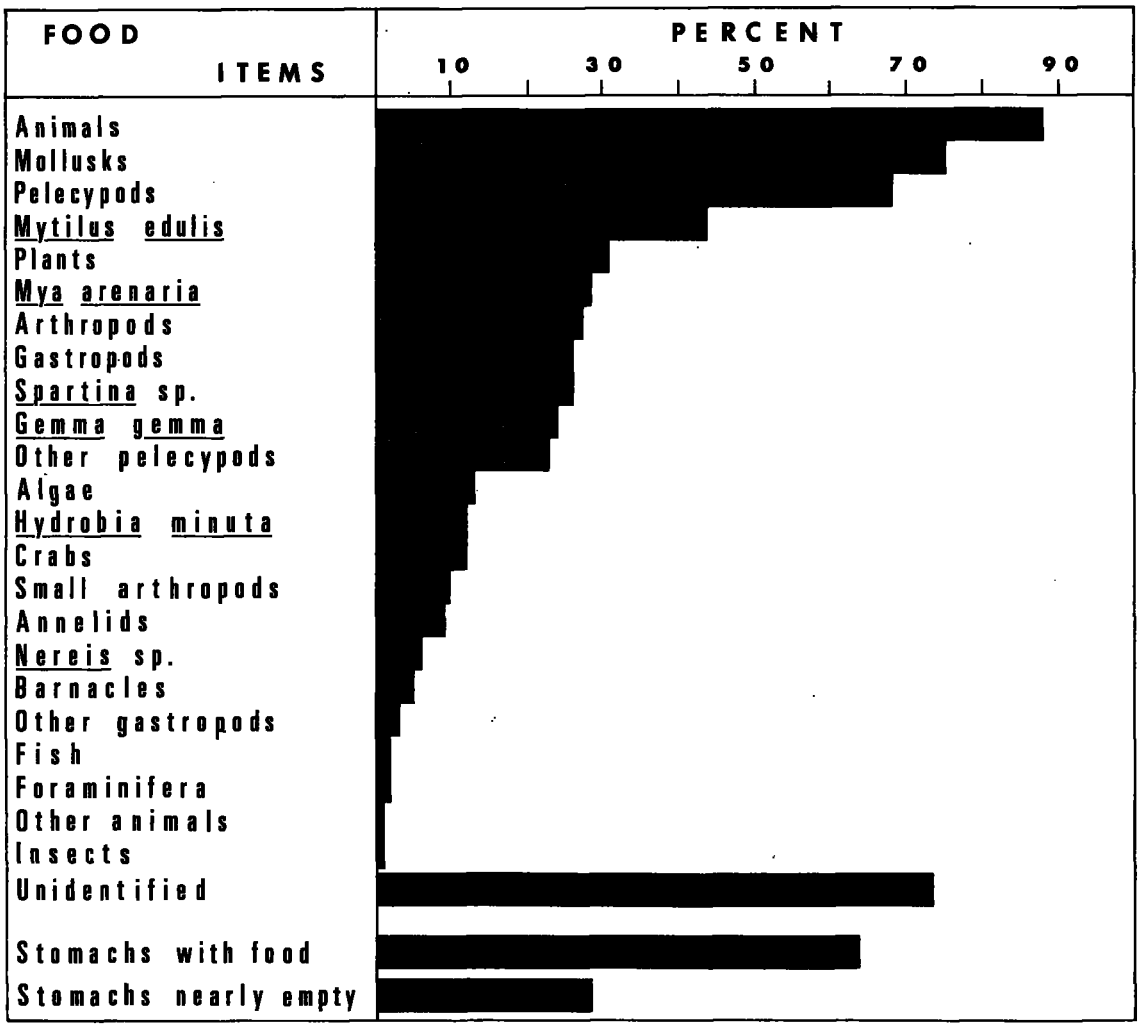
Annelids	Arthropods
Nereis sp.	Crabs
Glycera sp.	*Pagurus* sp.
Clymenella sp.	*Cancer irroratus*
Mollusks	*Carcinus maenas*
Pelecypods	*Limulus polyphemus*
Solemya velum	Small arthropods
Mytilus edulis	Isopods
Modiolus demissus	Amphipods
Mysella planulata	Natantia
Gemma gemma	Barnacles
Petricola pholadiformis	*Balanus* sp.
Tellina sp.	Other animals
Macoma sp.	Foraminifera
Ensis directus	Colonial hydroids
Mya arenaria	Insects
Gastropods	Fish
Littorina sp.	Plants
Polinices sp.	Algae
Odostomia sp.	*Spartina* sp.
Hydrobia minuta	

Both animal and plant foods occurred in the stomachs, but not with equal frequency (fig. 3); only one-third of the 3,979 stomachs with food contained plants, whereas 88 percent contained animals. Mollusks, and especially pelecypods, were the most frequent animal foods in the stomachs, and *Mytilus* was the most frequent species. *Mya*, *Gemma*, and other pelecypods occurred in about one-fourth of the stomachs. Only the plant food *Spartina* was found in as many stomachs as some of the pelecypod species. Remains of large arthropods and fish, probable indicators of cannibalistic and scavenging food habits, respectively, were in few stomachs; obviously green crabs are essentially omnivorous.

THE FEEDING CAPABILITIES OF GREEN CRABS

Certain items in the stomachs and observations of feeding in the laboratory provided information on the food-gathering capabilities of green crabs. A few stomachs contained the bodies and thoroughly crushed shells of barnacles. The presence of mussels with the barnacles in some stomachs suggested that one food was eaten incidentally to the other. In the laboratory, however, green crabs ate barnacles alone; they used their chelae to tear individual barnacles from clusters adhering to wood and glass. The eating of barnacles, thus, was not necessarily contingent upon the ingestion of another food. Occasionally a stomach contained gastropod meats, identified by the presence of a radula but no shell fragments. Green crabs were not seen eating gastropods in the laboratory, but perhaps the snails were eaten in the same fashion as *Mya*. The crabs usually exposed the meats of *Mya* 10 mm. long or longer by crushing or chipping off pieces of the shell with the chelae. Then they easily severed the adductor muscles, tore out pieces of meat, and ate them. Only the largest clams resisted attacks by green crabs. MacPhail et al. (1955) and Dearborn [3] found that *Mya* with shells equal in length or shorter than the width of the carapace of a green crab were successfully broken into and devoured. In the laboratory, I saw clams shorter than 10 mm. picked up, crushed by the chelae, and then ingested nearly whole. Many nearly intact valves were found in the stomachs—some in crabs as small as 10 to 19 mm. These results suggested that green crabs probably ate whole animals more frequently than Dearborn believed. Crescent-shaped pieces of *Spartina* were sometimes found in green crab stomachs. In the laboratory green crabs ate the stems of *Spartina* by holding them in their chelae so that the mouthparts surrounded one end. Dow and Wallace (1952) provided additional observations on the

[3] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER
Mollusks	13.9
Pelecypods	9.4
Gastropods	4.6
Hydrobia minuta	4.1
Mytilus edulis	4.1
Gemma gemma	3.1
Mya arenaria	1.2
Other pelecypods	1.0
Other gastropods	.1
Annelids	.06
Nereis sp.	.06
Other annelids	.004
TOTAL NO. of CRABS	3,979

FIGURE 3.—The relative importance of foods, analyzed by the percentage frequency of occurrence per sample of crabs and by the average numbers of certain animals per stomach, in the stomachs of 3,979 green crabs collected in 1954–56.

use of chelae by green crabs, and Borradaile, Potts, Eastham, and Saunders (1958) described the holding, severing, and chewing action of the green crab's mouthparts.

Carthy (1958) discussed accessory sense organs other than eyes which may help to direct green crabs to food. I observed how the chemical senses arouse green crabs in the laboratory. Ten crabs, from which the eye stalks had been removed, were held in an aquarium where 54 *Mya* lived in the sand. During 18 days of observation, all the crabs remained buried in the sand and did not search for the clams. On the 18th day, when juice of the quahog (*Mercenaria mercenaria*) was poured into the aquarium, the crabs almost immediately rose out of the sand and moved about, as if in search of food. Such an unoriented reflex action of the whole animal or kinesis to chemical stimuli was discussed by Allee, Emerson, Park, Park, and Schmidt (1949).

Abundance of certain foods undoubtedly affects predation by green crabs and is interrelated with their food-getting capabilities. Bottom samples taken in 1954 by Smith (1955) from areas protected from crabs by Saran screening had more *Mya* per square foot at Hales Cove than at Hampton Harbor. During the same year, more crabs contained *Mya* at Hales Cove than at Hampton Harbor. Thus, the crabs at Hales Cove reacted to the greater relative abundance of *Mya* by eating more of them.

Small animals were most numerous in the stomachs. Many crabs consumed large numbers of such small mollusks as *Gemma* and *Hydrobia* (table 4). Some pelecypods were ingested soon after setting, when they were very small. Smith (1955) observed that clams 2 to 12 mm. long were most abundant at Hales Cove in September and October and deduced that this phenomenon was probably an annual event. *Mya* occurred most frequently in green crab stomachs during September to November.

Some foods were eaten frequently by certain groups of crabs. *Spartina* was found most often in intertidal crabs (fig. 4), although crabs from both the intertidal and subtidal zones usually contained more animals than plants. Plant foods, especially *Spartina*, were abundant near the caves inhabited by green crabs and on islands that were relatively near the subtidal zone. Subtidal crabs contained animal foods, apparently from the clam flats, rather than *Spartina*.

TABLE 4.—*Numbers of certain organisms in selected specimens of green crabs*

Width of crab	Sex [1]	Food					
		Mytilus	*Gemma*	*Mya*	Other pelecypods	*Hydrobia*	Other food (not counted)
Mm.		*Number*	*Number*	*Number*	*Number*	*Number*	
43	M		165	2		18	None
48	M		181	1		50	Algae and *Spartina*
48	F		123	4		92	Algae
52	F		23			355	None
53	F		17			382	*Spartina*
49	F		18			309	None
44	F	159			1		Algae and *Spartina*
58	F	236		3	2		Foraminifera and *Spartina*
53	F	120		7	2		None
57 [2]	M	32		35	17		Crabs, algae, and *Spartina*
65	F	24		48	74		Algae and *Spartina*
32	F	48		22			Crabs, algae, and *Spartina*
42	F	6		83	7		Small arthropods and *Spartina*

[1] M = male; F = female.

[2] The stomach of the crab also contained one *Nereis*.

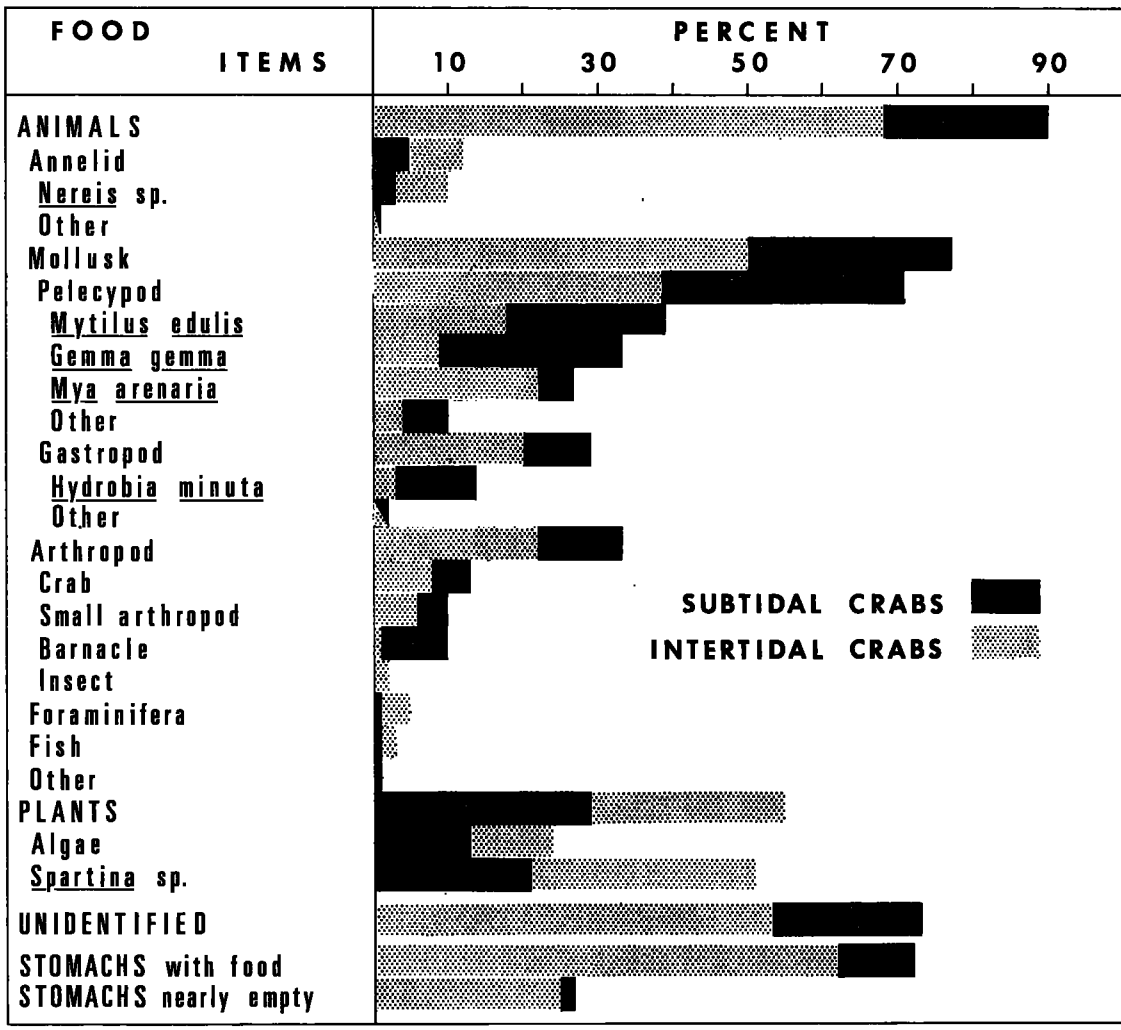
THE INFLUENCE OF CRAB SIZE ON FEEDING HABITS

I analyzed the relation of crab size to stomach contents because food habits sometimes change as an animal grows. The stomach contents differed between crabs less than 30 mm. wide and those 30 mm. wide and larger (fig. 5). The groups are designated as small and large in the text to simplify presentation. The original data on food occurrence are separated by size intervals of 10 mm.

In general, all sizes ingested the same kinds of foods and differences in food were minor. The smallest crabs were perhaps exceptions because fewer different kinds of food were eaten.

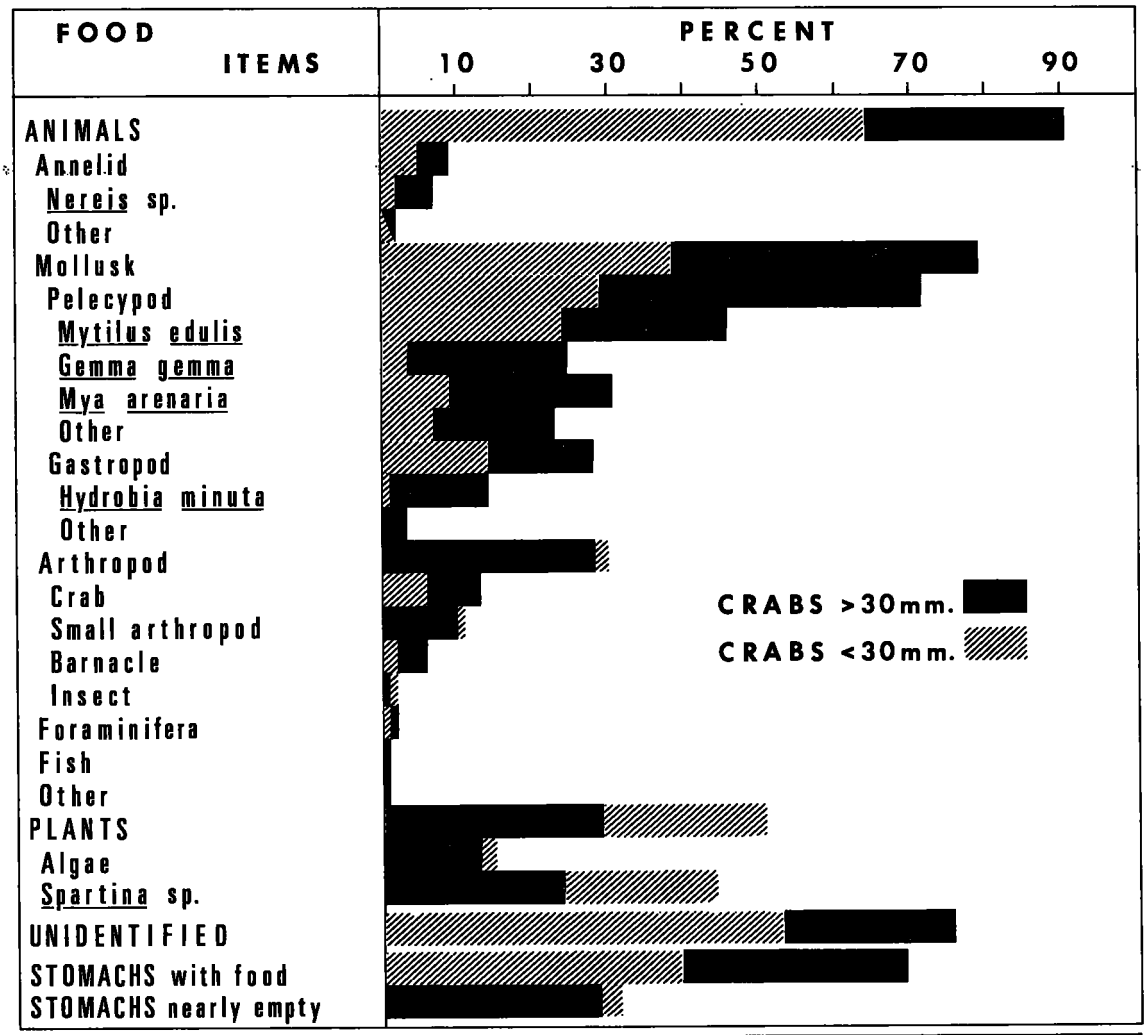
Plants and soft-shelled animals were most frequent in the stomachs of small crabs. More small than large crabs contained *Spartina*, but the frequency of algae was nearly equal in crabs from the two size groups. Small crabs also ate animals, but only small arthropods and insects were more common in small than in large crabs. Numerous stomachs of small crabs contained small, chitinous fragments, probably from small arthropods.

Large crabs contained hard-shelled foods, such as mollusks, more often than did small crabs. Large crabs concentrated on the clam flats when feeding,



FOOD ITEMS	AVERAGE NUMBER	
	INTERTIDAL	SUBTIDAL
Annelid	0.11	0.05
Nereis sp.	.11	.05
Other	<.1	<.01
Mollusk	2.5	17.5
Pelecypod	2.0	10.2
Mytilus edulis	.4	2.3
Gemma gemma	.4	6.7
Mya arenaria	1.0	.9
Other	.1	.2
Gastropod	.6	7.3
Hydrobia minuta	.3	6.7
Other	<.1	<.1
TOTAL NO. of CRABS	847	1,300

FIGURE 4.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs caught from the intertidal (shaded bars) and subtidal (black bars) zones during 1954 and 1955.



FOOD ITEMS	AVERAGE NUMBER	
	CRABS LESS THAN 30 mm.	CRABS MORE THAN 30 mm.
Annelid	0.03	0.07
Nereis sp.	.02	.06
Other	.01	.01
Mollusk	2.1	15.3
Pelecypod	1.7	10.2
Mytilus edulis	1.0	4.4
Gemma gemma	.1	3.4
Mya arenaria	.2	1.3
Other	.4	1.1
Gastropod	.5	5.0
Hydrobia minuta	.1	4.5
Other	—	.1
TOTAL NO. of CRABS	651	3,328

FIGURE 5.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in small green crabs less than 30 mm. wide (shaded bars) and in large ones 30 mm. wide and larger (black bars).

even though the whole intertidal zone, including the banks where *Spartina* grows, was available to them. Pits dug by green crabs were not found in the banks where some *Mya* lived in the sediments and among the plant roots. Apparently the crabs could not burrow easily into these compact sediments, like the gravel and cobble sediments described by Dow and Wallace (1952). Instead, the green crabs dug numerous pits in the clam flats. Large crabs frequently contained *Mya* and other animals living in the sediments that required some digging to obtain, but few ate *Spartina*.

Most small crabs lived near the banks. Small arthropods, plants, small *Mytilus*, and gastropods, which were frequent in and beneath the vegetation on the banks, provided small crabs with a convenient source of food. Finger-sized holes in the banks, mats of algae, and a thick growth of *Spartina* provided likely protection from predation. Several observations indicated that small crabs inhabited the banks but not the subtidal zone. In 1954, I trapped and dredged green crabs in the subtidal zone and searched the banks for them. All sizes were taken in the banks (fig. 6), but the traps and dredge caught many large, but few small crabs. These observations held true for samples collected during 1955 and 1956. In all 3 years, 47 percent of the 1,323 crabs caught in the intertidal zone and only 1 percent of the 2,656 crabs caught in the subtidal zone were small.

The near absence of small green crabs in the subtidal zone could have been misleading if the mesh size of the dredge (51 mm.) had permitted them to escape. When this same dredge was used on September 6 and 8, 1955, in Rhode Island, however, 108 of the 123 crabs caught were less than 10 mm. wide. These small crabs were picked out of clusters of recently set mussels and also were entangled in algae and eelgrass. Although this example was outstanding, many other dredge samples off Rhode Island included some small crabs and entangling debris. Entangling debris, then, partially closes the dredge meshes and aids in the capture of very small crabs. Debris, in the form of old *Mya* shells and *Spartina*, nearly filled each drag made at Plum Island River, but only one small green crab was caught. Similar debris was occasionally taken at Lufkins Flat, along with 27 small crabs. I conclude that small green crabs were scarce in the subtidal zone at Plum Island River but perhaps were occasionally more abundant at Lufkins Flat than the dredge samples indicated.

THE DIURNAL FEEDING HABITS OF GREEN CRABS

Green crabs are rarely seen in the unflooded intertidal zone during the daytime; most migrate to and from the intertidal zone with the tide (Dexter, 1947; Edwards, 1958), and others hide in bank caves and beneath sods during low water. Both diurnal and tidal activity rhythms were reported for green crabs by Naylor (1958); peaks of activity were during darkness and high tide.

Activity of green crabs in relation to tide and time of day probably affected the results of stomach analyses. The effects of diurnal activities on feeding habits were studied by examining stomachs of crabs dredged during two successive low tides. At most collection dates in 1956, one sample was taken just after sunrise and another late in the afternoon, before sunset. The crabs collected had had the opportunity to feed in the flooded intertidal zone during the high tide preceding capture, during the night or the day, respectively. The total number of stomachs per sample was used to obtain the percentage frequency of occurrence of food items and the average numbers ingested per crab. A preference to feed during a particular time of day is emphasized by this method if either the morning or afternoon samples contain a preponderance of crabs with empty stomachs.

The morning samples had more crabs than the afternoon samples (table 5). A chi-square test indicated significant differences from an expected 1:1 ratio (Plum Island River chi-square=47.42, d.f.=5, $P < 0.01$; Lufkins Flat chi-square=65.72, d.f.=6, $P < 0.01$). The number of crabs containing food and the average number of counted food items per crab both were greater in the morning than in the afternoon (fig. 7). Data on crabs with and without food were tested with chi-square (Plum Island River chi-square=6.79, d.f.=1, $P < 0.01$; Lufkins Flat chi-square=29.28, d.f.=1, $P < 0.01$).

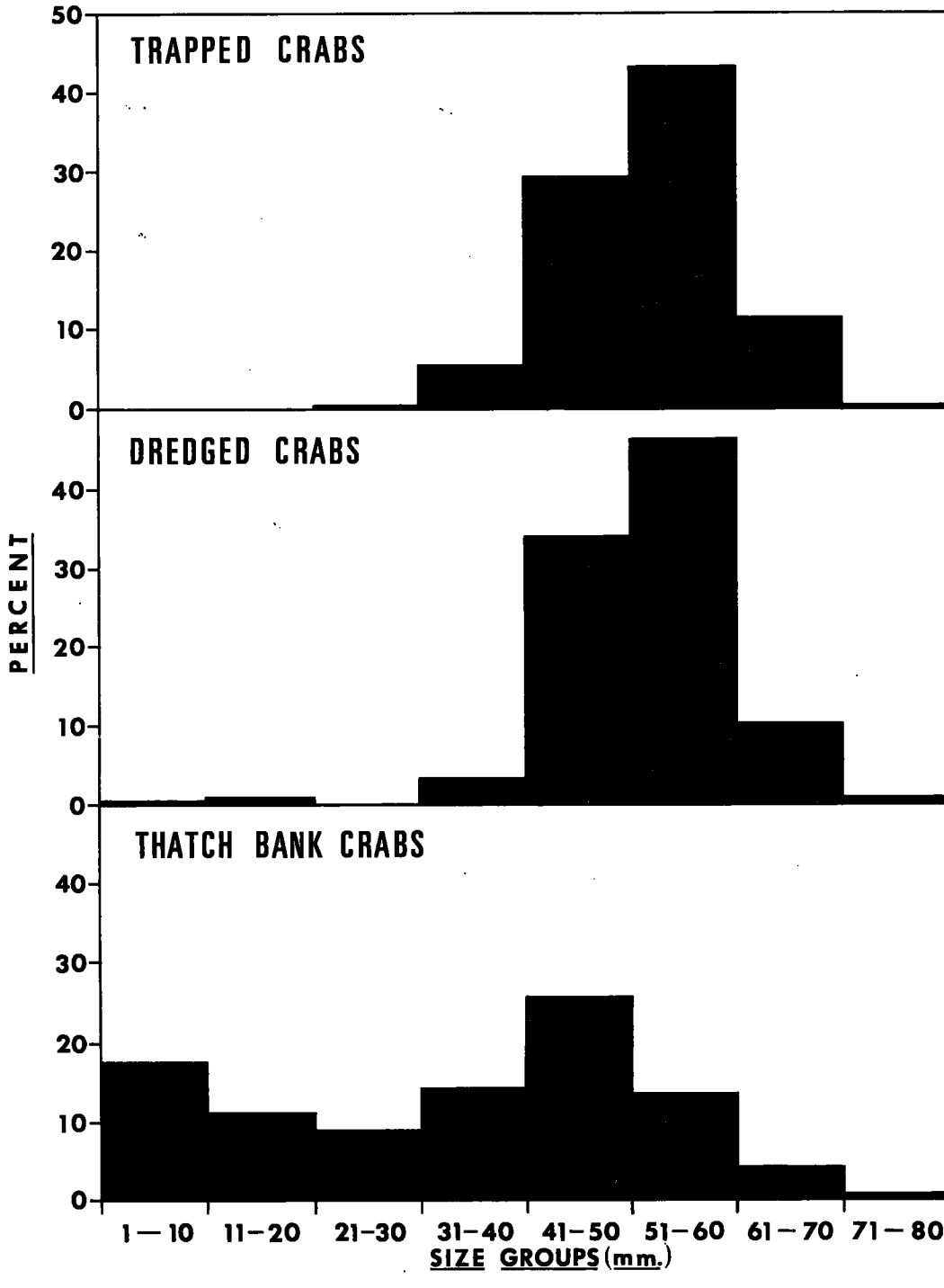
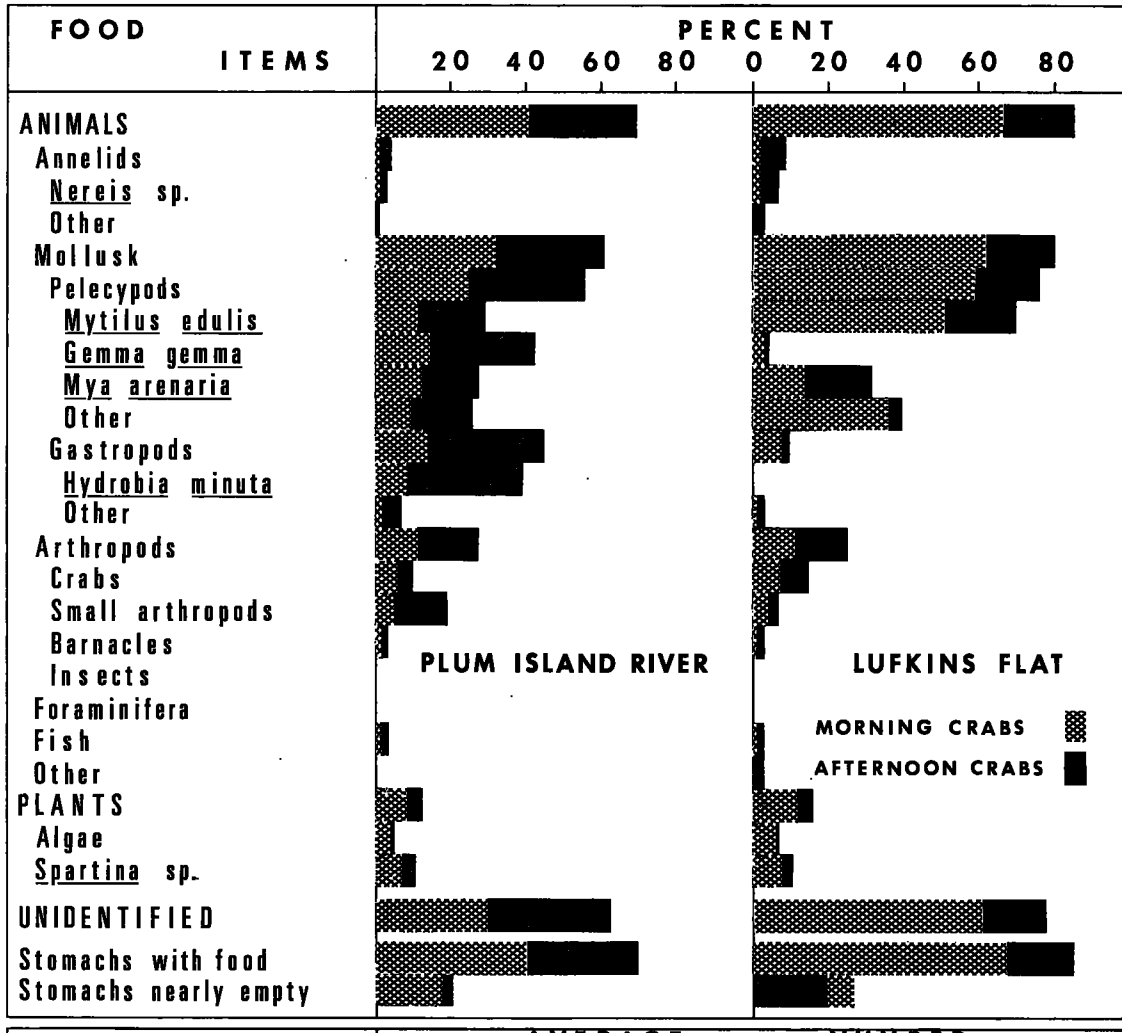


FIGURE 6.—The percentage frequency of occurrence, by 10-mm. size groups, of green crabs dug from the thatch banks in the intertidal zone and dredged and trapped in the subtidal zone during 1954.



FOOD ITEMS	AVERAGE NUMBER			
	MORNING	AFTERNOON	MORNING	AFTERNOON
Annelids	0.03	0.0	0.03	0.02
Nereis sp.	.02	.0	.03	.02
Other	.01	.0	.0	.0
Mollusks	17.3	3.8	13.1	12.1
Pelecypods	6.0	1.9	12.6	12.0
Mytilus edulis	1.0	.5	9.2	8.1
Gemma gemma	3.1	.7	<.1	<.1
Mya arenaria	.9	.4	1.4	.7
Other	1.0	.4	2.0	3.1
Gastropods	11.3	1.8	.5	.1
Hydrobia minuta	10.8	1.4	.0	.0
Other	.2	.1	.3	<.1
TOTAL NO. of CRABS	271	169	403	296

FIGURE 7.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs dredged in the morning (shaded bars) and afternoon (black bars) during 1956 at Plum Island River and Lufkins Flat.

TABLE 5.—*Number of green crabs caught in the morning and afternoon at Plum Island River and Lufkins Flat during 1956*

Locality and date	Drags during each morning and each afternoon	Crabs caught during collection period		Total crabs
		Morning	Afternoon	
Plum Island River	*Number*	*Number*	*Number*	*Number*
June 11	6	34	22	56
July 23	8	27	26	53
Aug. 6	9	25	25	50
Sept. 4	6	67	10	77
Sept. 21	2	26	26	52
Oct. 19	4	61	9	70
Total	35	240	118	358
Lufkins Flat				
June 11	5	26	16	42
July 23	5	59	20	79
Aug. 6	5	52	20	72
Sept. 5	8	54	53	107
Sept. 22	8	45	46	91
Oct. 5	4	49	4	53
Oct. 20	3	98	12	110
Total	38	383	171	554

OTHER FACTORS THAT INFLUENCE FEEDING HABITS

TEMPERATURE

The food consumption of the green crab may be affected by extremes in water temperature. Green crabs were presumed to be influenced by adverse temperature if less than half of the stomachs had food; if more than half of the stomachs with food were also nearly empty; and if no other factors were suspected to have prevented feeding.

The number of crabs containing food clearly declined in eight samples from the intertidal zone (table 6); seven samples were collected when the water temperatures were 11.5° C. and lower, and the crab stomachs contained only shell fragments; and one sample was collected when the water temperature was 26° C. Two other samples were borderline examples because slightly more than half of the crabs had recently fed. If the sample on August 26, 1955 is excluded, the total of 9 samples included 696 crabs; 208 contained food, but of these 129 (62 percent) were nearly empty. Thus, only 79 (38 percent) had eaten when the temperatures were 12° C. or less.

Eleven intertidal samples contained crabs that had clearly been feeding when the water temperatures were 9° C. or higher (table 6). The total of 11 samples included 619 crabs; 431 contained food, and only 82 (19 percent) of these were nearly empty. Therefore, 349 of the crabs (81 percent) had eaten when the temperatures were 9° C. or higher.

TABLE 6.—*Water temperatures and the percentage frequency of occurrence of food in green crabs from the intertidal zone, 1954–56*

Date	Temperature	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
1954	° *C.*	*Percent*	*Percent*	*Percent*	*Number*
Sept. 16	(1)	60	90	10	35
Sept. 23	16.0	61	68	32	51
Oct. 5	16.5	68	56	44	50
Oct. 19	(1)	76	86	14	72
Oct. 22	13.0	82	100	0	11
Nov. 2	9.6	83	94	6	93
Nov. 5	9.0	79	79	21	96
Nov. 18	(1)	62	89	11	113
Dec. 6	.0	11	38	62	72
Dec. 8	2.5	44	30	70	45
Dec. 22	1.0	27	38	62	155
1955					
Jan. 12	0	0	0	0	27
Jan. 27	.7	23	10	90	44
Feb. 16	2.0	29	17	83	83
Apr. 18	11.5	39	25	75	83
May 19	15.0	64	74	26	36
July 23	18.0	55	85	15	49
Aug. 26	26.0	38	33	67	8
Oct. 21	12.0	62	37	63	13
Oct. 21	10.5	42	58	42	137
Nov. 23	2.0	30	53	47	50

[1] No observation.

Most crabs caught in the subtidal zone were collected when the water was warm. A few exceptions indicated feeding at temperatures lower than 12° C. Table 7 includes the dates when the water temperatures at the dredge sites were less than 12° C. More than 50 percent of the crabs sampled on or near these dates contained food and less than half of the stomachs containing food were classified as nearly empty. These data suggested that temperatures as low as 7° C. do not suppress feeding. Activity, and presumably feeding as well, probably ceased at some temperature below 7° C. because on November 23, 1955, when the water temperature was 2° C., no green crabs were caught in the subtidal zone at either sampling area.

TABLE 7.—*Low water temperatures and the percentage frequency of occurrence of food in green crabs from the subtidal zone at Plum Island River and Lufkins Flat, 1954–56*

Place and date	Temperature	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
Plum Island River	° *C.*	*Percent*	*Percent*	*Percent*	*Number*
Nov. 5, 1954	9.0	68	69	31	62
Nov. 7, 1955	10.0	90	61	39	49
May 11, 1956	10.0	50	0	0	2
Oct. 5, 1956	10.0	79	77	23	62
Oct. 19, 1956	10.0	87	83	17	61
Nov. 15, 1956	7.5	67	87	13	24
Lufkins Flat					
Apr. 18, 1955	11.5	55	36	64	20
Oct. 21, 1955	10.5	77	65	35	44
Nov. 7, 1955	10.0	83	84	16	69
May 11, 1956	8.0	85	80	20	58
Oct. 20, 1956	9.5	95	83	17	98
Nov. 5, 1956	7.0	93	88	12	71

SALINITY

The feeding of green crabs was limited less by low salinities than by low temperatures in Plum Island Sound. Green crabs maintain a homoiosmotic condition when subjected to diluted sea water by actively taking up ions through the gills, increasing their oxygen consumption, and expending energy (Scheer, 1948; Waterman, 1960). Duval (1925) found that green crabs lived permanently in salinities as low as 11 p.p.t. (parts per thousand), but lower salinities killed them within 24 to 48 hours. Green crabs sometimes seek temporary shelter in moist caves, crevices, and seaweeds when the water in the estuary is drastically diluted (Broekhuysen, 1936; Nicol, 1935).

Salinities fell below 11 p.p.t. only at Plum Island River and only on three occasions (table 8). The proportions of crabs containing food were similar during periods of high and low salinity. Only slightly fewer crabs were caught per drag and fewer food items were counted in the stomachs of crabs caught when the salinity was low. The influence of low salinity on feeding was not apparent, even though the values were below the reported tolerance limits for green crabs.

TABLE 8.—*Low salinity and the percentage frequency of occurrence of food in green crabs at Plum Island River, 1955–56*

Date	Salinity	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
	p.p.t.	*Percent*	*Percent*	*Percent*	*Number*
Apr. 18, 1955	9.0	75	87	13	20
Nov. 7, 1955	7.4	90	61	39	49
May 11, 1956	7.6	50	0	0	2

SEX

Female green crabs were sometimes predominant in the dredge catches. An analysis of the sex ratio and frequency of occurrence of food by sex indicated that feeding differed with sex at Plum Island River.

Many more female than male crabs from Plum Island River contained mollusks (fig. 8). Six other food items also occurred slightly more often in female than male crabs. Female crabs from Plum Island River were only slightly more numerous than males in the total catch and were relatively more abundant than males for a shorter period of time than at Lufkins Flat (fig. 9). The total predation on mollusks by female crabs at Plum Island River was greater than by males, not only because more females were present to feed at certain times of the year, but because they ate more mollusks than did the males.

Differences were not appreciable between the stomach contents of male and female crabs caught from Lufkins Flat (fig. 8), but more female than male crabs were caught in nearly every collection (fig. 9). The total predation by females was greater than that by males only because females were more abundant.

EGG BEARING

In both sample areas fewer ovigerous crabs contained food (table 9) than nonovigerous, even though the kinds of food eaten by the two types of crabs were the same. The reduction in food intake may be accounted for by Dearborn's[4] observations that although ovigerous crabs readily accepted food in the laboratory, they are generally less active. The dredge catches indicated that fewer ovigerous than nonovigerous crabs were feeding; only 5.5 percent of the females from Plum Island River and 4.6 percent from Lufkins Flat were ovigerous.

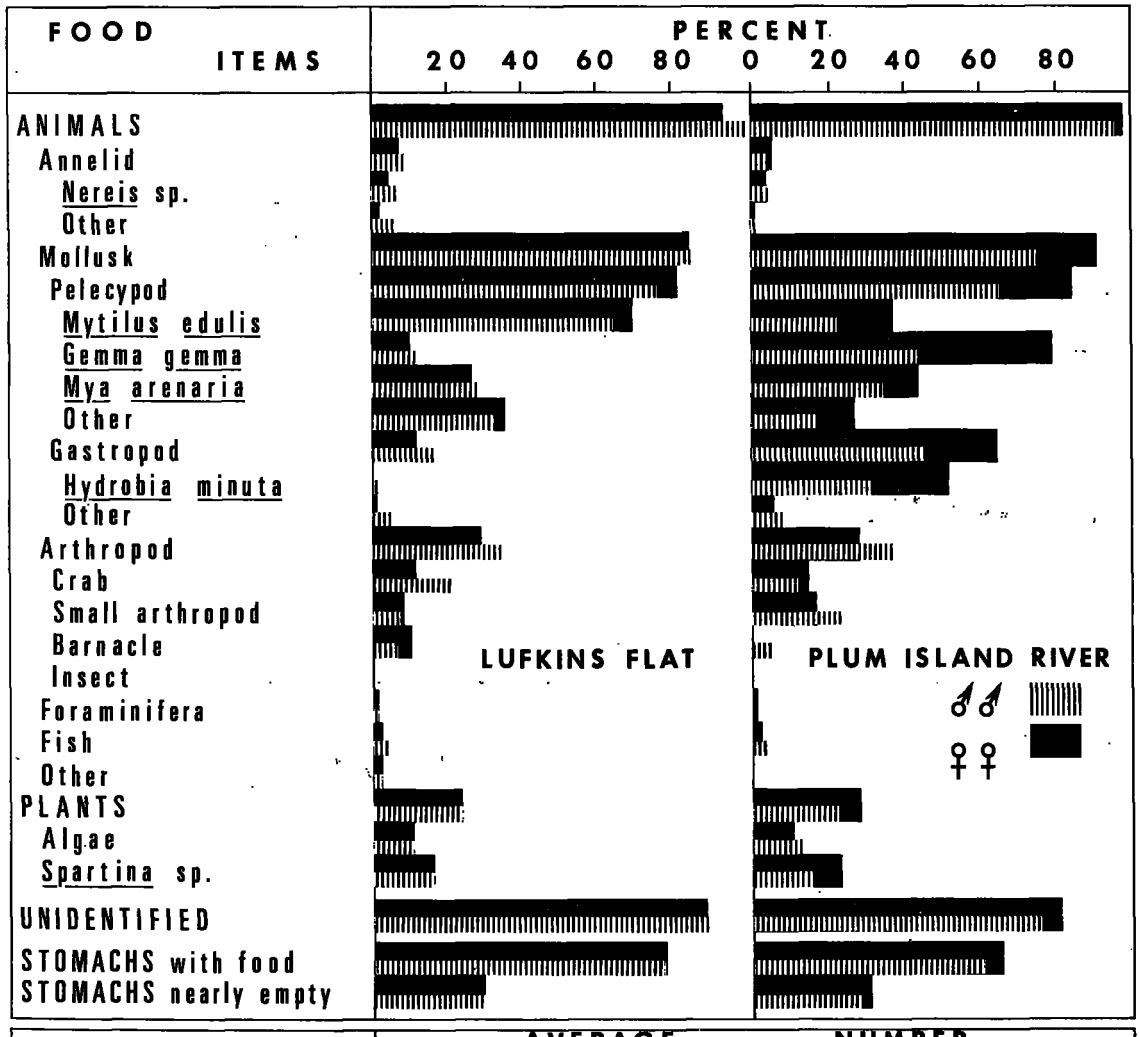
TABLE 9.—*Percentage frequency of occurrence of ovigerous and nonovigerous female green crabs that contained food at Plum Island River and Lufkins Flat, 1955–56*

Female condition and place	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total females
	Percent	*Percent*	*Percent*	*Number*
Ovigerous				
Plum Island River	29	56	44	31
Lufkins Flat	51	42	58	47
Nonovigerous				
Plum Island River	67	70	30	529
Lufkins Flat	80	72	28	981

MOLTING

As with other crustaceans, the green crab must molt its hard exoskeleton to grow. While preparing for ecdysis and hardening the exoskeleton after ecdysis, the crab would be likely to change its feeding habits because its claws and mouthparts are too soft to handle some of the usual foods. To determine the degree of change in food during molting, green crabs caught during 1956 were separated into five groups, based on molting condition. One group, the premolt crabs, was

[4] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER			
	MALES	FEMALES	MALES	FEMALES
Mollusk	13.2	13.1	23.3	6.1
Pelecypod	12.0	12.7	10.1	15.4
Mytilus edulis	8.1	8.5	.5	1.8
Gemma gemma	1.4	.7	8.4	11.0
Mya arenaria	1.1	1.5	.8	1.6
Other	1.4	2.1	.4	1.0
Gastropod	.7	.5	13.2	17.8
Hydrobia minuta	.3	.1	12.3	17.2
Other	.1	.2	.2	.2
TOTAL NO. of CRABS	350	1,028	505	560

FIGURE 8.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items between the sexes of green crabs caught during 1955 and 1956 (males, shaded bars; females, black bars)

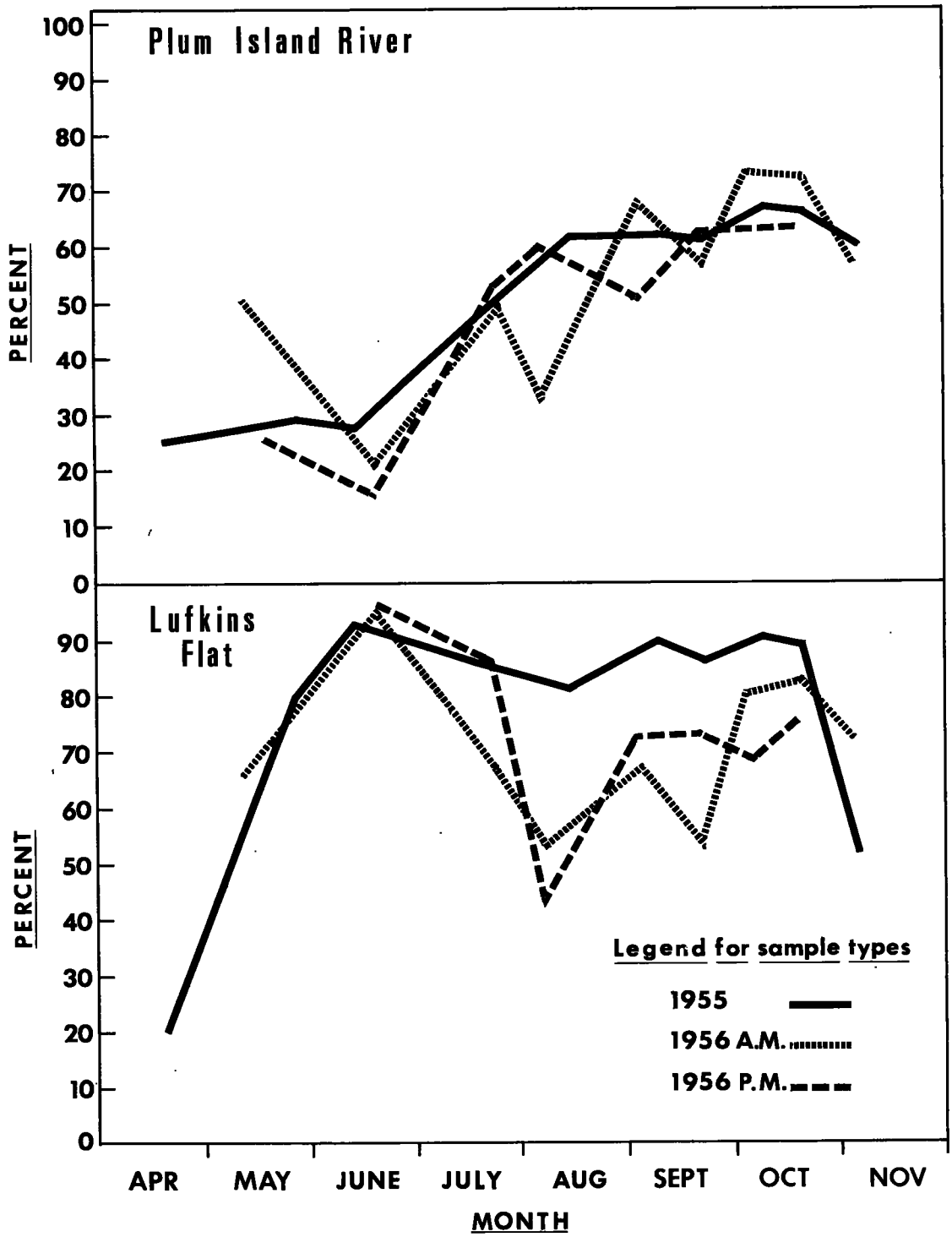


FIGURE 9.—The percentage frequency of occurrence of female green crabs in the dredge catches at Plum Island River and Lufkins Flat during 1955 and 1956.

easily separated while the stomachs were examined because the old stomach is replaced just before ecdysis. A second group included recently molted crabs with very soft shells. The next two groups, moderately soft-shelled and nearly hard-shelled crabs, were separated on the basis of the ease with which the carapace indented under finger pressure. The carapaces of hard-shelled crabs, the fifth group, were rigid and cracked if enough force was exerted.

The food habits of premolt and recently molted crabs were particularly affected (fig. 10). A few of these crabs contained bits of shell presumably ingested before ecdysis took place. Thus, like other brachyuran crabs (Waterman, 1960), green crabs stop feeding just before and after ecdysis.

Occurrence of food increased as the shells of molted crabs progressively hardened. Most of the moderately soft-shelled and nearly hard-shelled crabs contained *Gemma*, *Hydrobia*, small arthropods, and algae, and all of the typical foods were found in both groups. All foods, except those mentioned for moderately soft-shelled crabs, occurred more often and in larger numbers in nearly hard-shelled crabs than in any other group. This finding suggested that nearly hard-shelled crabs had a greater appetite than hard-shelled crabs. Nevertheless, the total predation by hard-shelled crabs was greater than that of nearly hard-shelled crabs because the crabs are in the hard-shelled condition for a longer period of time (Waterman, 1960).

MATING

Stomach analysis of a few male crabs, each caught clasping a female, indicated that they ceased feeding during the mating act. Only 2 of the 10 mated males from Plum Island River contained food, and both were nearly empty. No mated pairs were caught at Lufkins Flat.

THE GENERAL PREDATORY ECOLOGY OF GREEN CRABS

Green crabs eat other foods than those listed in table 1. I collected stomachs from Maine which contained *Anomia* sp., whereas *Aquipecten irradians* and *Zostera marina* occurred in some from Rhode Island. Spear [5] found during a laboratory study that green crabs ate small hard clams, *Mercenaria mercenaria* (6–10 mm.), in preference to larger ones (20–25 mm.). Green crabs almost destroyed small hard clams planted experimentally in Wickford Harbor, R.I., by Warren S. Landers (oral communication). Dearborn [6] found the following foods acceptable to green crabs: *Crassostrea virginica*, *Astarte castanea*, *Pectin grandis* (= *Placopecten magellanicus*), *Nucula* sp., *Modiolus modiolus*, *Callocardia* (=*Pitar*) *morrhuana*, *Spisula solidissima*, *Saxicava* (=*Hiatella*) *arctica*, *Fundulus* sp., *Laminaria* sp., *Littorina littorea*, and *L. obtusata*. Such variety in the diet of green crabs is undoubtedly due to their omnivorous feeding habits.

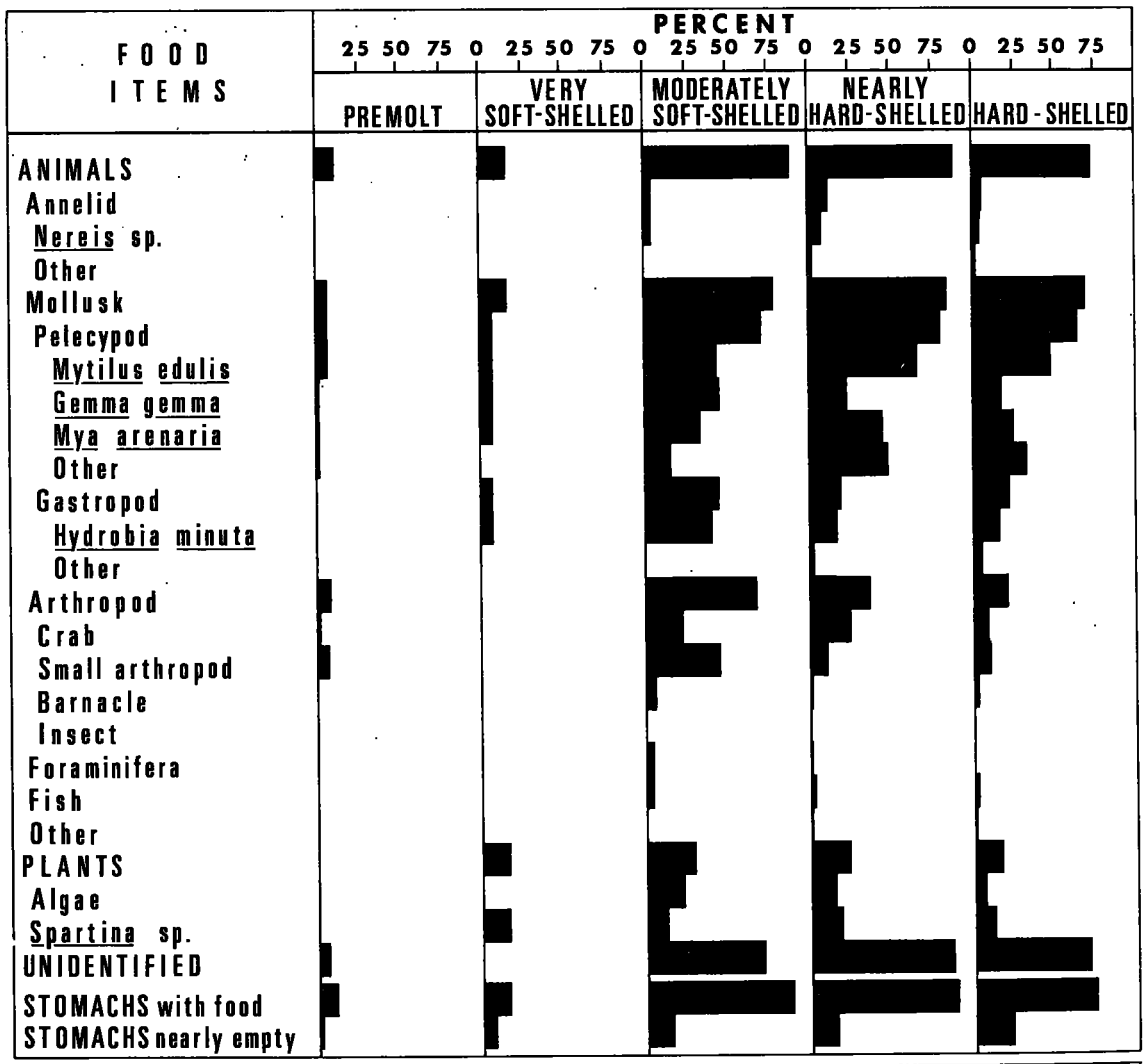
The green crab's ability to grasp, crush, and tear apart food probably permits scavenging for foods such as dead fish; however, they are not exclusively scavengers because they eat many live foods and may actually prefer fresh food to carrion. Fishermen replace old decomposed bait because they say fresh bait catches more green crabs. Some fresh, recently killed food is available from natural causes. While using free diving gear, I saw green crabs quickly pick up and eat small herring that sank to the bottom after being killed or stunned by gulls.

Samples of crabs taken by traps or dredges or from bank caves indicated that the population of green crabs in Plum Island Sound was large. Evidence of intraspecific competition was meager, however, even though the foods eaten by all sizes of crabs were qualitatively similar. The incidence of cannibalism, a possible measure of extreme competition, was low. Actually there was more reason to suppose that intraspecific competition was circumvented. Small crabs, which would be the most vulnerable to cannibalism because of their size, did not mix with the large crabs. Presumably the separation of small from large crabs enabled them to grow and develop their food-gathering abilities without the necessity of competing with large crabs. The omnivorous feeding of green crabs also serves to reduce intraspecific competition and to permit a large population to inhabit an area.

Predator control methods, developed during investigations of the decline in soft-shell clams, reduced the effects of green crabs on the clam flats. Fences (Smith, 1954; Smith et al., 1955) and

[5] Spear, Harlan S. 1955. Notes on laboratory experiments on feeding habits of green crabs. [U.S.] Fish Wildl. Serv., Clam Invest., Boothbay Harbor, Maine, 5th Conf. Clam Res.: 45. [Mimeographed.]

[6] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER				
Annelid	0.0	0.0	0.0	0.07	0.02
Nereis sp.	.0	.0	.0	.07	.01
Other	.0	.0	.0	.0	<.01
Mollusk	.1	.3	10.0	28.9	10.8
Pelecypod	.1	.3	7.0	22.6	7.9
Mytilus edulis	.1	.0	1.5	14.8	4.6
Gemma gemma	<.1	.2	3.4	1.4	.9
Mya arenaria	.1	.1	.6	3.2	.9
Other	<.1	.0	1.4	3.2	1.6
Gastropod	.0	.1	3.0	6.3	3.0
Hydrobia minuta	.0	.1	2.9	6.0	2.6
Other	.0	.0	.0	.1	.2
TOTAL NO. of CRABS	43	15	37	217	1,044

FIGURE 10.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs before and after molting.

chemical barriers (Hanks, 1961) were used to control predation by green crabs. These devices were usually installed in an area during early spring and maintained until late fall because green crabs feed for 6 to 7 months of the year.

The entire population of crabs may not be feeding actively at any one time in Plum Island Sound. Few ovigerous females were caught by dredging, but many of these samples were taken when, according to Broekhuysen (1936), ovigerous females would be scarce. Nevertheless, this study and unpublished records of green crabs caught by the staff of the Bureau of Commercial Fisheries indicated that ovigerous females were generally less active than nonovigerous crabs. A total of 124 females and 4 males were caught in three collections from the outflow of a hydraulic dredge that was excavating channels in the Merrimack River basin during June 1953; 94 percent of the females were ovigerous. At the same time traps and a scallop dredge fished near the area caught 24 males and 31 females, but only one of the females was ovigerous. Apparently ovigerous females are generally inactive and buried in the bottom substrate where the scallop dredge does not catch them.

The inconsistent feeding habits of each sex in the two areas sampled suggested that some aspect of their behavior may also be dissimilar. Male green crabs actively seek females that are about to molt, as they can mate only with soft-shelled individuals. It is not completely known how males select females that are about to molt, but Broekhuysen (1936) believed that as female crabs approach ecdysis they become passive to the advances of male crabs. Upon finding such a female, the male picks her up and holds her upside down beneath his body. The female may be carried by the male for several days before the female molts and mating takes place. While seeking and holding a female, the male's search for food probably is restricted.

To obtain indirect evidence of readiness for mating, I counted female green crabs in the premolt condition (data combined for 1955 and 1956) and found 4.8 percent at Plum Island River and 0.5 percent at Lufkins Flat. Males in the Plum Island River area, then, may have been more actively seeking mates than feeding because molting females were more available there. The time spent seeking and holding a mate may have contributed to the observed differences in the feeding habits between the sexes at Plum Island River.

These observations do not contradict Dearborn's [7] conclusion that male and female green crabs have similar food habits, because he held each crab in a separate container. In the absence of mates, male crabs probably had feeding habits similar to those of nonmolting females, and were, thus, like the crabs caught at Lufkins Flat.

Female green crabs were probably more destructive than males to the soft-shell clam population in Plum Island Sound. At least, relatively more female crabs were caught at both sample areas during the fall, when Smith (1955) found newly settled juvenile *Mya* abundant. An abundance of small-sized food, at a period in the crab's life history when molting, mating, low temperatures, and salinity were minor factors limiting the population's feeding habits, undoubtedly contributed to the decline of the clam fishery in Plum Island Sound.

SUMMARY

1. The green crab is an omnivore, but pelecypods formed a dominant part of the diet of crabs collected from Plum Island Sound, Mass., and vicinity.

2. Green crabs exhibit raptorial feeding abilities, aided by accessory organs which direct them to sources of food. The abundance, size, and kind of foods influence feeding.

3. Pelecypods were most frequent in crabs 30 to 59 mm. wide even though all sizes contained essentially the same kinds of food.

4. The feeding habits of green crabs were regulated by the time of day and the tides. The greater frequency of food in crabs caught during low tide and just after sunrise suggests that feeding is heaviest at night and at high tide.

5. Activity, and presumably feeding as well, probably were restricted at water temperatures below 7° C.

6. Low salinity apparently did not influence feeding.

7. Female crabs were relatively more numerous than males in the fall and, thus, were probably more destructive of pelecypods in Plum Island Sound.

[7] Footnote 1.

8. Ovigerous females were relatively inactive and, thus, less destructive of pelecypods than non-ovigerous females.

9. Feeding by crabs preparing for ecdysis and subsequent hardening of the exoskeleton was generally reduced, except for crabs that had nearly hard shells.

10. Feeding of male crabs apparently is markedly reduced during the mating act.

ACKNOWLEDGMENTS

Fenner A. Chace, Jr., Curator, Division of Marine Invertebrates, U.S. National Museum, provided the taxonomic background for the valid generic name of the green crab, namely, *Carcinus* rather than *Carcinides*. Lionel Sheppard, former Clam Commissioner of Ipswich, Mass., assisted during many of the dredge collections. Franklin C. Daiber of the University of Delaware read the manuscript and made helpful suggestions.

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EARLY LIFE HISTORY AND SPAWNING OF THE ALBACORE, *THUNNUS ALALUNGA*, IN HAWAIIAN WATERS

BY HOWARD O. YOSHIDA, *Fishery Biologist*

BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY
HONOLULU, HAWAII 96812

ABSTRACT

Thirty-five juvenile albacore were found in the stomachs of 4,568 billfishes captured in Hawaiian waters between July 1962 and April 1966.

Regressions of standard length on lengths of various segments of the vertebral column, determined from measurements made on 21 intact specimens caught in the Pacific Ocean, were used to estimate the lengths of the fragmentary specimens. A linear regression was used to describe the first year's growth of albacore. By use of the regression, expected lengths for various ages, in days, up to 1 year were obtained. One-year-old albacore were estimated to be 38 cm. in standard length. The spawning season for albacore in Hawaiian waters peaks in May and probably extends from March to September.

The albacore (*Thunnus alalunga*) in the North Pacific are believed to constitute a single subpopulation, the adults of which support fisheries off the coasts of North America and Japan. The age and growth of adult albacore have been estimated and hypotheses have been developed on their migrations among the fisheries (Otsu, 1960; Clemens, 1961; Otsu and Uchida, 1963).

Basic information on young albacore before they are recruited into the commercial fisheries is sketchy, however. Descriptions of larval albacore appear in the literature, but they need verification. Matsumoto's (1962) description of larval albacore differs significantly from that of Yabe and Ueyanagi (1962). Yabe, Ueyanagi, Kikawa, and Watanabe (1958) and Yoshida (1965) published descriptions of the anatomy of juvenile albacore, and Asano (1964) published observations on the morphology. The present report treats aspects of the early life history of albacore before their recruitment into the commercial fisheries. Growth in the first year of life is estimated and inferences are made on the spawning habits of the adults.

The juvenile albacore for this study came from the stomachs of billfishes, which are good collectors of juvenile tunas (Yabe et al., 1958; Yoshida, 1965). The Honolulu fish markets were an excellent source of billfishes from which stomachs could be sampled with relatively little difficulty. Although the abundance of billfishes varied seasonally, stomachs were available from every month in a 46-month period between 1962 and 1966. The billfish stomachs yielded 35 juvenile albacore. Skipjack tuna (*Katsuwonus pelamis*), the most numerous juvenile tuna, was about 24 times more numerous than albacore. Smaller numbers of juvenile yellowfin tuna (*T. albacares*), bigeye tuna (*T. obesus*), and other tunas and tunalike fishes were found.

COLLECTION AND EXAMINATION OF STOMACHS

Stomachs of 4,568 billfishes were examined from July 1962 to April 1966—3,751 striped marlin (*Tetrapturus audax*), 477 blue marlin (*Makaira nigricans*), 268 shortbill spearfish (*Tetrapturus angustirostris*), 34 black marlin (*Makaira indica*), 31 sailfish (*Istiophorus orientalis*), and 7 unidentified billfishes. The stomachs of striped marlin, blue marlin, and shortbill spearfish contained juvenile albacore.

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Most of the stomachs came from billfishes captured by vessels of the Hawaiian longline fishery. Otsu (1954) and Shomura (1959) gave detailed descriptions of that fishery. The catches are landed at the United Fishing Agency and the Fishing Co-Op of Hawaii in Honolulu, where the fish are sold at auction. The stomachs and information on the date of landing, locality of capture, weight, and sex for each fish were made available by the fish market personnel or the purchasers of the fish.

The vessels usually fished within sight of land. Thus, most of the stomachs came from billfishes captured within about 37 km. of the main Hawaiian islands. A few of the stomachs, however, came from billfishes caught as far as 644 km. from Oahu.

From 1962 to 1965, stomach samples were also collected from billfishes captured in the Hawaiian International Billfish Tournament, held annually since 1959 at Kona, Hawaii. The rules of the tournament limited the fishing area to the lee of the island of Hawaii.

The striped marlin were 4 to 148 kg.; the size distribution showed modes between 16 and 20 kg. and between 36 and 40 kg. The blue marlin were 16 to 364 kg.; a prominent mode was present between 60 and 70 kg. The shortbill spearfish were 14 to 38 kg.; a mode was present between 12 and 16 kg. The sailfish were 14 to 38 kg.; black marlin, from 36 to 290 kg.

The stomach samples from the Honolulu markets were taken to the laboratory and either examined immediately or preserved in 10 percent Formalin[1] for later examination. The samples from the billfish tournaments were shipped to the laboratory after preservation in 10 percent Formalin. In the laboratory, the stomach contents were initially sorted for tuna and tunalike specimens, which were later identified to species. The tuna specimens, which were affected in varying degrees by digestion, could be identified by their skeletons (Yabe et al., 1958; Matsumoto, 1963; Yoshida, 1965).

LENGTH OF JUVENILE ALBACORE

Few juvenile albacore from the billfish stomachs were intact. To estimate the SL (standard length) of the fragmentary specimens, which usually included part of the vertebrae, I determined the relation between the standard length and the lengths of various vertebral segments. On 21[2] relatively undamaged specimens (table 1) I measured the standard length, lengths of the vertebral column (39 vertebrae), precaudal vertebrae (1st–18th vertebrae), caudal vertebrae (19th–39th vertebrae), 1st to 9th vertebrae, and 19th to 28th vertebrae. The data indicated that all the relations were linear. The regressions describing the relations are:

Standard length on length of:

(1) vertebral column, $l = -0.2825 + 1.2762L$ ($s = 0.218$),

(2) precaudal vertebrae, $l = 0.0634 + 2.8843L$ ($s = 0.429$),

(3) caudal vertebrae, $l = -0.4370 + 2.2744L$ ($s = 0.298$),

(4) 1st–9th vertebrae, $l = 0.3200 + 6.3963L$ ($s = 0.788$),

(5) 19th–28th vertebrae, $l = -0.4579 + 4.4282L$ ($s = 0.289$),

where l is the standard length (cm.), L is the length (cm.) of the vertebral fragments, and s is the standard deviation from regression.

TABLE 1.—*Measurements of standard length and various vertebral column lengths of 21 juvenile albacore found in stomachs of billfish caught in Pacific Ocean*

Specimen No.	Standard length	Length vertebral column	Length precaudal vertebrae	Length caudal vertebrae	Length 1st–9th vertebrae	Length 19th–28th vertebrae
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	85	68	30	38	13	20
2	88	69	29	39	13	20
3	74	61	25	35	10	18
4	257	200	86	114	38	58
5	354	281	122	159	54	81
6	105	85	35	50	17	25
7	184	147	65	83	29	43
8	143	116	50	66	19	34
9	78	62	25	37	11	18
10	119	97	43	54	19	28
11	118	94	41	53	18	28
12	113	90	38	52	19	27
13	113	92	40	52	18	27
14	121	99	42	57	19	29
15	99	80	34	46	15	24
16	53	41	17	23	8	12
17	86	71	31	40	14	20
18	328	257	112	145	53	75
19	230	182	80	102	35	53
20	230	184	83	101	35	52
21	185	149	64	85	27	44

[1] Trade names referred to in this publication do not imply endorsement of commercial products.

[2] These specimens were from stomachs of predators captured not only in Hawaiian waters but in various localities in the North and South Pacific. I believe this fact should not affect the results. A covariance analysis applied to the relation between standard length and vertebral column length for North and South Pacific juvenile skipjack tuna showed no significant differences between the samples in the mean vertebral column length and slope of the lines.

I estimated the lengths of 26 of the 35 specimens with the regressions. The longest vertebral fragment available was always used to estimate the lengths. For example, if the vertebral column was intact, the regression with the length of all vertebrae as the variable was used rather than any of the other regressions. Pertinent data on the juvenile albacore are in table 2.

TABLE 2.—*Record of juvenile albacore from stomachs of billfishes caught in Pacific Ocean, 1962–66*

Date	Albacore	Predator		
	Standard length	Species	Weight	Location of capture (off the coast of)
	Cm.		*Kg.*	
August 1, 1962 [1]	18.4	Blue marlin	132.4	Kona, Hawaii.
August 13, 1962 [1]	[2] 13.0	Striped marlin	29.5	Waianae, Oahu.
September 13, 1962.[1]	[2] 18.1	Blue marlin	93.9	Do.
November 2, 1962 [1]	25.7	Striped marlin	29.9	Do.
Do	[2] 28.0	do	32.2	Do.
August 16, 1963	[2] 11.1	do	19.5	Do.
September 16, 1963	[2] 14.2	Blue marlin	65.8	Kalapana, Hawaii.
November 4, 1963	[2] 16.0	Shortbill spearfish.	15.9	Do.
November 7, 1963	[2] 11.9 [2] 11.4	Blue marlin	59.4	Do.
February 6, 1964	[2] 31.0	Striped marlin	19.5	Napoopoo, Hawaii.
February 20, 1964	35.4	do	147.9	241 km. south of Oahu.
February 25, 1964	[2] 33.6 [2] 35.5	do	17.2	161 km. south of Oahu.
March 4, 1964	[2] 34.6	do	26.8	West Lanai.
March 17, 1964	[2] 35.0	do	20.9	Waianae, Oahu.
June 29, 1964	[2] 9.5	Shortbill spearfish.	10.9	Do.
July 17, 1964	[2] 11.0	do	12.7	483 km. south of Oahu.
July 27, 1964	[2] 9.0	Striped marlin	12.7	Waianae, Oahu.
August 3, 1964	[2] 12.8	Shortbill spearfish.	10.9	483 km. south of Oahu.
September 15, 1964	[2] 9.5	do	13.6	Upolu Pt., Hawaii.
November 3, 1964	[2] 14.5	Striped marlin	39.9	Waianae, Oahu.
August 24, 1965	[2] 12.0	Blue marlin	52.2	Do.
Do	[2] 7.8	Shortbill spearfish.	15.0	Cape Kumukahi, Hawaii.
August 26, 1965	[2] 12.2	do	13.2	Waianae, Oahu.
Do	13.1	Blue marlin	72.6	Do.
October 6, 1965	17.8	do	49.4	Do.
October 18, 1965	[2] 19.8	Striped marlin	36.7	Ilio Pt., Molokai.
October 28, 1965	16.7	do	22.2	Cape Kumukahi, Hawaii.
November 4, 1965	[2] 12.1	Shortbill spearfish.	5.4	Do.
November 8, 1965	17.4	Striped marlin	33.6	Do.
November 10, 1965	25.0	do	36.7	483 km. south of Oahu.
November 12, 1965	[2] 16.4	do	29.0	Waianae, Oahu.
December 20, 1965	[2] 18.1	Blue marlin	42.6	Do.
January 20, 1966	28.9	Striped marlin	39.0	Do.

[1] Data from Yoshida (1965).
[2] Estimated from regressions.

AGE AND GROWTH

Because the juvenile albacore were collected from the stomachs of billfishes, any size selectivity by the billfishes could affect the analysis of the growth rate of the juveniles. Bias could be introduced by interspecific and intraspecific differences in the size of juveniles eaten by billfishes (e. g., larger billfish preying on larger juveniles). It is possible that billfishes do not feed on small juveniles. Fish shorter than 7 cm. SL were not found in the stomachs of the billfishes.

Other factors that may affect the estimation of growth are (1) changes in spawning season from year to year (the data for all years were pooled), (2) individual variation in growth, and (3) size-associated differences in schooling behavior and distribution of juvenile albacore so that the entire size range of juvenile fish would not be available to the predators. These factors are probably only a few of the many that may affect the data. I assume that all these factors have not seriously biased the data and that the juveniles eaten by billfishes are fairly representative of the population.

The standard length of the juvenile albacore is plotted against sampling date in figure 1. As would be expected, a considerable amount of variation in the size of juveniles is evident, particularly between August and November. Despite the scatter of the points, an increase in size with time is evident. A test showed that a second-degree polynomial provided a better fit to the data than a linear regression ($F=7.491^*$; $d.f.=1, 32$). It was decided, however, to use the simpler linear regression because of the possible heterogeneity of the data, as discussed above. For example, most of the larger juveniles were found in striped marlin stomachs.

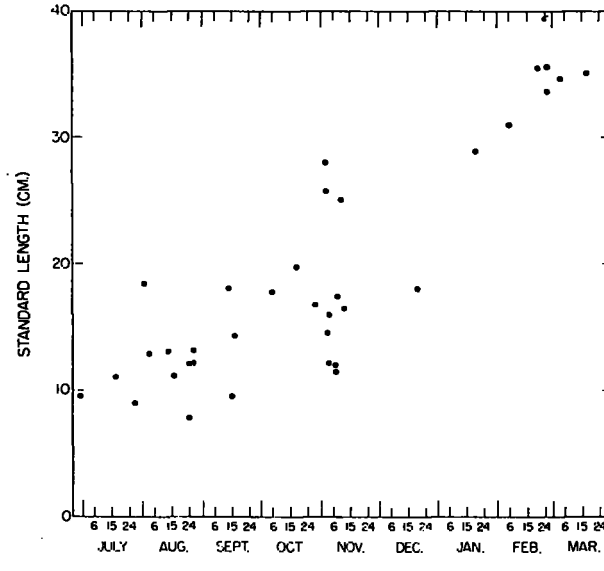

FIGURE 1.—The size and sampling date of juvenile albacore found in billfish stomachs.

For an initial approximation of the growth of the juveniles, a linear regression was fitted to the data with the hatching date set arbitrarily on April 1. Then, assuming a hatching size of 3 mm.,[3] I extrapolated the regression to obtain a better estimate of the hatching date, which proved to be in early May. The regression was then recalculated with May 1 as the hatching date. The linear growth is represented by

$$l = 0.349248 + 0.104184T$$

where l is standard length (cm.) and T is age in days. Figure 2 shows the regression and the observed data. Table 3 gives estimated lengths at various ages.

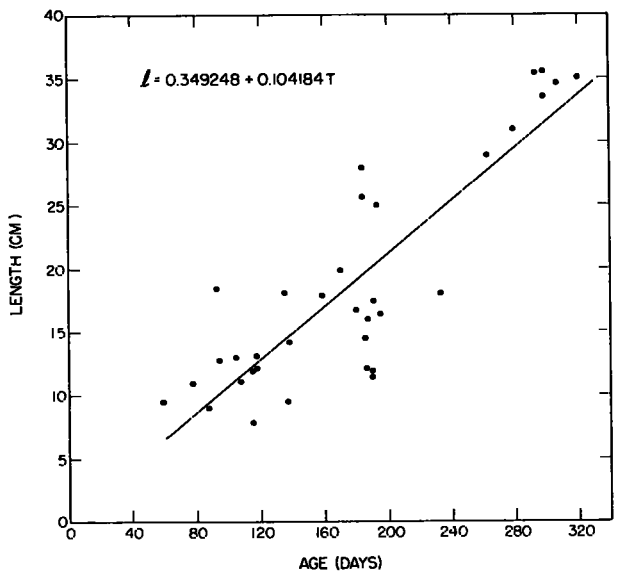

FIGURE 2.—Growth of juvenile albacore found in billfish stomachs.

TABLE 3.—*Expected lengths (derived from the linear regression) at various ages of juvenile albacore from billfish stomachs*

Age*	Standard length	Age*	Standard length
	Linear regression		Linear regression
Days	*Cm.*	*Days*	*Cm.*
60	6.6	240	25.3
90	9.7	270	28.5
120	12.8	300	31.6
150	16.0	330	34.7
180	19.1	360	37.8
210	22.2	365	38.4

*The age is based on an estimated hatching date of May 1 and should be considered only tentative.

[3] Matsumoto's (1958) observations suggest that tuna larvae are about 2 to 3 mm. long at hatching.

The data from this study have a bearing on an unresolved problem in the biology of albacore—that of determining the absolute age of the fish. Various investigators, using scales and vertebrae for aging, have reported conflicting results in determining the absolute age of albacore. Others attempted to estimate the age of groups of albacore that appear regularly in the commercial catch. Investigators now generally agree that the modal groups in the Pacific albacore fisheries represent year classes, but disagree on the ages assigned to the year classes (Clemens, 1961; Otsu and Uchida, 1963).

The expected length that I estimated for 1-year-old fish is most similar to that given by Aikawa and Katō (1938), who made one of the earlier studies on the age and growth of albacore. Their results, however, were not generally accepted because they postulated rectilinear growth. Otsu (1960) was not entirely satisfied with the results of fitting a Gompertz curve to his growth data, which indicated that albacore required 3 years to grow about 30 cm. TL[4] (total length). In a later study Otsu and Uchida (1963) speculated that albacore 30 to 35 cm. TL, which sometimes appear in the commercial catches, were probably 1-year-old fish, and albacore 50 to 55 cm. TL were 2-year olds. Clemens (1961) and Bell (1962), on the other hand, assigned lengths of 52 cm. and 57.3 cm. TL, respectively, to 1-year-old albacore.

SEASONAL AND LENGTH DISTRIBUTION OF JUVENILE ALBACORE

Catch per unit of effort is often used to assess apparent abundance of fishes. For this study I used the number of juveniles per 100 billfishes as an index of apparent abundance. Juvenile albacore were found in stomachs of only three (striped marlin, blue marlin, and shortbill spearfish) of the five billfish species examined. In calculating the monthly apparent abundance of juveniles, however, I used the total of all billfish species for each month. I assumed that (1) no differences exist among the billfish species in relative efficiency in capturing prey and the apparent abundance of all the billfish species did not greatly change over the years and that (2) billfishes will feed on juvenile albacore when they are available, not selecting

[4] Total length as defined by Marr and Schaefer (1949).

other prey in preference to juvenile albacore, or vice versa.

Serious error may result if my first assumption was not valid. Figure 3 shows the monthly distribution of striped marlin, blue marlin, and shortbill spearfish used in this study. These numbers generally reflect the seasonal abundance of these billfishes around Hawaii. Striped marlin are almost always more abundant than blue marlin and shortbill spearfish. Seasonally, striped marlin are most abundant from November to June and blue marlin are most abundant from June to September. Although the distribution of shortbill spearfish in figure 3 shows peaks in April and August, the seasonal abundance of this species is not well defined around Hawaii. Because of interspecific and intraspecific differences in seasonal abundance, differences in catching efficiency among the billfish species may affect estimates of juvenile albacore abundance. No attempt was made to test whether differences did exist in catching efficiency because the data were inadequate.

The second assumption is probably justified; studies on the food habits of billfishes indicate that they are broadly carnivorous (Royce, 1957).

Because of the small number of juveniles, the apparent abundance on a seasonal basis is shown in figure 4, for all years combined. Juvenile albacore occurred in billfish stomachs in all months except April and May; they were most numerous between August and November. The juveniles were generally larger in the winter than in the summer and fall. The large juveniles that were collected between January and March were most likely the progeny of spawning the previous spring.

My observations are consonant with the hypothesis of Otsu and Uchida (1963) that albacore spend their larval and early juvenile stages in subtropical waters and that the older juveniles then migrate into temperate waters. Otsu and Uchida also speculated that small albacore are probably abundant generally throughout temperate waters, but are not available to the commercial fisheries until they are 2 or 3 years old. Occasionally, small albacore (about 35 cm. TL) appear in the catches of the United States west coast and Japanese pole-and-line fisheries.

No attempt was made to find differences in abundance among areas, for example around the various islands, in Hawaiian waters. It is not realistic to do so because longline fishing is not random throughout the islands (Otsu, 1954). Because billfishes are fast-moving and can probably travel many miles in a single day, the location of their capture may not necessarily coincide with that at which they preyed on the juveniles.

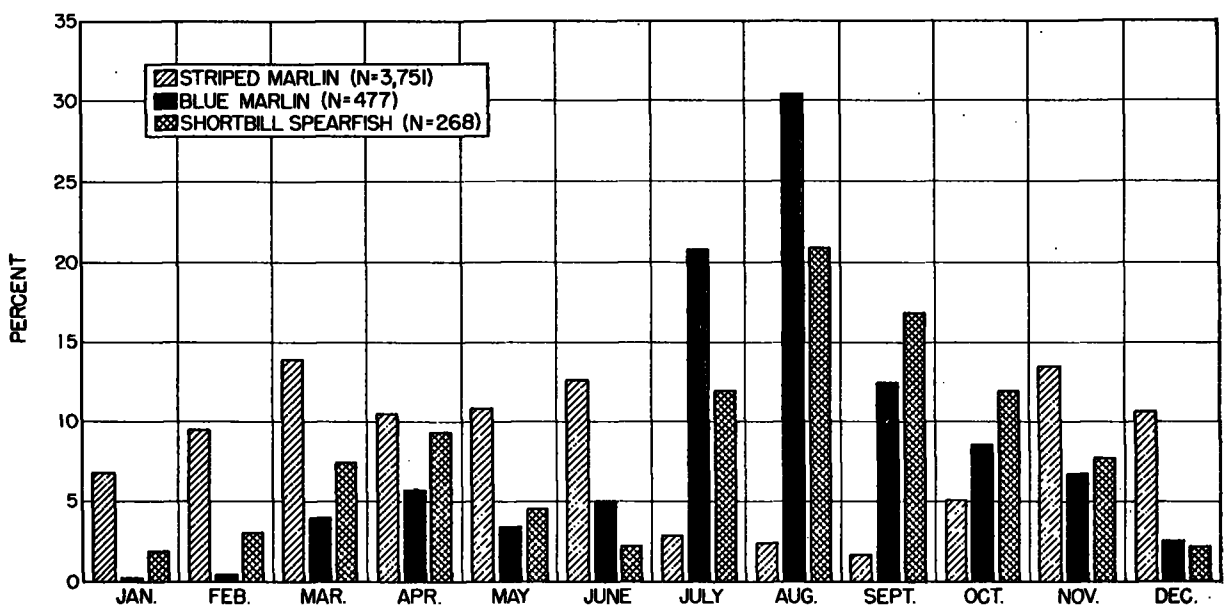

FIGURE 3.—Seasonal distribution of catches of striped marlin, blue marlin, and shortbill spearfish off Hawaii, 1962–65.

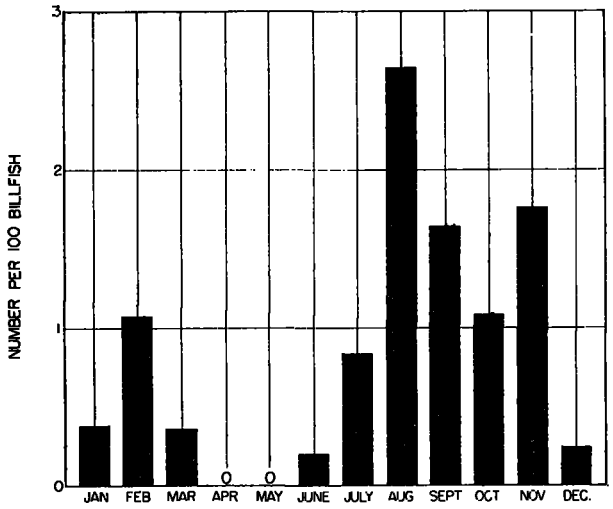

FIGURE 4.—Apparent seasonal abundance of juvenile albacore in Hawaiian waters, 1962–65.

SPAWNING

Yoshida (1965) reported that juvenile albacore occur near the Hawaiian Islands and tacitly assumed that albacore spawned in these waters. The most direct method of determining the spawning habits of fishes is to observe the spawning activity, where possible. Another method is to determine the seasonal and areal distribution of freshly fertilized ova and newly hatched larvae. Because these observations are not available, however, inferences on spawning must be made on indirect evidence.

Otsu and Uchida (1959), who examined albacore ovaries, indicated that albacore in the central and eastern North Pacific (between lat. 30° to 50° N. and the 180th meridian to the U.S. west coast) were either sexually immature fish or were adults that did not show signs of being near spawning. Adult albacore caught near Hawaii, however, showed evidence of active spawning during the summer. Furthermore, the northern limits of the distribution of all tuna larvae in the longitudes of the Hawaiian Islands are lat. 30° N. in the summer and 25° N. in the winter (Walter M. Matsumoto, personal communication). Finally, the wide size range of the juveniles around Hawaii suggests that they probably do not move great distances. I conclude, therefore, that albacore do spawn in Hawaiian waters and that the resulting juveniles spend at least part of their early life in these waters.

As noted earlier, the growth curve provided an estimate of early May as the time albacore larvae hatched. For all practical purposes the hatching and spawning periods can be considered coincident; Matsumoto (1958) estimated that the incubation period of fertilized tuna ova was not more than 4 days. The 5-percent confidence limits for the extrapolated hatching date suggest that albacore may spawn from March to September. I can conclude that albacore spawning around Hawaii peaks in May and may extend from March to September. These observations are not unlike that of Otsu and Uchida (1959), who postulated summer spawning for albacore in Hawaiian waters.

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SOME EFFECTS OF HYDRAULIC DREDGING AND COASTAL DEVELOPMENT IN BOCA CIEGA BAY, FLORIDA [1]

BY JOHN L. TAYLOR AND CARL H. SALOMAN, *Fishery Biologists*
BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY
ST. PETERSBURG BEACH, FLA. 33706

ABSTRACT

Filling of 1,400 hectares (3,500 acres) of bay by hydraulic dredging has reduced the area of Boca Ciega Bay, Fla., by about 20 percent since 1950. An estimate of the annual standing crop destroyed is 1,133 metric tons (798 kg. per hectare, dry whole weight) of sea grass and about 1,812 metric tons (1,277 kg. per hectare, dry weight) of associated infauna. In terms of annual production, the loss of biological resources is far greater—minimum estimates are 25,841 metric tons of sea grass, 73 metric tons of fishery products, and 1,091 metric tons of infauna exclusive of meiofauna. Natural areas remaining in the Bay support local and offshore fisheries and are of value for recreation, public utilities, commerce, and industry. At an estimated value of $988 per hectare per year, worth of the estuarine area already eliminated is $1.4 million annually. In addition, inestimable secondary losses occur, principally from sedimentation, turbidity, and domestic sewage.

Boca Ciega Bay is a part of Tampa Bay, Fla., where coastal development and progressive deterioration of water quality have adversely influenced plant and animal production. This report describes some biological and physical changes that followed alteration of the bay and compares estuarine conditions in dredged areas with those in relatively undisturbed areas.

Hydraulic dredging became an accepted means of creating coastal upland in Florida about 1920, and has since proved an efficient means of providing waterfront real estate of premium value. Dredging was not a serious threat to coastal resources until after 1950 when coastal construction started on a large scale, especially along the lower east coast and the low-energy strand of the west coast from Tampa Bay southward. Profit and permissive attitudes toward the sale of submerged land contributed to rapid disposal of vast public holdings along much of Florida's 14,400 km. (9,000 statute miles) of tidal coastline. Bay filling has been little regulated, and in most situations biological and recreational resources of estuarine waters have been disregarded by coastal developers and governing authorities (Davis, 1956; Brunn and De Grove, 1959; Kidd, 1963).

Legislation to control dredge-fill projects in Florida appeared first in 1957 (Section 253.122 Florida Statutes, 1957), and the following year all such projects became subject to Federal review (Fish and Wildlife Coordination Act, P.L. 85–624). Unfortunately, under these laws the sale and development of submerged land remained largely arbitrary and most efforts to stop landfills in estuaries have been unsuccessful (Arnold, 1967).

Guidelines for appraisal of estuarine areas were proposed by Thompson (1961), and more positive measures are now being taken to conserve marine resources and provide for their rational use in Florida as well as in other parts of the country and abroad (Florida Statutes, chapter 67–393; Gilmour, 1965; Hutton, 1964; Tukey, 1965; Cain, 1966; Caldwell, 1966). Encouraging, too, is the

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fact that developers of bayfill projects have recently demonstrated a willingness to preserve some natural features on development sites (Gresham, 1967; Sykes, 1967).

In Florida and other States bordering the Gulf of Mexico, dredging and other forms of estuarine destruction damage fisheries because most of the species taken in sport and commercial fisheries live in estuaries during part or all of their life cycle (Skud and Wilson, 1960; Sykes and Finucane, 1966). Premium estuarine habitats that support the fisheries are vegetated, littoral biotopes containing populous, stable, and highly productive communities (Humm, 1956; Odum and Hoskin, 1958; Pomeroy, 1959; Odum, 1961; Margalef, 1963; Moore, 1963; Livingstone, 1965; Stephens, 1966; O'Gower and Wacasey, 1967).

Commercial fisheries in the Gulf of Mexico account for one-third of the Nation's marine landings and are worth about $114 million annually (Lyles, 1966). The landings could probably be increased two to five times through greater fishing effort, and use of species not now fished would raise these figures even higher (Schaefer, 1965; Pirie, 1967). In addition, production in some estuaries will certainly increase when methods are developed for culture of certain fishes, crustaceans, mollusks, and marine plants (Allen, 1963; Loosanoff and Davis, 1963; Shelbourne, 1964; Boney, 1965). Thus, perhaps the most timely argument against further destruction of estuarine habitats is the present and potential value of these areas for production of food (Tressler and Lemon, 1951; Hornig, 1966). Other nondestructive uses of estuaries, such as recreation, are compatible with fisheries and greatly add to the cash value of estuarine acreage, particularly in resort areas like Boca Ciega Bay.

DESCRIPTION OF AREA

Boca Ciega Bay lies within Tampa Bay, midway along the west coast of peninsular Florida. Separated from the Gulf of Mexico by a chain of barrier islands, Boca Ciega Bay merges with Tampa Bay on the south and extends 25.6 km. (16 miles) north as a narrow coastal lagoon (fig. 1). Water area is about 70 km.^{2} (27 square miles) and water depth over nearly 80 percent of the area is 1.8 m. or less (Olson, 1953; Olson and Morrill, 1955).

Bayfills occupy about 1,400 hectares (3,500 acres) and have reduced the water area by nearly 20 percent (Saloman, 1965). Aerial photographs taken before and after major dredging illustrate how coastal development has reshaped Boca Ciega Bay in less than a generation (figs. 2–9).

In areas that remain relatively undisturbed, sediments are a firm mixture of shell and sand (Goodell and Gorsline, 1961). They support luxuriant beds of sea grass except in deep depressions and channels where light is inadequate. Turtle grass (*Thalassia testudinum* König) is the most common species, but in many places any of three other species may be present (Phillips, 1960a, 1962).

The first comprehensive study of Boca Ciega Bay began in 1955 as a joint project of the Florida Board of Conservation and the Fish and Wildlife Service (Hutton, Eldred, Woodburn, and Ingle, 1956). The objectives were to determine commercial and recreational assets of the lagoon and focus attention on undesirable consequences of past and pending dredge-fill operations. Although the report did not impede bayfill construction, it described many biological and physical features of the bay. Subsequent work on the biology of Boca Ciega Bay included that of Springer and Woodburn (1960), Phillips (1960b), Dragovich and Kelly (1964), Saloman (1965), Sykes and Finucane (1966), and Bullock and Boss.[2]

PROCEDURE

Sampling began in September 1963 at 31 stations. Ten of these (BC series) had been previously sampled by biologists of the Florida State Board of Conservation (Hutton et al., 1956). The other 21 (D and PB series) were in natural areas, deeply dredged canals, and a variety of habitats influenced to some degree by dredging. On the basis of an evaluation of initial collections at all stations, we selected six (PB series) to represent conditions at dredged and undredged locations. Sampling at these stations began in November 1963 and continued at 3-month intervals for 9 months (February, May, and August 1964). Four stations (PB 1, 3, 5, and 6) were in undredged areas, and two (PB 2 and 4) were in dredged access canals be-

[2] Bullock, Bob, and Chuck Boss. The ecological distribution of the marine mollusks in Boca Ciega Bay—1962. On file at Department of Biology, Florida Presbyterian College, St. Petersburg, Fla. 33711.

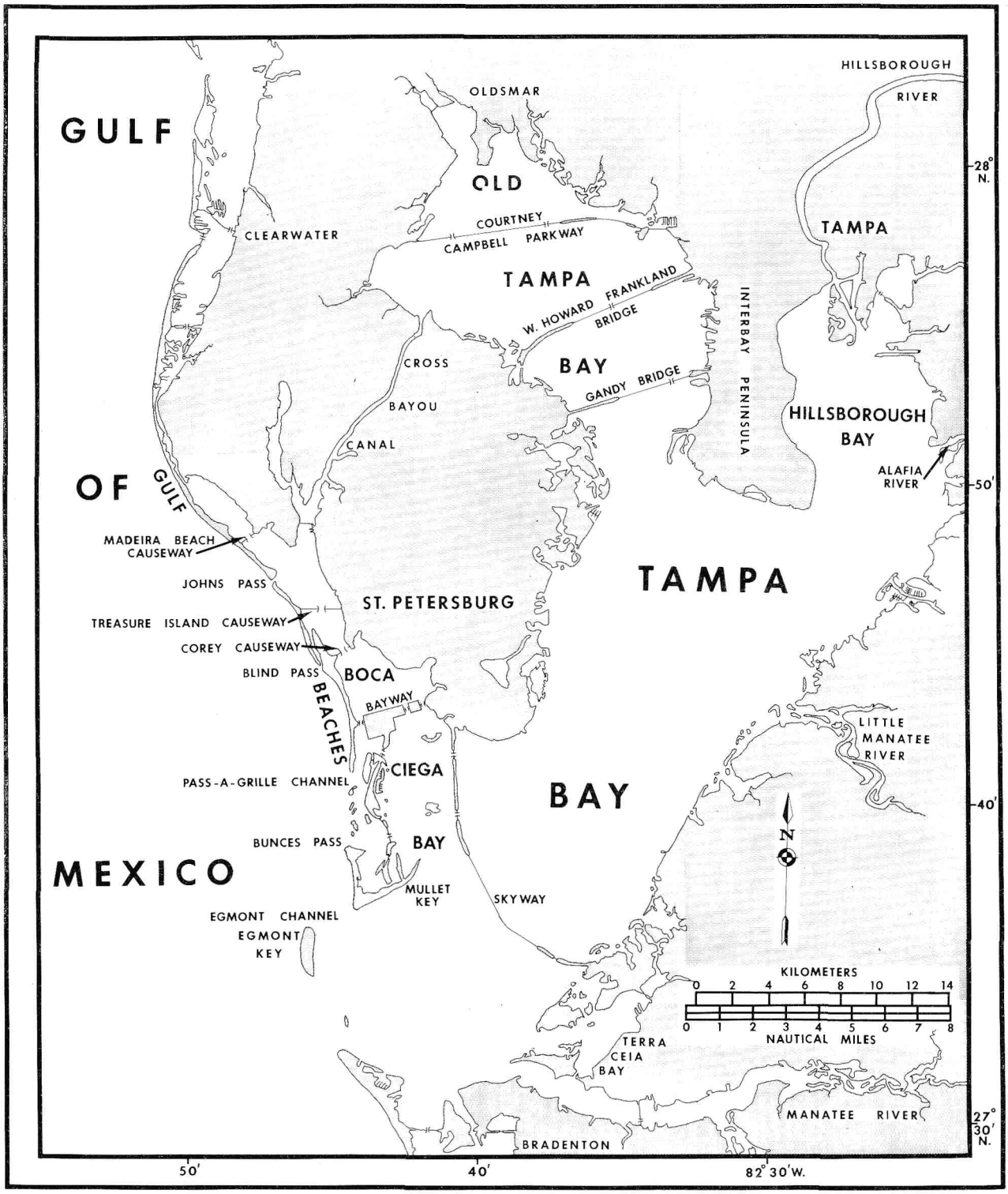

FIGURE 1.—Boca Ciega Bay and Tampa Bay, Fla.

FIGURE 2.—Southern Boca Ciega Bay in 1953 before major bayfill construction (photograph courtesy of Airflite, St. Petersburg, Fla.).

tween bayfills. In addition, four areas of the bay (A, B, C, and D) were sampled in August 1964 to estimate the biomass of turtle grass and infauna (figs. 10 and 11). At all sampling stations, water was collected at surface and bottom for physical and chemical analyses, sediment samples were obtained for textural and chemical analyses, and biological collections were made for benthic invertebrates, plants, and fishes.

Measurements were made of water temperature, salinity, pH, total phosphorus, dissolved oxygen, secchi disc depth, chlorophyll *a*, and primary production following methods described by Saloman, Finucane, and Kelly (1964)—see table 1. Supplemental data on water quality were used to show long-term hydrological changes that have occurred throughout Tampa Bay as a result of coastal development (tables 2–5). The supplementary data are from the following published reports and unpublished data of the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla.: Odum (1953), Hutton et al. (1956), Marshall (1956), Finucane and Dragovich (1959, 1966), Pomeroy (1960), Dragovich, Finucane, and May (1961), Saloman et al. (1964), Dragovich, Kelly, and Finucane (1966), Saloman and Taylor (1968), May and Johnson (unpublished data on

FIGURE 3.—Southern Boca Ciega Bay in 1963 showing Pinellas County Bayway and other bayfill areas (photograph courtesy of Airflite, St. Petersburg, Fla.

chlorophyll *a* and primary productivity),[3] and the U.S. Weather Bureau (unpublished water temperature data for Egmont Key).[4]

Sediments and infauna were collected with a shovel in water as deep as 1 m. and with a bucket dredge at greater depths (Taylor, 1965). A subsample of about 500 cc. was withdrawn from each bottom sample for sediment analysis. Each subsample was sealed in a moist condition and later analyzed at Florida State University.[5] Particles of sand size and larger were separated from silt and clay by wet sieving through a screen of 62-micron mesh. Material remaining on the sieve was dried and subdivided by use of a series of nested screens mounted on a mechanical shaker. The fine fraction that passed the 62-micron mesh was sized electronically in a Coulter counter.[6] Clay minerals were examined by X-ray diffraction, and chemical analyses were made for carbonates, organic carbon, and organic nitrogen. Statistical calculations were made by computer and included mean

[3] May, B. Z., and Lucius Johnson. On file at Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla. 33706.

[4] On file at U.S. Weather Bureau, Tampa International Airport, Tampa, Fla. 33614.

[5] Sediment analyses were under the direction of H. Grant Goodell, Sedimentological Laboratory, Florida State University, Tallahassee, Fla. 32306.

[6] References to trade names in this publication do not imply endorsement of commercial products.

FIGURE 4.—Central Boca Ciega Bay near Corey Causeway in 1949 before major bayfill construction (photograph courtesy of Airflite, St. Petersburg, Fla.

grain size, standard deviation (sorting), skewness, and kurtosis.

In addition to the collection of bottom organisms taken by shovel and dredge, the epibenthos was sampled at all stations by a bottom drag fitted with fine netting (Taylor, 1965). Infauna was removed from sediments in a Tyler No. 24 screen of 30-cm. diameter and 0.701-mm. mesh. To distinguish small specimens from debris, rose bengal dye was added to material concentrated by screening (Jones, 1961). Ten percent sea-water Formalin used to fix specimens was replaced later by 70 percent isopropanol.

Fishes were collected at each station with either a 4.8-m. semi-balloon trawl or a 21-m. beach seine. The trawl was hung with a 3.75-cm. stretch mesh body fitted with a 1.25-cm. bag liner. The seine had a stretch mesh of 1.25 cm. in the end sections and 0.08 cm. in the bag. In addition, a 7.5-cm. stretch mesh trammel net, 90 m. x 1.8 m., was fished each sampling period at the entrance of access canals where stations were located. Fishes, invertebrates, and plants taken in nets and by bottom samplers were sorted, enumerated, and identified. Animals in each group are not treated in detail in the present report, although some are mentioned because of their prominence in bayfill canals.

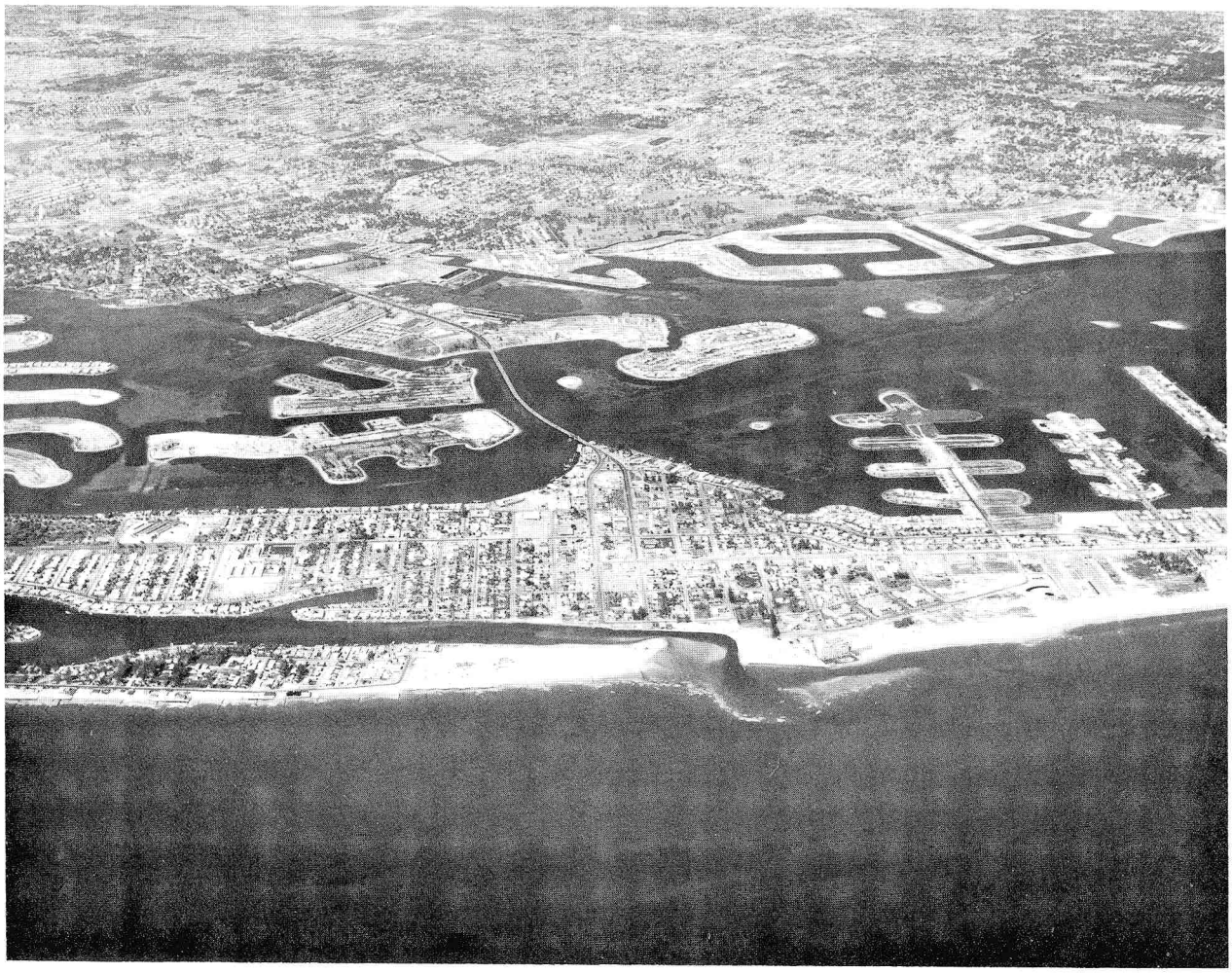

FIGURE 5.—Central Boca Ciega Bay near Corey Causeway in 1963 showing bayfill areas (photograph courtesy of Airflite, St. Petersburg, Fla.).

Quantitative samples for estimates of biomass were taken in August 1964 with a 0.25 m.^{2} plug sampler that extracts sediments to a depth of 22.5 cm. (fig. 12). In operation, the sampler is pushed into the sediment and then dug out with a shovel which covers the bottom of the sampler and retains the sediment plug. Total weights of plants and infauna from grass beds were determined from sets of triplicate samples taken in representative stands of turtle grass in lower, central, and upper Boca Ciega Bay (areas A, B, and C, fig. 10). Infaunal biomass from unvegetated bottom was determined from a single set of three samples in the central part of the bay shoreward of station D–5 in area D (fig. 11). Wet and oven-dried plants and wet whole animals were weighed on a Mettler K–7 balance. Dry whole weight of animals was arbitrarily calculated at 15 percent of wet whole weight because most of the animals in all samples were polychaete worms, small crustaceans, and small mollusks (Sanders, 1956; Thorson, 1957). Large mollusks and crustaceans that appeared sporadically in bottom samples were disregarded in calculations of standing crop because of the bias they would have introduced. Consequently, figures for dry whole weight of animals are conservative, particularly in lower Boca Ciega Bay (area A), where the southern hard-shell clam (*Mercenaria*

FIGURE 6.—Central Boca Ciega Bay near Treasure Island Causeway in 1949 before major bayfill construction (photograph courtesy of Airflite, St. Petersburg, Fla.

campechiensis) and pink shrimp (*Penaeus duorarum*) are abundant (Saloman, 1965; Taylor and Saloman, 1967). Biomass estimates of turtle grass are also minimal because the sampler did not collect roots and rhizomes that penetrate sediments beyond 22.5 cm. (9 inches).

TEMPERATURE, SALINITY, AND pH

Temperature, salinity, and pH of Boca Ciega Bay are similar to those in water near the mouth of Tampa Bay because land drainage is not appreciable and four passes lead directly to the Gulf of Mexico. Furthermore, there is little or no stratification of water masses in unprotected parts of the bay because of shallow depths and tidal and wind-driven circulation (table 1).

The most detailed record of water temperature for lower Tampa Bay comes from daily observations over 18 years by the U.S. Coast Guard at Egmont Key. The monthly means correspond closely to means of our water temperature data for 1963–64 and to means of other records from Boca Ciega Bay between 1961 and 1965 (tables 1 and 2). The range of water temperature over shallow flats, however, is considerably greater than the range of monthly means. For example, Phillips (1960b) recorded 36.9° C. from water standing over turtle grass in July 1958, and a low of 4.8° C.

FIGURE 7.—Central Boca Ciega Bay near Treasure Island Causeway in 1963 showing bayfill areas (photograph courtesy of Airflite, St. Petersburg, Fla.).

was recorded near shore at Mullet Key on January 31, 1966 (Saloman and Taylor, 1968).

Water temperature is usually the same in the open bay and in bayfill canals, except in winter when periodic cold fronts create a temporary thermocline in deep water. At such times, bottom water may be 4 to 5° C. warmer than surface water and serves as a refuge for polythermal fishes (Kinne, 1963). If cold weather persists for more than a few days, however, bottom water becomes cold and sequestered fishes may die. During prolonged cold in February 1966, John H. Finucane (unpublished data)[7] observed mass mortality among snook, *Centropomus undecimalis* (Block), in bayfill canals of Boca Ciega Bay.

Average salinity in Boca Ciega Bay (32 p.p.t.) approaches that of the nearshore Gulf and is at least 10 p.p.t. higher than water in northern reaches of Old Tampa Bay and Hillsborough Bay (table 3). Even though the major portion of annual rainfall (127 cm.) comes in the summer and fall, seasonal fluctuations of salinity in the lagoon are slight. Appreciable changes occur only in surface water directly south of Lake Seminole Dam

[7] Unpublished data (quarterly report) on file, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla. 33706.

FIGURE 8.—Northern Boca Ciega Bay near Johns Pass in 1952 showing first bayfill areas (photograph courtesy of Airflite, St. Petersburg, Fla.).

at station PB–1 (fig. 10 and table 1). Stable and relatively high salinity in Boca Ciega Bay and the temperate or subtropical water temperature favor the occurrence of a large number and diversity of marine plants and animals (Gunter, 1961; Kinne, 1964).

In the sea, pH is generally near 8 and remains stable unless affected by abnormally high photosynthetic activity, rapid temperature change, or anoxic conditions on the sea floor (Skirrow, 1965). In Boca Ciega Bay the observed pH range of 7.2 to 8.5 is normal for water of nearly oceanic salinity (Park, Hood, and Odum, 1958; Reid, 1961). Within any single sampling period pH on the surface and bottom at each station varied no more than one unit.

OXYGEN

Daytime concentrations of oxygen on the surface and bottom of dredged and undredged stations were at least 3.5 ml./l. in all seasons (table 1). In more recent work, however, less than 2 ml./l. was recorded in June and August from bottom water at a dredged location in the central part of Boca Ciega Bay near station PB–4 (Dragovich et al., 1966). These recent data show that oxygen is re-

FIGURE 9.—Northern Boca Ciega Bay near Johns Pass in 1963 showing bayfill areas (photograph courtesy of Airflite. St. Petersburg, Fla.).

duced in summer over the soft sediments of access canals. Tidal movements in the bay probably make some oxygen available throughout the water column at most times, but occasional reductions limit some marine animals (Emery and Stevenson, 1957; Reish, 1959).

Elsewhere in Tampa Bay, marked oxygen reduction near the bottom has been recorded only in Hillsborough Bay (Saloman et al., 1964), where pollution from sewage is heavy, summer water temperature is high, and water circulation is poor. Additional bayfill development in Boca Ciega Bay would increase sewage volume, impede water circulation, and further reduce dissolved oxygen.

PHOSPHORUS AND NITROGEN

Phosphorus concentration was high in surface and bottom water at dredged and undredged locations. At dredged locations, bottom concentration was generally higher than surface concentration. At undredged locations, however, concentration did not vary consistently with water depth (table 6). Phosphorus was probably reduced in calm, surface water between finger-fills by deposition of sorbed phosphates bound to particles of silt and clay (Pomeroy, Smith, and Grant, 1965).

Nitrogen was not measured in this study, but other data show that it is plentiful in Boca Ciega Bay (table 4).

FIGURE 10.—Boca Ciega Bay showing station locations (BC and PB series, and biomass stations A, B, and C), bayfill areas (black), and proposed bayfill areas (shaded).

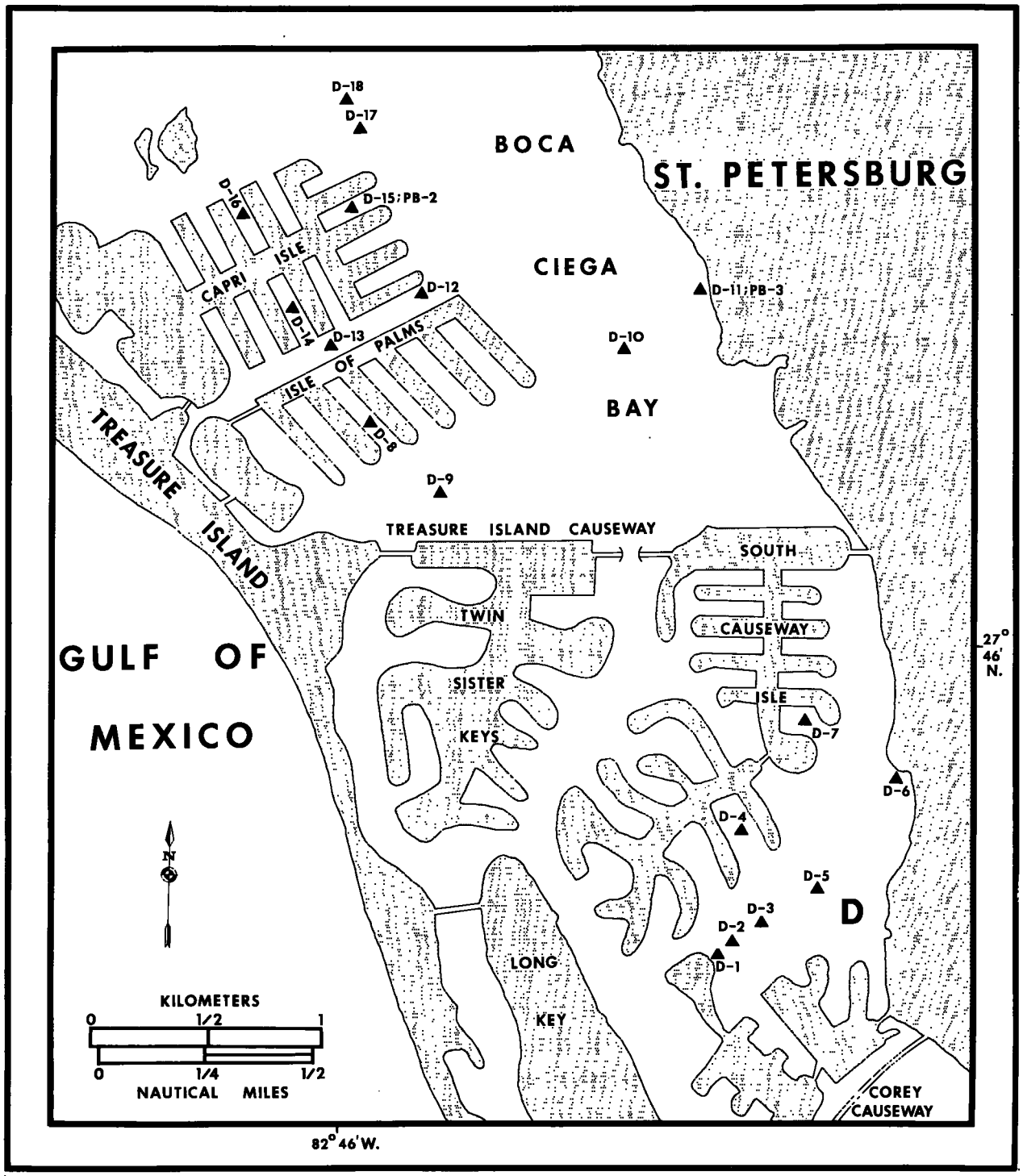

FIGURE 11.—Boca Ciega Bay north of Corey Causeway showing station locations (D–1 through D–18, and biomass station D).

TABLE 1.—*Hydrological measurements from surface and bottom water at sampling stations in undredged and dredged areas of Boca Ciega Bay, Fla., 1963–64*

Date and stations	Depth	Temperature	Salinity	pH	Dissolved oxygen	Total phosphorus	Secchi disc depth	Chlorophyll *a*	Primary production
NOVEMBER 1963									
Undredged stations:									
PB-1	*M.*	°*C.*	*P.p.t.*		*Ml./l.*	*μg.at./l.*	*Cm.*	*Mg./m.*³	*G.C/m²/day*
Surface	0	20.9	29.6	8.0	4.6	16.6	105.0	13.1	0.52
Bottom	2	20.6	30.3	8.2	5.2	5.0			
PB-3									
Surface	0	19.8	31.9	8.2	4.7	22.1	100.0	11.1	.48
Bottom	2	19.4	31.9	8.2	5.5	21.4			
PB-5									
Surface	0	20.0	31.8	7.9	4.9	15.6	92.5	9.5	.44
Bottom	3	20.0	31.9	8.1	4.9	14.1			
PB-6									
Surface	0	20.5	32.5	8.1	5.3	1.1	240.0	1.5	.17
Bottom	4	20.4	32.8	8.0	5.2	17.3			
Mean surface value		20.3	31.5	8.1	4.9	13.9	134.4	8.8	.40
Mean bottom value		20.1	31.7	8.1	5.2	14.5			
Dredged stations:									
PB-2									
Surface	0	18.4	32.4	8.1	4.5	5.9	105.0	9.5	.37
Bottom	4	18.5	32.0	8.2	4.1	18.6			
PB-4									
Surface	0	19.8	31.7	8.0	4.4	4.7	130.0	12.9	.81
Bottom	4	19.7	31.7	8.0	4.0	1.1			
Mean surface value		19.1	32.1	8.1	4.5	5.3	118.0	11.2	.59
Mean bottom value		19.1	31.9	8.1	4.1	9.9			
FEBRUARY 1964									
Undredged stations:									
PB-1									
Surface	0	13.8	20.3	8.1	5.3	8.8	80.0	13.0	.44
Bottom	2	14.7	29.2	7.9	5.6	5.0			
PB-3									
Surface	0	15.2	29.7	8.5	7.8	3.8	92.5	4.6	.16
Bottom	2	13.9	31.0	7.8	6.1	3.9			
PB-5									
Surface	0	15.2	29.0	8.4	5.9	6.7	88.5	17.0	.25
Bottom	3	15.2	29.0	8.1	5.9	7.4			
PB-6									
Surface	0	14.7	31.6	8.1	5.4	6.4	112.5	13.3	.24
Bottom	4	14.6	31.7	7.2	5.4	7.1			
Mean surface value		14.7	27.7	8.3	6.1	6.4	93.1	12.0	.27
Mean bottom value		14.6	30.3	7.8	5.8	5.9			
Dredged stations:									
PB-2									
Surface	0	13.8	29.7	8.1	6.6	3.2	82.5	7.7	.27
Bottom	4	13.8	30.2	8.0	5.8	2.8			
PB-4									
Surface	0	14.7	28.2		5.9	5.4	82.5	18.9	.07
Bottom	4	14.5	28.8	8.1	5.3	5.4			
Mean surface value		14.3	29.0	8.1	6.3	4.3	82.5	13.3	.17
Mean bottom value		14.2	29.5	8.1	5.6	4.1			

TABLE 1.—*Hydrological measurements from surface and bottom water at sampling stations in undredged and dredged areas af Boca Ciega Bay, Fla., 1963–64*—Continued

Date and stations	Depth	Temperature	Salinity	pH	Dissolved oxygen	Total phosphorus	Secchi disc depth	Chlorophyll *a*	Primary production
MAY 1964	*M.*	°*C.*	*P.p.t.*		*Ml./l.*	*µg.at./l.*	*Cm.*	*Mg./m.*³	*G.C/m.²/day*
Undredged stations:									
PB–1									
Surface	0	27.0	33.6	7.8	3.6	6.1	87.5	9.9	.55
Bottom	2	26.8	33.4	8.0	3.8	6.2			
PB–3									
Surface	0	28.0	33.8	7.9	5.0	4.3	110.0	7.1	.48
Bottom	2	27.0	33.8	8.1	4.9	4.8			
PB–5									
Surface	0	27.9	32.9	7.9	4.1	12.4	115.0	3.5	.25
Bottom	3	27.7	32.9	7.9	3.9	10.9			
PB–6									
Surface	0	28.5	34.7		4.9	7.5	150.0	2.2	.19
Bottom	4	28.5	34.5	8.2	5.0	5.4			
Mean surface value		27.9	33.8	7.9	4.4	7.6	115.6	5.7	.37
Mean bottom value		27.5	33.7	8.1	4.4	6.8			
Dredged stations:									
PB–2									
Surface	0	27.3	34.0	8.0	4.5	4.1	142.5	6.6	.59
Bottom	4	26.6	34.1	8.3	4.0	4.9			
PB–4									
Surface	0	27.3	33.6		4.0	6.3	130.0		
Bottom	4	27.2	33.6		3.6	10.8			
Mean surface value		27.3	33.8	8.0	4.3	5.2	136.3	6.6	.59
Mean bottom value		26.9	33.9	8.3	3.8	7.9			
AUGUST 1964									
Undredged stations:									
PB–1									
Surface	0	29.8	27.7	7.8	4.5	15.8	45.0	28.2	.67
Bottom	2	27.7	31.8	7.9	3.8	11.8			
PB–3									
Surface	0	30.1	33.9	8.1	6.3	9.5	100.0	6.4	.33
Bottom	2	29.8	33.8	8.1	4.9	8.6			
PB–5									
Surface	0	30.5	33.3	7.4	4.8	12.9	125.0	4.5	.32
Bottom	3	30.0	33.3	8.4	4.8	13.3			
PB–6									
Surface	0	31.1	34.0	8.1	5.6	13.6	147.5	6.7	.59
Bottom	4	30.1	33.9	8.2	4.4	15.5			
Mean surface value		30.4	32.2	7.9	5.3	13.0	104.4	11.5	.48
Mean bottom value		29.4	33.2	8.2	4.5	12.3			
Dredged stations:									
PB–2									
Surface	0	30.7	34.3	7.9	5.2	7.1	105.0	10.6	.59
Bottom	4	29.8	34.4	7.9	3.5	7.2			
PB–4									
Surface	0	29.7	33.6	8.0	4.4		125.0	3.9	.28
Bottom	4	29.5	33.8	8.2	3.4	12.4			
Mean surface value		30.2	34.0	8.0	4.8	7.1	115.0	7.3	.44
Mean bottom value		29.7	34.1	8.1	3.5	10.8			

TABLE 2.—*Mean monthly surface water temperature (°C.) from observations (daily at 0700 hours) near Tampa Bay entrance (Egmont Key) 1948–65,[1] and Boca Ciega Bay (near station PB–4) 1961–65*[2]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Egmont Key, Fla.:												
Mean low	13.9	12.7	16.3	20.0	25.1	27.5	27.9	28.5	27.0	24.0	19.4	14.6
Mean high	20.2	20.8	23.0	24.4	26.8	29.4	30.5	30.6	29.7	27.1	23.7	21.1
Mean	16.3	17.3	19.7	22.3	25.9	28.5	29.6	29.8	28.6	25.5	21.1	17.5
Boca Ciega Bay, Fla.:												
Mean	14.2	16.5	19.3	23.6	25.5	29.8	29.3	30.2	28.7	25.3	21.8	16.9

[1] U.S. Weather Bureau, Tampa International Airport, Tampa, Fla. 33614. [2] Saloman et al., 1964; Dragovich et al., 1966; Finucane and Dragovich, 1966.

TABLE 3.—*Mean monthly surface water salinity (p.p.t.) for areas of Tampa Bay and adjacent Gulf of Mexico, 1954–65*[1]

Areas	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly mean
Old Tampa Bay:													
Upper	20.0	18.6	21.1	23.5	22.8	26.4	22.5	22.6	18.3	21.4	21.4	23.1	21.8
Middle	23.4	21.8	22.3	23.8	24.9	26.5	25.8	22.3	21.6	21.4	22.4	23.7	23.3
Lower	25.8	25.8	25.3	25.8	26.9	27.6	26.9	24.6	22.6	23.8	23.7	24.7	25.3
Hillsborough Bay:													
Upper	19.7	22.2	19.3	22.8	19.8	23.6	19.3	19.1	16.6	21.3	22.3	23.0	20.8
Lower	21.3	21.2	21.4	22.3	21.3	25.9	23.6	20.4	22.0	22.9	25.2	25.6	22.8
Tampa Bay:													
Upper	25.6	24.6	22.7	23.0	25.9	27.5	26.5	22.0	21.2	22.7	24.8	25.8	24.4
Middle	27.5	26.8	25.0	25.0	28.1	29.0	29.0	23.4	24.3	25.8	26.5	27.5	26.5
Lower	30.5	29.3	28.5	30.6	31.4	31.8	32.2	30.3	29.1	29.8	30.5	30.7	30.4
Terra Ceia Bay	27.6	25.5	27.6	30.2	31.1	31.6	29.9	24.4	25.4	28.4	30.0	30.2	28.5
Egmont Key	31.9	31.9	31.5	31.5	33.1	34.1	34.3	32.4	30.7	31.0	31.7	31.8	32.2
Boca Ciega Bay	31.7	32.0	30.7	31.8	33.2	34.0	33.4	31.3	31.2	31.9	32.5	32.1	32.1
Gulf of Mexico	33.4	33.7	33.4	34.0	34.6	35.1	35.0	34.1	34.0	33.9	33.7	33.7	34.1

[1] Finucane and Dragovich, 1959; Dragovich et al., 1961; Saloman et al., 1964; Finucane and Dragovich, 1966; Dragovich et al., 1966.

TABLE 4.—*Surface values of total phosphorus, 1952–66, total nitrogen, 1961–66,[1] and nitrogen-phosphorus ratio (N/P)*[2] *for areas of Tampa Bay, Fla.*

Area	1952–53	1954	1955	1956	1957	1958	1959	1960	1961		1962		1963		1964		1965		1966	
	P	P	P	P	P	P	P	P	N	P	N	P	N	P	N	P	N	P	N	P
	μg.at./l																			
Area I—Old Tampa Bay:																				
January									44.5	20.6	31.2	29.9	33.7		37.6	23.6	26.1	24.6		
February									24.2	23.7	35.8	22.3	33.7	29.1			15.7	27.6		
March									42.6	14.6	43.0	18.5	49.6	28.2			55.8	18.7		
April	7.7								47.0	18.5	63.5	32.5	39.1	22.3			62.4	20.7		
May									54.4	23.9	36.4	25.9	27.6	24.9			40.7	28.7		
June									50.2	28.0	31.7	19.6	27.6				62.8	30.1		
July									47.7	21.5	74.1	19.4	25.4				36.4	11.9		
August									46.6	21.4	42.8	25.5	69.4	24.2	83.1	25.5	46.3	14.0		
September	8.1								57.0	21.6	58.4	21.2	52.4	26.6	46.4	23.7	61.7	25.1	58.8	25.5
October									41.7	26.2	35.4	29.8	36.0	5.6	43.3		66.6	28.2	64.3	19.3
November									38.9	18.5	27.2	30.9			33.6	24.6	47.9	22.1	48.4	18.3
December									39.4	22.3	62.2	23.2	31.8	18.5	28.0	21.6	46.1	22.1	47.5	19.3
Yearly mean	7.9								44.3	22.2	45.0	23.1	43.5	22.2	38.1	24.8	57.2	24.4	47.1	21.6
N/P									.9		.9		.9		.6		1.3		1.0	
Area II—Hillsborough Bay:																				
January													37.9	36.1	48.1					
February													55.3	25.5	50.7					
March													57.0	23.5	47.4					
April	18.7													27.9	60.7					

See footnotes at end of table.

TABLE 4.—*Surface values of total phosphorus, 1952–66, total nitrogen, 1961–66,*[1] *and nitrogen-phosphorus ratio (N/P)* [2] *for areas of Tampa Bay, Fla.*—Continued

Area	1952–53 P	1954 P	1955 P	1956 P	1957 P	1958 P	1959 P	1960 P	1961 N	1961 P	1962 N	1962 P	1963 N	1963 P	1964 N	1964 P	1965 N	1965 P	1966 N	1966 P
Area II—Hillsborough Bay—Continued																				
May													41.0	42.7	45.4					28.6
June													38.3	23.2	30.7					25.4
July													77.4	22.7	43.6					10.1
August													60.9	29.5	73.9				69.6	11.2
September	23.9										59.2	23.3	55.7	26.0	50.1				90.7	23.0
October											50.5	31.4	49.7	16.9	44.1				95.5	18.7
November											75.3	32.6			67.4				73.3	19.9
December											41.4	16.4	60.7	22.1	47.6				71.8	18.2
Yearly mean	21.3										56.6	25.9	53.4	26.9	50.8				80.2	19.4
N/P											1.0		.9						1.8	
Area III—Tampa Bay:																				
January								22.8		24.5	21.0	23.2	35.6	33.3					26.8	22.4
February								23.6		23.0			28.5	22.5					31.3	8.8
March								28.3			46.8	19.5	44.1	26.0	33.0				58.3	19.7
April	3.5							23.7			31.3	31.0	54.0	9.6	59.3				76.6	11.4
May								22.6				24.9	31.4	25.2	37.6				37.0	31.7
June								22.7		24.2	37.7	24.3	30.0	22.0					45.0	20.8
July								20.9		26.9	40.6	20.7	32.1	18.4	28.7				44.8	10.1
August								21.1			42.1	20.5	34.0	25.0	26.0		79.3	20.2	50.1	10.7
September	9.2							27.9	50.7	32.5	29.0	18.8		27.0	20.7		71.4	19.1	56.5	28.5
October									36.7	24.5	33.4	29.1	37.9	19.0	28.7		49.4	24.6	61.9	17.5
November								21.1	34.3	19.5	42.2	31.4			27.4		42.0	21.0	51.1	17.9
December								23.5	25.1	18.0	48.2	14.5	38.6	10.4	20.0		44.7	20.5	46.7	18.1
Yearly mean	6.4							23.5	36.7	24.1	37.2	23.4	36.6	22.6	31.3		57.4	21.1	48.8	18.1
N/P									.7		.7		.7				1.1		1.2	
Area IV—Tampa Bay Entrance:																				
January								2.1	26.9	7.7	33.3	10.9			26.1				14.7	6.2
February				13.6				3.9	18.1	4.7			22.0	10.6	21.2				13.0	5.5
March				9.7				8.4		3.9	45.4	3.0	20.5		19.4				44.0	15.2
April				4.9				3.9			31.2	8.6	29.4	8.6	12.8				42.0	13.7
May				1.7				3.6	19.6	5.2	36.7	4.5	23.6	7.1	28.7				34.0	8.6
June				9.8				4.9	47.3	5.1	26.8	7.7	27.1	8.8	11.7				47.6	13.9
July				5.4				4.6	34.2	2.8	24.9	8.2	32.6	9.6	39.0				37.8	10.4
August								4.4			36.3	12.5	22.0	10.6	23.1		32.7	11.4	39.4	10.3
September	4.2		21.6	15.9				6.4	39.0	5.7	23.2	9.2	33.7	14.4	22.8		62.6	11.3	51.6	17.4
October			18.3	9.5				10.5	46.4	16.2			28.0	11.6	17.6		37.9	10.6	62.3	17.3
November				12.7				6.3	36.2	13.4	28.0	14.3			21.0		53.1	5.6	44.8	15.0
December			4.0					3.6	25.3	13.6	34.4	7.0	28.6	7.9	13.7		32.7	5.8	47.7	12.0
Yearly mean	4.2		14.6	9.2				5.2	32.6	7.8	32.0	8.6	26.8	9.9	21.4		43.8	8.9	39.9	12.2
N/P									2.5		1.3		1.3				2.0		1.5	
Area V—Boca Ciega Bay:																				
January								1.4			27.6	3.3			23.3		42.1	3.9	25.1	6.7
February								4.1			22.8	3.3	36.8	4.7	26.7	1.5			39.1	4.4
March						2.2		3.9			37.2	3.2	29.7	11.8	26.4	7.9			60.7	9.1
April		2.4				2.2		4.4			28.7	4.9		13.2	14.7				50.1	6.0
May						2.5		4.1			47.4	2.0	26.1	4.4	50.3	11.4			36.4	15.1
June						3.7		5.8			39.4	10.6	33.3	10.1		11.2			64.8	10.2
July						2.6		5.3			40.7	7.8	32.6	13.4		16.0			31.4	11.2
August						2.8		5.4			32.8	9.7	25.7	11.4	63.9		51.9	15.4	48.1	11.4
September						3.7		7.0		57.4	8.6	38.6	14.4		9.0	29.9	13.4	42.1	10.1	47.2	15.3
October						1.5		5.9		39.0	11.3			39.4	18.1			55.1	14.3	49.6	14.2
November		.8				2.3		2.5		30.3	6.9	25.2	12.8	29.0	4.3		9.0	42.4	6.7	41.3	8.9
December						1.1		3.1		43.2	5.3	35.3	4.0	31.8	3.1		6.5	38.6	4.2	47.6	7.5
Yearly mean		.8	2.4			2.5		4.4		42.5	8.0	34.2	7.0	32.6	9.4	33.6	9.6	45.4	9.1	45.1	10.0
N/P										3.0		2.5		1.7		1.7		2.0		2.0

[1] Odum, 1953; Hutton et al., 1956; Finucane and Dragovich, 1959, 1966; Dragovich et al., 1961; Saloman et al., 1964; Dragovich et al., 1966; Saloman and Taylor, 1968.

[2] To calculate the nitrogen-phosphorus ratio, μg.at./l. values for nitrogen and phosphorus have been converted to parts per million (p.p.m.) by multiplying by 0.014 (nitrogen) and 0.031 (phosphorus).

TABLE 5.—*Surface values of chlorophyll a (mg./m.³), 1952–66, and primary production (G. C/m.²/day), 1962–66, for areas of Tampa Bay, Fla.*[1]

Area	1952–53		1958		1962		1963		1964		1965		1966	
	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.
Area I—Old Tampa Bay:														
January	2.0						3.3	0.32			1.6	0.44	8.1	0.22
February							1.7	.11					3.5	.14
March							6.8	.72	4.0	0.34	2.4	.29	3.6	.16
April	3.1						9.4	.61	6.3	1.34	7.1	.81	5.0	.24
May	3.1						3.9	.54	3.7	.61	2.1	.35	9.8	.37
June							10.4	1.26	1.8	.29			5.0	.28
July							20.0	.90	5.3	.48			5.1	.22
August							8.9	.96	3.9	.32	26.6	1.26	7.7	.43
September	9.9				10.9		15.2	.56	2.6	.32	9.1	.52	5.0	.28
October					15.2	0.97	5.9	.51			8.9	.41	6.5	.46
November					5.0	.39			5.1	.45	11.8	.56	3.1	.17
December					6.4	.41			12.6	1.13	8.1	.30	5.2	.25
Yearly mean	4.5				9.4	.59	8.6	.65	5.0	.59	8.6	.55	5.6	.27
Area II—Hillsborough Bay:														
January	4.6						25.9	1.79			5.5			
February							9.3	.71				.77		
March							25.7	.57	8.3	.51	7.1			
April	4.6						4.7	.23	27.5	1.41	3.6	.79		
May	7.9						16.1	1.26	.8	.33	6.0	.43		
June							4.9	.25	1.6	.13		.99		
July							27.1	1.66	13.7	2.08				
August							35.4	1.49	26.5	1.43				
September	13.3				18.8		29.0	.79	16.2	.70				
October					10.2	.19	11.3	.77						
November					14.7	.95			4.9	.23				
December					16.0	.61			8.2	.62				
Yearly mean	7.6				14.9	.58	18.9	.95	12.0	.83	5.6	.75		
Area III—Tampa Bay:														
January							2.2	.13			1.0	.14	7.6	.26
February							10.4	.82					6.4	.26
March							5.7	.64	4.7	.54	5.5	.65	5.6	.26
April	6.9						11.5	.64	13.4	.62	5.4	.37	6.3	.31
May							4.4	.42	4.1	.43	3.1		4.1	.16
June							3.6	.21	.6	.30			5.3	.30
July							3.0	.19	10.6	.77			8.4	.36
August							3.9	.43	4.3	.37	10.8	.52	12.7	.65
September	9.3				7.5		9.2	.56	8.7	.50	22.4	.74		
October					5.0	0.57	5.1	.22			4.8	.22		
November					11.0	.73			3.7	.21	10.5	.52		
December					3.0	.31	7.6	.59	2.6	.16	10.7	.44		
Yearly mean	8.1				6.6	.53	6.1	.48	5.9	.43	8.3	.45	7.1	.32
Area IV—Tampa Bay Entrance:														
January	1.7										2.2	.30	1.2	.04
February							2.8	.32					3.3	.14
March							1.6	.21	1.7	.38	3.9	.66	2.3	.10
April							1.9	.27	3.0	.54	2.4	.36	1.4	.07
May	3.1						6.1	.69	.7	.23	1.2	.10	2.5	.11
June							9.3	.54	.4	.07			2.6	.10
July							3.3	.47	2.9	.14			8.4	.40
August							2.8	.28	3.1	.31			6.9	.35
September	10.0				1.6		6.0	.75	5.3	.79	9.9	.52	8.2	.46
October					8.2	.57	1.9	.25			8.9	.37	21.1	.95
November					5.0	.49			11.4	.57	3.2	.15	5.9	.22
December					5.7	.41	3.8	.16	.7	.12	6.4	.26		
Yearly mean	4.9				5.1	.49	4.0	.39	3.2	.35	4.8	.34	5.8	.27

See footnote at end of table

TABLE 5.—*Surface values of chlorophyll a (mg./m.³), 1952–66, and primary production (G.C/m.²/day), 1962–66, for areas of Tampa Bay, Fla.*[1]—Continued

Area	1952–53		1958		1962		1963		1964		1965		1966	
	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.	Chlor. *a*	Primary prod.
Area V—Boca Ciega Bay:														
January							7.5	.30	11.1	.47			9.1	.30
February							7.9	.27	7.4	.32			1.8	.07
March							6.2	.30	7.9	.41			19.3	.89
April	5.1						3.8	.28	4.5	.30			13.8	.67
May	3.4						5.0	.34	3.4	.22			4.7	.18
June					9.0	.71	6.5	.37	3.9	.25			15.8	.89
July			3.5		8.3	.51	7.6	.43					10.6	.45
August					8.7	.44	6.2	.36					9.2	.53
September					9.0	.44	10.0	.46			5.1	.26	8.1	.47
October					8.8	.47	5.0	.27			10.1	.41	11.6	.61
November	3.1				9.2	.40	6.7	.31			9.0	.41	5.5	.31
December					7.4	.32	9.5	.40			15.0	.59	7.1	.41
Yearly mean	3.9		3.5		8.6	.47	6.8	.34	6.4	.33	9.8	.42	9.7	.48

[1] Marshall, 1956; Pomeroy, 1960; May and Johnson, unpublished data, on file at Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla.; Saloman et al., 1964; Finucane and Dragovich, 1966; Dragovich et al., 1966; Saloman and Taylor, 1968.

Compared with average concentrations of phosphorus and nitrogen in surface sea water, Boca Ciega Bay has about five times more phosphorus and four times as much nitrogen (Sverdrup, Johnson, and Fleming, 1942; Armstrong, 1965; Vaccaro, 1965). Even when compared with other estuarine systems of the Atlantic and Gulf Coasts, Boca Ciega Bay and the other areas of Tampa Bay rank high in these elements (Newcombe and Brust, 1940; Williams, 1954; Riley and Conover, 1956; NcNulty, Reynolds, and Miller, 1959; Lackey, 1963; Mackenthun, 1965; Saville, 1966).

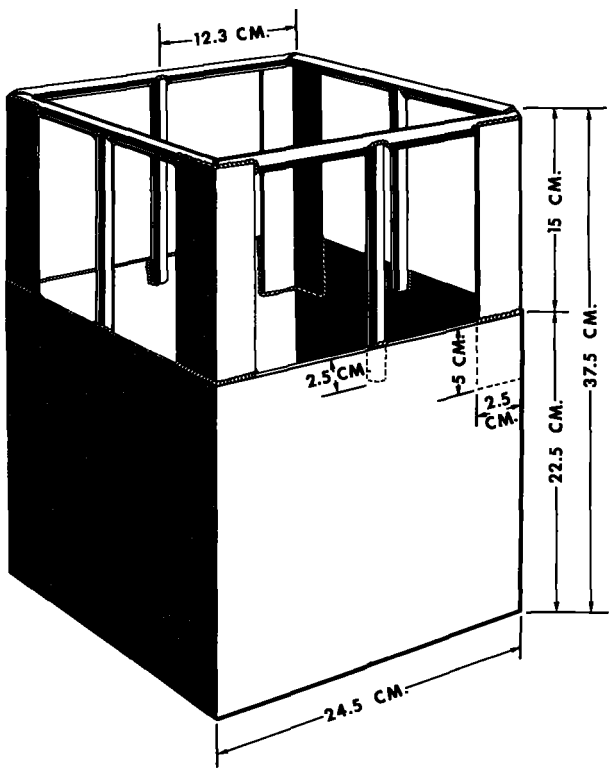

FIGURE 12.—Bottom sampler of stainless steel (0.25 m.²) used for sampling vegetation and infauna.

Under natural conditions, phosphorus and nitrogen enter Tampa Bay mainly through discharge from rivers and springs (Dragovich and May, 1962; Dragovich, Kelly, and Goodell, 1968). The major contribution of phosphorus enters Hillsborough Bay through the Alafia River from mining operations in extensive phosphatic deposits east of Tampa. On the basis of water analyses made in the early 1950's phosphorus in Hillsborough

TABLE 6.—*Mean total phosphorus from surface and bottom water of undredged and dredged sampling stations in Boca Ciega Bay, Fla., 1963–64*

	Undredged		Dredged	
	Surface	Bottom	Surface	Bottom
	µg.at./l.			
1963				
November	13.9	14.5	5.3	9.9
1964				
February	6.4	5.9	4.3	4.1
May	7.6	6.8	5.2	7.9
August	13.0	12.3	7.1	10.8
Mean	10.2	9.9	5.5	8.2

Bay has remained at about its present level since 1952 or before (Odum, 1953)—see table 4. In areas of the estuary less affected by mining runoff, high concentrations of phosphorus and nitrogen recorded since the early 1960's are due to an increase in industrial and domestic sewage. Population in the area around Tampa Bay was less than one-half million in 1950, rose to about three-fourths million by 1960, and is now near 1 million. As population rose, the method of sewage disposal was converted from septic tanks to treatment plant in the late 1950's and early 1960's. This change introduced treated sewage directly into all areas of the estuary. In Boca Ciega Bay, the mean annual concentration of total phosphorus rose from 2.5 μg.a./l. in 1954–58 to 4.4 in 1959, and 8 by 1961. At present, total phosphorus averages 10 μg.a./l. and total nitrogen 45.1 μg.a./l., and sewage volume is about 17 million gallons per day (secondary treatment) from outfalls located throughout the lagoon. Along with progressive eutrophication of Boca Ciega Bay, counts of coliform bacteria have risen so high that shellfishing has been prohibited near all outfalls and in all waters of the bay north of Pinellas County Bayway (fig. 13)—Pinellas County Health Department, personal communication.

Relative as well as total concentration of nitrogen and phosphorus influences the occurrence and abundance of marine life (Raymont, 1963). Within limiting values, studies of marine plankton indicate that growth and reproduction of marine phytoplankton are greatest when the ratio of nitrogen to phosphorus is 10 or higher (Odum, Lackey, Hynes, and Marshal, 1955; Lackey, 1963). In Boca Ciega Bay the observed N/P is about 2. The disproportionately high level of phosphorus may limit kinds and numbers of phytoplankton in the lagoon and perhaps explains why plankton blooms are infrequent and planktonic primary production is not extremely high (Dragovich, Kelly, and Kelly, 1965; Rounsefell and Dragovich, 1966; Dragovich and Johnson, 1966).

Attached algae and sea grasses also respond to eutrophy. McNulty (1961) noted an abundance of *Gracilaria blodgettii* Harvey, other red algae, and the green alga *Ulva lactuca* Linnaeus in Biscayne Bay, Fla., before pollution abatement. Wilkinson (1964) found a direct relation between eutrophication of a New Zealand estuary and marked increase of two green algae, *Ulva* sp. and *Enteromorpha* sp. He wrote that foul odor of hydrogen sulphide was emitted from decay of algal mats and that white paint was turned black on homes nearby. Production of hydrogen sulphide by *Enteromorpha* has also been studied by Baas Becking and Mackay (1956).

Species of *Gracilaria* have been implicated in reports of offensive odors arising from Hillsborough Bay (Florida State Board of Health, 1964). The Federal Water Pollution Control Administration is now investigating this matter. In Boca Ciega Bay, *Gracilaria* is present, as are *Ulva* and *Enteromorpha*. We observed windrows of *Ulva lactuca* in bayfill access canals after residents reported objectionable odors in the central part of the bay in the spring of 1965. Further nutrification of Boca Ciega Bay would increase growth of these and perhaps other filamentous algae that become fetid as they decompose.

TURBIDITY

Data from 1963–64 show that secchi discs were visible to depths greater than 150 cm. only in southern Boca Ciega Bay (PB–6), well away from bayfill developments (table 1). Here, average light transmission through the water column is 53 percent of incident radiation at about 40 cm. beneath the surface (Saloman et al., 1964). In contrast, water in the open bay nearer bayfills is turbid. Within protected waters of access canals, however, transparency approaches that of the lower bay. For example, average monthly light transmission in one canal was 45 percent at 40 cm. (Saloman et al., 1964). Even so, canal bottoms are far too deep to receive light required for the growth of sea grass.

Much of the silt and clay raised by dredging will eventually be removed from circulation in the lagoon by biological fixation and tidal transport (Dapples, 1942; Ginsburg and Lowenstam, 1958; Van Stratten and Kuenen, 1958; Phillips, 1960a; Lyntz, 1966). Until water is clarified by these processes, turbidity will continue to limit biological production in central and northern parts of Boca Ciega Bay.

CHLOROPHYLL *A* AND PRIMARY PRODUCTION

Neither chlorophyll *a* nor rate of planktonic primary production differed consistently in

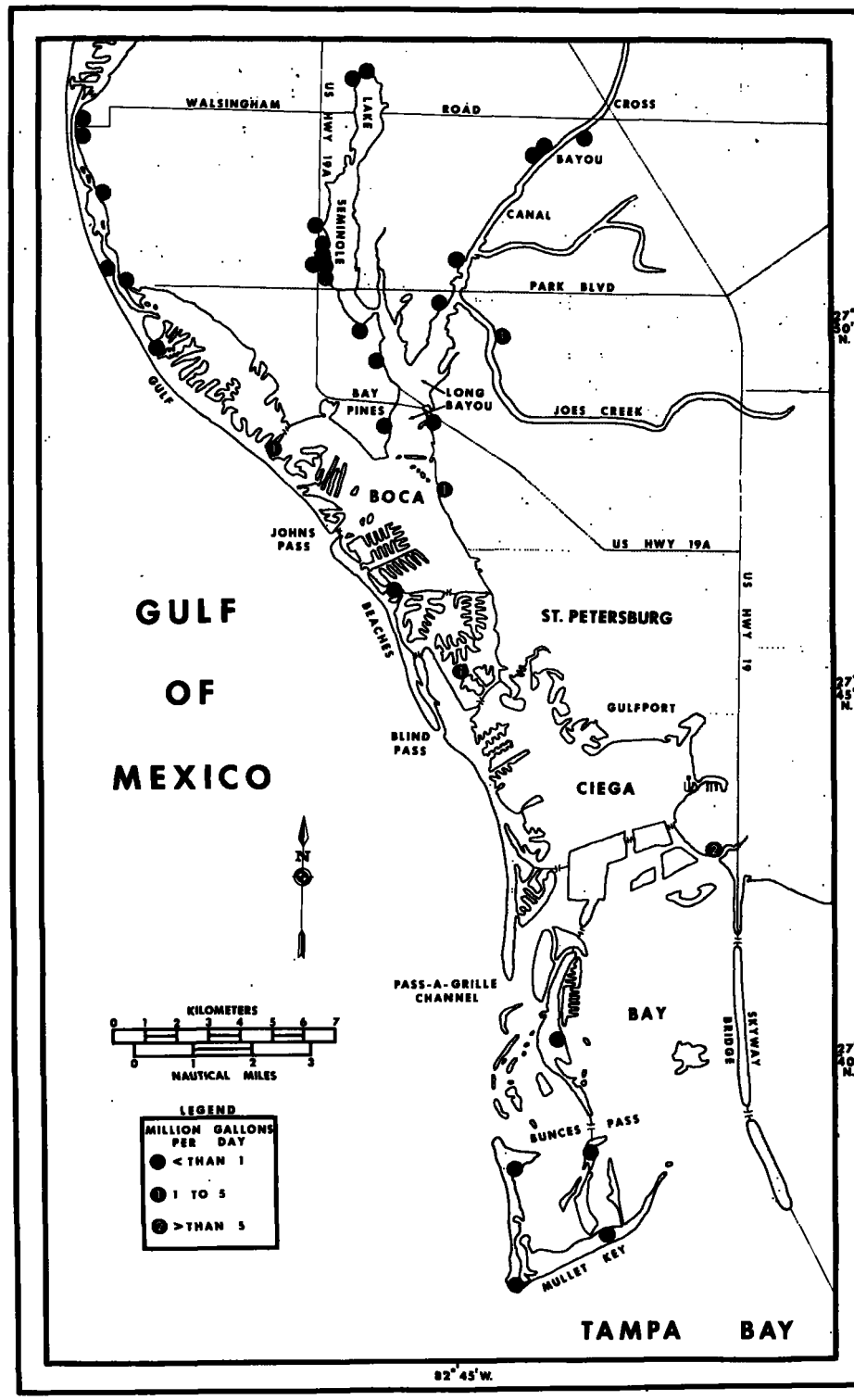

FIGURE 13.—Approximate sewer outfall locations and discharge volumes (secondary treatment) in Boca Ciega Bay, Fla. 1966.

dredged and undredged locations. Chlorophyll *a* did not fluctuate seasonally. Low primary production noted in February may be due to turbid conditions rather than lack of nutrients or limitation by another factor, such as temperature (table 1). Except for higher values in extremely eutrophic Hillsborough Bay, pigment and production figures (table 5) are both similar to those recorded for other areas of the estuary as well as other estuarine waters of the southeast (Ragotzkie, 1959; Odum and Wilson, 1962; Williams, Murdock, and Thomas, 1966; Saville, 1966; Dragovich and Johnson, 1966).

In 1962–66, mean chlorophyll *a* in Boca Ciega Bay was 8.6 mg./m.^{3} and mean primary production by phytoplankton was 0.40 G.C/m.^{2}/day. The most extensive data for chlorophyll *a* and primary production in Boca Ciega Bay are from daily observations by May and Johnson [8] between June 1962 and June 1964 (table 5). These figures show a slightly lower mean annual value for chlorophyll *a* (7.3 mg./m.^{3}) but the same value for mean annual production (0.40 G.C/m.^{2}/day). Earlier data indicate about a twofold rise in chlorophyll *a* since 1952, following nutrification of the lagoon by sewage (table 5).

Actually, the productivity figures given above for Boca Ciega Bay are misleading and far too low because sea grasses and unicellular and filamentous benthic algae add to the production that was recorded only for phytoplankton. Pomeroy (1960), who considered photosynthetic contributions by all hydrophytes in his study of primary production in lower Boca Ciega Bay, concluded that an average value is about 5 G.O_2/m.^{2}/day. Odum and Hoskin (1958) gave a value of about 5 grams of dry organic material per day. On the basis of an allowance of 0.5 G. of C for each gram of organic matter produced (May, 1966), this is equivalent to about 2.5 G.C/m.^{2}/day or nearly six times the estimates of daily production in the lagoon by phytoplankton alone. The main point to be made is that under natural conditions primary production from a variety of photosynthetic taxa far exceeds production in turbid waters where photosynthetic activity of benthic flora has been reduced or eliminated (Blinks, 1955; Odum, McConnell, and Abbott, 1958; Pomeroy, 1959).

[8] See footnote 3.

SEDIMENTS

Sediments of Tampa Bay are mainly a firm mixture of sand and shell containing little silt or clay (Goodell and Gorsline, 1961). Soft deposits are localized in upper reaches of Old Tampa Bay, Hillsborough Bay, natural depressions, and dredged bottom of bayfill access canals, where the weight percentage of silts and clays may exceed 90 percent. In Boca Ciega Bay the sediments in undredged areas averaged 94 percent sand and shell whereas the sediments in dredged canals averaged 92 percent silt and clay (table 7).

The ooze measured in two dredged pockets between bayfill fingers extended downward to a depth of about 3.6 m. The upper 30 cm. was dark, semifluid, and sulphurous; below was an unconsolidated horizon of gray clay. The predominantly organic upper layer consists of decomposing detritus that accumulates in the canals. The origin of the underlying clay has not been determined, but it seems likely that a thick stratum of clay was uncovered in the dredging which extended some distance below a bay floor veneer of sand and shell. To judge from the uniformity of the viscous clay layer, this material was redeposited after dredging ceased and now lies too deep to be reworked by normal water movements. Clay settles out of suspension slowly and may form deposits to 364 m. or more beyond dredging sites (Phillips, 1960a; Mackin, 1961; Hellier and Kornicker, 1962; Odum, 1963; Woodburn, 1965). Thus, resident benthos far from fill and borrow areas may be suffocated by sedimentation from dredging operations.

MACROBIOTA

Analysis of biological samples in Boca Ciega Bay supplements earlier studies in undredged areas and contrasts these findings with a scarcity of macrobiota found in bayfill canals.

DIVERSITY AND ABUNDANCE

In the first comprehensive survey of Boca Ciega Bay, Hutton et al. (1956) recorded nearly 200 plant and animal species from marine and tidewater communities and presented fishery statistics that attest to the importance of commercial and sport species. Later a notable addition was made

to the list of algal species by Phillips (1960b); Springer and Woodburn (1960) brought the list of fishes from Tampa Bay up to 108; and unpublished work by Bullock and Boss[9] increased the recorded number of mollusks in Boca Ciega Bay from 30 to 175. Nearly 700 species of marine plants and animals have been identified from our sampling in 1963–64 and from other work in the area. Among the major taxa are about 180 species of mollusks, 120 polychaete worms, 60 decapod crustaceans, 20 echinoderms, 110 fishes, and 200 plants.

Comparative records show that stations inside deeply dredged canals contain less than 20 percent of the species we recorded for the bay. If fishes are excluded from the species total, nearly 100 percent of the organisms recorded come from collections made outside dredged areas. Invertebrates collected in bayfill canals consisted of only a few polychaete worms, mollusks, blue crabs, and pink shrimp. We conclude, therefore, that soft deposits in the canals are in some way unsuitable for most bottom invertebrates found in other areas of the bay. Thorson (1957) and others have demonstrated that larvae of many benthic forms are sensitive to sediment composition and will not metamorphose from a planktonic stage until contact is made with suitable bottom. In 10 years, recolonization of canal sediments has been negligible and it appears doubtful that soft sediments of bayfill canals will

[9] See footnote 2.

TABLE 7.—*Comparison of sediments at undredged and dredged stations in Boca Ciega Bay, Fla. (1963–64), showing depth, mean grain size, percentage of shell and sand by weight (particle size <4 ∅), percentage of silt and clay by weight (particle size >4 ∅), and percentage of total carbon by weight*

Station	Depth	Mean grain size	Percentage of shell and sand by weight	Percentage of silt and clay by weight	Percentage of total carbon by weight
Undredged:	*Meters*	*Phi units (∅)* [1]	*Percent*	*Percent*	*Percent*
BCA	2	3.5	81	19	1.7
BCH	2	2.5	95	5	.5
BCC	1	2.5	96	4	.7
BCE	7	2.6	99	1	.2
BCG	1	2.3	97	3	.6
BCI	3	3.4	87	13	1.3
BCL	1	1.9	98	2	.6
BCM	2	3.0	95	5	.7
PB-6; BCN	3	1.4	98	2	.4
D-1	3	2.8	98	2	.4
D-2	1	2.5	98	2	.4
D-3	1	2.5	88	12	1.4
D-5	2	2.6	97	3	.8
D-6	1	2.8	96	4	.8
D-9	2	2.8	96	4	.5
D-10	2	3.0	89	11	1.0
PB-3; D-11	1	2.9	92	8	.4
D-17	2	2.8	96	4	.5
D-18	1	3.4	85	15	1.3
PB-1	2	2.6	99	1	.3
PB-5	3	2.5	98	2	.4
Means	2	2.7	94.2	5.8	.7
Dredged:					
BCH	3	7.1	12	88	4.6
D-4	4	6.5	6	94	.6
D-7	4	6.3	5	95	8.9
D-8 [2]	2	4.6	60	40	6.6
D-12 [2]	1	.8	99	1	.2
D-13 [3]	4	4.0	83	17	.9
D-14	4	7.0	7	93	3.8
PB-2; D-15	4	7.0	6	94	1.3
D-16	4	6.3	14	86	1.3
PB-4	4				
Means	3.9	6.7	8.3	91.7	3.4

[1] The phi unit is a logarithmic transformation of the Wentworth grade scale of particle size (Krumbein and Pettijohn, 1938).

[2] Berm of canal not included in calculation of mean.

[3] Transitional bottom not included in calculation of mean.

ever support a rich or diverse infauna. The existence of soft sediments does not necessarily preclude the presence of a diverse and abundant bottom fauna (Barnard and Hartman, 1959; Sanders, 1960), but where sediments are highly organic, deposition rapid, and dissolved oxygen low, the benthos is likely to be impoverished (Pratt, 1953; Bader, 1954; Reish, 1959; McNulty, Work, and Moore, 1962; McNulty, 1966).

Forty-nine species of fishes were caught at stations in dredged canals. None were demersal, and the absence of this type of fish in the catch may be due to lack of food organisms on and in bottom deposits. In contrast, 80 species of fish were collected at stations outside bayfill canals. Even though waters in the open bay accounted for a greater number of fish species, 30 percent more fish were netted within dredged canals. One species, the bay anchovy, *Anchoa mitchilli* (Valenciennes), was most common in the canal catch but the Cuban anchovy, *Anchoa cubana* (Poey), and the scaled sardine, *Harengula pensacolae* (Goode & Bean), were also abundant.

BIOMASS AND PRODUCTION

The major benthic habitats in Boca Ciega Bay are turtle grass beds, unvegetated bottom, and oyster reefs. All contain large numbers of species, but the grass bed community is outstanding because it is widespread and highly productive.

Extensive beds of turtle grass now exist only south and east of the Pinellas County Bayway (fig. 1). Poorer stands are located in central and northern parts of the bay, but only in very shallow water. Representative beds were sampled to compare standing crop in the relatively undisturbed southern section of the bay (area A) with that in extensively dredged central (area B) and northern (area C) sections (fig. 10). Dry whole weight of turtle grass in areas A, B, and C averaged 1,198, 1,008, and 320 g./m.^{2}, respectively. The figure for area C agrees with other biomass estimates of turtle grass in the Gulf of Mexico, but values from areas A and B are two to three times greater (Phillips, 1960a; Odum, 1963). Maximum development of turtle grass probably occurs in the Caribbean where Burkholder, Burkholder, and Rivero (1959) have observed stands having a biomass of 2,800 g./m.^{2} dry weight.

Pomeroy (1960) reported an average biomass of about 81 g./m.^{2} for turtle grass sampled randomly along a transect across lower Boca Ciega Bay. This figure seems low, but no doubt includes values from samples in some sparsely vegetated areas. Since bayfills cover bare and vegetated bottom, 80 g./m.^{2} is probably a reasonable factor for calculating total biomass of turtle grass that has been covered by bayfills in Boca Ciega Bay. Using 1,400 hectares (3,500 acres) as the filled area of the bay, we compute that standing crop of turtle grass buried by filling is at least 1,133 metric tons. If the area of bayfill canals and other borrow areas were included in this calculation, the figure would be nearly doubled.

Our estimate of total primary production in Boca Ciega Bay is based on work by Pomeroy (1960) and studies in vegetated Texas bays by Hellier (1962) and Odum and Wilson (1962). An average production figure would be about 5 G.O_2/m.^{2}/day (ca. 2.5 G.C/m.^{2}/day) which is roughly equivalent to 18,206 kg./ha./yr. (16,243 lbs./acre/yr.) of dry organic material or an annual loss of about 25,841 metric tons (28,425 tons) for the 1,400 hectares (3,500 acres) of the bay now filled.

No quantitative study has been made of biomass of animals living among blades of turtle grass, although Moore (1963) and Stephens (1966) estimated the abundance of small invertebrates, and drop-net samples in Texas bays gave data on some larger invertebrates and fishes (Hellier, 1958, 1962; Jones, Ogletree, Thompson, and Klenniken, 1963). The drop-net studies gave a mean annual standing crop of about 15 g./m.^{2} wet weight (3 g./m.^{2} dry weight—20 percent of wet weight) (Vinogradov, 1953). Annual fish production is also about 3 g./m.^{2} in Texas bays or about 30 kg./ha./yr. (27 lbs./acre/yr.) (Hellier, 1962). This figure is below an estimate by Sykes (1963) for fishery production in Gulf estuaries (52 kg./ha./yr., or 46 lbs./acre/yr.). Using Sykes' estimate, we calculate that filling of 1,400 hectares (3,500 acres) has reduced fishery production in Boca Ciega Bay by 73 metric tons (80 tons) per year.

Biomass of invertebrate infauna living among roots and rhizomes of turtle grass was calculated from wet whole weight of animals recovered by sieving 0.25 m.^{2} plug samples collected in areas A, B, and C. At area D, the infauna biomass was determined in the same manner for unvegetated

bottom (fig. 10). Mean wet weights of infauna in areas A, B, C, and D were 912, 560, 128, and 80 g./m.^{2}, respectively. Thus, the density of sea grass and abundance of infauna were positively correlated. If 85 percent of wet whole weight is weight of contained water and inert structures, dry weight of infauna from luxuriant beds of turtle grass in the lower bay was about 137 g./m.^{2} This figure is high in comparison with other biomass figures for estuarine waters (Sanders, Goudsmit, Mills, and Hampson, 1962). Bayfills in Boca Ceiga Bay have reduced the standing crop of bottom invertebrates by about 1,812 metric tons (1,993 tons)—calculated from relatively low infaunal biomass of area C.

Figures for the annual production of infauna are much higher. Sanders (1956) estimated infaunal production at two to five times the standing crop and indicated that the larger factor very likely applied in tropical situations. We arbitrarily selected four as a multiplier, and calculated infaunal production in the best stands of turtle grass at about 548 g./m.^{2}/yr. (5,466 kg./ha./yr., or 4,877 lbs./acre/yr. dry weight). Even in poor grass beds at area C infaunal production would be about 768 kg./ha./yr. or 685 lbs./acre/yr. This figure multiplied by the 1,400 hectares (3,500 acres) now in bayfills puts the loss of infaunal production at about 1,091 metric tons (1,200 tons/yr.). If more refined collecting had been done (screening at less than 0.701-mm. mesh), the addition of biomas from meiobenthos would have added considerably to the figures reported for macrobenthos alone, and the annual production of meiobenthos would very likely be equivalent or somewhat greater than the estimate for macrobenthos (Weiser, 1960; McIntyre, 1964).

ESTUARINE EVALUATION

Products and other values provided by the Nation's tidewaters are so numerous and diverse that their true worth is difficult to compute. Nonetheless, a number of attempts have been made to estimate the cash value of estuarine acreage. In the northeast, notable contributions were made by Shuster (1959); Fogg (1964); Jerome, Chesmore, Anderson, and Grice (1965); Jerome, Chesmore, and Anderson (1966); and Cain (1966). Pertinent details of estuarine evaluations along the Gulf of Mexico were abstracted and annotated by Woodburn (1965).

On the basis of these estimates, we conclude that fishery production alone in Tampa Bay estuary has an annual value of about $741/ha. ($300/acre). In addition, these waters are used by public utilities, industry, and commerce and serve recreational requirements of nearly a million residents[10] and 1½ million annual vacationers.[11] Hence, total worth of each water acre in the estuary can be conservatively estimated at $988/ha. ($400/acre) per year. At this rate, the 1,400 hectares (3,500 acres) covered by bayfills in Boca Ciega Bay represent an annual loss of about $1.40 million, which if capitalized at 6 percent would total a natural investment of $23.3 million. This accounting is not complete because the undesirable aspects of coastal development extend well beyond bulkheads and outfalls.

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[11] St. Petersburg Times, July 19, 1966.

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PHOTOGRAPHIC ATLAS OF SOCKEYE SALMON SCALES

BY KENNETH H. MOSHER, *Fishery Biologist*

BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY
SEATTLE, WASHINGTON 98102

ABSTRACT

Photographic plates of sockeye salmon scales, with explanatory text, illustrate in detail the variations in scale features in this species. These illustrations of zones of freshwater and ocean growth (and of complete scales) can be used as: (1) standards to which scales under study may be referred for determination of age and race, (2) guides in choosing scale characters for racial and other studies, and (3) aids in the training of scale scientists. Examples of regenerated, resorbed, and other atypical scales are also shown.

Sockeye salmon *(Oncorhynchus nerka)* is the most valuable species of Pacific salmon in North America and has been the subject of scientific study since the 1870's. Most of the extensive research for the INPFC (International North Pacific Fisheries Commission) by Canada, Japan, and the United States now is directed toward this species. Many of these projects use data obtained from study of the scales of sockeye salmon.

Sockeye salmon spend their early lives in fresh water, migrate to the North Pacific Ocean, and finally return to their natal streams to spawn and die. The growth zones formed on the scales record the growth of each individual fish. The fresh- and salt-water zones differ from each other in appearance. The zones can reveal the number of years that the fish spent in each environment; they also divulge the year in which the fish was hatched and the year it migrated to sea. Scale features have been used in age studies of sockeye salmon since 1910 (Gilbert, 1913). Recently, scale features have also been used in racial studies to determine the origin of fish taken at sea (Krogius, 1958; Kubo, 1958; Kubo and Kosaka, 1959; Henry, 1961; Mosher, Anas, and Liscom, 1961; Anas, 1963; Mosher, 1963; and Anas, 1964).

No detailed information has been published, however, on how to interpret the scales. The purpose of this atlas is to show the features of sockeye salmon scales in detail so that workers can interpret the scales they are working with to provide the data required in their studies.

A section on the use of the atlas in age studies and for describing scale features follows the illustrations of the scale features.

MATERIALS AND METHODS

Scientists of BCF (Bureau of Commercial Fisheries) have examined many thousands of sockeye salmon scales in recent years to supply information to the United States Section of INPFC. From these thousands I have selected certain scales to illustrate the variations in scale characters among fish. Variations may be genetic or environmental, or both, but generally many of the differences in the characters of scales are linked to geographic localities; therefore, a study of these variations offers a means of determining the mainland (racial) origin of fish taken beyond their natal streams.

For scale studies, workers of the research agencies of the INPFC (Fisheries Agency of Japan, Fisheries Research Board of Canada, and BCF) collect scales from the side of the fish as shown in Mosher, 1963. The "preferred scale" is in the second scale row above the lateral line in the diagonal scale row downward from the posterior edge of the dorsal fin. If this scale is missing on both sides of the fish, a scale is taken as close as possible to the preferred position, but not from the lateral line or the first row above or below the line.

The plates of the atlas are made from negative

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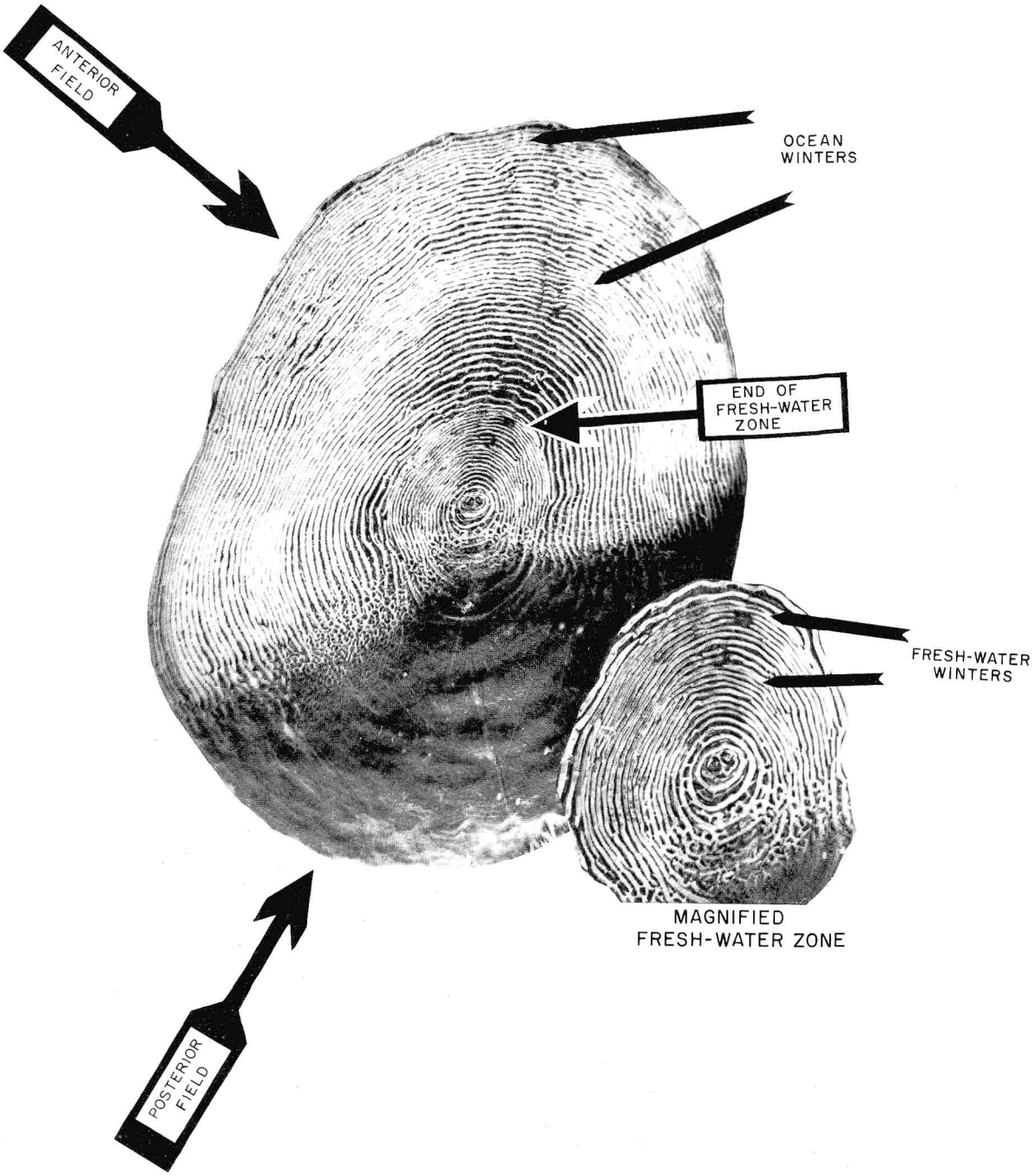


PLATE 1.—Sockeye salmon scale.

prints of projected plastic impressions of scales.[1] Explanations and descriptions of the various features accompany the plates.

The original plates were assembled on 15- by 20-inch mounting sheets. Magnification of the individual scales and scale sections was adjusted for reduction onto the usual 8- by 10½-inch page; in this reduction, however, the clarity of the scale characters varies somewhat; therefore, I suggest that the reader keep a small magnifying glass (2 to 4X) handy for examination of specific portions of the plates as needed.

Examples of negative and positive prints of scales, a comparison of scales and their plastic impressions, the appearance of scale features under various magnifications, a glossary of terms used in scale studies, and the method of making the photographs are presented in the appendix.

The following order of topics has been chosen as the most useful for study of scales from sockeye salmon:

1. Gross features of sockeye salmon scales (plates 1 and 2).
2. Circuli, winter zones, and ages in the fresh-water growth zone (plates 3, 4, and 5).
3. Transition zone between fresh-water and ocean growth (plate 6).
4. Appearance, number, and spacing of circuli, winter zones, and ocean ages in the ocean growth zone (plates 7-11).
5. Age group combinations in sockeye salmon (plates 12-16).
6. Anomalies which make some scales unusable for age and racial studies (plates 17, 18, and 19).
7. Use of the atlas.
8. Appendix.

FEATURES OF SCALES FROM SOCKEYE SALMON (Plate 1)

Under magnification, a sockeye salmon scale shows two distinct areas: (1) The anterior or sculptured field, which was embedded in the scale pocket and (2) the posterior or unsculptured field, which protruded from the scale pocket and overlapped the adjacent posterior scale pockets. The examples shown in plate 1 and plate 2 illustrate these and other gross features described below. Scales of Pacific salmon are cycloid scales.

ANTERIOR FIELD

The upper surface of the anterior field is sculptured with ridges (circuli) and grooves (interspaces). See Koo and Finn (1964) for photographs of magnified cross sections of salmon scales. Under magnification the circuli and interspaces appear as alternating light and dark concentric "rings" which result from differences in transmission of light through the grooves and ridges of the translucent scale material.[2] The contrast between circuli and interspaces varies from high (heavily marked circuli) to low (lightly marked circuli).[3] Circuli are formed on the edge of the scale as it grows (Neave, 1936; Welander, 1940; Wallin, 1957). When the scales are growing rapidly (in late spring and summer), the circuli are deposited relatively far apart and have a broad and heavy appearance and texture (as if drawn with a blunt pencil or stub-tipped pen). The periods of retarded growth (in the fall, winter, and early spring) show on the scale as bands of circuli lying closer together than the circuli of the summer growth zone. These bands have been called annual marks, annual rings, winter zones, winter checks, winter growth zones, resting zones, or annuli.[4] Where zone dimensions are needed, most salmon scale workers measure to the last circulus of this band of closely spaced circuli.

The circuli laid down while the fish is in fresh water are of finer texture than those deposited later while the fish is in the ocean (as if drawn with a sharp pencil or fine-tipped pen). This cen-

[1] See Mosher (1950) for a description of the scale projector. See Clutter and Whitesel (1956) or Koo (1962a) for a description of the method of making plastic impressions of the scales.

[2] The circuli appear as the light rings in the negative prints and the interspaces as the dark rings (see appendix plate 3).

[3] The differences in contrast between circuli and interspaces are not as evident in the photographs as they are when the scales or scale impressions are examined directly. For reproduction I have adjusted the contrast between the light and dark tones to near maximum wherever possible.

[4] Annuli of sockeye salmon scales, unlike those of most other fish, are bands of closely spaced circuli formed during the winter and early spring. The usual definition of an annulus as a line of discontinuity between successive growth zones does not describe most annuli in the ocean growth zones of the sockeye salmon scale. Such lines of discontinuity often occur between the fresh-water and ocean growth zones whether or not an annulus is present and often occur on the scale at various places not related to the presence of the bands of closely spaced circuli which form each winter.

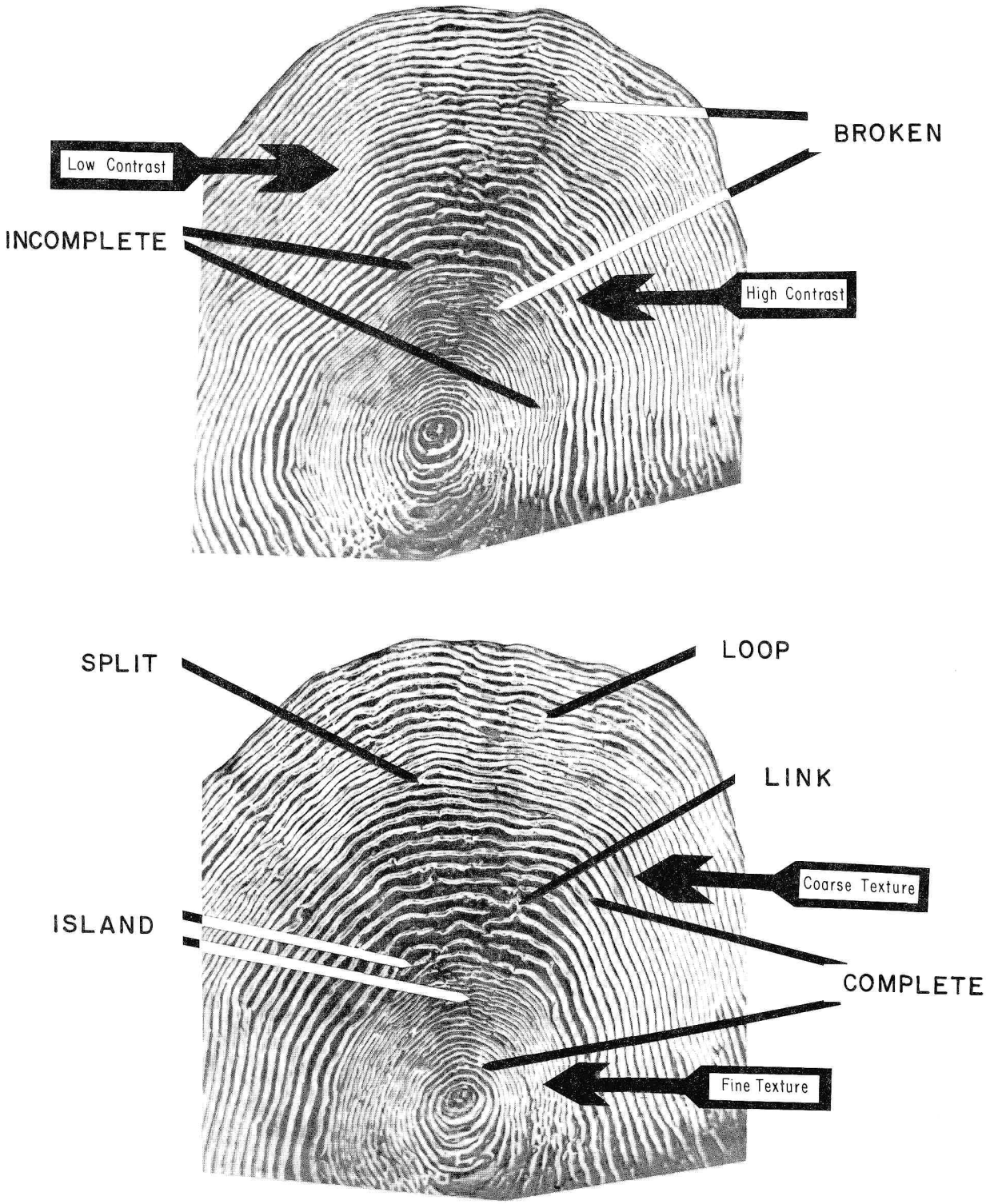


PLATE 2.—Types of circuli.

tral zone of closely spaced circuli is often called the nucleus. The area enclosed by the first circulus is called the focus of the scale or the central platelet. Only the first few circuli encircle the focus; the rest are arcs that do not extend into the posterior field.

POSTERIOR FIELD

The posterior field is a relatively clear area without distinctive growth features. It photographs black because it is uniformly translucent (see appendix plate 3).

TYPES OF CIRCULI (Plate 2)

The circuli of fresh-water and ocean growth may be described as:

1. Complete, or regular—circuli that are unbroken over most of their arc.
2. Incomplete, or irregular—circuli that are broken, split, or otherwise discontinuous in the anterior portion of their arc. Several types of incomplete or irregular circuli may be identified as follows:
   a. Broken—circuli that are broken or discontinuous in the anterior portion of their arc.[5]
   b. Split—circuli that divide into two or more circuli.
   c. Incomplete—circuli that end in a cul-de-sac against another one or two circuli, or circuli that are not complete around the anterior field of the scale.
   d. Island—a small segment of a circulus that is not joined to another circulus, but stands by itself.
   e. Loop—a segment of one or two circuli that form a loop.
   f. Link—an interconnection between adjacent circuli.
   g. Miscellaneous—circuli that are modified in various other ways.

FRESH-WATER (LACUSTRINE) GROWTH

Plates 3, 4, and 5 show the fresh-water portions of adult sockeye salmon scales and give examples of zones of complete, "average," and irregular circuli; various types of winter zones; and various fresh-water ages. The same criteria can be applied to scales from young salmon collected in fresh water.

FRESH-WATER CIRCULI (Plate 3)

This plate shows examples of different types of circuli in fresh-water growth of ages 1., 2., and 3.[6] See plate 2 for examples of various types of circuli. Figures labeled A are scales with predominantly complete circuli; those labeled B are more or less "average" scales, some circuli complete, others broken and irregular; and those labeled C are scales with predominantly broken and irregular circuli. Arrows indicate end of winter growth.

On the North American side of the Pacific Ocean complete circuli generally predominate on scales of fish from Bristol Bay, Karluk River, Fish Creek (in Cook Inlet), Alaska; Skeena and Fraser Rivers, British Columbia; and the Columbia River. On the Asian side of the Pacific, complete circuli occur frequently on scales of fish from the Ozernaia, Kamchatka, and Dalinaia Rivers of Kamchatka.

Broken and irregular circuli predominate on scales of fish collected in the Aleutian Islands, the Alaska Peninsula, Cook Inlet (except Fish Creek), and Southeastern Alaska; Smith and Rivers Inlets, British Columbia; and in Blinjinaia and Bolshaia Rivers of Kamchatka.

Fish scales from any area may have some complete and some broken circuli in the fresh-water zones.

WINTER ZONES IN FRESH-WATER GROWTH (Plate 4)

As mentioned previously, winter zones are formed when the growth of the scale slows down during the fall, winter, and early spring. The circuli are formed closer together and are broken or otherwise interrupted so that the winter growth zone shows up as a band of circuli more closely spaced than the adjacent circuli nearer

[5] Krogius (1958) used counts of broken circuli as a scale character in racial studies.

[6] Age designation of salmon in reference to fresh-water life only follows the recommendations of Koo (1962b): an Arabic numeral indicating the winters the fish spent in fresh water from hatching, followed by a dot.

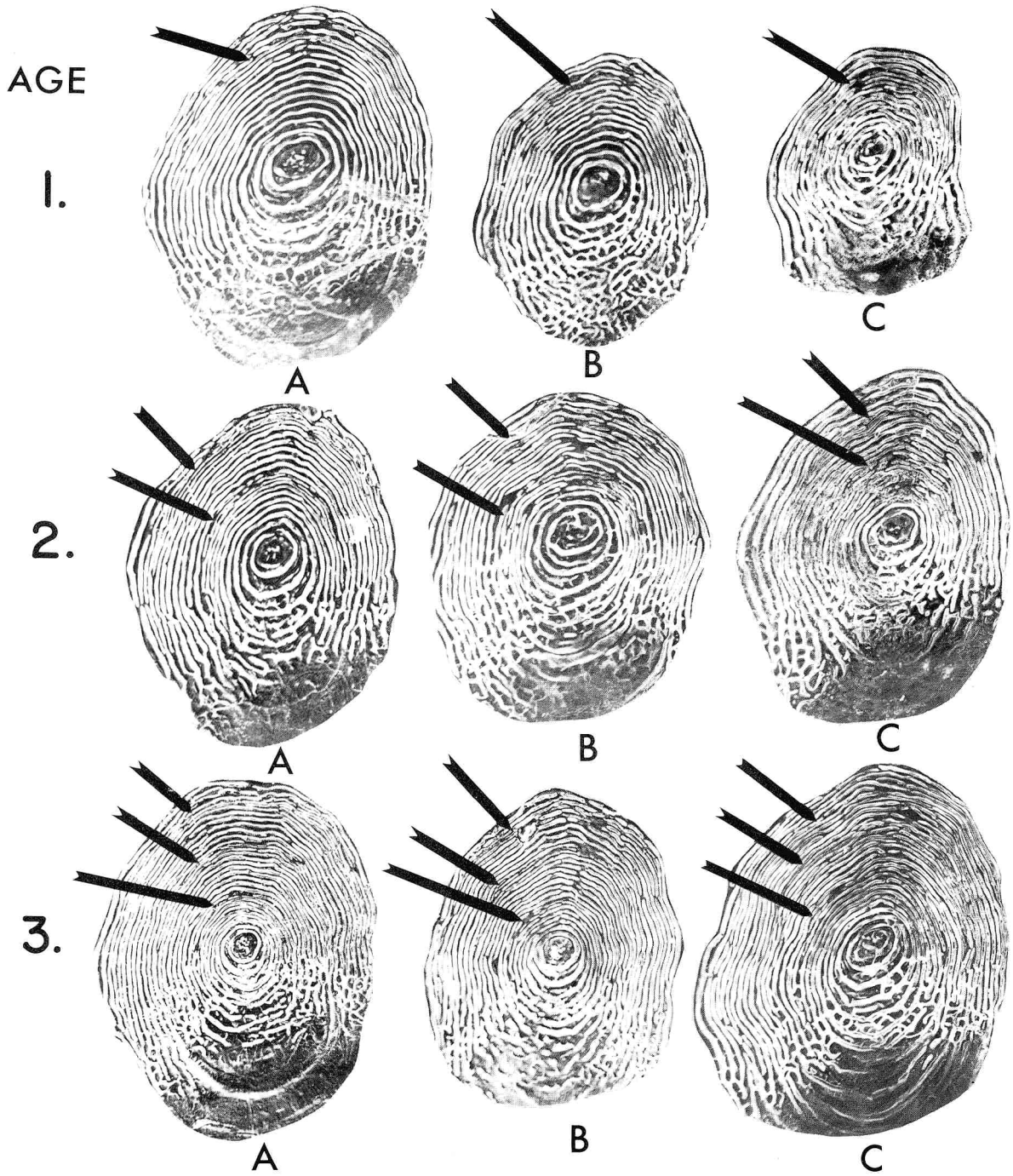


PLATE 3.—Fresh-water circuli.

PLATE 4.—Winter zones in fresh-water growth.

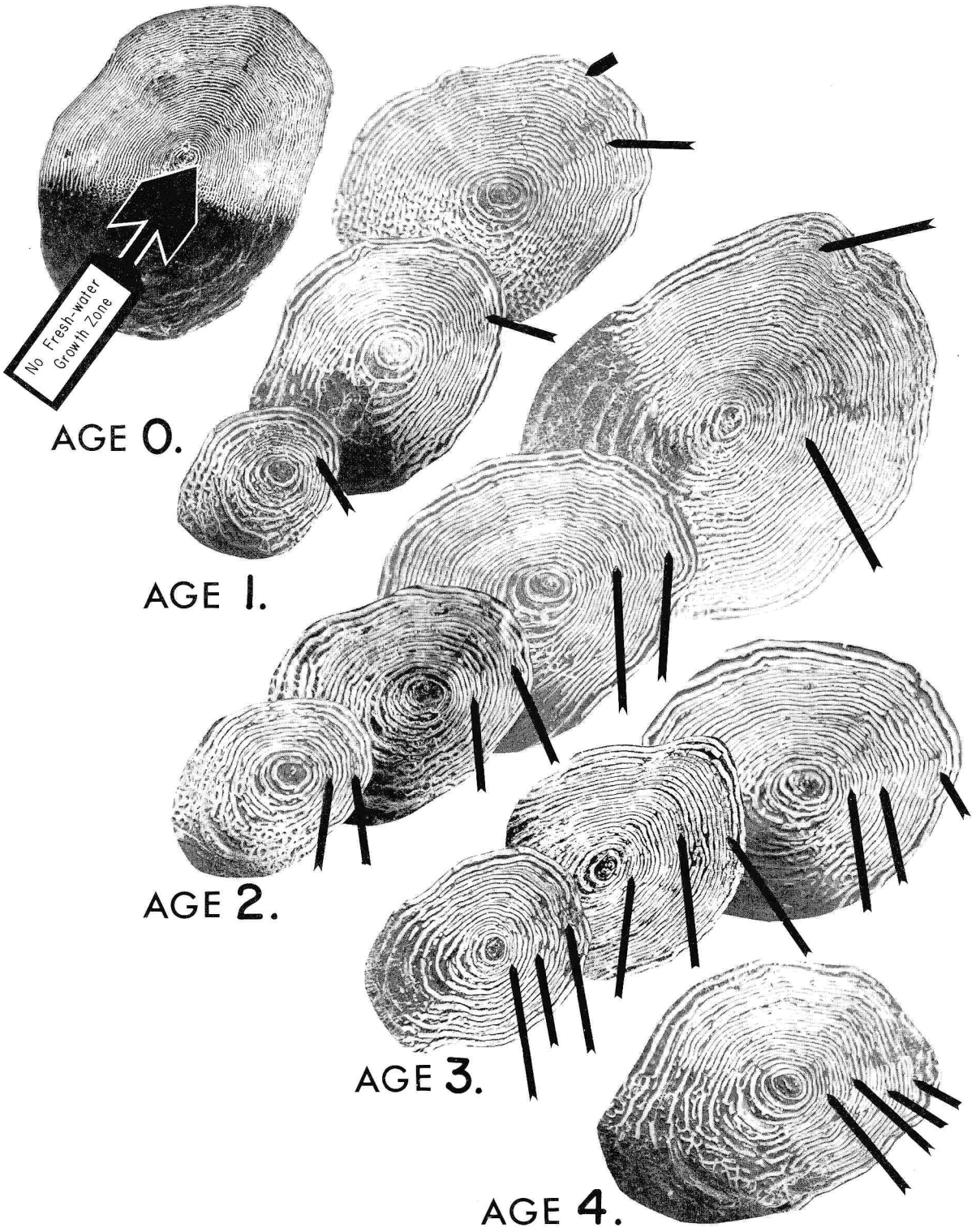


PLATE 5.—Fresh-water ages.

to the focus or to the edge of the scale. Because the circuli of the fresh-water zone are closer together and more finely lined and the growth zones may be composed of fewer circuli than in the ocean, the winters of fresh-water growth are sometimes indistinct and difficult to identify.

To assist in interpretation of the fresh-water zone, winter growth zones are classified into four types (numbers 1 to 4 in plate 4 correspond with the following descriptions):

1. Those made up of two or three circuli close together. This type of winter zone is the most distinct and easiest to identify and measure because it looks almost like a continuous line around the anterior field. The width of the arrows indicates the relative width of the winter zone.
2. Those made up of three or more circuli lying close together in a narrow band. This type of zone is relatively easy to identify, but less easy to measure or delimit than those of type 1.
3. Those made up of a number of complete or broken circuli lying close together in a broader band than those of type 2.
4. Those made up of a few circuli that are not much closer together than the adjacent circuli of the summer growth. These zones are diffuse and difficult to identify and measure.

FRESH-WATER AGES (Plate 5)

Plate 5 shows the range of fresh-water ages and the range of sizes of fresh-water zones of each age that may be found in sockeye salmon scales. The complete scale of the 0. age fish is magnified about 20 X. All other photographs are of the fresh-water zones of scales from adult sockeye salmon and show the relative sizes of the various zones as they appear when projected at about 40 X. The winters in fresh water are indicated by arrows.

Age 0. A complete scale from a fish in its third year that migrated to the ocean soon after hatching, magnified about 20 X. The few sockeye salmon that migrate seaward early in their first year usually reach the ocean before scales are formed; thus, their scales lack a fresh-water growth zone. Additional examples are shown in plate 12 and in Koo (1962c).

Age 1. Scales from fish that migrated seaward after one growing season in fresh water (in the second year). Small to large zones are illustrated. The small zone is typical of fish from Southeastern Alaska and some British Columbia areas. The large zone is typical of fish from Fish Creek, Cook Inlet, Alaska. (The stub pointer near the top of the upper scale in this series indicates the end of the transition zone; see plate 6.)

Age 2. Scales from fish that migrated to the sea after two full growing seasons in fresh water (in their third year). Small to very large zones are shown. The small zone is common in fish from Asian areas. The very large ones have been found only in fish from Dalinaia River, Kamchatka.

Age 3. Scales from fish that migrated to the sea after three full growing seasons in fresh water (in their fourth year). Small to large zones illustrated. The small zone is common in fish from Asian areas.

Age 4. A scale from a fish that migrated to sea after four full growing seasons in fresh water (in its fifth year). Fish of this fresh-water age are rare.

TRANSITION ZONE BETWEEN FRESH-WATER AND OCEAN GROWTH (Plate 6)

Correct interpretation of the zone of transition between fresh-water and ocean growth is important in age determination. Many disagreements on the age of individual sockeye salmon can be traced directly to different interpretations of this portion of the scales.

In most areas of western Alaska, new growth beyond the zone of narrow winter circuli is evident on the margin of nearly all scales of young fish in fresh water by mid-June (Koo, 1962a; and Mosher[7]) and earlier in areas to the south.

[7] Mosher, Kenneth H. Time of fresh-water annulus formation on the scales of young sockeye salmon from western Alaska. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash. [Manuscript.]

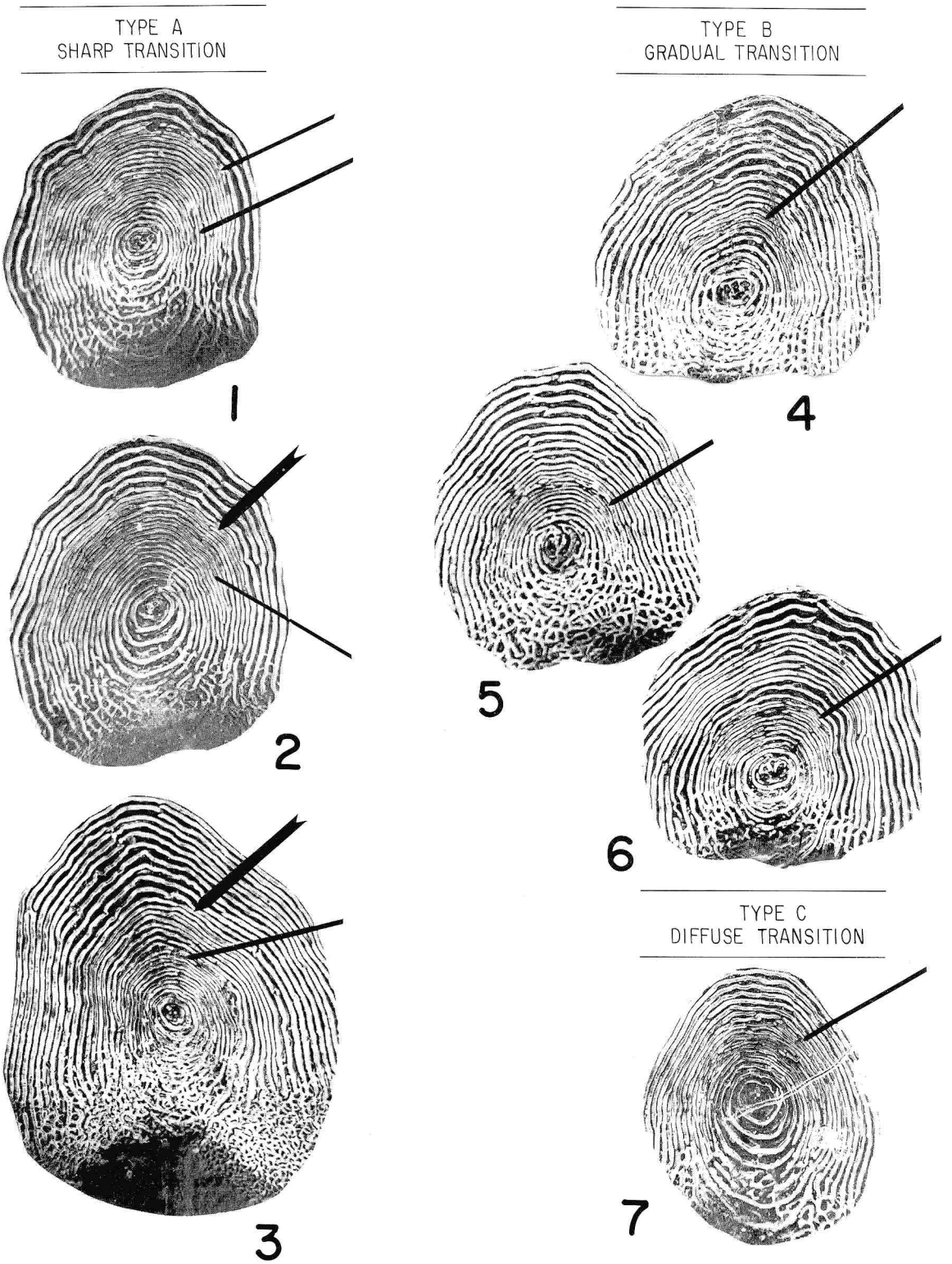


PLATE 6.—Transition zone between fresh-water and ocean growth.

Wider, darker circuli usually are laid down after this zone in the year in which the fish migrates seaward. If the fish reaches the ocean about the time this zone of narrow circuli is completed, the transition from narrow, light-textured fresh-water circuli to wider, heavier textured ocean circuli is abrupt. If the winter zone is completed before the fish reaches salt water, however, a varying number of circuli, intermediate in appearance between the fresh-water and ocean circuli, may be formed. This type of growth is called plus, transitional, intermediate, incidental, or spring growth.[8]

If the transition zone merges gradually into the ocean growth zone, it is usually easy to identify, although not to delimit. If, on the other hand, an adventitious mark (called a "migration check") forms and the zone is large, the migration check might be mistaken for another fresh-water winter (Mosher[9]).

Three general types of transition between fresh-water and ocean growth zones can be identified: type A, sharp or abrupt; type B, gradual; and type C, diffuse. These general types can be found in fish of all fresh-water ages.

Examples of the three types of transition zones are shown in plate 6. (The winter zones are indicated by arrows, and the migration checks in figures 2 and 3 by wider arrows.)

Type A. Sharp or abrupt transition is shown by the following photographs:

Figure 1. No plus growth. The transition from the fine-lined, closely spaced fresh-water circuli to the widely spaced ocean circuli is sudden. This type of transition poses no problems for accurate age determination.

Figure 2. Little plus growth after the winter zone formed. A migration check is between the transitional growth and the ocean growth. That the portion of the scale between the two arrows is plus growth is evident from the narrowness of the zone and the appearance of the circuli, which are intermediate in width and spacing between the circuli of the fresh-water and ocean growth zones.

Figure 3. Extensive plus growth after the winter zone formed. The weak migration check at the end of the transition might be mistaken for another winter in fresh water. Note, however, that the seven or eight circuli immediately preceding the broad, widely spaced circuli of the ocean zone are intermediate in width and spacing between the circuli of the fresh-water and ocean growth zones.

Type B. Gradual transition is shown by the following photographs:

Figure 4. No plus growth. The two or three circuli following the winter zone gradually expand into the broader ocean-type circuli.

Figure 5. Little plus growth. A few circuli of intermediate type are present, and the boundary of the transition is difficult to identify.

Figure 6. Extensive plus growth. The zone of intermediate growth is wide. Because there is no migration check at the end of the plus growth, the chance is small that it will be interpreted as another year's growth in fresh water.

[8] The term "spring growth" is usually applied to the intermediate or plus growth observed on scales of seaward migrant fish, not adult fish.

[9] Mosher, Kenneth H. The plus or intermediate growth of sockeye salmon scales. Bureau of Commercial Fisheries, Biological Laboratory, Seattle, Wash. [Manuscript.]

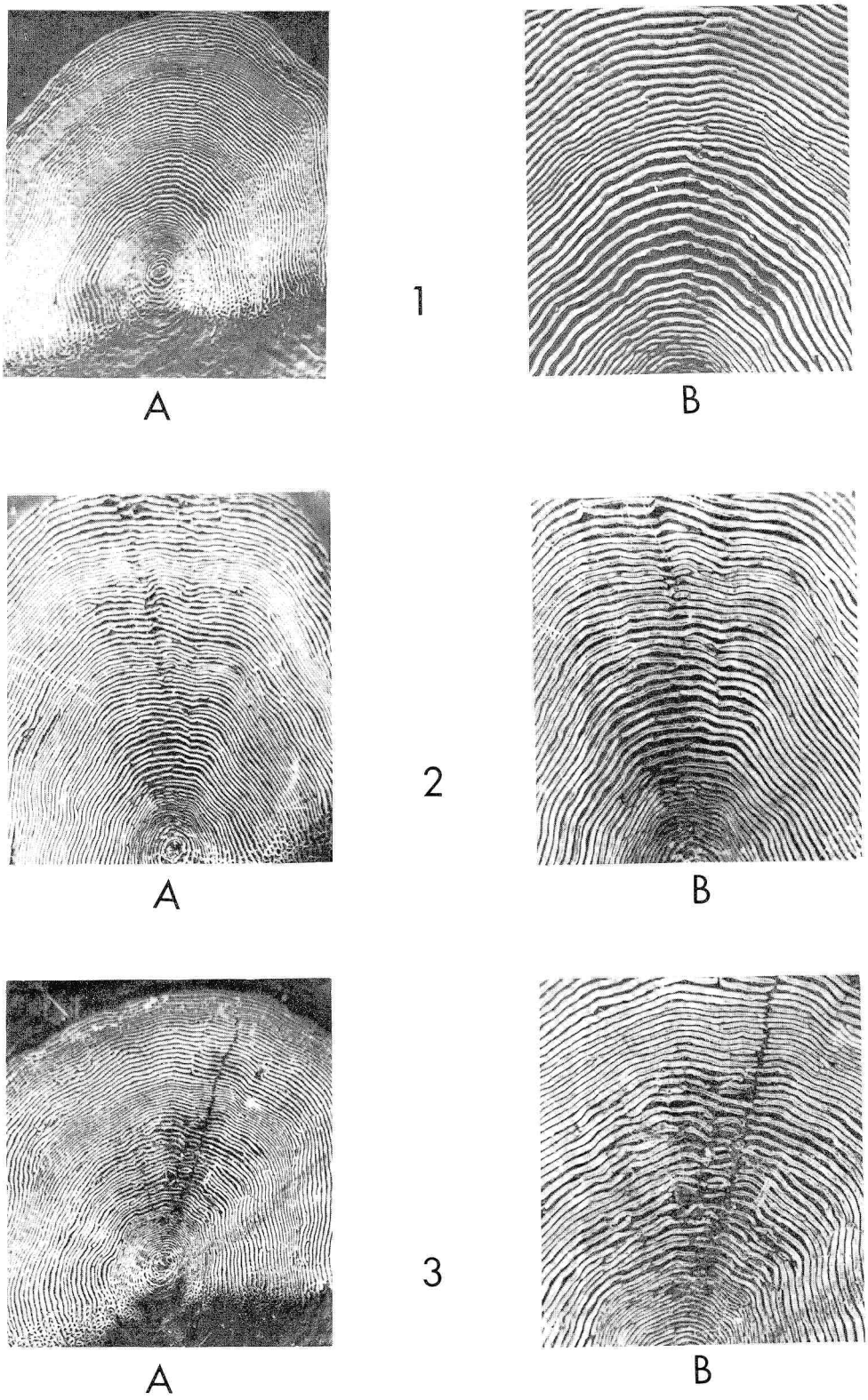


PLATE 7.—Appearance of ocean growth zones based on type of circuli.

Type C. Diffuse transition is shown in figure 7. The transition between the fresh-water and ocean growth is so broken up by irregular circuli that the exact boundaries of the fresh-water and plus growth (if any) are difficult to determine.

OCEAN GROWTH

The following plates show details of the ocean growth zone, including the variations in:

1. appearance of zones based on type of circuli (plate 7).
2. number of circuli (plate 8).
3. spacing of circuli within the zones (plate 9).
4. appearance of the winter zones (plate 10).
5. ocean ages (plate 11).

APPEARANCE OF OCEAN GROWTH ZONES BASED ON TYPE OF CIRCULI (Plate 7)

The relative numbers of complete and interrupted circuli affect the appearance of the different ocean zones and the ease and accuracy with which measurements and counts of circuli and winters of life can be made. See plate 2 for examples of various types of circuli. Three broad categories of ocean growth zones, based on the circuli, are illustrated in plate 7. Each category is illustrated by two photographs.

Figure A shows the major portion of a scale magnified about 20 X; figure B, which is the central portion of the same scale magnified about 40 X, shows the circuli of the first ocean zone in greater detail. The categories of ocean-growth zones are described as follows:

Category 1. A scale with mostly complete circuli in the ocean-growth zones.

Category 2. A scale with complete and irregular circuli in the ocean-growth zones (an "average" scale).

Category 3. A scale with nearly every circulus broken or otherwise interrupted in the ocean-growth zones.

NUMBER OF OCEAN CIRCULI (Plate 8)

The mean number of circuli in the first ocean growth zone of scales from adult fish differ by geographical areas (table 1). The largest mean numbers are on scales of sockeye salmon from Rivers Inlet, British Columbia. Mean numbers of circuli tend to be progressively lower on scales of North American fish taken southward to the Columbia River and northwestward to Bristol Bay, Alaska. Scales from Asian fish have greater mean numbers of circuli than the Bristol Bay sockeye. This difference in mean numbers of circuli holds true in all ocean zones but is most pronounced in the first ocean zone.

The scales in plate 8 were selected to show the numerical differences in the number of circuli in the first ocean zone (number of circuli between each pair of pointers) among sockeye salmon from different geographical areas, as follows:

Figure 1. Asia, 25 circuli.

Figure 2. Bristol Bay, 22 circuli.

Figure 3. Ketchikan, Alaska (as representative of the area from Cook Inlet to the Nass River, British Columbia), 27 circuli.

Figure 4. The Skeena River, British Columbia, 29 circuli.

Figure 5. Rivers Inlet, British Columbia, 32 circuli.

Figure 6. The Columbia River, Oregon-Washington, 26 circuli.

SPACING OF OCEAN CIRCULI (Plate 9)

Spacing of circuli within the ocean growth zones may also vary between scales from fish collected in different geographical areas. In general, scales with relatively large numbers of circuli in the first ocean zone tend to have more uniformly spaced circuli than those with fewer circuli. On scales from Bristol Bay fish, the widest spaced circuli are usually deposited near the closely spaced fresh-water portion. On scales from Asian fish, the widest spaced circuli are often deposited just before the closely spaced winter ocean circuli. On scales from fish taken east and southeastward of Bristol Bay, the position of the widest spaced circuli of the ocean zones is less consistent. They may occur in the same position as in the Bristol Bay or the Asian

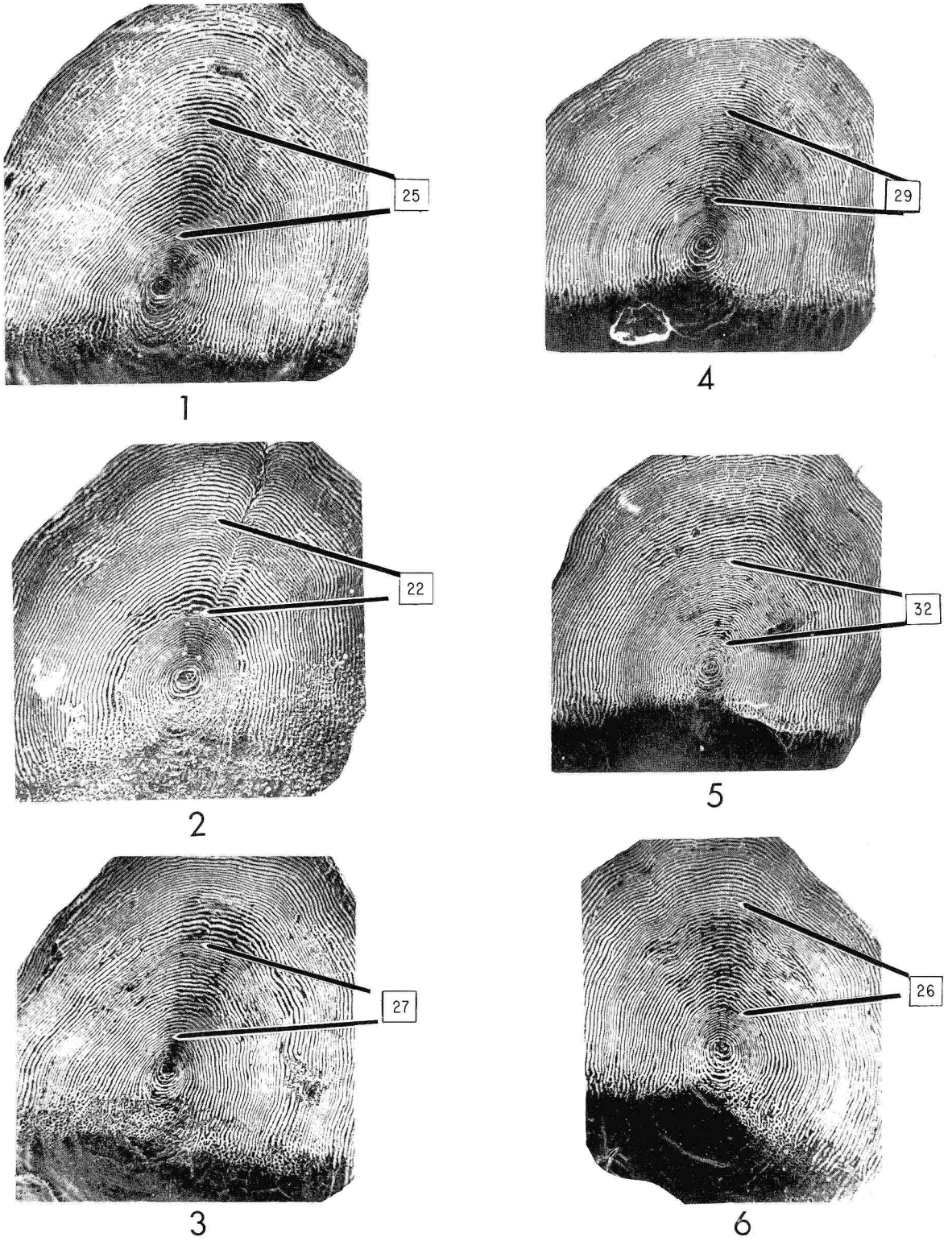


PLATE 8.—Number of ocean circuli.

TABLE 1.—*Percentage frequency distribution[1] and mean number of circuli in the first ocean zone of scales from sockeye salmon collected in 1963*

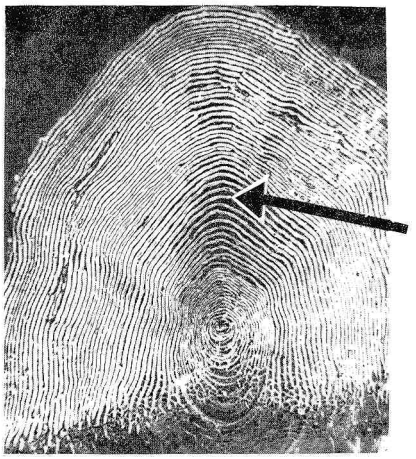
[Asterisks indicate modes]

Number of circuli	Alaska				British Columbia				
	Asla [2]	Bristol Bay[2]	Chignik [3]	Cook Inlet[2]	Nass [2]	Skeena [3]	Rivers Inlet [3]	Fraser [3]	Columbia River[3]
	Percent								
13	0.2	....	....	....	....	....	....	....	....
14	.5	....	....	....	....	....	....	....	....
15	.2	0.5	....	....	....	....	....	....	....
16	....	1.5	....	....	....	....	....	....	....
17	.5	4.4	....	....	....	....	....	....	....
18	1.4	9.1	0.6	....	....	....	....	....	....
19	3.1	14.7	1.4	0.4	0.6	....	....	....	....
20	6.5	*19.1	2.3	2.0	1.5	....	....	....	....
21	9.0	18.7	4.5	4.6	2.0	....	....	....	0.9
22	9.3	14.5	8.5	7.3	1.8	0.6	....	....	4.0
23	11.9	10.0	14.2	10.4	2.6	1.7	....	0.3	7.3
24	*15.9	5.2	*17.3	14.6	5.6	4.8	....	3.4	9.8
25	15.4	1.7	15.6	*17.8	9.2	10.5	0.3	9.2	14.0
26	10.6	.5	13.4	16.0	13.0	15.1	.9	12.9	*18.0
27	5.9	.1	9.9	12.1	*14.4	*15.6	1.2	*14.7	16.8
28	3.8	....	6.0	7.9	12.2	13.6	2.9	*14.7	12.2
29	2.5	....	3.7	3.7	10.2	12.2	6.2	13.6	8.2
30	1.4	....	2.0	2.1	10.2	10.2	8.8	11.5	5.2
31	1.0	....	.6	1.1	9.0	6.8	12.0	6.9	2.4
32	.7	....	....	....	5.4	4.0	*14.7	4.3	.9
33	.2	....	....	....	1.7	2.3	*14.7	4.3	.3
34	....	....	....	....	.4	1.1	11.5	2.8	....
35	....	....	....	....	.2	.6	7.9	1.1	....
36	....	....	....	....	....	.6	7.4	.3	....
37	....	....	....	....	....	.3	6.2	....	....
38	....	....	....	....	....	....	3.5	....	....
39	....	....	....	....	....	....	1.5	....	....
40	....	....	....	....	....	....	.3	....	....
Mean number of circuli	24.1	20.6	24.7	25.1	27.5	27.9	32.8	28.4	26.3
Number of fish	156	650	88	145	98	88	85	87	82

[1] Actual frequencies smoothed according to Henry (1961).

[2] Combined 1. and 2. fresh-water ages.

[3] 1. fresh-water ages only.



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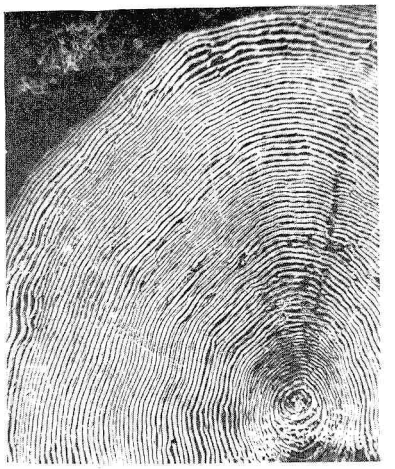

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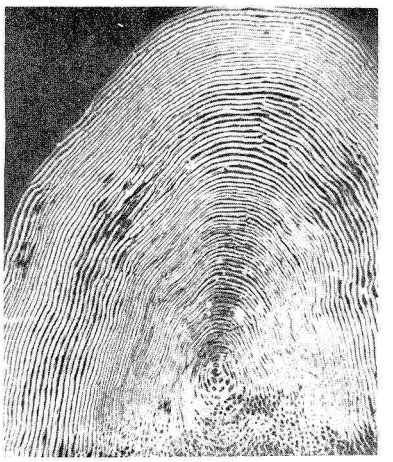

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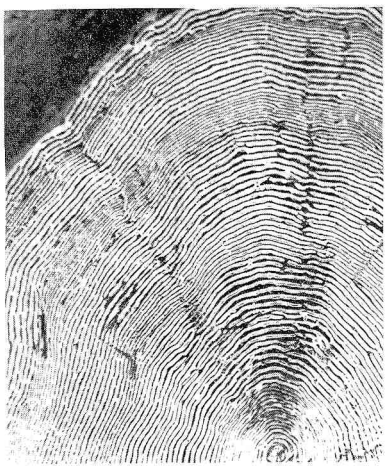

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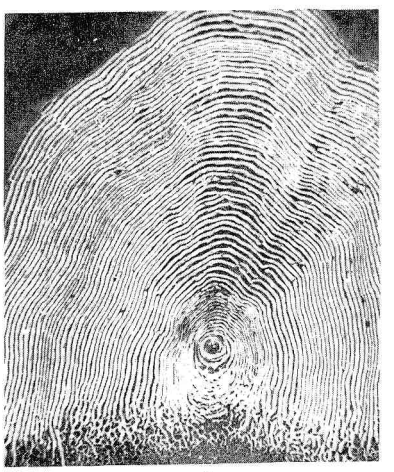

6

PLATE 9.—Spacing of ocean circuli.

fish, but often the circuli are so uniformly spaced that no area of widest spacing can be identified.

Plate 9 shows examples of these variations in spacing of circuli within the first ocean growth zone, as follows:

Figure 1. A scale from an Asian sockeye salmon with the widest spaced circuli (arrow) immediately preceding the winter ocean growth.

Figure 2. A scale from a Bristol Bay sockeye salmon with the widest spaced circuli (arrow) formed immediately after migration to the ocean.

Figure 3. A scale from a Cook Inlet sockeye salmon with a summer growth zone of widely and uniformly spaced circuli.

Figure 4. A scale from a Skeena River sockeye salmon with a summer growth zone of uniformly spaced circuli.

Figure 5. A scale from a Rivers Inlet sockeye salmon with a summer growth zone of evenly and closely spaced circuli.

Figure 6. A scale from a Columbia River sockeye salmon with a summer growth zone of widely and uniformly spaced circuli.

WINTER ZONES IN OCEAN GROWTH (Plate 10)

Winter zones in the ocean growth result from slower scale growth in the fall, winter, and early spring, during which time the circuli are formed closer together than during the faster growth in the late spring and summer. Zones of winter growth in the ocean, like those in the fresh-water portion of the scale, also vary in appearance; they may be classified into four general groups on the basis of appearance (winter zones in the illustrations are numbered as follows):

1. Clear-cut zones made up of a number of closely spaced circuli.
2. Zones made up of circuli less closely spaced or more numerous than those of group 1.
3. Diffuse zones the boundaries of which cannot easily be identified. Whereas the circuli are closer together than the adjacent summer growth zones, either the difference between the spacing of circuli is so slight or the narrowing of the circuli into the winter zone is so gradual that it is difficult to be sure of the exact boundaries of the zone.
4. Winter zones characteristic of the first ocean zone of most sockeye salmon from Rivers and Smith Inlets, British Columbia, where the circuli are often only slightly closer together than the closely spaced circuli of the summer growth.

The winters of ocean life of the fish not only must be accurately identified for age determination, but their location and boundaries must be measured exactly in many racial and other studies; therefore, scales with diffuse winter zones (group 3) may be difficult or impossible to use in some of these studies.

AGE GROUPS BY NUMBER OF WINTERS IN THE OCEAN (Plate 11)

Sections of sockeye salmon scales showing ocean growth zones illustrate the range of ocean ages found in this species.[10] Arrows indicate the winter growth zones.

.0 — only a few months in the ocean, no winter growth zone
.1 — one winter in the ocean
.2 — two winters in the ocean
.3 — three winters in the ocean
.4 — four winters in the ocean
.5 — five winters in the ocean

SCALES WITH DIFFERENT COMBINATIONS OF FRESH-WATER AND OCEAN AGE

All the combinations of fresh-water and ocean age that I have found in sockeye salmon are illustrated in plates 12 to 16. Age designations of adult salmon follow the recommendations of Koo (1962b). Two methods may be used—the European method or the Gilbert and Rich (1927) method. The Gilbert and Rich method is used on the following plates; in the text, age designa-

[10] Age designation of salmon in reference to marine life only follows the recommendations of Koo (1962b): a dot followed by the number of winters the fish spent in the ocean.

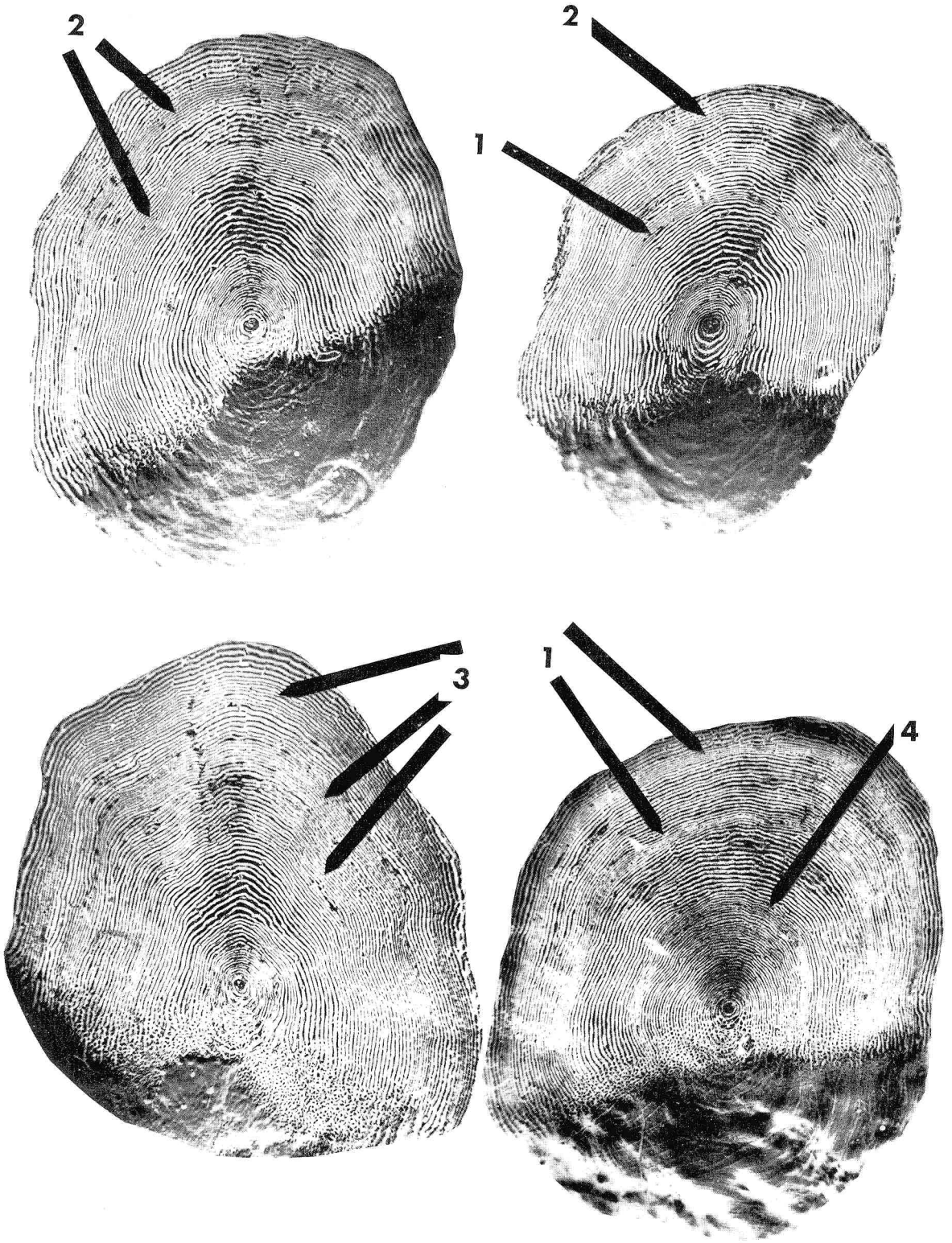

PLATE 10.—Winter zones in ocean growth.

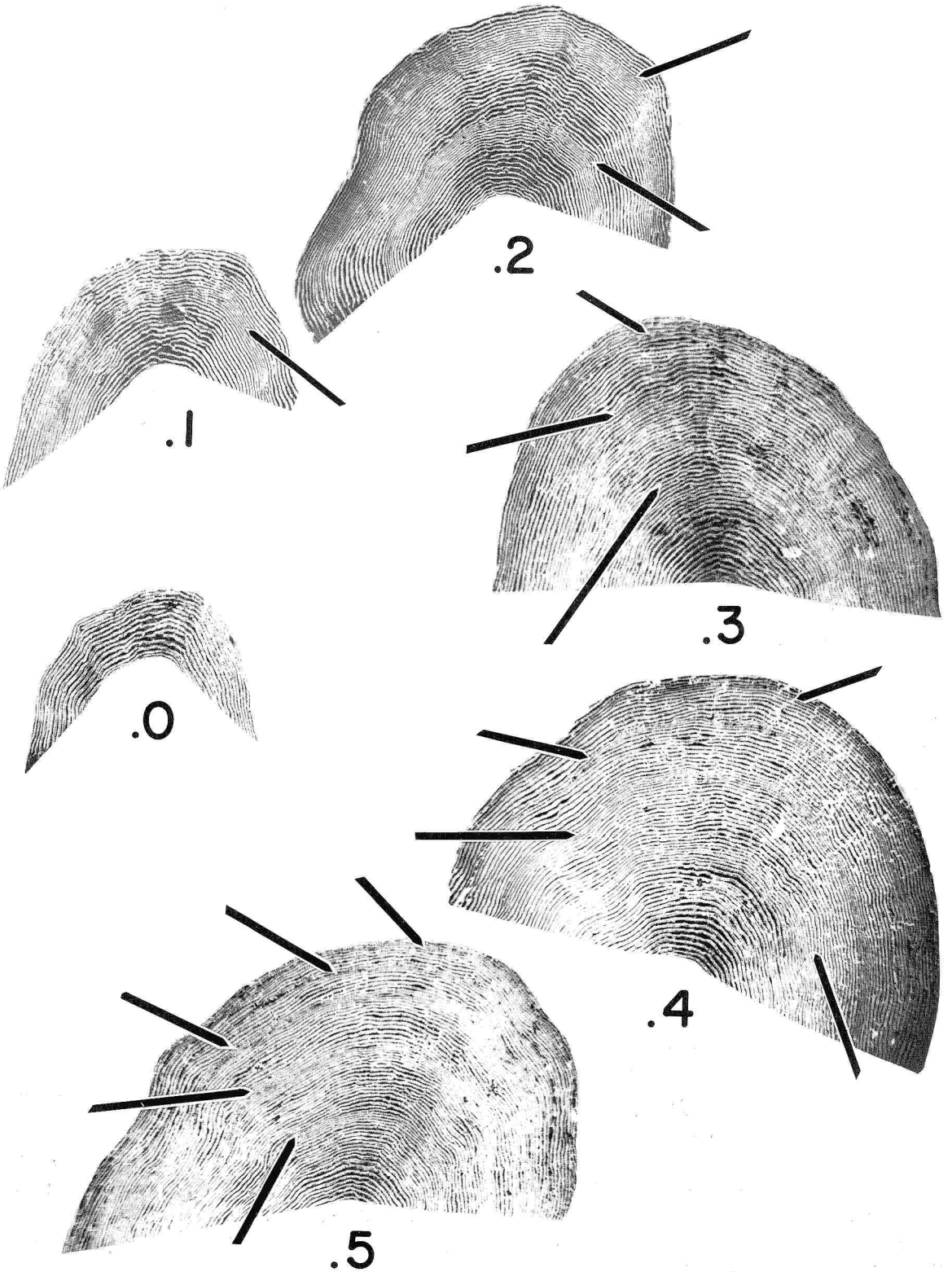

PLATE 11.—Age groups by number of winters in the ocean.

tion by the European method is shown in parentheses.

In the Gilbert and Rich designations, an Arabic numeral indicates the number of winters from spawning of the parents to capture. A second digit, usually written as a subscript, indicates the winters from spawning of the parents to seaward migration. Because the fish do not form scales until after the first winter in the gravel, the number of winters of growth is one less than shown by the age formula, but the fish is in the indicated year of life. To assign a fish to its parent brood year, subtract the first digit from the year of capture; e.g., a fish of age group 5_3 caught in 1965 was produced by the spawning in 1960 and migrated to the ocean in 1963. Scientists of the U.S.S.R. use a modified Gilbert and Rich system in which the age is computed from hatching instead of spawning of the parents (Krogius, 1958; Chugunova, 1959).

In the European method, the number of winters the fish spent in fresh water from hatching and in the ocean are separated by a dot. To determine the year of spawning that produced the fish, add 1 to the sum of the two digits and subtract from the year of capture.

A comparison of the major age groups in the three methods of age designation follows:

Gilbert and Rich	European	U.S.S.R.
4_1	0.3	3_0
4_2	1.2	3_1
5_2	1.3	4_1
5_3	2.2	4_2
6_3	2.3	5_2
6_4	3.2	5_3
7_4	3.3	6_3

Runs of sockeye salmon often include individuals, considerably smaller than the average, that have returned to spawn after only one winter at sea. These fish are known as "jacks" as they are almost invariably males, except in the Columbia River where they may be of either sex.[11]

In the following plates the winter growth zones are indicated by arrows—wide arrows in the ocean portion of the scale (plates 12-18) and narrow arrows in the fresh-water portion (plates 13-18). Stub arrows when present indicate the end of plus growth.

[11] Occasionally the small females in the Columbia River are called "jennies."

AGE GROUPS WITH NO SCALE GROWTH IN FRESH WATER (Plate 12)

Fish of these age groups migrate to the sea before or immediately after scale formation. Because most sockeye salmon live in fresh water for a year or more, few scales of these ages are collected; they are usually in the 3_1 and 4_1 age groups.

Examples of these age groups are shown:

Age group 2_1. (0.1) one winter in the ocean zone. Spawning fish are "jacks."

Age group 3_1. (0.2) two winters in the ocean zone.

Age group 4_1. (0.3) three winters in the ocean zone.

Age group 5_1. (0.4) four winters in the ocean zone.

AGE GROUPS WITH ONE GROWING SEASON IN FRESH WATER (Plate 13)

These age groups make up many of the important runs of sockeye salmon. From the Columbia to the Copper River, and in the Wood River-Nushagak system in Bristol Bay, fish with this fresh-water history predominate every year.

Fish of a given year class may first be present in a spawning run as age group 3_2 ("jacks"); dominate the run the next year as age group 4_2 and (in some areas) the following year as age group 5_2; and provide occasional 6_2's and 7_2's in subsequent years. Thus, it is possible that fish of a year class with one growing season in fresh water could be present in the spawning migration over a 5-year period, but in most areas the period lasts only 3 or 4 years.

Examples of the following age groups are shown:

Age group 2_2 (1.0). One winter in fresh water, none in the ocean. (This illustration is from an immature fish, not an adult.)

Age group 3_2 (1.1). One winter in fresh water, one in the ocean.

Age group 4_2 (1.2). One winter in fresh water, two in the ocean.

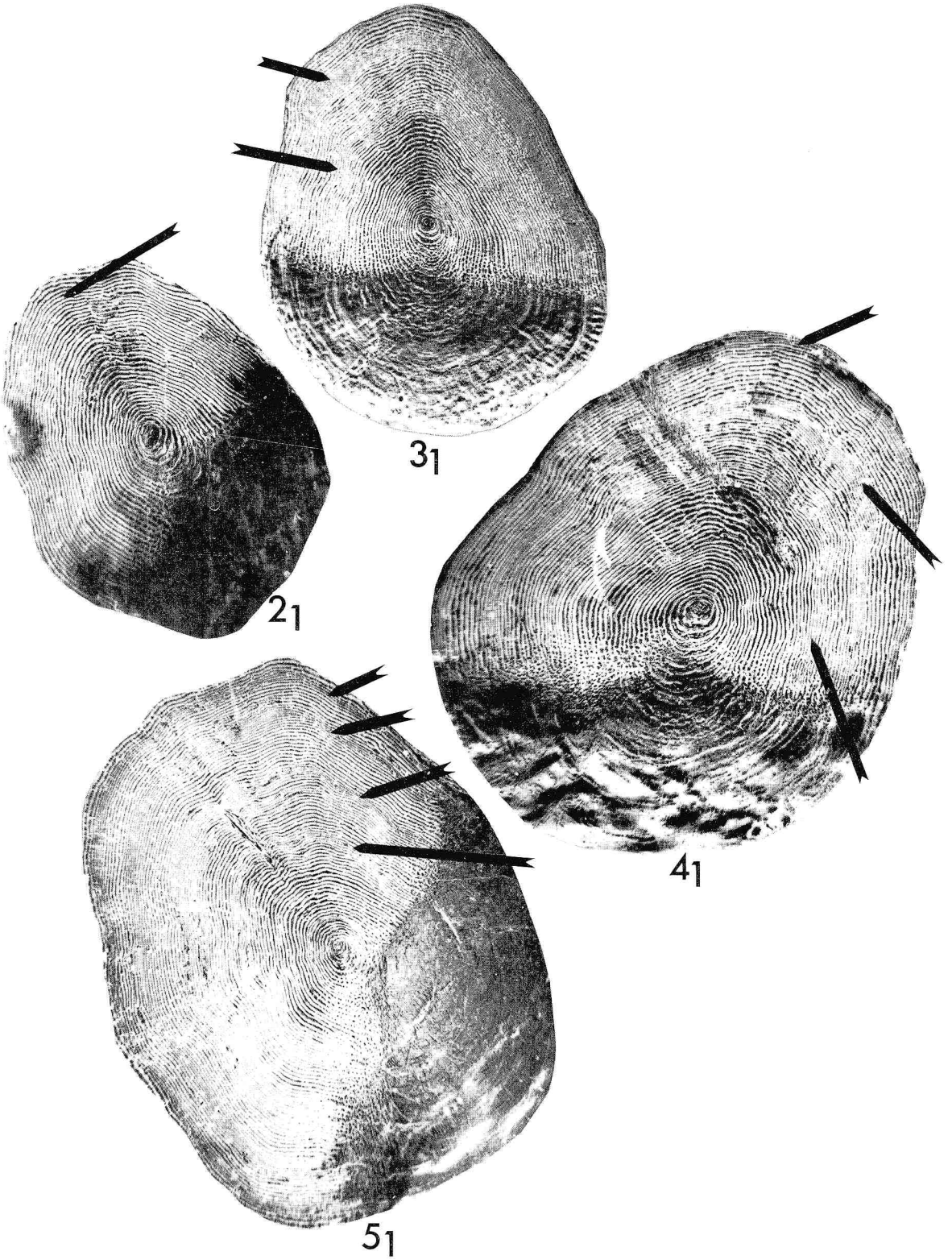

PLATE 12.—Age groups with no scale growth in fresh water.

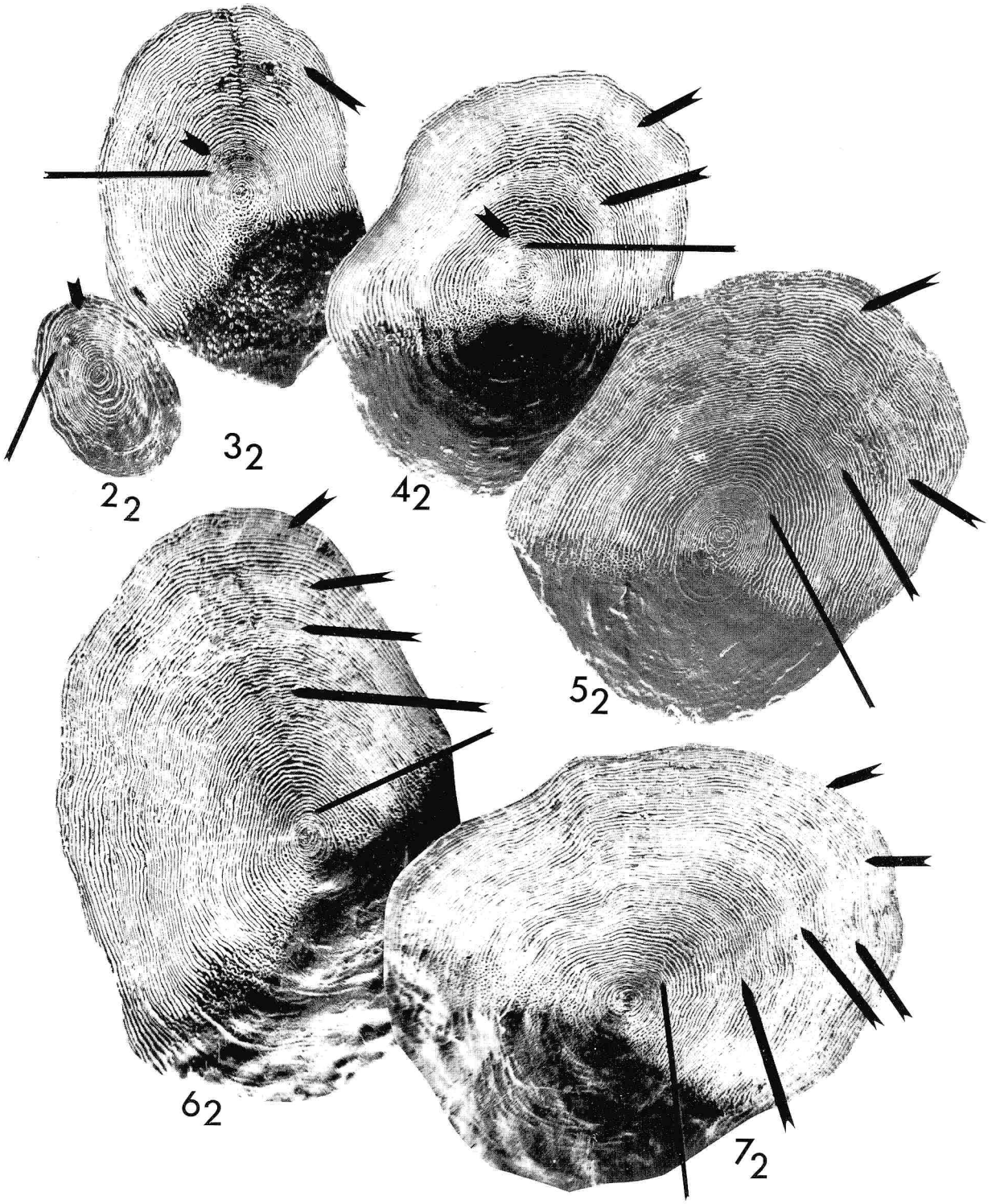

PLATE 13.—Age groups with one growing season in fresh water.

Age group 5_2 (1.3). One winter in fresh water, three in the ocean.

Age group 6_2 (1.4). One winter in fresh water, four in the ocean.

Age group 7_2 (1.5). One winter in fresh water, five in the ocean.

AGE GROUPS WITH TWO GROWING SEASONS IN FRESH WATER (Plate 14)

These age groups also make up many important runs of sockeye salmon. The Ozernaia River in Asia, a number of tributaries of Bristol Bay, and Karluk River on Kodiak Island are areas where fish of these age groups predominate in the spawning runs in most years. Fish of a given year class may be in the spawning run one year as age group 4_3 ("jacks"); dominate the run the next year as age group 5_3 and (in some areas) the following year as 6_3's; and produce an occasional 7_3 the following year.

Examples of the following age groups are shown:

Age group 3_3 (2.0). Two winters in fresh water, none in the ocean. (This illustration is from an immature fish, not an adult.)

Age group 4_3 (2.1). Two winters in fresh water, one in the ocean.

Age group 5_3 (2.2). Two winters in fresh water, two in the ocean.

Age group 6_3 (2.3). Two winters in fresh water, three in the ocean.

Age group 7_3 (2.4). Two winters in fresh water, four in the ocean.

AGE GROUPS WITH THREE GROWING SEASONS IN FRESH WATER (Plate 15)

Fish of these age groups are common in the Karluk River, Alaska, and in some Asian areas. In some years they may make up a substantial portion of the spawning runs in these areas, primarily as age groups 6_4 and 7_4. Examples of the following age groups are shown:

Age group 4_4 (3.0). Three winters in fresh water, none in the ocean. (This illustration is from an immature fish, not an adult.)

Age group 5_4 (3.1). Three winters in fresh water, one in the ocean.

Age group 6_4 (3.2). Three winters in fresh water, two in the ocean.

Age group 7_4 (3.3). Three winters in fresh water, three in the ocean.

Age group 8_4 (3.4). Three winters in fresh water, four in the ocean.

AGE GROUPS WITH FOUR GROWING SEASONS IN FRESH WATER (Plate 16)

In areas where fish with three growing seasons in fresh water are common, occasional fish stay in fresh water another year. These fish are rare. Examples of the following ages are shown:

Age group 6_5 (4.1). Four winters in fresh water, one in the ocean.

Age group 7_5 (4.2). Four winters in fresh water, two in the ocean.

Age group 8_5 (4.3). Four winters in fresh water, three in the ocean. This group is very rare.

SCALES WITH IRREGULAR OR DEFORMED FEATURES

Some scales are of little or no value for age or racial study because they are regenerated (plate 17). Others may be unsuited for these studies because of resorption (plate 18), or for a number of other reasons (shown in plate 19).

REGENERATED SCALES (Plate 17)

When a salmon loses a scale, a new one rapidly replaces it.[12] The new scale does not form circuli until it approximates the size of the scale that was lost. Normal scale growth then resumes, and circuli form regularly thereafter. Regenerated areas range from a small portion of the center of the scale to almost the complete scale. When a scale is lost from large fish, the resulting regenerated scale is often of atypical size and shape.

Scales that were regenerated before the fish migrated to the sea can be used to determine the

[12]Unpublished results of my experiments a few years ago showed that lost scales of coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon were replaced and had resumed normal growth within 1 month, even in fish which were in poor physical condition.

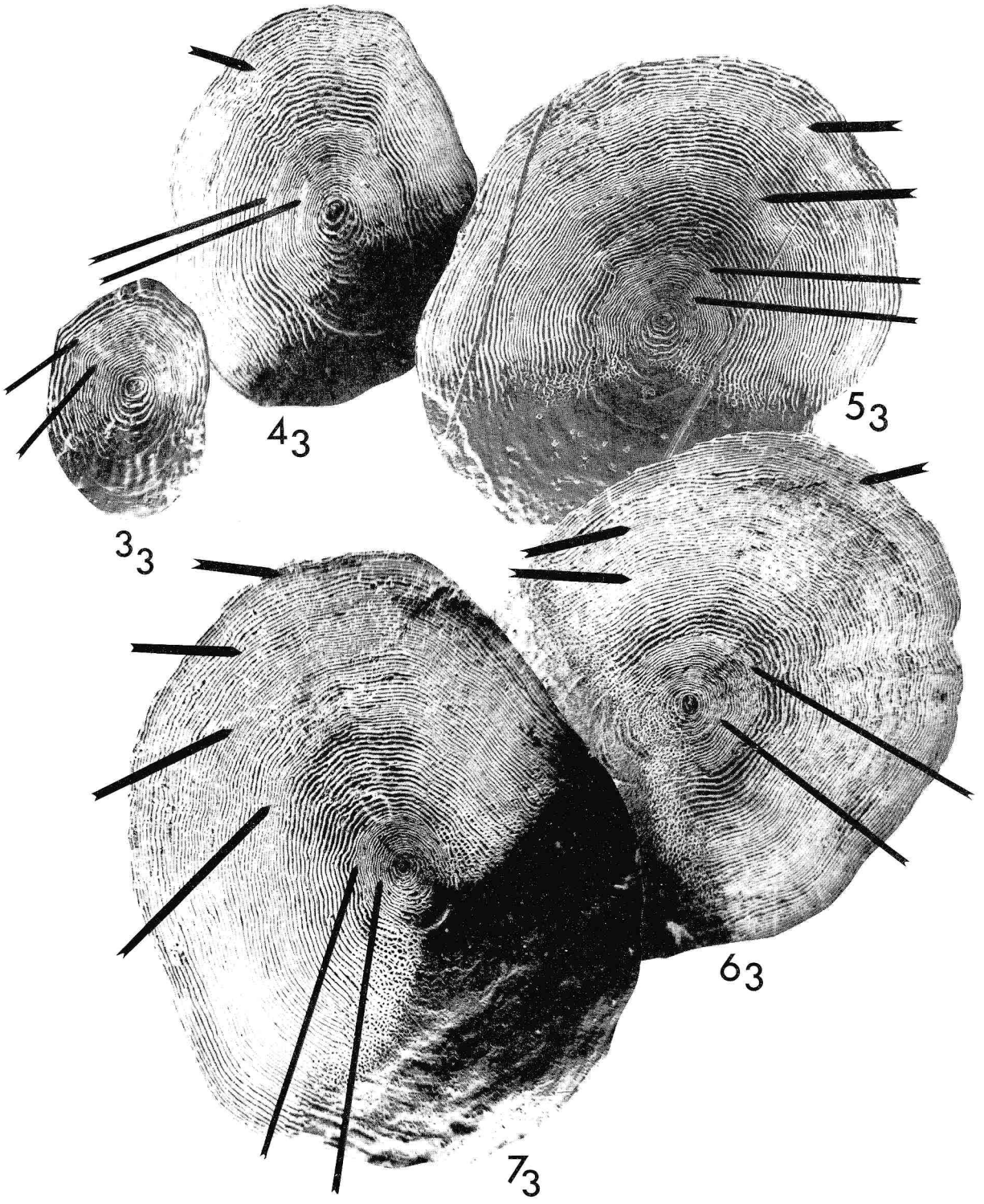

PLATE 14.—Age groups with two growing seasons in fresh water.

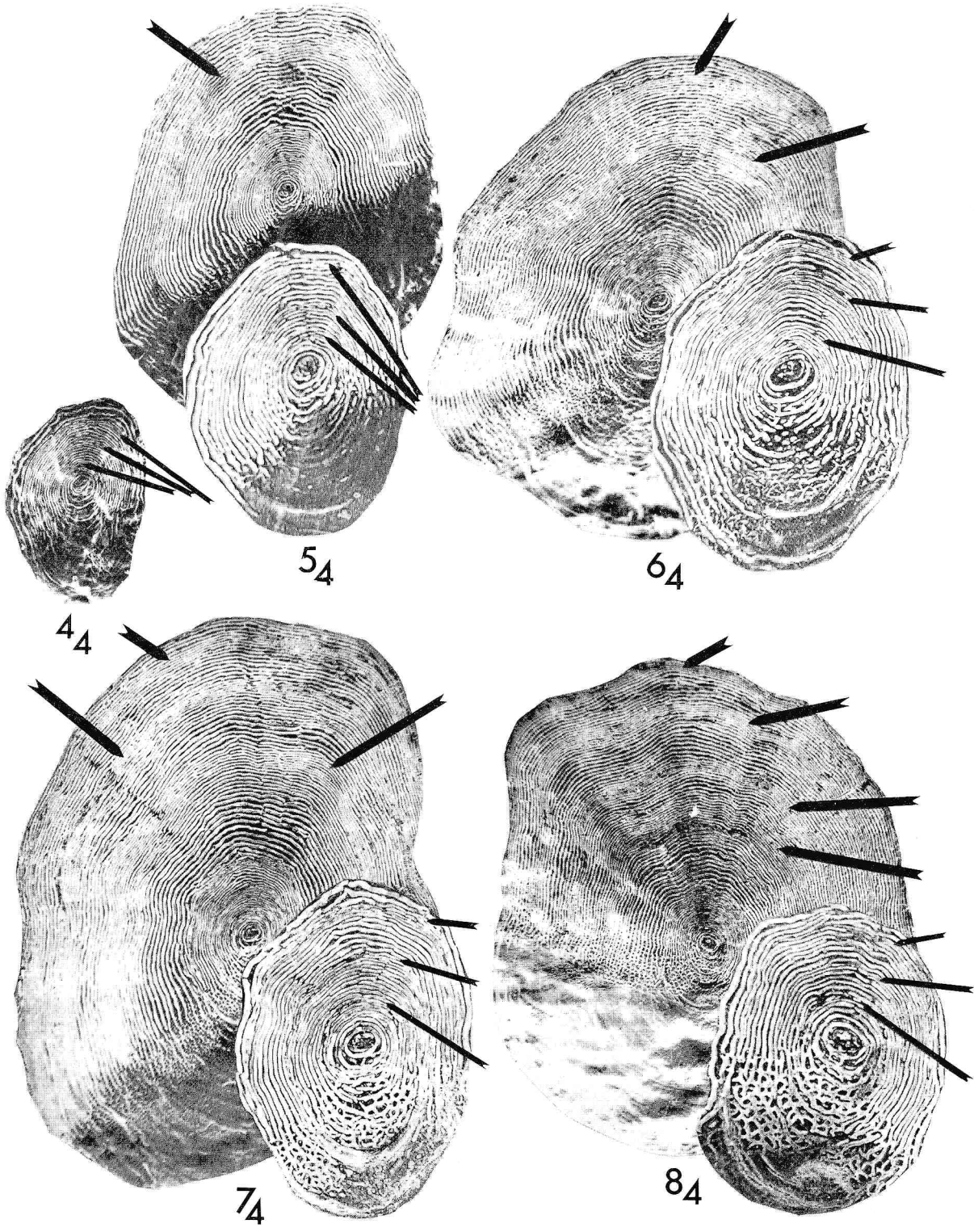

PLATE 15.—Age groups with three growing seasons in fresh water.

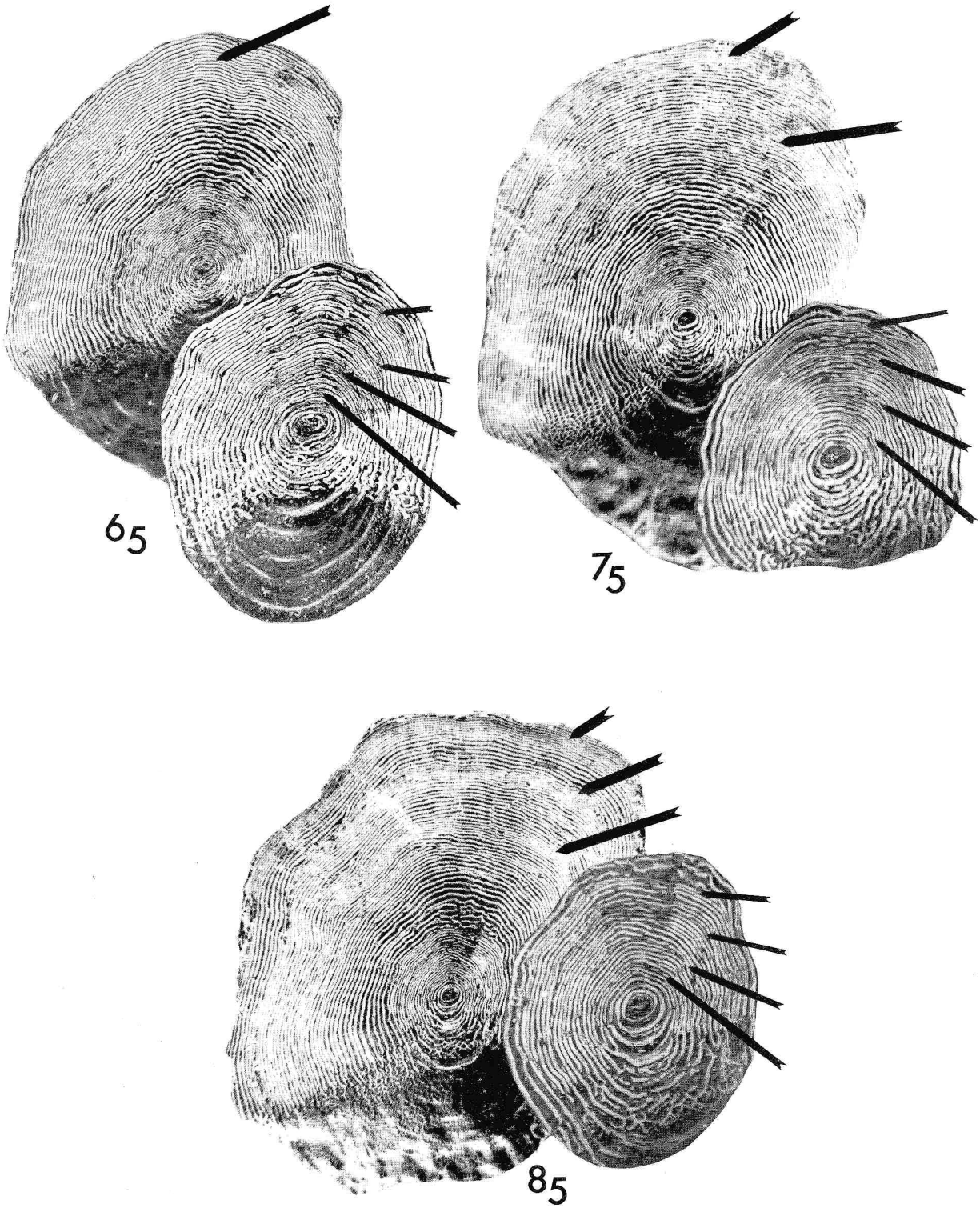

PLATE 16.—Age groups with four growing seasons in fresh water.

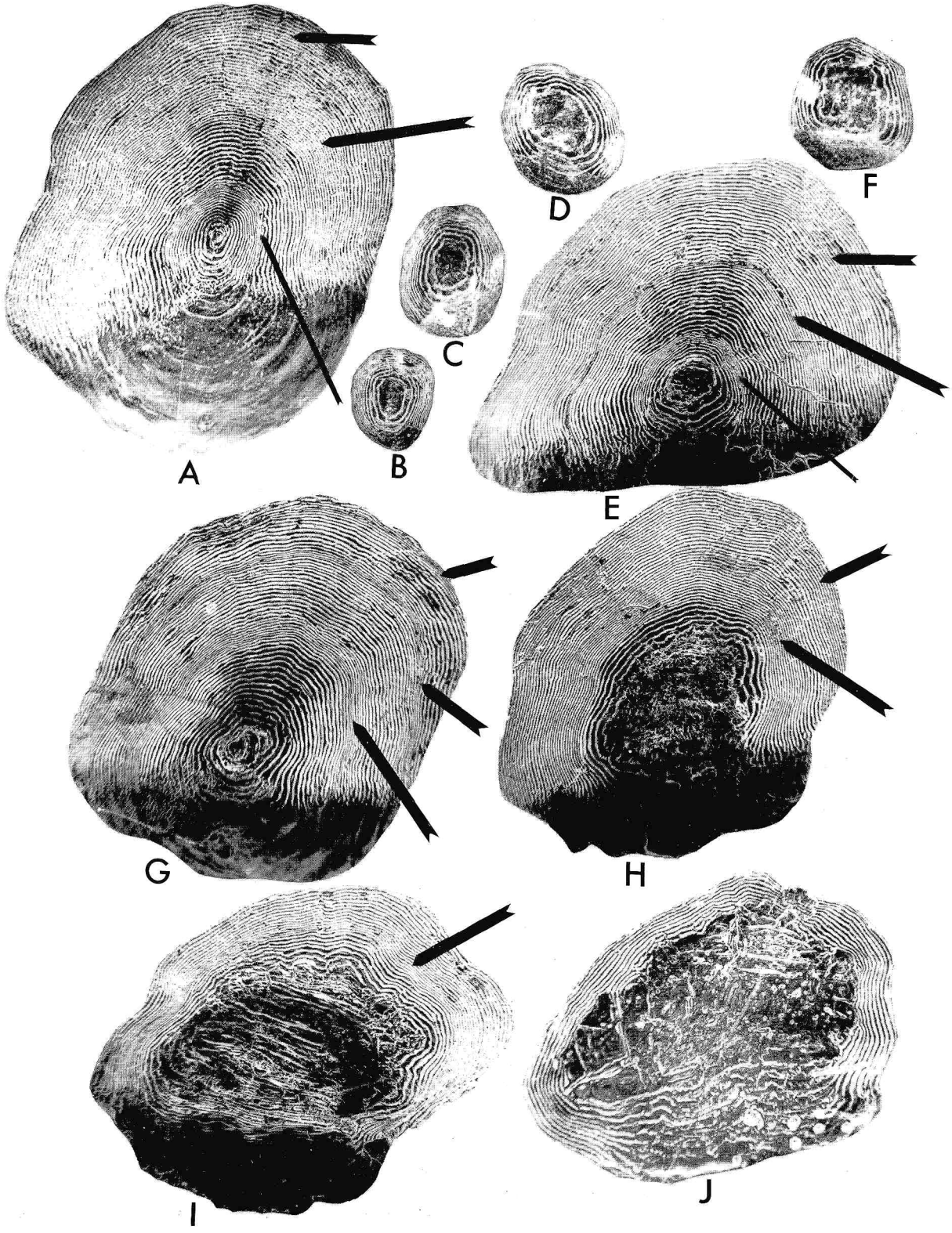

PLATE 17.—Regenerated scales.

ocean age of the fish, but only those that were replaced before the first winter reveal the total age.

Regenerated scales may be used to back-calculate the year of scale loss; for instance, scales taken from scars on the body of the fish may show the number of years since the injury. This technique can be applied to fish with gill net marks.

The scales on plate 17 are arranged to show increasing amounts of regeneration. Figures A and B, D and E, and F and G are pairs; the large scale of each pair shows about the same amount of regeneration of the fresh-water zone as the small scale of the pair. To illustrate how regenerated scales may be used to date an injury that removed the original scale, I arbitrarily assume that all the scales from adult fish on this plate were collected in the summer of 1965.

Scale A. A scale from an adult sockeye salmon shows regeneration of only a few central circuli; the fish spent one winter in fresh water and two winters in the ocean. This scale replaced one lost in 1962, a short time after the original scale was formed.

Scale B. A scale from a young sockeye salmon taken in fresh water shows regeneration that involves only a few circuli. At adult size the scale of this fish would look much like scale A.

Scale C. A scale from a young sockeye salmon. This scale shows a larger area of regeneration.

Scale D. A scale from a young sockeye salmon shows regeneration of about half of the scale.

Scale E. A scale from an adult sockeye salmon shows regeneration that involves about half of the fresh-water zone (scale D). This scale shows that the fish spent two winters in the sea and at least one in fresh water. This fish also lost the original scale in 1962; the age of the fish at that time could have been from a few months to over a year. The total age of the fish cannot be determined from this scale.

Scale F. A scale from a young sockeye salmon shows regeneration of most of the scale.

Scale G. A scale from an adult sockeye salmon shows regeneration of the entire fresh-water zone (scale F). This scale shows only that the fish spent three winters in the ocean and that the scale replaced one lost in 1962.

Scale H. A scale from an adult sockeye salmon shows regeneration of fresh-water growth and most of the first summer at sea. This scale shows that the fish spent two winters at sea after it lost the original scale in the summer of 1963.

Scale I. A scale from an adult sockeye salmon with only the winter and last summer's growth completed before capture. Because of extensive regeneration, even the ocean age of this fish cannot be determined. The scale is of slightly atypical shape; it replaced one lost in the summer of 1964.

Scale J. A scale from an adult sockeye salmon with only a few months' growth complete. The scale is atypical in size and shape; it replaced one lost in the spring of 1965 and is unusable for age or racial studies.

RESORBED SCALES (Plate 18)

At some time during the migration toward their spawning streams, sockeye salmon stop feeding and subsist on stored fat and other body materials. As they work their way up the streams, the material in the scales is resorbed. Resorption generally starts along the lateral margins of the scale near the base of the anterior field and progresses until the whole scale margin is affected. Scales taken from spawning fish may have only a small central portion left. On most resorbed scales taken from spawning fish the fresh-water growth may still be present, but usually the ocean growth zones are too badly eroded to permit determination of total age with confidence. With greatly resorbed scales, study of otoliths or length frequencies may be required to estimate the age of the fish.

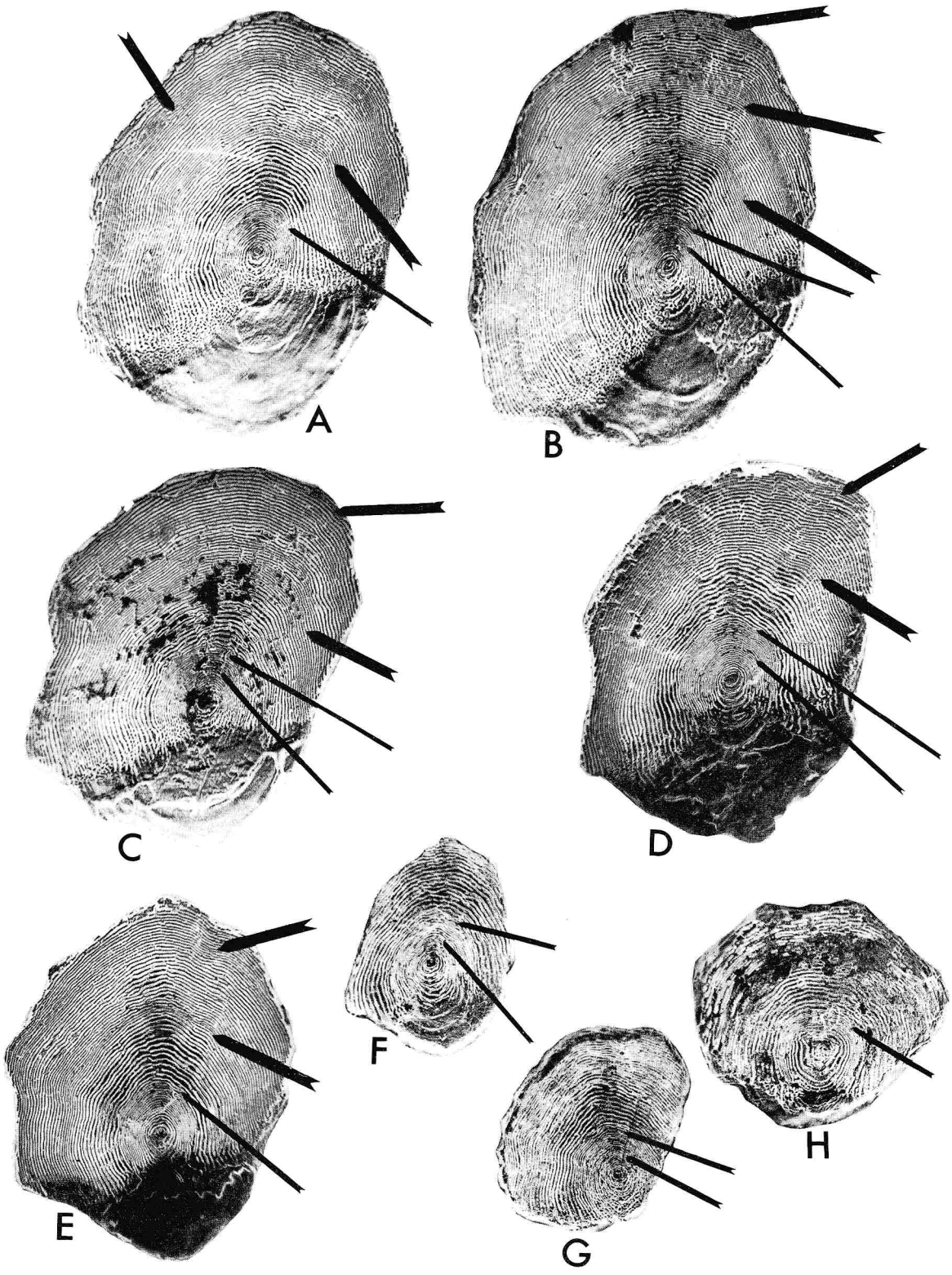

PLATE 18.—Resorbed scales.

The scales on this plate are arranged to show increasingly greater degrees of scale resorption, from A to H.

Scales A and B. These scales show slight resorption. Age determination is possible with these scales.

Scales C and D. These scales show considerable resorption. Age determinations are subject to error.

Scale E. This scale shows a greater amount of resorption than scales C and D, age determination is subject to considerable doubt.

Scales F and G. Only the fresh-water growth and a portion of the first year's ocean growth of these scales remain. Determination of total age is not possible.

Scale H. This scale shows considerable resorption and a regenerated center; it is useless for age or racial studies.

OTHER SCALES NOT SUITED FOR AGE OR RACIAL STUDIES (Plate 19)

Scales can be unusable for a number of reasons other than regeneration or resorption, as shown by the following examples:

Scale A. Scales may be distorted with atypical sculpturing. These scales often adjoin regenerated scales.

Scale B. Scales of adult and young fish may have a twisted center or other distorted area. If the growth pattern is not too badly distorted, the correct age may be determined from the scale.

Scale C. Scales may have scars (arrow). Here again, if the damage is not too serious, the correct age may be determined. Scars are more common in the ocean growth zones than in the fresh-water zone—perhaps because the scales of small fish are more easily lost than displaced in the scale pocket.

Scale D. Scales from the lateral line have a trough or tubelike structure that forms part of the lateral line organs. Scales near the lateral line may also be distorted to a varying degree, but some may be usable.

Scale E. Scales of atypical size and shape occur near the bases of the fins and the operculum; they should not be used for age or racial studies as they usually have fewer circuli than preferred scales.

USE OF ATLAS

Now that we have examined the features of sockeye salmon scales in detail, we are ready to use the atlas for specific purposes. This section is divided into two parts: (1) The use of the atlas in age studies and description of the scale features and (2) the use of the atlas in racial and other studies.

USE OF THE ATLAS FOR AGE STUDIES AND DESCRIPTION OF IMPORTANT SCALE FEATURES

This section demonstrates the use of the atlas to describe the physical features of the scale and to determine the fresh-water, ocean, and total age of the sockeye salmon from its scales. Compare the scale being studied with the plates in sequence, starting with plate 3. Compare the individual features of the scale with the variations shown on the appropriate reference plate. Select the one that is most similar to the feature under study.

The scale shown in plate I is used here to illustrate this method. Compare the scale in plate I with the various reference plates as follows:

Plate 3. Column A, chiefly regular, unbroken circuli.

Plate 4. First winter zone in the fresh-water growth is of type 1, sharp, the second is of type 2, moderately sharp.

Plate 5. Fresh-water age 2., medium-sized zone.

Plate 6. A sharp transition from fresh-water growth to ocean growth without plus growth. Type A (like fig. 1).

Plate 7. First ocean growth zone is of type 1; circuli are chiefly unbroken and uniformly spaced. Second ocean growth zone is of type 2, "average."

PLATE 19.—Other scales not suited for age or racial studies.

Plate 8. The first ocean zone has 24 circuli; the second has 21.

Plate 9. The widest spaced circuli of the first ocean zone are near the fresh-water growth; in the second ocean zone, they are near the previous winter zone.

Plate 10. Both ocean winter zones are of type 2, "average."

Plate 11. This fish is ocean age .2.

Plates 12 to 16. This fish is of age group 5_3 (2.2), shown on plate 14.

USE OF ATLAS FOR RACIAL AND OTHER STUDIES

Numerous scale characters are being used to determine the continent of origin of sockeye salmon when they are caught away from natal streams. Some scale characters and methods of analysis were reported by Krogius, 1958; Kubo, 1958; Kubo and Kosaka, 1959; Henry, 1961; Mosher et al., 1961; Anas, 1963; Mosher, 1963; and Anas, 1964. Methods now under study to determine the stream of origin range from identification based on appearance of the scale to multivariate techniques that make use of scale data collected with precision. Although numerous characters have been examined for racial studies, many more could be defined and used; some of the additional characters might be better than ones now in use.

This atlas can be used to (1) find additional characters for racial study, (2) decide which circuli or parts of circuli to count or measure for consistent results, (3) provide a basis for developing "standard" descriptions of the scale characters of sockeye salmon from the different spawning regions of North America and Asia, and (4) choose characters for special studies in which data on sockeye salmon scales are used.

No specific list of additional characters is given here, but ingenuity and imagination of the scientist in discovering and developing use of scale characters and methods of analysis will open new possibilities for the study of sockeye salmon.

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APPENDIX A

GLOSSARY OF TERMS

Adventitious mark or check.—A nonperiodic interruption in the regular pattern of scale growth. The check may or may not resemble a winter growth zone. See plates 6 (migration checks), 19B (twisted areas), and 19C (scar).

Annual ring, annulus, resting zone, winter ring, winter zone, winter mark, year mark, or year ring.*—A concentration of circuli or a series of interrupted circuli denoting a winter of life of the fish. See plates 1, 4, and 10.

Annulus.—See annual ring and footnote 4.

Anterior field, sculptured field.*—The portion of the scale that was embedded in the scale pocket toward the head of the fish and is sculptured with circuli. See plate 1. All plates show anterior fields.

Bases of circuli.—On the sockeye salmon scale only the first few circuli encircle the center or focus of the scale. The circuli beyond these first few are arcs. The ends of the circuli at the posterior field are their bases.

Central platelet or focus.—The area enclosed by the first or central circulus.

Circulus (plural, circuli), stria, or sclerite.*—A ridge on the upper surface of the anterior field of the scale. See Neave (1936), Welander (1940), or Wallin (1957). The circuli and interspaces (grooves) appear under magnification as concentric light and dark rings around the anterior field of the scale. All plates show circuli.

Clear field or area, posterior field or area.*—The portion of the scale which protrudes from the scale pocket toward the tail of the fish. This portion of the scale is a relatively clear area without distinctive growth features. See plate 1.

Focus.—See central platelet.

Fresh-water growth, fresh-water zone, fresh-water growth zone, lacustrine growth, lacustrine zone, lacustrine growth zone, or nucleus.*—The central portion of the scale formed while the fish was in fresh water. See plates 1 and 3 through 5.

Incidental growth, incidental zone, incidental growth zone, intermediate growth, intermediate zone, intermediate growth zone, plus growth, plus zone, plus growth zone, transitional zone, transitional growth zone, transitional zone, or spring growth.*—The portion of some scales between the fresh-water and the ocean growth

* here and later indicates the term I prefer.

zones where the difference between the fresh-water and ocean type circuli is not clear. See plate 6.

Intercirculus space, interspace.—A groove between two circuli. See circuli.

Intermediate growth, intermediate zone, intermediate growth zone.—See incidental growth zone.

Interspace.—See intercirculus space.

Lacustrine growth, lacustrine zone, lacustrine growth zone.—See fresh-water growth.

Marine growth, marine zone, marine growth zone, ocean growth, ocean zone, or ocean growth zone.*—The portion of the scale formed while the fish was in the ocean. See plates 1 and 7 through 11.

Migration check. — An adventitious check formed on some scales at the end of the incidental or plus growth. See plate 6.

Nucleus.—See fresh-water growth.

Ocean growth, ocean zone, ocean growth zone.*—See marine growth.

Plus growth, plus zone, plus growth zone.*—See incidental growth.

Posterior field or area.*—See clear field.

Regenerated scale.—A scale that replaces one that has been lost. The new scale grows without the formation of circuli until it reaches the approximate size of the scale which was lost. See plate 17.

Resorbed or eroded scale.*—A scale with the margins eroded because of sexual maturation. See plate 18.

Resting zone.—See annual ring. This term is often used by Japanese scientists.

Scar.—An abrupt change in the regular pattern of scale growth marked by a displacement of the natural configuration of the circuli. See plate 19C.

Sclerite.—See circulus. This term is widely used in Europe.

Sculptured field or area.—See anterior field.

Spring growth or spring growth zone.—See incidental growth and footnote 8.

Stria.—See circulus.

Transition zone, transitional growth, transitional growth zone, transition zone.—See incidental growth.

Winter ring, winter mark, or winter zone.*—See annual ring.

Year mark or year ring.—See annual ring.

APPENDIX B

EFFECT OF MAGNIFICATION ON APPEARANCE OF SCALE FEATURES (Appendix Plate 1)

The magnification which should be used for examination of scales from sockeye salmon varies with the size of the scales, the intended use of the data, and the preference of the scientist. The photographs in appendix plate 1 show how features of sockeye salmon scales appear at different magnifications and indicate the relative magnifications for various scale studies. (The arrows indicate the same feature on each scale section.)

Scale sections (shown at various magnification) follow:

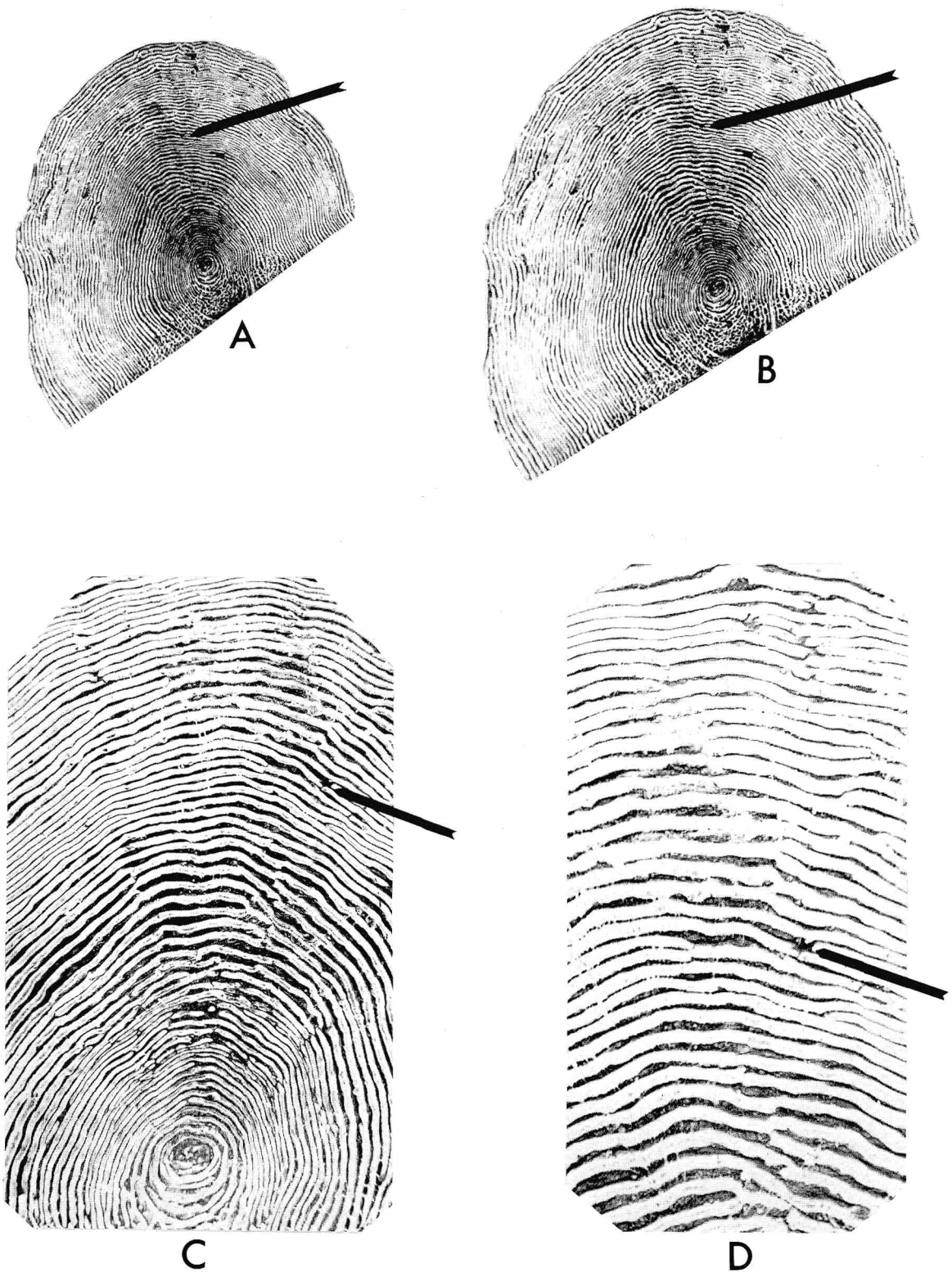
Section A. About 19 X. Note how difficult it is to identify any of the scale features on this photograph.

Section B. About 25 X. Note that the ocean winter zones are distinct at this magnification, but the fresh-water features are difficult to determine.

Section C. About 50 X. The ocean winter zones are less distinct at this magnification, but the details of the fresh-water zone are clear.

Section D. About 100 X. The ocean winter zones are very difficult to identify and delimit at this magnification.

Thus, the scales should be studied first at a magnification of between 25 X and 50 X to observe the whole scale in perspective and the details of the ocean zone. Then a magnification of between 50 X and 100 X should be used for the fresh-water zone, counts, and measurements of circuli, . . . These ranges of magnification are suggested as a starting point, because the exact magnification needed depends on the use of the data and on the temperament and visual habits of the investigator.



APPENDIX PLATE 1.—Effect of magnification on appearance of scale features.

APPENDIX C

APPEARANCE OF SCALES AND SCALE IMPRESSIONS (Appendix Plate 2)

Impressions of scales in plastic offer a number of advantages over the use of the scales themselves:

1. The effect of dirt on the scales is minimized—especially dirt on the unsculptured surface.
2. Duplicates can be made that are exact copies of the scales.
3. Impressions are easier to file and store than scales mounted on glass slides and the chance of breakage is reduced.

The process of making plastic impressions was described by Clutter and Whitesel (1956) and by Koo (1962a). Impressions made with a cold roller are not as satisfactory for salmon scales as those made with the heat-press method. (In 1955, a series of salmon scale impressions made with a jeweler's cold roller were compared with those made with a heat press. The heat-press impressions were greatly superior.)

In appendix plate 2, scale A shows a section of a sockeye salmon scale, and scale B shows an impression of the same scale section. The photograph of the impression shows slightly sharper circuli with less fuzziness from dirt and foreign material on the surface of the scale. Note that the photograph of the impression was reversed for comparison.

APPENDIX D

APPEARANCE OF NEGATIVE AND POSITIVE PRINTS (Appendix Plate 3)

When plastic impressions are made of the scales, the ridges on the scale surface become valleys in the impressions. Koo and Finn (1964) found that the sharp troughs of the impressions and the ridges on the scales both appear as dark rings when examined by transmitted light. When either the scale or its impression is examined by reflected light, these structures appear as light rings. Because the circuli and adjoining interspaces over much of the scale have about the same width, and because some workers project the scales by transmitted light and others use dark-field techniques for direct microscopic examination, it makes little difference whether the scale photograph is a positive or a negative print.

In appendix plate 3 there is an example of each type: Scale A is a positive print and scale B a negative print of the same sockeye salmon scale.

The only real difference in the prints is in the posterior field where growth features are absent anyway. The density of the negative print more nearly matches the image seen under the projector, or through the microscope; negative prints, therefore, were used in making this atlas.

APPENDIX E

TECHNIQUES OF PHOTOGRAPHING SCALES

The scales were photographed by placing a piece of high-contrast photographic enlarging paper under the image from a scale projector set up in a darkroom. The image was first carefully focused on a white paper in a printing frame. Then, with only a darkroom safelight on, a piece of the enlarging paper was substituted for the focusing paper, exposed, developed in a high-contrast paper developer (minimum exposure-maximum development), and fixed, washed, and dried in the usual manner.

Positive prints can be made by taking a picture of a scale with a microscope camera (a single lens reflex camera on a microscope), or by photographing the projected image with a camera, then exposing and processing the same as for any photograph of a high-contrast subject.

APPENDIX PLATE 2.—Appearance of scales and scale impressions.

APPENDIX PLATE 3.—Appearance of negative and positive prints.

GROWTH OF JUVENILE BLUE CRABS, *Callinectes sapidus* RATHBUN, IN THE ST. JOHNS RIVER, FLORIDA

By Marlin E. Tagatz, *Fishery Biologist*

Bureau of Commercial Fisheries Biological Laboratory
Beaufort, N.C. 28516

ABSTRACT

Relative growth was studied by holding juveniles (20–139 mm. wide) in anchored floats. The floats were at two locations—one in salt water and one in fresh water. Molt intervals were similar at both sites, but the average growth was generally more per molt in salt water. From April to mid-November, the mean molt interval was 11 days for crabs 20 to 29 mm. wide; it increased to 41 days for crabs of 130 to 139 mm. Frequency of molting decreased in winter, but most juveniles 20 to 59 mm. wide molted two or three times. Growth increments per molt varied from 7.8 to 50 percent. Mean increment, by 10-mm. width groups, was 20.9 to 34.2 percent. Estimates of increase in width with age indicate that most blue crabs in the St. Johns River reach harvestable size (width of 120 mm.) within 1 year after hatching.

This report presents the results of studies from April 1964 to March 1966 on growth increments, molt intervals, and the effects of salinity and temperature on growth of juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. Johns River, Fla. This information on growth is needed to estimate the time required for crabs of any particular size to reach harvestable size.

Because the juvenile (postlarval) crab has a rigid shell, it can grow only when it molts. The shell is composed of chitin strengthened by the deposition of calcium salts (Rees, 1963). Before molting, the crab forms a new exoskeleton inside the old shell, which then loosens. During molting, the carapace separates from the abdomen along the sides of the undersurface, and in a few minutes, the crab backs out of the old shell (fig. 1). Initially, the new shell is soft and wrinkled. Water, absorbed after molting, stretches the thin and elastic new cuticle and increases the size of the crab. Crabs grow from the first postlarval crab stages, about 2.5 mm. wide, to full size after 18 to 23 molts (Van Engel, 1958). In the St. Johns River, the width of fully grown blue crabs ranges from less than 100 mm. to more than 240 mm.

Few studies have been made on the rate of growth of juvenile blue crabs. Churchill (1919) used the limited number of molting records available at that time for Chesapeake Bay crabs and attempted to determine size at various instars and the frequency of molting from hatching to maturity. He found that time between molts was progressively longer with increase in size. The first few molts were a few days apart and the last at intervals of a month or more. He reported that growth ceases from October until late April or early May and that the animals probably do not molt at temperatures less than 60° F. (15.5° C.). Studies with blue crabs over 29 mm. wide by Gray and Newcombe (1938) and on smaller crabs by Newcombe, Sandoz, and Rogers-Talbert (1949) provide the best published data on growth. The mean increases in width of the various instars ranged from 15 to 48 percent; the mean was 25 percent for males and 27 percent for females. No information was obtained on molt intervals because the animals were held for only one molt.

Numerous reports of unusually large blue crabs in low-salinity waters and very small adult crabs in high-salinity waters suggest a possible negative correlation of size with salinity of the water in which growth occurs (Newcombe, 1945; Porter, 1956; Cargo, 1958; Fischler, 1959; Tagatz, 1965). Van Engel (1958) believed that crabs in low salinity absorb more water at the time of the molt and, thus, increase more in size than crabs that molt in water of higher salinity.

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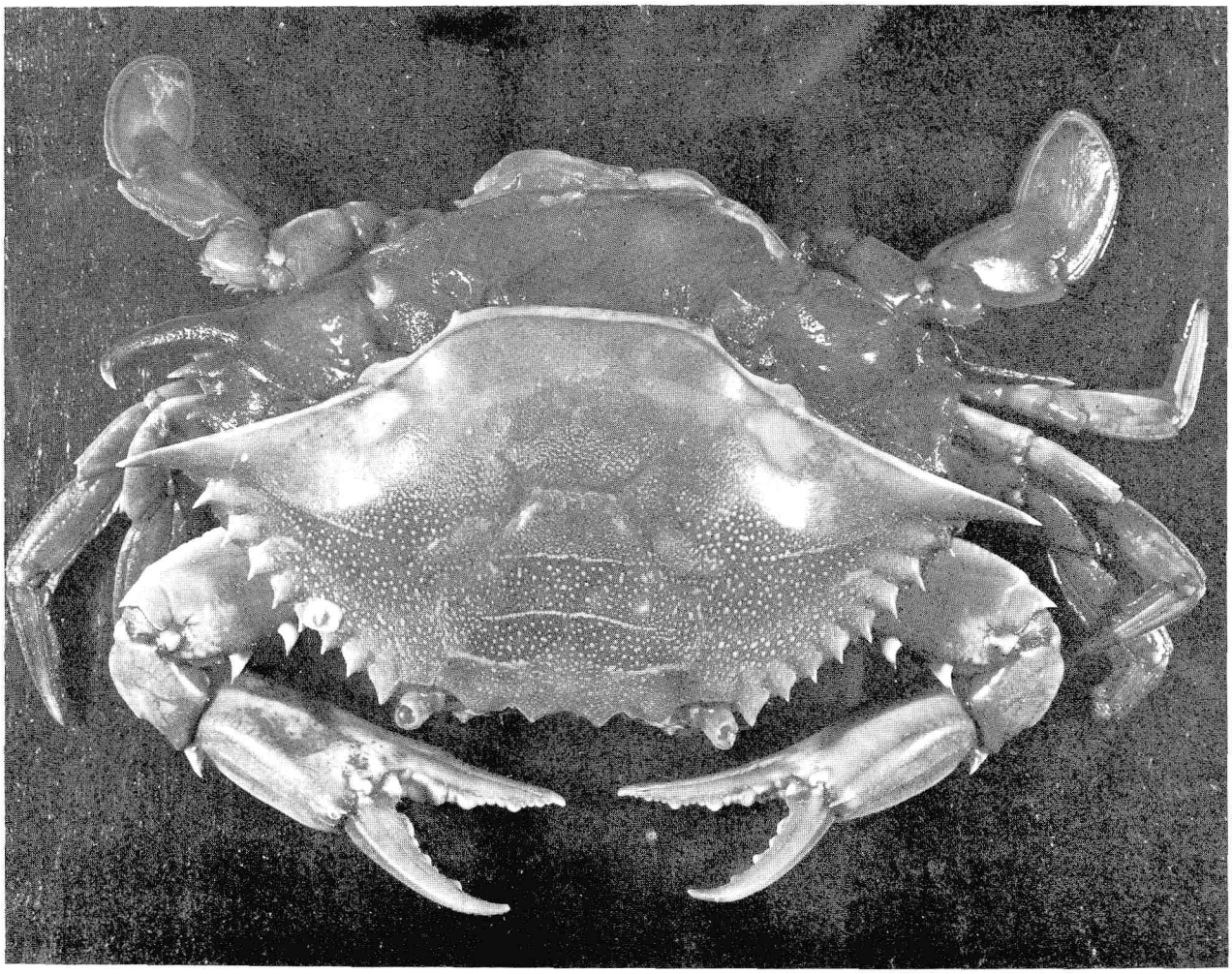

FIGURE 1.—A molting blue crab emerging from its old shell.

MATERIALS AND METHODS

Juvenile blue crabs, 20 to 139 mm. wide, were held in wooden floats in salt water (salinity greater than 5 p.p.t.—parts per thousand) from April 1964 to March 1965 and in fresh water (salinity less than 1 p.p.t.) from April 1965 to March 1966. Studies in salt water were in Cedar Point Creek, a tidal tributary of Clapboard Creek, which enters the St. Johns River 15 km. from the Atlantic Ocean. Studies in fresh water were in the St. Johns River near Green Cove Springs, 90 km. upstream from the mouth of the river. Both sites were natural habitats for crabs in the size range used.

Two hundred crabs in four floats were used at each location. The floats had hinged covers and were about 3 m. long, 1½ m. wide, and ½ m. deep. A 15-cm.-wide rim allowed three-fourths of the float to hang submerged. Each float had 50 compartments, 24 cm. by 24 cm. by 46 cm. deep, covered with 6.4-mm.-mesh hardware cloth.

Blue crabs were collected near the floats, and only one animal was put in each compartment (to prevent cannibalism). About 2,000 of those captured were measured for length-width ratio.

Three times each week crabs were fed, those that had molted were measured, and the dead ones were removed. The crabs normally were supplied with more cut fish than they would eat. I measured carapace width and length of each animal that had molted since the last observation; shell hardness indicated the day of ecdysis. Width

is the distance between the tips of the large lateral spines, and length the distance between the median anterior notch and the posterior margin. Measurements of crabs that died within a week after molting were not used in estimating growth. Except for length-width ratio, I discuss growth in terms of width.

Salinity and temperature were measured at each observation. Salinity determinations, obtained within 2 hours of low tide at Cedar Point Creek, probably were near minimum values for this site. Salinities at Green Cove Springs were always less than 1 p.p.t.—the lowest concentration detectable with the hydrometer. Blue crabs and other marine forms are able to live in the upper St. Johns River because it has a high concentration of calcium chloride and also localized areas of high sodium chloride (Odum, 1953).

I defined as summer studies those from early April to mid-November and as winter studies those from near the end of November through March. Summer work ended earlier in salt water because of damage to the floats from a September storm. During the summer, crabs were replaced (randomly collected near floats) when they died, escaped, attained maturity, or surpassed 139 mm. All new crabs were used at the start of winter, and none were replaced.

LENGTH-WIDTH RATIO

Length-width ratios were obtained for blue crabs 10 to 149 mm. wide captured in the St. Johns River (table 1). For comparison, I have included the data given by Newcombe et al. (1949) for Chesapeake Bay blue crabs. The two sets of data show similar changes in body form with growth. As size increases, the length-width ratio decreases. For St. Johns River crabs the ratio expressed as a percentage was 50 in juveniles 10 to 19 mm. wide and decreased to less than 42 in crabs over 119 mm. wide. In crabs over 69 mm. wide, males were proportionally longer than females.

The body proportions of blue crabs from the St. Johns River differed from those of crabs from the Chesapeake Bay. In every width class the Chesapeake Bay crabs had a greater mean length than the St. Johns River crabs. Geographic variation is to be expected in an animal as widely distributed as the blue crab.

TABLE 1.—*Length-width ratios of blue crabs from St. Johns River, Fla., and Chesapeake Bay*

Sex and width	St. Johns River				Chesapeake Bay [1]			
	Crabs	Mean width	Mean length	Length/width	Length/width	Mean length	Mean width	Crabs
Mm.	*Number*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Number*
Males:								
10–19	10	16.8	8.4	50.0	53.2	9.2	17.3	13
20–29	67	25.4	12.5	49.2	53.3	13.6	25.5	17
30–39	130	34.7	16.4	47.3	49.7	17.7	35.6	16
40–49	122	44.1	20.7	46.9	49.4	22.4	45.3	27
50–59	88	54.4	25.3	46.5	48.6	26.5	54.5	32
60–69	69	63.9	29.3	45.8	48.5	31.7	65.4	35
70–79	69	74.7	34.6	46.3	47.5	35.3	74.3	31
80–89	93	83.8	37.7	45.0	46.9	40.1	85.4	37
90–99	65	94.4	42.2	44.7	47.2	44.2	93.7	39
100–109	54	103.8	45.3	43.6	46.2	48.3	104.6	38
110–119	52	114.9	49.4	43.0	45.7	52.7	115.3	37
120–129	52	124.2	51.5	41.5	46.2	57.9	125.3	32
130–139	46	133.8	54.3	40.6	44.8	60.2	134.4	35
140–149	22	145.0	59.0	40.7	44.9	65.4	145.7	42
Females:								
10–19	11	16.8	8.4	50.0	53.9	8.9	16.5	22
20–29	78	25.3	12.4	49.0	52.5	12.8	24.4	21
30–39	129	34.6	16.5	47.7	50.3	18.4	36.6	19
40–49	136	44.4	20.7	46.6	49.7	22.5	45.3	50
50–59	119	54.3	25.3	46.6	49.0	27.1	55.3	83
60–69	102	63.7	29.5	46.3	48.1	31.1	64.6	103
70–79	116	74.4	33.8	45.4	47.1	35.1	74.5	79
80–89	100	84.1	37.7	44.8	46.5	39.2	84.3	65
90–99	103	94.7	41.4	43.7	45.2	42.6	94.3	58
100–109	48	103.9	44.3	42.6	45.2	47.3	104.7	38
110–119	58	113.7	48.0	42.2	44.0	50.1	113.8	32
120–129	30	124.5	50.3	40.4	44.4	55.4	124.7	34
130–139	11	132.6	53.4	40.3	44.5	59.0	132.7	25
140–149	13	143.8	55.8	38.8	41.7	60.6	145.3	21

[1] Data from Newcombe et al. (1949).

RELATIVE GROWTH

Observations on growth were made during summer and winter.

SUMMER

I obtained data on 1,085 molts in salt water (April 1 to September 15, 1964) and on 1,152 in fresh water (April 24 to November 15, 1965).

Water temperatures were somewhat similar at the sites, but salinities differed by as much as about 26 p.p.t. The mean water temperature was 26.8° C. in salt water (range, 13.8°–32.1° C.) and 25.8° C. in fresh water (range, 16.2°–31.5° C.). Mean salinity (readings taken within 2 hours of low tide) at the Cedar Point Creek site was 18.8 p.p.t. (range, 7.5–25.8 p.p.t.); at Green Cove Springs, salinity was always less than 1 p.p.t.

Confinement did not appear to inhibit growth of blue crabs. The experimental animals ate readily, remained pugnacious, and many molted six or seven times. Growth increments of crabs that molted more than once in confinement averaged about the same as those for crabs of comparable size that molted only once.

Growth increments were highly variable in each size group, but no blue crab molted without some increase in size. The smallest increase in width was 7.8 percent; the largest, 50 percent. Mean percentage growth per molt by 10-mm.-width groups was 20.9 to 34.2 (table 2), and the groups averaged 26.7 for females, 23.9 for males, and 25.3 for females and males combined. Among larger crabs, females usually had greater width increments (at greater ages, they are relatively wider than male crabs). On the assumption of homogeneous variance about the regression of postmolt width on premolt width, an analysis of covariance indicated significant interaction of sex and salinity on growth ($P < 0.01$). Because of this interaction the separate effects of salinity on males and females were examined. Each sex showed significant differences in growth between fresh and salt water ($P < 0.05$). All crabs less than 80 mm. wide and many larger ones had greater average growth in salt water (fig. 2).

Some factor other than salinity appears to account for larger crabs in certain low-salinity waters. In the present experiments and in earlier ones on the terminal molt of female blue crabs (Haefner and Shuster, 1964), decrease in salinity did not produce increase in size.

Female blue crabs undergo a final molt at which they become sexually mature. This stage is easily recognizable because the abdomen changes shape from triangular to semicircular (the last stage of males cannot be determined from external appearance). In the St. Johns River, as in Chesapeake Bay (Tyler and Cargo, 1963), the sizes at the last two instars overlap widely. The smallest mature female measured was 99 mm. wide, and the largest immature female was 177 mm.

I obtained data on the terminal molt of 170 females (83–139 mm. wide)—85 at each site. Most growth generally took place at this molt. The mean increase in width was 34.4 percent (range, 19.6–50) in salt water and 30.2 percent (range, 20.5–47.4) in fresh water.

The variability of growth of juvenile crabs causes irregularity in the recruitment of harvestable crabs (larger than about 120 mm. wide) and in the time of crab maturity. For example, of two 21-mm.-wide males that molted seven times in salt water from May to August (in 101 days and 103 days), one attained 139 mm. and the other only 115 mm. The smaller crab would be more likely to escape the fishery to complete its life history (crabs smaller than 120 mm. made up less than 5 percent of the commercial catch). Another example is the difference in growth of two females in salt water that were 34 mm. wide in spring. One matured after four molts and 78 days (114 mm.); the other after seven molts and 179 days (175 mm.). The individual maturing at 114 mm. did not attain harvestable size and probably would have spawned in summer. The 175-mm. female was acceptable for market during its last two instars and had it escaped the fishery it probably would have spawned in fall.

TABLE 2.—*Relative growth of blue crabs, by 10-mm.-width groups and by sex, in salt (S) and fresh (F) water, St. Johns River, Fla., April 1 to November 15, 1964 and 1965*

Width and habitat	Males			Females		
	Crabs	Mean increase and standard deviation	Range	Crabs	Mean increase and standard deviation	Range
Mm.	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*
20–29						
S	17	27.4±5.9	15.4–38.5	13	23.8±7.9	10.3–39.1
F	50	20.9±5.5	11.1–34.6	48	21.3±3.7	11.1–30.4
30–39						
S	39	23.3±7.1	10.2–37.8	42	24.7±6.8	12.8–35.9
F	93	22.3±5.4	10.8–33.3	108	21.8±5.0	10.8–33.3
40–49						
S	74	24.2±7.4	11.4–41.9	64	23.4±7.0	11.1–44.2
F	93	21.9±6.1	9.3–35.7	120	22.7±5.2	9.5–32.6
50–59						
S	73	24.4±6.9	11.9–40.0	77	24.2±5.7	11.5–40.0
F	70	21.0±6.0	7.8–36.5	85	23.2±6.8	8.5–34.0
60–69						
S	65	24.4±6.9	8.3–39.3	75	28.2±7.0	13.6–44.1
F	38	23.1±6.2	10.1–41.2	69	25.7±6.0	11.7–39.3
70–79						
S	66	26.2±7.1	8.1–39.7	62	27.0±8.1	13.5–43.0
F	32	24.4±5.5	14.7–35.1	62	26.3±6.8	7.9–40.3
80–89						
S	58	24.4±6.3	8.4–37.6	74	28.1±6.6	13.8–44.8
F	24	25.0±6.3	12.9–37.6	47	28.2±6.1	10.0–39.0
90–99						
S	52	25.9±6.9	12.6–41.0	55	28.2±8.5	11.7–48.9
F	22	24.7±5.8	14.3–36.4	47	28.9±7.3	14.3–47.4
100–109						
S	43	26.4±5.7	9.7–36.1	39	29.4±6.8	16.0–45.7
F	5	26.0±7.8	18.0–35.6	23	30.4±7.3	15.8–43.5
110–119						
S	30	24.4±4.7	13.4–30.4	30	34.2±9.3	14.8–50.0
F	13	24.6±4.2	19.8–31.8	35	28.5±5.4	13.4–39.6
120–129						
S	16	22.5±5.5	9.4–31.4	6	28.0±3.9	23.4–32.8
F	24	23.1±4.0	15.4–28.9	18	27.7±4.0	20.5–37.2
130–139						
S	13	21.6±5.1	14.1–33.6	2	30.2±2.0	28.8–31.6
F	16	22.7±3.4	16.9–28.5	10	26.9±4.4	22.3–35.8

WINTER

Blue crabs grow during the winter in the St. Johns River but more slowly than in summer. I observed 287 molts among crabs in salt water (November 20, 1964, to March 31, 1965) and 258 in fresh water (November 22, 1965, to March 31, 1966).

Water temperatures in winter averaged 11.8° C. lower in salt water and 13.5° C. lower in fresh

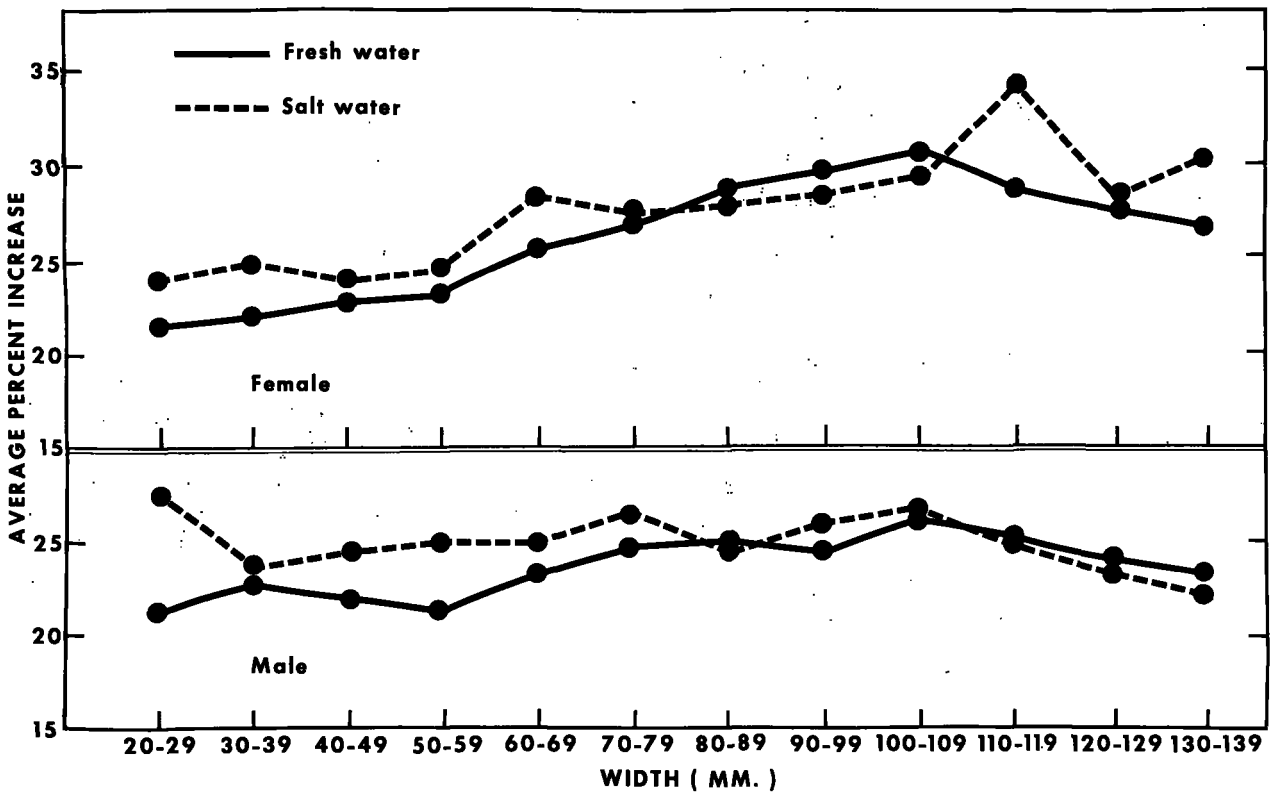

FIGURE 2.—Relative growth per molt of female and male blue crabs in fresh and salt water, St. Johns River, Fla., April 1 to November 15, 1964 and 1965.

water than in summer; salinities at the salt water station were 4.3 p.p.t. lower. Mean water temperature was 15° C. in salt water (range, 8.3°–22.9° C.) and 12.3° C. in fresh water (range, 3.8°–18.2° C.). Salinity at the Cedar Point Creek site averaged 14.5 p.p.t. (range, 6–23.3 p.p.t.).

Relative growth per molt in winter was similar to that in summer. Crabs were less active and consumed less food but generally were in good condition.

MOLT INTERVAL

Information was collected on molting in summer and winter.

SUMMER

More than one-half (1,256) of the molts in summer (April 1 to November 15) from crabs that molted more than once provided information on molt interval.

Molt intervals appeared to be affected by the size of crabs and by season but not by sex and salinity. I found little difference in molt interval between males and females or between salt and fresh water. The time between molts increased with increasing body size (table 3). The smallest crabs (20–29 mm. wide) molted after an average of 11 days, and those over 120 mm. wide after an average of 42 days. Molt intervals of crabs within each size group varied greatly but usually were shortest during the warmest months, June to September. Most juveniles 30 to 39 mm. wide in April reached harvestable size after 4 months, but crabs that had the same width in June were harvestable after 3 months with the same number of molts. Crabs that molted after particularly long periods grew little or died.

Information was obtained on the time needed for the terminal molt of 101 female blue crabs (83–139 mm. wide). The final molt interval for 85 percent of these crabs ranged from 25 to 50 days. Two females molted in as few as 18 days. Large crabs (above 110 mm. wide) averaged 5 days longer than smaller ones. In salt water (crabs averaged 106 mm. wide), the mean interval

TABLE 3.—*Molt interval in the blue crab, by 10-mm.-width groups, St. Johns River, Fla., April 1 to November 15, 1964 and 1965*

[Salt- and fresh-water data combined; ranges in parentheses]

Width group	Crabs		Mean molt interval, standard deviation, and range	
	Male	Female	Male	Female
Mm.	*Number*	*Number*	*Days*	*Days*
20–29	23	18	12±5.0 (7–25)	10±2.4 (7–17)
30–39	61	77	15±4.6 (7–34)	13±3.8 (6–27)
40–49	100	101	17±6.1 (8–38)	18±6.1 (9–42)
50–59	101	99	21±7.9 (9–51)	20±9.0 (9–49)
60–69	67	87	23±9.2 (11–54)	21±10.3 (9–68)
70–79	69	51	22±8.5 (11–64)	24±9.5 (11–59)
80–89	46	65	28±10.5 (16–68)	26±11.5 (14–77)
90–99	52	47	31±9.1 (20–64)	30±8.8 (17–60)
100–109	36	39	32±9.2 (21–65)	33±7.2 (20–52)
110–119	29	38	34±7.8 (19–53)	39±10.2 (18–61)
120–129	17	15	43±12.0 (22–68)	43±8.4 (26–59)
130–139	13	5	41±9.6 (27–56)	41±7.4 (35–54)

before the final molt was 38 days (range, 18–77 days); in fresh water (crabs averaged 117 mm.), it was 40 days (range, 18–61 days).

WINTER

Data on molt intervals (from animals that molted more than once in confinement) were obtained on 112 crabs in salt water and 96 in fresh water during winter (November 20 to March 31). The time between molts was three to four times as long in winter as in the rest of the year. The mean interval was 46 days for crabs 20 to 29 mm. wide and rose to 124 days for an individual 92 mm. wide (table 4). Most juveniles 20 to 59 mm. wide molted two or three times, but many of those larger than 99 mm. did not molt (table 5).

Temperature has a major influence on the molt interval. In Chesapeake Bay, growth of blue crabs usually ceases during the colder months from November to early April (Van Engel, 1958). In the St. Johns River, low temperatures delay but do not prevent molting. I observed crabs shedding their old shells at water temperatures as low as 3.8° C. Molting in winter was less frequent at the lower water temperatures. The numbers of molts were about the same in November and March (mean water temperature 16° C.) as during the 3 months, December–February (mean water temperature 12.5° C.). Extended observations in fresh water indicated that almost all of the crabs that did not grow in winter molted during the first 3 weeks of April (mean water temperature had risen to 18.2° C.).

TABLE 4.—*Molt interval in the blue crab, by 10-mm.-width groups, St. Johns River, Fla., November 20 to March 31, 1964–65 and 1965–66*

[Salt- and fresh-water data combined]

Width group [1]	Crabs	Molt interval	
		Mean and standard deviation	Range
Mm.	*Number*	*Days*	*Days*
20–29	16	46±25.8	21–96
30–39	48	47±15.8	20–100
40–49	49	59±17.8	22–94
50–59	35	72±17.3	28–101
60–69	37	79±18.1	46–118
70–79	18	91±19.4	69–123
80–89	4	106±17.0	81–120
90–99	1	124	

[1] Crabs wider than 99 mm. did not molt more than once.

ESTIMATE OF ABSOLUTE GROWTH

Mean percentage growth per molt (25.3) and mean molt interval per size group (for summer and winter) were used with relevant data from laboratory experiments on blue crabs less than 20 mm. to obtain gross estimates of increase in body size with age. Although the floats would not hold crabs smaller than 20 mm. wide, I have data on two individuals that reached this size when hatched and reared in the laboratory. After metamorphosis to the first crab stage, one of these crabs went through 10 molts in 68 days to reach 23 mm.; the other took nine molts and

TABLE 5.—*Frequency of molting of blue crabs, by 10-mm.-width groups, St. Johns River, Fla., November 20 to March 31, 1964–65 and 1965–66*

[Salt- and fresh-water data combined; no crabs molted more than three times]

Width group	Crabs	1 molt	2 molts	3 molts
Mm.	*Number* [1]	*Number*	*Number*	*Number*
20–29	40	40	39	22
30–39	43	43	40	14
40–49	58	58	46	2
50–59	46	46	33	0
60–69	37	37	10	0
70–79	31	31	1	0
80–89	41	40	0	0
90–99	24	19	0	0
100–109	12	7	0	0
110–119	25	14	0	0
120–129	27	3	0	0
130–139	6	0	0	0

[1] Not included are 10 crabs that died before molting once. Deaths after one molt: 1(20–29), 1(30–39), 1(40–49), and 1(60–69); after two molts, 1(40–49).

69 days to reach 20 mm. The mean percentage growth per molt was the same as in larger crabs. To estimate the time needed to attain harvestable size, I used 25.3 percent to calculate relative increases from the 1st crab stage (2.5 mm.) to a 19th crab stage (142 mm.), applied mean molt intervals, and allowed 1½ months for larval development (Costlow and Bookhout, 1959). These calculations indicate that most blue crabs in the St. Johns River reach harvestable size within 1 year after hatching (table 6).

TABLE 6.—*Estimated growth by month of St. Johns River, Fla., blue crabs hatched in April, July, and October*

Month	Maximum width		
	Mm.	*Mm.*	*Mm.*
April	[1] 1		
May	5		
June	12		
July	23	[1] 1	
August	46	5	
September	58	12	
October	90	23	[1] 1
November	113	46	5
December	113	46	8
January	113	58	10
February	113	58	12
March	142	72	15
April		90	29
May		113	46
June		142	72
July			90
August			113
September			142

[1] Larvae.

MORTALITY OF EXPERIMENTAL ANIMALS

I recorded deaths of 94 blue crabs in salt water and 212 in fresh water during the summer. Mortality was 8 percent for crabs 20 to 79 mm. wide and 19 percent for those 80 to 139 mm. Most crabs that died were well past the average molt interval of their size group.

Only eight animals died in salt water (two after molting once) and seven in fresh water (three after molting once) during the winter—a mortality of 3 percent.

Year-round mortality at ecdysis was 36 crabs (salt water, 11; fresh water, 25) out of a total of 2,782 molts. The few deaths at ecdysis indicate that molting in itself may not be a critical source of mortality. In nature, however, crabs are easy prey immediately after they emerge from their shells.

SUMMARY

From April 1964 through March 1966, juvenile blue crabs (20–139 mm. wide) were held in floats in St. Johns River to determine growth increments, molt intervals, and the effects of salinity and temperature on growth.

Measurements of 2,000 blue crabs, 10 to 149 mm. wide, collected in the river indicated that the length-width ratio decreased as the animals grew. This decrease was less among males than females.

In salt water (salinity greater than 5 p.p.t.), data were obtained on 1,085 molts during the summer (April 1 to November 15) and on 287 during the winter (November 20 to March 31); in fresh water—on 1,152 molts in summer and 258 in winter.

Growth increments per molt varied from 7.8 to 50 percent in summer, and mean increment, by 10-mm.-width groups, was 20.9 to 34.2 percent. Among larger crabs, females usually had greater width increments than males. Percentage growth in the terminal molt of females averaged 34.4 in salt water and 30.2 in fresh water. Males and females showed significant difference in growth between fresh and salt water. Each sex generally averaged the most growth per molt in salt water.

Relative growth per molt in winter was similar to that in summer.

Molt intervals in the summer did not appear to be affected by the sex of the crab and the salinity of the water, but were affected by crab size and water temperature. The smallest crabs (20–29 mm. wide) molted after an average of 11 days and animals over 120 mm. wide after an average of 42 days. Molt intervals usually were shortest during the warmest months. The interval of the terminal molt of females averaged 38 days in salt water (mean width, 106 mm.) and 40 days in fresh water (mean width, 117 mm.).

The time between molts was three to four times as long in winter as in summer. Most juveniles 20–59 mm. wide molted two or three times, but many of those larger than 99 mm. did not molt.

Calculations based on the data presented indicate that most blue crabs in the St. Johns River reach harvestable size within 1 year after hatching.

Year-round mortality at ecdysis at both sites was only 36 crabs out of a total of 2,782 molts; other deaths totaled 285.

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DISTRIBUTION OF BROWN SHRIMP (*Penaeus aztecus aztecus* IVES) AS RELATED TO TURBID WATER PHOTOGRAPHED FROM SPACE[1]

BY MILTON J. LINDNER, *Fishery Biologist,* AND JAMES S. BAILEY,[2] *Research Oceanographer*
BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY
GALVESTON, TEXAS 77550

ABSTRACT

Visual evidence of probable relief currents in the northwestern Gulf of Mexico is provided for the first time by photographs taken from Gemini spacecraft. After rectification of photographs of the Continental Shelf off the Texas Coast, a comparison of the position of relief currents to areas of high shrimp production indicates that photography from space can be a valuable tool for fishery research.

Oceanographers long have predicted the existence of relief or rip currents between Galveston and Corpus Christi, Tex. (Sweitzer, 1898; Smith, Medina, and Abella, 1951; Curray, 1960), and navigators have called the area the "Whirlpool of the Gulf" (U.S. Coast and Geodetic Survey, 1949). The offshore relief currents result from the convergence of southerly and northerly currents, which causes a piling up of water that is relieved by an offshore flow. The buildup and eventual release of waters in the Galveston-Corpus Christi area are continuously recurring sequences of events related to the total Gulf system.

Visual evidence of countercurrents, which have never before been documented by oceanographic techniques, is apparently provided by figure 1. This figure is a reproduction of a color photograph taken by NASA (National Aeronautics and Space Administration) from an altitude of 330 km. on November 14, 1966. In addition to showing the distribution of suspended material in bay and Gulf waters, the discharge patterns from the bays, the major eddy currents, and the relative direction of the currents, we believe it illustrates clearly the long-suspected phenomenon of rip or relief currents.

Sediments in the water provide the contrast that permits us to see the interaction of the coastal current systems. Perhaps the most obvious feature is the discharge of sediment at the entrances to Lake Charles, La., and Sabine Lake and Galveston Bay, Tex. Large volumes of sediment in these areas are being carried into the Gulf and immediately transported southward by an alongshore current. Less noticeable but vastly larger are two areas of discolored water south of Galveston that extend eastward. These plumes of suspended material are aligned by moving water and most likely represent the areas of rip or relief currents predicted by oceanographers. The plumes, outlined in figure 2, are believed to be semipermanent features of the Gulf current system, although their locations, intensity, and dimensions undoubtedly fluctuate throughout the year. Obviously, they must have some effect on the bottom sediments and nutrient supply.

Our conclusions admittedly are conjectural because of the lack of necessary detailed physical and chemical data from oceanographic and bottom surveys made in and around the areas under consideration. A definite relation does exist, however, between the shrimp catch, trawling frequency, and the plumes shown in figure 2.

Rectification of the Gemini photograph to ONC (Operational Navigation Chart) No. 24 (fig. 3) revealed that the plumes were in BCF (Bureau of Commercial Fisheries) statistical area 19 and the lower portion of area 18 (fig. 4). The best

[1] Contribution No. 276, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex. 77550.
[2] Present address: TRW Systems, 1 Space Park, Redondo Beach, Calif. 90278.

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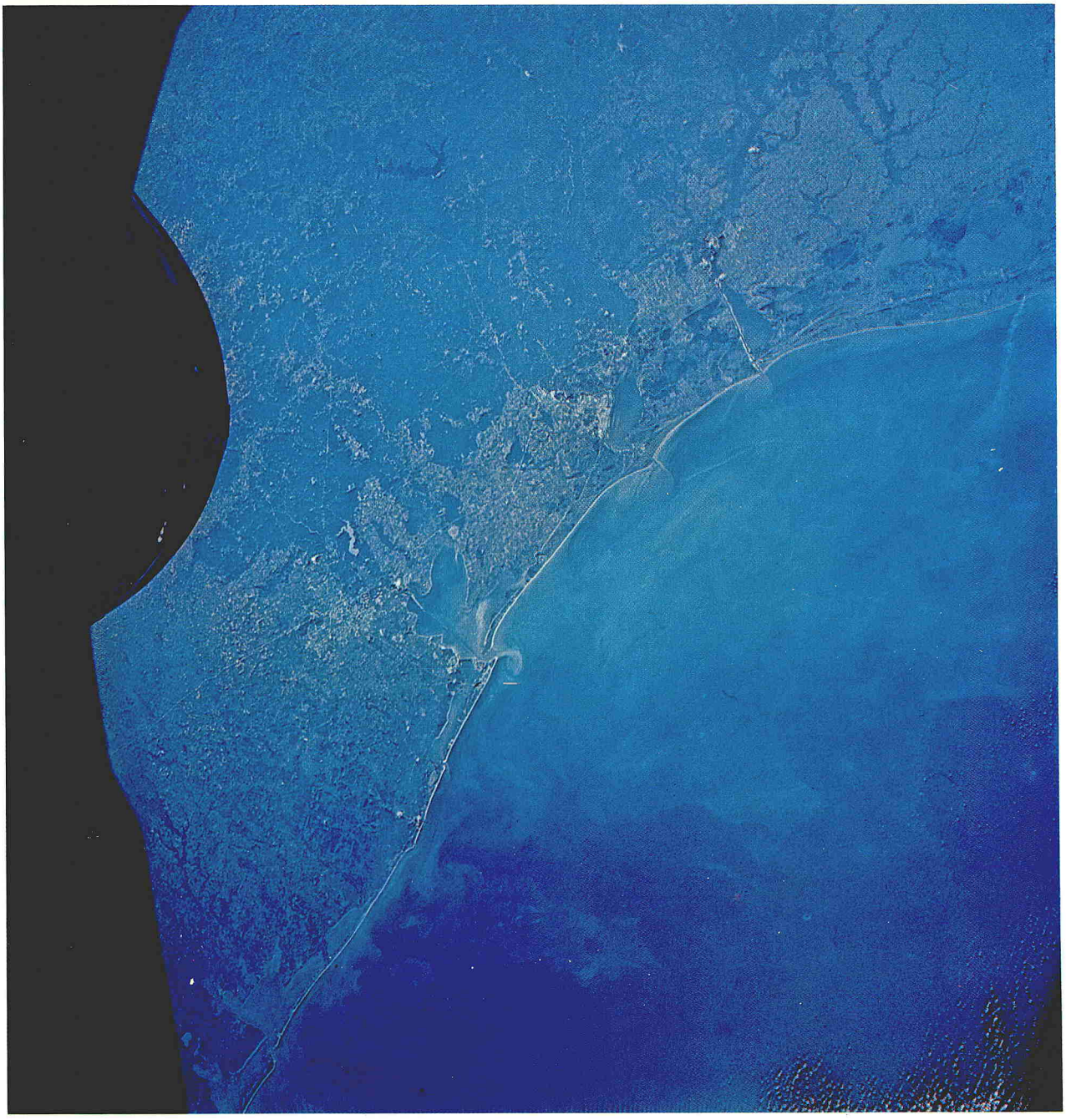

FIGURE 1.—An unrectified Gemini photograph of the northwestern Gulf of Mexico, from an altitude of 330 km. Matagorda Bay, Tex., is to the lower left and White Lake, La., to the upper right. The direction of the wind can be determined from the smoke trailing offshore near White Lake. The discharge patterns from the bays and the southerly alongshore currents are plainly visible. What appear to be offshore relief currents are evident south and east of Galveston, Tex. The white dots along the right margin are clouds; a portion of the Gemini craft is on the left margin. (NASA color photograph S–66–63034, taken by James A. Lovell, Jr., and Edwin E. Aldrin, Jr., November 14, 1966 (1300 hours local time), during Gemini Flight XII).

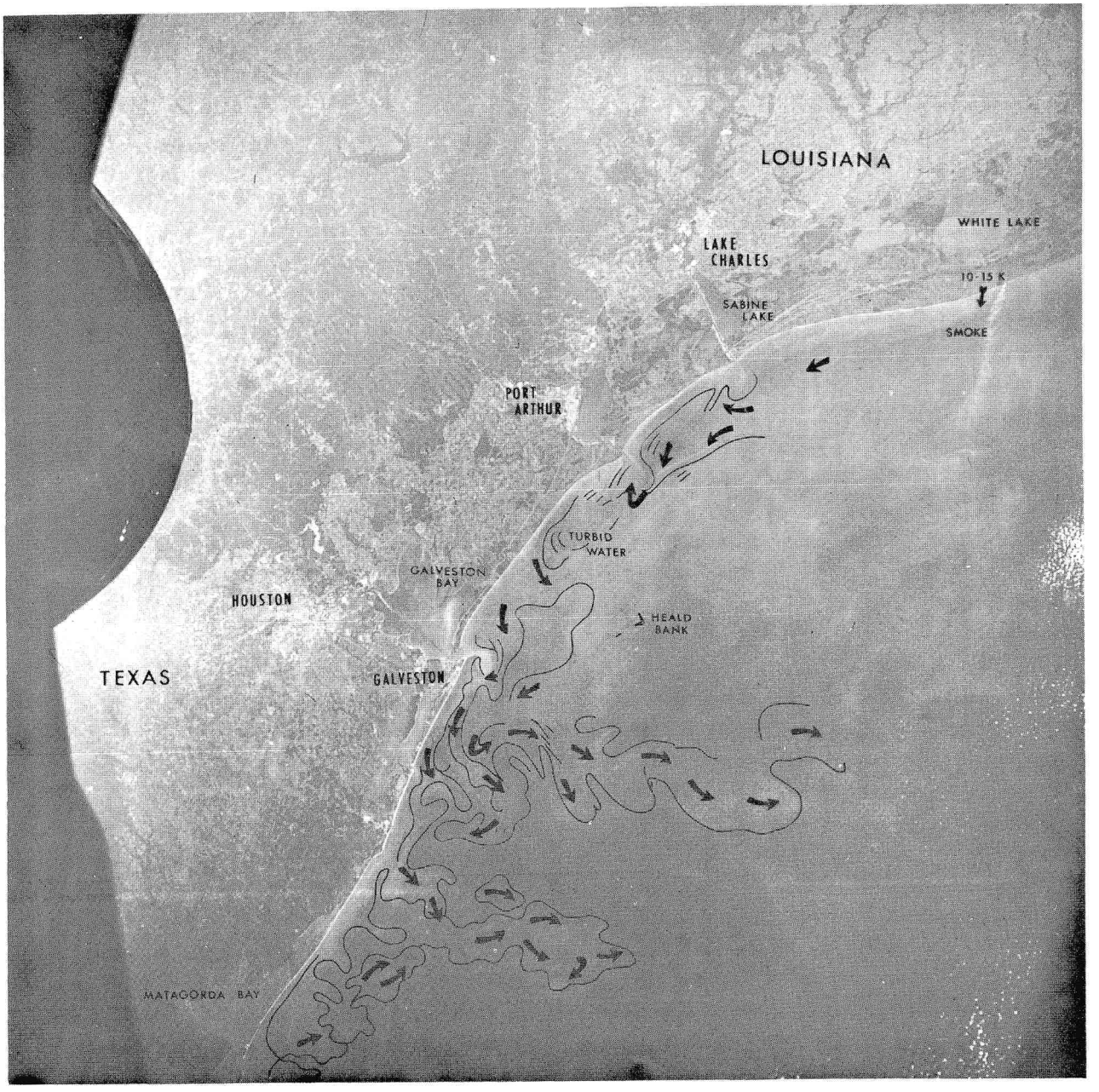

FIGURE 2.—This reproduction of figure 1 shows the alongshore southerly currents and what we believe to be the offshore relief or rip currents south and east of Galveston, Tex.

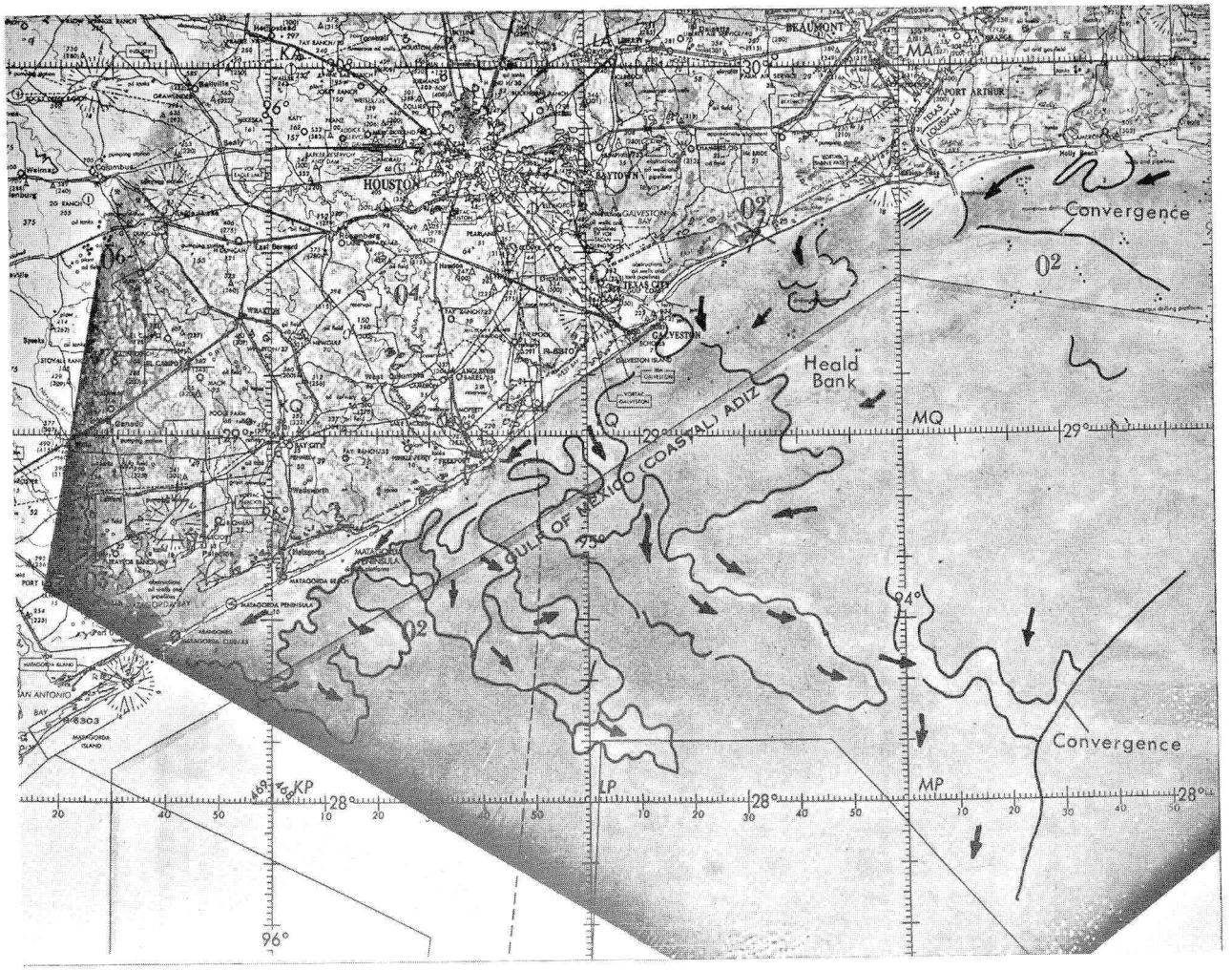

FIGURE 3.—An image of *ONC No. 24*, superimposed over a portion of figure 1 (rectified). The plumes have been outlined, and the directions of the currents are shown by arrows.

fishing grounds for brown shrimp (*Penaeus aztecus aztecus* Ives) in the northern Gulf of Mexico are known to be consistently in this region. In November 1966 (when the Gemini photograph was taken) about 57 percent of the catch of brown shrimp along the Texas Coast came from statistical area 19 and about 54 percent of the fishing effort was expended in this area (table 1). In 1956–66 about 43 percent of the brown shrimp caught in Gulf waters along the Texas Coast came from statistical area 19 (table 2).

Additional evidence for the relation between the plumes and brown shrimp fishing is provided by data gathered in July–September 1964 by personnel of the BCF Biological Laboratory, Galveston, Tex. During this period, which is the height of the brown shrimp season, an extensive interview campaign was undertaken to determine, by 10-minute grids, the areas most frequented by vessels fishing for brown shrimp. These data have been

TABLE 1.—*Catch and fishing effort for brown shrimp, by statistical areas, in the Gulf of Mexico along the Texas Coast, November 1966* [1]

Statistical area	Catch		Effort (trips)	
	Metric tons	*Percent*	*Number*	*Percent*
18	36.7	4.6	119	9.5
19	450.4	56.9	684	54.4
20	99.4	12.6	166	13.2
21	205.5	25.9	288	22.9
Total	792.0	100.0	1,257	100.0

[1] Source: Gulf Coast shrimp data, reported by depth and area of capture, species, size, number of trips, and days fished, November 1966. U.S. Fish Wildl. Serv., Curr. Fish. Statist. 4358.

TABLE 2.—*Catch of brown shrimp (heads-off), by statistical areas, in the Gulf of Mexico along the Texas Coast* [1]

Year	Statistical area				
	18	19	20	21	Total
	Thousands of metric tons				
1956	2.2	3.1	3.3	1.4	10.0
1957	2.4	5.3	3.4	1.6	12.7
1958	2.2	2.8	4.6	1.3	10.8
1959	2.3	4.9	3.6	2.5	13.4
1960	3.4	7.0	2.9	1.7	15.0
1961	1.1	2.5	2.1	1.3	7.0
1962	1.0	3.4	2.4	.8	7.6
1963	1.6	6.1	2.0	1.8	11.5
1964	1.2	4.0	2.4	1.0	8.6
1965	1.9	6.4	1.9	1.6	11.8
1966	1.3	5.7	2.6	2.0	11.6
Total	20.6	51.2	31.2	17.0	120.0
Percentage	17.1	42.7	26.0	14.2	100.0

[1] Source: Published records of the U.S. Department of the Interior, Bureau of Commercial Fisheries.

superimposed on the rectified Gemini photograph in figure 5. Clearly, fishing intensity was heaviest in and near the plumes.

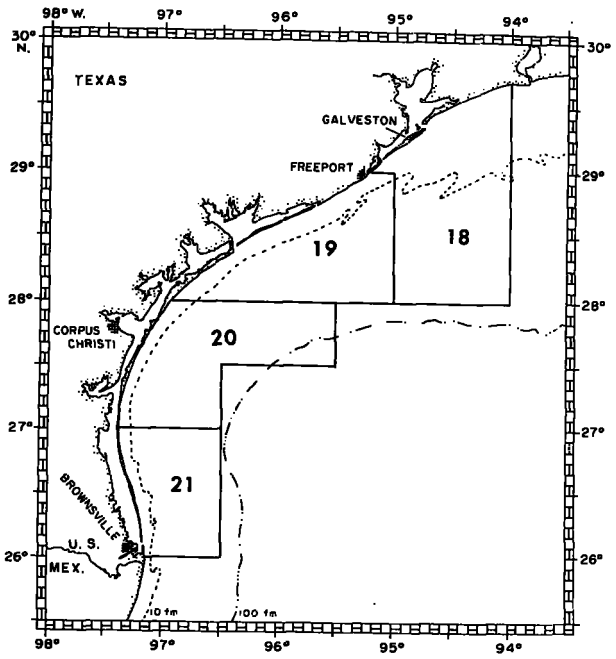

FIGURE 4.—Statistical areas along the Texas Coast. By interviewing fishermen, BCF employees are able to record data on daily landings and fishing effort by statistical area. The recording of catch and effort by this method began in January 1956. Comparison of this figure with figure 3 shows that the relief plumes lie in statistical area 19 and the lower portion of 18.

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FIGURE 5.—An overlay on figure 3 that demonstrates the relation between the plumes and fishing intensity for brown shrimp. The numbers in the 10-minute grids represent the total number of vessels fishing in each grid in July–September 1964. Only those grids are numbered where 25 or more vessels fished.

PHYSICAL AND CHEMICAL LIMNOLOGY OF BROWNLEE RESERVOIR, 1962–64

By Wesley J. Ebel and Charles H. Koski, *Fishery Biologists*
Bureau of Commercial Fisheries Biological Laboratory
Seattle, Washington 98102

ABSTRACT

The physical and chemical features of Brownlee Reservoir are discussed in relation to seasonal change, inflow and outflow, operation of the dam, modified environment of river below the dam, and possible effects of these factors on behavior, passage, and survival of salmon (*Oncorhynchus* spp.).

Temperature, oxygen concentration, and current were the most critical factors affecting the distribution and survival of salmon. Water temperature above 26.7° C. and oxygen concentration below 3 p.p.m. limited the area of suitable habitat during midsummer; environmental conditions in the spring, fall, and winter were suitable, if not optimal. The reservoir had a significant effect on the temperature and oxygen concentrations of the Snake River below the dam. In October, discharge from the reservoir was 5° C. warmer than the water entering the reservoir; oxygen concentration was 5 p.p.m. lower than in the inflow. This condition reversed in June and July.

Current velocities and directions changed significantly with changes in river inflow, discharge rate, and surface level of the reservoir. Passage by juvenile salmonids through the reservoir was affected by changes in reservoir temperature, length, oxygen concentrations, and velocity and direction of the current.

The U.S. Department of the Interior began intensive research in 1961 to solve problems of fish passage at high dams. Primary consideration was given to the study of factors that might affect the survival and passage of adult and juvenile salmonids (*Oncorhynchus* spp.) under the conditions anticipated for the Middle Snake River Basin. Brownlee Reservoir, completed in 1958, provided an area in which to examine the effects of a large impoundment on migrating salmon. The Bureau of Commercial Fisheries began limnological studies (physical and chemical) in July 1962 and continued them through October 1964; the study on the effects of various environmental factors on the behavior and passage of salmonids was directed principally toward water quality and current.

Brownlee Reservoir lies at the head of the Snake River canyon in hilly and semiarid, open-range country between the borders of northeastern Oregon and midwestern Idaho (fig. 1). At full pool, the reservoir begins about 16 km. downstream from Weiser, Idaho, and continues northerly in a nearly straight course for 92 km. to Brownlee Dam. Average width is less than 0.8 km.; maximum depth at full pool is about 92 m. At full capacity, the reservoir has an area of 6,100 hectares and contains 217,000 hectare-meters, or 1.8×10^9 m.^{3} of water.

Three main tributaries—the Snake, Powder, and Burnt Rivers—and many small, intermittent streams enter the reservoir. The upper 23 km. above the mouth of Burnt River is relatively shallow and essentially a river. Depth increases sharply below Burnt River; currents in the remaining 69 km. are weak when the reservoir is at full pool. The slope of the reservoir's basin, its depth, geographic location, and especially its thermal characteristics, are such that it fits some of the criteria used by Welch (1952) and Hutchinson (1957) to describe "temperate lakes of the second order."

An obvious difference between a reservoir such

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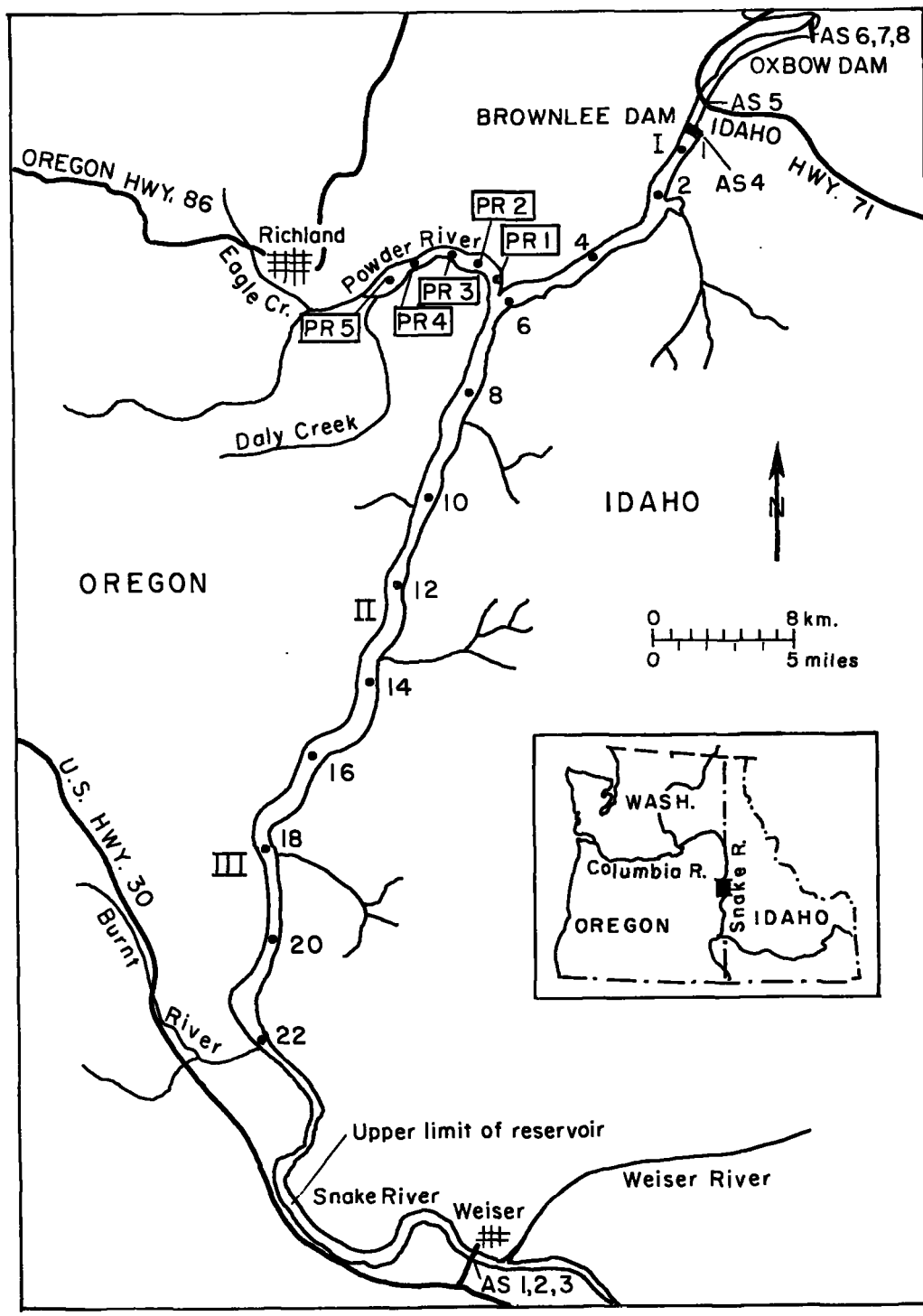


FIGURE 1.—Brownlee Reservoir, showing principal limnological sampling stations. The twelve Arabic numerals without a letter prefix were the main sampling stations; Roman numerals indicate location of continuous current recorders. Stations PR 1–5 were frequently sampled stations in the Powder River and AS 1–8 were frequently sampled stations located upstream and downstream from Brownlee Reservoir.

as Brownlee and a natural river-lake system is the depth at which the water is discharged. Flows from a reservoir are usually discharged at depth, whereas flows from a lake are discharged from the surface. At Brownlee, the turbine intake is 36.6 m. below normal pool level. The spillway discharges from the surface and from a depth of 35.4 m. Fluctuation in water level is considerable during late fall and winter; the reservoir is lowered as much as 32.8 m., depending on forecasts of expected spring runoff. The fluctuations lead to terraced mudbanks that are unproductive areas. Average volumes of water from the Snake River at Weiser, Idaho, range from 255 c.m.s. (cubic meters per second) in late summer to 1,132 c.m.s. in the spring. Maximum rate of flow during the study period was about 1,416 c.m.s.[1]

METHODS

Sampling stations were established throughout Brownlee Reservoir and at certain locations upstream and downstream from the reservoir to measure physical and chemical properties of its water. Temperature, dissolved oxygen concentration, and current were the principal factors studied. The location of sampling stations and the techniques and equipment used are described.

SAMPLING LOCATIONS AND TECHNIQUES

We established sampling stations throughout the reservoir and at certain locations upstream and downstream from it (fig. 1). Twelve main stations were spaced about 6 km. apart on the axis of the reservoir. They extended from 1 to 69 km. above the dam. Occasional sampling was done between these main stations. Additional stations along the Snake River included sites on State highway 30 at the bridge in Weiser, State highway 71 on interstate bridge below Brownlee Dam, and on the catwalk below the Oxbow and Brownlee power plants. Other stations were at Eagle Creek (on the Powder River) and at five places in the Powder River arm of Brownlee Reservoir. Water samples were also collected at fish-trapping sites throughout the reservoir during the periods of migration by salmon.

All permanent stations were sampled once every 2 weeks during summer stratification of the water in 1962 and once a month in winter and early spring after turnover of the water in 1963–64. Permanent stations were marked by Styrofoam[2] buoys anchored to concrete blocks to assure sampling at the same location each period.

Four sets of diurnal observations were made in addition to the routine sampling. These observations covered either a 24- or 48-hour period; samples were taken every 3 to 6 hours.

To secure temperature profiles from top to bottom and define the epilimnion, thermocline, and hypolimnion when present, depth and conductivity readings were recorded with each temperature change of 0.55° C. as read from a Whitney thermistor and conductivity meter. The thermistor was calibrated daily with a certified laboratory thermometer and checked periodically at various depths with a mercury reversing thermometer. The conductivity meter was calibrated daily.

During periods of stratification, water samples were taken in 2½-liter plastic Van Dorn bottles to determine dissolved oxygen and other characteristics in each of the three water masses. Before and after stratification, sampling was from the surface to the bottom at intervals up to 15 m. Samples were kept in an insulated cooler to minimize chemical changes that might be caused by increasing temperature. Dissolved oxygen was determined by the unmodified Winkler method (American Public Health Association, 1960); a second subsample was drawn and placed in a plastic bottle for later determination of free carbon dioxide, sulphate, turbidity, total and phenolphthalein alkalinity, and pH. Duplicate samples from some of the same casts were collected at least once every sampling day to check accuracy of all determinations.

Daily maximum and minimum air temperatures, precipitation, and wind direction and velocity were recorded at two stations. Meteorological data were received from the weather station operated by Radio Station KWEI at Weiser, Idaho. A second weather station was established near station 14 on the west side of the reservoir.

A temperature profile was determined by taking the temperature from top to bottom and recording the depth at every temperature change of 1° F.

[1] A flow of 2,209 c.m.s. was recorded in December 1964 (after the study ended).

[2] Trade names referred to in this publication do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

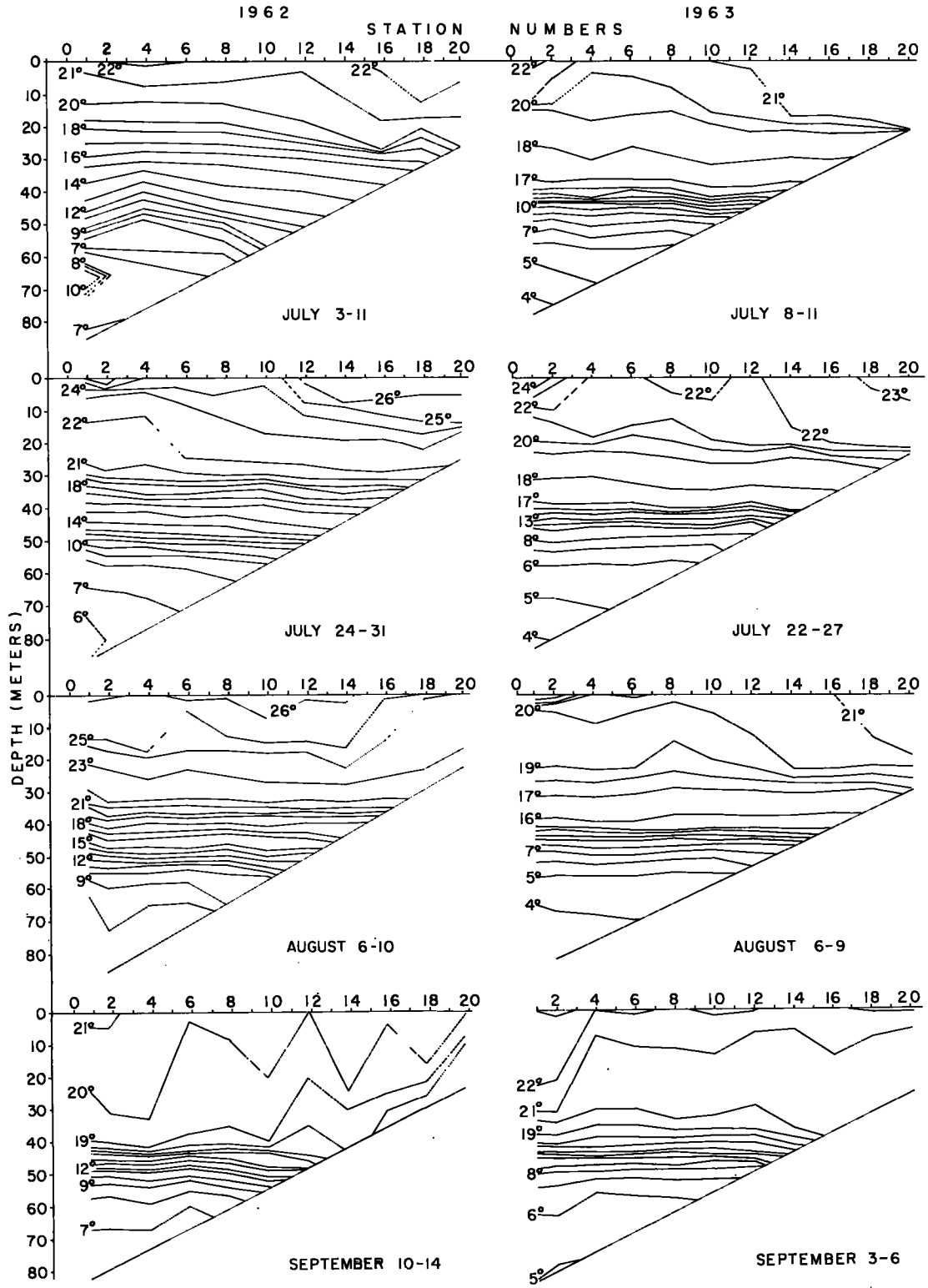


FIGURE 2.—Temperature profiles (° C.), Brownlee Reservoir. Comparison of months, July 1962 to June 1964.

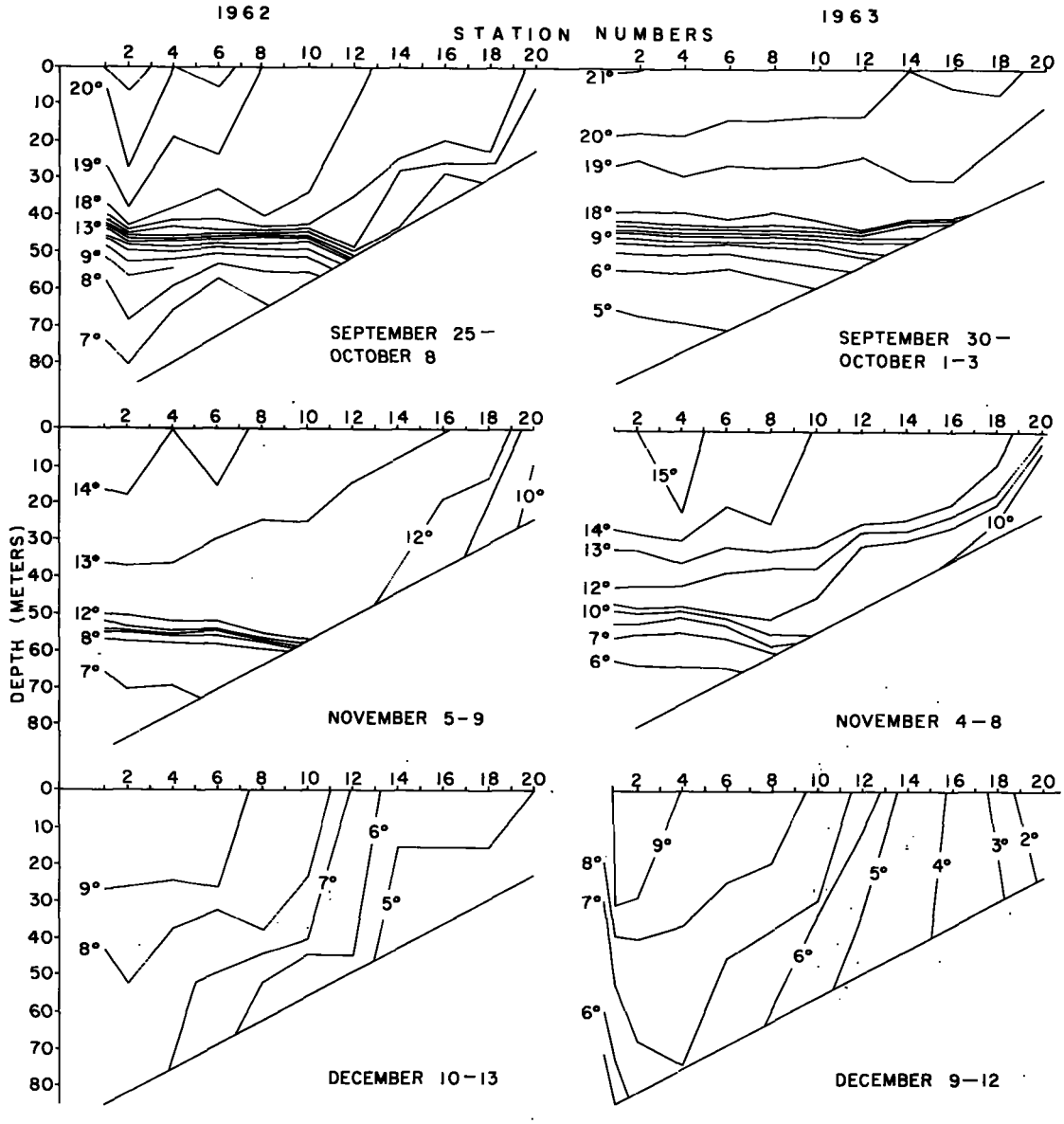


FIGURE 2.—Continued

(0.55° C.). Conductivity readings were also recorded at each change of 1° F. Temperature data were then graphed to determine the depths of the epilimnion, thermocline, and hypolimnion.

Along with Secchi disc readings, air temperature, wind velocity and direction, other atmospheric conditions also were recorded routinely at each station.

Mean volumes of flow from the Snake River into the reservoir and discharges from Brownlee Reservoir were computed during each sampling period. Mean temperatures of the inflow and outflow volumes were also computed for each period from thermograph, Whitney thermistor, and laboratory thermometer records. Table 1 summarizes temperature and inflow-outflow computations.

CURRENT MEASUREMENTS

Measurement of current velocity and direction with three Savonius-type current meters began in the fall of 1963. The meters were used as continuous current recorders at a given depth and loca-

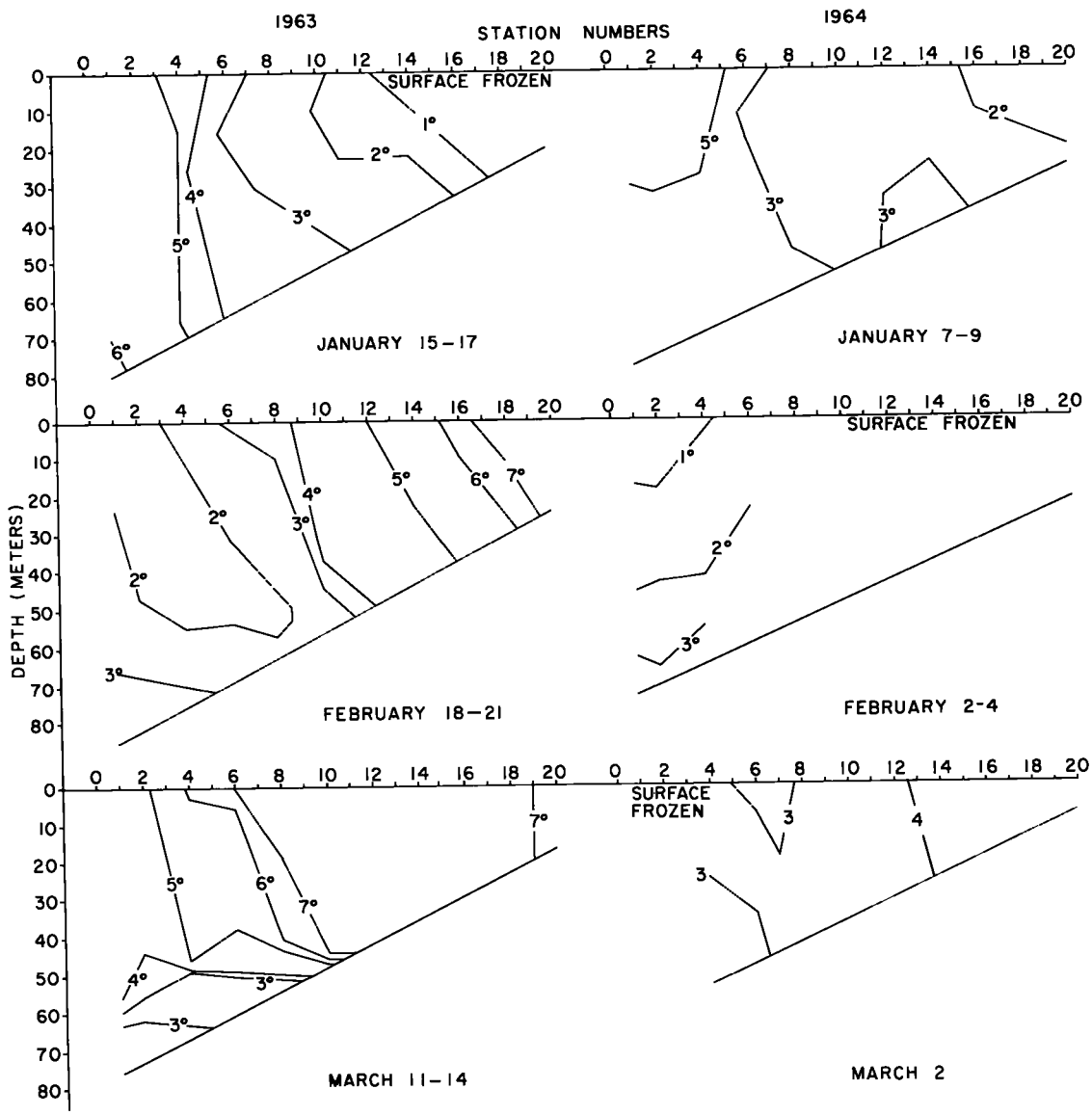


FIGURE 2.—Continued

tion and as mobile instruments to determine current patterns at any given time under any condition. Data were recorded under the following conditions: (1) during maximum reservoir drawdown; (2) at sustained minus 13-m. level with spill; (3) during fill-up without spill; (4) at full pool with high spill; and (5) at full pool without spill. The current meters, when used as continuous current recorders, were placed at midchannel stations in the lower, middle, and upper reservoir (I, II, and III, respectively, fig. 1) at a depth of 3 m. When the current meters were used as mobile instruments, measurements were made at the established limnological stations.

LABORATORY ANALYSES

Laboratory methods for analysis of samples followed standard methods (American Public Health Association, 1960). Quality control measures described for maintaining reagent normalities of sodium thiosulfate were also instituted and performed before each period. Sodium hydroxide, sulfuric acid, and reagents used in the field were checked immediately before each sampling period and renewed when necessary.

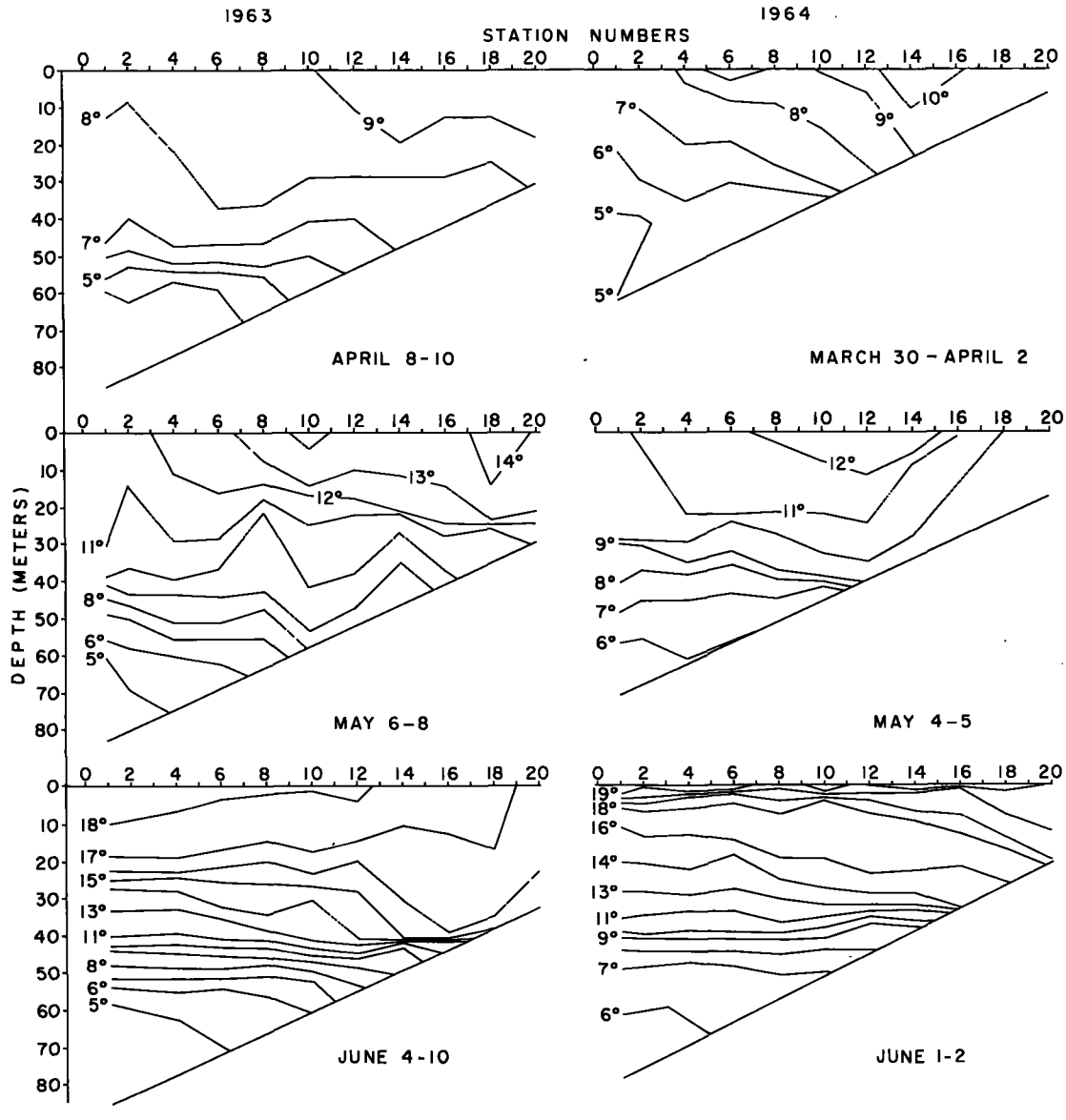


FIGURE 2.—Continued

PHYSICAL AND CHEMICAL PROPERTIES

Temperature, oxygen concentration, current, and other physical and chemical data are presented. Changes in these properties are described, and comparisons are made between years. Diurnal fluctuations of special interest are also described.

TEMPERATURES

The temperature regime of Brownlee Reservoir differs somewhat from that in large, deep lakes, but nevertheless shows the seasonal thermal changes of deeper lakes in the temperate zone: spring turnover, formation of thermocline, and fall turnover. In January 1963, the isotherms were vertical from upper reservoir to the dam (fig. 2). Temperatures in the upper portion ranged from 0.5° to 1.6° C.; those at the lower end ranged between 3.3° and 5.5° C. The isotherms remained vertical until mid-March; then the isotherms began to align horizontally at depths below 49 m. The January–March period is analogous in a

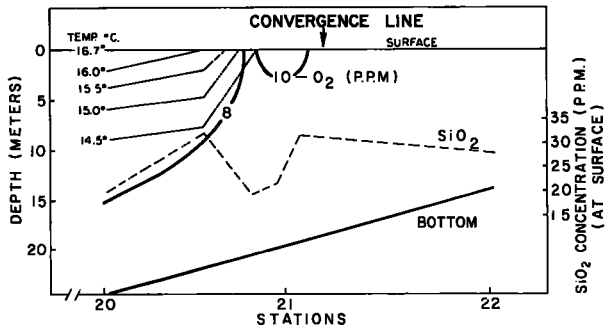


FIGURE 3.—Water temperature, oxygen concentrations, and silicon dioxide concentrations of Brownlee Reservoir from stations 20 to 22 at the time of formation of a visible convergence line, October 23, 1963.

sense to the "spring turnover" in lakes. Temperatures at this time ranged from 0.5° to 7.2° C.

Vertical stratification continued to strengthen after mid-March, and by early June a thermocline began to develop in the upper reservoir. Also in June, a visible convergence line (Frey, 1963) was observed in the upper reservoir near station 20. The cooler, heavier water from the Snake River dipped at this point and flowed under the warmer, lighter water of the reservoir. This condition was repeated in the fall (fig. 3). A sharp increase in temperature, higher concentration of oxygen (10 p.p.m.), and a dip in concentration of silicon dioxide were characteristic chemical and physical features observed in the vicinity of the convergence line in October 1963.

The temperature difference was 2.2° to 2.7° C. from one side of the convergence line to the other most of the time that the line could be identified. The temperature gradient near the visible line usually was extended over 0.8 km. The extreme difference of 2.7° C. during one sampling period, however, was from one side of the boat and the other. Turbidity readings and oxygen concentrations were higher upstream from the line, whereas conductivities were lower downstream. Wind action and the extent of discharge at the dam seemed to control the movement of the line upstream or downstream in the reservoir, as well as the sharpness of the temperature gradient.

The thermocline continued to develop during late spring and early summer of 1963; it was well defined from the upper reservoir to the dam by July 8. The stratification was then complete with a well-defined epilimnion, thermocline, and hypolimnion. Temperatures ranged from 15° to 25.5° C. in the epilimnion, 10° to 15.5° C. in the thermocline, and 3.9° to 9.5° C. in the hypolimnion.

Stratification continued until mid-October 1963, when the convergence or shear line was again formed. The heavier, cooler water from the river flowed under the warm epilimnion and evidently eroded the thermocline; distinct separation of isotherms was gradually eliminated until only a remnant of the thermocline remained in November. The reservoir was again in a state of turnover by December 9 when isotherms aligned vertically (fig. 2). Temperatures in the Powder River arm were nearly identical to those in the main reservoir.

The general patterns of the isotherms in 1962 and 1963 were similar except for time of formation of the thermocline. During the summer of 1962 a well-defined thermocline was not formed until early September, whereas in 1963 it was established by late June. Temperature ranges for the various months also differed; the greatest difference was in August. In 1962 the maximum was 27.2° C. whereas in 1963 it was 25.5° C. The temperature range for the epilimnion in August 1962 was 20.5° to 27.2° C.; in 1963 it was between 16.6° and 25.5° C. The reservoir temperatures gradually and consistently increased in 1962 without abrupt changes until September. In 1963 the trend was the same until the last of May, when a brief reversal occurred. The combination of heavy rain and melting snow in the headwaters caused a large volume of cool water to enter the Snake River above the reservoir (table 1). This mass of water cooled the entire upper end of the reservoir about 3.3° C. (see fig. 4).

Although air temperatures in June, July, and August 1962 were warmer than for the same period in 1963 (table 2), the thermocline developed earlier in 1963 than in 1962. The later formation of the thermocline in 1962 was due to the extent of reservoir drawdown and the length of the subsequent filling period. The drawdown in the winter of 1961 and ensuing months prolonged fill-up in the spring and early summer of 1962; it took place over a significant depth of 13.7 m. and caused enough water circulation to delay formation of the thermocline, despite the warmer air temperatures that year. By contrast, drawdown in the winter

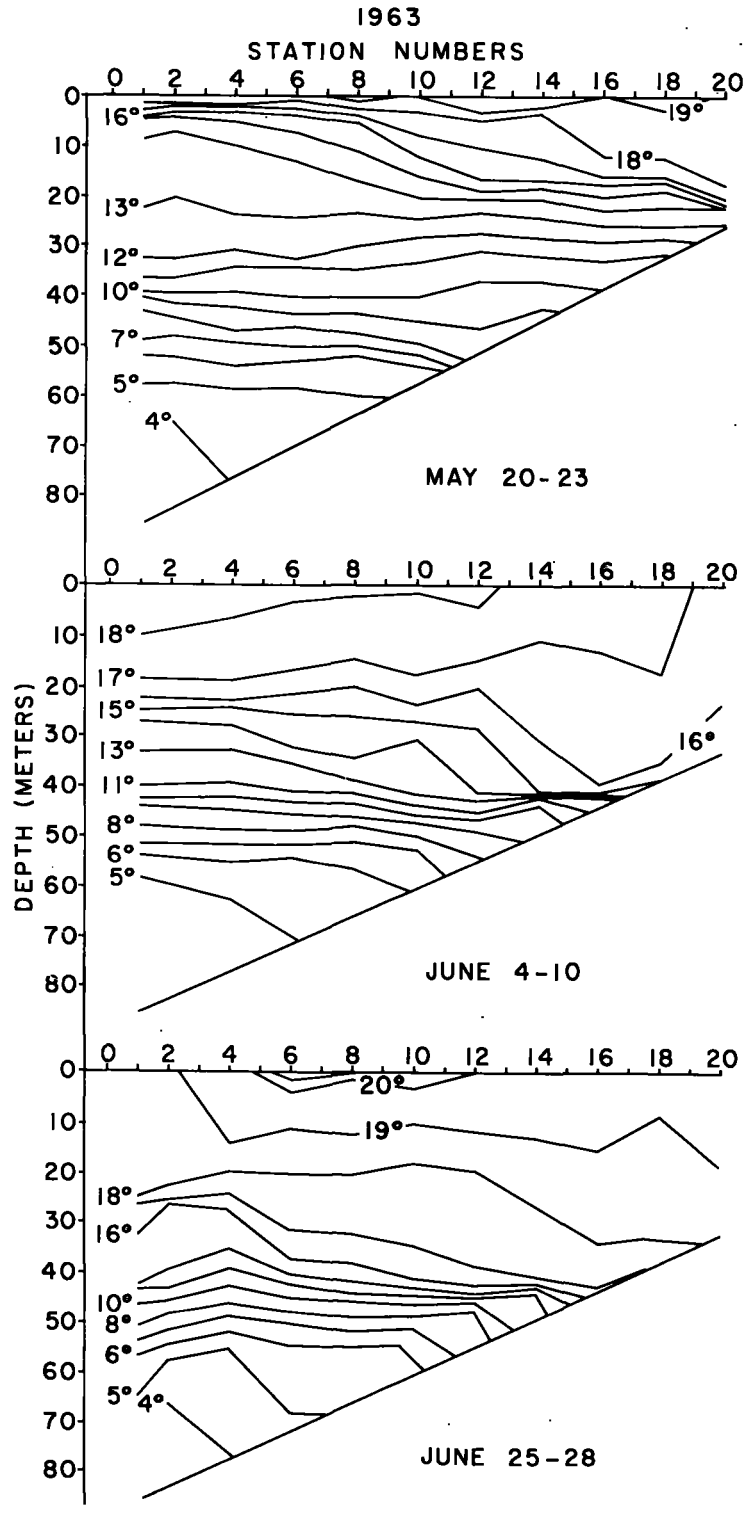


FIGURE 4.—Temperature isotherms (°C.), Brownlee Reservoir, May to June 1963. Cooling effect of cold river inflow is shown for June 4 to 10.

TABLE 1.—*Mean water temperature and mean volume of flow from the Snake River into Brownlee Reservoir and discharge at Brownlee Dam, May 1962 to June 1964*

Sample period	Mean temperature, Snake River at Weiser	Mean inflow at Brownlee	Mean discharge at Brownlee	Mean temperature at Brownlee [1] turbine outlets
1962	° *C.*	*C.m.s.*	*C.m.s.*	° *C.*
May 1–5	14.6	589.0	492.2	12.5
June 1–15	18.4	485.5	452.7	16.0
June 19–29	20.9	405.9	316.9	18.1
July 3–11	21.2	262.7	215.8	17.8
July 16–23	21.9	257.1	271.8	18.9
July 24–31	25.1	266.2	265.1	18.9
Aug. 6–10	23.3	314.9	389.6	20.4
Aug. 14–21	22.2	293.5	288.8	20.8
Aug. 22–28	22.2	293.0	268.2	21.1
Sept. 10–14	20.0	345.5	330.2	20.7
Sept. 25–Oct. 8	18.9	401.7	438.5	18.9
Oct. 10–16	13.9	510.5	453.1	16.9
Oct. 22–26	13.9	448.0	465.5	14.7
Nov. 26–30	7.5	442.9	418.5	10.3
Dec. 10–13	5.6	398.3	435.4	8.3
1963				
Jan. 15–17	5.6	341.9	542.1	6.1
Feb. 18–21	6.7	397.1	485.9	1.7
Mar. 11–14	8.9	371.7	379.3	4.7
Apr. 8–10	9.0	574.8	278.3	7.8
May 6–8	13.6	482.3	692.3	10.0
May 20–23	19.2	603.2	497.8	12.8
June 4–10	15.9	1,061.1	972.7	15.1
June 25–28	18.7	872.2	867.2	18.1
July 8–11	22.4	284.0	286.9	19.2
July 22–25	23.6	281.5	301.6	20.0
Aug. 6–9	23.1	296.6	288.7	20.0
Sept. 3–6	20.2	361.0	388.8	21.1
Oct. 1–3	16.7	366.2	401.6	20.0
Nov. 4–8	10.3	385.7	381.6	14.2
Dec. 9–12	4.4	387.2	444.6	7.7
1964				
Jan. 7–9	1.1	369.1	571.3	4.4
Feb. 2	3.3	371.0	401.8	3.3
Mar. 2	3.9	396.4	431.0	6.1
Mar. 30–Apr. 2	8.9	703.7	418.8	----------
May 4–5	11.7	773.1	835.7	----------
June 1–2	16.0	675.4	183.5	----------

[1] Courtesy of Bureau of Commercial Fisheries, River Basins Studies, Boise, Idaho.

of 1962 was relatively minor—only 6.4 m.; fill-up was short in 1963 and was completed by early May. As a result, the thermocline was formed fully 2 months earlier than in 1962.

OXYGEN CONCENTRATIONS

The chronological changes in oxygen concentrations permit description of seasonal changes and estimates at particular times (fig. 5).

Seasonal changes are described best by starting with January 1963, when dissolved oxygen concentrations approached saturation throughout the reservoir at all depths; conditions changed little until March when some decrease was evident below 49 m. Concentrations by May dropped to 1 p.p.m. on the bottom at stations 14 and 15, where the reservoir first receives a deposit of silt from the Snake River. Oxygen content of the entire reservoir ranged between 1 and 7 p.p.m.

Oxygen depletion continued at the lower depths from May until November when turnover began. The oxygen content near the surface (0–15 m.) increased in some areas, however, and generally ranged from 4 to 13 p.p.m. Increase of oxygen at the surface was presumably due to algae, which were readily visible throughout the reservoir. Lowest concentrations of oxygen came in August, when all water below 25 m. had a concentration of 3

TABLE 2.—*Air temperature at Weiser, Idaho,[1] and on west bank at station 14, Brownlee Reservoir, June 1962 to June 1964*

Locality and month	1962			1963			1964		
	Average maximum	Average minimum	Average median	Average maximum	Average minimum	Average median	Average maximum	Average minimum	Average median
	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	°*C.*
Weiser, Idaho:									
January				1.3	−8.5	−3.3	0.9	−9.8	−4.5
February				10.4	−.8	4.8	1.8	−12.5	−5.4
March				13.6	−.7	6.4	9.6	−3.2	3.2
April				15.4	1.8	8.6	12.3	1.4	6.8
May				23.9	6.6	15.2	22.4	4.6	13.6
June	29.2	9.4	19.3	25.5	9.6	17.6	25.6	9.2	17.4
July	32.2	13.3	22.7	31.6	9.5	20.6	----------		
August	30.2	11.4	22.7	32.8	11.2	21.9	----------		
September	26.5	6.8	16.7	28.7	9.2	19.0	----------		
October	17.8	2.9	10.3	20.6	3.7	12.1	----------		
November	10.1	−.6	4.8	9.9	−.8	4.5	----------		
December	4.6	−2.2	1.2	.6	−7.5	−3.6	----------		
Station 14, Brownlee Reservoir:									
January							2.9	−4.2	−.7
February				12.4	1.9	7.2	4.4	−4.3	.1
March				13.9	2.1	8.0	10.8	−.2	5.3
April				16.7	3.6	10.1	16.6	3.4	10.1
May				25.1	10.5	17.8	22.6	7.8	15.2
June				27.3	12.9	20.1	25.9	12.3	19.1
July				34.2	16.2	25.2	----------		
August				34.5	18.4	26.4	----------		
September				28.8	15.2	22.0	----------		
October				22.2	17.9	20.1	----------		
November				11.3	3.1	7.2	----------		
December				3.0	−2.8	.1	----------		

[1] Courtesy of radio station KWEI.

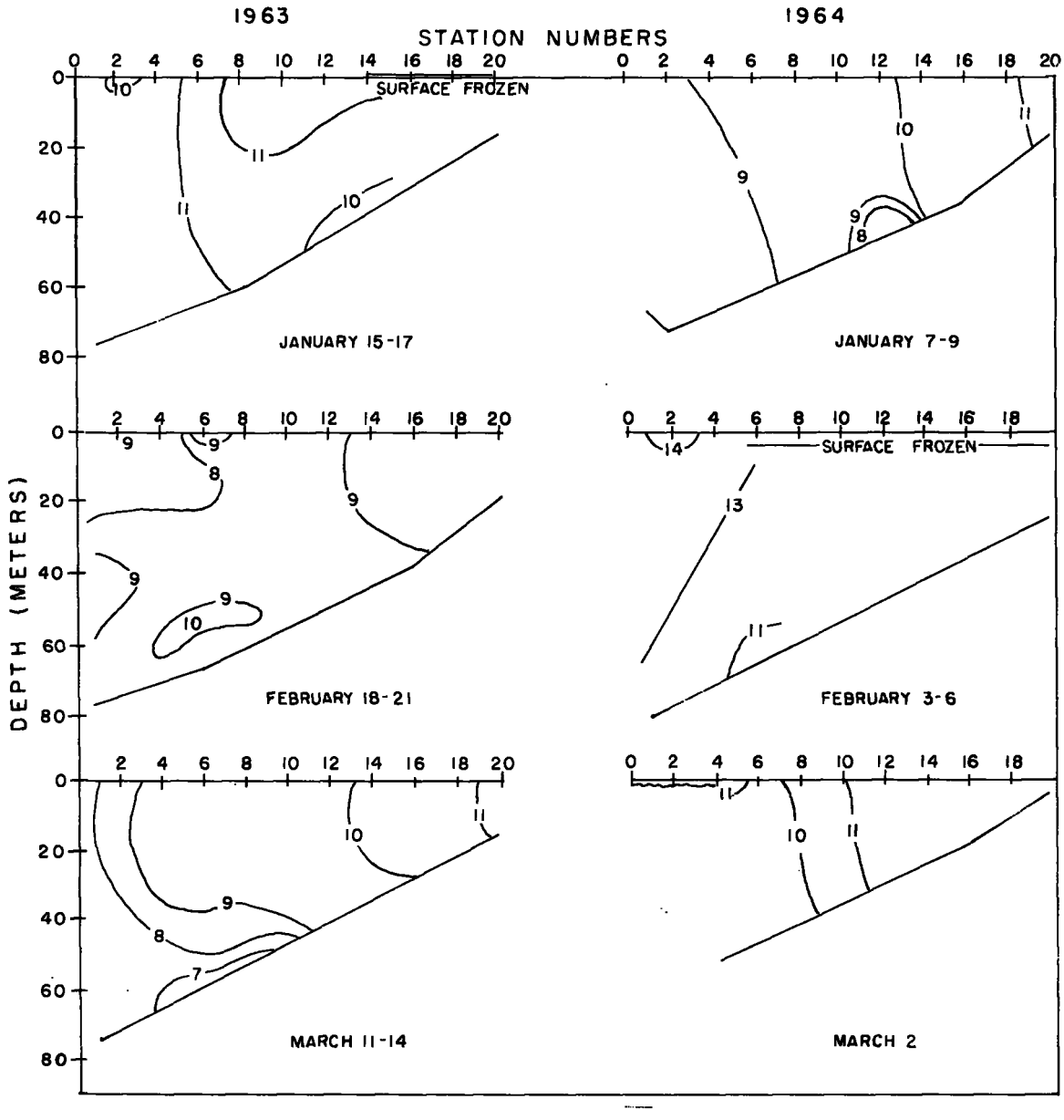
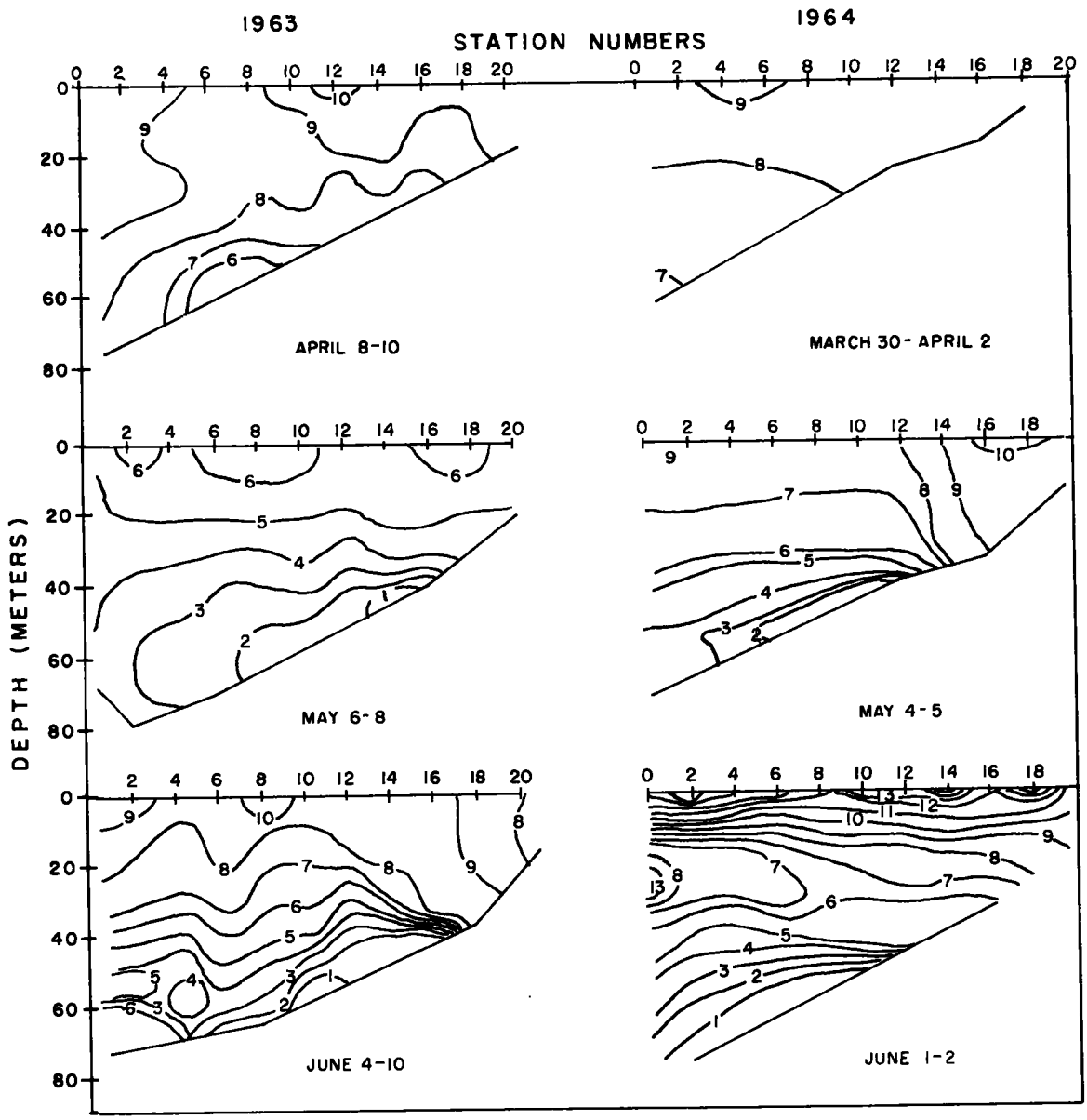


FIGURE 5.—Dissolved oxygen (p.p.m.) profiles, Brownlee Reservoir. Comparison of months for July 1962 to June 1964.



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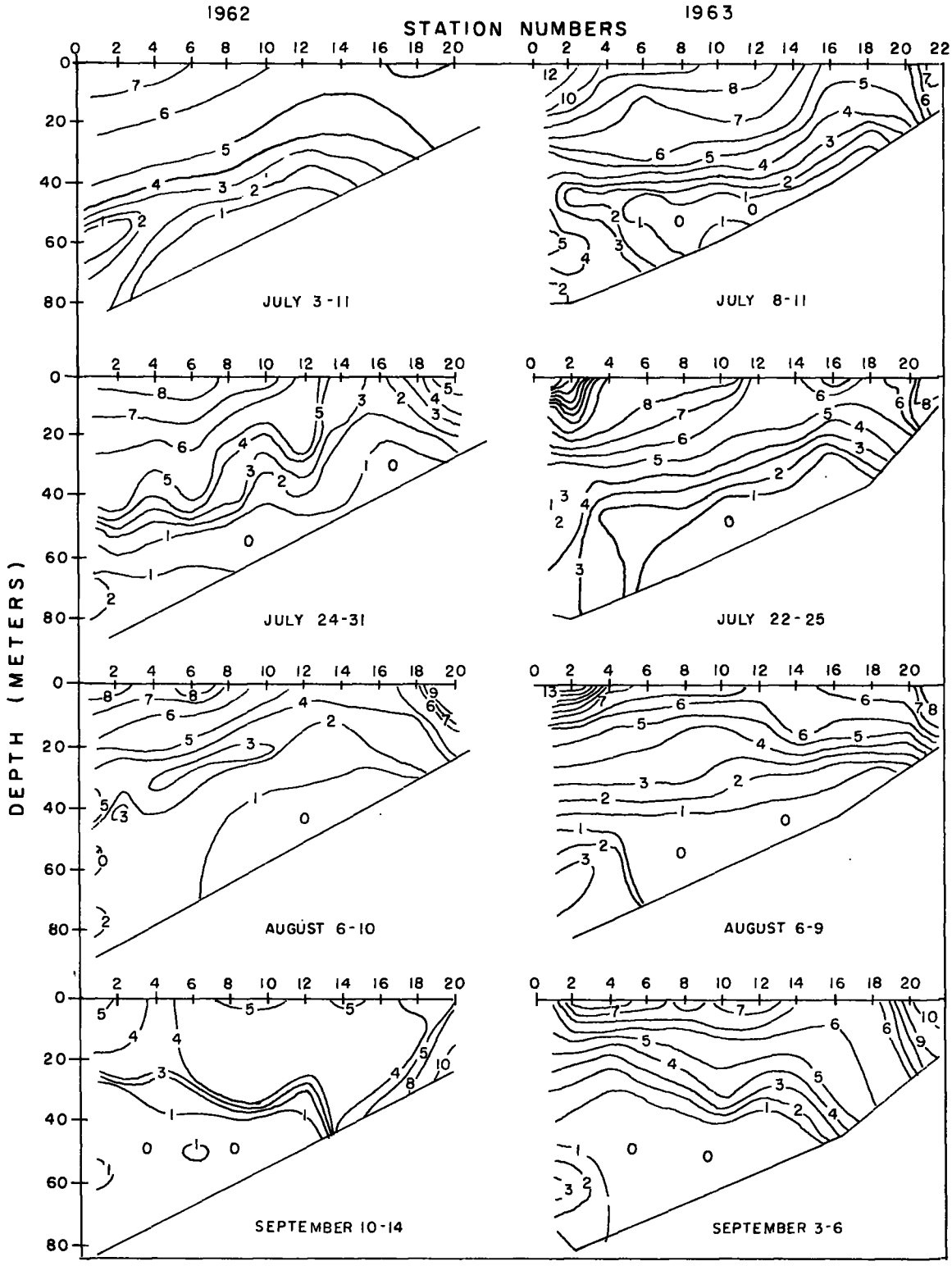

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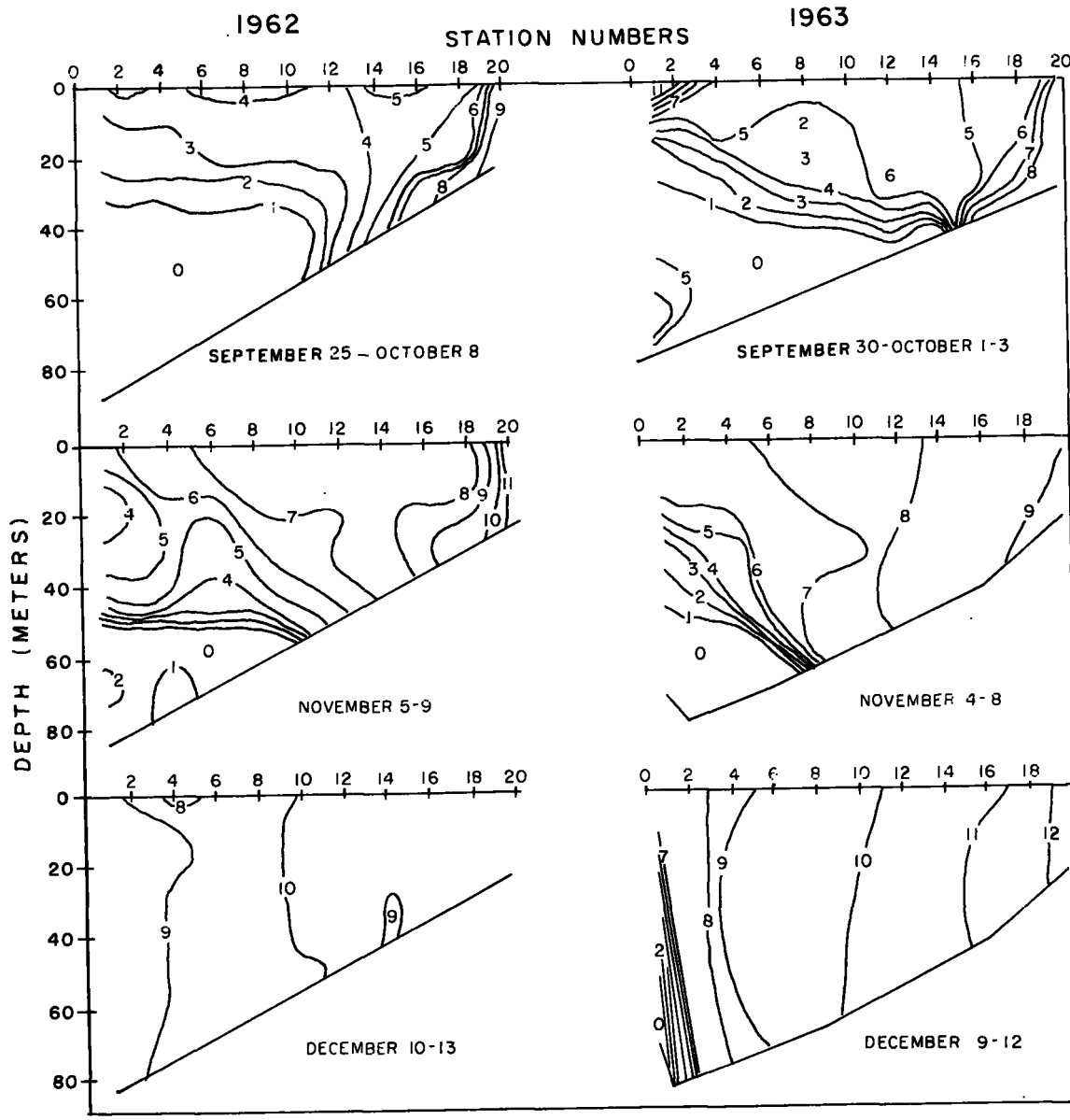

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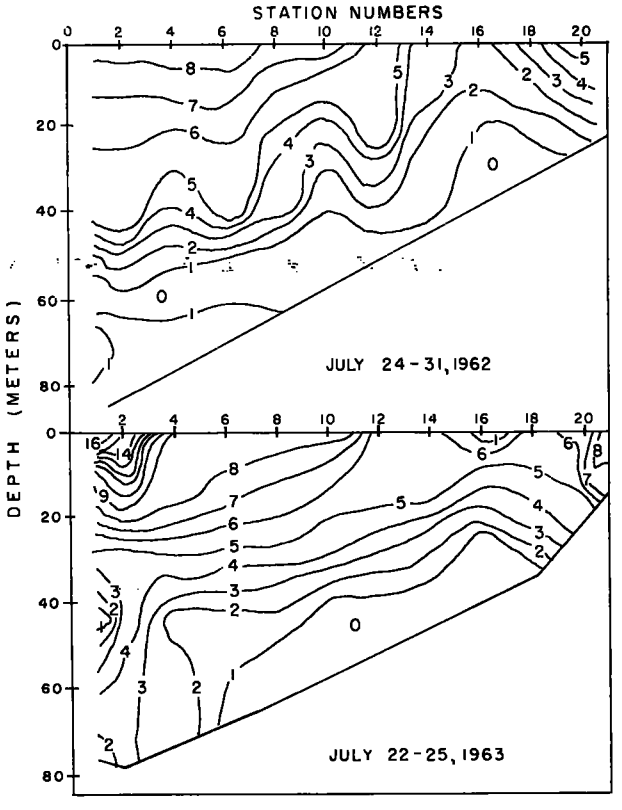


FIGURE 6.—Comparison of oxygen concentrations in Brownlee Reservoir July 1962 and July 1963. Note pronounced oxygen block at upper end of reservoir (stations 14 to 18) in 1962.

p.p.m., or less, and most of the water below 15 m. had 4 p.p.m. or less. This condition persisted through September but was alleviated somewhat in the upper end of the reservoir by October because of cooler inflow from the Snake and Burnt Rivers. By November, nearly two-thirds of the reservoir water contained 7 to 9 p.p.m. dissolved oxygen.

A small remnant of the hypolimnion remained at the dam in December, but more than nine-tenths of the reservoir had completely overturned; oxygen concentrations ranged from 7 to 12 p.p.m. Concentration changes were similar in the Powder River arm.

Oxygen records indicated that location of the turbine intake at 37 m. below normal pool level created sufficient circulation adjacent to the dam to bring some of the oxygenated water from the epilimnion down to the hypolimnion from July through October. Oxygen concentrations in this area for the same months in 1962 were almost identical.

An oxygen block or area of oxygen depletion (fig. 6) similar to that described by Fish and Wagner (1950) and Ellis (1942) was present in late July, 1962; it could be traced progressively through the reservoir in successive months (fig. 5). This block was not observed in 1963, although some evidence suggested that it was beginning to form. Shortly thereafter, the incipient block disintegrated.

Another major difference in the graphs of oxygen concentrations is that concentrations in September 1962 were considerably lower in the epilimnial waters than they were during the same month in 1963. Very possibly the oxygen block, higher air temperatures, and lower inflow from the Snake River all contributed to the lower epilimnial concentrations of oxygen in September 1962.

CONDUCTIVITY, pH, AND OTHER CHEMICAL PROPERTIES

Total alkalinity, phenolphthalein alkalinity, carbon dioxide, hydrogen-ion concentration, silicon dioxide, sulphates, turbidity, and conductivity were obtained for the surface, middepth, and bottom. Ranges for each year are presented; variation with depth, during the year and from one year to the other, is described.

Alkalinity was generally similar for comparable periods during the 27 months of study. Concentrations (fig. 7) ranged from 68 to 202 p.p.m. for 1962–63 and from 86 to 225 p.p.m. for 1963–64. Concentrations were highest in December, January, February, and March; they were lowest during May and June and increased through one summer. These concentrations were undoubtedly governed in part by the trend in alkalinity in the Snake River and in other tributaries (table 3). Alkalinity concentrations were fairly uniform during December and January when the reservoir was nearly homothermous and oxygen concentrations were nearly uniform. Range in concentrations was widest during the summer, when the reservoir was stratified.

The highest alkalinity occurred in the hypolimnion during June, July, and August. Precipitation of normal carbonates by aquatic organisms and

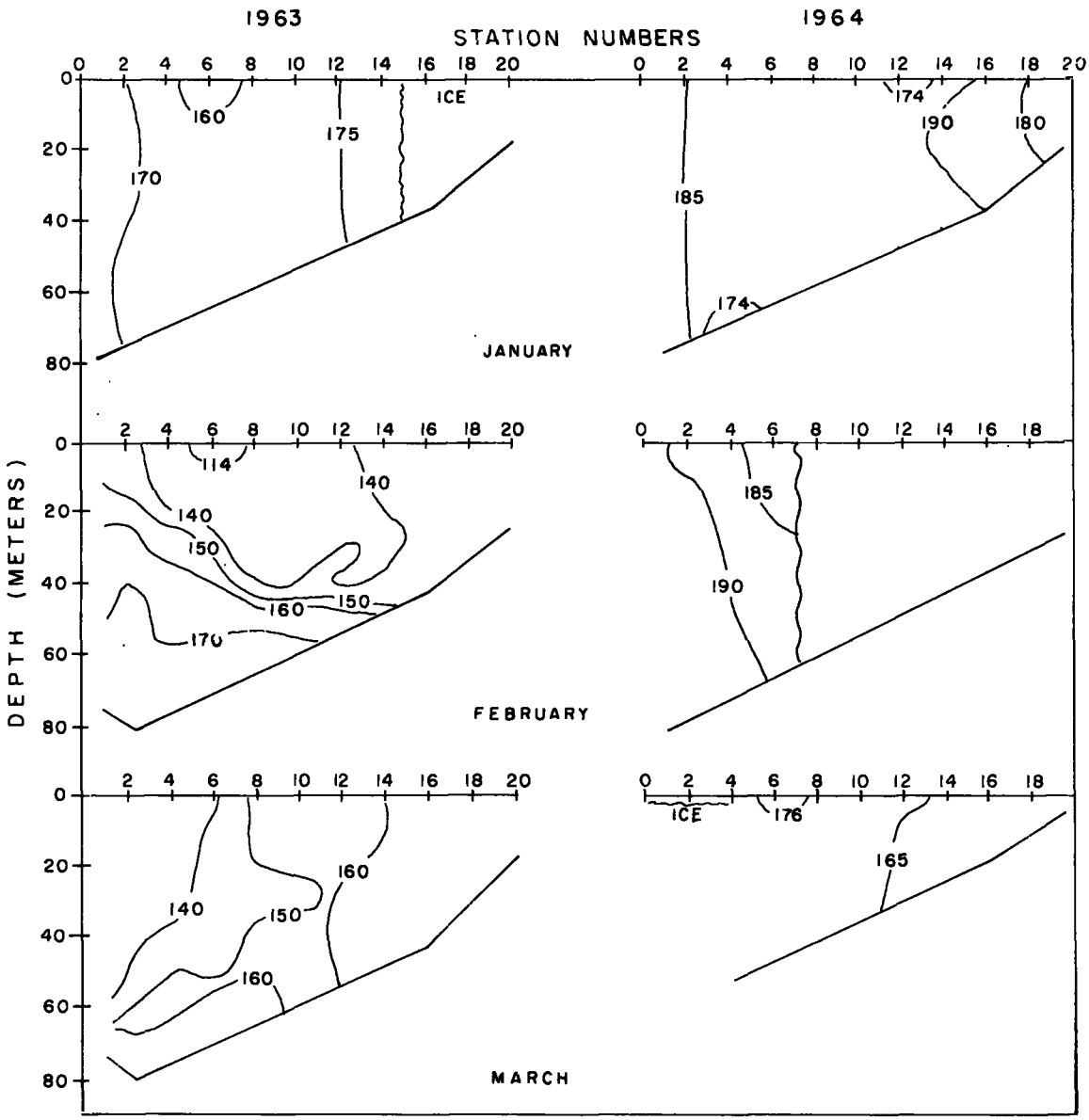
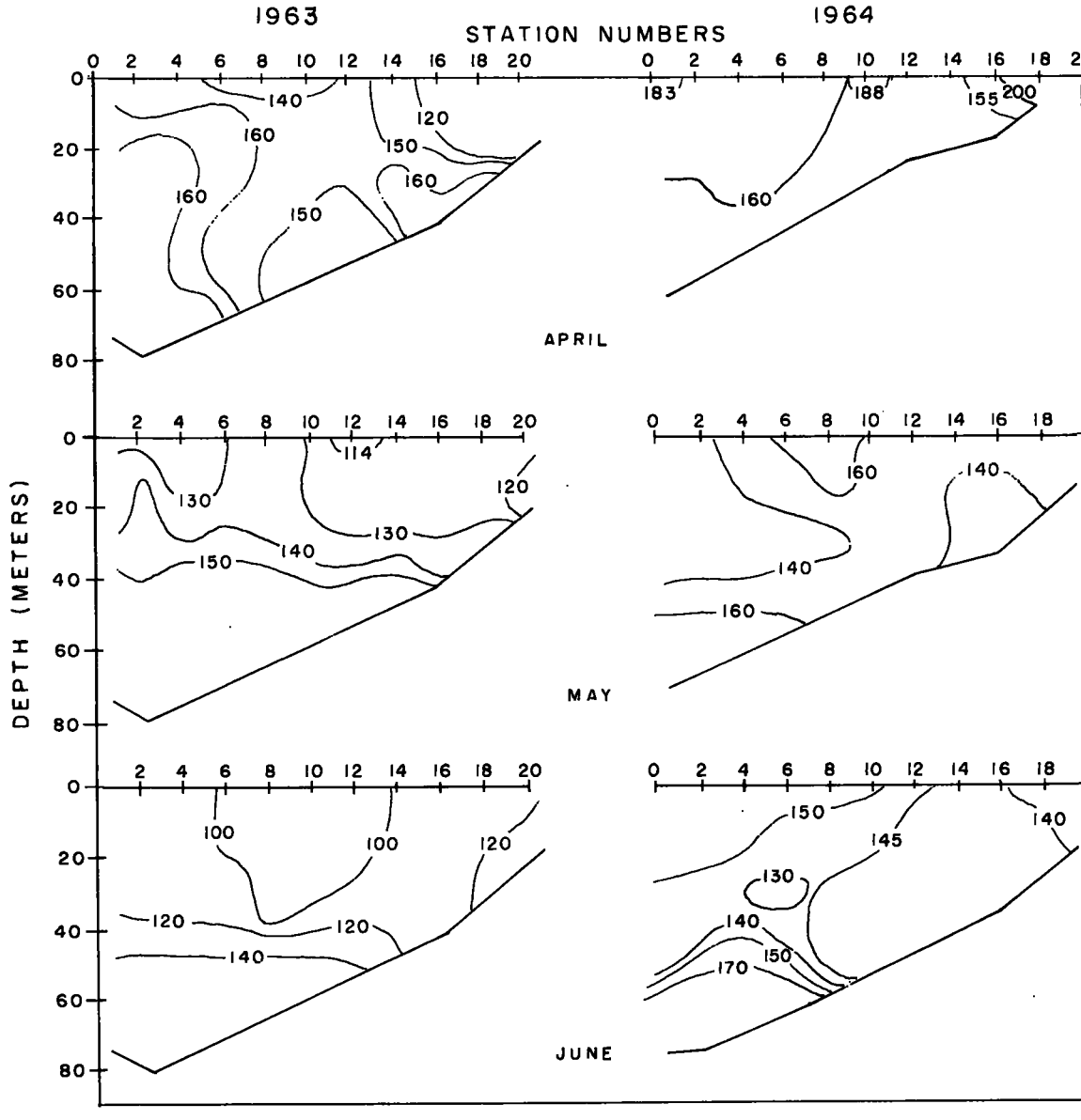


FIGURE 7.—Total alkalinity (p.p.m.), Brownlee Reservoir, July to December 1962 and 1963 and January to June 1963 and 1964.



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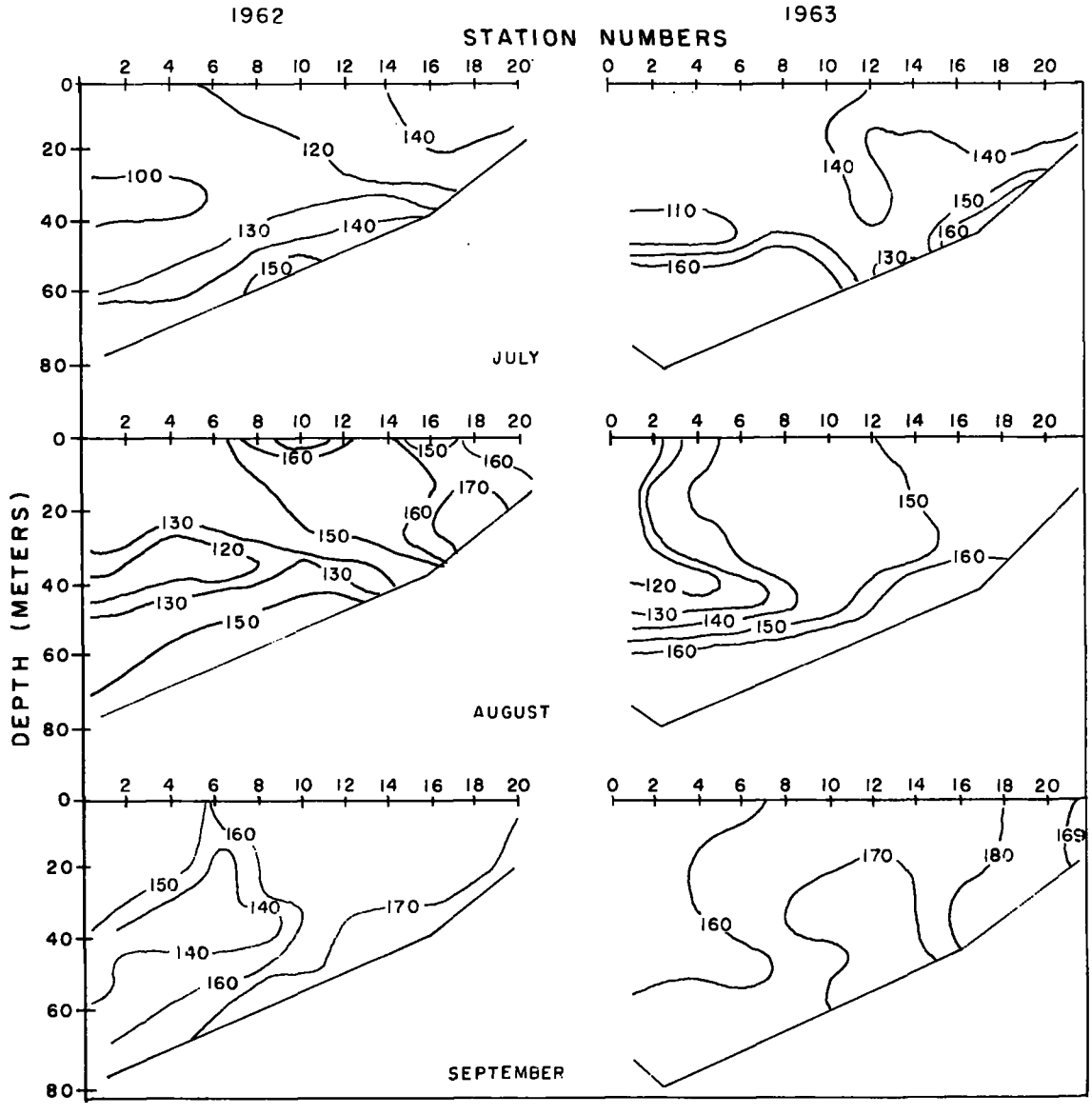

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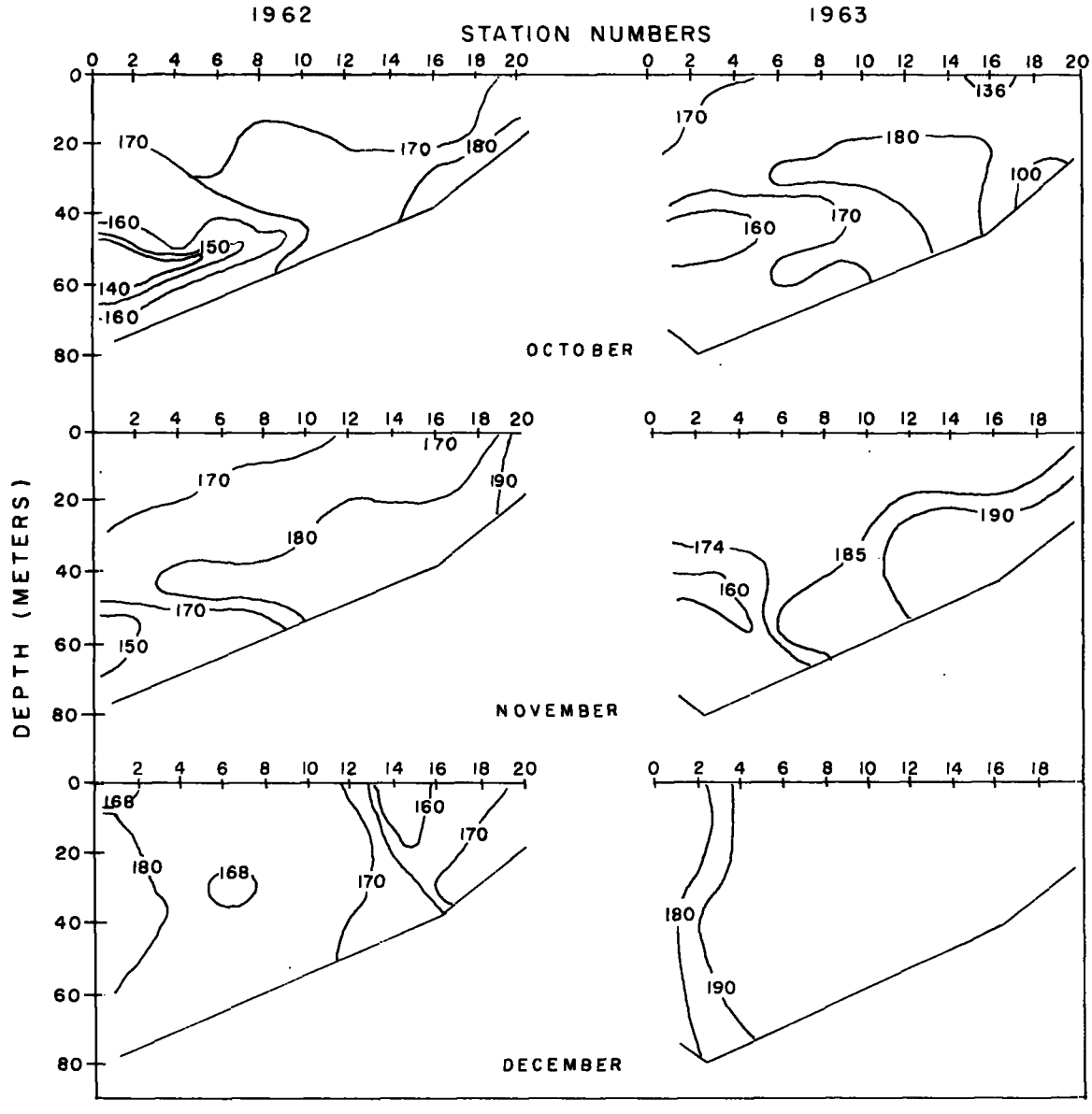

FIGURE 7.—Continued

TABLE 3.—*Surface temperature and chemical characteristics of water in Snake River (at Weiser, Idaho), Powder River, and Eagle Creek, January 1963 to June 1964*

Year and month	Total alkalinity	Phenolphthalein alkalinity	CO_2	pH	Temperature	O_2	SO_4	SiO_2
Snake River:								
1963:	*P.p.m.*	*P.p.m.*	*P.p.m.*		*°C.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
January	175	5	0.0	8.6	5.6	11.6	35	6
February	147	2	.0	----	6.7	10.0	46	61
March	168	12	.0	----	8.3	11.4	43	47
April	141	9	.0	8.4	8.9	11.5	39	31
May	119	12	.0	----	14.4	8.9	8	34
June	115	12	.0	----	21.7	10.1	6	15
July	139	15	.0	----	23.3	10.8	12	58
August	176	0	6.2	7.5	23.3	6.6	53	40
September	175	0	2.6	7.8	21.7	8.0	54	83
October	186	6	.0	7.6	16.7	9.0	43	34
November	190	13	.0	8.1	10.0	10.3	58	28
December	191	15	.0	8.2	4.4	12.2	46	50
1964:								
January	180	1	.0	8.6	.6	13.1	51	39
February	179	13	.0	8.2	3.3	15.4	50	47
March	169	4	.0	7.8	3.9	11.2	42	52
April	99	3	.0	7.7	7.8	9.7	29	7
May	171	6	.0	8.5	11.7	9.8	51	8
June	130	14	.0	----	15.6	11.2	34	64
Powder River:								
1963:								
January	----	----	----	----	----	----	----	----
February	104	0	4.4	7.7	3.3	11.7	22.5	67
March	109	0	[1] 4.0	7.7	5.0	11.6	7.0	66
April	122	0	1.8	7.7	7.2	14.1	3.0	36
May	149	10	.0	8.1	16.1	8.7	1.5	54
June	185	11	.0	8.1	26.7	7.3	9.0	125
July	209	14	.0	[1] 8.8	24.4	8.7	1.5	15
August	265	12	.0	[1] 8.5	27.8	7.2	22.0	22
September	265	9	.0	8.0	25.6	8.2	13.0	25
October	239	14	.0	[1] 8.5	14.4	11.0	18.0	15
November	224	22	.0	[1] 8.9	9.4	12.0	19.0	31
December	181	0	4.4	8.0	2.2	12.6	36.0	58
1964:								
January	Frozen	----	----	----	----	----	----	----
February	150	6	.0	8.0	2.2	16.7	20.0	25
March	136	[1] 5	.0	8.4	5.6	13.9	5.5	36
April	82	0	2.0	7.6	----	10.2	125.0	60
May	136	1	.0	8.2	15.6	10.6	42.0	11
June	150	0	7.0	----	14.4	8.6	11.0	74
Eagle Creek:								
1963:								
January	64	0	[1] 7.0	7.4	4.4	12.1	6.0	3
February	66	0	3.5	7.8	3.3	12.4	5.0	16
March	69	0	[1] 6.0	7.3	5.0	12.2	3.5	25
April	68	0	1.8	7.4	6.1	9.9	3.5	10
May	56	0	1.8	7.0	11.7	10.2	1.0	19
June	29	0	3.5	7.2	15.0	9.8	1.0	45
July	58	[1] 0	.0	7.1	21.1	8.4	1.0	6
August	151	0	2.6	7.6	27.8	6.7	3.0	19
September	149	9	.0	8.2	27.8	9.7	3.0	42
October	146	0	15.0	7.2	18.3	8.8	3.5	19
November	85	[1] 0	.0	7.8	10.0	10.7	4.0	36
December	87	0	3.5	7.5	3.3	12.2	2.0	42
1964:								
January	100	0	7.9	7.9	1.1	13.0	4.5	39
February	86	[1] 6	.0	7.6	2.2	15.5	8.0	22
March	78	6	.0	8.0	6.7	12.6	1.5	26
April	62	[1] 0	.0	7.6	8.9	10.8	8.0	35
May	75	1	.0	8.1	14.4	10.6	25.0	11
June	36	0	4.0	----	8.3	10.6	4.5	34

[1] Computed from Moore (1938).

their subsequent conversion to bicarbonate by carbonic acid probably accounted for the higher readings. The large local variation in the concentration was probably caused by currents, algae, and changes in alkalinity of the inflowing river.

The samples were also analyzed for normal carbonate. Concentrations for July 1962 through June 1963 ranged from 0 to 30 p.p.m.; for 1963–64, the range was 0 to 21 p.p.m. Maximum concentrations were in the surface layer (0–15.2 m.). The lower depths contained no normal carbonate during July and August, when production of algae was high and stratification complete. This condition was similar to that in lakes described by Welch (1952). Decomposition of algae and other organic material at the lower depths apparently liberated enough carbon dioxide to convert all carbonate to bicarbonate. This assumption is supported by the fact

that concentrations of high carbon dioxide were at the lower depths.

Concentrations of carbon dioxide were low in the spring and early summer, but high in the fall. Free carbon dioxide was lacking in January of both years. The range in concentration (p.p.m.) for 1962–63 (July–June) was 0 to 12 for the surface, 0 to 11 for the 30.5- to 45.7-m. layer, and 0 to 19 for the 45.7-m. layer to the bottom. The ranges for 1963–64 were 0 to 19, 0 to 23, and 0 to 43 for the surface, middepth, and bottom. Highest values were at the lower depths. Concentrations were not only far below the lethal levels indicated by Ellis (1937) but usually below the harmful level (39.2 p.p.m.) indicated by McKee and Wolf (1963).

Hydrogen-ion concentration (pH) in the reservoir ranged from 7 to 8.9. The high pH of the Snake River (table 3) throughout the year accounted for the high readings in the reservoir. The readings were highest in surface water where concentrations of normal carbonate were highest. The range in pH of the surface water in 1963, for example, was 7.7 to 8.9, but the range at lower depths, 46 m. to bottom, was 7 to 8.3. Neutral values of 7 were typical near the bottom during August and September, when the reservoir was well stratified. Decomposition of organic material apparently liberated enough carbon dioxide into the hypolimnion to lower the pH to this level. Concentrations were slightly higher on the bottom during these same 2 months in 1962. The pH ranged from 7.5 to 8.5 throughout the year in most of the water mass, indicating that Brownlee Reservoir is relatively alkaline in comparison with other lakes and reservoirs in the United States.

Conductivity readings, which were adjusted to 20° C., ranged from 253 to 867 micromhos. Values were low in the spring, progressively higher during the summer, and low again in the late fall after the turnover. During stratification, the highest readings were usually in the surface layer and the lowest readings in the hypolimnion. This phenomenon is the reverse of what would be expected if conductivity fluctuated with total alkalinity. Conformity with the expected relation (when the highest conductivity readings were in the hypolimnion) existed only in July and August of 1962 and 1963 and only in the lower part of the reservoir. Apparently some electrolytic substance, other than those sampled, was reduced at the lower depths. Ellis (1940) found that conductivities paralleled alkalinities and sulfates and that all three were higher at the lower depths. Although conductivity reached 867 micromhos, this figure was still below the level

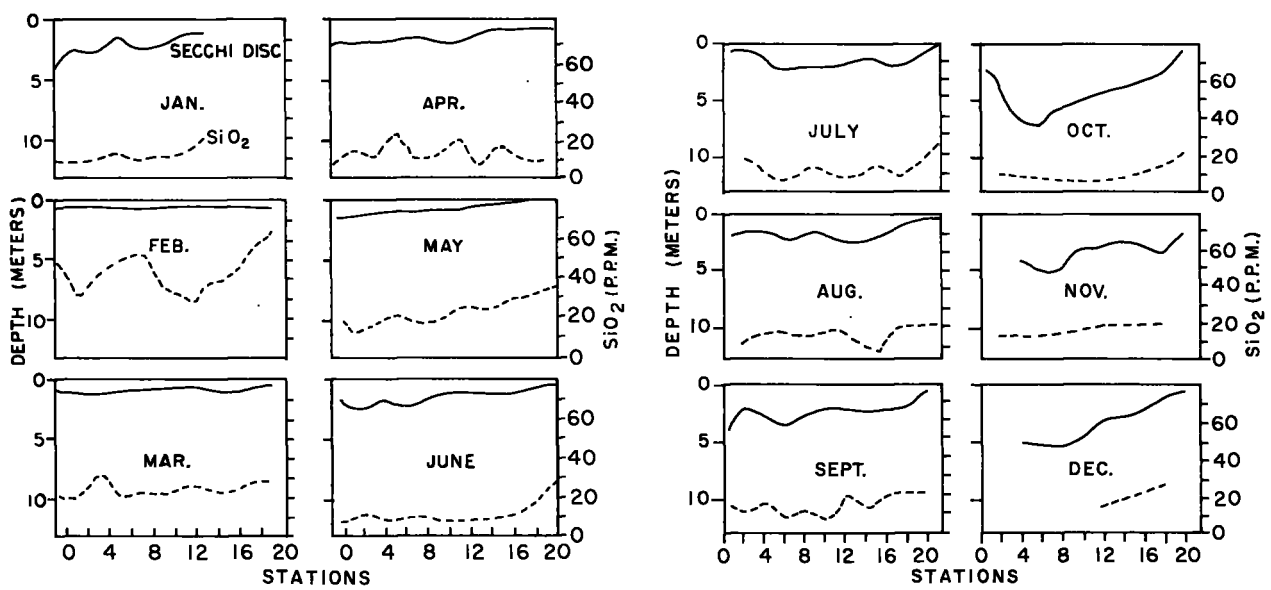

FIGURE 8.—Comparison of Secchi disc readings (solid lines) and surface silicon dioxide concentrations (broken lines) in Brownlee Reservoir, January to December 1963.

(1,000) set by Ellis (1944) as the upper limit of conditions favorable to fish life.

The range in sulfate concentrations for July 1962 to June 1964 was 2 to 69 p.p.m. The value throughout the reservoir was 15 to 50 p.p.m. during most of the year, which is considered the optimum range for aquatic life (McKee and Wolf, 1963). Sulfate concentrations were highest in the surface waters and lowest in the deeper waters during most of the year. This distribution may account in part for the lower conductivities at the lower depths mentioned earlier.

Secchi disc readings and silicon dioxide concentrations for 1963 are shown in figure 8; the readings were typically low when silicon dioxide concentrations were high. Turbidity showed an annual cycle comparable to that of total alkalinity and was greatest in February (Secchi disc 0.3–0.6 m.) during drawdown, when silt deposited in the upper reservoir was recirculated by the turbulent river inflow. Turbidity continued high throughout the spring and early summer and then gradually decreased through the fall. The highest Secchi disc readings (lowest turbidity) were in October at stations 4 and 6 (7.1 and 7.6 m.). The Snake River above Brownlee Reservoir remained turbid throughout the year; the maximum reading in the river was 0.6 m. Hence, the uppermost portion of the reservoir was always rather turbid.

Several authors have analyzed the relation between turbidity and plankton production and, hence, with fish production. Their conclusions vary depending on the characteristics of the water mass studied and on their interpretation of available data. For example, Van Oosten (1948) found no correlation, whereas Langlois (1941) indicated a high correlation. The large phytoplankton blooms on the surface of Brownlee Reservoir throughout the summer indicated that high turbidity did not seriously hinder primary production near the surface.

DIURNAL OBSERVATIONS OF LIMNOLOGICAL CONDITIONS AND CONDITIONS AT TRAP SITES

Four diurnal studies were carried out from June 1962 to June 1964 to measure fluctuations under unusual conditions during mortalities at a fingerling trap site, or to determine diurnal fluctuations at the end of winter or in late summer. Studies were made September 5 and 6, 1962, July 17 and 18, August 19 and 20, 1963, and May 12 and 13, 1964. The studies in the early spring (May 1964) and late summer (September 1962) showed that diurnal variations in temperature and water chemistry were minor. Temperatures in the reservoir in September and May did not change more than 1.1° C. Maximum change in oxygen concentration was 1.3 p.p.m. in September and 3 p.p.m. in May. Changes in concentrations of other factors were similarly minor.

The diurnal observation at a floating fish trap at station 18 was done to determine if water temperature and chemistry contributed to the high mortality of young salmon captured on July 17, 1963. Samples were taken at 1500 hours on July 18 and every 3 hours over the ensuing 24-hour period at the trap and at a point 30 m. outward from it. The samples at the two sites did not differ significantly. Water temperatures ranged from 22.1° to 23° C. at the 6-m. level and from 22.3° to 23.3° C. at the surface. Diurnal variation was 1.1° to 1.65° C. at the surface; the temperature was highest in the early afternoon. Dissolved oxygen concentrations ranged from 3.2 p.p.m. to 2 p.p.m. on the surface and from 2.1 p.p.m. to 1.6 p.p.m. at the 6-m. level. No cyclic trend in oxygen concentrations appeared. The high temperatures and the low dissolved oxygen concentrations apparently were major factors in the high mortality of captured fish. Concentrations of pH, carbon dioxide, and sulfates were suitable for survival of fish (Ellis, 1937, 1944); diurnal fluctuations were lacking.

A day-night study also was done in the Powder River arm of Brownlee Reservoir on August 19 and 20, 1963. The purpose was to determine the extent of diurnal variation in water chemistry and temperature in an area of high concentrations of algae. A series of samples was taken from the surface to the bottom at stations PR4 (PR4 located midway between PR3 and PR5) and PR5, in a relatively shallow pond at the head of the arm, and at station PR3, at midarm. Surface water temperatures varied 2.3° C. through the day-night cycle, ranging from 20.5° to 22.8° C. Diurnal fluctuation in dissolved oxygen concentrations at the three stations was high; maximum variation at the surface was at PR4, where the range was 6.8 to 14 p.p.m. Concentrations were

high in the late afternoon when algal activity was greatest. Concentration of dissolved oxygen at the surface dropped to 5.6 p.p.m. at station PR5 in the early morning hours.

Free carbon dioxide concentrations were 3.5 to 12.3 p.p.m. from 9 to 15 m. in all samples at station PR3, and no diurnal change was apparent. Hydrogen-ion concentrations ranged from 7.4 to 8.3 in the surface waters at all stations.

Additional limnological sampling was done throughout March, April, and May 1963 at sites of surface trap nets to measure limnological conditions at each trap during the peak migrations of salmon fingerlings. All sampling was during daylight, normally between 0800 and 1600 hours. Oxygen concentrations remained saturated or near saturation (8–15 p.p.m.). Water temperatures warmed gradually as the season progressed but remained favorable for fish until the end of May, when they rose to 23.9° C. All chemical determinations were within acceptable limits for fish. Samples taken at the trap sites did not differ appreciably from those taken at established stations in the same general areas of the reservoir.

CURRENTS

Continuous and instantaneous current measurements are discussed in this section as well as wind and other factors that affect surface currents. Surface currents were considered of primary importance because most of the fingerling migrants remained near the surface during the peak of the downstream migration. Surface currents were, therefore, recorded continuously to provide an accurate description during any period. Instantaneous measurements were made during five periods

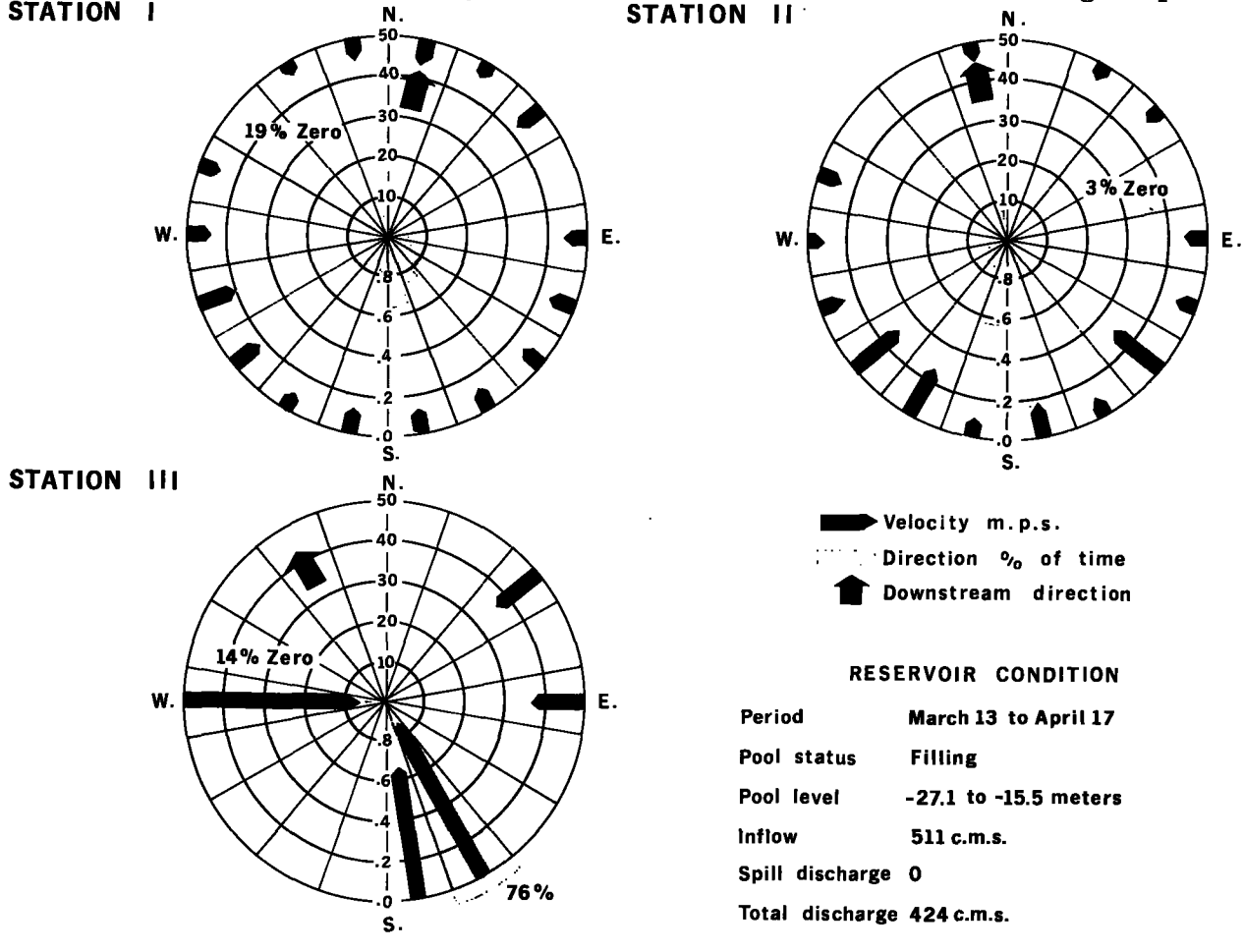

FIGURE 9.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s. scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during maximum drawdown, March 13 to April 17, 1964. Direction of current reads toward point of wedge.

at times of major changes in reservoir conditions. These periods are the same as those described under continuous recording except for the period described as fill-up at minus 20.4 m. from full pool level. The instantaneous measurements provide information on subsurface currents.

Continuous Current Measurements

The averages (percentages of time) are given for surface current direction and velocity readings (m.p.s.) recorded by continuous current recorders at three midchannel stations (station I—lower reservoir; station II—midreservoir; station III—upper reservoir) during each of five periods. These periods covered the major changes in inflow and outflow and fluctuations of reservoir level from maximum drawdown in March 1964 through fill-up in August 1964—the time of the major fingerling migration through the reservoir. All current meters were maintained at a depth of 3 m.

The terms "downstream," "upstream" (reverse), and "cross reservoir" are used throughout this section of the report to describe direction of currents. Upstream and downstream currents did not deviate more than 60° from the downstream axis; the others were cross currents.

Conditions in the reservoir include maximum drawdown, sustained minus 13.4-m. level with spill, fill-up with no spill, full pool with high spill, and full pool without spill.

Maximum drawdown.—Maximum drawdown (minus 27.1 m.) was on March 18, 1964. The mean

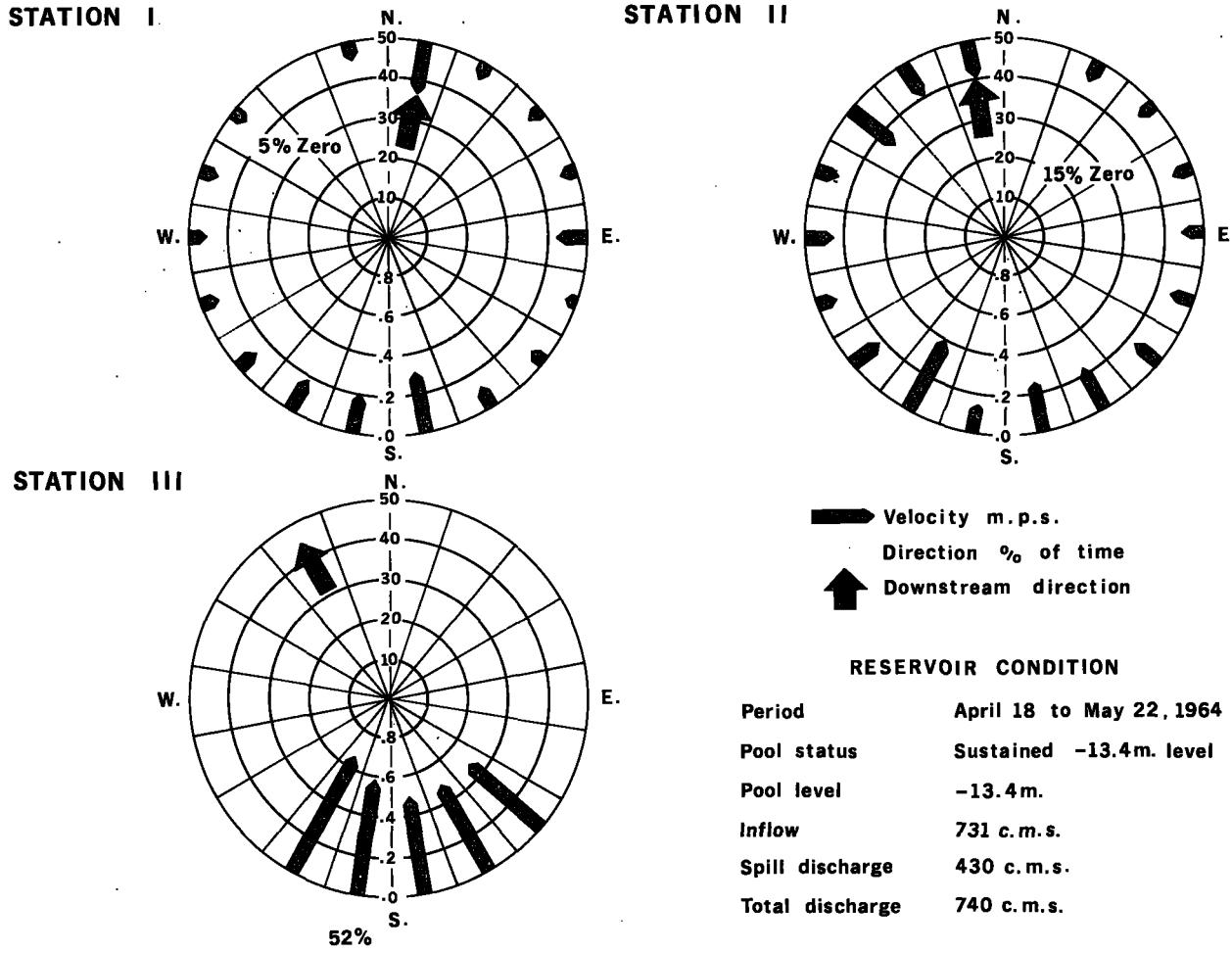

FIGURE 10.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s. scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during sustained 13.4-m. level with spill, April 18 to May 22, 1964. Direction of current reads toward point of wedge.

daily outflow (turbine discharge only) from March 13 through April 17 (fig. 9) was 424.4 c.m.s.; the average daily inflow was 511.5 c.m.s. No water was discharged through the spillway. These conditions resulted in gradual filling. Currents were well oriented downstream at stations II and III and reasonably so at station I. Downstream orientation varied from 40 percent in the lower part of the reservoir (station I) to 85 percent in the upper part (station III). Velocities ranged from zero at station I to 0.26 m.p.s. at station III.

Sustained minus 13.4-m. level with spill.—The reservoir was maintained near the minus 13.4-m. level from April 18 through May 22. The average inflow was 731.7 c.m.s., and the mean spillway discharge was 430.4 c.m.s. The rest of the inflow was discharged through the turbines at Brownlee Dam.

The percentage of downstream currents at stations I and III increased considerably over that of the previous period. Downstream orientation increased from 40 to 82.6 percent at station I and from 85 to 100 percent at station III (fig. 10). The percentage of downstream currents at station II decreased from 68 to 49 percent. Some upstream and cross-reservoir currents were also recorded at this station. Velocities ranged from 0.015 m.p.s. at station I to 0.21 m.p.s. at station III.

Averages of currents during 3 days separated by 3-day intervals over a period of decreasing discharge in 1964 are compared in figure 11.

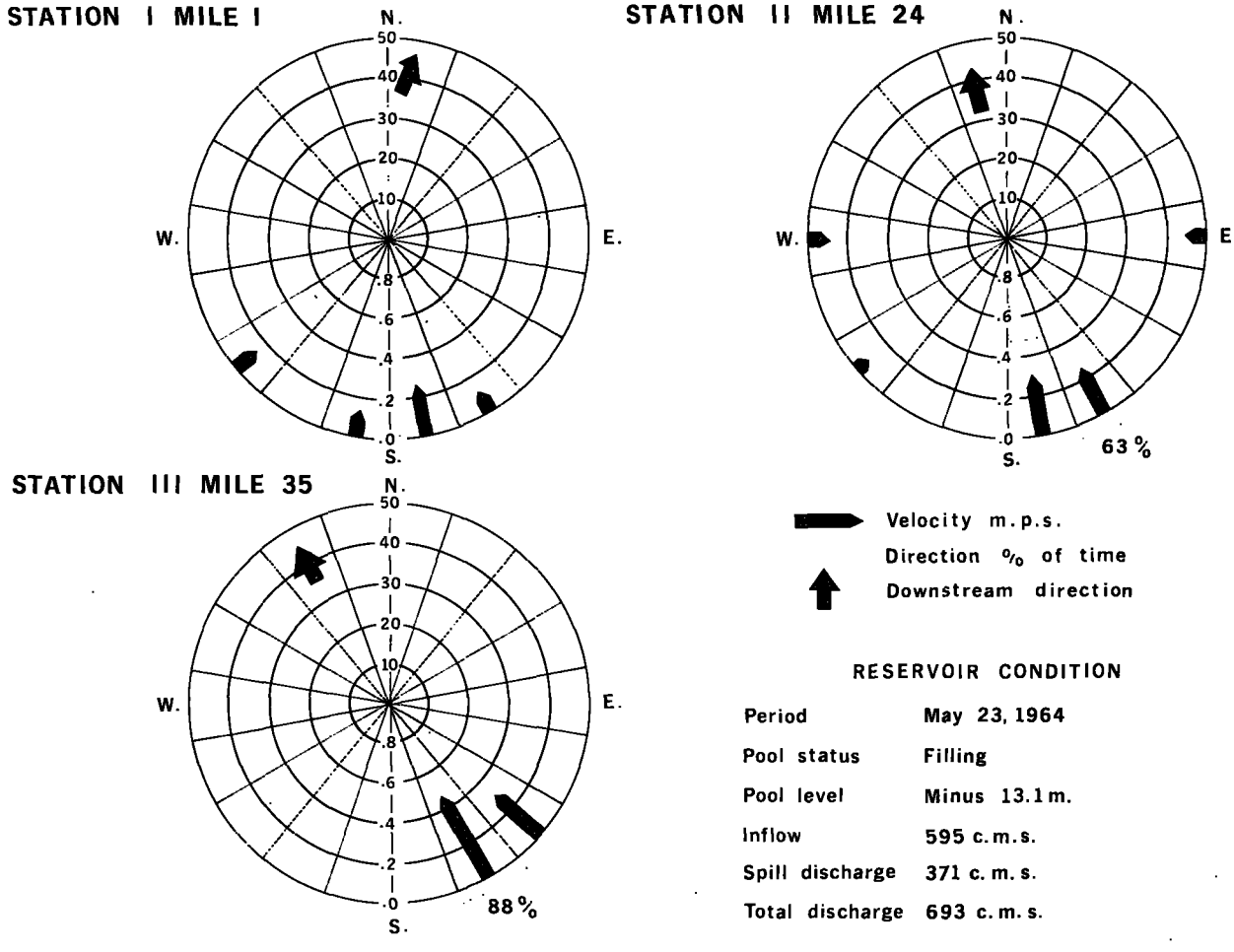

FIGURE 11.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s., scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir for three 24-hour periods during rapidly decreasing discharge at the 13.1-m. level (May 23, 26, and 29, 1944). Direction of current reads toward point of wedge.

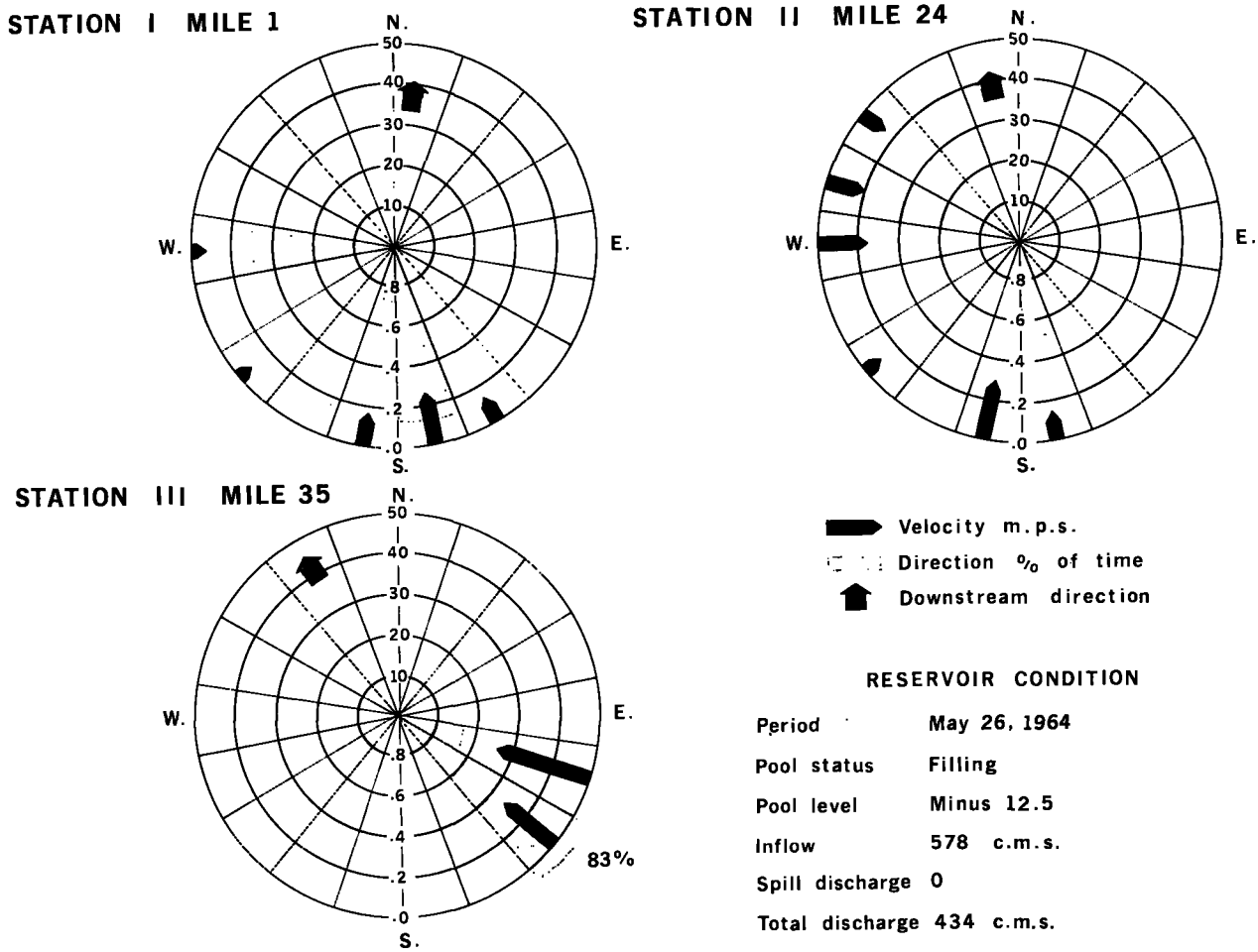

FIGURE 11.—Continued

The influence of the reduced discharge on currents is readily apparent. On May 23, a day of surface spill and high total discharge, all three stations showed nearly 100-percent downstream orientation of currents. On May 26, the spill was closed and the total discharge was reduced. Current direction at station II shifted from 88 percent downstream to about 58 percent cross reservoir. On May 29, the total discharge was reduced further. A high percentage of the currents at the downstream end and in the middle of the reservoir (stations I and II) were oriented upstream. Downstream orientation of currents at station III shifted slightly; this change may have resulted from the subsequent filling action rather than from the reduced discharge. Currents remained well oriented downstream at station III throughout the period because the reservoir is essentially river-run in this area at this level.

Fill-up with no spill.—Spilling ceased on May 26, and filling of the reservoir resumed. Figure 12 shows the weekly average current velocities and directions during fill-up from the minus 10.1- to minus 4.9-m. level. Downstream currents decreased at all three stations from those recorded during the previous period (minus 13.1 m.). Upstream currents were about as frequent as downstream currents at station I and II. Currents were still downstream 95 percent of the time at station III. Velocities ranged from zero at station I to 0.17 m.p.s. at station III. Velocity was zero 20 percent of the time at station I.

Full pool with high spill.—The currents from June 13 to 26, when the reservoir was full and a large volume of water was being discharged over the spillway, are described in figure 13.

Currents were weak and downstream orientation was lacking during filling and at full pool im-

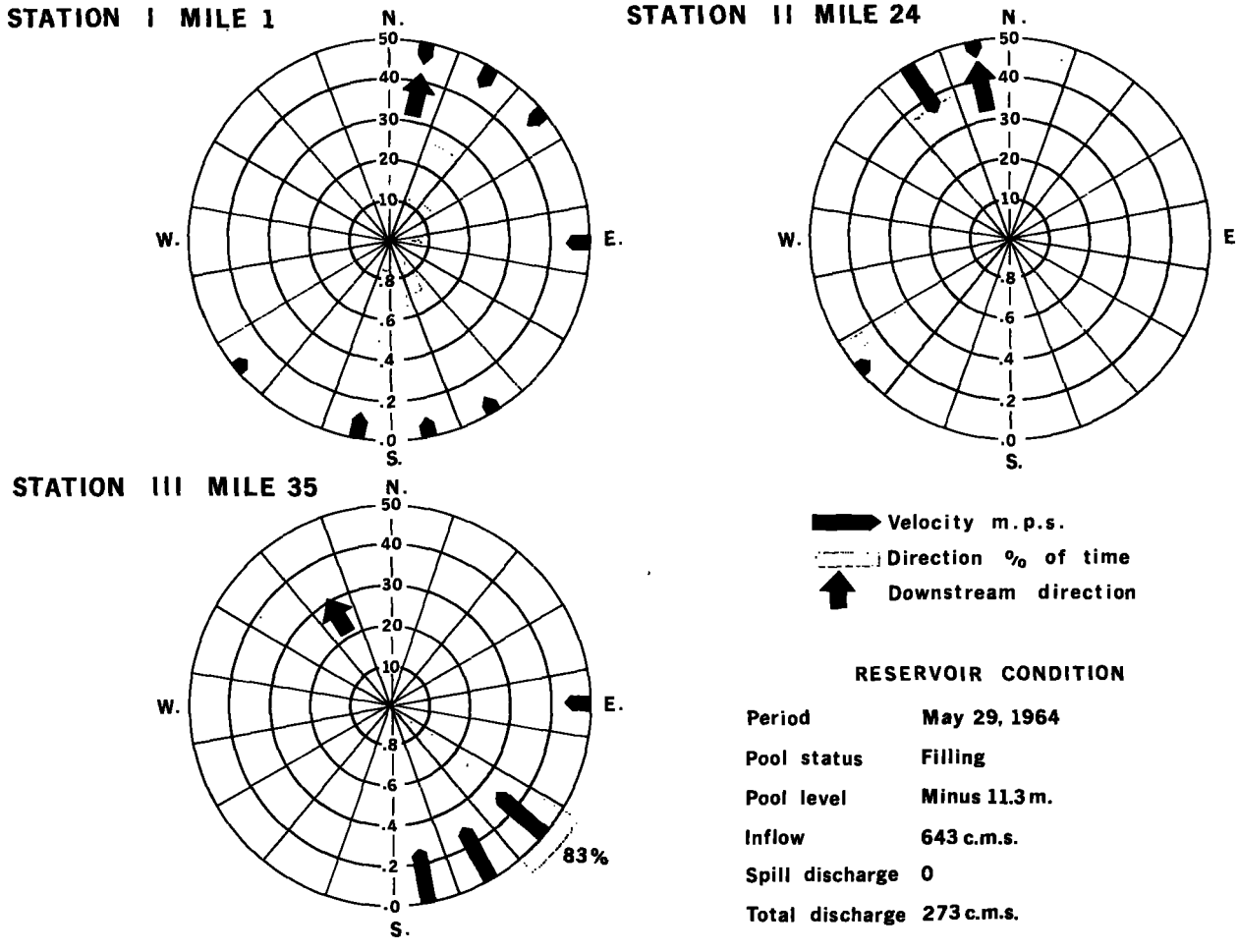

FIGURE 11.—Continued

mediately before spilling (fig. 12). Spilling began again on June 9 and by June 12 had reached about 708 c.m.s. and through June 13–26 averaged 1,013 c.m.s. This spilling caused currents at station I to be oriented downstream; currents were downstream 93 percent of the time. The percentage of zero readings (66 percent) was high at midreservoir (station II). Currents at the upper end of the reservoir were oriented downstream 49 percent of the time; water velocities here ranged from 0.07 to 0.18 m.p.s. Vertical and counter currents undoubtedly accounted for the lack of downstream orientation at the upstream end of the reservoir. Thus, for the period of high inflow and high spill at full pool, currents in the lower reservoir were well oriented in a downstream direction, but the discharge had little influence on currents at midreservoir. Velocities increased in the upper reservoir, but downstream orientation of the currents was not visibly stronger.

Full pool without spill.—The reservoir remained at full pool without spill from July 2 to August 25, 1964. The mean daily inflow was 316.2 m.p.s.; the average outflow was 312.3 m.p.s. The reservoir was thermally stratified, and the thermocline was well defined. Downstream movement of surface water was negligible—weak upstream and downstream currents were nearly equal. Current readings of zero were common at midreservoir (fig. 14).

Instantaneous Current Measurements

Instantaneous measurements of current direction and velocity at the limnological stations under the five reservoir conditions are presented. We reasoned that some knowledge of subsurface currents could be gained from these measurements and that

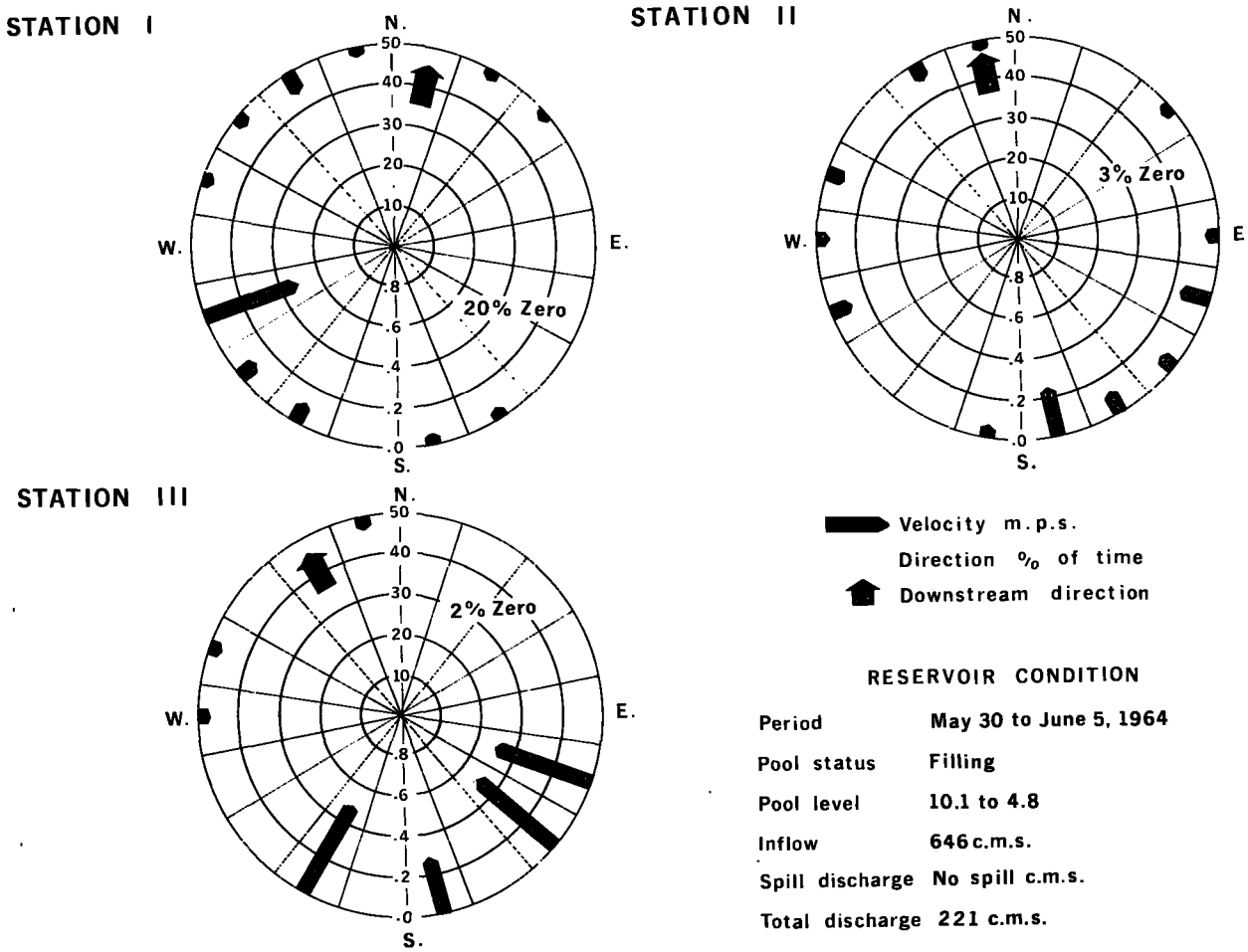

FIGURE 12.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s., scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during filling with no spill, May 30 to June 5, 1964. Direction of current reads toward point of wedge.

this information might later help us to understand the movement of juvenile salmonids.

As in the continuous current measurements, the instantaneous current measurements were made of maximum drawdown, fill-up with no spill, sustained minus 13.4-m. level with spill, full pool with high spill, and full pool without spill. The effect of wind on the currents was measured also.

Maximum drawdown.—Measurable currents were evident from surface to bottom at most stations throughout the reservoir during maximum drawdown in March 1964 (fig. 15). Velocities varied from 0.08 to 0.51 m.p.s. in the upper end of the reservoir and from 0.00 to 0.15 m.p.s. in the lower end. The direction pattern of surface currents was generally downstream, but some upstream currents were recorded below the surface.

Fill-up with no spill.—Few currents were detectable at the greater depths from station 10 downstream during fill-up in April 1964 at the minus 20.4-m. level (fig. 16). All readings at station 10 (midreservoir) were zero. Temperature data at this time indicated the start of vertical stratification. All readings in the lower end of the reservoir were less than 0.15 m.p.s.

Sustained minus 13.4-m. level with spill.—Velocity and direction were recorded in April at the minus 13.4-m. level when the spillway discharge was about 141.6 c.m.s. and when inflow was about 991.2 c.m.s. This minimal spill and increased inflow

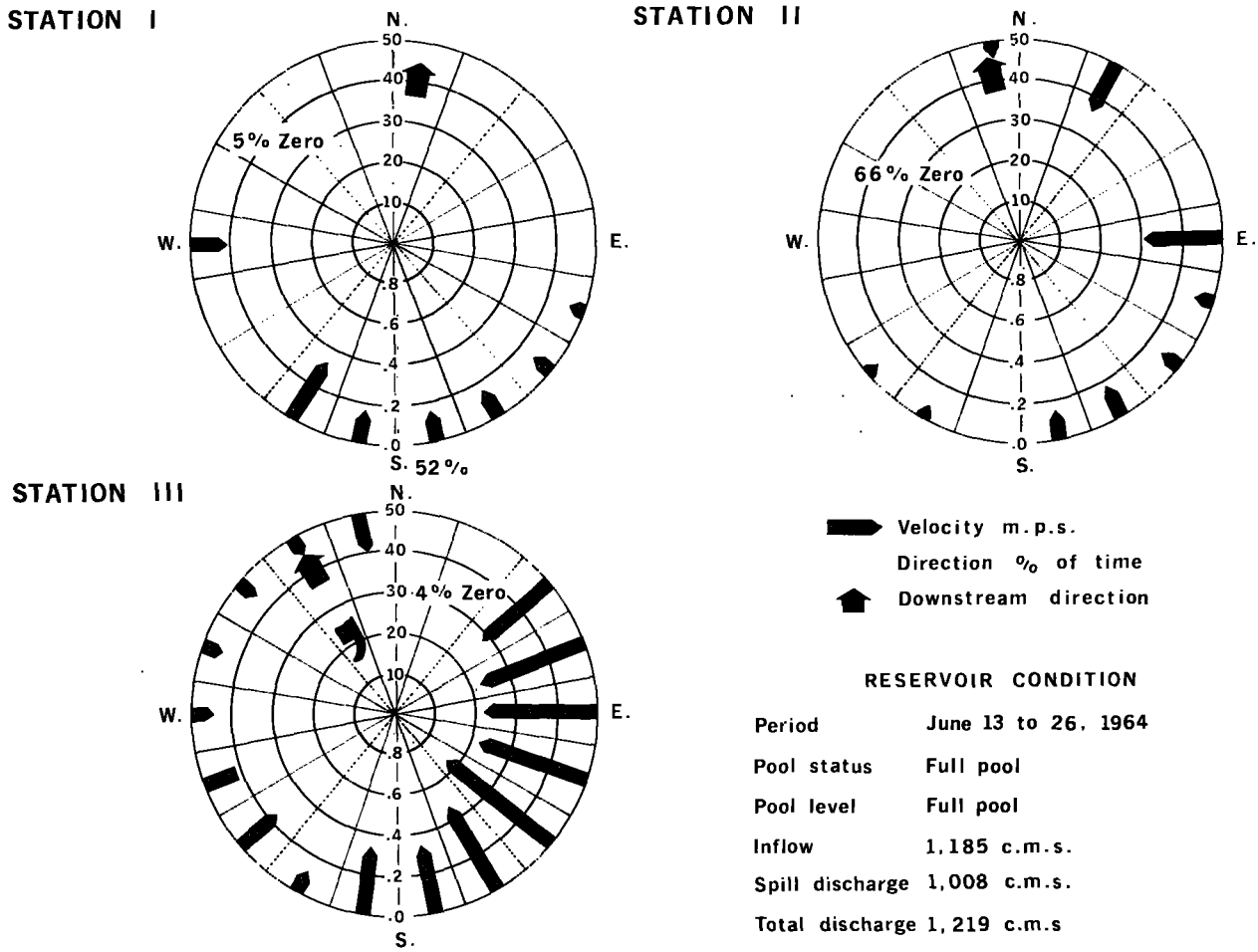

FIGURE 13.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s., scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during full pool with spill, June 13 to 26, 1964. Direction of current reads toward point of wedge.

caused measurable currents at station 10 (fig. 17), where readings from top to bottom ranged from 0.06 m.p.s. to zero. Velocities at the lower end of the reservoir still remained below 0.15 m.p.s. Generally, most currents at the surface were downstream and were measurable from station 20 to the dam.

Full pool with high spill.—Instantaneous current measurements were made again on June 24 and 25, 1964 (fig. 18), when the reservoir was at full pool and when the spill was 1,049.1 c.m.s. Currents were measurable from station 20 to the dam from the surface to 30.5 m. All readings below 38.1 m. were zero in the lower end of the reservoir. Velocities in the upper end of the reservoir ranged from 0.04 to 0.30 m.p.s.; in the lower end of the reservoir, velocities ranged from 0.00 to 0.14 m.p.s. The maximum of 0.14 m.p.s. in the lower reservoir was at the 22.9-m. depth at station 6. The direction of currents was generally downstream in the upper levels throughout the reservoir, but some upstream currents were detected in the lower levels at the upstream end.

Full pool without spill.—Instantaneous current measurements at full pool without spill began on July 1 and continued through October 1964. All data were similar to those for August 18 to 20 (fig. 19). Directions of flow at the time of thermal stratification were erratic: velocities rarely exceeded 0.08 m.p.s. even in the upper reservoir

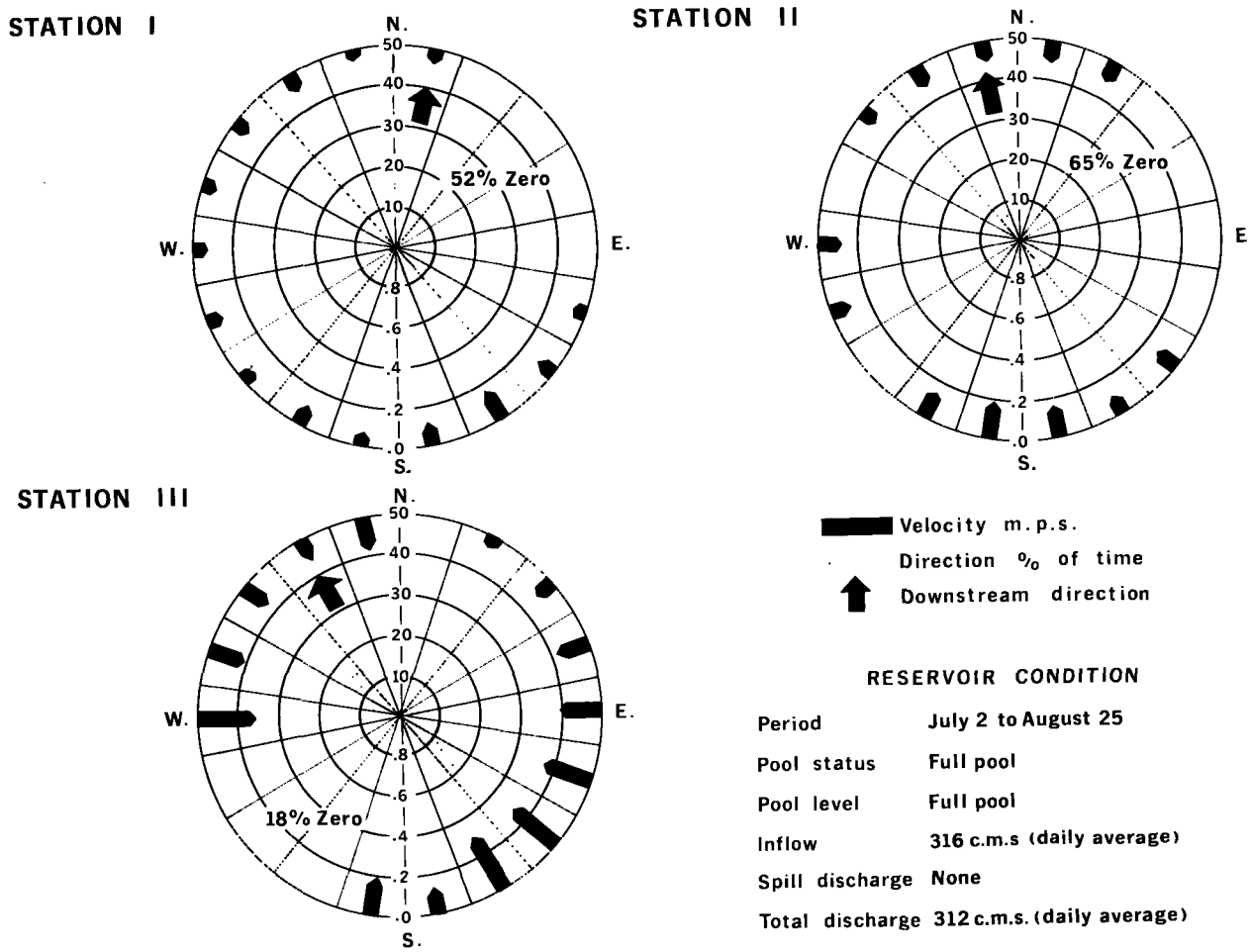

FIGURE 14.—Direction (percentage of time, indicated by scale between center and upper margin of each figure) and average velocity (m.p.s. scale between center and lower margin) of currents recorded at 3-m. depth in Brownlee Reservoir during full pool with no spill, July 2 to August 25, 1964. Direction reads toward point of wedge.

(station 20). Velocities and directions of surface currents seemed to depend primarily upon velocities and directions of the wind.

Effect of wind on currents.—The wind near station 14, measured at a set time each day, showed a trend. In contrast, the currents were recorded 24 hours. In future studies of this type, we recommend that wind direction and velocity be measured continuously along with direction and velocity of surface water current at each station so that they can be directly correlated.

Wind direction and velocity had a considerable influence on surface currents. The wind was predominantly northerly or southerly, rarely easterly or westerly (tables 4 and 5). The reservoir flows generally from south to north; thus, the primary effect of wind was either to increase or diminish the velocity of the prevailing surface currents. A wind of high velocity and relatively long duration was required to reverse a prevailing surface current of more than 0.03 m.p.s.

Wind apparently had the least effect near the head of the reservoir, where the inflow had comparatively high velocity during all reservoir stages except at full pool with low inflow. Wind had a decided effect on the lower and middle sections of the reservoir (stations I and II), where velocities rarely exceeded 0.25 f.p.s. (0.08 m.p.s.). Effects were significant at these areas during all reservoir stages except at maximum drawdown. Instantaneous sampling indicated that wind could affect measurable currents to a depth of 8 m.

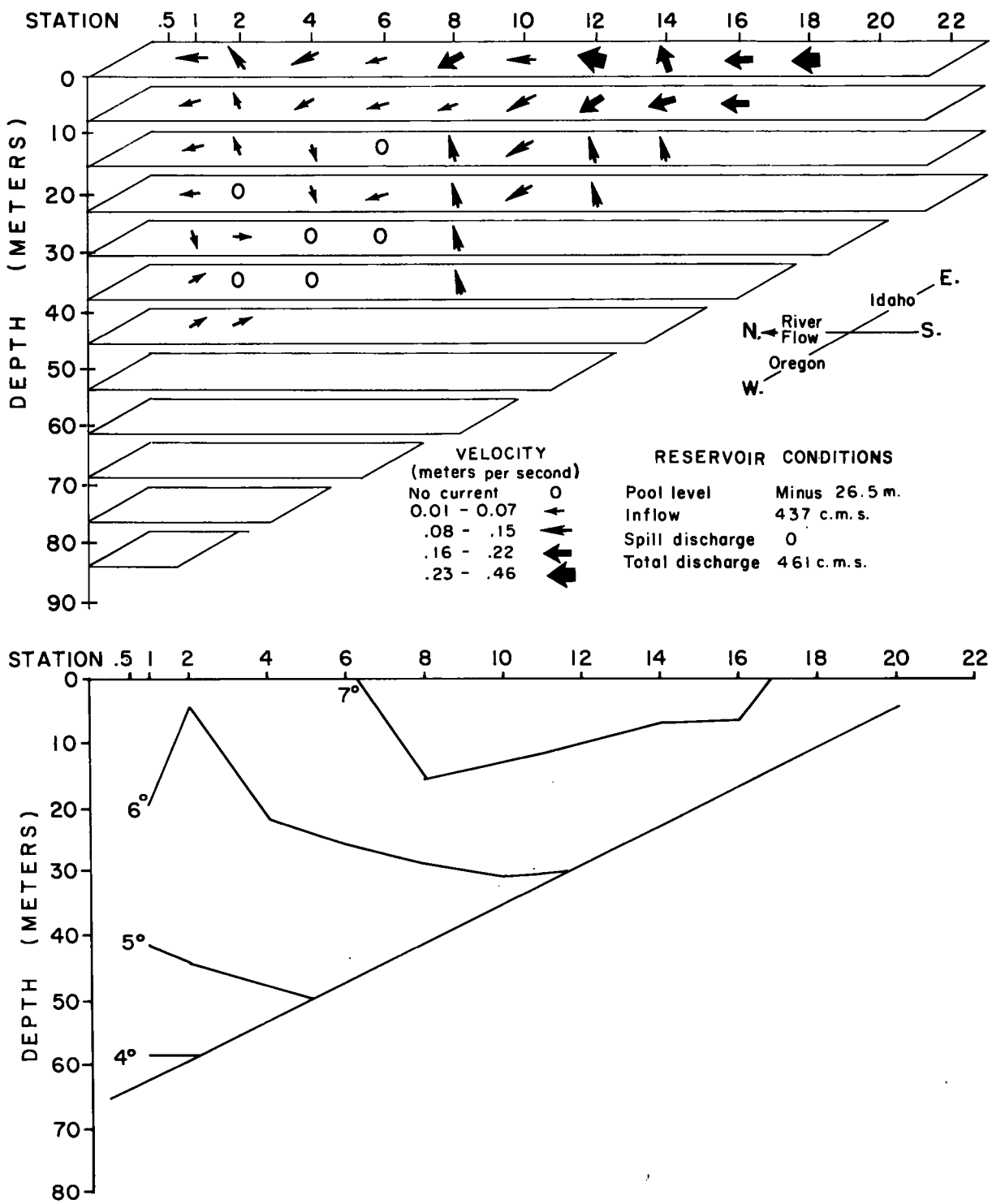

FIGURE 15.—Instantaneous current and temperature readings in Brownlee Reservoir during maximum drawdown, March 23 to 25, 1964.

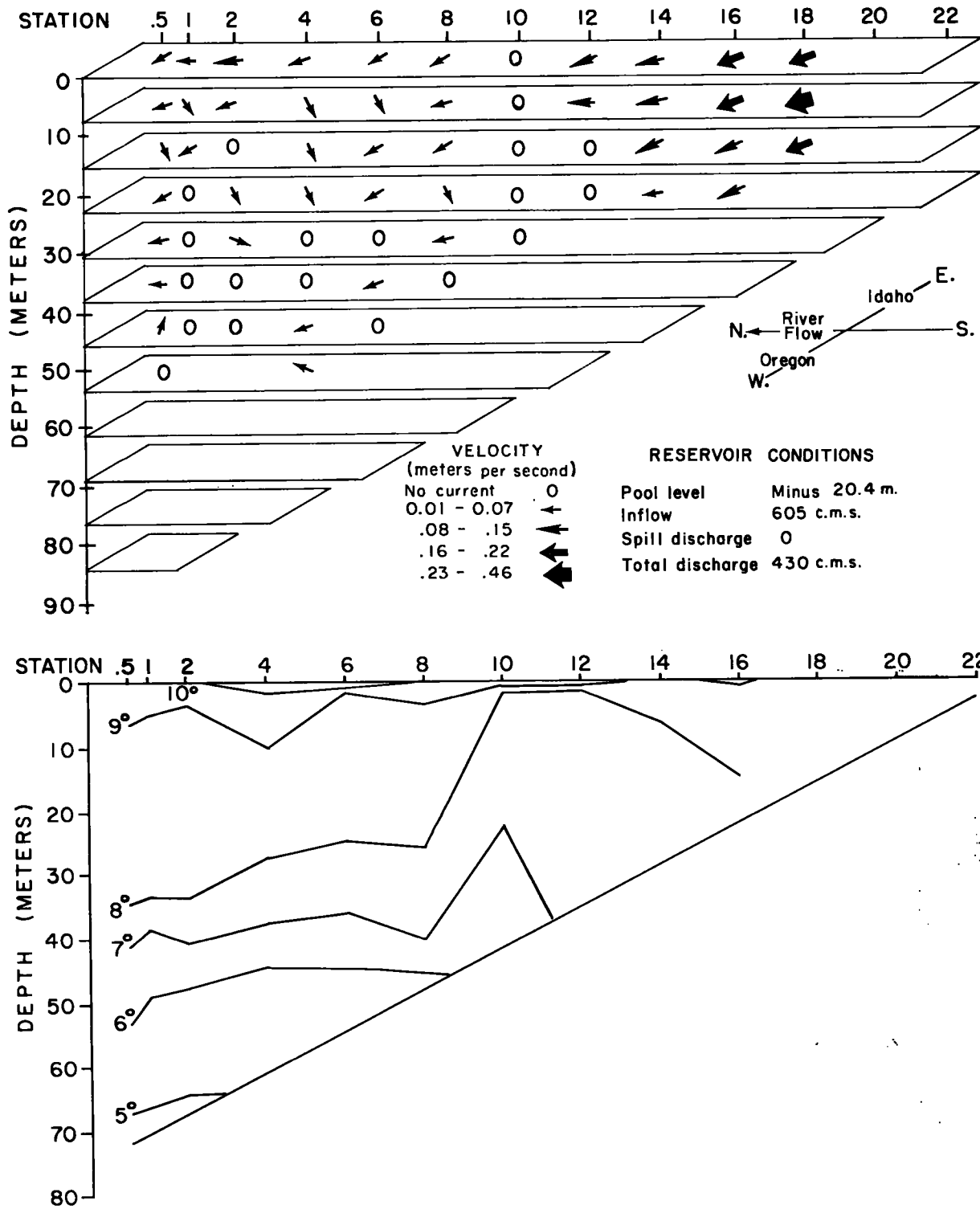

FIGURE 16.—Instantaneous current and temperature readings in Brownlee Reservoir during filling with pool at minus 20.4 m., April 7 to 10, 1964.

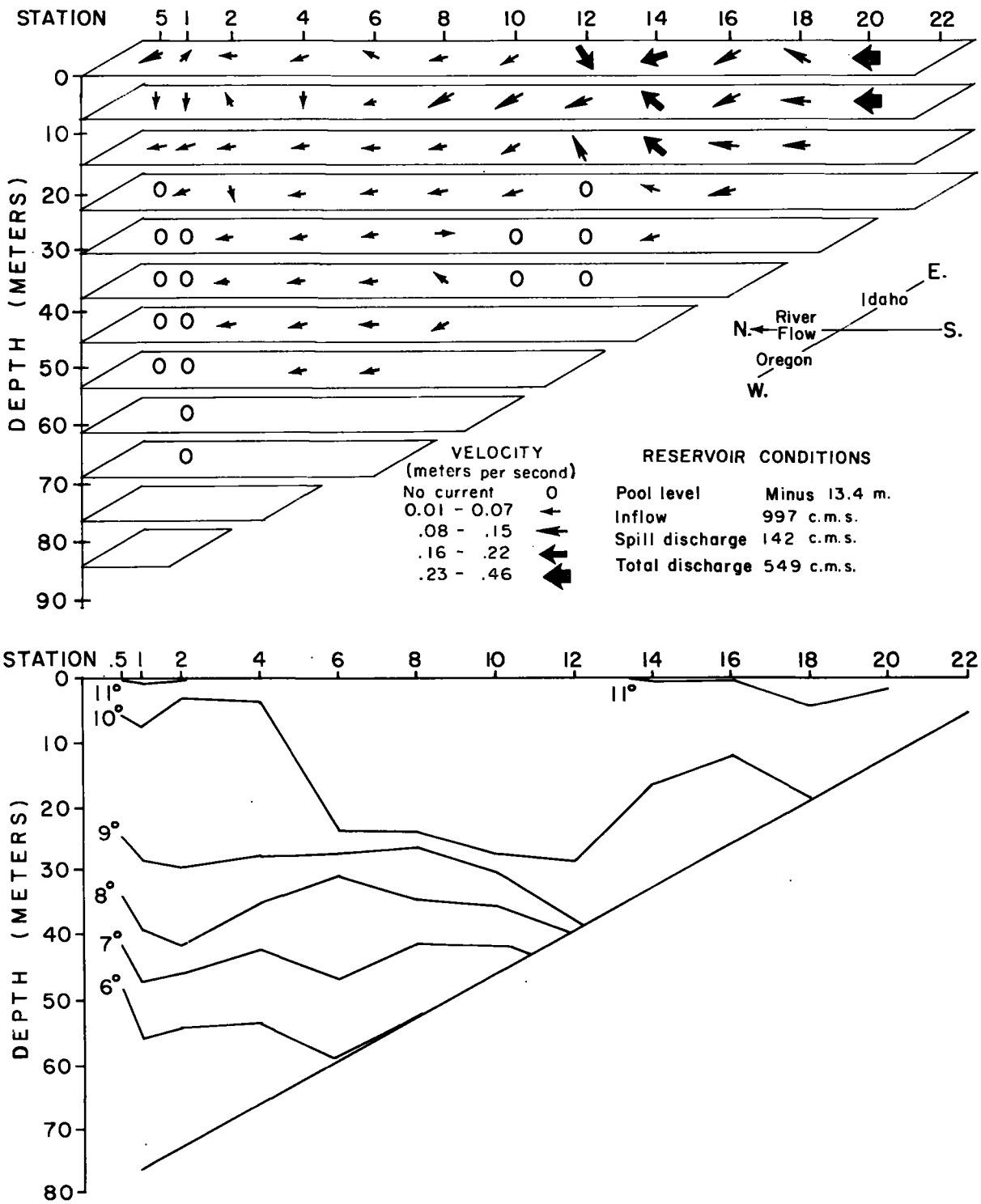

FIGURE 17.—Instantaneous current and temperature readings in Brownlee Reservoir during moderate spilling and with pool level sustained at minus 13.4 m., April 20 to 23, 1964.

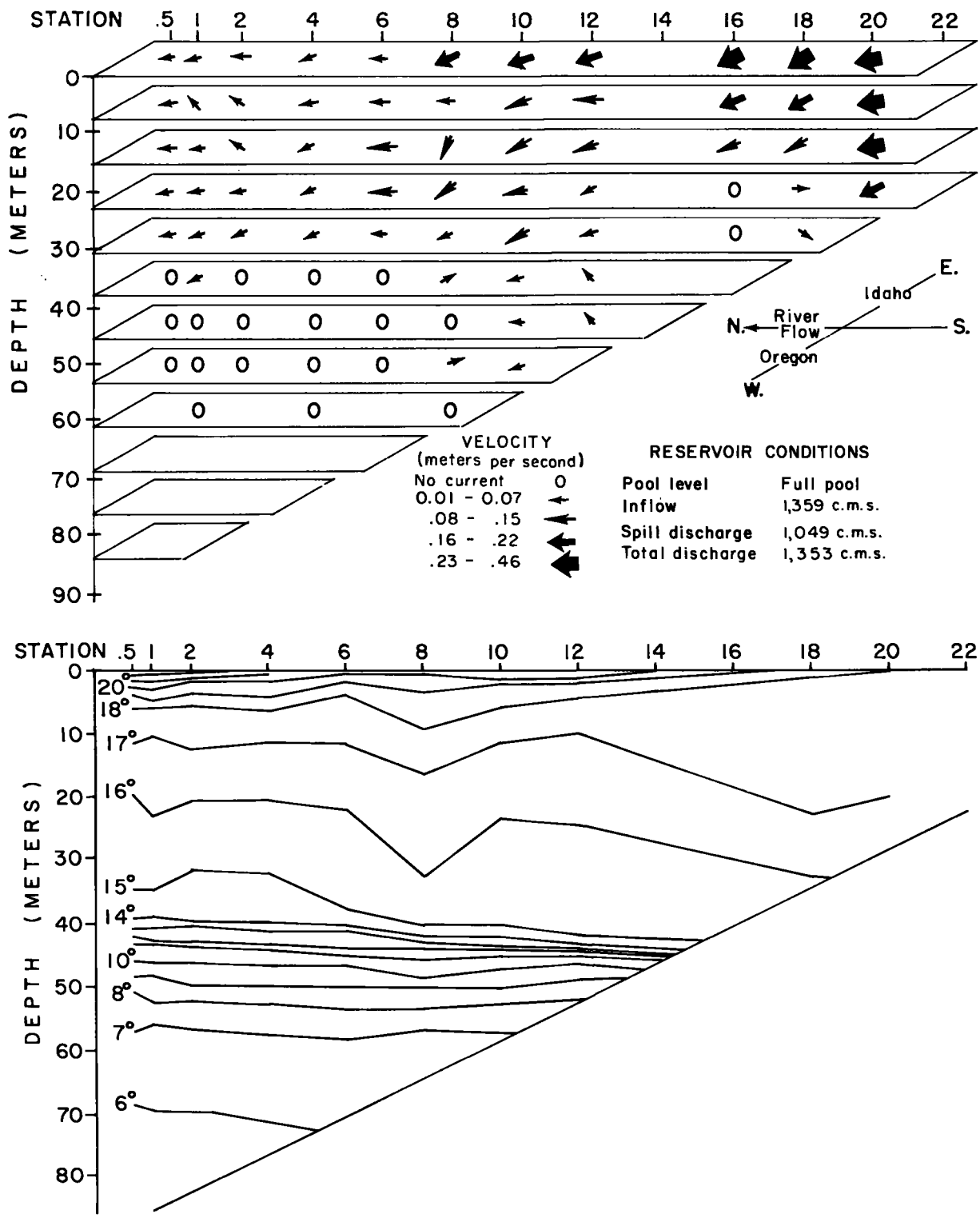

FIGURE 18.—Instantaneous current and temperature readings in Brownlee Reservoir during a heavy spill at full pool, June 24 to 25, 1964.

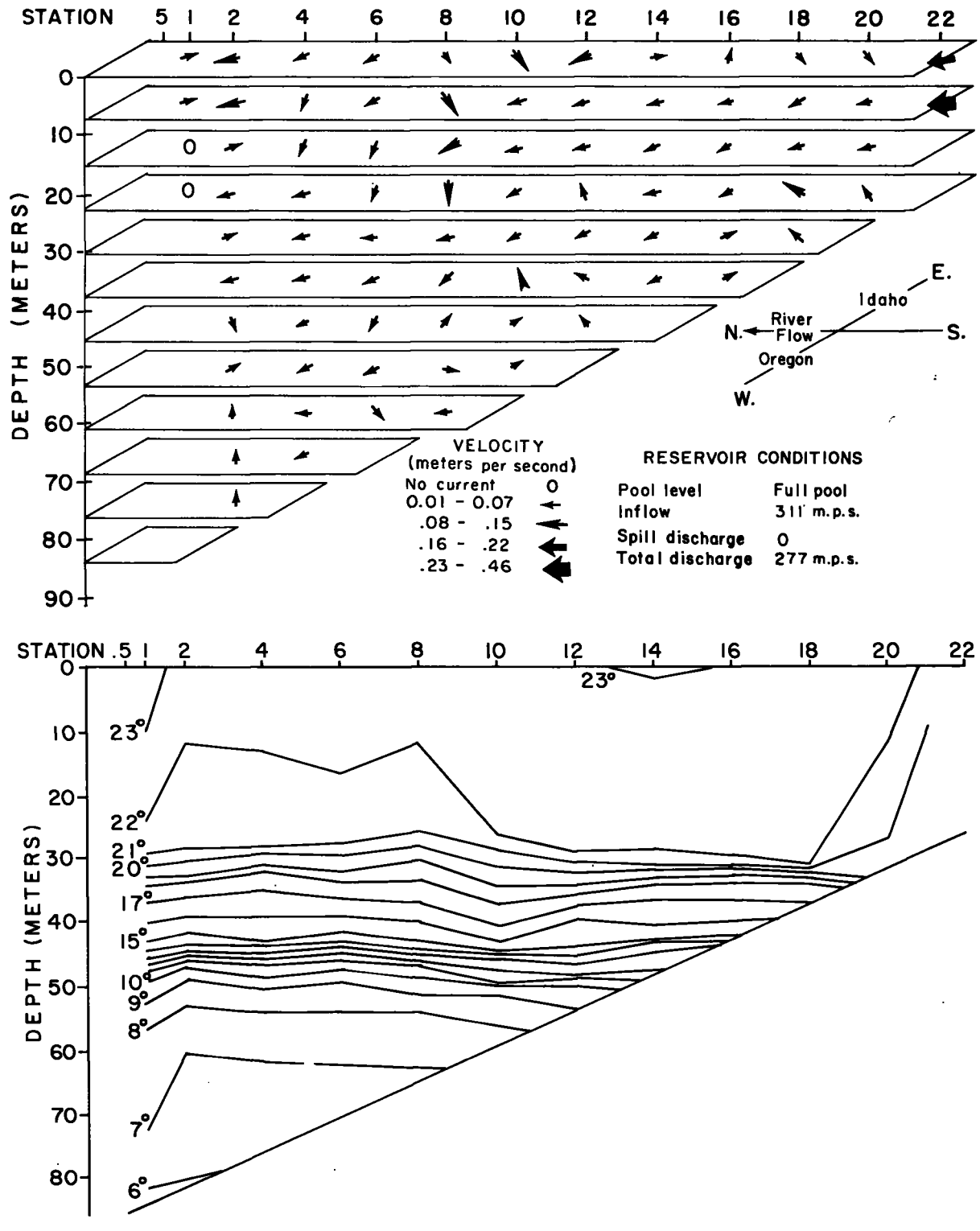

FIGURE 19.—Instantaneous current and temperature readings in Brownlee Reservoir during full pool at no spill and low discharge, August 18 to 20, 1964.

TABLE 4.—*Prevailing wind direction at station 14 during 5 reservoir stages (determined from single daily observations), March to August 1964*

Reservoir stage	Date	Wind direction		
		North	South	Calm
		Percent		
Maximum drawdown	Mar. 6–Apr. 17	36	25	39
Sustained pool minus, 13.1 m.	Apr. 18–May 22	57	17	26
Fill-up—no spill	May 30–June 5	57	0	43
Full pool—spill	June 13–June 26	50	22	28
Full pool—no spill	July 2–Aug. 25	73	2	25

Factors That Influence Surface Currents

Surface currents are highly important because most of the juvenile salmonids were near the surface upon entry into the reservoir and for some time thereafter. The primary factors that affected surface currents at the three stations were as follows:

Station I (lower reservoir)—rate of discharge and wind

Station II (middle reservoir)—reservoir drawdown, rate of discharge, and wind

Station III (upper reservoir)—reservoir drawdown and rate of river inflow

Surface currents at station I were not well oriented downstream except when the rate of discharge was increased at the spill (figs. 10, 11, and 13). Wind was the main factor affecting currents when there was no spill.

Currents at station II were well oriented downstream during two periods—maximum drawdown at minus 27.1 m. and at the minus 13.4-m. level with spill (figs. 9 and 10). During the rest of the study period, currents at station II were oriented upstream about as often as downstream. The wind again seemed to exert a disorienting influence.

Currents at station III were well oriented downstream except at full pool and at full pool with spill. Although wind seemed to be the most important disorienting factor at full pool, it had less effect on the surface currents at the upper end of the reservoir than at the middle and lower areas. Water velocities at station III were usually in excess of 0.15 m.p.s.; consequently, considerable wind was needed to alter significantly the general downstream current pattern. A wind of high velocity blowing in a reverse direction for a short time might deflect the surface current somewhat, but it would not reverse it.

The instability of currents in the upper end of the reservoir during full pool with spill and high river inflow (fig. 13) was probably due to the spill rather than to the wind. Possibly a seiche effect was created during the heavy spill, which caused strong vertical currents near the convergence line. Repeated observations of the movement of the convergence line indicated a definite shift downstream during spilling. When the convergence line moved downstream to the vicinity of the current monitor at station III, the downstream orientation of the current suffered a definite breakdown.

EFFECTS OF BROWNLEE RESERVOIR ON WATER QUALITY OF SNAKE RIVER

Temperature, dissolved oxygen, and total alkalinity were measured in 1963 at three stations along the Snake River: (1) above Brownlee Reservoir (Weiser, Idaho), (2) below Brownlee Dam (interstate bridge), and (3) below Oxbow Dam (powerhouse tailrace). The data are plotted in figure 20 to show the effect of the Brownlee-Oxbow complex on the inflowing river waters from April through December. Upstream from

TABLE 5.—*Wind velocities and direction recorded during instantaneous current measurements in Brownlee Reservoir, March to August 1964*

Station No.	Dates									
	Mar. 23–25		Apr. 7–10		Apr. 20–23		June 24–25		Aug. 18–20	
	Direction	Velocity	Direction	Velocity	Direction	Velocity	Direction	Velocity	Direction	Velocity
		km.p.h.		*km.p.h.*		*km.p.h.*		*km.p.h.*		*km.p.h.*
0.5			S	8.0	Calm		Calm		NW	6.4– 8.0
1	SE	16.1	S	12.8–14.5	S	8.0–16.1	Calm		SE	9.7–11.3
2	SW	3.2	Calm		S	8.0	Calm		S	9.7–12.8
4	Calm		NE	4.8– 8.0	N	6.4– 8.0	Calm		SE	8.0– 9.7
6	S	9.7	Calm		Calm		S	9.7–12.8	NE	16.1–20.9
8	S		Calm		Calm		S	9.7–12.8	NE	16.1–19.3
10	S	8.0–16.1	S	1.6– 3.2	NW	32.2	S	6.4– 9.7	N	12.8–16.1
12	S	8.0–16.1	SW	3.2– 4.8	NW	8.0–16.1			N	16.1–19.3
14	S	16.1	S	1.6– 3.2	NE	8.0	S	4.8– 8.0	N	6.4– 8.0
16	S	16.1	Calm		SW	3.2– 4.8	S	4.8– 8.0	N	6.4– 9.7
18	S	1.6	NE	16.1–32.2	NE	8.0	Calm		NW	4.8– 6.4
20					Calm		Calm		NW	12.8–16.1
22									W	9.7–12.8

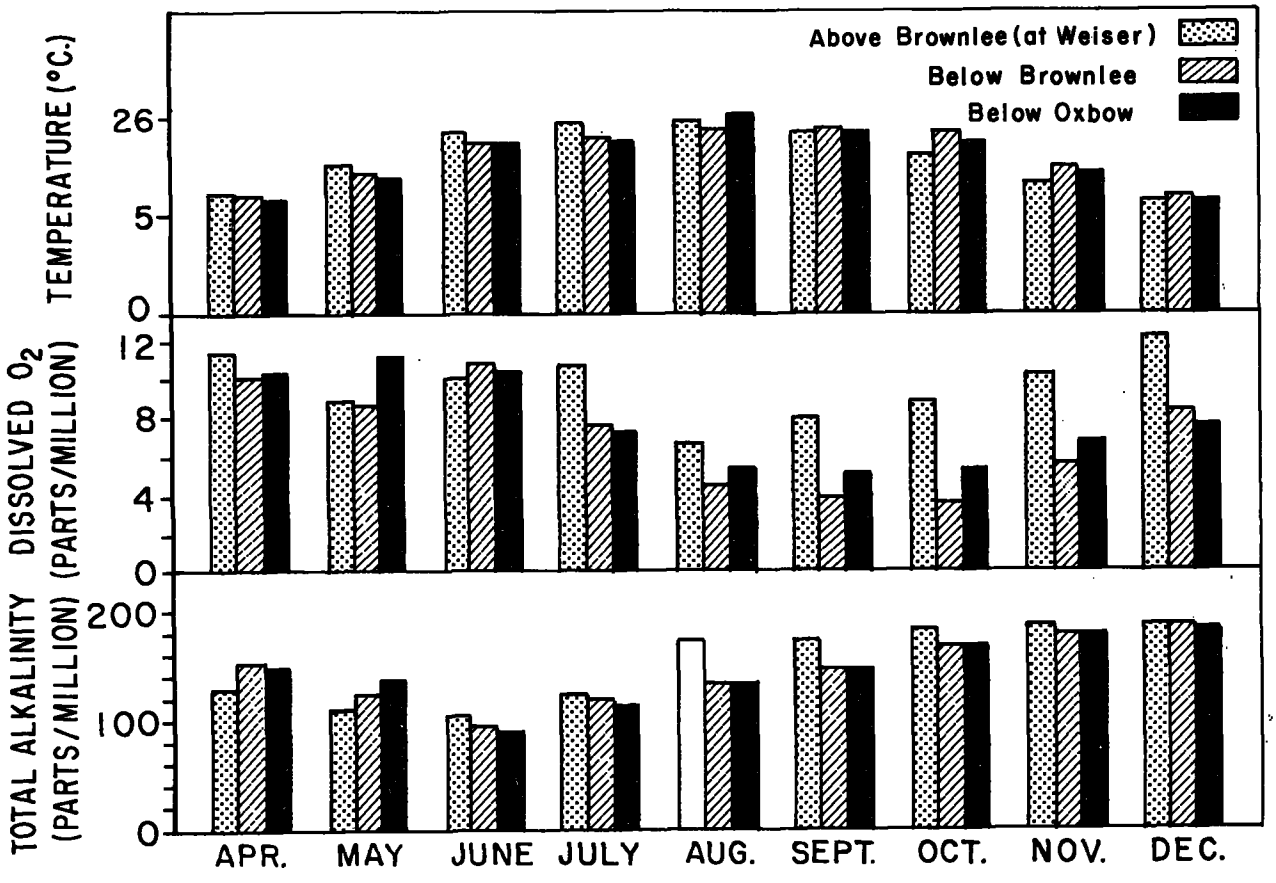

FIGURE 20.—Temperature, dissolved oxygen, and alkalinity in the Snake River above Brownlee Reservoir, below the reservoir, and below Oxbow Dam, 1963.

Brownlee Reservoir, the Snake River had a rapid increase in temperature from April through August, whereas below Brownlee and Oxbow Dams it showed a definite lag in warming. Temperatures were nearly identical at all three stations in September. The trend from October through December reversed in the spring and summer; i.e., inflowing water cooled rapidly, and outflowing water was warmer than inflowing water for several months. Outflow at Oxbow Dam was slightly cooler than that from Brownlee Reservoir; nevertheless, it remained warmer than the inflowing Snake River water.

Dissolved oxygen concentrations in the river upstream from Brownlee Reservoir remained relatively high through July 1963, declined sharply in August, and gradually increased in September. During the same period dissolved oxygen concentrations below Brownlee were much lower than those in the inflowing water except during heavy spilling discharge in June. Undoubtedly, removal of subsurface water (through turbine intakes) from oxygen-depleted layers in the reservoir caused the lower concentrations of oxygen below Brownlee Dam. Readings fell below 5 p.p.m. from August through October, a condition which approached the critical limit for survival of salmonids (Ellis, 1944), especially when these levels were accompanied by water temperatures in excess of 21.1° C. Oxygen concentrations below Oxbow Dam were somewhat higher; apparently some oxygen was restored in the Oxbow Dam area. Improvement below Brownlee and Oxbow Dam began in November, 2 months after increases in the river above Brownlee.

Measurements of total alkalinity indicated a delay in trends similar to that of temperature and oxygen. In August, the alkalinity of inflowing water increased sharply, whereas the increase in outflowing water was gradual. About 4 months

passed before alkalinity below the reservoirs reached that of the inflowing water in August. Again, the delaying effect of the reservoir is apparent.

POSSIBLE EFFECTS OF LIMNOLOGICAL CONDITIONS ON SALMON

The most important environmental factors that could affect the migration, distribution, and survival of juvenile salmonids in Brownlee Reservoir were water temperatures, dissolved oxygen concentrations, and currents.

Temperature tolerance ranges and temperature preferences of juvenile salmon have been determined by several authorities. Brett (1952) listed maximum temperatures for survival of young salmon between 23.8° and 25.1° C. Ferguson (1958) placed the temperature preference for chinook salmon (*Oncorhynchus tshawytscha*) and pink salmon (*O. gorbuscha*) at 11.7° C. Donaldson and Foster (1941) concluded that young sockeye salmon (*O. nerka*) fingerlings were barely able to maintain themselves at 21.1° C. and could not tolerate water as high as 25.5° C. for more than a few days.

Ellis (1944), McKee (1952), and Fisher (1963) discussed dissolved oxygen levels. Ellis stated that dissolved oxygen content of not less than 5 p.p.m. was favorable to a mixed fauna of food and game fish of the "warm water type." McKee indicated that a dissolved oxygen concentration of 3 p.p.m. was minimal for fresh-water fishes. Fisher found that oxygen levels were definitely correlated with growth of coho salmon (*O. kisutch*). In general, high dissolved oxygen concentrations increased growth, and low levels retarded growth.

The temperature and oxygen requirements for salmonids were not always met in Brownlee Reservoir; at times the movement of salmonids was restricted or perhaps seriously impaired. From late July through September, high surface water temperatures and low oxygen concentrations in the hypolimnion limited the survival area to a layer between 15.2 and 30.5 m., where temperatures ranged from 18.3° to 23.9° C. and oxygen fluctuated between 0 and 7 p.p.m. In some zones temperatures ranged from 12.8° to 15.5° C., but these areas were either completely void of oxygen or blocked off by water masses with no oxygen. Thus, horizontal as well as vertical distribution of salmonids was affected by temperature and oxygen. When oxygen blocks were present in the upper reservoir in late July, fish could have been forced up- or down-reservoir by serious oxygen depletion and high temperatures. Growth and survival of individuals remaining in the reservoir during August and September could have been reduced, especially in years when oxygen concentrations were extremely low and temperatures rose to nearly lethal levels. For example, oxygen and temperature were at much more critical levels for salmonids in August 1962 than in August 1963.

Alkalinities, pH, and conductivities were within acceptable limits for fish life, although conductivity and pH reached nearly critical levels at times. Sulfate and alkalinity concentrations during most of the year were suitable if not optimal for aquatic life. McKee and Wolf (1963) stated that the range in concentration of sulfate in U.S. waters that supported good game fish was 11 to 90 p.p.m. They also stated that alkalinity, when caused almost entirely by bicarbonate, did not seem to harm aquatic life. Concentrations of sulfate in Brownlee Reservoir fell within this range, and alkalinity was primarily bicarbonate.

Several authors examined the relations of total dissolved solids, total alkalinity, and conductivity to productivity; most of them found a positive correlation. Northcote and Larkin (1956) indicated, in their study of 100 British Columbia lakes, that total dissolved solids were the most important factor in determining the general level of productivity. Lakes with the highest productivity had total dissolved solids in excess of 100 p.p.m. At the time of one study, the total dissolved solids of Brownlee Reservoir were well in excess of 100 p.p.m. Even though sufficient nutrients were apparently available for high productivity, critical values of temperature and oxygen during midsummer tended to restrict the growth and movement of salmonids in Brownlee Reservoir.

Two of the diurnal studies showed variations in temperature and oxygen concentrations that probably influenced vertical movements of salmonids. Variations in temperature amounted to 1.65° and 2.2° C. in 24-hour periods during July and August 1963, when variations in oxygen concentrations also were significant. Cooling of the surface waters in the evening and early morning may have enabled salmonids to move toward the

surface. Oxygen depletion at the lower depths also may have induced them to move toward the surface.

Diurnal studies in the spring and fall did not show significant variations in either temperature or chemical characteristics of water that might have noticeably affected the movement or behavior of fish. In general, the environment in Brownlee Reservoir was suitable for juvenile salmonids in the spring, winter, and late fall, but marginal during the late summer and early fall.

Movements of salmonids were affected by currents during drawdown and periods of increased inflow and outflow. The maximum effect came during maximum drawdown when current velocities were highest and direction was strongly oriented downstream. Laboratory experiments by Gregory and Fields (1962) indicated that juvenile coho and chinook salmon showed significant responses to currents with a velocity as low as 0.0039 m.p.s.

Studies at Brownlee Reservoir showed that the direction of water currents significantly influenced the passage of young salmonids. This finding was substantiated by analyses of changes in water current and subsequent changes in success of passage by juvenile migrants.[3]

The most obvious downstream orientation of currents was at maximum drawdown, minus 27.1 m., and at minus 13.4 m. at high inflow and outflow. Conversely, the downstream current was weakest at full pool. Studies by Durkin and Park [4] on rates of movement and by Sims [5] on escapement of juvenile salmonids indicated that passage through the reservoir was more successful in the spring of 1964 than in the two previous springs. In 1964, two favorable conditions existed: (1) a fairly high river inflow and (2) relatively low reservoir level throughout most of the downstream migration period. Conceivably, then, fingerlings would have greater success in passing through reservoirs of this type if it were possible to create conditions similar to those described without inflicting heavy financial loss to power companies or greatly interfering with water conservation and irrigation practices.

Fall chinook salmon are the most likely of adult migrant salmonids to be affected by the reservoir environment. Water temperatures below Oxbow Dam during peak migration were 2.7° to 4.9° C. higher than corresponding temperatures in the Snake River above the impoundments. At the same time, dissolved oxygen concentrations below Brownlee and Oxbow Dams were considerably lower than concentrations in the inflowing water above these reservoirs. The combination of these two conditions could place additional stress on adult migrants during fall.

SUMMARY AND CONCLUSIONS

Studies of the physical and chemical limnology of Brownlee Reservoir in relation to migrations of salmon began in July 1962 and continued through October 1964. Sampling stations were established throughout the reservoir, above and below the reservoir, and in the main tributaries. Factors studied were water temperature and chemistry, turbidity, weather, river inflow and outflow, and currents.

Temperatures and oxygen concentrations in the spring, late fall, and winter were suitable for salmonids. On the other hand, excessively high epilimnial temperatures (up to 27.2° C.) and dangerously low oxygen concentrations (0–4 p.p.m.) prevailed in August and September. Salmon were forced to occupy a relatively marginal area for survival. Trends in oxygen concentration and temperature in the epilimnial layer of the upper end of the reservoir were significantly influenced either by large volumes of water entering from the Snake River and tributaries or by large discharges at the dam.

A thermocline or metalimnion developed each year. The formation was accompanied by severe oxygen depletion in all areas below the epilimnion. The thermocline was formed fully 2 months earlier in 1963 than in 1962. Time of formation appeared to depend more on the extent of the drawdown and timing of the filling period than on air temperature and volume of water entering the reservoir. A substantial drawdown (minus 12.2 m.) followed by a prolonged filling period delayed formation of the thermocline in 1962, whereas a minimal drawdown (minus 6.1 m.) accompanied with rapid filling accelerated the formation in 1963.

[3] Durkin, Joseph T., and Donn L. Park. Behavior of juvenile salmonids in Brownlee Reservoir. Bureau of Commercial Fisheries, Fish-Passage Research Program, Seattle, Wash. [Manuscript in preparation.]

[4] See footnote 3.

[5] Sims, Carl W. Escapement of juvenile salmonids from Brownlee Reservoir. Bureau of Commercial Fisheries, Fish-Passage Research Program, Seattle, Wash. [Manuscript in preparation.]

An oxygen block appeared in early summer at the upper end of the reservoir in 1962. No distinct block was recorded in 1963, but some oxygen depletion was detected in the same areas.

Changes in temperature and oxygen concentrations were significant during 24-hour sampling periods in July and August. These changes could have influenced diurnal vertical movements of salmonids. Diurnal changes in temperature and oxygen concentrations were not significant during spring and fall.

Carbon dioxide, silicates, sulfates, hydrogen-ion concentration, conductivity, alkalinity, and turbidity were within acceptable limits for fish life, although hydrogen-ion concentrations and conductivity reached nearly critical values at times.

Continuous recordings of surface currents in 1964 indicated that downstream orientation of currents and current velocity changed significantly during five reservoir stages: (1) maximum drawdown, (2) minus 13.4-m. level with high inflow and outflow, (3) fill-up without spill, (4) full pool with heavy spill, and (5) full pool without spill. The conditions of currents for downstream movement of salmonids were best during maximum drawdown and at the minus 13.4-m. level with high inflow and outflow.

Instantaneous measures of current velocity and direction indicated that current velocities increased throughout the reservoir at a maximum drawdown of 27.1 m.; measurable velocities were detected at most depths from the upper to the lower end of the reservoir. Velocities decreased and current directions became erratic during fill-up. Significant spills at the dam increased currents and changed direction of the flow in the upper levels throughout most of the reservoir during April and June 1964.

Wind velocities influenced surface currents in the lower and middle reservoir. The effect of wind was strongest at midreservoir, where current velocities were lowest. A strong wind of 32 km.p.h. or more could reverse the direction of the surface current at all sections of the reservoir.

Brownlee Reservoir significantly affected the temperatures and oxygen concentrations of the Snake River below the reservoir. Temperatures below Brownlee Dam were about 5° C. higher than temperatures in the river above the reservoir during October. Conversely, oxygen concentrations below the dam were 5 p.p.m. lower than in the inflow. These conditions were reversed in June and July. In general, the reservoir had a buffering effect on temperatures, oxygen concentrations, and alkalinity.

The main conclusions bearing on movements of salmon were:

1. Temperatures, oxygen concentrations, and currents are the most critical of the environmental factors that can affect the distribution and survival of salmon in Brownlee Reservoir.

2. Environmental conditions for salmon at Brownlee Reservoir are suitable, if not optimal, in the spring, late fall, and winter. Growth, movement, and survival of resident juvenile salmon during the late summer and early fall can be seriously restricted.

3. Diurnal physical and chemical changes are not sufficient to cause any radical change in the behavior of salmon during the spring and fall. Diurnal variations in the summer, however, can significantly influence vertical movements of salmon within a 24-hour cycle.

4. Surface and subsurface currents are significantly affected by changes in reservoir level and volumes of inflow and outflow. These changes can influence success in passage of juvenile salmon.

5. Brownlee Reservoir alters the water quality of the Snake River below the dam in the spring and fall. These changes are of particular importance to adult fall-run salmon migrants because the reservoir at this time not only delays the cooling cycle of the river but also lowers the oxygen content to nearly critical levels for salmon.

ACKNOWLEDGMENTS

John R. Donaldson, Oregon State University, critically reviewed this paper. The U.S. Department of the Interior Geological Survey and Idaho Power Company provided data on Snake River flows. Donald Montgomery, project leader of this study in 1962, provided the data for that year.

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CHANGES IN ABUNDANCE OF THE GREEN CRAB, *CARCINUS MAENAS* (L.), IN RELATION TO RECENT TEMPERATURE CHANGES

BY WALTER R. WELCH, *Fishery Biologist*

BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY

W. BOOTHBAY HARBOR, MAINE 04575

ABSTRACT

Trap catches, shore surveys, and fishermen's reports demonstrated that declining abundance of green crabs in northern New England was associated with particularly cold winters and a cooling trend in the water. Since the mid-1950's, the once great abundance of green crabs in northeastern Maine has declined to a scarcity or total absence. Abundance in southwestern Maine and in Massachusetts has fluctuated widely, and moderate abundance in Rhode Island decreased consistently through 1959.

Mass mortalities of green crabs in winter coincided with periods of severe cold. The general abundance and commercial catch of the soft-shell clam (*Mya arenaria*), a common prey of the green crab, increased markedly during the period of decline of the crabs.

Although the decrease in abundance of green crabs is clearly associated with lower temperatures, the relation is not necessarily direct; there are a number of ways in which low temperature, in combination with lowered salinity, low dissolved oxygen, and other unidentified factors, may affect abundance.

The green crab, *Carcinus maenas* (L.), has undergone major changes in abundance and distribution along the northeast Atlantic Coast since the late 1800's. Scattergood (1952) traced the spread of the species northward to Casco Bay in southwestern Maine by the early 1900's, to scattered localities in central Maine by the late 1930's, and finally into far northeastern Maine and New Brunswick by 1951. He concluded that green crabs, if present at all in northeastern Maine, were scarce in 1939–42. Glude (1955) narrowed the period of greatest increase of green crabs along the Maine Coast to 1948–51 and recorded their spread to Wedgeport, Nova Scotia, by 1954 (fig. 1). The Fisheries Research Board of Canada (1961) reported that the species had extended its range as far east as Lockeport, Nova Scotia, 64 km. beyond Cape Sable.

The green crab is of minor commercial importance as bait for sport fishermen south of Cape Cod. A limited fishery in Maine, New Hampshire, and Massachusetts supplies this market.

The major interest in the species in the United States lies in its importance as a predator. Dow and Wallace (1952) pointed out the significance of the green crab as a predator on the soft-shell clam (*Mya arenaria*). Glude (1955) and MacPhail, Lord, and Dickie (1955) presented evidence to show the seriousness of predation by green crabs on clams in Maine, New Brunswick, and Nova Scotia.

The purposes of this paper are to document changes since the peak of abundance in the mid-1950's and to relate these changes to concurrent changes in temperature.

SOURCES OF INFORMATION

I have used data from three sources: (1) Records of surface sea-water temperature kept at Boothbay Harbor from 1905 through 1967; (2) estimates of the abundance of green crabs and soft-shell clams by biologists, wardens, and fishermen; and (3) quantitative sampling of green crab populations.

RECORDS

Records of surface sea-water temperature were kept at the BCF Biological Laboratory, Boothbay Harbor, Maine, from 1905 through 1967. From 1905 through 1949, thermometer readings were made thrice daily at the station wharf. From 1950 on, instruments have recorded the temperature, sensed at 1.68 m. below mean low water. Infrequent gaps in the recorded data were filled in from temperatures read in flowing water tanks. Daily, monthly, and annual means were derived from the three daily thermometer readings and hourly readings from the recordings. Figure 2 shows the

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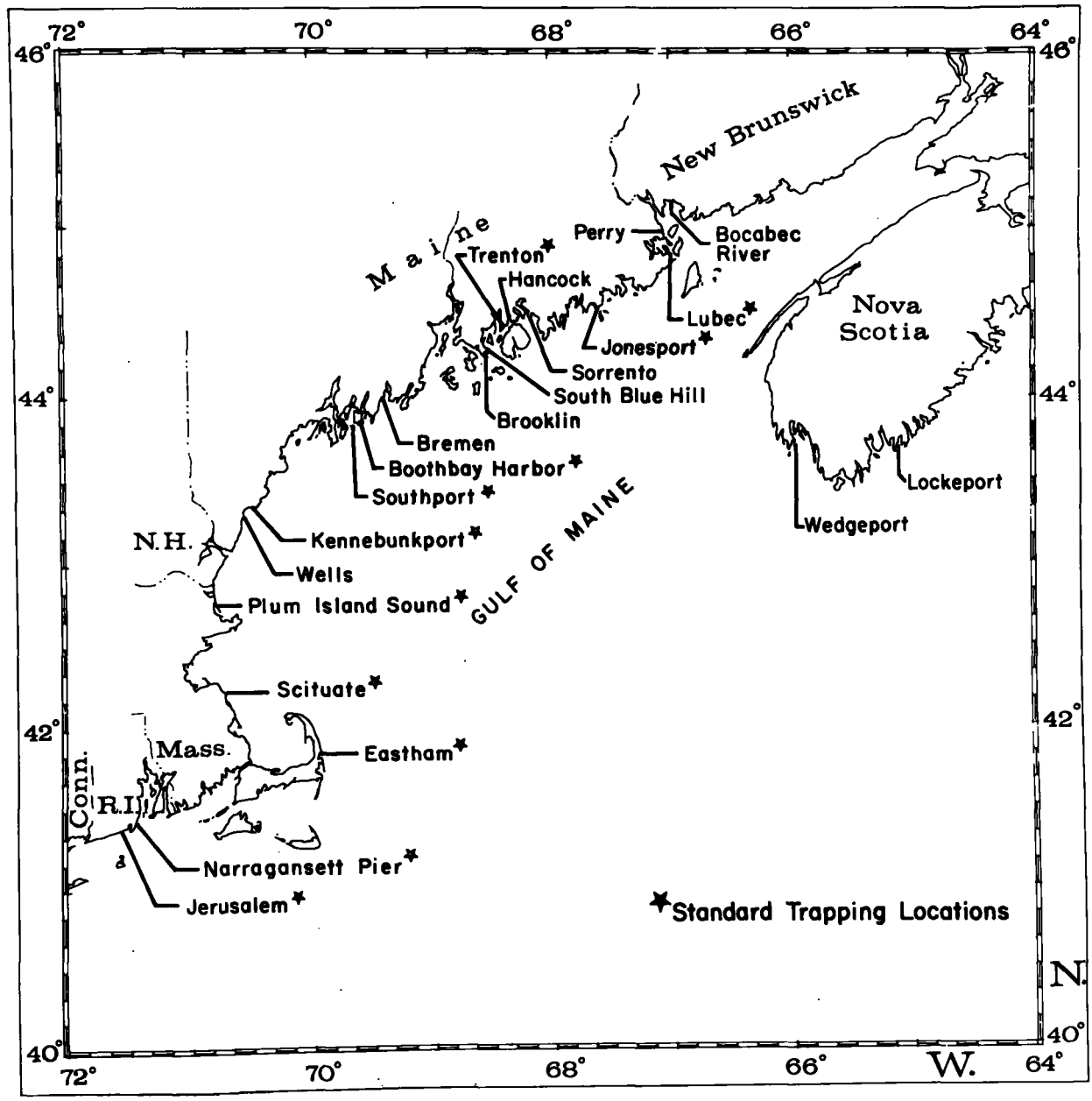

FIGURE 1.—Location of trapping sites and other areas mentioned in text.

annual means and means for the coldest month of each year.

ESTIMATES

Estimates of the abundance of green crabs and soft-shell clams from the early 1920's to 1951 were obtained from two sources. First, F. E. Goucher, the Clam Commissioner of Essex, Mass., who dug clams for over 22 years, wrote of his own and other fishermen's observations in northern Massachusetts.[1] Second, about 100 coastal wardens and fishermen were interviewed in cooperation with the Maine Department of Sea and Shore Fisheries. Their recollections applied to Maine, but the information reported for southwestern Maine agreed well with that of Goucher (see footnote 1) for northern Massachusetts.

[1] Goucher, Franklyn E. 1951. Commentary of a clam digger. Unpublished manuscript on file at the BCF Biological Laboratory, Boothbay Harbor, Maine.

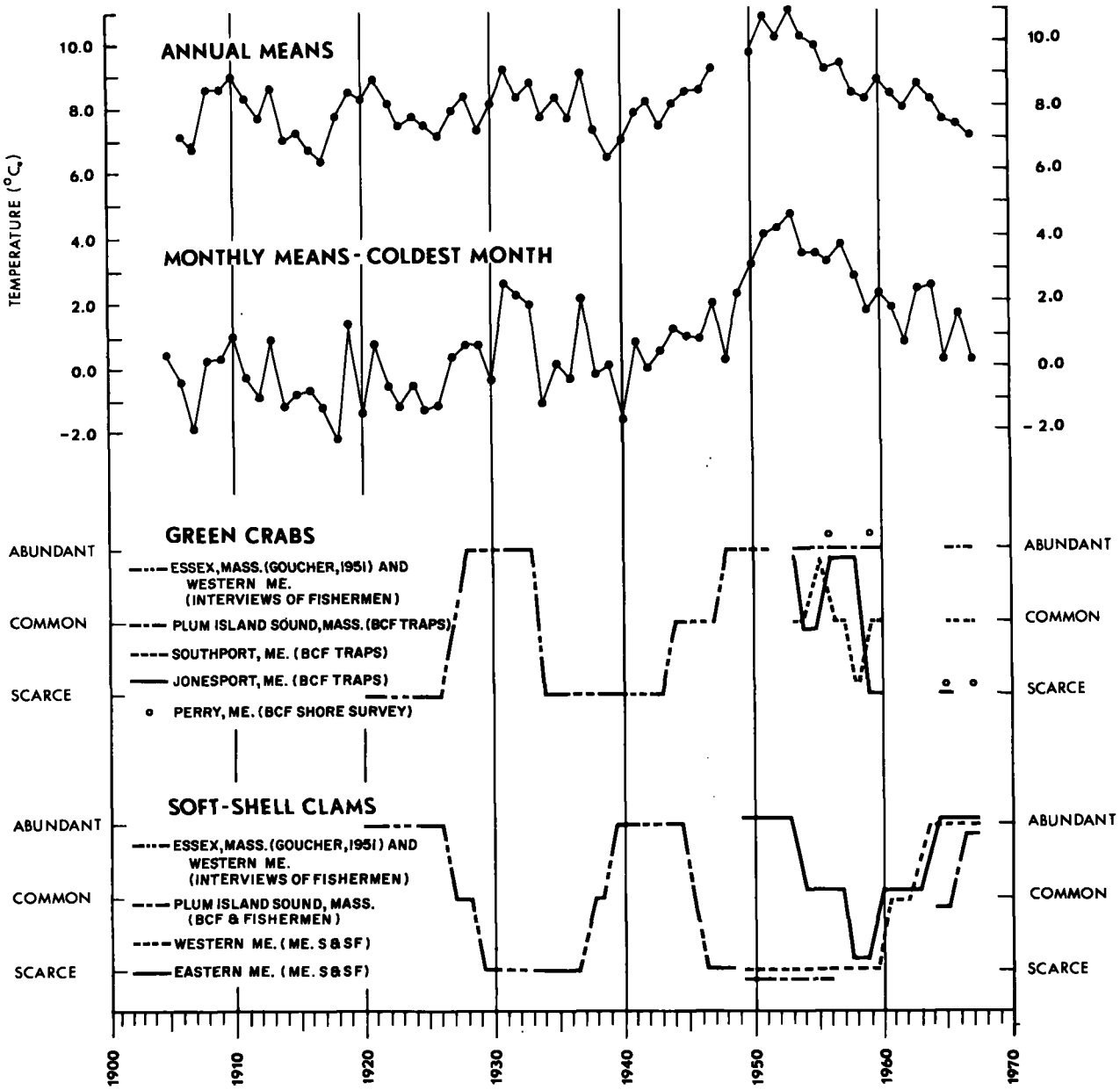

FIGURE 2.—Comparison of annual mean temperatures and lowest monthly mean temperature for each of the years 1905–67, with the abundances of green crabs and soft-shell clams. Equal levels of abundance occurring at the same time and place are shown as slightly displaced lines.

Estimates of the abundance of clams from 1949 through 1967 were furnished by biologists of the Maine Department of Sea and Shore Fisheries.

QUANTITATIVE SAMPLING

BCF biologists used standardized methods to trap crabs in various locations from 1953 through 1960 and 1965 through 1967. The specially designed traps (fig. 3) were built to the same dimensions, were baited with 4.5 kg. of fresh or frozen herring each day, and were fished at the same locations in the same depth of water each time. The traps were fished for 24 hours on 2 consecutive days during the first week of each month from late spring to late fall, when the crabs were most active. The catch and old bait were removed each day. The crabs were sexed, counted, measured, and destroyed. The catch per trap per day, used

FIGURE 3.—Standard trap used for sampling green crab populations. The deep, sheet-metal funnel prevents escape. The outside dimensions are 81 cm. long by 61 cm. wide by 34 cm. high.

as a measure of abundance, was calculated for each month and each location.

Occasional shore surveys in the intertidal zone supplemented trap catches. The surveys were at low tide in widely scattered areas where traps were not being fished and where there was good to excellent cover for crabs. During a timed search, requiring at least 1 man-hour of effort, all crabs that could be found in the open, under seaweed or stones, or in burrows, were collected, sexed, counted, and measured. Abundance was expressed as the number of crabs found per man-hour of effort expended.

CHANGES IN ABUNDANCE OF GREEN CRABS

In 1953–67 green crab populations were sampled to detect major changes in abundance. Because the month of maximum catch varied from year to year and place to place, I have used only the maximum monthly mean catch per trap per day for each year when comparing years and areas (fig. 4). Individual trap catches at any location during one monthly trapping period (3 traps for 2 days, or 6 catches) showed an average variation of ± 15 percent around the mean, with an extreme of ± 40 percent. This degree of variability in catch limits the quantitative value of the trapping surveys, but the trends were consistent with general observations and the results of the shore surveys.

The possibility of reducing crab populations by trapping was tested by fishing 18 traps daily for 36 consecutive days in a 5.7-hectare (14-acre) cove. A total of 33,760 crabs was removed at an average catch rate of 52 crabs per trap per day, but there was no significant reduction in numbers by the

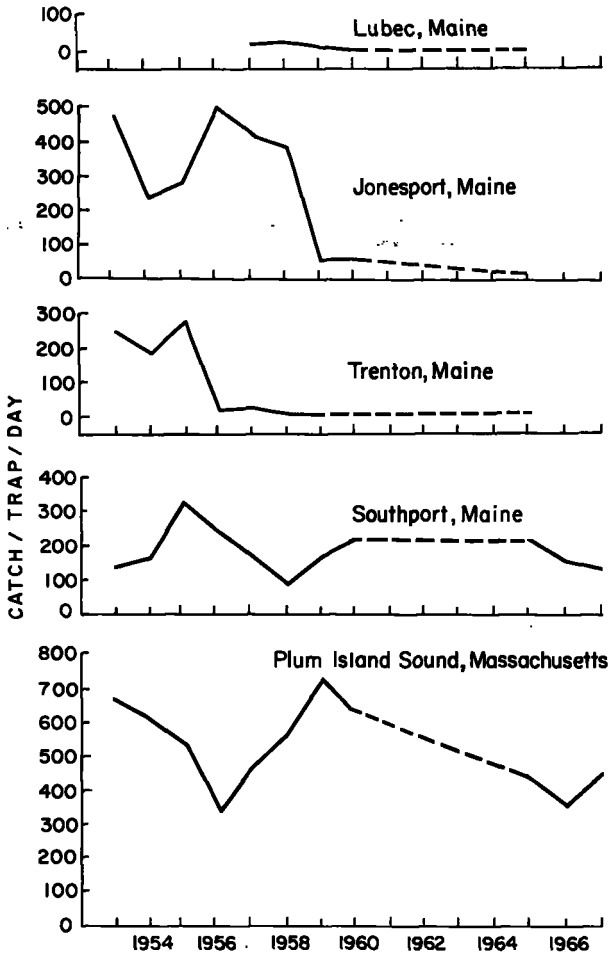

FIGURE 4.—Greatest monthly mean catch of green crabs per trap per day in each year, 1953–67. Locations are arranged from northeast (top) to southwest (bottom). Broken lines indicate periods when no trapping was done.

end of the period. In Canada, MacPhail et al. (1955) fished two traps daily for 24 days and removed 14,915 crabs without a drop in catch. It appears that, in areas where crabs are generally abundant, they move about sufficiently to fill any gap temporarily caused by trapping.

The most radical changes in abundance have been in Canada and northeastern Maine. During the summer of 1954, MacPhail et al. (1955) trapped an average of 343 crabs per trap per day for 24 days in a rocky area of the Bocabec River in New Brunswick, Canada. Soon after 1954 the green crab population started a continuous decline; the catch per trap dropped to 53 in 1958, 41 in 1959, and 7½ in 1960 (Fisheries Research Board of Canada, 1961).

In Perry, Maine, on Passamaquoddy Bay, shore surveys yielded 552 crabs per man-hour in August 1956 but only 7 per man-hour in September 1965. At nearby Lubec, where trapping was not started until 1957, maximum monthly catches were 13 and 16 crabs per trap per day in 1957 and 1958, but dropped to zero by 1960 and were still zero in 1965.

Trap catches at Cummins Beach, Jonesport, Maine, ranged between 235 and 500 crabs per trap per day in 1953–58, dropped to 50 in both 1959 and 1960, and to 6 in 1965. Shore surveys made in September 1965 at two locations near Jonesport yielded 3 and 11 crabs per man-hour.

In Trenton, Maine, at the Mount Desert Island bridge, where trapping began in 1953, catches dropped abruptly from a maximum of 271 crabs per trap per day in 1955 to 5 and 8 in 1956 and 1957. Catches then dropped to zero in 1958 and were still zero in 1965. A shore survey in nearby Sorrento yielded 14 crabs per man-hour in September 1965.

Trap catches have fluctuated in 1953–67 at Southport in central Maine and Plum Island Sound in northern Massachusetts; and over shorter periods in Boothbay Harbor and Kennebunkport, Maine, and in Scituate and Eastham, Mass. None of these fluctuations have reached points as low as those given above for northeastern Maine and Canada.

Two locations in Rhode Island showed a more gradual but consistent decline of crabs over several years. At Narrow River in Narragansett Pier maximum monthly means dropped steadily from 127 crabs per trap per day in 1956 to 51 in 1959. At Potter Pond Outlet in Jerusalem the means dropped from 334 in 1955 to 88 in 1959. The abundance in later years was not determined.

CHANGES IN WATER TEMPERATURE

The trend in coastal sea-water temperature has changed markedly since the early 1950's when the importance of the green crab was first being realized in northern New England. I have shown (Welch, 1967) that the peak of warming of surface sea water at Boothbay Harbor, Maine, since 1905 was in 1953 (annual mean, 11.1° C.); that the subsequent trend has been toward lower temperature (1967 annual mean, 7.3° C.); and that, although both summer and winter tempera-

tures have followed the same downward trend as the annual means, the decreases have been greater during the winters. Lauzier (1965) has shown that air and sea temperature trends similar to those recorded at Boothbay Harbor have occurred at various points along the western north Atlantic Coast from Atlantic City, N.J., to Halifax, Nova Scotia, and stations over the Scotian Shelf. The sea temperature trend at St. Andrews, New Brunswick, is of particular interest because the station is on Passamaquoddy Bay, a part of the Bay of Fundy where observations were made on crab abundance, and because the general trend is similar to that at Boothbay Harbor. The peak of the warming period at St. Andrews was in 1951, and the temperature declined rapidly after 1954.

RELATION OF CRAB ABUNDANCE TO TEMPERATURE CHANGE

Past records in different areas have indicated that the green crab suffers from extreme or sudden decreases in temperature and apparently prospers in periods of increasing temperature. Broekhuysen (1936), working near Den Helder, Netherlands, found that the development of the eggs of this species was most successful within an optimum range of water temperature and salinity and that a combination of low temperature and low salinity adversely affected egg development and probably the development of adults as well.

Glude (1955) associated increases in green crab abundance with the increase in sea-water temperature—especially winter temperature—and speculated on ways in which temperature could affect the crabs. He also pointed out that Goucher (see footnote 1) had recorded an increase in green crabs at Essex, Mass., between 1926 and 1933 (a period of warming); an abrupt decrease of crabs after the very severe winter of 1933–34; and an increase in abundance again from 1944 to 1951, coincident with the most recent warming period.

Taylor, Bigelow, and Graham (1957) discussed the changes in distribution and abundance of numerous marine animals during the period when information on abundance and temperature has been available. They mentioned that too little was known about the life history of the green crab to say what environmental factors affected it so favorably, but that the winter temperatures of the mid-1950's seemed sufficiently high to account for the northward extension of its range.

Waugh (1964) and Crisp (1964), investigating the effects of the severe winter of 1962–63 on marine life in southern England and North Wales, respectively, found heavy mortality among adult green crabs, but smaller individuals seemed less affected. During most of January and February 1963 the water temperature was about 5° C. below normal, often reaching well below 0° C.

Along the Maine Coast, the most drastic and noticeable decreases in crab abundance were during the winter of 1955–56. Mean monthly water temperatures at Boothbay Harbor for December 1955 (4.9° C.) and January 1956 (3.4° C.) were the coldest in 8 years. These conditions occurred at a time when crab abundance was near an alltime high and when fishermen and others had been alerted to the threat of the green crab. Throughout 1956, I received numerous reports attesting to a decrease in the numbers of crabs seen along the shore or taken in lobster traps during the summer. Of greatest interest were the reports of dead crabs during the winter.

On the Skillings River, in Hancock, Maine, clam diggers observed that green crabs became very active during a thaw in January and were out in the open on the clam flats. The temperature dropped suddenly, and shortly thereafter many dead crabs were found along the shores. This area is near the trapping location at Trenton, where catches dropped sharply from 1955 to 1956.

A lobsterman reported that when the ice broke up in Blue Hill Bay in 1956 he saw large numbers of green crabs washed up along the South Blue Hill shore.

Another lobsterman reported many dead green crabs during the winter of 1955–56 at Herrick Bay in Brooklin, Maine. During the following summer, he found the crabs far less numerous in his lobster traps there.

At Sams Cove, Bremen, Maine, in January 1956, BCF biologists saw hundreds of dead and dying green crabs on muddy bottom at 0.3 to 1.2 m. below mean low water. Heavy ice cover prevented us from examining much of the bottom, but we found crabs lying on the bottom at a time when they would normally be buried. We do not know when the conditions occurred that killed the

crabs nor do we know what those conditions were. A few days after the crabs were found, temperature, salinity, and dissolved oxygen in the water between the ice cover and bottom were within the normal range for green crabs. Winter mortality was sufficiently heavy to reduce trapping and shore collections during the following summer to about one-tenth the catches of the previous year.

During the winter of 1958–59 BCF biologists observed another winter kill in southwestern Maine. Monthly mean water temperatures from January through March 1959 were the lowest for all 3 months since 1948. Monthly mean air temperatures for December and February were the lowest for those months since 1917 and 1934, respectively (U.S. Environmental Science Services Administration, 1967). In the tidal marshes in Wells, where many crabs overwinter intertidally in burrows in banks of *Spartina* sod, we found hundreds of dead crabs of both sexes and all sizes. Trap catches in the marshes during the 1959 season were much smaller than in previous years, and the proportion of small crabs in the catch was much higher. This last observation seems to confirm Waugh's (1964) and Crisp's (1964) observations that the smaller individuals of the species suffer less from the effects of low temperature than do the larger ones.

CONCURRENT CHANGES IN CLAM ABUNDANCE

Although the primary purpose of this paper is to report on changes in green crab abundance, the importance of the species as a clam predator justifies mention of changes that have taken place in Maine soft-shell clam stocks as a result of decreased predation. Glude (1955) demonstrated correlations among the increase of green crabs, the decrease of soft-shell clams, and the increase in water and air temperatures. Because of the overwhelming abundance of crabs, he predicted a bleak future for the clam industry if the weather continued mild.

During clam population surveys in the period of heavy predation, BCF biologists consistently found evidence of adequate annual sets of clams; however, each year class was regularly destroyed as the individual clams became large enough for the crabs to find. Nevertheless, the reproductive potential existed for the recovery of clam stocks at any time when predation either decreased naturally or was controlled by man.

The decreasing abundance of crabs during the late 1950's caused a lessening in the effects of predation on the clams and resulted in an increasing supply of clams. Catches of clams have improved markedly in recent years in the two southwestern counties of Maine and to a lesser extent in the rest of the State (fig. 5). In the northeastern counties, where the decrease in crabs has been most pronounced, catches have also increased, but to a far less extent because of an unfavorable market. Reports from clam diggers, coastal wardens, and the resident State biologist, have indicated that clam flats in the northeastern area are well populated with market-size clams (fig. 2). During the course of the crab surveys, I have confirmed these reports by sampling a number of clam flats. Year classes of the past 3 to 5 years were represented consistently in the samples, and usually sufficient market-size clams were present to make clam digging worthwhile.

SUMMARY OF EFFECTS OF TEMPERATURE ON ABUNDANCE OF GREEN CRABS

Carcinus maenas is markedly affected by temperature changes. Documentation is sufficient to show that mass mortalities are often associated with unusually cold winters and that widespread increases and decreases in abundance are associated with long-term warming and cooling trends.

The direct correlation of abundance of green crabs with water temperature and the inverse correlation of abundance of clams with abundance of crabs is compared in figure 2. The close relation of the very low February temperatures of 1934 to the scarcity of crabs later in the same year as observed by Goucher (see footnote 1), and the ensuing increase in the number of clams is especially notable.

There are many ways in which this crab may be favorably affected by higher temperature, either directly or indirectly. Scattergood (1952) pointed out that numerous means have long been available to aid in the spread of the green crab northward—for example, the transportation of larvae by ocean currents, or of adults in fish and lobster shipments. Survival and successful reproduction did not

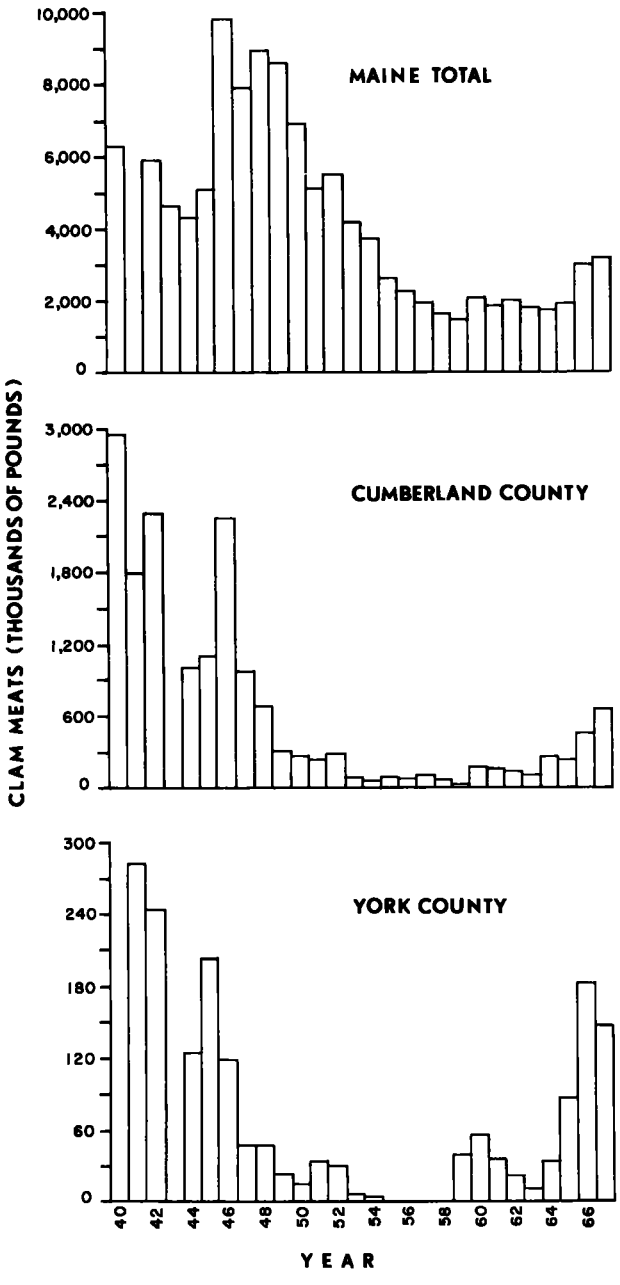

FIGURE 5.—Landings of soft-shell clams in Maine and Maine's southwestern counties, 1940–67. County totals for 1940–46 from Dow and Wallace (1961); Maine totals for 1940–56 from Power (1958); and county totals for 1947–67 and Maine totals for 1957–67 from Fish and Wildlife Service (1948–68). No totals were available for York County, 1940 and 1943; Cumberland County, 1943; and Maine, 1941. Landings in York County in 1955–58 were less than 300 lbs.

occur, however, until a certain stage of the warming trend had been reached.

Similarly, the effects of low temperature may be direct or indirect, short- or long-term. Broekhuysen's (1936) evidence and ideas on the deleterious effects of combined low temperature and low salinity may apply to upper estuaries and semienclosed bays. Since *Carcinus* consumes considerably more oxygen in dilute sea water than in water of normal salinity (Waterman, 1960), unfavorable temperature, salinity, and dissolved oxygen may combine to provide an environment lethal to *Carcinus*.

As the species ordinarily seems tolerant of low temperature, lowered salinity, or low dissolved oxygen when the conditions are met singly, it is more likely that widespread reduction in numbers results from more complex causes or chronic conditions. Examples might be the ones described in the foregoing section, "Relation of Crab Abundance to Temperature Change," in which unseasonable warming brought the normally dormant crabs out into the open where they were later killed by falling temperature, or where an excessively long dormant period, caused by a long, cold winter with heavy icing of the shore, may have been fatal.

In the northern part of its range, *Carcinus maenas* is apparently among the most responsive of common marine animals to temperature change; consequently, the species may be a useful indicator of changes in the environment that affect associated animals to a less obvious but perhaps no less serious extent.

ACKNOWLEDGMENTS

Wardens John F. Anderson, Chester E. Brown, Richard E. Coffin, Bertram E. Davis, Daniel J. Johnson, and Ralph Pinkham of the Maine Department of Sea and Shore Fisheries; Massachusetts Town Shellfish Officers Howard L. Anderson and Walter O'Neil; and, especially, retired Massachusetts State Shellfish Officer Daniel B. Pierce sampled with traps in several areas. Biologist Malcolm Richards of the Maine Department of Sea and Shore Fisheries assisted in many of the shore surveys.

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EGG-TO-MIGRANT SURVIVAL OF SPRING CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) IN THE YAKIMA RIVER, WASHINGTON

By Richard L. Major and James L. Mighell, *Fishery Biologists*
Bureau of Commercial Fisheries Biological Laboratory
Seattle, Washington 98102

ABSTRACT

Egg-to-migrant survival for the 1957–61 broods ranged from 5.4 to 16.4 percent—the first estimates of survival of chinook salmon in a large river system.

Spring chinook salmon spawn in the American, Bumping, and Naches Rivers and Rattlesnake Creek—tributaries of the Yakima River—and in the upper stretch of Yakima River proper. For both sexes, spawning fish in the upper Yakima River are smaller than those in the other areas. Mean lengths (mideye to end of hypural plate) were 45.5 and 57.3 cm. for the males and females in the upper Yakima River and 65.4 and 71 cm. for the males and females in the other areas.

Spring chinook salmon migrate to sea in their second year. Larger fish migrate earlier in the season than do smaller fish. Seaward migration reaches a peak at Prosser, Wash., on the lower Yakima River between April 14 and May 19. Movement tends to be nocturnal.

Knowledge about the life history of a species of fish is fundamental to its effective management. For Pacific salmon (*Oncorhynchus* spp.), some conception is required of survival from the egg to the seaward migrant stage. Survival from egg to migrant has been measured for four of the five species that spawn in North America—sockeye, pink, chum, and coho salmon (*O. nerka, O. gorbuscha, O. keta,* and *O. kisutch*)—but comparable information is almost completely lacking for chinook salmon (*O. tshawytscha*). For the race of chinook salmon known as spring chinook, survival has never been measured mainly because this race spawns in large river systems where sampling is difficult.[1]

The Columbia River, although its runs have been reduced to a fraction of their former size, continues to be a major producer of spring chinook salmon. To estimate the egg-to-migrant survival of a population of spring chinook salmon, the Bureau of Commercial Fisheries began a study in 1957 on the Yakima River, a tributary of the Columbia River in south-central Washington (fig. 1). The Yakima River was chosen because a trap in a diversion canal at Prosser, Wash., on the lower river provided a unique opportunity to sample the seaward migration. The trap allowed us to estimate the number of seaward migrants each year. Comparison of the number of migrants with the number of eggs deposited by the female spawners in the appropriate brood year yielded an estimate of survival to the seaward migrant stage. This paper is a summary of our work on the Yakima River from 1957 to 1963.

SPAWNING OF SPRING CHINOOK SALMON

The aim of our studies of adult spring chinook salmon was to estimate the number of eggs deposited. We had to determine (1) the distribution and abundance of redds, (2) the size, age, and fecundity of the spawners, and (3) the number of eggs retained by female spawners.

DISTRIBUTION AND ABUNDANCE OF REDDS

The spawning grounds of spring chinook salmon in the Columbia River system were originally delineated in the 1930's (Bryant and Parkhurst, 1950). For the Yakima River system, the following

[1] Seasonal races of chinook salmon in the Columbia River system are classified as spring, summer, or fall chinook depending on the time of year that the adults enter the river to spawn. In tributaries that contain more than one seasonal race, the spawning of spring chinook salmon is separated in time and space from the spawning of the other races.

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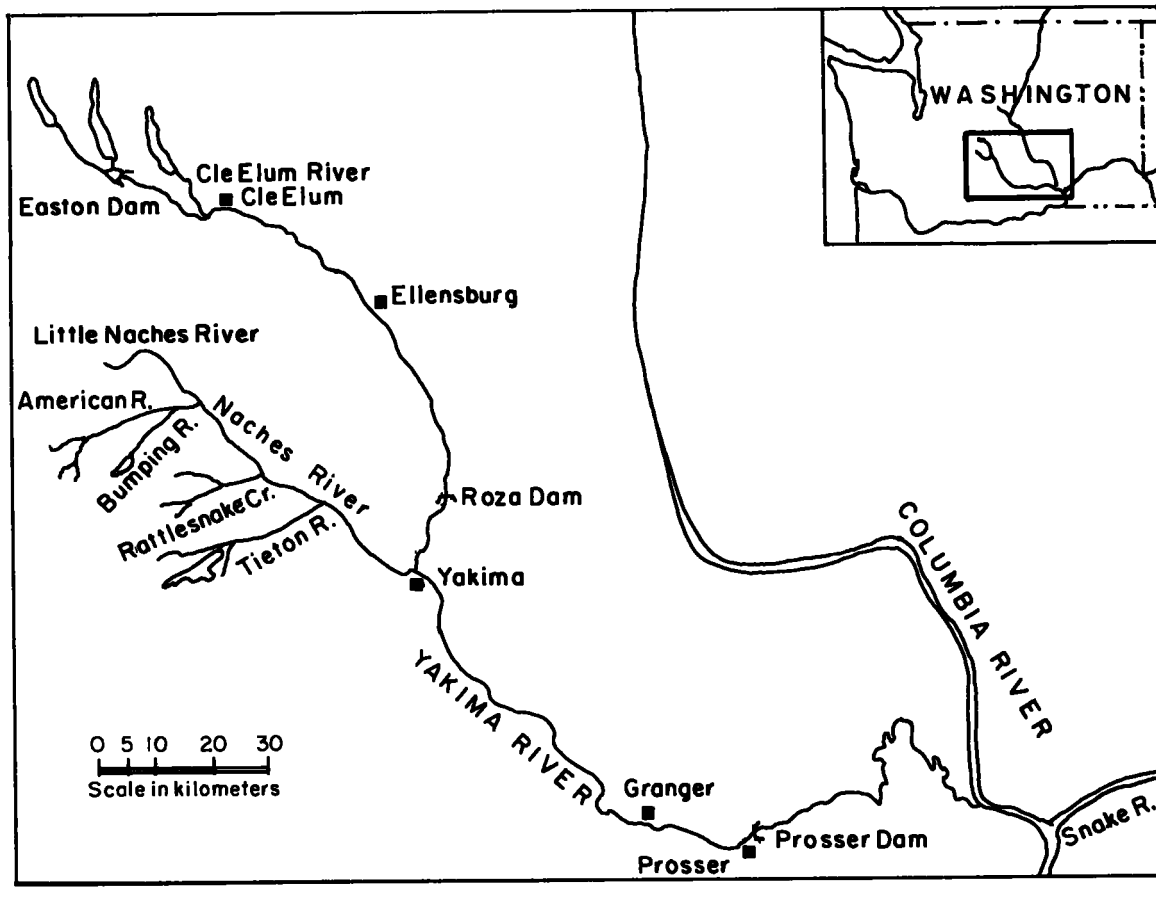

FIGURE 1.—Yakima River system and locations important to present study.

areas were listed: Yakima River from Easton Dam to Ellensburg, Naches River from the confluence of the Little Naches and Bumping Rivers to the confluence with the Tieton River, and Little Naches, Bumping, and American Rivers and Rattlesnake Creek. We surveyed these and other likely areas in 1957 but found that, except for a few scattered redds in the Cle Elum River, spawning was still confined to the areas reported by Bryant and Parkhurst (1950). We surveyed only the latter areas and the Cle Elum River in 1958–61.

Surveys were made in a standard manner. Working in pairs or alone, depending on the width of the stream, we counted the redds and the live fish as we waded downstream or floated downstream in rubber boats (table 1). If necessary, the surveys were repeated weekly until no unspawned fish were sighted. This precaution minimized the possibility that we might overlook redds made by females that were late arrivals.

Distribution of redds (fig. 2) varied little from year to year and agreed closely with Bryant and Parkhurst (1950).

TABLE 1.—*Number of spawning redds of spring chinook salmon in the Yakima River system, 1957–61*

Stream	Spawning redds				
	1957	1958	1959	1960	1961
	Number	*Number*	*Number*	*Number*	*Number*
Naches River and tributaries:					
American River	479	137	100	27	23
Bumping River	41	67	55	31	30
Little Naches River	106	16	22	3	2
Naches River	94	34	108	57	103
Rattlesnake Creek	44	30	21	8	8
Subtotal	764	284	306	126	166
Upper Yakima River: (Yakima River from Easton Dam to Ellensburg and the Cle Elum River)	1,216	531	255	184	175
Total	1,980	815	561	310	341

Spawning was distributed over a 6-week period. Peak of spawning was usually within the following dates:

American River, Aug. 8 to 12.
Bumping River, Sept. 5 to 10.
Little Naches River, Sept. 1 to 5.
Naches River, Sept. 1 to 5.
Rattlesnake Creek, Aug. 28 to Sept. 2.
Upper Yakima River, Sept. 17 to 22.

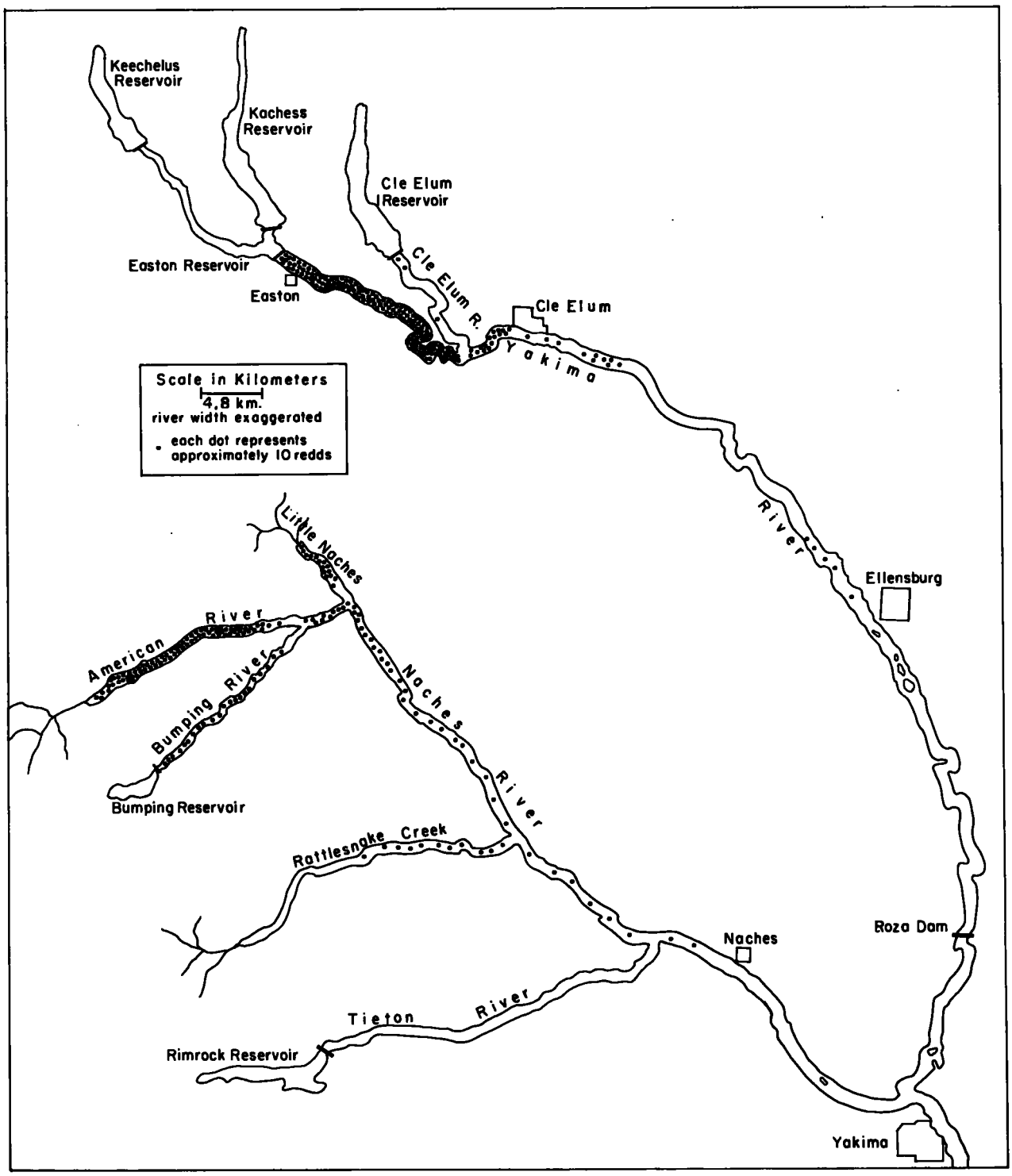

FIGURE 2.—Distribution of spawning redds of spring chinook salmon in the Yakima River system, 1957–61.

SIZE, AGE, AND FECUNDITY OF THE SPAWNERS

All of the spawned-out carcasses that could be retrieved were measured. Two measurements were obtained for each fish: fork length and mid-eye to posterior end of the hypural plate. The latter measurement excludes the snout and tail—appendages that are usually distorted on spawning salmon. The snout becomes elongated, particularly in the male, and the tail of the female is damaged in digging the redd.

Length-frequency curves by sex for the upper Yakima River and Naches River subareas (fig. 3) show that fish of both sexes are longer in the Naches River subarea than in the upper Yakima River subarea.[2] Mean lengths are 45.5 and 65.4 cm. for the males and 57.3 and 71 cm. for the females in the respective areas. The frequency distribution of length of males from the Naches River subarea is trimodal with peaks at 40, 61, and 79 cm. These modes correspond to those in samples of spring chinook salmon that are captured in the gill net fishery at the mouth of the Columbia River—fish that belong to age groups 1.1, 1.2, and 1.3, respectively.[3] Only two modes—at 40 and 55 cm.—appear in the length-frequency curve of males from the spawning area in the upper Yakima River subarea. These modes are comparable to the modes of the 1.1 and 1.2 age groups in the fishery. Females from the Naches River subarea have a single mode at 73 cm., which corresponds to the mode of females of the 1.3 age group in the fishery. Females from the upper Yakima River subarea have a single mode at 57 cm., which corresponds to the mode of the 1.2 age group in the fishery. We were unable to verify these gross length-age relations with scale data; the scales from spawned-out fish were so deteriorated that ocean ages were undeterminable.

NUMBER OF EGGS RETAINED BY FEMALE SPAWNERS

In 1960 and 1961, 82 females were examined for the number of eggs retained after spawning. Results were: 0 eggs—47 fish; 1 to 10 eggs—22 fish; 11 to 100 eggs—10 fish; and over 100 eggs—3 fish. The number of eggs retained by the spawning females does not appear to have any great effect on estimates of egg deposition.

ESTIMATED NUMBER OF EGGS DEPOSITED

Number of eggs deposited, $\hat{Y}$, was estimated by the formula

$$\hat{Y}=\sum_{i=1}^{6} n_i \hat{Y}_i$$

where n_i is the number of redds in stream (i), and $\hat{Y}_i$ is the estimated mean fecundity of the female spawners in stream (i). Here, in turn, $\hat{Y}_i = -3{,}634+105.51\ X_i$ where X_i is the mean fork length in cm. of female spawners in stream (i). The values −3,634 and 105.5 were reported by Galbreath and Ridenhour (1964), who investigated the fork length-fecundity relation of chinook salmon in the Columbia River. We used the dual measurements taken on the spawning grounds to convert to fork lengths the mideye to hypural plate measurements. These fork lengths are subject to error introduced by the elongation of the snout in the male and the wearing away of the caudal fin rays of the female in redd building. Although we were unable to measure this error, we believe it to be small.

The number of eggs deposited in the Yakima River system as a whole and that of each subarea declined markedly between 1957 and 1961 (table 2).

SEAWARD MIGRATION AND SURVIVAL OF PROGENY

We designed our studies with young salmon to estimate the number of fish that migrated seaward each spring. To make this estimate, we trapped and counted a sample of migrating fish each day during the 1959–63 migrations and from these partial counts made daily and seasonal estimates.

Sampling was at Prosser, Wash., on the lower Yakima River where a 3-m.-high dam creates a pool from which a canal transports water to a power plant 25 km. downstream. A battery of electrically powered rotary screens, 1.6 km. downstream from the entrance of the canal, diverts fish into an underground conduit which returns fish to the river. Just before it reenters the river, the conduit is equipped with a trapping system which, when activated, captures all fish that are being returned to the river (fig. 4). An aerial photograph of the area was the basis for a

[2] The upper Yakima River subarea, by our definition, includes that part of the Yakima River and its tributaries that lies above the confluence of the Yakima and Naches Rivers; the Naches River subarea includes the Naches River and its tributaries; and the main Yakima River is that part of the river that lies downstream from the confluence of the Naches and Yakima Rivers.

[3] The method of designating age follows the scale formulas of Koo (1962). The number of winters at sea is shown by an Arabic numeral preceded by a dot; similarly, the number of winters that the salmon spent in fresh water (not counting the winter the egg was in gravel) is shown by an Arabic numeral preceding a dot. Both are shown by two Arabic numerals separated by a dot. A salmon of age 1.2 spent 1 winter in fresh water and 2 winters in the ocean; the fish is 3 years old and in its fourth year of life.

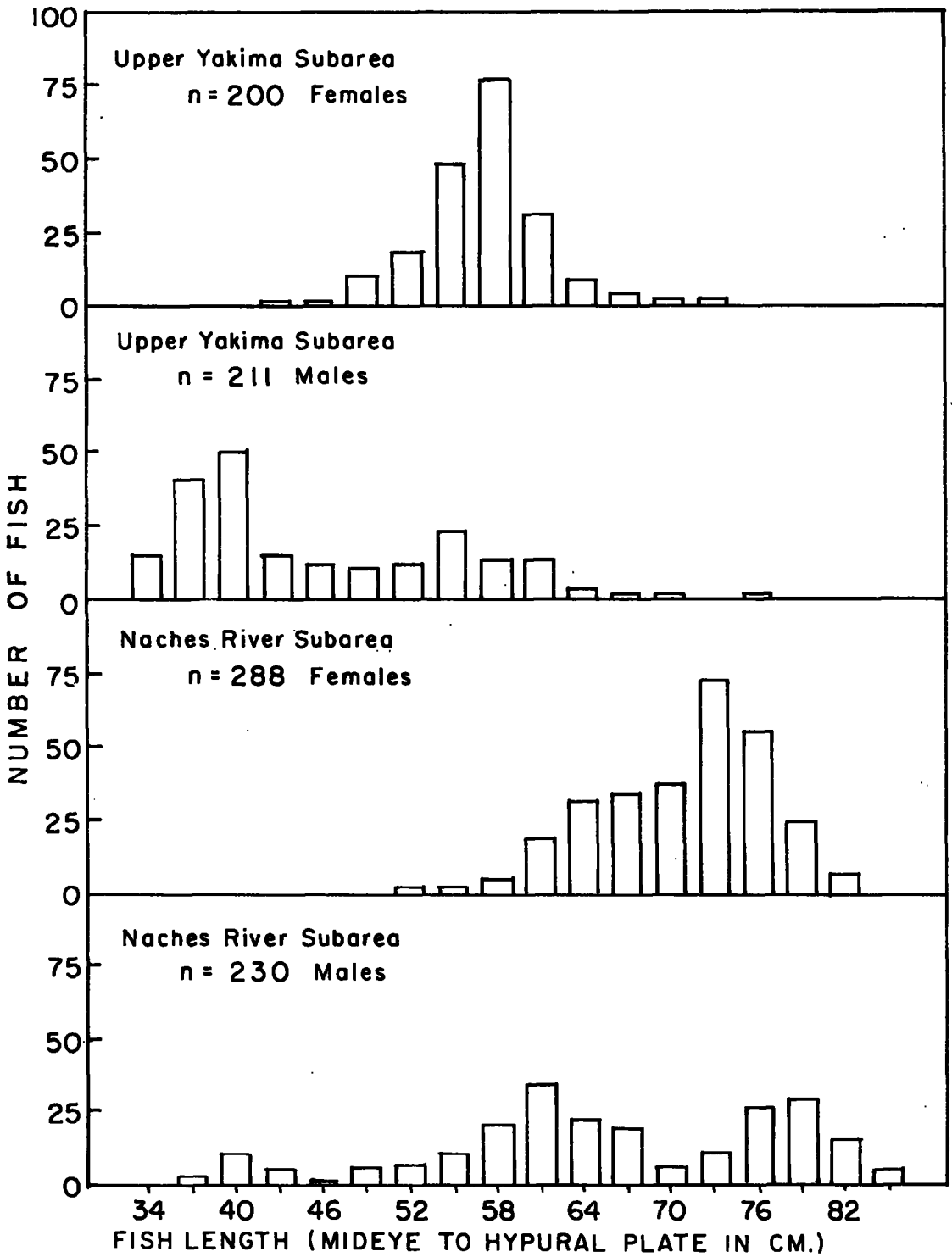

FIGURE 3.—Length-frequency distribution of adult spring chinook salmon in the Yakima River system, 1957–61.

TABLE 2.—*Estimates of number of eggs deposited by spring chinook salmon in the Yakima River system, 1957–61*

Year, subarea, and stream	Redds counted	Mean fork length of female spawner	Mean fecundity	Eggs deposited
	Number	*Centimeters*	*Number of eggs*	*Millions*
1957:				
Naches subarea:				
American River	479	86 1.	5,446	2.609
Bumping River	41	87.1	5,553	.228
Little Naches River	106	80.7	4,877	.517
Naches River	94	85.3	5,354	.503
Rattlesnake Creek	44	80.2	4,832	.213
Subtotal	764			4.070
Upper Yakima subarea	1,216	70.3	3,784	4.600
Total	1,980			8.670
1958:				
Naches subarea:				
American River	137	86.1	5,448	.747
Bumping River	67	80.8	4,888	.328
Little Naches River	16	84.0	5,231	.084
Naches River	34	84.3	5,255	.179
Rattlesnake Creek	30	81.1	4,926	.148
Subtotal	284			1.486
Upper Yakima subarea	531	66.1	3,342	1.774
Total	815			3.260
1959:				
Naches subarea:				
American River	100	89.7	5,831	.583
Bumping River	55	81.5	4,961	.273
Little Naches River	22	84.7	5,304	.117
Naches River	108	86.0	5,443	.588
Rattlesnake Creek	21	78.4	4,639	.097
Subtotal	306			1.658
Upper Yakima subarea	255	68.2	3,565	.910
Total	561			2.568
1960:				
Naches subarea:				
American River	27	84.2	5,250	.142
Bumping River	31	81.7	5,003	.155
Little Naches River	3	82.6	5,081	.015
Naches River	57	79.5	4,754	.271
Rattlesnake Creek	8	80.2	4,832	.039
Subtotal	126			.622
Upper Yakima subarea	184	66.3	3,358	.618
Total	310			1.240
1961:				
Naches subarea:				
American River	23	86.2	5,459	.126
Bumping River	30	80.1	4,816	.144
Little Naches River	2	82.6	5,081	.010
Naches River	103	86.2	5,464	.563
Rattlesnake Creek	8	80.6	4,867	.039
Subtotal	166			.882
Upper Yakima subarea	175	68.2	3,564	.624
Total	341			1.506

sketch to describe the function of the canal-conduit system. The trapping system is shown diagrammatically in figure 5.

Procedures for studying seaward migration were similar for all years. Trapping began about April 1 when young salmon were not yet abundant and continued until they became scarce—sometime in June. Fish were removed from the trap with dip nets at 8 a.m., 12 noon, 4 p.m., and 12 midnight. The trapping "day" used here extended from 8 a.m. of the calendar day indicated to 8 a.m. of the following day. Fish other than salmon were counted and released. Young salmon were transferred into tubs for closer inspection before they were counted and released.

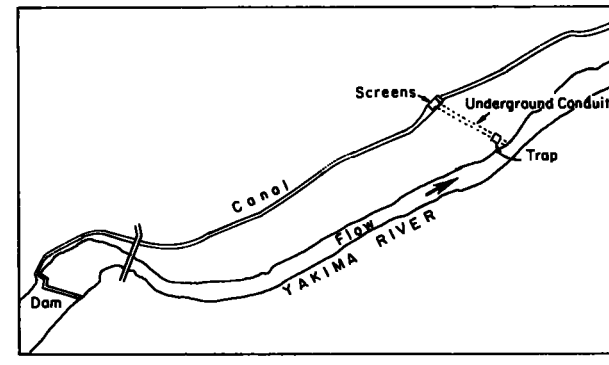

FIGURE 4.—Diagrammatic sketch of the system for sampling the seaward migration at Prosser. Low dam diverts water into the canal; screens divert fish into an underground conduit that carries them to the traps and eventually to the river.

Once a week a sample of young chinook salmon was anesthetized in a 1:20,000 solution of MS 222. Fork length to the nearest millimeter was recorded from each fish. Weight to the nearest gram was recorded from a randomly selected subsample of about 50 fish per week. Scales, selected from a stratified subsample, were placed between pairs of glass slides and later examined with a microscope to determine the age of the fish.

AGE AND SIZE OF SEAWARD MIGRANTS

Scales from 1,458 young chinook salmon captured at Prosser from 1959–63 revealed that fish were either in their first or second year of life. Certain differences between the age groups are noteworthy. First, the two age groups do not appear at Prosser at the same time; fish that are in their second year appear in early April, but fish that are in their first year do not appear until June. Second, when samples that contain fish of both age groups are viewed in tubs, the first-year fish (even the few that are as long as the fish in their second year) are readily distinguishable by their stouter bodies.

We reasoned that the stouter, first-year migrants were not spring chinook salmon but rather fall chinook salmon—progeny of adult fall chinook salmon that spawn near Granger, 40 km. upstream from Prosser. If they were spring chinook salmon migrating downstream from the upriver spawning areas, they would have had to move through the midriver areas in the winter or spring. But this movement did not take place. We sampled the Yakima River system extensively with electro-

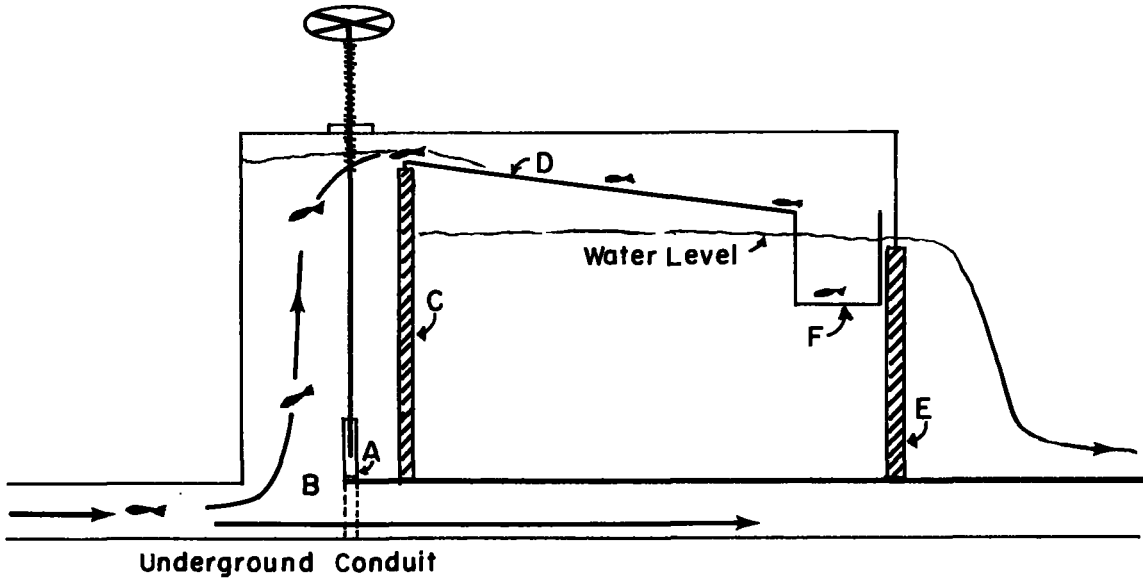

FIGURE 5.—Diagrammatic sketch of trapping system on bypass conduit on the Yakima River at Prosser. When valve (A) is open, fish pass directly to the Yakima River. To activate the trap, the valve is closed forcing the water and fish upward through a hole in the top of the conduit (B). Water flows over the top of the interior wall (C), through inclined plane screen (D), over a second interior wall (E), and on to the Yakima River. Fish and some water continue into trap (F).

fishing equipment in the winter and spring of 1958–63 but found no first-year fish in the mid-river stretches. Furthermore, no first-year fish migrated seaward past Roza Dam, 19 km. above the confluence of the Yakima and Naches Rivers, in either 1961 or 1962 (according to Donald Greenland).[4] Data presented here pertain only to spring chinook salmon, or fish that migrate seaward in their second year.

Length-frequency polygons of downstream-migrating spring chinook salmon (fig. 6) show that the modal length increased from 120 mm. in 1959 and 1960 to 125 mm. in 1961, 130 mm. in 1962, and 135 mm. in 1963. Present data are inadequate to explain the reason for the increase in modal length. Possible explanations include the availability of more food per young fish and differential growth and abundance of the several tributary subpopulations believed to be present.

Analysis of the length and weight data (table 3 and figure 7) clearly shows that the larger fish tend to migrate early in the season. The condition factor tends to increase—that is, the fish become heavier per unit length as the season progresses. This change is explained, at least in part, by the extended sojourn of the later migrating fish in water where the temperature is rising and food is becoming more abundant, and where their feeding becomes more intensive.

[4] Donald Greenland, Fishery Biologist, Bur. Commer. Fish., Columbia River Program Office, Portland, Oreg. Personal communication.

TIMING OF SEAWARD MIGRATION

The daily timing of the downstream migrations in 1959–63 was similar for all years (fig. 8). Generally the catches remained relatively stable between periods ending at noon, 4 p.m., and 8 p.m. and increased in the period ending at midnight. The hourly distribution of the catch between midnight and 8 a.m. is unknown, but the number of chinook salmon captured during the 8-hour period approximated the number taken from 8 p.m. to midnight. Thus, migration tended to be at night.

The week or weeks of heaviest seaward migration of spring chinook salmon at Prosser varied in 1959–63, but always fell between April 14 and May 19 (fig. 9).

SURVIVAL TO SEAWARD MIGRATION

We estimated the number of seaward migrants from the formula:

$$\hat{N}=\sum_{i=1}^{n}\hat{N}_i=\sum_{i=1}^{n}Ci(32.5/f_i)$$

where $\hat{N}$ is the estimated number of spring chinook salmon migrating seaward, $\hat{N}_i$ is the estimated

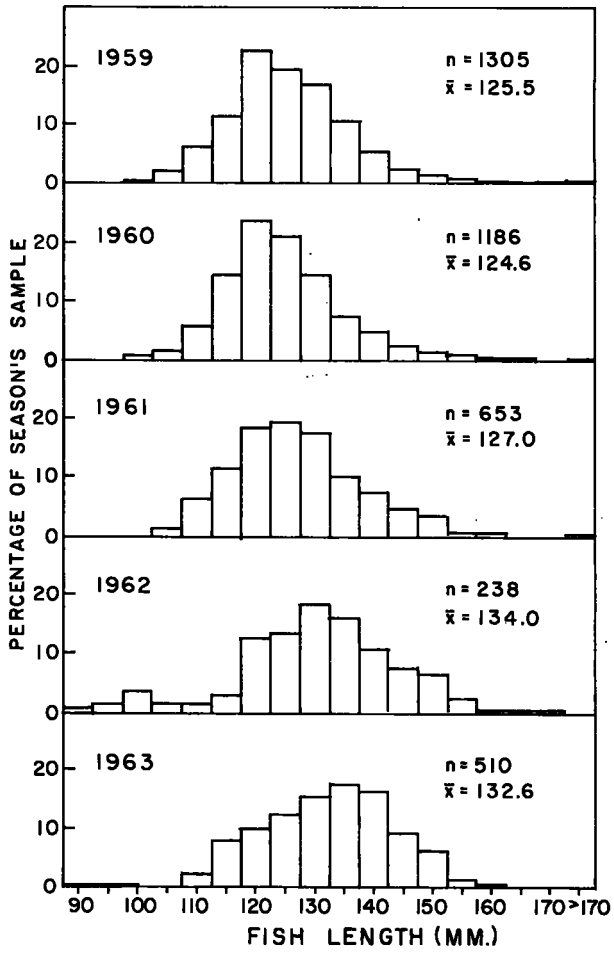

FIGURE 6.—Length-frequency distribution of Yakima River spring chinook salmon captured during their seaward migration at Prosser, 1959–63.

TABLE 3.—*Mean length, mean weight, condition factor, and size of samples of spring chinook salmon taken at Prosser, 1959–63*

Date (week ending)	Fish	Mean fork length	Mean weight	Condition factor
	Number	*Millimeters*	*Grams*	
1959:				
April 14	50	128.4	23.8	1.13
21	50	129.6	24.4	1.12
28	49	127.7	23.2	1.12
May 5	50	121.8	20.7	1.15
12	50	122.9	20.1	1.08
19	48	120.0	20.0	1.16
26	50	124.0	21.9	1.15
June 2	29	125.3	22.8	1.16
9	15	119.5	20.0	1.17
After June 9	23	117.6	19.5	1.20
1960:				
April 7	28	130.5	24.1	1.09
14	50	125.3	20.7	1.06
21	50	132.7	25.3	1.08
28	53	127.7	21.9	1.05
May 5	102	123.8	20.0	1.06
12	50	125.8	21.8	1.10
19	49	119.2	19.1	1.13
26	50	123.8	20.7	1.09
June 2	50	121.4	20.3	1.13
9	50	120.4	20.7	1.19
After June 9	51	121.8	21.8	1.21
1961:				
April 7	52	132.3	25.2	1.09
14	50	136.0	26.9	1.07
21	50	124.7	21.0	1.08
28	50	130.2	23.2	1.05
May 12	104	123.6	20.8	1.10
19	48	120.4	19.2	1.10
June 9	19	118.3	18.7	1.13
1962:				
April 14	50	137.7	28.7	1.10
21	50	139.4	29.6	1.09
28	50	130.3	23.7	1.07
May 19	33	125.7	21.7	1.09
June 2	37	129.5	24.5	1.13
After June 9	18	127.9	25.0	1.19
1963:				
April 7	30	143.9	31.6	1.06
14	33	138.2	29.6	1.12
21	38	141.4	29.7	1.05
28	45	138.6	28.4	1.07
May 5	110	133.5	26.7	1.12
12	40	136.3	27.3	1.08
19	37	131.8	24.2	1.06
26	42	130.7	23.8	1.07
June 2	32	127.8	21.7	1.04
9	60	120.1	19.0	1.10
After June 9	42	121.4	20.7	1.16

TABLE 4.—*Egg-to-migrant survival of young spring chinook salmon in the Yakima River (brood years 1957–61)*

Brood year	Egg deposited	Seaward migration	Survival
	Millions	*Thousands*	*Percent*
1957	8.670	464	5.4
1958	3.260	319	9.8
1959	2.568	194	7.6
1960	1.240	177	14.3
1961	1.505	246	16.4

number migrating on day (i), Ci is the number captured in the trap on day (i), and f_i is the estimated flow in cubic meters per second of the Yakima River at Prosser on day (i) (U.S. Geological Survey, 1961–65). Canal flow is constant at 32.5 $m.^3$ per second. This method requires the assumptions that the number of fish per volume of water is the same in the canal as in the river and that the mortality in the canal is the same as that in the adjacent stretch of river. The number of migrants that were caught in the trap and the total number that we estimated to have migrated seaward at Prosser are shown in figure 10 by day and year.

Estimates of the number of seaward migrants, estimates of the number of eggs deposited in the appropriate brood year, and the percentage survival are shown in table 4 and figure 11. Survival ranged from 5.4 to 16.4 percent; the average was 10.7 percent. The low survival of the 1957 brood was caused—to a great extent—by an unnatural condition that did not recur in the other years. In 1957 an estimated 30 to 50 percent of the eggs deposited in the upper Yakima River subarea succumbed to exposure when, in October and November, the water level was artificially lowered and maintained 2 feet below what it had

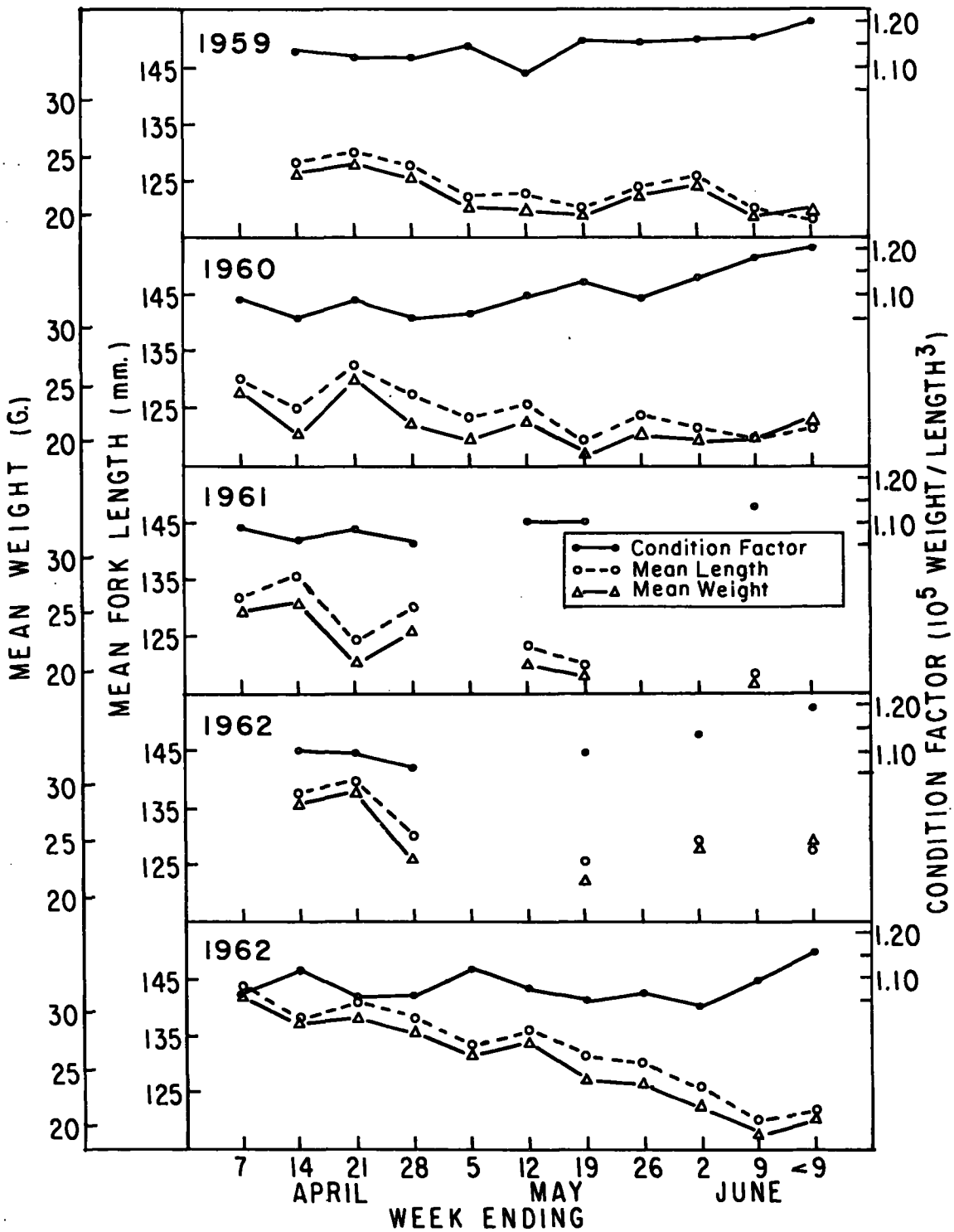

FIGURE 7.—Mean length, mean weight, and condition factor of Yakima River spring chinook salmon captured during their seaward migration at Prosser, 1959–63.

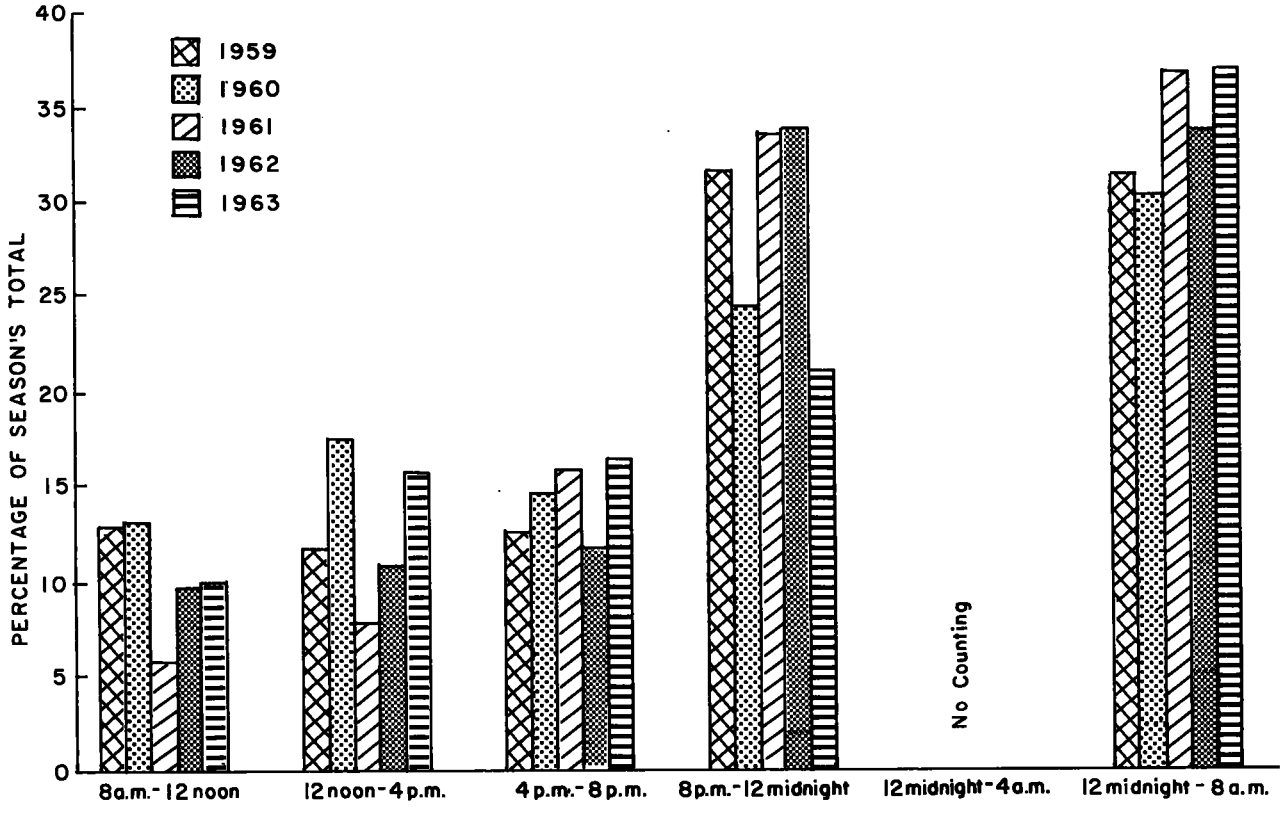

FIGURE 8.—Daily distribution of Yakima River spring chinook salmon captured during their seaward migration at Prosser, 1959–63.

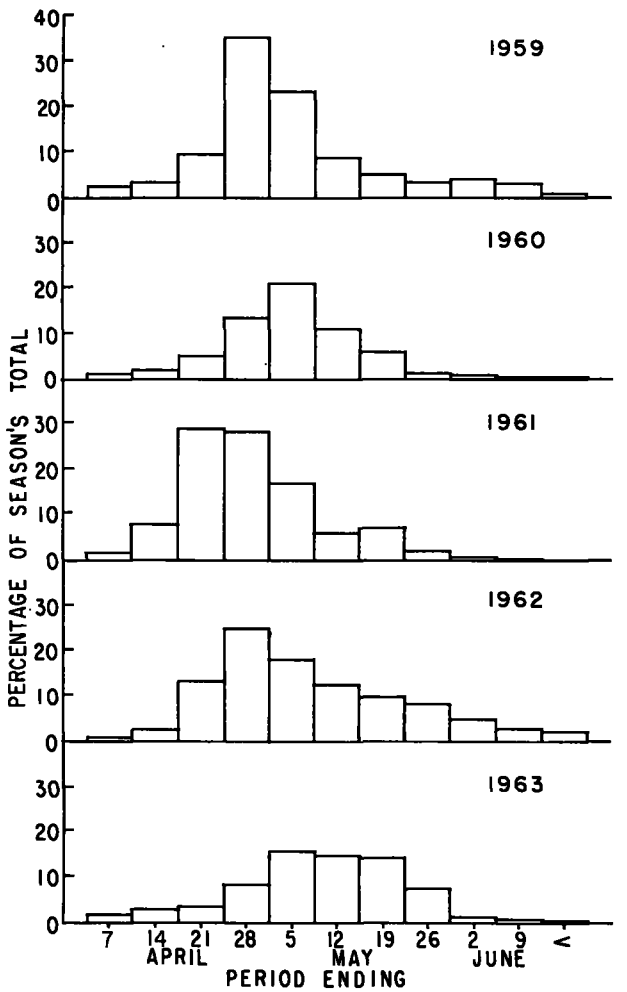

FIGURE 9.—Seasonal distribution of Yakima River spring chinook salmon captured during their seaward migration at Prosser, 1959–63.

been when the fish spawned in late September (Quentin Edson).[5] In subsequent years, per an agreement between the State of Washington Department of Fisheries and the U.S. Bureau of Reclamation—the agency controlling the flow of water over Easton Dam, a relatively uniform minimum flow was maintained from September until February when the young fish emerge from the gravel.

Estimates of survival from the egg to the seaward migrant stage for Pacific salmon are summarized in table 5. Prior to the present study, survival of chinook salmon had been estimated

[5] Quentin Edson, Fishery Biologist, City of Tacoma, Department of Public Utilities, Tacoma, Washington. Personal communication.

TABLE 5.—*Survival from egg to seaward migrant for five species of Pacific salmon*

Species and location	Survival, egg to seaward migrant: Range	Survival, egg to seaward migrant: Average	Period	Source of information
	Percent	*Percent*	*Years*	
Sockeye salmon:				
Cultus Lake, B.C.	1.01–3.22	1.87	4	Ricker, 1966.
Babine Lake, B.C.	1.34–5.18	3.77	5	Do.
Lakelse Lake, B.C.	.60–5.05	1.86	7	Do.
Port John Lake, B.C.		3.00	(1)	Do.
Chilko Lake, B.C.		8.00	(1)	Do.
Dalnee Lake, U.S.S.R.	.005–1.05	.28	10	Hanamura, 1966.
Pink salmon:				
McClinton Creek, B.C.	6.90–23.80	(1)	6	Neave, 1966a.
Morrison Creek, B.C.	4.70–6.70	(1)	2	Do.
Hooknose Creek, B.C.	.90–37.20	(1)	13	Do.
Lakelse River, B.C.	18.00	(1)	1	Do.
Kispiox River, B.C.	23.00	(1)	1	Do.
Kitwanga River, B.C.	15.00	(1)	1	Do.
Wahleach Creek, B.C.	37.00	(1)	1	Do.
Sashin Creek, Alaska	.10–21.80	6.33	22	McNeil, 1966.
Karymai Spring, U.S.S.R.	.02–5.70	1.96	6	Semko, 1954.
Chum salmon:				
Nile Creek, B.C.	.08–13.60	(1)	8	Neave, 1966b.
Hooknose Creek, B.C.	.96–22.00	0	13	Do.
Karymai Spring, U.S.S.R.	.68–4.20	2.16	7	Semko, 1954.
Coho salmon:				
Nile Creek, B.C.	.76–2.10	1.27	4	Godfrey, 1965.
Hooknose Creek, B.C.	.70–3.96	1.30	10	Do.
Minter Creek, Wash.	.70–9.65	1.71	11	Do.
Waddel Creek, Calif.	1.16–1.56	1.43	4	Do.
Chinook salmon:				
Fall Creek, Calif.	7.00–32.00	14.50	4	Wales and Coots, 1955.
Yakima River, Wash.	5.35–16.35	10.70	5	Present study.

[1] Not reported.

only in Fall Creek, Calif., and the usefulness of these values is limited. Fall Creek is a small atypical spawning stream and the progeny of the Fall Creek chinook salmon population migrate to sea in their first year of life (a characteristic of fall chinook, pink, and chum salmon, but not of spring or summer chinook salmon; the latter races, like sockeye and coho salmon, usually spend 1 year or more in fresh water before migrating to sea).

Relative to all other species, the limits within which the percentage survival of spring chinook salmon in the Yakima River fluctuates are neither wide nor narrow but reasonably moderate. Egg-to-migrant survival of spring chinook salmon in the Yakima River is generally higher than that for sockeye salmon and coho salmon—other species whose young spend 1 year or more in fresh water. The results of the various studies are not strictly comparable, however, because migrants are trapped at varying and sometimes unspecified points in time and distance from the nursery areas and the sea. Young spring chinook salmon trapped at Prosser must yet migrate 600 km. to the sea.

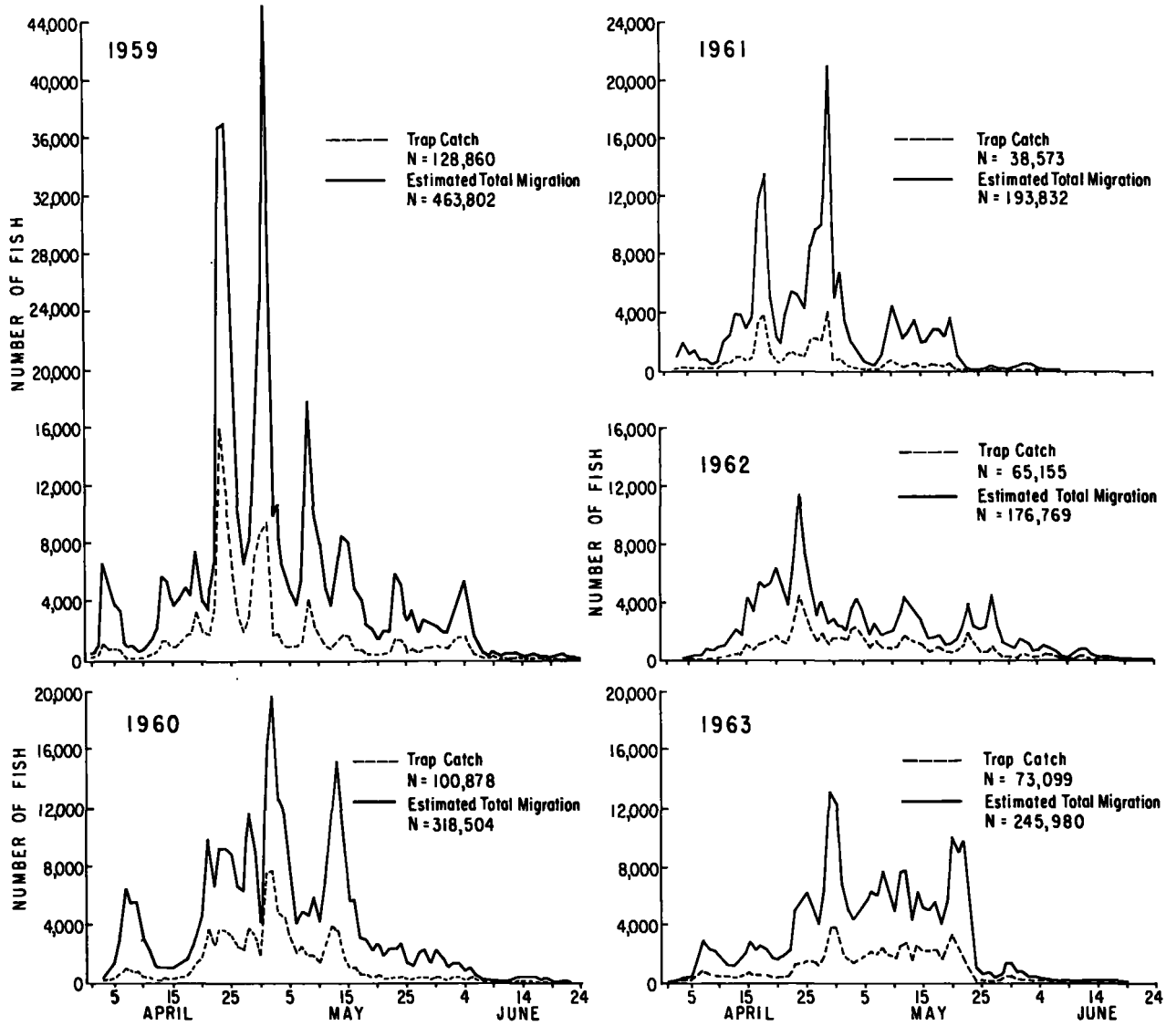

FIGURE 10.—Seaward migration of Yakima River spring chinook salmon at Prosser, 1959–63. Number captured in the trap are shown by broken lines. Solid lines indicate the calculated totals for the entire river (trap and remainder of the river).

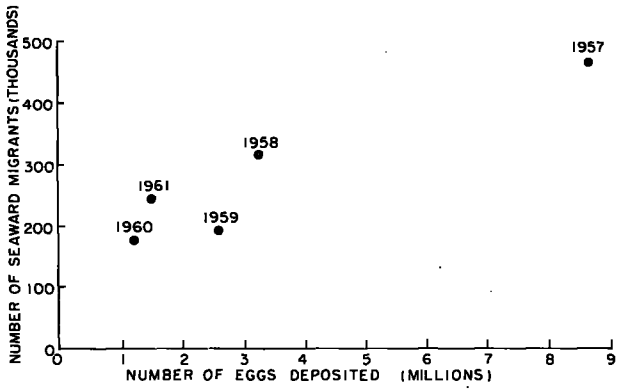

FIGURE 11.—Estimated number of seaward migrants and estimated number of eggs deposited, Yakima River spring chinook salmon, brood years 1957–61.

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CONTRIBUTION OF COLUMBIA RIVER HATCHERIES TO HARVEST OF FALL CHINOOK SALMON (*Oncorhynchus tshawytscha*)

BY DONALD D. WORLUND,[1] ROY J. WAHLE,[2] AND PAUL D. ZIMMER[2]

ABSTRACT

A marking experiment was designed in which fall chinook salmon (*Oncorhynchus tshawytscha*) from 12 Columbia River hatcheries were marked in 4 consecutive years to estimate their contribution to the sport and commercial fisheries. The study was planned and is being executed by scientists of the Fisheries Research Board of Canada, Bureau of Commercial Fisheries, and fishery agencies of the States of Washington, Oregon, California, and Alaska.

Sampling for marked fish is being conducted in most ocean fisheries for chinook salmon from Monterey, Calif., to southeast Alaska, as well as on the Columbia River. The 1963–66 returns from the first year's release (1961 brood) of 5.4 million marked fish make it possible to obtain a preliminary estimate of the contribution of the total hatchery releases as represented by this marked group.

The estimated catch of 1961-brood fish that originated from the hatcheries under study was 287,326, or about 10 percent of the total catch of chinook salmon of that brood in the fisheries sampled. The estimated net value of this catch (to the fisherman) was about $1,900,000, whereas the cost to produce them was $831,000. The benefit to cost ratio was 2.3:1.

The net value of the catch of fall chinook salmon of the 1961 brood that originated from all Columbia River hatcheries (including those not participating in the marking experiments) was estimated at $2,055,000.

The U.S. Fish and Wildlife Service has financed the Columbia River Fishery Development Program, a cooperative effort of the States of Oregon, Washington, and Idaho, since its inception in 1949. The Bureau of Commercial Fisheries Columbia Fisheries Program Office, Portland, Oreg., administers this project, which is designed to increase production of salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) in the Columbia River.

A major accomplishment of the program has been the construction and modernization of 19 salmon producing hatcheries on the lower 290 km. (180 miles) of the river. These hatcheries, managed by the Bureau of Sport Fisheries and Wildlife and the States of Washington and Oregon, were built primarily to offset the loss of natural spawning and rearing areas for salmon and steelhead trout caused by water development projects.

Releases of fall chinook salmon have varied from less than 10 million fish from 6 hatcheries in 1949 to about 56 million from 14 hatcheries in 1966. The contribution of these large releases to the commercial and sport fisheries, however, is unknown. Past marking experiments have demonstrated that hatchery releases contribute to the fisheries, but because such experiments were limited and designed for other purposes, the contribution has not been estimated.

A marking experiment was undertaken in 1962 by the Columbia Fisheries Program Office to estimate the contribution of hatchery-reared fall chinook salmon to the fisheries. The experiment was confined to 12 hatcheries that have propagated about 90 percent of all fall chinook salmon artificially reared in the Columbia River. Data collection will be completed by the end of 1969; however, sufficient information is presently available for preliminary estimates of the contribution to the fisheries by one group (1961 brood) of hatchery-reared fall chinook salmon.

[1] Statistician, Bureau of Commercial Fisheries Biological Laboratory, 2725 Montlake Boulevard East, Seattle, Wash. 98102.

[2] Fishery Biologists, Bureau of Commercial Fisheries Columbia Fisheries Program Office, 811 Northeast Oregon Street, Portland, Oreg. 97208.

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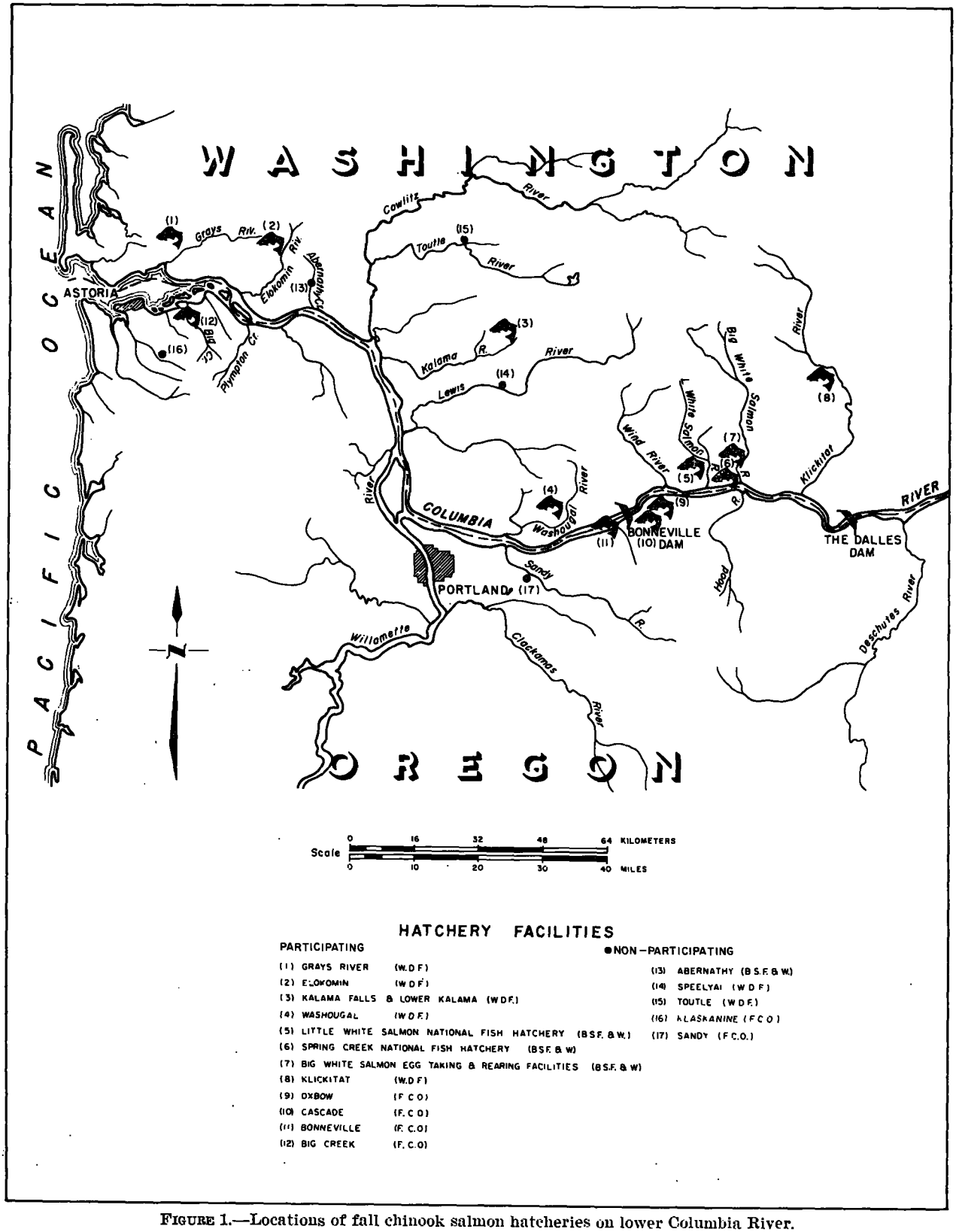


HATCHERY FACILITIES

PARTICIPATING

(1) GRAYS RIVER (W.D.F.)
(2) ELOKOMIN (W.D.F.)
(3) KALAMA FALLS & LOWER KALAMA (W.D.F.)
(4) WASHOUGAL (W.D.F.)
(5) LITTLE WHITE SALMON NATIONAL FISH HATCHERY (B.S.F. & W.)
(6) SPRING CREEK NATIONAL FISH HATCHERY (B.S.F. & W.)
(7) BIG WHITE SALMON EGG TAKING & REARING FACILITIES (B.S.F. & W.)
(8) KLICKITAT (W.D.F.)
(9) OXBOW (F.C.O.)
(10) CASCADE (F.C.O.)
(11) BONNEVILLE (F.C.O.)
(12) BIG CREEK (F.C.O.)

●NON-PARTICIPATING

(13) ABERNATHY (B.S.F. & W.)
(14) SPEELYAI (W.D.F.)
(15) TOUTLE (W.D.F.)
(16) KLASKANINE (F.C.O.)
(17) SANDY (F.C.O.)

FIGURE 1.—Locations of fall chinook salmon hatcheries on lower Columbia River.

The 12 hatcheries are distributed over about 250 km. (155 miles) of the Columbia River (fig. 1). Big Creek Hatchery, the lowermost station, and Klickitat Hatchery, the uppermost, are on tributaries about 40 and 290 km. (25 and 180 miles), respectively, above the river mouth. Some hatcheries (Bonneville, Cascade, Oxbow, Little White Salmon, and Spring Creek) are adjacent to the Columbia River and release their fish directly into the river. In contrast, fish released at Klickitat Hatchery must travel about 40 km. (25 miles) to reach the main stem of the Columbia.

Artificial propagation procedures are similar at all hatcheries raising fall chinook salmon. Adults normally return to these hatcheries and are spawned during September and October. Depending upon water temperatures, fry typically reach the free swimming stage in February or March and are then placed in ponds. The young fish are released from the hatchery 90 to 120 days later at an average length of 6 to 8 cm. (2–3 inches). During the following 5 years, they are available to commercial and sport fisheries from southeast Alaska to central California. Some fish mature and return to the Columbia River during their second, third, fourth, and fifth years; however, most are in their third (age 3) and fourth years.

This report (1) describes the design of the marking experiment and (2) presents an estimate of the contribution (catch) to the fisheries by the 1961-brood hatchery releases and an estimate of the benefit-cost ratio. This is the first basic analysis of data collected under the hatchery evaluation study directed by Paul D. Zimmer of the Columbia River Fishery Development Program. Several research laboratories and individuals are analyzing data from this study and will develop much additional information.

DESIGN OF EXPERIMENT TO ESTIMATE HATCHERY CONTRIBUTION TO FISHERIES

The general approach for estimating the hatchery contribution of fall chinook salmon was to identically mark the same fraction (about 10 percent) of each hatchery's production and then sample for this mark in the commercial and sport fisheries. From the number of marked fish recovered and the sampling ratio, together with the fraction originally marked (or expected marked to unmarked ratio), we can estimate the number of hatchery-reared fall chinook salmon in the catch. In addition to the "common mark" (i.e., mark applied to portion of fish at all hatcheries under study), "special marks" were used at selected hatcheries each year to examine the variations in contribution among hatcheries. Supplemental data were also collected in an attempt to explain the expected variations among hatcheries and to test some of the assumptions underlying the experimental techniques and estimating procedures.

The success of the marking experiment required the efforts of many people and the cooperation of fishery agencies on the Pacific Coast (table 1). All marking and mark recovery activities were under the direct supervision of experienced biologists.

MARKING

The marking phase of the study began in June 1962 and was completed in June 1965. The 1961–64 broods (progeny of adults that spawned in 1961, 1962, 1963, and 1964) were marked. The "common mark" consisted of removing the adipose fin and a portion of the right or left maxillary bone. The clipped right maxillary was used to identify the 1961 and 1963 broods and the clipped left maxillary the 1962 and 1964 broods (table 2).

TABLE 1.—*Responsibilities of agencies participating in the marking and mark recovery phases of the Columbia River fall chinook hatchery contribution study, 1962–68*

Function	Execution	Supervision	Agency [1]
Coordinating and supervising	Biologist	Biologist	BCF
Obtaining fish for marking	Hatchery personnel	Biologist and hatchery manager	WDF, FCO, BSFW
Marking	Fish markers	Biologist	WDF, FCO, BSFW
Sampling hatchery releases	Hatchery personnel	Biologist and hatchery manager	WDF, FCO, BSFW
Sampling catch for marked fish	Mark samplers	Biologist	ADFG, FRBC, WDF, FCO OGC, CFG, BCF
Sampling hatchery returns and natural spawning populations for marked fish.	do	do	WDF, FCO, BSFW

[1] ADFG—Alaska Dept. of Fish and Game; FRBC—Fisheries Research Board of Canada; WDF—Washington Dept. of Fisheries; FCO—Fish Commission of Oregon; OGC—Oregon Game Commission; CDFG—California Dept. of Fish and Game; BCF—Bureau of Commercial Fisheries; BSFW—Bureau of Sport Fisheries and Wildlife.

TABLE 2.—*Ages of marked Columbia River fall chinook salmon in catches and escapements by brood (1961–64) and sampling years (1963–69)*

Brood	Mark[1]	Release site	Year of sampling						
			1963	1964	1965	1966	1967	1968	1969
			Years old						
1961	Ad-RM	12 hatcheries	2	3	4	5			
	Ad-LV-RM	Spring Creek	2	3	4	5			
	Ad-RV-RM	Kalama	2	3	4	5			
	RV-RM	Ox Bow	2	3	4	5			
	LV-RM	Elokomin	2	3	4	5			
1962	Ad-LM	12 hatcheries		2	3	4	5		
	Ad-LV-LM	Spring Creek		2	3	4	5		
	Ad-RV-LM	Kalama		2	3	4	5		
	RV-LM	Cascade		2	3	4	5		
	LV-LM	Grays River		2	3	4	5		
1963	Ad-RM	12 hatcheries			2	3	4	5	
	Ad-LV-RM	Spring Creek			2	3	4	5	
	Ad-RV-RM	Kalama			2	3	4	5	
	RV-RM	Klickitat			2	3	4	5	
	LV-RM	Big Creek			2	3	4	5	
1964	Ad-LM	12 hatcheries				2	3	4	5
	Ad-LV-LM	Spring Creek				2	3	4	5
	Ad-RV-LM	Kalama				2	3	4	5
	RV-LM	Little White Salmon				2	3	4	5
	LV-LM	Bonneville				2	3	4	5
Number of marks in catches and escapements			5	10	15	20	15	10	5

[1] Ad: Adipose; LV: Left ventral; RV: Right ventral; LM: Left maxillary; RM: Right maxillary.

To obtain the fish for marking, a sampling tool (Hewitt and Burrows, 1948) was modified to remove a random "10 percent" sample. This device is a circular net consisting of 10 equal pie-shaped sections that fits into a cylindrical liner such that all fish contained in the cylinder must pass through one of the sections (fig. 2). The sample for marking was obtained by closing one of the sections. In practice, the sampling device was placed in a tub partially filled with water. Fish were removed from a pond in groups weighing about 18 kg. (40 pounds) each and placed in the sampler, and the device was then raised; the closed section retained the sample for marking. The fish that passed through the open sections remained in the tub and were placed in another pond. This procedure was followed until all fish in each pond were processed.

At each hatchery, fish selected for marking were first anaesthetized with MS–222 [3] (tricaine methanesulfonate), then the markers used bent-nosed dissecting scissors to remove certain fins and maxillaries. Marked fish were held in hatchery troughs for recovery from the anaesthetic and returned to the group of unmarked fish from which they were removed. To ensure proper control of quality, 25 marked fish from each marker were examined daily. In addition, fish that died shortly after marking were carefully examined in an effort to detect improper handling.

The entire production of each hatchery was sampled at time of release (3–8 weeks after marking) to estimate the proportion and numbers of marked fish released. The procedure for obtaining this sample was the same as for selecting fish for marking, except that fish initially removed by the closed section of the sampler were pooled and sampled again. The resultant sample (about 1 percent of the total production) was sorted into marked and unmarked groups and counted and weighed. These counts, together with an estimate of the proportion removed by the particular sampler, were used to estimate the proportions and numbers of marked fish in the release.

RECOVERY OF MARKS

The recovery phase of the investigation began in 1963 and will end in 1969 (table 2).

Sampling for marked fish was designed to cover four areas: major ocean fisheries from southeast Alaska to central California, Columbia River fisheries, parent hatcheries, and certain natural spawning grounds.

Sampling for marks in each area consists of recording numbers of fish examined for marks and the numbers recovered with each type of mark. In addition, all marked fish and a sample of unmarked fish are examined for age, length, and weight. It was recognized that occurrence of marks and compositions of age and size would change with time; thus, the sampling season was stratified into small units (usually biweekly for the ocean and weekly for the Columbia River fisheries).

The general fisheries being sampled are ocean commercial and sport; Columbia River commercial and sport; and Puget Sound sport. For purposes of sampling, most fisheries were further stratified by port of landing. Exceptions are the Alaska and British Columbia troll, purse seine, and gill net fisheries; Columbia River commercial and sport fisheries; and Puget Sound sport fishery, in which the stratification is by area of catch. The specific fisheries being sampled are listed in table

[3] Trade names referred to in this publication do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

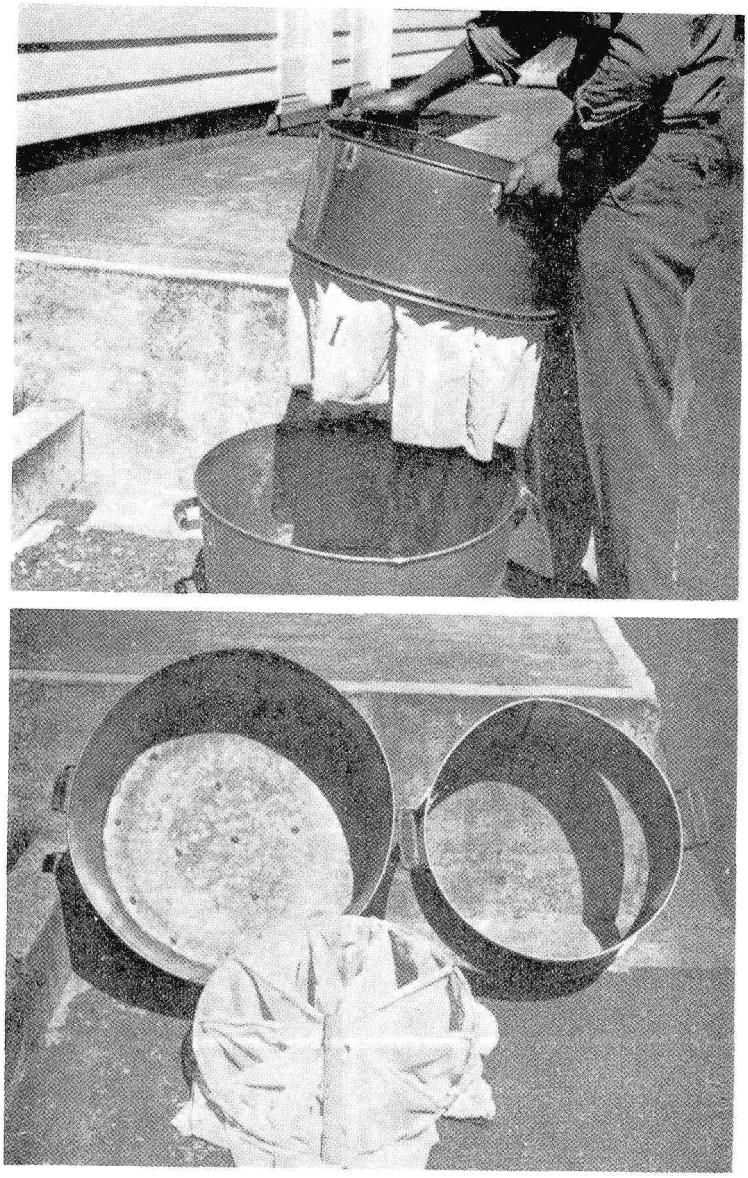


FIGURE 2.—Ten-part sampling net used to obtain fish for marking and to estimate the numbers of marked and unmarked fish released.

3 and shown in figure 3. General sampling levels for each time-location stratum were predetermined; typically, about 20 percent of the catch is sampled for marks, and from 50 to 100 unmarked fish are sampled to obtain age, length, and weight.

Catch data for each time-location stratum are provided by the management agencies. For most fisheries, the catch of chinook salmon in numbers of fish is an estimate. Commercial catches are estimated either from the total weight of landings and an estimate of average fish size or from total salmon landings (numbers) and an estimate of species composition. Estimates of sport catches are from measures of total effort and catch per-unit-effort or from salmon punch cards (filled out by anglers) together with independent sampling by the management agency.

Because the catch of hatchery-reared fish depends on length and timing of the fishing seasons as well as on the numbers of fish available, an estimate of the numbers of hatchery fish which escape the fishery is required to measure the

TABLE 3.—*Areas where catches were examined for marked fall chinook 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
Southeast Alaska		Zones 1, 3–15, 18, 22	Zones 1, 6, 8, 11, 15, 18, 19.		
British Columbia		Alaska area Zones 29, 40–43, Area C.	Zones 29, 40, 41–43		Zones 40–43
Washington ocean	Sekiu	Seattle	Juan de Fuca Strait.		
	Neah Bay	Neah Bay	Grays Harbor.		
	La Push	La Push	Willapa Bay.		
	Westport	Westport.			
	Ilwaco	Ilwaco.			
Puget Sound	Zones 6–12.				
Oregon ocean	Warrenton	Astoria.			
	Depoe Bay	Tillamook.			
	Newport	Nestucca.			
	Florence	Depoe Bay.			
	Reedsport	Newport.			
	Coos Bay	Florence.			
	Gold Beach	Reedsport.			
	Brookings	Coos Bay.			
		Port Orford.			
		Brookings.			
California ocean	Crescent City	Crescent City.			
	Eureka	Eureka.			
	Fort Bragg	Fort Bragg.			
	San Francisco	San Francisco.			
	Monterey	Monterey.			
Columbia River	Zones 1–5		Zones 1–6	Klickitat River.	

hatchery output. For this reason, plans for mark sampling also included examining the fish returning to the hatcheries and searching for marked fish on certain natural spawning grounds.

Fish returning to the hatcheries are counted and examined for marks. At each hatchery an effort is made to obtain data on age, length, and sex for 25 to 50 unmarked fish per week. In addition to searching for marks at the 12 participating hatcheries, returns to 5 other hatcheries (Abernathy, Speelyai, Toutle, Klaskanine, and Sandy; fig. 1) are also examined for marks.

To estimate natural spawning of hatchery-reared fish, surveys were conducted on hatchery streams as well as those adjacent to or near the hatcheries under study. These streams are Klickitat, Big White Salmon, Little White Salmon, Wind, Washougal, Kalama, Lewis, Elokomin, and Grays Rivers and Plympton and Big Creeks. These surveys were designed to estimate size of the total spawning population, as well as to sample for marks, age, and length.

All data collected during the recovery phase of the study are recorded on a standard form (fig. 4). Data on a group of fish examined for marks are recorded according to the format along the upper part of the form; data for individual marked recoveries are recorded on the same form according to the format along the lower part. A scale sample from each marked fish is sent along with the form to the Fish Commission of Oregon's mark processing center, where the age is determined and entered on the form.[4] Samples of individual unmarked fish are recorded and processed in the same way as the marked fish.

After appropriate coding (e.g., type of mark, fishery and gear, and port of landing) the data are transferred to data processing cards from which tabulations are made. The tabulations are then forwarded to the Biometrics Unit at the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash., where they are collated with catch information, and a summary report of each year's sampling effort is assembled.

SOURCES OF VARIATION

Two major sources of variation in the contribution of hatcheries are being considered. The first is the variation from year to year, which is the reason for extending the marking experiment over four brood years. The second source of variation is among hatcheries. To examine this, a group of fish at each of the four hatcheries was marked with a unique fin clip each year. Spring Creek and Kalama Hatcheries were allotted a special mark each year, and two additional special marks were rotated among eight of the remaining hatcheries so all hatcheries, except two, received special

[4] In some instances (British Columbia and Washington fisheries), ages are determined by the agency that collects the data.

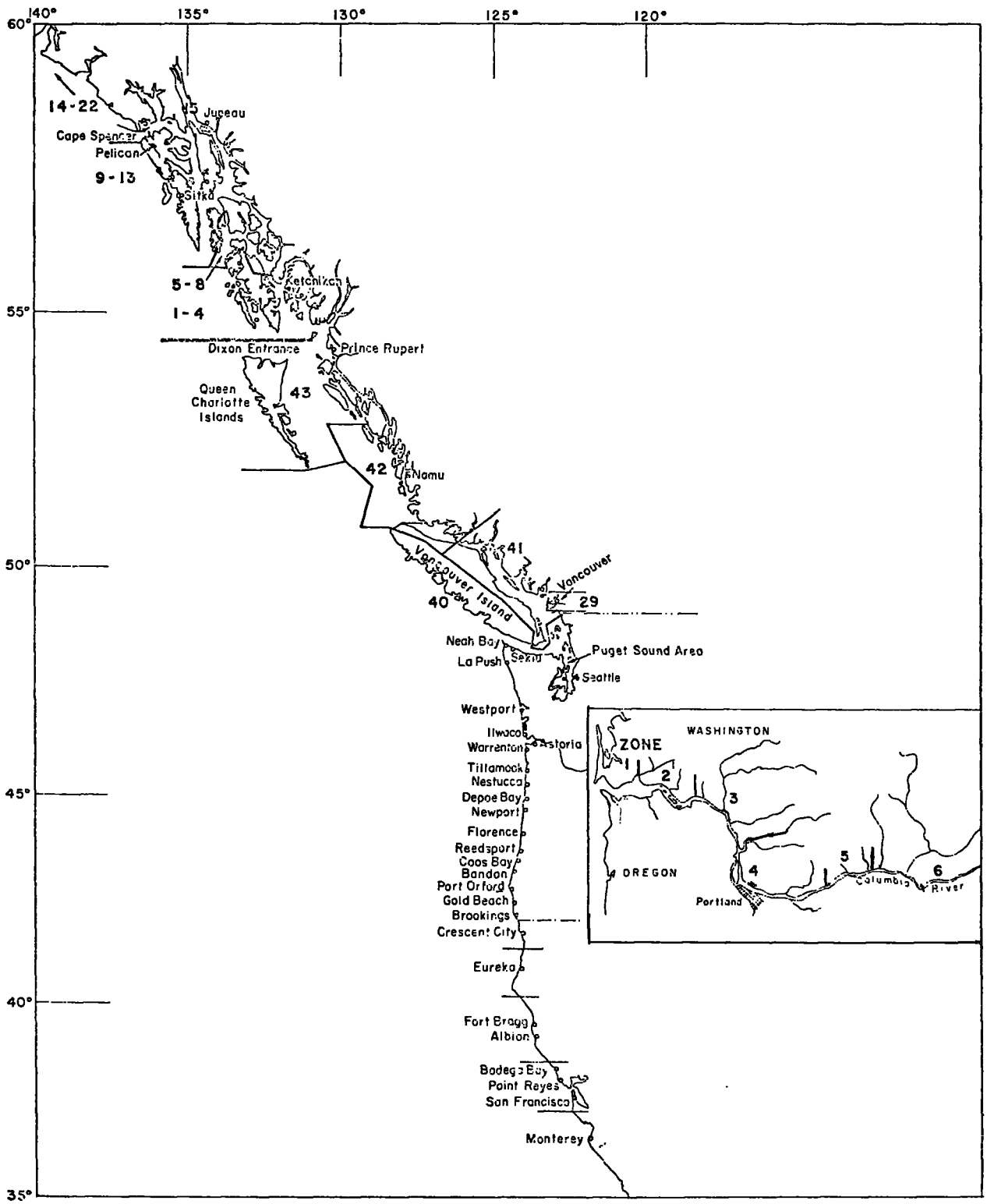


FIGURE 3.—Ports and zones sampled for marked fall chinook salmon of Columbia River origin.

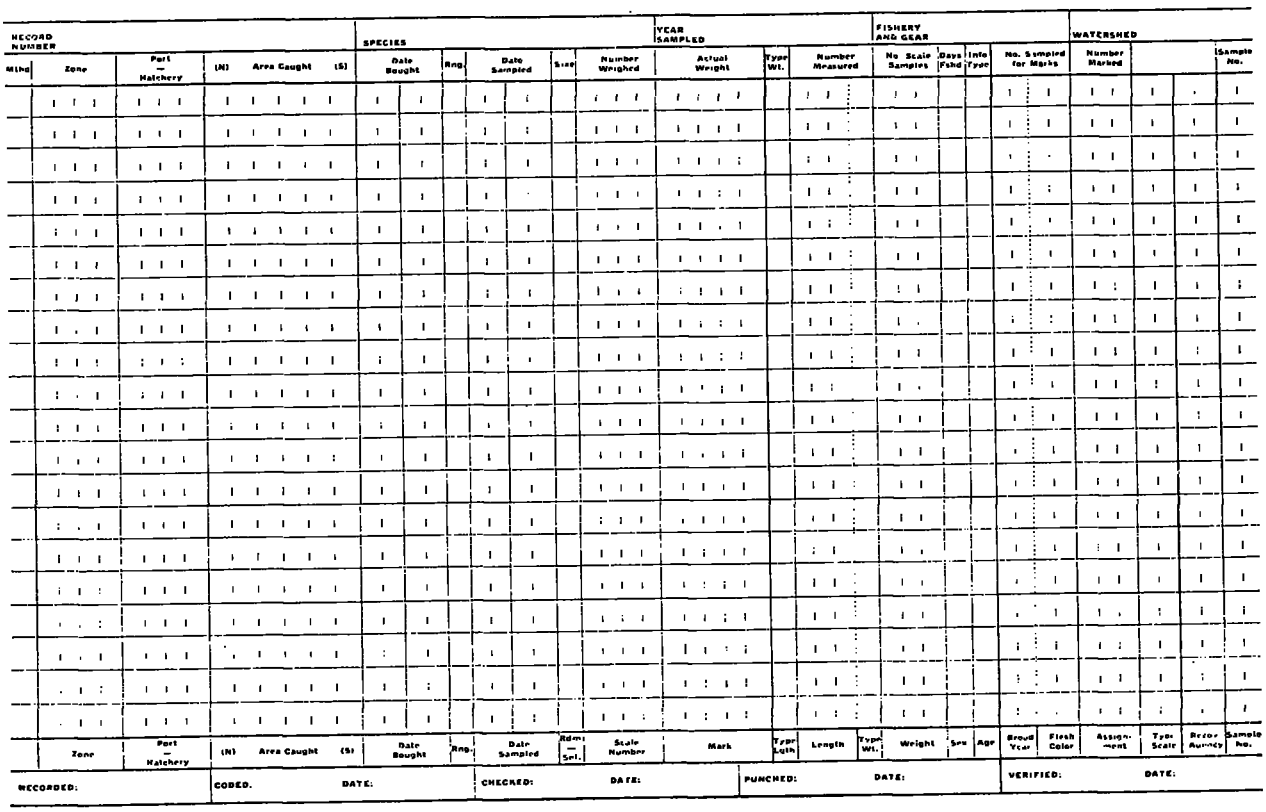


FIGURE 4.—Form for recording mark recoveries and biological data.

marks. Marks selected were the excised right or left ventral fin, with and without the adipose fin. In addition, part of the left maxillary bone was removed in the even numbered brood years and part of the right maxillary in odd numbered brood years. These marks, together with the hatcheries involved and expected age of appearance in the sampling area, are shown in table 2.

Procedures for selecting fish, marking them, and sampling them at release to estimate mark ratios were the same as described earlier for the common (adipose-maxillary) mark.

Certain items of information concerning the rearing history were collected at each hatchery to explain some of the expected variations in contribution between hatcheries and between years. This information included numbers of adults spawned, incidence of disease in adults,, mortalities during incubation of eggs and rearing of young, incidence and treatment of disease in progeny, diet, fish size at release, and water temperatures during incubation, rearing, and at the release site.

For the same purpose, groups of marked and unmarked fish obtained at time of release from each hatchery underwent numerous tests at Abernathy Salmon Cultural Laboratory. Variables of interest included physical capabilities, body composition, hematology, and pathology. Physical capability of each group of fish was indexed by use of a stamina tunnel; body composition of protein, lipid, ash, water and glycogen was determined by proximate analyses; hematology consisted of hematocrit determinations and chemical measurements of blood plasma to determine levels of calcium, phosphorus, chloride, glucose, protein, albumin, cholesterol, icteric index, creatinine, uric acid, ammonia, and urea; and pathology included examinations for disease organisms from which a "disease index" was determined.

ESTIMATING PROCEDURES

The contribution (catch) of hatchery-reared fish will be estimated, as noted earlier, from data on the proportion of hatchery fish that were marked (or expected marked to unmarked ratio), the chinook

salmon catch by time period within a season for a particular fishery, the number of fish examined for marks, and the number of marked fish recovered. In addition to obtaining an estimate of the catch of a given age group of hatchery fish, we are estimating the percentage contribution of hatchery fish to the total catch of that age group. This makes it necessary to subdivide the catch by age group on the basis of an estimated age composition.

For a particular fishery (e.g., Washington ocean sport fishery at Westport) let:

c_i = catch during i^{th} period

n_i = number of fish examined for marks during i^{th} period

n_{ijk} = number of marked fish with the k^{th} kind of mark and of the j^{th} age group recovered during the i^{th} period

p_{ijk} = proportion of n_i having k^{th} kind of mark and of the j^{th} age group

$= n_{ijk}/n_i$

Then an estimate of the catch of fish with the k^{th} kind of mark and of the j^{th} age group for the i^{th} period is:

$$m_{ijk} = p_{ijk} c_i \qquad (1)$$

An estimate of the catch of all marked fish of the j^{th} age group for the i^{th} period is:

$$m_{ij.} = c_i \sum_k p_{ijk} = \sum_k m_{ijk}$$

and an estimate of the catch of all marked fish of all age groups for the i^{th} period is:

$$m_{i..} = \sum_j m_{ij.}$$

The estimated catch of unmarked fish during the i^{th} period is then:

$$u_i = c_i - m_{i..}$$

If g_{ij} is the proportion of the sample of unmarked fish belonging to the j^{th} age group for the i^{th} period, then an estimate of the catch of unmarked fish of the j^{th} age group for the i^{th} period is:

$$u_{ij} = g_{ij} u_i$$

Hence, the estimate of the total catch (marked and unmarked) of the j^{th} age group for the i^{th} period is:

$$c_{ij} = u_{ij} + m_{ij.}$$

and the estimated seasonal catch of marked and unmarked fish of the j^{th} age group is:

$$c_{.j} = \sum_i c_{ij} \qquad (2)$$

Now, if we designate a particular hatchery evaluation mark (e.g., adipose-right maxillary) by setting $k=1$ in equation (1), then an estimate of the seasonal catch of Columbia River hatchery fish of the j^{th} age group having that mark is:

$$m_{.j1} = \sum_i p_{ij1} c_i \qquad (3)$$

If, for example, we are interested in marked hatchery fish (adipose-right maxillary mark) of the 1961 brood, then their estimated catch in 1963 as 2-year-old fish is:

$${}_3m_{.21} = \sum_i ({}_3p_{i21})\ ({}_3c_i)$$

where the presubscript denotes the last digit of the sampling year. Similarly, the estimated catch in 1964 as 3-year-old fish is:

$${}_4m_{.31} = \sum_i ({}_4p_{i31})\ ({}_4c_i)$$

and the estimated catch in 1965 as 4-year-old fish is:

$${}_5m_{.41} = \sum_i ({}_5p_{i41})\ ({}_5c_i)$$

and similarly for still later years of capture.

An approximate variance estimate for $m_{.j1}$ is:

$$V(m_{.j1}) = C^2 \sum_i (w^2{}_i p_{ij1}/n_i) + V(C)\left[(\sum_i w_i p_{ij1})^2 - \sum_i w^2{}_i p_{ij1}/n_i\right] \qquad (4)$$

where $C = \sum_i c_i$, $w_i = c_i/C$ and $V(C)$ is the variance of the estimated seasonal catch. If the catch, C, is known, then only the first item in (4) contributes to the variance estimate.

Now if ${}_ar_{j1}$ is the expected proportion of Columbia River hatchery fish of the j^{th} age group in sampling year "a," which is marked with a particular mark (e.g., let $k=1$ for adipose–right maxillary), then an estimate of the seasonal catch of hatchery fish (marked and unmarked) of the j^{th} age group in sampling year "a" is (from equation 3):

$${}_aH_j = {}_am_{.j1}/{}_ar_{j1} \qquad (5)$$

Hence, if, as in the example above, we are interested in the contribution of the 1961–brood hatchery fish, then an estimate of their catch (marked and unmarked) in 1963 as 2-year-old fish is:

$${}_3H_2 = {}_3m_{.21}/{}_3r_{21}$$

Likewise then, the estimated catch in 1964 as 3-year-old fish is:

$${}_4H_3 = {}_4m_{.31}/{}_4r_{31}$$

and similarly for the 1965 and 1966 sampling years.

An alternative procedure for estimating the seasonal catch of hatchery fish of the j^{th} age group in sampling year "a" is:

$$ {}_aH_j = ({}_aM_{.j1}/{}_aq_{j1}) + \sum_{k=1}^{5} {}_aM_{.jk} \qquad (6) $$

where ${}_aq_{j1}$ is the expected marked (adipose–right maxillary) to unmarked ratio. The first term in this equation is an estimate of the catch of unmarked hatchery fish, and the second term is the estimated total catch of marked hatchery fish (summed over the five marks identifying hatchery fish).

The percent contribution of hatchery fish to the catch of the j^{th} age group in year "a" is then (from equation 2): ${}_aP_j = 100({}_aH_j/{}_ac_{.j})$.

Equations (5) and (6) are the basic equations for estimating the catch of Columbia River hatchery-reared fall chinook salmon of a given age in a given year. The numerator, ${}_aM_{.j1}$, in equation (5) is the estimated number of marked fish (adipose–right maxillary) in the catch at a particular fishery-port combination. As stated before, the denominator, ${}_ar_{j1}$, is the expected proportion that ${}_aM_{.j1}$ is of the total catch of hatchery fish of the same age group. Granting certain assumptions (set forth in the following section), the proportion of adipose-right maxillary marked fish in the hatchery releases is an estimate of ${}_ar_{j1}$. Hence, if r is the proportion of marked fish in the 1961 brood hatchery releases, we set

$$ {}_3r_{21} = {}_4r_{31} = {}_5r_{41} = {}_6r_{51} = r $$

So, we assume that the expected proportions of marked age 2 hatchery fish in 1963, age 3 fish in 1964, etc. are identical and equal to the proportion of marked fish in the releases of the 1961 brood hatchery fish.

The estimated proportion of marked fish in the total release of each brood year from the 12 hatcheries is based on estimates of the proportion of marked fish in the release and the size of release at each of the hatcheries. These latter estimates were obtained from a sampling procedure at the time of release at each of the hatcheries. If N_0 is the total number of fish released from a hatchery, then the number of fish removed by the sampling device at the first stage of sampling is:

$$ N_1 = s_1 N_0 $$

where s_1 is the actual proportion of the total number of fish removed by the sampling device. These fish, N_1, were then sampled again. If s_2 is the actual proportion of the total number of fish, N_1, removed by the sampling device during the second stage of sampling, then the number of fish which comprise the final sample is:

$$ N_2 = s_2 N_1 = s_2 s_1 N_0 $$

Hence, if s is an estimate of the proportion of fish removed by the sampler during a single stage (i.e., s is an estimate of both s_1 and s_2), then an estimate of the numbers of fish released, N_0, is:

$$ N = N_2/s^2 $$

The estimated proportion of fish removed by the sampling device was obtained from a number of trials using known numbers of fish, and the number of fish removed by the sampling device, N_2, was counted and sorted into the marked and unmarked groups. Thus, if M is the count of marked fish, then the estimated proportion of marked fish in the release is simply:

$$ r = M/N_2 $$

If N_i and r_i are the above estimated quantities for the i^{th} hatchery, then the estimated proportion, r, of marked fish in the total release from all hatcheries is:

$$ r = \sum_i w_i r_i $$

where $w_i = N_i/\Sigma N_i$

An estimate of the marked to unmarked ratio for the hatchery releases is similarly obtained.

ASSUMPTIONS

Several assumptions are inherent in the foregoing method of estimating the contribution of hatchery-reared fall chinook salmon to the fisheries. Three basic assumptions are:

1. A marked fish is identifiable as a marked fish throughout its life.
2. All observed chinook salmon having the kind of mark used on the hatchery-reared fish are indeed hatchery fish.
3. Chinook salmon are correctly aged from scale examinations and information on size of fish and date of capture.

In addition, we assume that marked fish behave like the unmarked hatchery fish. In particular we must assume:

4. Marked and unmarked hatchery fish have the same survival rates and maturity schedules.
5. Marked and unmarked hatchery fish have the same ocean distribution and are equally vulnerable to the fisheries.

Finally, because part of all hatchery releases bear the same mark, we assume that:

6. Either the ocean distribution and timing of migration of fish from each of the hatcheries are the same or the same proportion of each hatchery's production is marked.

The appropriateness of the estimating procedures described above is obviously dependent upon the validity of these assumptions. For this reason, the results must be considered as preliminary until sufficient data are collected to judge their validity. For example, if marked and unmarked fish have different survival rates, then the marked to unmarked ratio in the hatchery release is not appropriate [in equation (6)] and some adjustment should be made. To test the assumptions, additional studies and data collections were incorporated within the design of the marking experiment.

In connection with the first assumption (permanence of fin marks), marked juvenile fish were held and periodically examined to determine degree of mark regeneration. Also, illustrated forms on which missing fins or parts of fins are shaded out provide information on the samplers' interpretation of marked fish (fig. 5).

To test the second assumption (origin of fish marked with hatchery marks), fish were examined for natural marks while being marked. In addition, the cooperating fishery agencies agreed not to use the combination of marks used in this study on any group of 1965–brood chinook salmon. This group will be sampled as 2-, 3-, and 4-year-old fish during the 1967, 1968, and 1969 sampling years. Any observed marks of the kind used in this study will be from the natural loss of fins.

A test of scale readers was designed to test the third assumption (accuracy of age assignments). Scales from 400 marked fish of known age were submitted to six readers from the Fisheries Research Board of Canada, Washington Department of Fisheries, Oregon Game Commission, Fish Commission of Oregon (two readers), and Bureau of Commercial Fisheries. Length of fish and date of capture were available for each scale.

The fourth assumption (equality of survival rates and maturity schedules) will be examined from data on a different type of mark applied to fish at one of the hatcheries. At Little White Salmon Hatchery, a fraction of the 1964 brood was marked with TM 50 (oxytetracycline) that was added to the diet. This mark was selected to identify a hatchery stock because it apparently does not affect their growth or survival (Weber and Ridgway, 1967). As a result, some of the fish are double marked—with a finclip and TM 50. Returns to the hatchery in 1966, 1967, 1968, and 1969 will be examined for changes since release in the proportion of TM 50 marked fish which also have the finclip. In addition to the TM 50 marking at this hatchery, data bearing on the changes in marked to unmarked ratios (i.e., finclip vs. totally unmarked) between release and return will be available from the returns to each of the participating hatcheries.

With the resources available, we could not test the fifth assumption (equality of ocean distribution and vulnerability). Indirect evidence may be obtained, however, by comparing the ocean distribution of marked fish with the distribution as determined by past tagging experiments in the ocean.

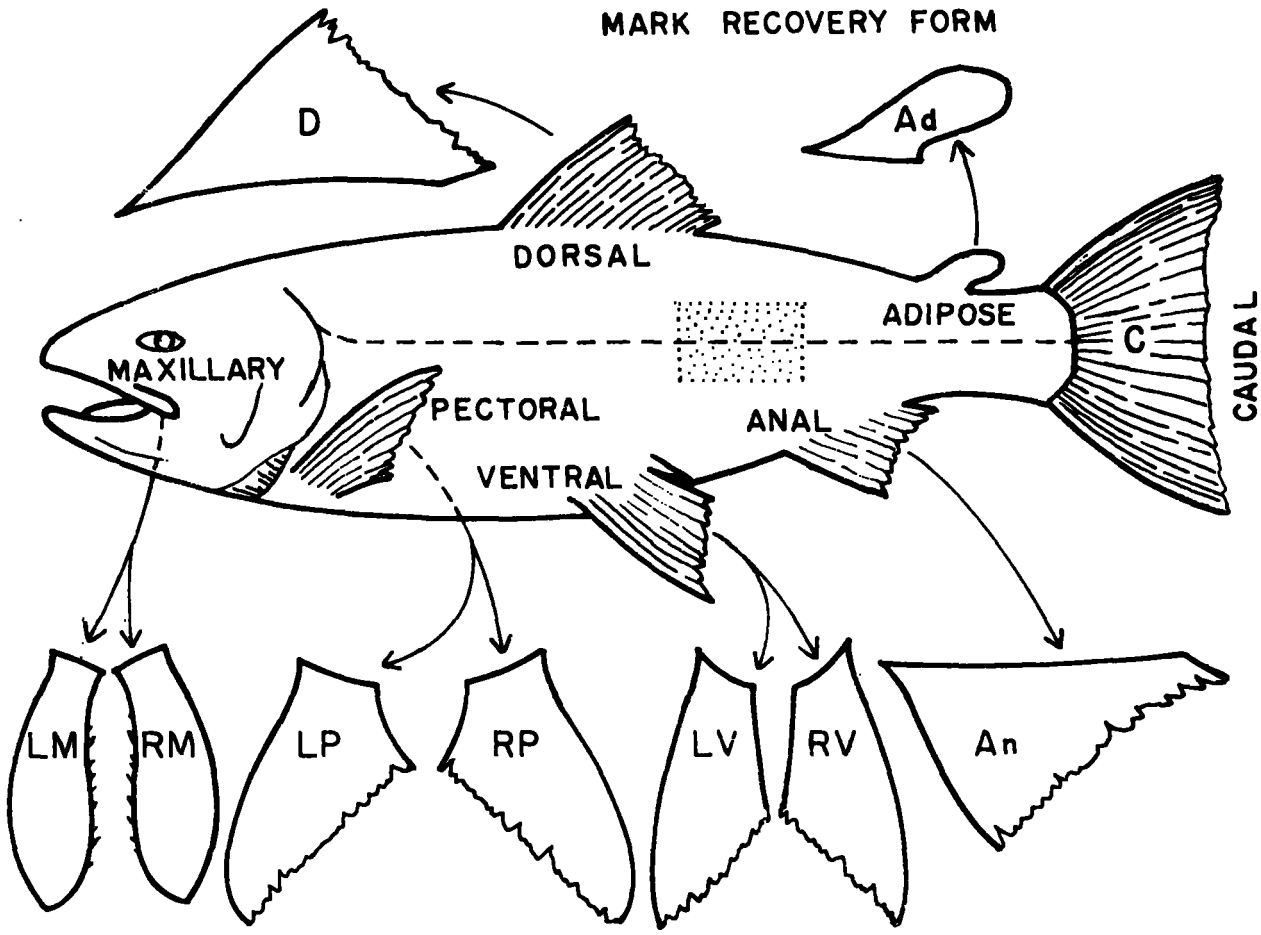
The sixth assumption (equality of ocean distribution or proportion marked among hatcheries) will be examined from data collected in that part of the study designed to examine the variations in contribution between hatcheries and, of course, from the data collected from each hatchery at the time of release.

RELEASES OF FISH

The marking phase of the hatchery contribution study (concluded in 1965) included marking a portion of the fall chinook production of each of the 12 hatcheries with the same mark; marking a portion of the production of 4 hatcheries with a unique mark; measuring the quality of marking; examining hatchery fish for naturally missing fins; and obtaining samples of fish to determine regeneration of marks and for measuring certain physical and physiological characteristics of the releases for each of the brood years. Analyses of these latter data in terms of explaining

AGENCY:

SCALE ENVELOPE NO.



COMMENTS:

FIGURE 5.—Form for recording type of mark observed.

sources of variation must await completion of the study.

Table 4 shows for each mark type and brood year the estimated numbers of chinook salmon released and the proportions of fish that were marked, and ratios of marked-to-unmarked fish. Detailed data for each hatchery are given in appendix tables 1, 2, 3, and 4.

During the 4 years of marking (i.e., 1961-64 broods), 213 million fall chinook salmon were released from the hatcheries under study. Included were 21.3 million fish with the adipose-maxillary mark. This mark, common to all of the 12 hatcheries, was 9.9 to 10.1 percent of the releases. In addition, the release included 9.6 million fish with special marks unique to individual hatcheries. These special marks were 9.1 to 30.5 percent of the yearly releases from the hatcheries where used.

Samples of over 100,000 marked fish were examined each year and graded according to quality of mark. A score of 5 was assigned for a good mark, 3 for an acceptable mark, and 0 for an unacceptable mark. Average scores were 4.9, 4.9, 4.9, and 4.8 for 1961, 1962, 1963, and 1964 broods, respectively. The lowest average score for any hatchery-mark type combination was 4.1; all remaining scores were greater than 4.5. Although a certain

TABLE 4.—*Estimated numbers and mark ratios of fall chinook salmon released from study hatcheries for 1961–64 brood years*

Brood year	Mark	Origin of mark	Marked release	Marked and unmarked release	Marked/ Marked and unmarked	Marked/ unmarked
			Number	*Number*		
1961	Ad-RM	All hatcheries	5,446,439	53,653,214	0.1015	0.1193
1962	Ad-LM	do	5,249,079	52,470,003	.1000	.1163
1963	Ad-RM	do	5,986,464	60,112,063	.0996	.1155
1964	Ad-LM	do	4,638,237	46,778,552	.0992	.1175
		Subtotal	21,320,219	213,013,832		
1961	Ad-LV-RM	Spring Creek	1,133,019	10,925,933	.1037	.1308
	Ad-RV-RM	Kalama	475,964	4,906,845	.0970	.1210
	LV-RM	Elokomin	480,533	1,575,000	.3051	.5075
	RV-RM	Oxbow	450,446	4,549,959	.0990	.1241
1962	Ad-LV-LM	Spring Creek	866,892	8,408,267	.1031	.1299
	Ad-RV-LM	Kalama	437,669	4,599,326	.0952	.1173
	LV-LM	Grays	241,494	1,359,761	.1776	.2437
	RV-LM	Cascade	541,158	4,217,910	.1283	.1667
1963	Ad-LV-RM	Spring Creek	751,243	7,467,629	.1006	.1264
	Ad-RV-RM	Kalama	456,158	4,883,937	.0934	.1156
	LV-RM	Klickitat	521,610	2,888,208	.1806	.2501
	RV-RM	Big Creek	579,967	1,985,838	.2920	.4770
1964	Ad-LV-LM	Spring Creek	600,953	6,554,455	.0917	.1139
	Ad-RV-LM	Kalama	319,412	3,496,560	.0914	.1129
	LV-LM	Bonneville	957,110	9,887,575	.0968	.1205
	RV-LM	Little White Salmon	797,345	8,365,579	.0953	.1184
		Subtotal	9,610,973			
		Total	30,931,192			

amount of subjectivity is inherent in such a scoring system, these values indicate that a high quality was attained.

During the marking, over 30 million fingerlings were examined for naturally missing adipose and ventral fins. A total of 156 missing adipose and 201 missing ventral fins were observed. Although insignificant in relation to the fish examined, these numbers represent the frequency of naturally missing fins for these hatchery-reared fish only. A more direct measure of this source of error (i.e., occurrence of natural marks) in the hatchery contribution study will be possible during the years when fish of the 1965 brood are in the fishery. The marks used in the study were not applied to the 1965 brood.

Marked fingerlings obtained at time of release from the hatcheries were held in salt-water rearing ponds at Bowman Bay, Wash., for as long as 34 months. Periodic examinations were made to determine the extent of regeneration of the fin and maxillary marks, and the results are summarized in table 5.

Regeneration of the adipose mark was not apparent. Similarly, complete regeneration of the ventral mark did not occur. Some regeneration of the ventral mark, however, was apparent for a substantial portion of the fish in each group (up to 47 percent). In most cases, the ventral fin regenerated to less than 25 percent of its original size (as judged by the size of the paired ventral

TABLE 5.—*Regeneration of adipose fin, maxillary bone and ventral fin in test lots of fish, 1961–64 brood years, held at Bowman Bay, Wash.*

Adipose fin

Brood year	Age	Fish examined	Regeneration	
	Months	*Number*	*Number*	*Percent*
1961	20	115	0	0
1962	12	626	0	0
	23	452	0	0
	29	381	0	0
1963	12	872	0	0
	17	551	0	0
	26	371	0	0
	34	311	0	0
1964	14	416	0	0
	27	312	0	0

Maxillary bone

Brood year	Age	Fish examined	Complete regeneration	
	Months	*Number*	*Number*	*Percent*
1961	20	291	20	6.9
1962	12	1,079	32	3.0
	23	734	38	5.2
	29	652	76	11.6
1963	12	1,615	8	.5
	17	1,160	25	2.2
	26	774	26	3.4
	34	664	22	3.3
1964	14	751	12	1.6
	27	567	5	.9

Ventral fin

Brood year	Age	Fish examined	Regeneration			
			Less than 25 percent		Greater than 25 percent	
	Months	*Number*	*Number*	*Percent*	*Number*	*Percent*
1961	20	291	116	39.9	[1] 14	4.8
1962	12	1,079	444	41.1	64	5.9
	23	734	293	39.9	37	5.0
	29	652	247	37.9	39	6.0
1963	12	1,615	559	34.6	[2]	
	17	1,160	408	35.2	62	5.3
	26	774	310	40.0	41	5.3
	34	664	182	27.4	33	5.0
1964	14	575	211	36.7	22	3.8
	27	432	86	19.9	16	3.7

[1] Complete regeneration did not occur in any of the groups.
[2] Degree of regeneration was not determined.

fin). Even where the regeneration was greater (up to 6 percent of the fish examined), the marks were readily identifiable owing to a deformation of the fin rays.

The maxillary mark completely regenerated for varying proportions of the groups examined. The relatively high occurrence of regeneration for the 1961- and 1962-brood fish (6.9–11.6 percent) was the basis for removing more of the maxillary bone for the next 2 brood years. Only the tip of the maxillary was removed for the 1961 and 1962 broods. For the 1963 and 1964 broods, the maxillary was excised at a point below the middle of the eye. This change in marking procedure is reflected in the smaller percentages of fish with regeneration (1–3 percent) for the 1963 and 1964-brood fish.

It is likely that these test fish were examined in greater detail and under better conditions than can be expected in actual sampling. The results of the examinations, however, make it doubtful that fin regeneration is an important source of error in the total program. Maxillary regeneration causes some difficulties and will be considered in a later section.

MARK RECOVERIES AND ESTIMATED CATCH OF MARKED FISH

The mark-sampling phase of the program began in 1963 when the 1961-brood-year fish first entered some of the fisheries as 2-year-olds. During the first year, sampling was limited to the Washington and Oregon ocean fisheries, Columbia River fisheries, and hatchery returns. Beginning in 1964, sampling was expanded to include most chinook salmon fisheries from Monterey, Calif., to and including southeast Alaska. The results reported here concern recoveries of the 1961 brood in 1963, 1964, 1965, and 1966. Recoveries from this brood in 1967 were minor.

The total catches of chinook salmon in the fisheries that were sampled and numbers of fish examined each year for marks and for age are given in table 6. Over the 4 years of sampling, 23 percent of the catch of 8.5 million fish were examined for marks. In addition, 1.5 percent of the total catch was sampled for age determinations and other data (e.g., length and weight). Mark sampling percentages were 28.3, 26.6, 19.8, and 21.5 percent for 1963, 1964, 1965, and 1966, respectively.

TABLE 6.—*Catches of chinook salmon and number of fish examined for marks and age, 1963–66*

Year	Catch [1] chinook salmon		Sampled for marks	Sampled for age
	1961 brood	All ages		
	Number of fish			
1963	41,786	570,172	161,460	20,000
1964	1,565,549	2,671,976	709,660	33,000
1965	998,849	2,572,919	508,730	34,000
1966	206,765	2,645,537	569,265	40,000
Total	2,812,949	8,460,604	1,949,115	127,000

[1] Total catch is only for those fisheries sampled.

RECOVERIES OF MARKED FISH

Table 7 summarizes all marks of possible Columbia River hatchery origin (1961 brood year) recovered in the fisheries. Included in the table are recoveries of marks that could be the result of maxillary regeneration. A total of 9,573 marked fish of possible Columbia River hatchery origin were recovered during the 4 years of sampling. Although fairly large numbers of marked fish of the 1961 brood were recovered in 1966 and during the limited sampling in 1963, most of them were recovered as 3-year-old fish in 1964. Exceptions were the fish marked at Kalama Hatchery; slightly more of these fish were recovered in 1965 than in 1964.

The distribution of recoveries for each year by region of capture and type of fishery is shown in table 8. Only recoveries of the full marks are listed. The distribution of recoveries of the possible experimental marks was similar.

As 2-year-old fish, those with 1961-brood marks were recovered only in the Washington ocean sport and Columbia River gill net fisheries. Although many fisheries were not sampled in 1963, 2-year-old mark recoveries of the 1962- and 1963-brood fish indicate that the contribution of this age group to other fisheries is relatively minor. By 1964 the marked fish were distributed over the entire range of sampling. For ocean fisheries they appeared most frequently, however, in Washington and British Columbia catches (although not shown in table 8, the bulk of the British Columbia recoveries were from the troll fishery landings on the west coast of Vancouver Island). The distributions of recoveries in 1965 and 1966 were similar to 1964 but in fewer numbers.

The distributions of marked fish that originated from Spring Creek and Kalama Hatcheries were different. Proportionately more of the Kalama

TABLE 7.—*Marked 1961 brood-year chinook salmon of possible Columbia River hatchery origin recovered in the fisheries, 1963–66*

Origin of mark	Mark	Year of capture				Total
		1963	1964	1965	1966	
		Number of fish				
All hatcheries	Ad-RM	110	4,145	1,885	144	6,284
	Ad	79	561	189	30	859
Spring Creek	Ad-LV-RM	29	861	270	5	1,165
	Ad-LV	19	125	42	2	188
Kalama	Ad-RV-RM	5	248	268	64	585
	Ad-RV	1	17	35	5	58
Elokomin	LV-RM	0	38	18	2	58
	LV	3	75	57	21	156
Oxbow	RV-RM	3	54	16	5	78
	RV	3	65	55	24	147
Total		252	6,189	2,835	302	9,578

marks were recovered in the northern portions of the sampling range. For example in 1964, 3.3 times as many Kalama marks were recovered in the British Columbia troll fishery than were recovered in the Washington troll fishery. Such a comparison for Spring Creek marks shows a figure of 1.3 times. Moreover, Kalama marked fish were the only ones with marks (specific to a hatchery) recovered in the southeast Alaska fisheries.

Distributions of recoveries of marked fish that originated from Elokomin and Oxbow Hatcheries were similar to the distribution of Spring Creek recoveries, but the number of marks recovered was much smaller.

Recoveries of marked fall chinook salmon of the 1961 brood from the Columbia River escapement are presented in appendix table 5 and summarized in table 9. As in the ocean fisheries, most of the recoveries at the hatcheries were made in 1964. The exception was the relatively high 1965 recovery of marks originating from Kalama Hatchery.

Mark recoveries at hatcheries were obtained from examination of the entire hatchery returns. Therefore, it is impossible to make meaningful comparisons between hatchery recoveries and recoveries in tributary streams and fisheries, where only a portion of the populations was examined for marks.

ESTIMATED CATCHES OF MARKED FISH

As shown by equation (3), the total catch of fish with a particular mark is estimated for each stratum (fishery, port of landing or area of capture, and time period) from the catch and the proportion of fish having the mark in the catch sample. (It is assumed that a random sample is examined for marked fish and that all marked fish are observed.) The annual catch of fish with a particular mark is estimated for each fishery category (e.g., Washington troll fishery) by summing over the time periods and appropriate ports of landing

TABLE 8.—*Marked 1961-brood Columbia River chinook salmon recovered by year, region of capture, and type of fishery, 1963–66*

Origin and type of mark	Year	California		Oregon		Washington			Puget Sound	British Columbia			S.E. Alaska		Columbia River		
		Sport [1]	Commercial [2]	Sport	Commercial	Sport	Commercial		Sport	Troll	Gill net	Purse seine	Commercial		Sport	Commercial	
							Troll	Gill net					Troll	Gill net		Gill net	Dip net
		Number of recoveries															
All hatcheries (Ad-RM).	1963	(*)	(*)	0	0	88	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	22	(*)
	1964	0	4	18	102	389	1,057	2	(*)	1,654	1	1	0	0	1	880	36
	1965	0	0	7	6	91	128	3	0	505	1	0	2	0	0	1,106	6
	1966	0	1	0	0	13	14	0	0	63	0	(*)	0	(*)	0	53	0
Spring Creek (Ad-LV-RM).	1963	(*)	(*)	0	0	23	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	6	(*)
	1964	0	3	1	31	81	246	0	(*)	321	0	0	0	0	0	178	0
	1965	0	0	0	2	12	21	1	0	41	0	0	0	0	0	193	0
	1966	0	0	0	0	0	0	0	0	2	0	(*)	0	(*)	0	3	0
Kalama (Ad-RV-RM).	1963	(*)	(*)	0	0	5	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	0	(*)
	1964	0	1	0	7	20	49	0	(*)	161	0	0	1	0	0	9	0
	1965	0	0	0	2	14	35	1	0	104	0	0	5	0	0	107	0
	1966	0	0	0	0	1	4	0	0	24	0	(*)	2	(*)	0	33	0
Elokomin (LV-RM).	1963	(*)	(*)	0	0	0	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	0	(*)
	1964	0	1	1	4	3	14	0	(*)	12	0	0	0	0	0	3	0
	1965	0	0	0	2	3	2	0	0	2	0	0	0	0	0	9	0
	1966	0	0	0	0	0	1	0	0	1	0	(*)	0	(*)	0	0	0
Oxbow (RV-RM).	1963	(*)	(*)	0	0	3	0	(*)	(*)	(*)	(*)	(*)	(*)	(*)	0	0	(*)
	1964	0	0	2	9	8	23	0	(*)	4	0	0	0	0	0	8	0
	1965	1	0	1	1	0	3	0	0	7	0	0	0	0	2	1	0
	1966	0	0	0	0	2	0	0	0	1	0	(*)	0	(*)	0	2	0

*No sampling.
[1] All sport fishing is by rod and reel.
[2] Unless otherwise noted commercial fishing is by trolling.

TABLE 9.—*Recoveries of 1961-brood fall chinook salmon in the Columbia River escapement by type of mark, recovery location, and year of capture, 1963–66*

Origin of mark	Mark	Recovery location [1]											
		Study hatcheries				Other hatcheries				Tributary streams			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Numbers of recoveries											
All hatcheries	Ad-RM	100	1,296	679	57	(*)	4	1	0	(*)	53	104	9
	Ad	24	215	167	2	(*)	0	0	0	(*)	11	5	0
Spring Creek	Ad-LV-RM	41	364	121	1	(*)	0	0	0	(*)	1	1	0
	Ad-LV	5	51	23	1	(*)	0	0	0	(*)	0	0	0
Kalama	Ad-RV-RM	0	8	112	38	(*)	5	0	0	(*)	0	15	4
	Ad-RV	0	0	4	0	(*)	0	0	0	(*)	0	1	1
Elokomin	LV-RM	2	4	1	0	(*)	0	0	0	(*)	4	1	0
	LV	0	8	5	0	(*)	2	2	0	(*)	0	0	1
Oxbow	RV-RM	4	52	22	1	(*)	0	0	0	(*)	0	0	0
	RV	3	7	10	0	(*)	0	0	0	(*)	0	0	0
Total		179	2,005	1,144	100	(*)	11	3	0	(*)	69	127	15

*Not sampled.
[1] The "study hatcheries" include the 12 hatcheries participating in the marking program. "Other hatcheries" include Abernathy, Speelyai, Toutle, Klaskanine, and Sandy Hatcheries. "Tributary streams" include those tributaries listed in an earlier section.

(or area of capture). The same system is used to estimate the total number of marked fish in spawning populations of tributary streams.

Estimated numbers of marked 1961-brood fish caught in the fisheries, returning to the hatcheries and escaping to tributary streams, are listed in table 10. Estimated numbers include fish which had a partial mark only—not a complete double or triple mark—(e.g., Ad only instead of Ad–RM or Ad–LV only instead of Ad–LV–RM). These numbers are substantial—for example, we estimated that the fisheries took 2,710 adipose-only marked fish or about 14 percent of the number with the full mark (Ad–RM).

The partial marks were from naturally marked fish, from experimentally marked fish with complete regeneration of the maxillary mark, or possibly both. From the mark regeneration experiment described earlier, we expected complete regeneration of the maxillary mark for about 12 percent of the marked fish over a 2.5-year period. To determine if the percentages observed can be explained by the expected regeneration of the maxillary mark, it is necessary to make a detailed

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*

Region	Fishery type	Ad-RM				Ad				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Number of fish											
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	0	7	0	(*)	2	23	2	(*)	2	30	2
British Columbia	do	(*)	4,106	1,871	235	(*)	566	370	68	(*)	4,672	2,241	303
Washington	Sport	375	1,681	416	67	196	224	104	15	571	1,905	520	82
	Commercial	0	3,241	455	41	3	397	59	8	3	3,638	514	49
Oregon	Sport	0	72	26	0	0	93	16	0	0	165	42	0
	Commercial	0	324	10	0	0	45	12	0	0	369	22	0
California	Sport	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
	Commercial	(*)	23	0	6	(*)	0	4	0	(*)	23	4	6
Subtotal	Sport	375	1,753	442	67	196	317	120	15	571	2,070	562	82
	Commercial [1]	0	7,694	2,343	282	3	1,010	468	78	3	8,704	2,811	360
Columbia River fisheries	Sport	0	7	0	0	0	14	0	0	0	21	0	0
	Commercial [2]	72	2,151	3,544	176	76	297	92	24	148	2,448	3,636	200
Total	All fisheries	447	11,605	6,329	525	275	1,638	680	117	722	13,243	7,009	642
Columbia River escapement:													
Study hatcheries	[3]	100	1,296	679	57	24	215	167	2	124	1,511	846	59
Other hatcheries	[4]	(*)	4	1	0	(*)	0	0	0	(*)	4	1	0
Tributary streams		(*)	393	355	21	(*)	74	11	0	(*)	467	366	21
Total	Escapement	100	1,693	1,035	78	24	289	178	2	124	1,982	1,213	80

*Not sampled.
[1] Primarily troll fisheries.
[2] Primarily gill net.
[3] Twelve hatcheries participating in the marking program.
[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*—Continued

Region	Fishery type	Ad-LV-RM (Spring Creek)				Ad-LV				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Number of fish											
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
British Columbia	do	(*)	767	140	5	(*)	74	24	0	(*)	841	164	5
Washington	Sport	89	354	52	0	63	77	45	0	152	431	97	0
	Commercial	0	869	78	0	4	215	4	0	4	1,084	82	0
Oregon	Sport	0	5	0	0	4	44	4	0	4	49	4	0
	Commercial	0	73	16	0	0	8	4	0	0	81	20	0
California	Sport	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
	Commercial	(*)	15	0	0	(*)	10	0	0	(*)	25	0	0
Subtotal	Sport	89	359	52	0	67	121	49	0	156	480	101	0
	Commercial [1]	0	1,724	234	5	4	307	32	0	4	2,031	266	5
Columbia River fisheries	Sport	6	0	0	0	0	0	16	0	0	0	16	0
	Commercial [2]	19	453	608	10	3	65	61	7	22	518	669	17
Total	All fisheries	108	2,536	894	15	74	493	158	7	182	3,029	1,052	22
Columbia River escapement:													
Study hatcheries	[3]	41	364	121	2	5	51	23	1	46	415	144	3
Other hatcheries	[4]	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
Tributary streams		(*)	1	4	0	(*)	0	0	0	(*)	1	4	0
Total	Escapement	41	365	125	2	5	51	23	1	46	416	148	3

*Not sampled.

[1] Primarily troll fisheries.
[2] Primarily gill net.
[3] Twelve hatcheries participating in the marking program.
[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*—Continued

Region	Fishery type	Ad-RV-RM (Kalama)				Ad-RV				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Number of fish											
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	5	14	4	(*)	0	21	0	(*)	5	35	4
British Columbia	do	(*)	420	480	89	(*)	21	25	6	(*)	441	480	95
Washington	Sport	17	74	72	5	4	4	28	4	21	78	100	9
	Commercial	0	132	122	7	0	17	20	0	0	149	142	7
Oregon	Sport	0	0	0	0	0	0	0	0	0	0	0	0
	Commercial	0	18	4	0	0	3	0	0	0	21	4	0
California	Sport	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
	Commercial	(*)	2	0	0	(*)	0	0	0	(*)	2	0	0
Subtotal	Sport	17	74	72	5	4	4	28	4	21	78	100	9
	Commercial [1]	0	577	595	100	0	41	66	6	0	618	661	106
Columbia River fisheries	Sport	0	0	0	0	0	0	0	0	0	0	0	0
	Commercial [2]	0	32	377	106	0	6	22	5	0	38	399	111
Total	All fisheries	17	683	1,044	211	4	51	116	15	21	734	1,160	226
Columbia River escapement:													
Study hatcheries	[3]	0	8	112	38	0	0	4	0	0	8	116	38
Other hatcheries	[4]	(*)	5	0	0	(*)	0	0	0	(*)	5	0	0
Tributary streams		(*)	0	56	9	(*)	0	4	2	(*)	0	60	11
Total	Escapement	0	13	168	41	0	0	8	2	0	13	176	49

*Not sampled.
[1] Primarily troll fisheries.
[2] Primarily gill net.
[3] Twelve hatcheries participating in the marking program.
[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

examination of the data on mark recoveries and accuracy of determining the age of fall chinook salmon.

In test readings of scales from marked chinook salmon of known age, six scale readers correctly aged (total age) 83 percent of the 400 test scales (Godfrey, Worlund, and Bilton, 1968). Table 11 shows the estimated and actual percentage age compositions of the 400 test scales. From the results of this test, it appears that in any one year scale readers can estimate reasonably well the numbers of partially marked fish of a given age (and, hence, brood-year).

A summary of partially marked fish is presented in table 12; the data resulted from the combination of years and general mark types (e.g., Ad–LV and

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*—Continued

Region	Fishery type	LV-RM (Elokomin)				LV				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Number of fish											
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	0	0	0	(*)	4	51	15	(*)	4	51	15
British Columbia	do	(*)	28	7	6	(*)	60	46	63	(*)	88	53	69
Washington	Sport	0	8	15	0	12	55	27	0	12	63	42	0
	Commercial	0	45	5	3	0	64	22	10	0	109	27	13
Oregon	Sport	0	3	0	0	0	11	0	0	0	14	0	0
	Commercial	0	9	3	0	0	13	5	0	0	22	8	0
California	Sport	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
	Commercial	(*)	7	0	0	(*)	0	21	0	(*)	7	21	0
Subtotal	Sport	0	11	15	0	12	66	27	0	12	77	42	0
	Commercial [1]	0	89	15	9	0	141	145	88	0	230	160	97
Columbia River fisheries	Sport	0	0	0	0	0	0	0	0	0	0	0	0
	Commercial [2]	0	7	28	0	0	24	17	13	0	31	45	13
Total	All fisheries	0	107	58	9	12	231	189	101	12	338	247	110
Columbia River escapement:													
Study hatcheries	[3]	2	4	1	0	0	8	5	0	2	12	6	0
Other hatcheries	[4]	(*)	0	0	0	(*)	2	2	0	(*)	2	2	0
Tributary streams		(*)	5	2	0	(*)	0	0	2	(*)	5	2	2
Total	Escapement	2	9	3	0	0	10	7	2	2	19	10	2

*Not sampled.
[1] Primarily troll fisheries.
[2] Primarily gill net.
[3] Twelve hatcheries participating in the marking program.
[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

TABLE 10.—*Estimated number of marked fall chinook salmon of 1961 brood in catches, tributary spawning populations, and hatchery returns by type of mark, region of recovery, type of fishery, and year of capture, 1963–66*—Continued

Region	Fishery type	RV—RM (Oxbow)				RV				Total			
		1963	1964	1965	1966	1963	1964	1965	1966	1963	1964	1965	1966
		Number of fish											
Ocean fisheries:													
Southeastern Alaska	Commercial	(*)	0	0	0	(*)	0	41	2	(*)	0	41	2
British Columbia	do	(*)	8	16	6	(*)	59	51	77	(*)	67	67	83
Washington	Sport	11	43	0	9	10	52	21	75	21	95	21	84
	Commercial	0	58	9	0	0	29	14	8	0	87	23	8
Oregon	Sport	0	18	4	0	0	5	9	0	0	23	13	0
	Commercial	0	20	2	0	0	21	1	0	0	41	3	0
California	Sport	8	0	2	-------	(*)	0	0	0	(*)	0	2	0
	Commercial	(*)	0	0	0	(*)	0	71	3	(*)	0	71	3
Subtotal	Sport	11	61	6	9	10	57	30	75	21	118	36	84
	Commercial [1]	0	86	27	6	0	109	178	90	0	195	205	96
Columbia River fisheries	Sport	0	0	17	0	0	0	8	0	0	0	25	0
	Commercial [2]	0	24	3	16	2	14	16	5	2	38	19	21
Total	All fisheries	11	171	53	31	12	180	232	170	23	351	285	201
Columbia River escapement:													
Study hatcheries	[3]	4	52	22	1	3	7	10	0	7	59	32	1
Other hatcheries	[4]	(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
Tributary streams		(*)	0	0	0	(*)	0	0	0	(*)	0	0	0
Total	Escapement	4	52	22	1	3	7	10	0	7	59	32	1

*Not sampled.
[1] Primarily troll fisheries.
[2] Primarily gill net.
[3] Twelve hatcheries participating in the marking program.
[4] Toutle, Abernathy, Speelyai, Sandy, and Klaskanine Hatcheries.

Ad–RV were combined as were their corresponding full marks Ad–LV–RM and Ad–RV–RM). Under the hypothesis that the partial marks are primarily from maxillary regeneration, each entry is an estimate of percentage regeneration of the maxillary. For the returns to the hatcheries under study, the percentages of adipose-ventral and adipose-only marks (10.9 and 16.1) were similar to the expected magnitude of maxillary regeneration from the fin regeneration experiments. It is likely, therefore, that these partial marks in the hatchery returns were from maxillary regeneration. The same cause is not indicated for the ventral-only marks, which, in the hatchery returns, were about twice as numerous as expected.

If the percentage of partial marks in the ocean fisheries (compared with that observed for the hatchery returns) is generally high, then we

TABLE 11.—*Actual and estimated age composition of 400 test scales read by 6 scale readers*

Evaluation	Age composition (years)				
	2	3	4	5	6
	Percent				
Estimated	18.4	38.5	28.2	12.5	2.4
Actual	20.2	41.8	24.5	13.5	.0

would tend to reject the hypothesis that these marks are caused primarily by regeneration and conclude that many of these partial marks occurred naturally.

Because the Ad–RV and Ad–LV partial marks are double fin marks, we assume that their occurrence (in catch and hatchery returns) was primarily the result of maxillary regeneration. Hence, the data in the column Ad–EV of table 12 reflects the variability in rate of maxillary regeneration. When we compare the percent occurrence of Ad and EV marks with that of Ad–EV marks and the percentages of Ad and EV marks in the catches and at the hatcheries, the Ad mark appears to have been caused primarily by maxillary regeneration; and single RV or LV marks appear to have resulted from naturally marked fish in addition to maxillary regeneration.

In view of the above, we combined the estimated numbers of partially marked fish with their corresponding full mark for each mark type except for the LV and RV marks. On this basis

TABLE 12.—*Recoveries of partially marked fish by region of capture, type of fishery, and type of mark, 1963–66*

Region	Fishery type	Partial mark [1]		
		Ad-EV [2]	Ad	EV
		Percent		
Ocean fisheries:				
Southeastern Alaska	Commercial	47.7	79.4	100.0
British Columbia	do	7.4	13.9	83.4
Washington	Sport	25.3	17.5	74.6
	Commercial	17.7	11.1	55.0
Oregon	Sport	91.2	52.6	50.0
	Commercial	11.9	14.6	54.0
California	Sport			0
	Commercial	37.0	12.1	93.1
Subtotal	All	15.8	14.6	74.9
Columbia River fisheries	All	10.3	7.8	51.0
Columbia River escapement:				
Study hatcheries		10.9	16.1	27.7
Other hatcheries		0	0	100.0
Tributary streams		7.9	10.0	22.0
Subtotal		10.6	14.5	29.5

[1] Data in table are ratios (average for all years) of estimated numbers of partial marks to estimated sum of partial marks and corresponding complete marks expressed in percent.
[2] EV signifies "either ventral." Marks of same general type are combined.

TABLE 13.—*Estimated catch and escapement of marked fall chinook salmon of Columbia River hatchery origin by area of recovery, 1963–66*

Recovery category	Type of mark				
	Ad-RM [1]	Ad-LV-RM [1] (Spring Creek)	Ad-RV-RM [1] (Kalama)	LV-RM (Elokomin)	RV-RM (Oxbow)
	Numbers of fish				
Ocean fisheries	15,163	3,043	1,593	139	206
Columbia River fisheries	6,453	1,242	548	35	60
Total fisheries	21,616	4,285	2,141	174	266
Total escapement	3,399	612	238	14	79

[1] Includes partially marked fish.

the estimated numbers of marked fall chinook salmon of Columbia River hatchery origin in the catch and escapement are summarized in table 13.

Of the 1961 brood released from the 12 hatcheries with Ad–RM mark, we estimated that 21,600 were caught by the various fisheries between 1963 and 1966. An additional 3,400 fish escaped the fisheries and returned to spawn. The catch to escapement ratio for the 12 hatcheries is, therefore, about 6:1. For the four hatcheries represented by the other marks, this ratio was 12:1, 9:1, 3:1, and 7:1 (Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries, respectively).

The estimated catch of marked fish (Ad–RM) that originated from the 12 hatcheries relative to numbers released was 21,616/5,446,439 or 3.97 fish per 1,000 released. Considerable variation in contribution occurred between hatcheries. The catch per 1,000 fish released was 0.36, 4.50, 0.59, and 3.78 for Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries, respectively. Values for Elokomin and Oxbow Hatcheries are undoubtedly too low—some of the partial marks must have resulted from maxillary regeneration. If we assume that all the partial marks actually originated from Elokomin and Oxbow Hatcheries, their respective contribution would have been 1.53 and 1.95 per 1,000 fish released. These contributions still would be only one-half of those for Kalama and Spring Creek Hatcheries.

Before proceeding with the estimate of total contribution (marked and unmarked) of hatchery-reared fish to the catch, we will consider the precision of the estimate of the total catch of marked fish.

Equation (4), which provides an approximation of the variance of the estimated number of marks in the catch, requires an estimate of the

precision of the seasonal chinook catch for each of the fisheries. Such estimates are not published except in a few instances (e.g., California troll and Oregon ocean sport fisheries). Lacking this information, we have assumed that the seasonal chinook catches in each fishery (except for Alaska troll and the ocean gill net and purse seine fisheries) are estimated within 15 percent of the true value; i.e., the variance of the catch, V(C), is such that one-half the width of the 95 percent confidence interval, $2[V(C)]^{\frac{1}{2}}$, is 15 percent of the estimated catch, C. We then have:

$$V(C) = (0.5 \times 0.15 \times C)^2$$
$$= 0.0056\ C^2.$$

Where available (e.g., California troll), estimates of the precision of the catches are well within the assumed value.

In the Alaska troll fishery and the ocean net fisheries, catches are reported in numbers of fish. The variance of the catch and, therefore, the second term in equation (4) is zero for each of these fisheries.

Substituting these values of V(C) in equation (4) and summing over the strata (i.e., fisheries and years) gives 357,000; 26,000; 13,000; 1,100; and 2,300 as approximate variances for the estimated numbers of Ad–RM, Ad–LV–RM, LV–RM, and RV–RM marks, respectively, in the total catch. The resulting estimates of the 95 percent confidence intervals for the numbers of marked fish in the catch are: Ad–RM 21,616±5.6 percent; Ad–LV–RM 4,285±7.5 percent; Ad–RV–RM 2,141±10.6 percent; LV–RM 174±37.9 percent; RV–RM 266±36.1 percent; where, for example, the 5.6 percent refers to the estimated number of Ad–RM marks (21,616) in the catch. Although these confidence interval estimates are approximate, they illustrate the general level of precision of the estimated total number of marks in the catch.

ESTIMATED CATCH OF 1961-BROOD HATCHERY FISH

In estimating the total number of marked hatchery fish in the catch on the basis of an observed number of mark recoveries and a sampling ratio, as was done in the preceding section, we made certain assumptions. These are assumptions 1, 2, and 3, which dealt with the permanence of fin marks, origin of observed fish marked with the hatchery marks, and accuracy of age assignments. Data presented in the preceding section supported these assumptions.

Additional assumptions are inherent in the procedure for estimating the catch of unmarked and, hence, total catch of hatchery fish. These are assumptions 4, 5, and 6, which were listed previously.

From the distribution of mark recoveries it appears that chinook salmon from Kalama and Spring Creek Hatcheries had different ocean distributions. It is not likely, then, that the first part of assumption 6 (same ocean distribution of fish from each hatchery) is satisfied. This poses no problem, however, provided the second part of assumption 6 (same proportion of fish marked at each hatchery) is satisfied. In this regard, it appears from appendix table 1 that with the possible exception of Klickitat Hatchery, proportions of Ad–RM marked fish in the releases were much the same at all of the hatcheries. Accordingly, we consider that assumption 6 is reasonably satisfied.

Information to test the assumption (assumption 5) concerning the distributions of marked and unmarked hatchery fish is limited. The distribution of marked fish is available from the present study; however, concurrent data for unmarked fish are lacking. The only information available on this subject is from a review by Cleaver (1967) of past tagging experiments in the ocean. Of 290 tagged fish recovered in the Columbia River from these experiments (during 1925–52 in coastal areas from northern Oregon to Cape Fairweather, Alaska), only 13 were recovered in hatcheries. Twelve of the 13 recoveries, however, had been tagged in areas off the west coast of Vancouver Island, Canada—an area of high concentration of marked hatchery fish as shown by recoveries of the marked 1961 brood. Although this result is consistent with assumption 5, it does not, of course, conclusively support it. The assumption must, therefore, remain an assumption.

The validity of assumption 4 (equality of maturity schedules and survival rates between marked (Ad–RM) and unmarked hatchery fish) can be examined by comparing the ratios of marked to unmarked fish at times of release and return. The marked to unmarked ratios by type of mark and age of fish for the 1961-brood hatchery returns are given in table 14. Ratios for Elokomin (LV–RM) and Oxbow (RV–RM) hatcheries are not

presented because the number of recoveries was small.

TABLE 14.—*Marked to unmarked ratios for hatchery returns of 1961-brood chinook salmon by type of mark and age of fish*

Mark	Origin	Age (years)				
		2	3	4	5	All ages
		Marked/unmarked				
Ad-RM	All study hatcheries	0.059	0.063	0.075	0.106	0.067
Ad-RV-RM	Kalama	0	.016	.046	.092	.047
Ad-LV-RM	Spring Creek	.046	.038	.050	.062	.041
Ad-RM	Selected hatcheries [1]	.065	.067	.085	.081	.072

[1] Cascade, Oxbow, Little White Salmon, and Spring Creek Hatcheries.

The increase in ratios with age seems to indicate that marking had some delaying effect on the age of maturity. This effect was much greater for fish marked at Kalama than for fish marked at Spring Creek, although a similar type of mark was used. From the standpoint of survival, the ratios for all ages combined are smaller than those at release (table 4), thus indicating lower total survival for marked fish. The survival of Ad–RM marked fish, for example, was (0.067/0.1193)100=56.2 percent of that for the unmarked fish.

If the differences between the ratios of marked and unmarked fish at times of release and return are interpreted as indicative of delayed maturity or lower survival of marked fish, it is necessary to assume that all unmarked fish returning to a hatchery originated from that hatchery. It is apparent that straying [5] (provided the probability of straying is the same for marked and unmarked hatchery fish) reduces the marked to unmarked ratio for any given year of return. Thus, the indicated survival of marked fish relative to the survival of unmarked fish is too small. Also, if the probability that nonhatchery fish stray into a hatchery changes each year or is related to the age of fish, then the dilution of unmarked hatchery fish by nonhatchery fish in the return is disproportionate from year to year and the change in the marked to unmarked ratios with age of return is impossible to interpret.

Some of the hatcheries, such as Kalama Hatchery, are located on streams in which natural spawning occurs. In these cases, fish which are spawned at the hatcheries and comprise what we term "hatchery returns" are simply a selected sample (of various sizes in proportion to the total return) of adults returning to the stream. Marked to unmarked ratios would, therefore, be difficult to interpret in terms of the effects of marking on survival and age of maturity.

Only 5 of the 12 hatcheries (Bonneville, Cascade, Oxbow, Little White Salmon, and Spring Creek) are on streams that do not support natural spawning populations. Marked (Ad–RM) to unmarked ratios in the returns to four of these hatcheries, Bonneville Hatchery excluded,[6] are presented in table 14. The change in the ratio of marked to unmarked fish with age is not as pronounced as for the 12 hatcheries combined. In addition, the ratio, 0.072, for all ages is somewhat larger than it was for all 12 hatcheries, indicating that survival of marked (Ad–RM) fish relative to unmarked fish was (0.072/0.1193)100=60.4 percent.

Even for the four selected hatcheries, however, straying of nonhatchery fish into hatcheries is a possible source of error. Unfortunately, a direct measure of the extent of this straying is not available. General indications of straying of nonhatchery fish are obtained from observations of marked fish straying away from the hatcheries. Recoveries of specially marked fish released at Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries are presented in table 15. Of the recoveries of marked fish at hatcheries and on spawning grounds, 71.4, 6.3, 38.0, and 4.9 percent of Elokomin, Kalama, Oxbow, and Spring Creek fish were recovered at places other than the release site. The higher percentage of strays from Elokomin and Oxbow Hatcheries may possibly be explained by the fact that 75 percent of the fish released at Elokomin and 30 percent of the fish released at Oxbow were the progeny of fish spawned at Spring Creek Hatchery.

Some indication that younger fish stray more than older fish can be seen in table 15. Groves, Collins, and Trefethen (1968) tagged two groups of chinook salmon at Spring Creek Hatchery and released them into the main stem of the Columbia

[5] The term "straying" is used here in the sense that fish spawn or are spawned at a location other than their point of origin as fingerlings. Indeed, straying into a hatchery may be different from straying into a natural spawning area where the fish are free to leave again.

[6] Bonneville Hatchery is excluded because it is immediately below Bonneville Dam. The potential for straying may be greater if the fish are delayed in their upriver passage at the dam.

TABLE 15.—*Escapement recoveries of marked chinook salmon of 1961 brood by location of release and recovery and age of capture, 1963–66*

Recovery location [2]	Release location [1]															
	Elokomin				Kalama				Oxbow				Spring Creek			
	Age				Age				Age				Age			
	2	3	4	5	2	3	4	5	2	3	4	5	2	3	4	5
	Number of fish															
Grays River																
Big Creek			2													
Plympton		5														
Elokomin	2	2	0	0												
Abernathy																
Toutle																
Kalama						7	171	45								1
Lewis River (Speelyai)						5		4								
Washougal																
Tanner Creek (Bonneville)		1	1				4		1	12	5		1	1	1	
Eagle Creek (Cascade)										2			2	9		
Herman Creek (Oxbow)									1	35	12	1	1	6	2	
Wind River																
Little White Salmon									2	3	4					
Spring Creek		1				1	1				1		42	398	141	2
Big White Salmon														2		
Klickitat															4	
Total	2	9	3	0	0	13	176	49	4	52	22	1	46	418	148	3
Number of strays	0	7	3	0	0	6	5	4	3	17	10	0	4	18	7	1
Percentage strays	0	77.8	100.0	0	0	46.2	2.8	8.2	75.0	32.7	54.4	0	8.7	4.3	4.7	33.3
Percentage strays (all ages)			71.4				6.3				38.0				4.9	

[1] Elokomin: LV–RM; Kalama: Ad–RV–RM and Ad–RV; Oxbow: RV–RM; Spring Creek: Ad–LV–RM and Ad–LV.

[2] Recoveries in tributary streams were adjusted on the basis of the appropriate sampling ratios. Recovery locations are arranged in upstream order (see fig. 1).

River. A smaller fraction of the fish under 80 cm. (31.5 inches) long returned to Spring Creek than did the group over 80 cm. long (3-year-old chinook at Spring Creek average about 80 cm.).

These results offer an alternative explanation for the observed increase in the marked to unmarked ratio with age of return. That is, if the probability of straying is greater for younger fish than for older fish, as indicated above, then it is likely that the marked to unmarked ratio would increase with age even if marking had no effect on maturation.

Additional information of the effect of marking on maturation will be available later from the TM 50 marking experiment at Little White Salmon Hatchery. For the present, we will assume that marked and unmarked 1961-brood hatchery fish had the same maturity schedule.

Another point of interest in table 15 is that the fish generally strayed to areas near the hatchery of origin. Except for the one marked fish from Spring Creek recovered in the Kalama system all marked fish recovered at any great distance from the hatchery of origin were recovered upstream. If the pattern of straying is the same for nonhatchery fish, it is possible to obtain a maximum estimate of straying of nonhatchery fish into the four selected hatcheries—Cascade, Oxbow, Little White Salmon, and Spring Creek. These hatcheries are between Bonneville and The Dalles Dams (fig. 1). Most of the fall chinook salmon return to these hatcheries during the last week of August and September. Spawning occurs between mid-September and mid-October but is generally concentrated within a 2-week period.

Most (about 70 percent in 1965) of the fall chinook salmon that passed The Dalles Dam between August 26 and September 30 are generally brightly colored and are thought to spawn as much as a month later than the darker hatchery fish.[7, 8]

Because of the short duration of spawning at the four hatcheries, it is not likely that fish destined for areas above The Dalles Dam would contribute substantially to these hatchery returns. This generally agrees with the indicated "upstream" straying of the marked hatchery fish. That is, straying probably comes primarily from populations of fish that normally spawn near or downstream from the four hatcheries.

[7] Smith, Eugene M. 1966. Final report. A study to identify the race of fall chinook salmon whose spawning grounds will be inundated by the John Day impoundment on the Columbia River. Fish Comm. Oreg. Res. Div. (U.S. Army Corps Eng., Walla Walla Dist., contract DA–45–164–CIVENG–66–5). 53 pp. [Processed.]

[8] McKee, Thomas B. 1966. Deschutes River adult fall chinook holding study, 1965. Fish Comm. Oreg. Res. Div. (U.S. Army Corps Eng., Walla Walla Dist., contract DA–45–164–CIVENG–66–7). 26 pp. [Processed.]

The difference between fall chinook salmon counts [9] at Bonneville and The Dalles Dams is an estimate of the number of fish removed by the fishery and spawning (aside from mortalities and passage through navigation locks where they are not counted) between the two dams.[10]

By subtracting the number of returns to the four selected hatcheries and the number removed by the fishery from this estimate, we obtain a maximum estimate of the fish that spawned between the two dams at sites other than the four hatcheries—these are the fish that did not stray into the four selected hatcheries. The estimate is maximum because it includes losses between the two dams and fish that strayed from the four hatcheries. Finally, by applying age composition data and estimates of straying (from observed straying of fish marked at Spring Creek Hatchery, table 15), we obtain estimates of the number of 1961-brood nonhatchery fish spawned at the four selected hatcheries (table 16).

An example of the information in table 16 follows. In 1963 an estimated 11,759 fall chinook salmon spawned between the two dams but not at the four subject hatcheries. An estimated 14 percent, or 1,646, were 1961-brood fish. We assumed that these fish are the $(100-8.7)=91.3$ percent of the nonhatchery fish that did not stray into the four hatcheries. The 8.7 was the observed percentage of the 2-year-old fish straying from Spring Creek Hatchery (table 15). It follows that $(1,646/0.913)$—$1,646=157$ nonhatchery fish strayed into the hatcheries. Similar calculations for 1964, 1965, and 1966 give an estimated total of 2,126 nonhatchery fish of the 1961 brood that were spawned at the four selected hatcheries during the 4 years.

Total return of marked (Ad–RM and Ad-only) and unmarked fish to the four hatcheries was 1,898 and 26,538 fish, respectively (appendix table 5).

TABLE 16.—*Estimated number of nonhatchery chinook salmon of 1961 brood spawned at four hatcheries [1] between Bonneville and The Dalles Dams, 1963–66*

Item	Year of run				Total
	1963	1964	1965	1966	
Count at Bonneville Dam [2]	121,184	154,534	134,469	135,095	545,282
Count at The Dalles Dam [2]	66,473	56,150	87,096	69,018	278,737
Hatchery returns [1]	24,377	28,409	12,025	31,023	95,834
Catch [3]	18,575	23,338	25,051	7,008	73,972
Bonneville count minus The Dalles count minus hatchery return minus catch	11,759	46,637	10,297	28,046	96,739
Percent 1961 brood [4]	14	78	66	9	.....
Number of 1961 brood year not straying	1,646	36,377	6,796	2,524	47,343
Percent straying [5]	8.7	4.3	4.7	0	.....
Estimated number of 1961-brood fish straying into four hatcheries [1]	157	1,634	335	0	2,126

[1] Spring Creek, Little White Salmon, Oxbow, and Cascade Hatcheries.
[2] Counts for period August 26 to September 30.
[3] Chinook catch between Bonneville and The Dalles Dams for period August 26 to September 30. Sport catch not included.
[4] Estimated age composition from fishery samples.
[5] Estimates from Spring Creek mark (Ad-LV-RM), table 11. Assumed 0 for age 5 because of the small number of returns.

Subtracting the estimated number of nonhatchery strays, 2,126, from the unmarked return, we found the marked to unmarked ratio becomes $1,898/24,412=.078$. Estimated survival of marked relative to the unmarked fish is then $(.078/.1193)\ 100=65.4$ percent.

This procedure for estimating the number of nonhatchery fish entering the hatcheries is subject to error. If, for example, the percentage straying was as large as 10 percent (for each age group), then the estimated total of 1961-brood nonhatchery fish that entered the four hatcheries would be 5,260; the estimate of the survival of marked to unmarked fish would then be 74.6 percent. In spite of the inexactness, however, it seems clear that the small value of the marked to unmarked ratio observed in the hatchery returns relative to that in the hatchery releases cannot be solely attributed to straying of nonhatchery fish. Furthermore, it appears that the total survival of marked (Ad–RM) relative to unmarked 1961-brood-year fish could not have exceeded 70 percent.

In summary, it appears from the present data that assumption 6 (equality of proportions marked at each hatchery) is satisfied, but for the present we must assume that marked and unmarked hatchery fish have the same ocean distribution and maturity schedules. In addition, we will assume that total survival of marked fish was 70 percent of the survival of unmarked fish—and further, that all additional mortality of marked fish occurred during their first year of life.

[9] U.S. Army, Corps of Engineers. 1963–66. Annual fish passage report: North Pacific Division, Bonneville, The Dalles, McNary and Ice Harbor Dams, Columbia and Snake Rivers, Oregon and Washington. 1963–66. U.S. Army Eng. Dist., Corps Eng., Portland (Oreg.) and Walla Walla (Wash.). Various pagination.

[10] In an analysis of fishway counts (1957–65) at Bonneville and The Dalles Dams (among others), Fredd [11] found that the differences in counts of fall chinook salmon generally exceeded estimates of the numbers removed by the fishery and the numbers spawned in intermediate areas. He concluded that counting errors could not be a major contributor to the discrepancy, thus indicating a "loss" of fish between the two dams.

[11] Fredd, Louis C. 1966. Analysis of differences in fish counts at Columbia River dams, 1957–65. Fish Comm. Oreg. (U.S. Army Corps Eng. Portland Dist., contract DA–35–026–CIVENG–65–44), 47 pp. [Processed.]

On the basis of the preceding summary, estimates of the total catch of 1961–brood hatchery fish were made and are presented in table 17. These estimates were obtained from equation (6) and the estimated numbers of marked fish in the catch (table 10). For example, estimated 1964 total catch of hatchery fish (115,755) by the ocean commercial fisheries was computed as follows. First, the marked to unmarked ratio required in equation (6) was estimated by the product of the marked (Ad–RM) to unmarked ratio, 0.1193, at release (table 4) and the assumed relative survival of marked fish, 0.70. The catch of unmarked hatchery fish (104,227) was then estimated from the ratio: $104{,}227 = 8{,}704/(0.1193)(0.7)$ where 8,704 is the estimated catch of Ad–RM marked fish (including Ad-only). Estimated catches of the other marked hatchery fish were 2,031, 618, 89, and 86 for the Ad–LV–RM, Ad–RV–RM, LV–RM, and RV–RM marks, respectively.[12] The total catch of hatchery fish in 1964 is then simply the sum of the catches of marked and unmarked fish (i.e., $115{,}755 = 104{,}227 + 8{,}704 + 2{,}031 + 618 + 89 + 86$).

TABLE 17.—*Estimated catch of hatchery fall chinook salmon of 1961 brood by type of fishery and year of capture, 1963–66*

Fishery type	Year of catch				Total
	1963	1964	1965	1966	
	Number of fish				
Ocean sport	7,597	27,487	7,514	1,082	43,680
Ocean commercial	43	115,755	37,441	4,797	158,036
Columbia River sport	0	272	33	0	305
Columbia River commercial	1,942	32,349	48,275	2,739	85,305
Total	9,582	175,863	93,263	8,618	287,326

During the 4 years of sampling an estimated 287,326 fall chinook salmon that originated from the 12 hatcheries were caught. This number comprised about 10 percent of the total catch (2,812,949) of 1961-brood chinook salmon in the fisheries sampled. The fish from these hatcheries accounted for 23, 11, 9, and 4 percent of the catches of 1961-brood chinook salmon in 1963, 1964, 1965, and 1966, respectively.

An approximate interval estimate [13] (95 percent confidence interval) for the total catch of hatchery fish is 258,593 to 316,059 ($287{,}326 \pm 10$ percent). This estimate is rough and is presented solely to indicate the general level of precision of the estimated catch of hatchery fish (287,326) obtained under the assumptions stated previously. Sources of error other than sampling variation are in fact more important at this time. For example, if survival of marked relative to unmarked fish was 60 or 100 percent, rather than the assumed 70 percent, then the estimated catch of hatchery fish would have been 330,465 or 209,672, respectively. Both of these values are well outside the interval estimate. It should, therefore, be clearly understood that the above estimated catch of hatchery fish (287,326), although reasonable (but probably minimal), is preliminary.

ESTIMATED VALUE OF CATCH FOR 1961–BROOD HATCHERY FISH

To determine the benefit to cost ratio of the 1961-brood-year releases of fall chinook salmon from the 12 hatcheries under study, estimates were made of production cost for the 53.6 million fish released and of the net value of the 287,326 fish caught by the sport and commercial fisheries. In addition to the release of 53.6 million fish from the 12 hatcheries, 3.86 million fish were released from Abernathy, Speelyai, Toutle, Klaskanine, and Sandy Hatcheries. By making certain assumptions it is also possible to estimate the catch and value of these releases.

The cost of producing fish released from the 12 hatcheries was estimated from 1962 fiscal year costs at individual hatcheries. Costs were apportioned between the brood year-species groups at each hatchery on the basis of either estimated relative man-hours expended or relative size of each group. At each hatchery costs were divided into three categories:

1. Amortized and discounted capital investment
2. Fish food and drugs
3. Operational costs other than food

Capital investment in the hatcheries was amortized over 50 years and was charged a simple interest rate of 5 percent per annum,[14] which amounts to 7 percent of the total capital invest-

[12] Total estimates for LV–RM and RV–RM marks do not include the corresponding partial marks.

[13] Calculated by assuming that the variance of the estimate of the marked to unmarked ratio, $(.1193)(0.7) = 0.0835$, in the catch is such that 2 times the standard deviation is equal to 0.0835.

[14] Amortization period and discount rate are from J. A. Crutchfield, Department of Economics, University of Washington, Seattle, Wash. (personal communication).

ment chargeable to each year's operation. This 7 percent was then apportioned among the broods and species present by using the percentage of time spent caring for each group of fish. Cost of fish food and drugs during the fiscal year was apportioned according to the pounds of each brood year-species group produced.[15] Operational cost other than food and drugs was apportioned the same as capital investment. This category includes personal services, travel, transportation of items, communication services, rents and utilities, other contractual services, equipment, supplies and materials, and administration.

Klickitat Hatchery is used as an example of the above procedure. Table 18 shows the estimated cost ($68,773) to produce the 1961-brood fall chinook salmon at Klickitat Hatchery.

TABLE 18.—*Costs in rearing salmon at Klickitat Hatchery for fiscal year 1962, by brood and species*

Brood and species	Authorized and discounted capital investment	Fish food and related items	Operational costs other than food	Total
1961 fall chinook	$23,169.30	$4,959.82	$40,643.85	$68,772.97
1960 coho	6,360.20	4,046.17	11,157.14	21,563.51
1961 coho	12,366.10	2,871.48	21,517.33	36,654.91
1960 spring chinook	908.60	130.52	1,593.88	2,633.00
1961 spring chinook	2,725.80	1,044.17	4,781.63	8,551.60
Total	45,430.00	13,052.16	79,693.83	138,175.99

Capital investment through 1962 fiscal year for Klickitat Hatchery was $649,000. Seven percent, or $45,430, of this total, was attributable to the 1962 fiscal year. Because an estimated 51 percent of the man-hours was expended in caring for fall chinook salmon during fiscal year 1962, $23,169.30 (0.51 x 45,430) was the portion of the capital investment cost assigned to the fall chinook.

Total cost for food and drugs during the year at Klickitat Hatchery was $13,052.16. As 38 percent of the total weight of fish produced was fall chinook salmon, an estimated $4,959.82 (.38 x 13,052.16) of the food cost was assigned to them.

Total operational costs (other than food) were apportioned in the same manner as the capital investment. Hence, 51 percent or $40,643.85 of the year's operational cost ($79,693.83) was assigned to fall chinook salmon.

Adding these costs gives $68,772.97 as the estimated total cost in rearing the 1961-brood chinook salmon at Klickitat Hatchery. Following this procedure at each hatchery, we estimated the total cost in rearing the 1961-brood chinook salmon released at all hatcheries under study at $831,522.

To determine the benefit provided by the contribution of these hatchery releases to the commercial and sport fisheries, it is necessary to estimate their net economic value.

For commercially caught fish, the gross economic value was determined from estimated landings and average prices paid to fishermen in 1963–66. The standard benefit-cost technique would require the deduction of all associated costs, but on the basis of arguments similar to those presented by Crutchfield, Kral, and Phinney,[16] we assumed that the capacity of present commercial salmon fisheries in terms of vessels and gear is such that additional catches can be made with little increase in cost.

The above assumption is supported in part from an examination of recent catch and effort data for the Washington and British Columbia troll fisheries (table 19). The two fisheries accounted for over 90 percent of the estimated ocean commercial catch of hatchery fish. Beginning in 1958, the size (number of boats) of the troll fleet increased considerably. The increase was not accompanied, however, by a corresponding increase in the catch of chinook and coho salmon (target species of the troll fisheries). The average catch per boat for 1958–62 was 390–40 percent less than the average catch per boat of 650 for the preceding period (1952–57). Even with the increased catches during 1963–66, the average catch per boat (assuming the number of boats was at least as great as during 1958–62) was only about 550—again, considerably less than the 1952–57 level. It seems reasonably clear from these data that the catch capacity of the troll fleet of Washington and British Columbia is greater than their present success. Larger catches could, therefore, be made without investment in additional units of gear.

The assumption (excess fishing capacity) is also indicated for the Columbia River gill-net fishery, which together with the above two troll fisheries accounted for over 95 percent of the estimated com-

[15] Amount of food given to the various groups of fish at a hatchery is generally proportional to their weight.

[16] Crutchfield, James A., Kenneth B. Kral, and Lloyd A. Phinney. 1965. An economic evaluation of Washington State Department of Fisheries controlled natural-rearing program for coho salmon (*Oncorhynchus kisutch*). Wash. Dep. Fish., Res. Div. (U.S. Fish Wildl. Serv. contract #14-17-0007-246, Part II). 26 pp. [Processed.]

TABLE 19.—*Catch of chinook and coho salmon and number of boats in commercial troll fisheries of Washington and British Columbia, 1952–66*

Year	Catch of fish [1]	Boats [2]
	Millions	*Number*
1952	4.09	5979
1953	3.48	5410
1954	2.75	5240
1955	3.03	4560
1956	3.15	4277
1957	3.34	5061
1958	3.32	6606
1959	2.64	7511
1960	1.86	7390
1961	2.91	7654
1962	3.16	7115
1963	3.11	----------
1964	3.79	----------
1965	4.26	----------
1966	4.77	----------

[1] Washington State Department of Fisheries (1964) and International North Pacific Fisheries Commission (1952–66).
[2] Cleaver (1967): data are actually number of licenses sold.

mercial catch of hatchery chinook salmon of the 1961 brood. To conserve the chinook salmon resource, fishing seasons have been steadily shortened (Pulford, 1964). The length of the fishing season has been decreased from 272 days in 1936 to 101 days in 1960 and 80 days in 1966. It would seem, then, that the present fishery is capable of making additional catches without increasing the present number of fishing units.

We also assume that additional running expenses of vessels and labor costs—attributed to the contribution of these hatcheries to the salmon resource—are negligible for the present fisheries. This assumption is reasonable if one considers: (1) the estimated catch of hatchery fish (287,000 fish) is small compared to annual catches of salmon (e.g., Washington and British Columbia troll catches, table 19), and (2) crews of vessels engaged in fishing are effectively precluded from working at other occupations during closed fishing periods (Crutchfield et al.).[16]

Thus, the gross economic value to the commercial fisherman of additional catches of chinook salmon made possible by hatchery releases essentially constitutes a net benefit.

Estimation of net value for the catch of hatchery chinook salmon by sport fishermen was made from an assumed net value per fish of $8.87.[17] This value represents an estimate of the amount an angler is willing to pay for the right to fish. It was obtained by extrapolation from a 1962 survey of Oregon salmon-steelhead anglers reported upon by Brown, Singh, and Castle (1964).

Calculation of total net value ($1,917,003) of the commercial and sport catch of fall chinook salmon that originated from the hatcheries under study is shown in table 20. The benefit to cost ratio is obtained from the ratio $1,917,003/$831,522 and is estimated as 2.3 : 1.

This benefit to cost ratio applies, of course, only to chinook salmon at the study hatcheries. As indicated above for Klickitat Hatchery (table 18), other species of salmon (principally coho) are raised at these hatcheries. To fully use all production facilities, the hatchery complex is now managed on a multispecies basis. A more complete and meaningful benefit to cost analyses of the hatchery system must, therefore, await completion (1969) of the study of the contribution that hatchery-reared coho salmon make to the fisheries.

[16] U.S. Department of the Interior, Bureau of Commercial Fisheries, Division of Economics. 1966. An economic evaluation of Columbia River anadromous fish programs. 58 pp. [Processed.]

TABLE 20.—*Estimated value of the catch of fall chinook salmon of 1961 brood that were released from study hatcheries, by type of fishery*

Fishery	Age	Fish	Sample size	Average weight [1]		Total weight [1]		Value per unit catch [2]	Total value
		Number	*Number of fish*	*Lbs.*	*Kg.*	*Lbs.*	*Kg.*	*Dollars*	*Dollars*
Sport	All	43,985						[3] 8.870	390,147
Ocean commercial	2	43	27	4.00	1.81	172	78	.380	65
	3	115,755	2,040	8.45	3.83	978,130	443,689	.435	425,487
	4	37,441	538	15.20	6.94	572,473	259,653	.610	349,208
	5	4,797	56	18.71	8.49	89,752	40,712	.650	58,339
Columbia River commercial	2	1,942	22	6.11	2.77	11,866	5,381	.360	4,272
	3	32,349	870	17.98	8.16	581,635	263,838	.360	209,389
	4	48,275	1,135	26.10	11.84	1,259,978	571,528	.360	453,592
	5	2,739	57	28.13	12.76	77,048	34,950	.344	26,504
Total		287,325							1,917,003

[1] Weights for ocean commercial fisheries are dressed weights, and those for Columbia River fisheries are round weights. Original weights were in pounds for Ad–RM marked fish.
[2] Entries for commercial fisheries (dollars per pound) are based on prices paid for Washington State troll landings obtained from Dale Ward, Washington State Department of Fisheries (personal communication).
[3] See footnote 17 of text.

It must further be understood that hatchery methods have changed significantly since 1962. This change is reflected in the increased size of fish released from hatcheries. For example, the average weight of fall chinook salmon released from Columbia River hatcheries operated by Washington Department of Fisheries increased from 2.18 g. in 1962 to 3.89 g. in 1966.[18] It is likely, therefore, that survival of hatchery fish and, hence, the contribution of given numbers released has changed since 1962.

To estimate the value of the catch of 1961-brood fall chinook salmon from all Columbia River hatcheries, we must assume that the 3.86 million fish released from hatcheries not included in the study contributed to the fisheries in the same proportion as the fish released (53.65 million) from the hatcheries under study. On this basis the value of the catch of these releases would be:

$$137{,}832=\frac{(3.86)\ (1{,}917{,}003)}{(53.65)}$$

or about $138,000. The value of the catch of fish released from all hatcheries is then estimated as $2,055,000.

Because of the conservative nature of the estimate of survival of marked fish relative to unmarked fish, we believe that the estimated value of the catch of hatchery fish, as well as the benefit-cost estimate presented above, is minimal.

SUMMARY

1. During 4 years of marking at 12 hatcheries, 21.3 million fish (10 percent of the total production of 213 million) were marked with an adipose-maxillary mark. An additional 9.6 million were identified with special marks unique to a hatchery.

2. The 1961-brood release of 53.6 million fish included 5.4 million (10.1 percent of the total release) marked with a "common mark" (Ad–RM). Fish with marks unique to a hatchery were released from Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries.

3. Auxiliary data collected suggested that the quality of marking and the permanence of marks (except possibly for the maxillary mark in the 1961 and 1962 broods) were reasonably satisfactory.

4. During the first 4 years of mark sampling (1963–66), an average of 23 percent of the chinook salmon catch was examined for marked fish.

5. Except for 1963, sampling for marked fish was conducted in most chinook fisheries from Monterey, Calif., northward to southeast Alaska. In 1963, sampling was limited to the Washington, Oregon, and Columbia River fisheries.

6. A total of 9,573 marked fish from the 1961 brood of possible Columbia River hatchery origin were recovered during the 4 years. The majority, 6,189, were recovered as age–3 fish in 1964.

7. Although marked fish were recovered in the ocean fisheries over the entire range of sampling, most were recovered from landings made north of the Columbia River mouth (Washington and west coast of Vancouver Island fisheries).

8. Marked fish that originated from Kalama Hatchery were the only ones (specific to a hatchery) recovered in the southeast Alaska fishery. In general, proportionately more of the Kalama fish were recovered in the northern parts of the sampling range than were the marked fish originating from Elokomin, Oxbow, or Spring Creek Hatcheries.

9. An estimated total of 21,600 marked (Ad–RM) fish that originated from the 12 study hatcheries were caught. An additional 3,400 escaped the fisheries and returned to spawn.

10. The estimated average catch to escapement ratio for the hatcheries under study was about 6:1. For marked fish from Elokomin, Kalama, Oxbow, and Spring Creek Hatcheries this ratio was 12:1, 9:1, 3:1, and 7:1, respectively.

11. The catch of Ad-RM marked fish from all 12 hatcheries in terms of the numbers released was 3.97 per 1,000 released. This quantity was 4.50 and 3.78 for Kalama and Spring Creek Hatcheries, respectively. The contribution per 1,000 released for Elokomin and Oxbow Hatcheries was at most only one-half that for Kalama and Spring Creek.

12. By assuming that marked and unmarked hatchery fish have the same ocean distribution and maturity schedules and that survival of marked fish was 70 percent of the survival of unmarked fish, we estimated that the total catch of hatchery fish (marked and unmarked) was 287,326.

13. The estimated catch, 287,326, of hatchery fish comprised about 10 percent of the total catch

[18] Harry Senn, Washington State Department of Fisheries (personal communication).

of 1961-brood chinook salmon in the fisheries sampled.

14. If survival of marked relative to unmarked fish was 60 or 100 percent rather than the assumed 70 percent, then the estimated catch of hatchery fish would have been 330,465 or 209,672, respectively. The latter value is considered too low: it is not likely that the survival of marked fish exceeded 70 percent of the survival of unmarked fish.

15. The estimated cost of rearing the fall chinook salmon of the 1961 brood released from the study hatcheries was $831,522. The estimated net value to the fishermen of the catch of these fish was $1,917,003. The benefit to cost ratio was, therefore, 2.3:1.

16. The estimated total value of the catch of fall chinook salmon of 1961 brood that originated from all Columbia River hatcheries (including five hatcheries not participating in the marking experiment) was $2,055,000.

17. We considered that the estimated catch of hatchery fish, and, therefore, the value and benefit-ratio, is minimum.

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APPENDIX TABLE 1.—*Estimated numbers of fall chinook salmon fingerlings of 1961 brood released from Columbia River hatcheries*

Hatchery	Fish released		Proportion of fish marked				Fish marked			
			Proportion		Standard deviation		Total		Standard deviation	
	Total	Standard deviation	Ad-RM	Special mark	Ad-RM	Special mark	Ad-RM	Special mark	Ad-RM	Special mark
	Number	*Number*					*Number*	*Number*	*Number*	*Number*
Grays River	893,028	20,240	0.0051	(LV-RM)	0.00310		84,927		3,370	
Elokomin	1,575,000	33,888	.0937	0.3051	.00232	0.00366	147,578	480,533	4,837	11,838
				(Ad-RV-RM)						
Kalama	4,906,845	55,737	.1013	.0970	.00135	.00133	497,063	475,964	9,364	9,165
Washougal	2,314,940	46,983	.0932		.00191		215,752		6,219	
Little White Salmon	12,077,844	348,596	.1061		.00280		1,281,459		50,338	
				(Ad-LV-RM)						
Spring Creek	10,925,933	229,319	.1033	.1037	.00203	.00203	1,128,649	1,133,019	32,409	32,659
Big White Salmon	3,545,865	133,488	.0947		.00348		335,793		17,655	
Klickitat	3,177,958	133,217	.0891		.00508		283,155		20,075	
				(RV-RM)						
Oxbow	4,549,959	76,956	.1034	.0990	.00137	.00134	470,466	450,446	10,100	9,762
Cascade	4,842,554	81,014	.1015		.00132		491,519		10,401	
Bonneville	3,829,617	71,368	.1054		.00150		403,642		9,472	
Big Creek	1,013,671	26,210	.1050		.00292		106,435		4,039	
Total	53,653,214	568,071	.1015		.00088		5,446,439		74,630	

APPENDIX TABLE 2.—*Estimated numbers of fall chinook salmon fingerlings of 1962 brood released from Columbia River hatcheries*

Hatchery	Fish released		Proportion of fish marked				Fish marked			
			Proportion		Standard deviation		Total		Standard deviation	
	Total	Standard deviation	Ad-LM	Special mark	Ad-LM	Special mark	Ad-LM	Special mark	Ad-LM	Special mark
	Number	*Number*					*Number*	*Number*	*Number*	*Number*
				(LV-LM)						
Grays River	1,359,761	27,825	0.0936	0.1776	0.00249	0.00327	127,274	241,494	4,273	6,648
Elokomin	*2,391,219	61,000	.0934		.00195		223,340		7,360	
				(Ad-RV-LM)						
Kalama	4,599,326	102,405	.0938	.0952	.00135	.00136	431,206	437,669	11,272	11,632
Washougal	3,315,613	84,648	.0956		.00161		316,973		9,687	
Little White Salmon	11,588,405	171,575	.1022		.00088		1,183,865		20,298	
				(Ad-LV-LM)						
Spring Creek	8,408,267	146,575	.1033	.1031	.00105	.00105	868,574	866,892	17,521	17,496
Big White Salmon	3,438,295	55,505	.0993		.00160		341,554		7,818	
Klickitat	2,624,470	35,540	.0889		.00170		233,315		5,479	
Oxbow	4,916,873	76,396	.0951		.00127		467,595		9,576	
				(RV-LM)						
Cascade	4,217,910	66,149	.1021	.1283	.00141	.00156	430,649	541,158	9,000	10,735
Bonneville	4,635,279	73,539	.1139		.00150		527,958		10,895	
Big Creek	974,585	20,996	.0993		.00290		96,776		3,513	
Willard **										
Total	52,470,003	366,201	.1000		.00041		5,249,079		42,532	

*Includes an estimated 169,000 fish not sampled at release. ** Included in the release for Little White Salmon.

APPENDIX TABLE 3.—*Estimated numbers of fall chinook salmon fingerlings of 1963 brood releasea from Columbia River hatcheries*

Hatchery	Fish released		Proportion of fish marked				Fish marked			
			Proportion		Standard deviation		Total		Standard deviation	
	Total	Standard deviation	Ad-RM	Special mark	Ad-RM	Special mark	Ad-RM	Special mark	Ad-RM	Special mark
	Number	*Number*					*Number*	*Number*	*Number*	*Number*
Grays River	1,576,680	20,798	0.1023		0.00234		161,294		4,263	
Elokomin	2,383,919	31,374	.0912		.00181		217,413		5,179	
			(Ad-RV-RM)							
Kalama	4,883,937	85,028	.0987	0.0934	.00133	0.00130	482,176	456,158	10,490	10,119
Washougal	3,157,696	38,786	.0953		.00160		300,928		6,268	
Little White Salmon	11,915,503	186,493	.0036		.00084		1,115,614		20,208	
			(Ad-LV-RM)							
Spring Creek	7,467,629	131,916	.1032	.1006	.00111	.00110	770,659	751,243	15,934	15,607
Big White Salmon	2,448,904	49,017	.0998		.00191		244,401		6,768	
			(LV-RM)							
Klickitat	2,888,208	37,171	.0974	.1806	.00169	.00220	281,311	521,610	6,086	9,238
Oxbow	6,124,048	91,818	.1051		.00119		643,637		12,083	
Cascade	5,734,238	75,382	.0991		.00122		568,091		10,228	
Bonneville	9,545,463	141,289	.1059		.00095		1,010,865		17,515	
			(RV-RM)							
Big Creek	1,985,838	28,781	.0957	.2920	.00208	.00322	190,075	579,967	4,987	10,545
Total	60,112,063	356,945	.0996		.00037		5,986,464		42,071	

APPENDIX TABLE 4.—*Estimated numbers of fall chinook salmon fingerlings of 1964 brood released from Columbia River hatcheries*

Hatchery	Fish released		Proportion of fish marked				Fish marked			
			Proportion		Standard deviation		Total		Standard deviation	
	Total	Standard deviation	Ad-LM	Special mark	Ad-LM	Special mark	Ad-LM	Special mark	Ad-LM	Special mark
	Number	*Number*					*Number*	*Number*	*Number*	*Number*
Grays River	1,369,522	28,017	0.0938		0.00248		128,461		4,300	
Elokomin	2,069,739	32,740	.0935		.00204		193,485		5,199	
			(Ad-RV-LM)							
Kalama	3,496,560	67,730	.0993	0.0914	.00158	0.00152	347,248	319,412	8,691	8,215
Washougal	2,643,924	50,114	.1004		.00184		265,450		7,005	
			(RV-LM)							
Little White Salmon	8,365,579	120,972	.0995	.0953	.00108	.00105	832,221	797,345	14,996	14,550
Spring Creek	6,554,455	86,840	.1031	.0917	.00122	.00116	675,493	600,953	11,999	10,921
Big White Salmon	2,007,409	32,925	.0874		.00208		175,448		5,072	
Klickitat	2,935,065	54,478	.0934		.00172		274,135		7,174	
Oxbow	1,290,497	17,367	.0949		.00248		122,516		3,599	
Cascade	4,709,551	72,825	.1044		.00131		491,077		9,896	
			(LV-LM)							
Bonneville	9,887,575	121,640	.1000	.0968	.00093	.00092	988,974	957,110	15,242	14,876
Big Creek	1,448,676	19,111	.0988		.00241		143,129		3,964	
Total	46,778,552	258,073	.0992		.00044		4,638,237		32,729	

APPENDIX TABLE 5.—*Marked and unmarked returns of fall chinook salmon of 1961 brood year to Columbia River hatcheries and tributary streams*

Recovery location	Group	Year of return			
		1963	1964	1965	1966
		Number of fish			
Hatcheries:					
Grays River	Unmarked	0	35	34	0
	Ad-RM	0	0	1	0
Big Creek	Unmarked	103	902	281	6
	Ad-RM	5	33	20	0
	Ad	1	2	3	0
	LV	0	0	1	0
Elokomin	Unmarked	11	414	8	0
	Ad-RM	0	3	0	0
	Ad	0	1	0	0
	LV-RM	2	2	0	0
	LV	0	7	0	0
Kalama	Unmarked	49	434	2,429	411
	Ad-RM	0	20	134	47
	Ad	0	2	2	0
	Ad-RV-RM	0	7	111	38
	Ad-LV-RM	0	0	0	1
Washougal	Unmarked	14	53	12	3
	Ad-RM	1	2	0	0
Bonneville	Unmarked	369	2,527	1,867	13
	Ad-RM	13	157	84	1
	Ad	0	14	36	0
	Ad-LV	1	1	1	0
	Ad-RV	0	0	4	0
	LV-RM	0	1	1	0
	LV	0	0	1	0
	RV-RM	1	12	5	0
	RV	1	0	4	0
Little White Salmon	Unmarked	197	3,429	2,035	45
	Ad-RM	9	158	139	1
	Ad	1	45	41	0
	LV	0	0	1	0
	RV-RM	2	3	4	0
	RV	1	0	1	0
Cascade	Unmarked	156	2,010	1,078	38
	Ad-RM	5	117	64	1
	Ad	2	1	13	0
	Ad-LV-RM	2	8	0	0
	Ad-LV	0	1	0	0
	RV-RM	0	2	0	0
Spring Creek	Unmarked	922	10,374	2,849	32
	Ad-RM	57	641	190	6
	Ad	17	130	64	2
	Ad-LV-RM	38	353	119	1
	Ad-LV	4	45	22	1
	Ad-RV-RM	0	1	1	0
	LV-RM	0	1	0	0
	LV	0	0	2	0
	RV-RM	0	0	1	0
	RV	0	1	0	0
Oxbow	Unmarked	242	2,457	666	8
	Ad-RM	4	116	47	0
	Ad	3	16	8	0
	Ad-LV-RM	1	2	2	0
	Ad-LV	0	4	0	0
	LV	0	1	0	0
Oxbow	RV-RM	1	35	12	1
	RV	1	6	5	0
Big White Salmon	Unmarked	17	1,064	(*)	(*)
	Ad-RM	0	33	(*)	(*)
	Ad	0	4	(*)	(*)
	Ad-LV-RM	0	1	(*)	(*)
Klickitat	Unmarked	15	334	38	0
	Ad-RM	6	16	0	1
Toutle	Unmarked	(*)	956	1,289	107
Abernathy	Unmarked	(*)	1,797	661	0
	Ad-RM	(*)	1	0	0
	LV	(*)	2	2	0
Speelyai	Unmarked	(*)	1,202	2,084	0
	Ad-RM	(*)	4	0	0
	Ad-RV-RM	(*)	5	0	0
Tributary streams: [1]					
Big Creek	Unmarked	(*)	313	362	1
	Ad-RM	(*)	5	11	0
	Ad	(*)	0	2	0
	LV-RM	(*)	0	2	0
Kalama	Unmarked	(*)	6,330	2,884	120
	AD-RM	(*)	0	161	14
	Ad	(*)	45	7	0
	Ad-RV-RM	(*)	0	56	7
	Ad-RV	(*)	0	4	0
Little White Salmon	Unmarked	(*)	30	34	4
	Ad-RM	(*)	1	3	0
Big White Salmon	Unmarked	(*)	905	956	45
	Ad-RM	(*)	9	6	2
	Ad	(*)	1	0	0
	Ad-LV-RM	(*)	1	0	0
Klickitat	Unmarked	(*)	12,496	3,907	22
	Ad-RM	(*)	370	162	0
	Ad	(*)	22	0	0
	Ad-LV-RM	(*)	0	4	0
Plympton	Unmarked	(*)	333	172	1
	Ad-RM	(*)	8	4	0
	Ad	(*)	6	2	0
	LV-RM	(*)	5	0	0
Grays	Unmarked	(*)	87	36	0
	Ad-RM	(*)	0	2	0
Washougal	Unmarked	(*)	333	172	16
	Ad-RM	(*)	0	4	0
Wind	Unmarked	(*)	422	34	0
	Ad-RM	(*)	0	2	0
Lewis	Unmarked	(*)	643	160	1,835
	Ad-RM	(*)	0	0	5
	Ad-RV-RM	(*)	0	0	2
	Ad-RV	(*)	0	0	2
	LV	(*)	0	0	2
Elokomin	Unmarked	(*)	(*)	421	0

See footnotes at end of table.

APPENDIX TABLE 5.—*Marked and unmarked returns of fall chinook salmon of 1961 brood year to Columbia River hatcheries and tributary streams*—Continued

*Not sampled

[1] Total return of marked fish for tributary stream estimated from mark recoveries.

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EFFECTS OF PESTICIDES ON EMBRYONIC DEVELOPMENT OF CLAMS AND OYSTERS AND ON SURVIVAL AND GROWTH OF THE LARVAE

BY HARRY C. DAVIS AND HERBERT HIDU [1], *Fishery Biologists*

BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY

MILFORD, CONNECTICUT 06460

ABSTRACT

Fifty-two compounds were tested for their effects on embryos of the hard clam, *Mercenaria mercenaria*, and the American oyster, *Crassostrea virginica*, and on their larvae. The pesticides included 17 insecticides, 12 herbicides, one nematocide, four solvents, and 18 miscellaneous bactericides, fungicides, and algicides.

Most of the compounds affected embryonic development more than survival or growth of larvae. Some, however, drastically reduced growth of larvae at concentrations that had relatively little effect on embryonic development. It is necessary, therefore, to evaluate the effects of pesticides on all stages of the life cycle of an organism before the pesticide can be considered safe. Nevertheless, differences in toxicity to bivalve larvae among compounds of each category of pesticide are large enough that it should be possible to select compounds to control pest species without serious damage to commercial shellfish.

The extensive use in recent years of highly persistent pesticides for control of certain insects and undesirable plants, not only on agricultural lands but also on recreational areas, lakes, streams, and marshes, has made imperative an evaluation of the effects of these compounds on fish and wildlife. The eventual goal is to control undesirable species, with the least harm to the desirable members of the ecosystem. Attainment of this goal requires extensive knowledge of how each pesticide affects each species or representative species of the system. Also, the pesticide must be highly specific or be applied so that its dispersion is strictly limited.

Pesticides may enter the habitat of shellfish in several ways. One is by being carried there in runoff water from treated land areas. Cottam (1960) stated that 2 to 3 billion pounds (9.07 to 13.61 x 10^8 kg.) of pesticides are used annually in the United States on about 100 million acres (40.5 x 10^6 ha.) of land. Thimann (1964) stated that the United States used 175,000 short tons (158,760 metric tons) of insecticides in 1962 and about half that much of fungicides and herbicides. Doudoroff, Katz, and Tarzwell (1953) made laboratory tests of soils collected from toxaphene-treated fields and concluded that stream waters can be made toxic to fish by the drainage from such fields. Such runoff water may carry the pesticides in solution, adsorbed on suspended particles, or incorporated in plants and animals in the water. Certainly, large quantities of the pesticides that leach from the soil must eventually reach coastal marine waters and sediments.

A second, more direct, and perhaps more easily regulated method by which pesticides may enter the estuarine environment is the use of insecticides and herbicides on salt marshes and estuaries to control mosquitoes and undesirable plants. In some regions large areas are sprayed near shellfish beds. Pesticides used in this way probably create higher concentrations of the active ingredients in the estuarine water than are achieved by any other method.

Loosanoff, MacKenzie, and Shearer (1959 [2]), Loosanoff et al. (1960), and Loosanoff (1961) proposed the use of several pesticides for the control of certain predators and competitors of

[1] Present address: University of Maryland, Natural Resources Institute, Box 38, Solomons, Md. 20688.

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[2] Loosanoff, V. L., C. L. MacKenzie, Jr., and L. W. Shearer. 1959. Use of chemical barriers to protect shellfish beds from predators. Bur. Commer. Fish. Biol. Lab., Milford, Conn., Bull. 6, 23: 1-11.

commercial shellfish. The methods of application proposed by these authors, however, were designed to restrict the dispersal of the pesticide. Compounds relatively insoluble in water were dissolved in polychlorinated benzenes, which are themselves virtually insoluble in water—a characteristic that further limited the solubility of the pesticide. Moreover, the polychlorinated benzenes, which are heavier than sea water, were mixed with dry sand to anchor the pesticide to the bottom of the particular shellfish bed treated. This essentially two-dimensional treatment of limited areas with a control pesticide had little or no effect on pelagic or planktonic organisms.

Butler, Wilson, and Rick (1962) presented data on the effects of some pesticides on adult oysters and Davis (1960) reported the effects of 31 compounds, including several types of pesticides, on fertilized eggs and larvae of bivalves. The authors of the two papers considered the effect of pesticides on growth to be the most sensitive index for these mollusks.

The highest concentration of any pesticide that can be considered "safe" for use in waters in which valuable species of bivalves reproduce is the highest concentration that has no appreciable effect on survival of the developing embryo or on growth and survival of the fully formed veliger larvae. It is also necessary to determine the concentrations tolerated by spawning individuals and by organisms that serve as food for larval and adult bivalves (Ukeles, 1962).

A distinction is made between effects on development of the embryo and on survival and growth during the larval stage because tolerances of these two pelagic stages to a given toxicant are often markedly different. Growth of the veliger larvae, moreover, may be drastically retarded at concentrations of toxicants too low to cause direct mortality of either embryonic or larval stages. Such a retardation of growth, however, serves to prolong the pelagic life of the larvae and, thus, increases the chance for their loss through predation, disease, and dispersion.

This report summarizes the data obtained at the Bureau of Commercial Fisheries Biological Laboratory in Milford concerning the effects of various compounds used in control of various types of undesirable organisms, on the development of fertilized eggs of hard clams, *Mercenaria mercenaria*, and American oysters, *Crassostrea virginica*, and on the survival and growth of the larvae. The data, unfortunately, are not complete for all of the compounds tested. The work on pesticides at the laboratory in Milford has been terminated by transfer of pesticide work to the Bureau's Biological Laboratory at Gulf Breeze, Fla. In the early experiments the effects of the compounds on development of fertilized eggs were not determined and many were tested in only a single experiment. Furthermore, for some experiments in which growth of larvae in control cultures was not satisfactory, we can give only the data on development of fertilized eggs. The effects of a number of these pesticides on some of the algal foods of bivalve larvae have also been determined (Ukeles, 1962).

METHODS

Methods for spawning oysters out of season and standard methods for culturing the larvae have been described in detail by Loosanoff and Davis (1963). These methods were followed throughout the present series of experiments.

In most experiments all pesticides were tested at concentrations of 0.25, 0.50, 1, 2.5, 5, and 10 p.p.m. (parts per million), with duplicate cultures at each concentration. If a toxic range was not established in the first experiment, these concentrations were increased or decreased by a factor of 10 in the next experiment. Usually, however, the range of 0.25 to 10 p.p.m. included concentrations that had no effect and concentrations that caused 100 percent mortality. Stock solutions of water-soluble pesticides were made up in water; all others were made up in acetone, except for a very few that were insoluble in either water or acetone. The latter were used as water suspensions.

For observations on development of embryos, fertilized eggs were introduced into the test concentrations soon after release and fertilization, usually when the eggs were in the two-cell stage of development. Quantitative samples were taken 48 hours later to determine the percentage of the fertilized eggs in each culture that had developed to normal straight-hinge veliger larvae.

For tests to determine the effect of compounds on survival and growth of veliger larvae, we used cultures of 2-day-old larvae that had been reared to the straight-hinge stage under normal conditions. These larvae were then reared, in the different concentrations of substances being tested, for a

period of 10 days for clam larvae or 12 days for oyster larvae. Thus, when the quantitative samples were taken at the end of the period, the larvae were 12 and 14 days old, respectively. These periods represent the normal time of setting for the two species under good environmental conditions at the temperatures used (24°±1° C.).

We fed the test larvae a mixture of live flagellates, generally at a rate of 0.01 ml. of packed cells to each 1-liter culture per day. Sea water and test compound were renewed in the cultures every second day. The contents of a culture vessel were washed onto a stainless steel screen that retained the larvae but allowed the sea water and dissolved pesticide to pass through. The Pyrex[3] culture vessels used in the experiments were then thoroughly washed before the larvae and the fresh solution of pesticide in sea water were again added. The renewal of the culture medium every second day in this manner minimized the buildup of harmful metabolites and made it possible to maintain accurately the concentration of test compound at the desired level.

Quantitative samples, consisting of 1.6 percent of the total larval population of a culture, were taken at the end of the 2-day and the 12- or 14-day experimental periods and preserved for microscopic examination. We determined the survival by counting the number of larvae that had been living at the time of preservation. Survival values (table 1, cols. 1, 2) are expressed as a percentage (R) of the survival in control cultures and were calculated as follows:

$$R=\frac{\text{Average number of larvae in experimental cultures}}{\text{Average number of larvae in control cultures}}\times 100$$

Growth, or increase in mean lengths in the 12- and 14-day experiments (table 1, col. 3), is expressed as a percentage (G) of the increase in mean length of larvae in control cultures and was calculated as follows:

$$G=\frac{\text{Mean length of larvae in experimental cultures—mean length at 2 days}}{\text{Mean length of larvae in control cultures—mean length at 2 days}}\times 100$$

Mean length was determined by measuring the maximum length of the shell, parallel to the hinge line, of 100-oyster larvae or of 50-clam larvae from the preserved samples. The expression of results as percentages of the increase in mean length and survival of larvae in control cultures made possible the direct comparison of data from the different experiments.

Measurements of effects of toxicants on growth and survival of larvae are subject to considerable error due to random sampling error and variations introduced by the slight uncontrolled environmental differences between cultures. In addition, changes in sea water and food quality between successive experiments undoubtedly caused variation in observed effects. These factors must be taken into consideration in judging reliability of the data and in ascertaining safe and harmful levels of the test compound.

The standard error in measurements of growth is considerably greater for oyster larvae than for clam larvae. A length-frequency distribution of clam larvae receiving a given treatment is highly kurtotic, whereas that for oyster larvae exhibits this central tendency to a much lesser degree. Figure 1 shows the 95 percent confidence limits of the mean (± 2 SE_m) in microns, with N=100 for oyster larvae and N=50 for clam larvae, at the various mean lengths encountered in our experimental cultures.

After considering the variations encountered, in addition to sampling errors, we believe our

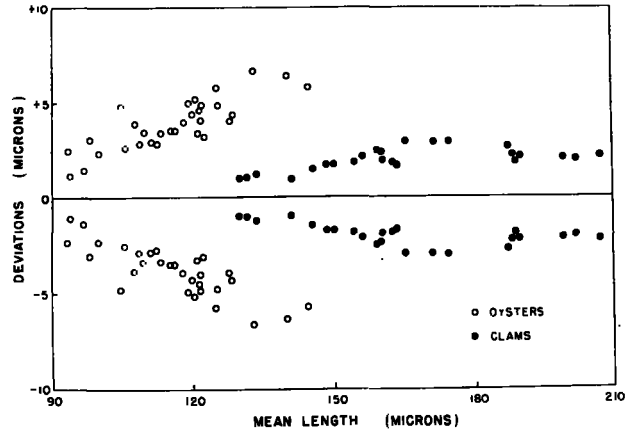

FIGURE 1.—The 95 percent confidence limits of measurements of mean lengths of oyster and clam larvae of different sizes. Values indicate ± 2 SE_m. N=100 for oyster larvae; N=50 for clam larvae.

[3] Trade names referred to in this publication do not imply endorsement of commercial products.

transformed values (G) for measurements of growth are generally accurate to about ±10 percent for oyster larvae and to about ±5 percent for clam larvae. The confidence limits for oyster larvae were not narrowed appreciably even by increasing N to 300; therefore, it was considered impractical to increase the number of measurements of oyster larvae sufficiently to reduce the error to that of measurements of clam larvae.

Errors involved in our techniques for determining numbers of larvae developing from fertilized eggs to straight-hinge larvae or the number surviving in growth experiments have been found to be about ±10 percent.

In any event, the effects of test compounds on larval growth and survival are readily distinguished, from random variation, by the regular stepwise reduction at each successive increase in concentration of the test chemical.

EFFECTS OF DIFFERENT COMPOUNDS ON EMBRYOS AND LARVAE

Table 1 shows the relative percentage of fertilized oyster and clam eggs that developed through normal embryonic stages into straight-hinge larvae, the relative percentage of larvae that survived, and the relative percentage increase in mean length when exposed to various pesticides and chemicals. We calculated the relative percentages, as has been previously stated, by using the survival and rate of growth of larvae in the control cultures of each experiment as 100 percent. The values given (except where noted) are averages for duplicate cultures at each concentration in each experiment. When more than one experiment was run, we combined the results of all experiments.

Some compounds were more toxic to embryos than to larvae (despite the much shorter exposure period of the embryos), although the reverse is generally indicated in our tests. The differences between the tolerance of developing embryos and larvae of oysters to the same pesticide are strikingly evident from the effects of the weedicides, Amitrol and Endothal (table 1). Embryos developed normally in higher concentrations of Amitrol (500 p.p.m.) than those at which larvae showed good growth (100 p.p.m.). In contrast, eggs could tolerate only 10 p.p.m. of Endothal, whereas larvae showed about normal growth at concentrations as high as 50 p.p.m.

The compounds we used in our tests differed widely in chemical composition and presumably have different modes and sites of action. It is not too surprising, therefore, that although the toxic levels of most compounds are about the same for clams and oysters, some are appreciably more toxic to one than to the other. The tolerance of oyster larvae to Endothal, for example, was considerably greater than that of clam larvae (although oyster embryos were slightly less tolerant than were clam embryos). Oyster larvae showed fair survival and normal growth at 25 p.p.m., whereas this concentration caused 100 percent mortality of clam larvae. In general, however, the rates of growth of clam larvae are less affected by toxicants than growth of oyster larvae.

As has been reported previously (Davis, 1960), some of the lower concentrations of certain compounds significantly accelerated growth of larvae (notably Sevin, Endothal, 2-4-D salt, phenol, and Sulmet—table 1). Although the reasons for this phenomenon are not clear, we believe it is the result of the bacteriostatic or, possibly, chelating effect of these compounds. Because growth of clam larvae is less affected by bacterial and algal toxins than is growth of oyster larvae, any bacteriostatic or chelating effect these compounds might have would be expected to have a less marked effect on growth of clam larvae than on growth of oyster larvae.

Synergistic Action of Solvent With Some Compounds

With certain pesticides, the solvent may act as a synergist and increase the toxicity of the compound, but with other pesticides the same solvent may show no such action. Acetone appeared to act as a synergist with Co-Ral but not with Di-Syston and Phygon. In experiments when the stock solutions of these three water-insoluble compounds were made up in acetone (appendix), the pair of control cultures receiving 100 p.p.m. acetone (the maximum concentration used in any of the experimental cultures) showed no significant reduction in growth or survival of either clam or oyster larvae. Survival and growth of clam larvae receiving Di-Syston and Phygon decreased progressively as the concentrations of these compounds increased, just as it did in various concentrations of the water-soluble toxicants (table 1). The toxic effects of Co-Ral, however, show a definite break in the middle of the

series that corresponds to the break in acetone concentrations.

To obtain the six concentrations of these acetone-soluble compounds, from 0.25 to 10 p.p.m., we used two stock solutions. The concentrations of 0.25, 0.5, and 1 p.p.m. of toxicants were obtained by increasing volumes of the less concentrated stock solution so that the concentrations of acetone were 25, 50, and 100 p.p.m. The concentrations of 2.5, 5, and 10 p.p.m. were achieved by increasing volumes of the more concentrated stock solution, again giving concentrations of acetone of 25, 50, and 100 p.p.m.

The stepwise decrease in survival and growth of clam larvae at 0.25, 0.5, and 1 p.p.m. Co-Ral, followed by better survival and growth at 2.5 p.p.m. and stepwise reduction at 5 and 10 p.p.m. indicates that the action of Co-Ral was being synergized by the acetone solvent (the action of Di-Syston and Phygon was not). The effect of Aldrin on clam embryos shows some evidence of similar synergism.

Variable Effects of Endrin and Dieldrin

Results of different experiments with these two compounds varied considerably even when acetone stock solutions were used. The results given for endrin and dieldrin, therefore, are the average values of a number of experiments but in some experiments tolerances were significantly below these averages. We assume that the variation in the several experiments was caused by differences in particle size and degree of suspension attained in the test culture, since these compounds are essentially insoluble in water. We would expect field observations on commercial applications to yield conflicting data, depending upon the degree of dispersion attained when the pesticide reaches the water.

Possible Indirect Effect of Compounds Through Food Chain

Ukeles (1962) showed that the tolerance for pesticides of some of the best algal foods for bivalve larvae was considerably lower than the tolerances of the larvae. Therefore, even a concentration of a pesticide that showed no effect on eggs or larvae might, indirectly, if used in the field, markedly reduce the growth of bivalve larvae by killing or preventing reproduction of the algae that serve as foods.

We believe the results given in table 1 are, at least primarily, the direct effect of these compounds on the embryos or larvae themselves because we are not dependent upon reproduction of the algae in our larval cultures. We add the food cells to our experimental cultures daily, and the pesticide would have an indirect effect through the food chain only if it destroyed the food cells. The concentration of Sulmet (sodium sulfamethazine) used routinely as a bactericide in our larval cultures, for example, is sufficient to inhibit or prevent reproduction of the algae used for food, yet it has no adverse effect on growth of larvae under our laboratory conditions of feeding.

Significance of TL_m Values

In table 2 we have listed the 24-hour TL_m (the concentration in p.p.m. that would cause an approximate 50-percent reduction in the number of eggs developing into normal straight-hinge larvae) for oyster and clam eggs. Also listed are the 12-day TL_m for clam larvae and the 14-day TL_m for oyster larvae. We believe the TL_m values listed are of value only for rough comparisons of toxicity because some compounds drastically reduce the rate of growth of larvae at concentrations too low to cause appreciable mortality or may kill embryos at lower concentrations than are required to affect growth or survival of larvae. Both endrin and dieldrin, for example, had 14-day TL_m's for oyster larvae greater than 10 p.p.m., yet either of these compounds, at concentrations of only 1 p.p.m., reduced the rate of growth of these larvae drastically. Other compounds, such as Nemagon, Aldrin, and toxaphene, permitted development of embryos at considerably higher concentrations than those at which the larvae could survive and grow. Conversely, other compounds, such as griseofulvin (on clams) and Endothal (on oysters), almost completely stopped embryonic development at concentrations too low to affect seriously survival and growth of the larvae.

In comparison with the TL_m values given for other species, the rankings of Amitrol, Endothal, Omazene, and Phygon are the same for clam and oyster larvae as Bond, Lewis, and Fryer (1960) found for largemouth bass, *Micropterus salmoides*, and two species of salmon, *Oncorhynchus kisutch* and *O. tshawytscha*. The median tolerance limits for the least tolerant stages in the life cycle of clams and oysters for these compounds, however,

were lower than the values given for fish. The 96-hour TL_m for bluegills, *Lepomis macrochirus*, to Co-Ral and Di-Syston, reported by Henderson, Pickering, and Tarzwell (1960), was also higher than that for the least tolerant stages of clams.

NEED FOR FURTHER STUDY

The examples cited indicate the need for evaluating all aspects of toxicity on rapidly growing and changing animals at each stage of their life cycle. The high tolerance of bivalve larvae to some of these pesticides also suggests that compounds can be chosen to control pest species without serious damage to commercial shellfish. Within the series of insecticides, for example, Davis (1960) showed that DDT was much more toxic to oyster larvae than lindane. Similarly, within the series of herbicides tested, Amitrol was "safe" at 100 p.p.m., whereas MCPA caused a significant reduction in the rate of growth of oyster larvae at all concentrations above 0.25 p.p.m. We believe, as Thimann (1964) suggested, that emphasis should be placed on developing "substances whose action is selective and on those which decompose quickly."

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Insecticides:	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Aldrin (2 experiments; acetone solution)	0.25				96	[2] 75	[2] 20
	.50				90	[2] 37	[2] 9
	1.00				71	0	
	2.50				86	0	
	5.00				83	0	
	10.00				64	0	
Co-Ral (2 experiments; acetone solution)	.0025	89	74	83			
	.0050	100	66	105			
	.01	103	87	92			
	.025	111	91	88			
	.050	98	90	72			
	.10	55	95	61			
	.25	0	104	49	95	87	89
	.50	0	99	38	97	72	67
	1.00	0	75	17	99	44	39
	2.50				88	74	57
	5.00				87	52	44
	10.00				42	5	14
DDT (1 experiment; water suspension)	.025		80	54			
	.050		0				
Dicapthon (1 experiment; water solution)	.10				112	91	89
	.20				91	88	87
	1.00				95	89	59
	2.00				60	94	65
	10.00				0	0	
Dieldrin [3] (4 experiments; 1 water suspension and 3 acetone solution)	.025	95	69	95			
	.05	75	68	79			
	.10	74	66	67			
	.25	67	53	30			
	.50	60	59	42			
	1.0	29	63	35			
	2.5	46	91	37			
	5.0	40	84	27			
	10.0	31	80	13			
Dipterex (1 experiment; water solution)	.025			67			
	.050			78			
	1.00		50	64			
Di-Syston (2 experiments; acetone solution)	.025	110	103	106			
	.050	98	99	116			
	.100	96	115	117			
	.25	103	97	101	99	91	98
	.50	82	91	80	92	81	96
	1.00	75	76	51	80	67	74
	2.50	53	64	9	75	2	14
	5.00	56	34	2	52	0	
	10.00	21	0		16	0	
Endrin [4] (5 experiments; 2 water suspension and 3 acetone solution)	.025	103	79	111			
	.050	91	67	70			
	.100	92	70	61			
	.25	52	67	38			
	.50	58	66	20			
	1.00	44	50	30			
	2.5	44	78	35			
	5.0	42	79	12			
	10.0	48	83	11			

See footnotes at end of table.

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]—Continued

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Insecticides—Continued	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Guthion (1 experiment; water solution)	.25	91			106	81	95
	.50	65			109	81	95
	1.00	0			31	38	98
	2.50						
	5.00	0			0	0	
	10.00	0			0	0	
Lindane (1 experiment; water solution)							
	.25	127			97	117	86
	.50	114			112	102	98
	1.00	84			111	100	101
	2.50						
	5.00	82			106	103	107
	10.00	43			60	67	71
Malathion (2 experiments; acetone solution)							
	.25	104	90	86			
	.50	95	88	90			
	1.00	101	66	77			
	2.50	89	52	74			
	5.00	85	20	72			
	10.00	42	3	41			
N-3452 (1 experiment; water solution)							
	.50	0	0				
	1.0	0	0				
	2.5	0	0				
	5.0	0	0				
N-3514 (1 experiment; water solution)							
	1.0	0	0		0	5	30
	10.0	0	0		0	0	
Parathion (1 experiment; water solution)							
	.025			103			
	.050			87			
	1.00			22			
Sevin (3 experiments; 1 water solution and 2 acetone solution)							
	.02	88	111	109	85		
	.025				97		
	.050				100		
	.10	96	113	119	77		
	.20	104	117	124	91		
	1.00	106	119	106	94	103	92
	2.00	90	135	72	77		
	2.50				64	85	30
	4.00	11	0		48		
	5.00				0		
	10.00	0	0		[2] 41		
TEPP (1 experiment; water solution)							
	1.00	100	101	80			
	2.50	91	93	70			
	5.00	100	101	61			
	10.00	74	90	41			
Toxaphene (2 experiments; acetone solution)							
	.25				84	33	21
	.50				91	11	5
	1.00				51	0	
	2.50				39	0	
	5.00				37	0	
	10.00				0	0	
Herbicides:							
Amitrol (2 experiments; water solution)							
	2.50	101	99	117			
	5.00	99	94	111			
	10.00	103	100	96			
	25.00	95	80	117			
	50.00	104	80	112			
	100.00	104	96	116			
	250.00	104	51	71			
	500.00	94	5	36			
	1,000.00	2	0				
Amitrol-T (1 experiment; water solution)							
	.25	93	91	116			
	.50	100	89	107			
	1.00	48	97	109			
	2.50	93	96	105			
	5.00	89	104	99			
	10.00	88	78	108			
2-4-D ester (1 experiment; acetone solution)							
	.025		95	99			
	.05		97	95			
	.10		80	89			
	.25	90	102	70			
	.50	89	98	100			
	1.00	80	0				
	2.50	89					
	5.00	85					
	10.0	27					

See footnotes at end of table.

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]—Continued

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Herbicides—Continued	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
2-4-D salt (2 experiments; water solution)	.025	----------	84	148	----------	----------	----------
	.05	----------	98	194	----------	----------	----------
	.10	----------	93	134	----------	----------	----------
	.25	84	92	124	----------	----------	----------
	.50	91	89	111	----------	----------	----------
	1.0	82	102	119	----------	----------	----------
	2.5	78	103	83	----------	----------	----------
	5.0	79	112	86	----------	----------	----------
	10.0	88	97	77	----------	----------	----------
	25.0	29	104	62	----------	----------	----------
	50.0	32	52	39	----------	----------	----------
	100.0	0	45	8	----------	----------	----------
Diuron (1 experiment; water solution)	.25	----------	----------	----------	92	128	99
	.50	----------	----------	----------	91	112	101
	1.00	----------	----------	----------	81	127	94
	5.00	----------	----------	----------	0	[5] 100	62
EMID (4 experiments; water solution)	.25	103	99	81	----------	----------	----------
	.50	101	92	99	----------	----------	----------
	1.0	107	95	87	----------	----------	----------
	2.5	101	106	94	----------	----------	----------
	5.0	101	106	82	----------	----------	----------
	10.0	90	98	78	----------	----------	----------
	25.0	2	61	47	----------	----------	----------
	50.0	0	11	1	----------	----------	----------
	100.0	0	0	----------	----------	----------	----------
Endothal (2 experiments; water solution)	.25	95	97	124	98	100	104
	.50	108	98	148	86	104	108
	1.00	101	97	129	85	103	104
	2.50	91	111	130	98	92	99
	5.00	102	109	129	93	91	91
	10.0	94	109	119	89	60	64
	25.0	57	74	96	76	0	----------
	50.0	1	48	90	51	0	----------
	100.0	0	2	18	0	0	----------
Fenuron (2 experiments; water solution)	.025	----------	----------	----------	100	92	[6] 76
	.050	----------	----------	----------	100	53	[6] 64
	.20	----------	----------	----------	100	69	[6] 38
	.25	----------	----------	----------	[7] 91	86	[7] 110
	.50	----------	----------	----------	[7] 92	[7] 75	[7] 115
	1.00	----------	----------	----------	[6,7] 98	[7,8] 95	[7,8] 119
	2.00	----------	----------	----------	[6] 97	[6] 0	[6] 0
	4.00	----------	----------	----------	[6] 98	[6] 0	[6] 0
	5.00	----------	----------	----------	[7] 95	[7] 115	[7] 109
	10.00	----------	----------	----------	[6] 115	[6] 0	[6] 0
MCPA (2 experiments; water solution)	.25	100	75	69	----------	----------	----------
	.50	103	89	99	----------	----------	----------
	1.00	99	89	110	----------	----------	----------
	2.50	94	88	86	----------	----------	----------
	5.00	96	80	77	----------	----------	----------
	10.00	80	89	61	----------	----------	----------
	25.00	0	64	30	----------	----------	----------
	50.00	0	8	14	----------	----------	----------
	100.00	0	0	----------	----------	----------	----------
Monuron (1 experiment; water solution)	.25	----------	----------	----------	93	120	114
	.50	----------	----------	----------	99	122	109
	1.00	----------	----------	----------	91	128	86
	5.00	----------	----------	----------	92	111	93
Neburon (1 experiment; water solution)	2.4	----------	----------	----------	0	0	----------
	4.8	----------	----------	----------	0	0	----------
Silvex (1 experiment; acetone solution)	.025	----------	89	128	----------	----------	----------
	.05	----------	101	108	----------	----------	----------
	.1	----------	99	91	----------	----------	----------
	.25	100	102	94	----------	----------	----------
	.50	81	85	38	----------	----------	----------
	1.0	75	0	----------	----------	----------	----------
	2.5	78	----------	----------	----------	----------	----------
	5.0	56	----------	----------	----------	----------	----------
	10.0	22	----------	----------	----------	----------	----------
Nematocide:							
Nemagon (2 experiments; acetone solution)	.25	----------	----------	----------	100	116	75
	.50	----------	----------	----------	98	97	30
	1.00	----------	----------	----------	100	14	21
	2.50	----------	----------	----------	98	<1	4
	5.00	----------	----------	----------	95	0	----------
	10.00	----------	----------	----------	86	0	----------
Solvents:							
Acetone (1 experiment; confirmed by others)	10.0	162	----------	----------	91	100	110
	25.0	----------	----------	----------	107	100	104
	50.0	122	----------	----------	98	100	91
	100.0	158	----------	----------	93	100	91
	250.0	----------	----------	----------	----------	100	87

See footnotes at end of table.

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]—Continued

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Solvents—Continued	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Allyl alcohol (1 experiment; water solution)	.25				95	0	
	.50				76	0	
	1.0				51	0	
	2.5				0	0	
	5.0				0	0	
	10.0				0	0	
Orthodichlorobenzene (1 experiment; acetone solution)							
	.25				107	121	95
	.50				94	111	98
	1.0				99	123	92
	2.5				94	107	97
	5.0				106	107	94
	10.0				79	82	86
Trichlorobenzene (1 experiment; acetone solution)							
	1.0	59			72	108	102
	10.0	21			58	69	104
Bactericides, fungicides, algicides, miscellaneous:							
Chloramphenicol (1 experiment; water solution)							
	.1				108	97	111
	.2				111	104	117
	1.0				106	84	104
	2.0				100	87	101
	10.0				107	90	81
	100.0				30	0	
Delrad (1 experiment; water solution)							
	.01		94	89		117	96
	.05		9	50		[2] 88	42
	.1		0			0	
	.2		0			0	
Dowicide A (1 experiment; water solution)							
	.25				104	70	114
	.50				86	136	119
	1.00				102	0	
	2.50				100	0	
	5.00				94	0	
	10.00				55	0	
Dowicide G (1 experiment; water solution)							
	.25				0	0	
	.50				0	0	
	1.00				0	0	
	2.50				0	0	
	5.00				0	0	
	10.00				0	0	
Griseofulvin (1 experiment; water solution)							
	.025					106	101
	.050					94	100
	.10					99	109
	.25				36	101	98
	.50				0	105	103
	1.00				0	86	101
	2.50				0		
	5.00				0		
	10.00				0		
PVP-Iodine (2 experiments; water solution)							
	.25					99	106
	.50					103	101
	1.00					108	102
	2.50				108	116	100
	5.00				103	85	97
	10.00				94	92	93
	25.00				1	82	56
	50.00				0	1	9
	100.00				0		
Nabam (1 experiment; water solution)							
	.5	0			0	118	9
	1.0	0			0	102	8
	2.5	0			0	0	
	5.0	0			0	0	
	10.0	0			0	0	
Nitrofurazone (1 experiment; water solution)							
	2.50				104	94	97
	5.00				111	101	83
	10.00				111	101	75
	25.00				119	87	53
	50.00				103	93	45
	100.00				102	80	23
Omazene (2 experiments; water solution)							
	.025	87	107	122	101	93	104
	.05	79	103	123	97	91	104
	.10	34	84	112	21	93	98
	.25	0	76	22	0	90	74
	.50	0	0		0	12	33
	1.00	0	0		0	0	

See footnotes at end of table.

TABLE 1.—*Percentage of eggs of American oyster and hard clam that developed normally, percentage of larvae that survived, and percentage increase in mean length, in the presence of different concentrations of chemicals* [1]—Continued

Compound	Concentration	Oysters			Clams		
		Eggs developing	Survival of larvae	Increase in length of larvae	Eggs developing	Survival of larvae	Increase in length of larvae
Bactericides—Continued							
Pentachlorophenol (1 experiment; acetone solution)	*P.p.m.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
	.025		115	104			
	.05		86	80			
	.10		0				
	.25	0	0				
	.50	0	0				
	1.00	0					
	2.50	0					
	5.00	0					
Pentachlorophenyl acetate (1 experiment; acetone solution)	.025		41	60			
	.05		0				
	.10		0				
	.25	0	0				
	.50	0	0				
	1.00	0					
	2.50	0					
	5.00	0					
Phenol (1 experiment; water solution)	.025	103			111	121	109
	.05	110			101	131	114
	.10	112			126	143	115
	.20	102			105	130	119
	1.0	103			99	137	125
	2.0	94			113	166	128
	10.0	102			95	149	55
	100.0	5			0	0	
Phygon (2 experiments; acetone solution)	.00025	110	106	100	97	99	99
	.0050	101	113	76	91	99	99
	.01	69	95	39	65	104	96
	.025	0	79	20	1	94	76
	.050	0	32	9	0	58	31
	.10	0	0		0	34	21
	.25				0	0	
	.50				0	0	
	1.00				0	0	
Roccal (1 experiment; water solution)	.1				97	80	86
	.2				45	0	
	1.0				0	0	
Rosin Amine D (1 experiment; acetone solution)	.025		5				
	.05		0				
	.10		0				
	.25	0	0				
	.50	0	0				
	1.00	0					
	2.50	0					
	5.00	0					
Sulmet (1 experiment; water solution of tinted veterinary formula)	.1				103	97	109
	.2				108	113	112
	1.0				111	103	106
	2.0				105	106	87
	10.0				95	113	83
	100.0				107	98	37
Sulmet (1 experiment; water solution of new untinted 1962 formulation)	50.00		90	150		111	97
	100.00		95	155		90	100
	150.00		94	148			
	200.00		108	138		114	101
	300.00		108	131		111	100
	400.00		110	121		108	98
	500.00		112	92		110	96
	600.00		101	72			
	1,000.00					98	85
TCC (1 experiment; water solution)	.0025					106	91
	.005					92	48
	.01					19	5
	.025				69	89	18
	.05				0	7	6
	.1				0	0	
	.25				0		
	.50				0		
	1.00				0		
TCP (1 experiment; water solution)	.025		100	116			
	.05		94	129			
	.10		96	117			
	.25	96	87	116			
	.50	62	99	114			
	1.00	2	85	14			
	2.50	20					
	5.00	0					
	10.00	0					

[1] Relative percentages calculated by using survival and growth rates of larvae in control cultures.

[2] 1 experiment only.

[3] Results with Dieldrin very erratic (see text).

[4] Results with Endrin very erratic (see text).

[5] 1 culture only; duplicate 97 percent mortality.

[6] 1st experiment.

[7] 2d experiment.

[8] 97 percent mortality in 1st experiment.

[9] 1 culture only; duplicate 100 percent mortality.

TABLE 2.—*Estimated concentrations (TL_m values), calculated by interpolation from data in table 1, at which 50 percent of the eggs of oysters and clams develops normally or 50 percent of the larvae survives*

Compound	Oysters		Clams	
	48-hr. TL_m eggs	14-day TL_m larvae	48-hr. TL_m eggs	12-day TL_m larvae
Insecticides:				
Aldrin			>10.00	0.41
Co-Ral	0.11	>1.00	9.12	5.21
DDT		.034		
Dicapthon			3.34	5.74
Dieldrin	.64	>10.00		
Dipterex		1.00		
Di-Syston	5.86	3.67	5.28	1.39
Endrin	.79	>10.00		
Guthion	.62		.86	.86
Lindane	9.10		>10.00	>10.00
Malathion	9.07	2.66		
N-3452	<.50	<.50		
N-3514	<1.00	<1.00	<1.00	<1.00
Parathion				
Sevin	3.00	3.00	3.82	>2.50
TEPP	>10.00	>10.00		
Toxaphene			1.12	<.25
Herbicides:				
Amitrol	733.70	255.44		
Amitrol-T	>10.00	>10.00		
2-4-D ester	8.00	.74		
2-4-D salt	20.44	64.29		
Diuron			2.53	>5.00
EMID	16.82	30.00		
Endothal	28.22	48.08	51.02	12.50
Fenuron			>10.00	>5.00
MCPA	15.62	31.30		
Monuron			>5.00	>5.00
Neburon			<2.4	<2.4
Silvex	5.90	.71		
Nematocide: Nemagon			10.00	.78
Solvents:				
Acetone	>100.00		>100.00	>100.00
Allyl alcohol			1.03	<.25
Orthodichlorobenzene			>100.00	>100.00
Trichlorobenzene	3.13		>10.00	>10.00
Bactericides, fungicides, algicides, miscellaneous:				
Chloramphenicol			74.29	50.00
Delrad		.031		.072
Dowicide A			>10.00	.75
Dowicide G			<.25	<.25
Griseofulvin			<.25	<1.00
PVP-Iodine			17.10	34.94
Nabam	<.50		<.50	1.75
Nitrofurazone			>100.00	>100.00
Omazene	.078	.34	.081	.378
Pentachlorophenol	<.25	.071		
Pentachlorophenyl acetate	<.25	<.025		
Pheriol	58.25		52.63	55.00
Phygon	.014	.041	.014	1.75
Roccal			.19	.14
Rosin Amine D	<.25	<.025		
Sulmet, tinted			>100.00	>100.00
Sulmet, untinted	>600.00	>600.00	>1,000.00	>1,000.00
TCC			.032	.037
TCP	.60	>1.00		

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APPENDIX

TABLE A–1.—*Source, solubility, and chemical names of compounds tested*

Common name	Chemical name	Solubility in p.p.m.	Source
Insecticides:			
Aldrin	Hexachlorohexahydro-endo, exo-dimethanonaphthalene.	Insoluble in water; 1,590,000 in acetone	Shell Chemical Corp.
Co-Ral	O,O-diethyl O-3-chloro-4-methyl-2-oxo-2H-1-benzopyran-7-yl phosphorothioate.	Insoluble in water; soluble in acetone	Chemagro Corp.
DDT	Dichlorodiphenyltrichloroethane	0.0002 in water (0.2 as colloid); 590,000 in acetone.	
Dicapthon	O-O-dimethyl-O(2 chloro-4 nitrophenyl) phosphorothioate.	Very low solubility in water; very low solubility in acetone.	American Cyanamid Co.
Dieldrin	Hexachloroepoxyoctahydro-endo, exo-dimethanonaphthalene.	Insoluble in water; 540,000 in acetone	Shell Chemical Corp.
Dipterex	O,O-dimethyl-1-hydroxy-2,2,2-trichloroethyl-phosphonate.	130,000 in water	Chemagro Corp.
Di-Syston	O,O-diethyl S-2-(ethylthio)ethyl phosphorodithioate.	25 in water; soluble in acetone	Do.
Endrin	Hexachloroepoxyoctahydro-endo, endo-dimethanonaphthalene.	"Insoluble" in water; "moderately" soluble in acetone.	Shell Chemical Corp.
Guthion	O,O-dimethyl S-4-oxo-1,2,3-benzotriazino-3(4H)-ylmethyl phosphorodithioate.	33 in water	Chemagro Corp.
Lindane	1,2,3,4,5,6-hexachlorocyclohexane	10 in water; 440,000 in acetone	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Malathion	O,O-dimethyl dithiophosphate of diethyl mercaptosuccinate.		American Cyanamid Co.
N-3452	Alkyl (C_8–C_{18}) dimethyl benzyl ammonium chloride.		Niagara Chemicals Division, Food Mach. & Chem. Corp.
N-3514	2-chloro-1-nitropropane	8,000 in water	Do.
Parathion	O,O-diethyl O-p-nitrophenyl thiophosphate.	20 in water	Chemagro Corp.
Sevin	1-naphthyl-N-methylcarbamate	1,000 in water; 300,000 in acetone	Union Carbide Chem. Co.
TEPP	Tetraethyl pyrophosphate	Miscible in water (hydrolyzes); miscible in acetone.	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Toxaphene	Mixture of polychloro bicyclic terpenes with chlorinated camphene predominating.	1.5 in water; 4,500,000 in acetone	Hercules Powder Co.
Herbicides:			
"Amitrol" Aminotriazole	3-amino-1H-1,2,4-triazole	Very soluble in water	
Amitrol-T	3-amino-1H-1,2,4-triazole with ammonium thiocyanate.	do	
2-4-D ester	Butoxyethanol ester of (2,4-dichlorophenoxy) acetic acid.	"Insoluble" in water	Thompson Hayward Chemical Co.
2-4-D salt	Dimethylamine salt of (2,4-dichlorophenoxy)acetic acid.	Very soluble in water	Do.
Diuron	3-(3,4-dichlorophenyl)-1,1-dimethylurea	42 in water	E. I. duPont de Nemours & Co.
EMID	2,4-dichlorophenoxy-acetamide	Very soluble in water	
Endothal	Disodium 3,6-endoxohexahydrophthalate	280,000 in water	Pennsalt Chemical Co.
Fenuron	3 phenyl-1,1-dimethylurea	2,900 in water	E. I. duPont de Nemours & Co.
MCPA	Dimethylamine salt of (2-methyl-4-chlorophenoxy) acetic acid.	Very soluble in water	American Chemical Paints Co.
Monuron	3-(p-chlorophenyl)-1, 1-dimethylurea	230 in water	E. I. duPont de Nemours & Co.
Neburon	1-n-butyl-3-(3,4-dichlorophenyl)-1-methylurea.	4.8 in water	Do.
Silvex	Butoxyethanol ester of (2,4,5-trichlorophenoxy)propionic acid.	0.014 percent in water; 15.2 percent in acetone.	
Nematocide:			
Nemagon	1,2-dibromo-3-chloropropane	1,000 in water; very soluble in acetone	Shell Chemical Corp.
Solvents:			
Acetone	Acetone	Miscible in water	Mallinckrodt Chemical Works.
Allyl alcohol	Propen-1-ol-3	do	Shell Chemical Corp.
Orthodichlorobenzene	o-dichlorobenzene	130 in water; miscible in acetone	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Trichlorobenzene	Trichlorobenzene	25 in water; miscible in acetone	Do.
Bactericides, fungicides, algicides, miscellaneous:			
Chloramphenicol	(Chloromycetin)D-(-)-threo-2-dichloroacetamido-1-p-nitrophenyl-1,3-propanediol.	2,500 in water; very soluble in acetone	Parke, Davis & Co.
Delrad	Dehydro-abietylamine acetate	Very soluble in water	Hercules Powder Co.
Dowicide A	O-phenylphenol, sodium salt	1,220,000 in water	Dow Chemical Co.
Dowicide G	Sodium pentachlorophenate, technical	330,000 in water	Do.
Griseofulvin	7-chloro-2',4,6-trimethoxy-6'-methyl-spiro[benzofuran-2(3H),1'-[2]cyclohexene]-3,4-dione.	10.0 in water	McNeil Laboratories, Inc.
PVP-Iodine	Polyvinylpyrrolidone-iodine complex	Very soluble in water	Antara Chemicals Division, General Analine & Film Corp.
Nabam	Disodium ethylenebis(dithiocarbamate)	do	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Nitrofurazone	5-nitro-2-furaldehyde semicarbazone	238 in water	Hess Clark Division, Vick Chemical Co.
Omazene	Copper dihydrazinium sulfate	"Very slightly" soluble in water	Olin Mathieson Chemical Corp.
Pentachlorophenol	Pentachlorophenol	80 in water; very soluble in acetone	Monsanto Chemical Co.
Pentachlorophenyl acetate	Pentachlorophenyl acetate		Niagara Chemicals Division, Food Mach. & Chem. Corp.
Phenol	Phenol	82,000 in water; very soluble in acetone	Mallinckrodt Chemical Works.
Phygon	2,3-dichloro-1,4-naphthoquinone	"Insoluble" in water	Niagara Chemicals Division, Food Mach. & Chem. Corp.
Roccal	Alkyl (C_8H_{17}–$C_{18}H_{37}$)dimethylbenzyl-ammonium chloride.	10 percent solution; very soluble in water.	Sterwin Chemicals, Inc.
Rosin Amine D	Rosin amine D (technical grade of dehydroabietylamine).	"Insoluble" in water; very soluble in acetone.	Hercules Powder Co.
Sulmet (tinted veterinary soluble)	(Sodium sulfamethazine)sodium(4,6-dimethyl-2-sulfanilamidopyramidine).	Very soluble in water	Agricultural Division, American Cyanamid Co.
Sulmet (untinted soluble)	do	do	Do.
"TCC"	3,4,4'-trichlorocarbanilide	"Insoluble" in water; 40,000 in acetone	Monsanto Chemical Co.
2,4,5 TCCPA	Propylene glycol to butyl ether esters of 2-(2,4,5-trichlorophenoxy)propionic acid.		

BIOLOGICAL STUDIES AND ESTIMATES OF OPTIMUM ESCAPEMENTS OF SOCKEYE SALMON IN THE MAJOR RIVER SYSTEMS IN SOUTHWESTERN ALASKA

By Robert L. Burgner, Charles J. DiCostanzo, Robert J. Ellis, George Y. Harry, Jr., Wilbur L. Hartman, Orra E. Kerns, Jr., Ole A. Mathisen, and William F. Royce[1]

ABSTRACT

An intensive research program was conducted in 1961 and 1962 by the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, and the Fisheries Research Institute, University of Washington, with the cooperation of the Alaska Department of Fish and Game. Many sockeye salmon river systems were studied concurrently with essentially the same techniques so that systems covering the entire range of production levels could be compared. The general objective of this research was to determine the optimum escapement of sockeye salmon for each of the major systems. This was accomplished through integration of the results of several related studies: (1) summarization and analysis of historical and current data on runs of adult sockeye salmon, (2) delineation and description of spawning areas and estimation of their capacities, (3) delineation and description of the nursery areas and estimation of their capacities.

The major systems studied were the Wood, Kvichak, Naknek, and Ugashik systems, which enter Bristol Bay; the Chignik system, on the south side of the Alaska Peninsula; and the Karluk system, on Kodiak Island. Adult sockeye salmon in the commercial catches and escapements, and sockeye salmon smolts, were counted and sampled. Spawning grounds were surveyed to determine their size and quality and the distribution and abundance of spawners. Bathymetric maps were prepared for some of the nursery lakes. Intensive limnological studies, including a major effort to measure primary productivity, were made on many nursery lakes. Several types of gear sampled juvenile sockeye salmon and associated species in the lakes. Interim optimum or target escapements required for highest production on a sustained-yield basis have been established for each major system.

The major task that the manager of a salmon fishery must undertake each year is to set a target escapement of fish to the spawning grounds for each salmon run (stock) under his management. He must have such a goal as a basis for numerous decisions that control the actual time, place, and method of fishing.

A correct decision is extremely valuable. The number of sockeye salmon *(Oncorhynchus nerka)* returning to a single river in Alaska may exceed 20 million in a single year, and each fish caught may be worth as much as $3 after being canned. Sometimes the number of adults returning to a system is much larger than the needed escapement; sometimes it is not large enough. Great year-to-year variability in the size of the run to a given system is common.

The manager must divide the return between catch and escapement, and he must do so in a way that ensures maximum sustainable yield. He must know the optimum escapement and then he must set a target escapement, having in mind the optimum and any modifications that may be indicated by the expected characteristics of the returning run and the expected conditions within the spawning and nursery areas. He will tend to set an escapement slightly higher than the optimum because his control of the fishery is not precise, and he is aware that the cost of slight underfishing is probably less than the cost of slight overfishing. In this way he attempts to make full use of the spawning and nursery areas.

The optimum escapement is usually considered to be the number of adults that will yield the greatest surplus of expected return over needed escapement. The optimum escapement is determined from the historical relation between

[1] The authors are listed alphabetically because no one is considered to be the senior author. Their addresses are: DiCostanzo, Ellis, and Hartman, Fishery Biologists, Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska 99821; Burgner, Kerns, Mathisen, and Royce, Fishery Biologists, Fisheries Research Institute, University of Washington, Seattle 98105; and Harry, Fishery Biologist, Bureau of Commercial Fisheries Biological Laboratory, Ann Arbor, Mich. 48103.

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recruitment, which usually is measured as the number of adults returning, and the parent escapement. A simplified example of this relation, developed partly from inference and partly from observation, is a curve that starts at zero and rises to the left of the replacement line (the 45° line representing replacement reproduction at various levels of escapement), so that over a considerable range of escapements the expected return is greater than the parent escapement (fig. 1). The distance between the curve and the replacement line represents surplus production. The curve, however, either levels off or declines because the capacities of the spawning area, the nursery area, or the ocean feeding ground have been exceeded; and an increased number of spawners will not increase the expected return.

In practice, a satisfactory curve is difficult to obtain. First, observations over many years that include values for the entire range of escapement sizes are needed for each run. These observations are not available for most runs in southwestern Alaska. Attempts to estimate the escapement on the basis of the catch per unit of effort of the fishery (International North Pacific Fisheries Commission, 1962) yielded uncertain results because the relation between the catch per unit of effort and the level of the escapement varied with changing gear, changing management practices, and changing effects of competition between units of gear.

Data on the catches of sockeye salmon from runs to Bristol Bay since 1955 present a special problem. The Japanese fishing fleet has intercepted parts of these runs at sea, and its catches in some years have nearly equaled those of United States fishermen in Bristol Bay. The total Japanese catch of Bristol Bay sockeye salmon is not known with reasonable accuracy, and we have no breakdown of their catch by river system.

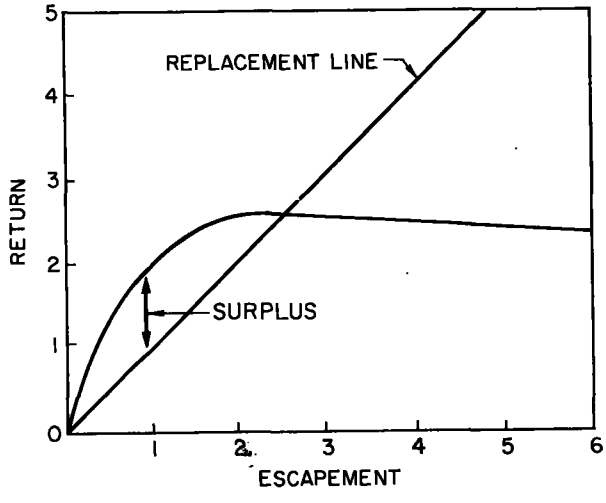

FIGURE 1.—Theoretical return-escapement relation of sockeye salmon.

Even when accurate catch and escapement data have been available, the relation between return and escapement has not been clearly defined—partly because of the cyclic nature of many sockeye salmon runs and partly because survival rates are greatly influenced by environmental conditions which differ from year to year. Obviously, it is desirable to measure abundance before the adults enter the fishery, particularly after completion of any critical part of the life cycle or residence in an environment that may limit production. The mortality of sockeye salmon in fresh water, from potential egg deposition to seaward-migrating smolt, is high and extremely variable; considerable evidence indicates that the fresh water rather than the marine environment usually places upper limits on the numbers of returning adults.

Thus, an important question is: What factors in the fresh-water environment are limiting the size of the sockeye salmon population in each system? First, the adult salmon must have access to spawning areas, and in some systems lack of access may be the limiting factor. Next, the spawning area must have gravel and water suitable for spawning and incubation of the eggs and for sheltering the fry until they emerge. Then, the young fish must find food and shelter for 1 or 2 years in the lake while they grow from a length of about 2.5 cm. to 7 to 13 cm.—smolt size. Finally, the smolts must be able to migrate successfully to sea.

In the sockeye salmon systems of southwestern Alaska, neither the adult's access to the spawning area nor the smolt's path of migration to the sea is restricted. It seems most logical, therefore, to seek limiting factors either during the salmon's life on the spawning grounds as adult, egg, larva, or fry or during its life in the lake as a growing juvenile. Our studies were planned on this assumption, and our task has been to determine approximately the number of spawners that can be expected to produce enough young to fully use the environment.

This report summarizes the data we now recognize as bearing on the question of optimum escapement. In it we recommend (where possible) optimum escapement for each of the sockeye salmon river systems in southwestern Alaska and discuss the factors that affect those levels. The recommendations are the best that we can prepare at this time. They are not the last word—that must await a more detailed understanding of the life of young sockeye salmon.

Commercial fishing for sockeye salmon in southwestern Alaska started in 1884, and the annual catch rose rapidly to more than 10 million fish by 1900 and was rarely less than this until after 1940.[2] Between 1913 and 1938 the annual production in the Bristol Bay area alone exceeded 20 million fish 10 times. The record of 24,700,000 was in 1938. More than half of the catch usually came from the Naknek-Kvichak district, where the fishery produced a record catch of almost 21 million fish in 1938.

During many of the years that the Federal Government managed the sockeye salmon fisheries of southwestern Alaska, desired escapements in the major river systems were established by law. The White Act of June 26, 1924, declared the intent of Congress to limit the catch to 50 percent of the returning salmon—that is, one fish in the escapement for each one in the catch. As our knowledge of the life history of sockeye salmon increased, it became apparent that in some years the stocks were so small that the entire returns were not adequate to use fully the spawning grounds or nursery areas; in other years the returns were so large that escapements of 50 percent were obviously excessive. This provision of the act was repealed on September 4, 1957.[3]

In autumn 1960 it became evident that a major research program was needed to supply additional biological information to be used in the management of the sockeye salmon and pink salmon *(O. gorbuscha)* of Alaska.

This need for information was emphasized by the escapement of more than 3 million adult sockeye salmon to the rivers of the Nushagak fishing district and more than 2 million to the Naknek River in 1959, and an escapement of almost 15 million to the Kvichak River in 1960. These possibly excessive escapements again raised many questions about optimum escapements. In spring 1961, the Secretary of the U.S. Department of the Interior submitted a revised budget in which he requested an increase of $1½ million for an intensified salmon research program in Alaska.

The study of sockeye salmon was undertaken by the BCF (Bureau of Commercial Fisheries Auke Bay Biological Laboratory). About half the funds and research were contracted to the FRI (Fisheries Research Institute, University of Washington). The two agencies together planned several projects on the major sockeye salmon systems.[4] Both organizations had historically worked in specific sockeye salmon river systems; they concentrated their efforts in these areas during this study. The FRI worked on the systems tributary to Nushagak Bay (the Igushik, Snake, Wood, and Nuyakuk systems) on the mainland, the Kvichak system at the head of the Alaska Peninsula, and the Chignik system on the Gulf of Alaska side of the Peninsula. The BCF worked on the Alagnak, Naknek, Egegik, and Ugashik systems of the Alaska Peninsula and the Karluk system on Kodiak Island (fig. 2). By mutual agreement, one agency or the other analyzed historic records of catch and escapement for individual systems.

The intensified program began in April 1961, and field work continued through the summer of 1962. Most of the techniques used by the two organizations were standardized. Field research guides and standardized data sheets were prepared.

The satisfactory execution of this large program required the effort of many biologists. The research responsibilities within the BCF and FRI were as follows.

For the BCF—George Y. Harry, Jr., and Charles J. DiCostanzo, assisted by Wilbur L. Hartman, were responsible for general planning and supervision. DiCostanzo directly supervised the compilation and analysis of the data on the historical and current catch and escapement of adults and on the records of counts of smolts. Hartman supervised the limnological research

[2] Extensive statistics on the catch and pack are available in Rich and Ball (1928), Simpson (1960), and in annual publications such as the Pacific Fisherman Yearbook and the Statistical Yearbook of the International North Pacific Fisheries Commission.

[3] Public Law 85-296.

[4] Each lake or group of connected lakes and its outlet to the ocean is termed a "system" and designated in this report by the name of the outlet or trunk river. For example, Amanka and Ualik Lakes are connected to the ocean through the Igushik River, and the system is, therefore, called the Igushik.

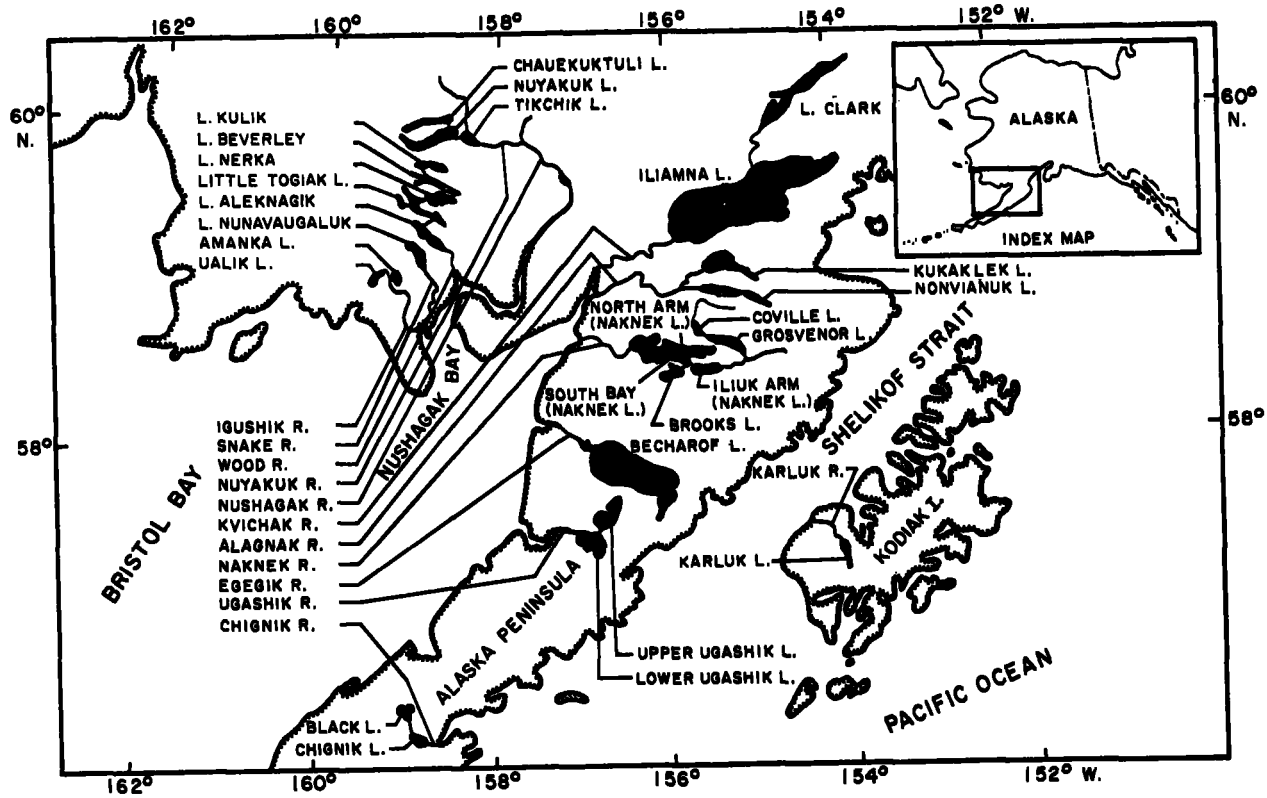

FIGURE 2.—Southwestern Alaska, showing major sockeye salmon river systems.

and assisted in studies of spawning ground capacities. John B. Owen helped compile and analyze historical and current records of catch and escapement. Herbert W. Jaenicke was responsible for counting smolts. Robert J. Ellis, William R. Heard, and Benson Drucker supervised studies of young fish. Ellis also assisted in studies of the spawning ground capacities. Richard Straty was responsible for studies of the timing of the migration of spawning fish in the Naknek system.

For the FRI—William F. Royce, Robert L. Burgner, and Ole A. Mathisen were responsible for general planning and supervision. Burgner and Ted S. Y. Koo supervised studies on the systems tributary to Nushagak Bay. Donald Rogers assisted in studies of the rearing areas in the systems tributary to Nushagak Bay. Mathisen, assisted by Orra E. Kerns, supervised studies on the Kvichak system. Royce supervised the studies of David Narver on the Chignik system.

Biologists who performed the research in each area compiled and analyzed the data on the historical and current catch and escapement in that area.

The Alaska Department of Fish and Game provided samples of scales and data for recent years on catch and escapement, length frequency of adults in escapements for many of the rivers, distribution of escapement for the Nushagak fishing district for 1960-62, and lengths, ages, and numbers of smolts for some rivers.

The broad aim of the intensified study of sockeye salmon was to determine the optimum escapement for each of the major systems in southwestern Alaska. In planning the investigation, we recognized that in the short time available little progress toward attaining our goal could be made by a detailed study of a single lake or river system. General principles applicable to each lake or system could be developed more rapidly by comparing the major sockeye salmon systems with respect to their salmon production and the factors in the spawning grounds or lakes that might limit this production. The bases for comparison were as follows: (1) type, quality, amount, and capacity of spawning areas; (2) type, quality, amount, and capacity of nursery areas; and (3) history and characteristics of sockeye salmon runs. Not all aspects

of the three categories are discussed for all of the systems because for some systems the data are too few.

PHYSICAL DESCRIPTION OF THE LAKES

A substantial portion of this study was devoted to obtaining physical data on the lakes of sockeye salmon systems in southwestern Alaska. All of these lakes were either formed or modified by glaciation during the Pleistocene (Mertie, 1938; Keller and Reiser, 1959). Except for the Alagnak system, the lakes lie at elevations less than 100 m. above sea level (table 1). In some systems tidal influence extends to or almost to the outlet of the lowest lake.

On the basis of geological and biological aspects, the systems studied fall into two general groups—"Mainland" and "Peninsula." The Mainland Systems drain into Bristol Bay along the west and north shores and include the Igushik, Snake, Wood, Nuyakuk, and Kvichak. Several of the Peninsula Systems enter Bristol Bay from the northeast and east—the Alagnak, Naknek, Egegik, and Ugashik. Two other systems that we place in the peninsula category enter the Pacific Ocean—the Chignik on the east coast of the Alaska Peninsula and the Karluk on the northwest shore of Kodiak Island.

TABLE 1.—*Morphometry and altitudes of major sockeye salmon lakes of southwestern Alaska*

System and lake	Lake area	Depth		Volume	Development of shoreline[1]	Altitude
		Maximum	Mean			
MAINLAND SYSTEMS	*Km.*[2]	*M.*	*M.*	*Km.*[3]		*M.*
Igushik system						
Amanka Lake	35	65	23	0.80	3.94	9
Ualik Lake	39	72	28	1.10	1.78	15
Total	74					
Snake system						
Lake Nunavaugaluk	89	162	57	5.10	1.94	14
Total	89					
Wood system						
Lake Aleknagik	83	110	43	3.57	4.22	10
Lake Nerka	201	164	39	7.84	5.70	21
Lake Beverley	90	188	55	4.95	3.46	30
Lake Kulik	45	160	77	3.47	2.80	43
Little Togiak Lake	6	77	30	.18	3.50	28
Total	425			20.01		
Nuyakuk (Tikchik) system						
Tikchik Lake	53	45	15	.80	2.44	95
Nuyakuk Lake	144	283	113	16.27	2.92	95
Lake Chauekuktuli	82	268	111	8.94	2.83	98
Total	279			26.01		

TABLE 1.—*Morphometry and altitudes of major sockeye salmon lakes of southwestern Alaska—Continued*

System and lake	Lake area	Depth		Volume	Development of shoreline[1]	Altitude
		Maximum	Mean			
MAINLAND SYSTEMS—Continued	*Km.*[2]	*M.*	*M.*	*Km.*[3]		*M.*
Kvichak system						
Iliamna Lake	2,622	301	44	115.31	2.75	15
Lake Clark	267	262	103	27.34	3.60	67
Total	2,889			142.65		
PENINSULA SYSTEMS						
Alagnak (Branch) system						
Kukaklek Lake	176				2.13	246
Nonvianuk Lake	121				1.95	192
Total	297					
Naknek system						
Coville Lake	33	53	19	.64	1.86	33
Grosvenor Lake	73	107	50	3.68	2.54	31
Naknek Lake						
North Arm	152	167	63	11.52	2.07	10
Iliuk Arm	94	173	96	9.00	1.71	10
South Bay	32	71	27	.86	1.41	10
West End	302	80	13	3.77	1.82	10
Brooks Lake	75	79	45	3.39	1.70	19
Total	790			32.86		
Egegik system						
Becharof Lake	1,132				2.26	15
Total	1,132					
Ugashik system						
Upper Ugashik Lake	208				1.72	3
Lower Ugashik Lake	177				1.70	3
Total	385					
Chignik system						
Chignik Lake	22	64	26	.60	2.40	5
Black Lake	39	6	3	.10	1.56	15
Total	61			.70		
Karluk system						
Karluk Lake	40	126	49	1.92	2.01	106
Total	40			1.92		

[1] Ratio of the length of the shoreline to the length of the circumference of a circle of area equal to that of the lake.

The geology of each general area is believed to be at least partly responsible for differences in water quality. Drainage areas of the Mainland Systems consist primarily of sedimentary rocks, which occasionally include local deposits of limestone. Minor bodies of igneous rocks and other products of volcanism also occur. In contrast, the drainage areas of the Peninsula Systems,

although containing sedimentary rocks, have proportionally much more igneous material (Keller and Reiser, 1959). The Alaska Peninsula is an area of current and historical volcanism, and drainages of the Peninsula Systems (including the Karluk) contain many deposits of volcanic ash.

The differences in seasonal changes of water level and turbidity in the lakes are also partly due to differences in geology. Water levels are lowest in the winter in all the systems. Because lakes of systems tributary to Nushagak Bay and those of the Chignik and Karluk systems receive most of their water from snowmelt and rainfall, water levels are highest during spring thaw and autumn rainy periods. In contrast, lakes of the other Peninsula Systems and of the Kvichak system are low in the spring and tend to rise during the summer because of melting ice fields and glaciers. Turbidity often varies widely among the lakes within a system because of the localized source of rock flour carried by glacial meltwater. Turbidity is highest during the summer, especially in lakes that receive glacial melt.

The sockeye salmon lakes in southwestern Alaska differ considerably in the length of their ice-free periods, and presumably the growing season also differs. In general, the lakes of the Mainland Systems that are farther from the influence of the oceanic climate have shorter ice-free periods than lakes nearer the coast. For instance, the lakes of the Nuyakuk system are farthest from the coast and are the last to become ice-free in the spring. The upper lakes of the Wood system do not usually become ice-free until after June 1, whereas Lake Aleknagik, the lowest lake in the Wood system, is usually free of ice during late May. In the Kvichak system, Iliamna Lake, because of its large size and greater exposure to ocean storms, loses its ice cover earlier and forms it later than Lake Clark. Breakup generally occurs by mid-May in Iliamna Lake, which occasionally has areas free of ice during mild weather in the winter.

Lakes of the Peninsula Systems, which are more influenced by the oceanic climate and generally more exposed to wind action, may be ice-free over long periods during the winter. The ice in the Naknek system generally breaks up in early May. Iliuk Arm seldom freezes over completely, and the other Naknek lakes frequently develop areas of open water during mild winters. Lakes of the Egegik and Ugashik systems, which are farther down the peninsula, freeze later (if at all) than the Naknek lakes, and the ice (if any) breaks up earlier. In the Chignik system the shallower lake, Black Lake, is free of ice sooner in the spring than Chignik Lake. Both lakes are generally open by early May and frequently develop areas of open water in the winter. The Karluk system is strongly influenced by the oceanic climate; the ice in Karluk Lake frequently begins to break up in April. The lake occasionally remains ice-free during mild winters.

The two lakes in the Igushik system, Amanka and Ualik, have similar areas, maximum and mean depths, and volumes but have different shoreline developments. Lake Amanka has two distinct basins, which are separated by a sill, but Ualik Lake has a single basin. The Kathlene River flows from Ualik Lake into Amanka Lake and enters the latter in its outlet basin.

Lake Nunavaugaluk, the single lake in the Snake system, is relatively deep and has only one basin and a relatively low shoreline development.

The four main lakes of the Wood system (excluding Little Togiak) are similar in average depth and shoreline development (if Lake Nerka is considered to be two separate lakes joined at their west ends). The deep end of each lake is to the west among the mountains, and the shallower east end extends into lowlands. All of the lakes have altitudes of less than 50 m. (table 1).

The lakes of the Nuyakuk system contrast in size and form. Tikchik Lake is relatively shallow. Lakes Chauekuktuli and Nuyakuk are larger and extremely deep—each has a mean depth of about 112 m. and a cryptodepression that exceeds 170 m.

The two major lakes of the Kvichak system are sharply dissimilar in size and other morphometric characters. Iliamna Lake is the largest body of fresh water in Alaska. Its east end lies among the mountains and has a deeply scoured basin with an irregular shoreline, and because of the many islands and bays, it has a high shoreline development value. The western two-thirds of the lake is relatively shallow and uniform in depth and has few islands and a low shoreline development. Lake Clark, much the smaller of the two major lakes of the system, empties into Iliamna Lake through the Newhalen River. It

lies in a long deeply glaciated valley and has a moderately high shoreline development, similar to the average of Iliamna Lake.

The Naknek system contains seven major interconnected lakes or basins all formed by glacial action. In general, the basins are elongate, deep, and steep sided. Within these basins, however, are representatives of most of the major physical and biological types of sockeye salmon lakes in southwestern Alaska. One exception is the lack of a basin as shallow and eutrophic as Black Lake of the Chignik system.

Three lakes of the Naknek system—Coville, Grosvenor, and Naknek—form a chain that drains through Naknek River into Bristol Bay. Coville Lake has the shallowest basin—mean depth, 19 m. It receives a great part of its water from snowmelt and runoff via 80-km.-long American Creek. Coville Lake acts as a settling basin for downstream Grosvenor Lake. Iliuk Arm of Naknek Lake receives drainage from Grosvenor Lake and from glacier fields via the Savonoski River, and from areas of volcanic ash and pumice in the Valley of Ten Thousand Smokes via the Ukak River. The heavy load of rock flour and volcanic materials from these drainages has a profound effect on the water quality and transparency of Iliuk Arm, and to a lesser extent on other areas of Naknek Lake. The South Bay basin of Naknek Lake receives water from Iliuk Arm and North Arm directly, and from Brooks Lake via 1.6-km.-long Brooks River. Brooks Lake receives snowmelt and runoff drainage from low mountains and extensive lowland wet tundra; the water is extremely clear. The North Arm basin of Naknek Lake has a restricted connection to South Bay because of a moraine that forms islands and shallow water along their common border. Drainage into North Arm is snowmelt and runoff, predominantly from areas of wet tundra. The west end of Naknek Lake leading to the outlet is less than 15 m. deep. The comparatively small and shallow northwest basin is separated from North Arm by a moraine and connected to the west end of Naknek Lake across a wide shoal.

Little is known about the morphometry of the remaining lakes in the Bristol Bay area. For lakes of the Alagnak, Egegik, and Ugashik systems we have only the information available from U.S. Geological Survey topographic maps.

The morphometry of the two major lakes of the Chignik system, Chignik and Black, is contrasting. Maximum and mean depths are only 6 and 3 m. for Black Lake, but they are 64 and 26 m. for Chignik Lake. Black Lake flows into Chignik Lake through Black River. Meltwater from an ice field on Mt. Veniaminoff enters Black River and, subsequently, Chignik Lake.

The Karluk system drains via Karluk River into Shelikof Strait on the northwest side of Kodiak Island. The system contains two small lakes and one large lake. The small lakes, Thumb and O'Malley, drain into separate basins of the large lake, Karluk. Karluk Lake is about 20 km. long, has a mean depth of 49 m., and appears to be of glacial origin. Drainage is snowmelt and runoff from a watershed composed predominantly of sedimentary rock.

LIMNOLOGY OF THE LAKES

The limnological studies were designed to help explain why the various lakes and systems produce salmon at different rates. In addition to morphometry of the lakes, we measured factors that other investigators have related to the biological productivity of lakes—chemical and thermal characteristics of the water. We measured biological productivity in terms of primary productivity and the standing crop of phytoplankton. The several measures of water chemistry and biological productivity are examined in relation to production of salmon.

WATER CHEMISTRY

The euphotic zones of the major sockeye salmon nursery lakes were sampled between May 1961 and November 1962 to determine their chemical characteristics. The number of determinations varies among characteristics and lakes, but sampling was concentrated in the more important systems (table 2). Standard methods of collection and analysis were used. In general, lakes of the Peninsula Systems contained higher concentrations of dissolved minerals than those of the Mainland Systems (table 3).

Total Dissolved Solids, Alkalinity, and pH

We have ranked the lakes according to total dissolved solids, total alkalinity, and pH (table 4). As would be expected, the rankings of the lakes by the three measurements tend to be similar, i.e., the more alkaline lakes tended to have higher total dissolved solids and generally higher pH values. Lakes of the Naknek, Chignik,

Nuyakuk, and Karluk systems rank highest in total dissolved solids, and those of the Igushik and Snake systems rank lowest. Usually the values for the three characteristics were similar in all of the lakes of a system. The concentrations of total dissolved solids in other deep-water lakes in the Northern Hemisphere (reported by Hutchinson, 1957) are generally higher than the values in sockeye salmon lakes of southwestern Alaska.

Several investigators have used total dissolved solids to predict lake productivity (cf. Larkin and Northcote, 1958; Rawson, 1942, 1961). A comparison of this characteristic with measures of lake productivity is made later.

TABLE 2.—*Months and depths of sampling and numbers of determinations of temperature and various chemical characteristics of sockeye salmon nursery lakes of southwestern Alaska, 1961-62*

System and lake	Month of sampling	Depth sampled	Determinations made: O_2	Temperature	Alkalinity	pH	Total dissolved solids	Mineral analysis
MAINLAND SYSTEMS		*M.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Igushik system								
Amanka Lake	Aug.	0–25	2	24	-----		2	2
Ualik Lake	Aug.	0–25	2	36	4	4	2	2
Snake system								
Lake Nunavaugaluk	Aug.	0–45	0	16	4	4	2	2
Wood system								
Lake Aleknagik	June-Oct.	0–45	34	192	52	52	10	10
Lake Nerka	June-Oct.	0–45	172	1,915	175	175	14	14
Lake Beverley	June-Oct.	0–45	21	194	26	26	8	8
Lake Kulik	June-Oct.	0–45	25	221	26	26	8	8
Little Togiak Lake	June-Oct.	0–45	34	225	30	30	7	7
Nuyakuk (Tikchik) system								
Tikchik Lake	Aug.	0–30	1	30	4	4	2	2
Nuyakuk Lake	Aug.	0–30	----------				2	2
Lake Chauekuktuli	Aug.	0–45	1	48	4	4	2	2
Kvichak system								
Iliamna Lake	June-Oct.	0–45	74	3,164	45	45	37	37
Lake Clark	June-Oct.	0–45	---	227	8	8	4	4
PENINSULA SYSTEMS		M.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Alagnak (Branch) system								
Kukaklek Lake	July-Aug.	20	8	17	7	8	4	8
Nonvianuk Lake	July-Aug.	25	9	20	9	9	4	8
Naknek system								
Coville Lake	June-Oct.	25	163	286	149	150	10	14
Grosvenor Lake	June-Oct.	45	198	553	178	178	10	15
Naknek Lake	June-May	35	260	742	254	255	14	19
Brooks Lake	June-May	35	249	675	243	249	15	20
Ugashik system								
Lower Ugashik Lake	Aug.	25	0	18	7	7	5	14
Chignik system								
Chignik Lake	June-Oct.	30	----------		61	54	15	15
Black Lake	June-Oct.	4.5	----------		43	41	11	12
Karluk system								
Karluk Lake	June-Oct.	45	214	557	227	222	15	15

TABLE 3.—*Chemical analyses of water from sockeye salmon nursery lakes of southwestern Alaska, 1961-62*

System and lake	Total dissolved solids	pH	Total alkalinity	Sodium	Potassium	Magnesium	Nitrate nitrogen	Silica	Iron	Manganese	Calcium	Boron	Copper	Strontium	Aluminum	Molybdenum
MAINLAND SYSTEMS	*P.p.m.*		*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
Igushik system																
Amanka Lake	21.5	7.80	10.84	0.55	<0.20	0.75	0.075	4.3	.010	.002	5.10	.007	.0003	.06	.005	.0015
Ualik Lake	17.5	7.13	10.50	.80	.35	.70	.020	2.1	.011	.001	3.95	.011	.0004	.08	.003	.0014
Snake system																
Lake Nunavaugaluk	18.0	7.16	10.42	.55	<.30	.65	.120	2.1	.010	.001	4.90	.007	.0003	.07	.003	<.0001
Wood system																
Lake Aleknagik	30.5	7.15	12.51	.63	.35	.95	.111	2.6	.006	.001	4.95	.008	.0003	.07	.004	.0004
Lake Nerka	20.7	7.14	11.99	.45	.37	.87	.167	2.2	.011	.001	4.68	.015	.0003	.06	.005	.0013
Lake Beverley	24.0	7.21	11.90	.80	<.33	.80	.160	2.8	.008	.001	4.23	.012	.0003	.07	.005	.0004
Lake Kulik	25.3	7.11	12.46	.68	.33	.68	.173	3.0	.009	.001	4.65	.005	.0003	.08	.004	.0015
Little Togiak Lake	35.0	7.29	18.69	.75	.50	1.33	.160	3.3	.006	.001	7.23	.013	.0002	.10	.004	.0006
Nuyakuk (Tikchik) system																
Tikchik Lake	42.0	7.34	22.45	.55	<.70	2.12	.090	5.4	.010	.001	7.70	.010	.0004	.09	.005	trace
Nuyakuk Lake	36.5	7.30	22.99	.40	Trace	1.55	.110	6.4	.007	trace	8.40	.017	.0004	.10	.005	<.0001
Lake Chauekuktuli	50.0	7.29	29.46	.40	Trace	2.60	.135	6.4	.005	trace	11.00	.009	.0004	.10	.003	.0003
Kvichak system																
Iliamna Lake	26.3	7.26	13.96	.83	.60	.83	.058	4.5	.011	<.003	5.11	.022	.0004	.06	.010	.0015
Lake Clark	32.0	7.28	19.59	.80	1.28	1.03	.113	8.6	.026	.001	6.75	.030	.0006	.09	.017	.0028

TABLE 3.—*Chemical analyses of water from sockeye salmon nursery lakes of southwestern Alaska, 1961-62—Continued*

System and lake	Total dissolved solids	pH	Total alkalinity	Sodium	Potassium	Magnesium	Nitrate nitrogen	Silica	Iron	Manganese	Calcium	Boron	Copper	Strontium	Aluminum	Molybdenum
PENINSULA SYSTEMS	*P.p.m.*		*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
Alagnak (Branch) system																
Kukaklek Lake	23.0	7.00	8.88	4.02	1.23	1.15	.018	1.1	----------		3.29	----------				
Nonvianuk Lake	32.5	7.21	10.54	3.25	.90	1.12	.017	4.1	.040	.01	5.33	.003				
Naknek system																
Coville Lake	51.6	7.13	25.28	3.18	.46	1.21	<.014	9.0	.052	.01	7.79	.003				
Grosvenor Lake	53.5	7.24	25.42	2.98	.47	1.89	<.014	7.7	.040	.01	6.90	.003				
Naknek Lake [1]	139.5	7.35	28.54	10.40	1.16	4.16	.087	9.3	.040	.01	18.16	.008				
Iliuk Arm	----------	7.27	28.61	----------					----------							
Brooks Lake	74.8	7.31	26.78	4.30	.95	2.18	.012	10.5	.041	.01	8.88	.004				
Ugashik system																
Lower Ugashik Lake	22.4	7.23	14.57	7.13	.80	1.28	.019	1.4	----------		4.81	----------				
Chignik system																
Chignik Lake	55.9	7.65	21.31	2.35	1.31	3.04	.026	12.9	.024	.002	7.43	.027	.0006	.07	.007	.0011
Black Lake	69.7	7.44	21.53	4.07	1.43	3.04	.014	12.6	.016	.002	10.36	.042	.0009	.12	.010	.0001
Karluk system																
Karluk Lake	42.9	7.25	25.22	3.32	.26	1.47	.036	.4	.042	.01	6.61	----------				

[1] Excluding Iliuk Arm. Iliuk Arm is considered separately because of the large amount of suspended glacial material.

TABLE 4.—*Ranking of sockeye salmon nursery lakes of southwestern Alaska according to total dissolved solids, total alkalinity, and pH, 1961-62*

Lake	System	Total dissolved solids	Total alkalinity	pH
Naknek [1]	Naknek	1	2	3
Brooks	Naknek	2	3	5
Black	Chignik	3	9	2
Chignik	Chignik	4	10	1
Grosvenor	Naknek	5	4	13
Coville	Naknek	6	5	20
Chauekuktuli	Nuyakuk	7	1	8
Karluk	Karluk	8	6	12
Tikchik	Nuyakuk	9	8	4
Nuyakuk	Nuyakuk	10	7	6
Little Togiak	Wood	11	12	8
Nonvianuk	Alagnak	12	20	15
Clark	Kvichak	13	11	10
Aleknagik	Wood	14	15	18
Iliamna	Kvichak	15	14	11
Kulik	Wood	16	16	22
Beverley	Wood	17	18	15
Kukaklek	Alagnak	18	23	23
Lower Ugashik	Ugashik	19	13	14
Amanka	Igushik	20	19	7
Nerka	Wood	21	17	19
Nunavaugaluk	Snake	22	22	17
Ualik	Igushik	23	21	20

[1] Excluding North Arm and Iliuk Arm.

TABLE 5.—*Mean equivalent proportions of the three major cations—sodium, calcium, and magnesium—in water samples from sockeye salmon lakes of southwestern Alaska, June to September 1961-62*

System and lake	Sodium	Magnesium	Calcium
MAINLAND SYSTEMS	*Percent*	*Percent*	*Percent*
Igushik system			
Amanka Lake	7	18	75
Ualik Lake	12	20	68
Snake system			
Lake Nunavaugaluk	7	17	76
Wood system			
Lake Aleknagik	8	22	70
Lake Nerka	6	22	72
Lake Beverley	11	21	68
Lake Kulik	9	18	73
Little Togiak Lake	6	22	72
Nuyakuk (Tikchik) system			
Tikchik Lake	4	30	66
Nuyakuk Lake	3	23	74
Lake Chauekuktuli	2	27	71
Kvichak system			
Iliamna Lake	10	19	71
Lake Clark	8	19	73
PENINSULA SYSTEMS			
Alagnak (Branch) system			
Kukaklek Lake	40	22	38
Nonvianuk Lake	28	18	54
Naknek system			
Coville Lake	22	16	62
Grosvenor Lake	21	25	54
Naknek Lake	27	20	53
Brooks Lake	23	22	55
Ugashik system			
Lower Ugashik Lake	47	16	37
Chignik system			
Chignik Lake	14	35	51
Black Lake	19	26	55
Karluk system			
Karluk Lake	24	20	56

Equivalent Proportions of Sodium, Calcium, and Magnesium

Lakes of the Mainland Systems clearly differ from those of the Peninsula Systems in the proportion (based on number of equivalents per million) [5] of each of the three principal cations —sodium, calcium, and magnesium. To deter-

[5] Equivalents per million are determined by multiplying the parts per million by the reciprocals of combining weights of the appropriate ions. The combining weight of an ion equals the atomic weight of the ion divided by its ionic charge.

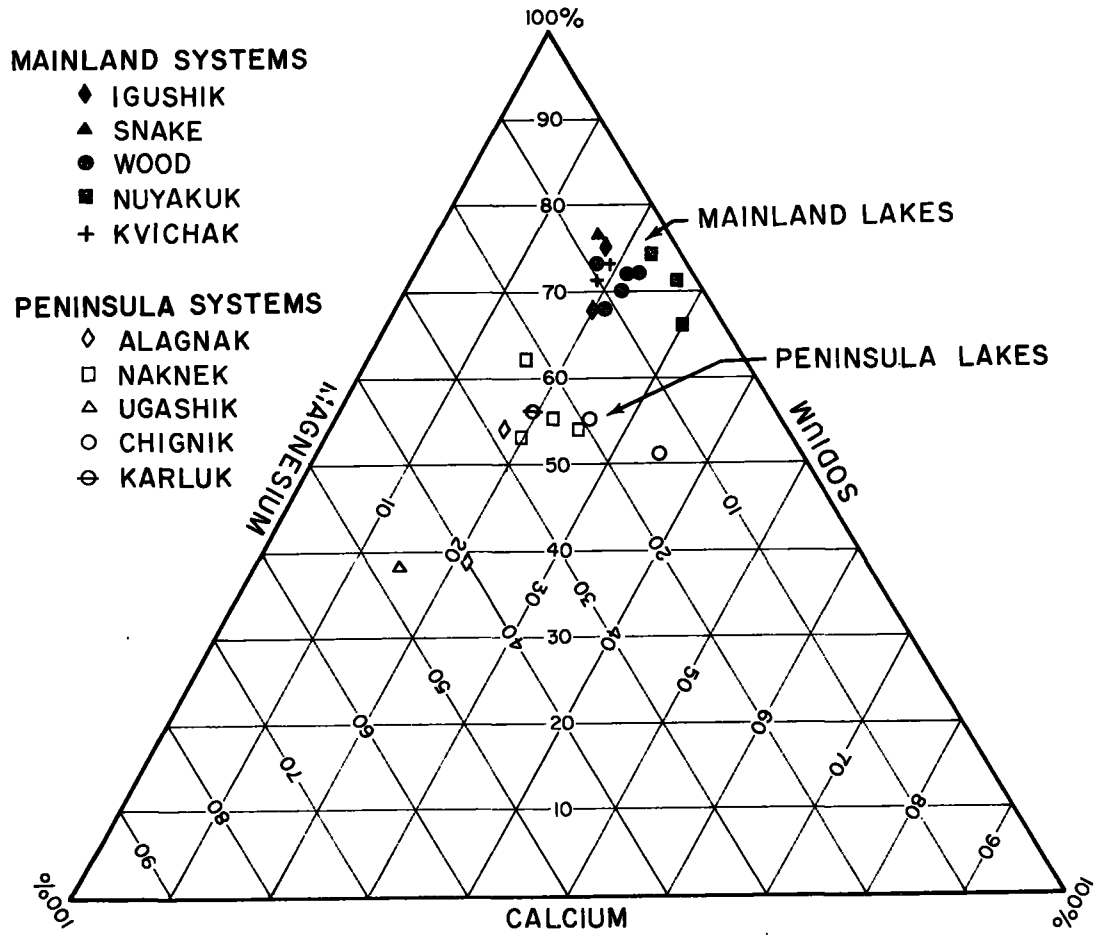

FIGURE 3.—Relative chemical proportions of the three major cations—sodium, calcium, and magnesium—in water samples from sockeye salmon lakes of southwestern Alaska. Each corner of a triangle is assigned a value of 100 percent for one of the cations. If a lake had equal equivalents of each cation, the value for that lake would be plotted in the center of the triangle. As the proportion of a cation increases toward 100 percent for that lake, the point is plotted closer and closer to the corresponding tip of the triangle.

mine these proportions, the concentrations of the three cations in equivalents per million were summed. Then the proportion of the total equivalents contributed by each cation was calculated (table 5). The data are presented graphically in figure 3.

The graphic analysis of the proportionate contribution of the three cations (fig. 3) reveals a similarity among the lakes of a system. Lakes of several systems—Wood, Nuyakuk, Naknek, and Chignik—show this grouping, which suggests that the sources of these elements (terrestrial and marine) influence all lakes within a system similarly. Figure 3 also shows that groups of lakes for systems on the mainland and on the peninsula do not overlap. Lakes of the Mainland Systems have proportionally more equivalents of calcium and less sodium than lakes of the Peninsula Systems. Our last comment on this analysis concerns lakes of the Nuyakuk system. In these waters the absolute concentrations of sodium were comparatively low (table 3), and the proportions of equivalents of sodium in relation to magnesium and calcium are also low (table 5).

Goldman (1960) found low concentrations of magnesium to be limiting to phytoplankton production in Brooks Lake during the summer of 1957. He concluded that magnesium at a low level, in comparison with other cations, was less available to the plankton because of the presence of relatively high quantities of sodium.

Other Nutrients and Trace Elements

We measured all of the dissolved chemicals our facilities permitted because more are either known or suspected to be important in the production of phytoplankton. In addition to those measurements previously discussed, we determined the concentrations of nitrogen, phosphorus, molybdenum, silica, iron, aluminum, boron, and copper.

Because nitrogen is essential for photosynthesis, it is commonly considered as a factor that may limit the production of phytoplankton. Although the ultimate source of nitrogen is the atmosphere, the combined nitrogen in lake water is derived primarily from inflowing waters (Hutchinson, 1957). Goldman (1960) found a nitrate-nitrogen deficiency in Brooks Lake in July and August 1957. In the lakes we studied concentrations of nitrate nitrogen were highest in the Mainland Systems and lowest in the Peninsula Systems (table 3). The lower values in the Peninsula Systems may be due in part to greater use of nitrate nitrogen in the higher production of phytoplankton.[6]

Some investigators have considered phosphorus as a possible limiting factor in the production of phytoplankton in sockeye salmon lakes (Krokhin, 1957; Nelson and Edmondson, 1955; Nelson, 1958; Goldman, 1960). Carcasses of adult salmon are considered an important source of replenishment of phosphorus to sockeye salmon lakes (Krokhin, 1957; Nelson and Edmondson, 1955). The limit of detectability of phosphate in our analysis of water samples was about 0.01 to 0.02 p.p.m. In general, concentrations of phosphorus were below these limits. Since a large part of the total phosphorus is bound in plankton, and phytoplankters are known to store more phosphorus than they need, the rate of phosphorus turnover largely controls the level in solution in water and, hence, determines its availability. Additional measurements and nutritional experiments are needed to establish whether availability of phosphorus is a factor that seriously limits production of phytoplankton in the lakes under study.

From limited nutritional experiments in 1962, Goldman (1964) concluded that low concentrations of molybdenum were limiting the phytoplankton growth in many lakes, including some sockeye salmon lakes of Bristol Bay. We measured molybdenum by colorimetric and spectrographic methods. Concentrations were low in all lakes. Comparison of spectrographic analyses of filtered water and phytoplankton from lakes of the Wood, Kvichak, and Chignik systems in 1964 indicates that molybdenum was generally detectable in water only. This finding indicates that phytoplankters were not concentrating the element. Experiments are needed to clarify the role of molybdenum in the production of phytoplankton.

Silica is necessary for the growth of diatoms and, "the main mechanism of loss of silica from lake waters is its utilization by diatoms. . . ." (Hutchinson, 1957). The peninsula lakes, except for Kukaklek and Lower Ugashik, had the highest concentrations of silica. Lakes of the Wood system had moderate levels; Karluk Lake, although highly productive, had considerably lower concentrations than the other lakes. It is likely that large amounts of silica are bound in the phytoplankton, especially in Karluk Lake, where Hilliard (1959) found that diatoms were the dominant phytoplankters throughout the year.

Some differences were found also between systems in concentrations of the other elements detected regularly in spectrographic analyses of water samples. Lakes in the Chignik system had the highest concentrations of iron, aluminum, boron, and copper; the Kvichak system followed. The concentrations of these elements were lower but fairly uniform in the lakes of the several systems tributary to Nushagak Bay. High concentrations of copper can inhibit growth of phytoplankton, but the concentrations found in this study were low.

Dissolved Oxygen

Concentrations of dissolved oxygen were near saturation whenever lakes were sampled, regardless of depth or season of year; winter samples through the ice were taken only in Naknek and Brooks Lakes.

THERMAL CHARACTERISTICS

Variation in both photosynthetic rates and water temperature during the summer is largely due to variation in solar radiation. Photosynthesis is at the base of primary productivity, and temperature greatly influences the rate of

[6] The low rates of productivity in the Ugashik and Alagnak systems are based on only one and two observations, respectively.

growth of fish; therefore, we measured solar radiation and water temperature in our limnology studies. Many data were collected, but only general comparisons were made among the systems.

Thermal stratification and development of thermoclines are most pronounced in lakes protected from the mixing action of strong and persistent winds. During our study, thermoclines usually were well developed in the upper lakes of the Wood system, which are generally protected from strong winds; they were less well defined in the lower, more exposed lakes. The larger, broadly exposed lakes, such as Iliamna and those of the Naknek system, were generally without thermoclines. Thermoclines were common in the smaller lakes, such as Chignik and Karluk, but were easily destroyed by the strong persistent winds which result from the lakes' exposure to the ocean climate.

PRIMARY PRODUCTIVITY AND STANDING CROP OF PHYTOPLANKTON

The measure of primary productivity used in this study was the rate of carbon fixation by phytoplankton per 4-hour midday incubation period throughout the water column, calculated on the basis of a square meter of the surface and a cubic meter in the euphotic zone. The rate of carbon fixation was determined by the in situ light- and dark-bottle C^{14} technique (method I of Steemann Nielsen, 1952). The measure of the standing crop of phytoplankton was the concentration of chlorophyll *a*. In general, rates of carbon fixation were lower in 1961 than in 1962, but the values for 1962 rather than the averages for 1961-62 are used here to compare lakes because productivity measurements were available for more lakes in 1962. These data along with concurrent measures of the transparency of the water (Secchi disk extinction values) are given in table 6.

The results of our measures of basic productivity are discussed by system.

Mainland Systems

Among lakes of the Mainland Systems, those of the Nuyakuk rank highest in concentrations of total dissolved solids and alkalinity; yet in the single series of observations in two lakes of the system (Tikchik and Chauekuktuli), phytoplankton production and standing crop were low. The average Secchi disk reading of more than 15 m. in Lake Chauekuktuli was the highest in any of the systems—a further indicator of low phytoplankton density; and the rate of carbon fixation per cubic meter had the lowest average for any of the lakes. Deficiencies of trace elements may limit productivity.

The single series of observations of photosynthetic rates in Ualik Lake of the Igushik system and Lake Nunavaugaluk of the Snake system indicated that they were intermediate in the ranking among all systems tested and were similar to those of the Wood system. The standing crops of phytoplankton, however, were lower.

The lakes of the Wood system had carbon fixation rates, chlorophyll *a* concentrations, and Secchi disk readings intermediate in the range of values for all systems. The photosynthetic rate and chlorophyll *a* concentration in Little Togiak Lake were slightly higher than in the other lakes. The differences among lakes in the Wood system were rather small.

Rates of carbon fixation were only slightly lower in lakes of the Kvichak system than in lakes of the Wood system. The photosynthetic rate per cubic meter in the euphotic zone and the chlorophyll *a* concentrations were as high in Lake Clark as in Iliamna Lake, but the total carbon fixed in the water column was less in Lake Clark because of the restricted depth of the euphotic zone (caused by rock flour). The Secchi disk extinction value was only 3.8 m. in Lake Clark, in contrast to 9.8 m. in Iliamna Lake and 8.7 to 12.6 m. in lakes of the Wood system.

Peninsula Systems

Among lakes of the Peninsula Systems, those of the Alagnak system ranked near the bottom in basic productivity and also had low standing crops of phytoplankton.

Lakes within the Naknek system had a wide range in productivity. Shallow Coville Lake is very productive and ranks next to lakes of the Chignik and Karluk systems in primary productivity and standing crop of phytoplankton, whereas deep and clear Brooks Lake is among the least productive systems. The Secchi disk readings in each lake were correspondingly low and high.

In the Ugashik system the primary productivity and standing crop of phytoplankton in Lower Ugashik Lake (the only lake examined) were about as low as in the Alagnak system.

Lakes of the Chignik system had by far the

TABLE 6.—*Primary productivity, chlorophyll a concentration, and water transparency for sockeye salmon nursery lakes of southwestern Alaska, 1962*

System and lake	Primary productivity: Determinations	Primary productivity: Mean carbon fixation per 4-hour period per square meter lake surface area	Primary productivity: Mean carbon fixation per 4-hour period per cubic meter in euphotic zone	Chlorophyll *a*: Determinations	Chlorophyll *a*: Mean concentrations	Water transparency: Samples	Water transparency: Mean Secchi disk reading
MAINLAND SYSTEMS	*Number*	*Mg.*	*Mg.*	*Number*	*Mg./l.*	*Number*	*M.*
Igushik system							
Amanka Lake	----	----	----	1	0.7	2	8.5
Ualik Lake	9	73	2.5	2	.8	3	9.7
Snake system							
Lake Nunavaugaluk	10	66	1.4	1	.6	1	13.0
Wood system							
Lake Aleknagik	240	65	2.0	8	1.3	25	8.7
Lake Nerka	659	58	1.7	22	.9	63	12.6
Lake Beverley	118	71	1.7	8	1.0	11	12.0
Lake Kulik	108	66	1.6	7	.8	11	11.5
Little Togiak Lake	133	73	1.9	6	1.4	14	10.4
Nuyakuk (Tikchik) system							
Tikchik Lake	10	52	1.6	3	.6	3	10.7
Nuyakuk Lake	----	----	----	2	.2	2	10.0
Lake Chauekuktuli	10	54	1.0	3	.5	3	15.3
Kvichak system							
Iliamna Lake	455	54	1.5	165	.8	24	9.8
Lake Clark	41	13	1.6	4	1.1	4	3.8
PENINSULA SYSTEMS							
Alagnak (Branch) system							
Kukaklek Lake	18	22	1.1	4	.6	3	10.2
Nonvianuk Lake	20	24	1.2	4	.5	4	13.2
Naknek system							
Coville Lake	411	99	5.9	80	1.0	72	5.4
Grosvenor Lake	553	61	2.9	85	.7	84	8.4
Naknek Lake [1]	810	59	3.4	86	.9	135	4.4
Iliuk Arm	----	----	----	----	----	----	.9
Brooks Lake	832	47	1.7	73	.5	154	10.8
Ugashik system							
Lower Ugashik Lake	20	41	1.2	4	.8	3	8.5
Chignik system							
Chignik Lake	311	242	13.5	41	15.3	41	1.9
Black Lake	137	121	33.4	26	5.4	28	1.6
Karluk system							
Karluk Lake	606	131	5.9	73	2.1	105	8.6

[1] Excluding Iliuk Arm. Iliuk Arm is considered separately because of the large amount of suspended glacial material.

highest photosynthetic activity and the greatest standing crop of phytoplankton of all lakes studied. Chignik Lake had a high average value for carbon fixed in the water column, but the rate per cubic meter in the euphotic zone was much higher in shallow Black Lake where a high rate of carbon fixation extended to the bottom. Although the low transparency in these two lakes was primarily due to heavy phytoplankton blooms, in Chignik Lake it was partially due to suspended rock flour.

In Karluk Lake, the rate of carbon fixation per cubic meter in the euphotic zone was high but considerably below the rate in the Chignik system. Because of the greater depth of the euphotic zone at Karluk Lake, however, the rate of carbon fixation per square meter of surface was greater than in Black Lake. The Secchi disk readings were 8.6 and 1.6 m., respectively, for Karluk and Black Lakes. The standing crop of phytoplankton in the Karluk system was second only to that of the Chignik system.

PRODUCTIVITY MEASUREMENTS AND SALMON PRODUCTION

Studies of the size of escapements and the growth of progeny indicate that in some systems at least (Wood, Kvichak, and Chignik), the growth of young salmon is slower when population densities are high (see later sections of this paper). This slow growth suggests that the abundance of food in the nursery lake limits

production. A primary aim of the limnological studies was to determine if those lakes that usually support high population densities of salmon are basically the more productive. In other words, do they have higher concentrations of dissolved plant nutrients, higher standing crops of phytoplankton, and higher rates of photosynthetic activity?

The only measure of salmon production available for all the systems is the average escapement for recent years. To use this measure we must assume that the average catch-to-escapement ratio is about the same for all systems. Although this ratio can vary somewhat, the escapement levels provide a useful index of salmon production.

The systems are ranked in table 7 according to: (1) the average sockeye salmon escapement per square kilometer of lake surface for 1955-62, (2) primary productivity as indicated by the rate of carbon fixation by photosynthesis per square meter of lake surface and per cubic meter in the euphotic zone, (3) the standing crop of phytoplankton as indicated by the concentration of chlorophyll *a*, and (4) the concentration of total dissolved solids.

The four systems with the higher rates of primary productivity (considering both rate per square meter and rate per cubic meter) produced more adult salmon per square kilometer of lake (Karluk, Chignik, Igushik, and Wood). Among the other systems the correlation between rates of primary productivity and salmon production is not marked. The number of observations was too small in several of the systems to give reliable averages for primary productivity and chlorophyll *a* values; hence, the true rankings of the lake systems may diverge from those given here.

The primary productivity and escapement per unit lake area for the Naknek system are unusual. Although this system does not rank high (no. 6) in rate of carbon fixation in the water column under a square meter of lake area, it does rank high (no. 3) in rate of carbon fixation per cubic meter in the euphotic zone. Furthermore, the escapement per unit lake area is a misleading statistic for this system because two basins, North Arm and Brooks Lake, make up about 32 percent of the area of the system but usually receive only about 5 percent of the escapement. These two basins also have the lowest rates of primary productivity in the system. If North Arm and Brooks Lake were not considered, the Naknek system would rank about no. 5 in terms of escapement and no. 4 or 5 in terms of primary productivity.

TABLE 7.—*Ranking of sockeye salmon nursery lakes of southwestern Alaska according to average escapement density (1955-62), primary productivity, standing crop of phytoplankton, and total dissolved solids (1961-62)*

System	Escapement per square kilometer		Primary productivity (rate of carbon fixation)		Standing crop of phytoplankton (chlorophyll *a* per liter)	Total dissolved solids in p.p.m.
			Per square meter lake surface area	Per cubic meter in euphotic zone		
	Rank	*Number*	*Rank*	*Rank*	*Rank*	*Rank*
Karluk	1	8,350	2	2	2	3
Chignik	2	8,070	1	1	1	2
Igushik	3	4,360	[1] 3	[1] 4	[1] 7	[1] 10
Wood	4	2,340	4	5	3	6
Alagnak	5	1,441	10	10	9	5
Ugashik	6	1,338	9	9	6	8
Kvichak	7	1,330	7	7	4	7
Naknek	8	1,122	6	3	5	1
Snake	9	290	[1] 5	[1] 8	[1] 8	[1] 9
Nuyakuk	10	280	[1] 8	[1] 6	[1] 10	[1] 4

[1] Only a few determinations were made: see tables 2 and 6.

Measurements of the standing crops of phytoplankton (chlorophyll *a* concentrations) and concentrations of total dissolved solids are not clearly related to rate of production of salmon. We cannot expect the standing crop of phytoplankton to be as sensitive a comparative measure of productivity as rates of carbon fixation because of the problems of unknown rates of turnover or utilization of phytoplankton by the zooplankton. Similarly, our measures of total dissolved solids do not give a good estimate of the potential of a system to produce salmon because the phytoplankters need a proper balance of nutrients.

CAPACITY OF SPAWNING GROUNDS

Our purpose in studying the capacity of the spawning grounds was to determine whether the space available is sufficient to produce enough salmon fry to use the nursery areas fully. In considering the amount of spawning ground as a limiting factor, we first present information on the size of past escapements and their characteristics. Next we will estimate potential spawning populations by using estimates of the space available for spawning, estimates of the space requirements of a spawning female, and

data on past spawning populations. Finally, we consider the question—is the capacity of the spawning grounds to produce young sockeye salmon less than or greater than the capacity of the lakes to rear them?

MEASURES OF ESCAPEMENT

Statistics on the escapements of sockeye salmon to the major river systems of southwestern Alaska are incomplete before 1955. Between 1900 and 1933, escapement counts were obtained at weirs in a few rivers. Since the late 1930's, rough estimates of escapements have been made by ground and aerial surveys. Weirs were reinstalled in the Chignik and Ugashik Rivers in 1949, in the Naknek River in 1950, and in the Egegik River in 1952. Intensive ground and aerial surveys of spawning grounds in the Wood system were started in 1946. On the Wood River in 1953, FRI first used observation towers to obtain sample counts for estimating escapements of migrating adult salmon. This technique has supplanted weirs in most areas and was extended to the Kvichak River in 1955; the Egegik in 1956; the Naknek, Ugashik, and Alagnak in 1957; the Igushik in 1958; the Nuyakuk in 1959; and the Snake in 1960 (fig. 2). Since 1921, weirs have been used in Karluk River except in 1958 and 1959 when counting towers were used. A weir is still used in the Chignik River.

Size of Escapements

Estimates of the size of escapements to the several river systems in 1955-62 (table 8) provide an index of the relative production of each system. Escapements may vary widely within a system and may be cyclic in some. For instance, in the Kvichak system (which is the only system with clearly defined cycles of abundance of sockeye salmon) the escapement in 1960 was almost 60 times that in 1955. In each of the next three largest systems—Wood, Naknek, and Egegik—the greatest escapements were only six to eight times the smallest. The escapements to Chignik and Karluk Rivers have not varied as much—in the Karluk system the largest was about four times the smallest, and in the Chignik system it was only twice the smallest.

Distribution of Spawners within Systems

Sockeye salmon use four major types of spawning grounds: streams tributary to lakes, rivers between lakes, outlet rivers (trunk streams), and lake beaches. The relative importance of each type varies among systems and from year to year within systems.

TABLE 8.—*Estimates of sockeye salmon escapements to major river systems of southwestern Alaska, 1955-62*

Year	Igushik	Snake	Wood	Nuyakuk	Kvichak	Alagnak	Naknek	Egegik	Ugashik	Chignik	Karluk
	(Thousands of fish)										
1955	[1] 500	[1] 30	1,383	[1] 16	251	[1] 172	273	269	77	447	386
1956	[1] 400	[1] 4	773	[1] 30	9,443	[1] 784	1,773	1,104	425	748	138
1957	[1] 130	[1] 3	289	[1] 67	2,843	127	635	391	215	509	221
1958	108	[1] 9	960	[1] 196	535	95	278	246	279	325	274
1959	644	[1] 140	2,209	49	680	825	2,232	1,072	219	411	444
1960	495	17	1,016	146	14,630	1,241	828	1,799	2,304	608	349
1961	294	5	461	80	3,706	90	351	702	349	407	297
1962	16	2	874	38	2,581	91	722	1,027	255	483	561
Average	323	26	996	78	4,334	428	886	826	515	492	334

[1] Aerial survey estimates by FRI.

Variation may be considerable in the age composition of sockeye salmon that use the different types of spawning grounds within a given system. The most striking difference is in the number of years the salmon have spent in the ocean. Although most adult sockeye salmon are 2- or 3-ocean fish (i.e., remain in the ocean 2 or 3 years before they return to spawn), the proportion varies among groups of fish occupying specific spawning areas from year to year. Three-ocean fish are larger than 2-ocean and are more susceptible to capture by the gill nets in Bristol Bay.

Natural fluctuations in the relative abundance of various components of a stock, combined with selective effects of the fishery, often lead to poor distribution of the escapement among the spawning grounds. The total escapement may be adequate for a system, but if the distribution of the escapement does not conform to the relative spawning capacities of various grounds, some grounds will be underutilized and others will be overutilized. Various races and age groups of sockeye salmon bound for the many spawning grounds of a system may pass through the fishery at different times. Therefore, the fishery that operates at different intensities through each season could harvest components at different rates—for example, through a combination of net selectivity and closed fishing times. This section examines the evidence bearing on these problems in the sockeye salmon systems of southwestern Alaska.

Igushik system.—The type of spawning grounds used varies greatly from lake to lake

TABLE 9.—*Distribution of spawning sockeye salmon among three types of spawning areas in lakes of the Wood system, 1955-62*

Lake and year	Fish spawning in—		
	Tributary creeks	Lake beaches	Rivers between lakes
	Percent	*Percent*	*Percent*
Aleknagik			
1955	55	0	45
1956	54	2	44
1957	38	2	60
1958	51	5	44
1959	29	5	66
1960	37	5	58
1961	10	2	88
1962	47	6	47
Average	40	3	57
Nerka			
1955	32	55	13
1956	11	43	46
1957	37	49	14
1958	17	74	9
1959	29	5	66
1960	37	49	14
1961	11	43	46
1962	32	55	13
Average	26	47	27
Beverley			
1955	0	95	5
1956	13	85	2
1957	29	70	1
1958	1	95	4
1959	1	95	4
1960	0	94	6
1961	14	76	8
1962	6	85	9
Average	8	87	5
Kulik			
1955	0	53	47
1956	0	49	51
1957	0	16	84
1958	0	90	10
1959	0	61	39
1960	0	63	37
1961	0	51	49
1962	0	88	12
Average	0	59	41

in the Igushik system. Most sockeye salmon spawn on the beaches at Lake Ualik and in the streams at Lake Amanka.

Wood system. — The distribution of adult sockeye salmon among the three types of spawning grounds in the Wood system differs markedly from lake to lake, but each lake has a characteristic distribution (table 9). For example, tributary creeks and the rivers between lakes receive the greatest part of the spawners in Lake Aleknagik (over 90 percent from 1955 to 1962), whereas in Lake Beverley almost 90 percent of the spawners use the lake beaches. The spawners in Lake Nerka are usually distributed about equally among the three types of spawning grounds. The year-to-year changes in distribution of the spawners in the system as a whole are largely the result of changes in the relative escapement to each lake.

Most sockeye salmon entering the Nushagak fishing district are bound for lakes of the Wood system. Tagging results in 1961 indicated that spawners bound for the different lakes of the Wood system may have passed through the fishery at different times. Overlap was considerable, however, and the same pattern of entry may not occur every year. Time of passage to the two major river spawning grounds, Agulowak and Agulukpak Rivers, was average for the system.

Although the percentages of 2-ocean and 3-ocean sockeye salmon in the run vary annually with year class strength and other undetermined factors, consistent differences in age composition tend to prevail among spawning groups. For instance, in 1960-62, samples of spawning sockeye salmon from Agulowak and Agulukpak

TABLE 10.—*Proportions of 3-ocean sockeye salmon in escapements from areas of the Wood system, 1960-62*

Year and sex	Agulowak River	Agulukpak River	Average for remaining areas
	Percent	*Percent*	*Percent*
1960			
Male	80	49	16
Female	84	66	18
1961			
Male	99	92	60
Female	100	96	69
1962			
Male	42	40	8
Female	76	64	7
Average	80	68	30

Rivers consistently had a higher proportion of 3-ocean fish than samples from other areas of the system (table 10).

Nuyakuk system. — The type of spawning grounds used also varies greatly among the lakes of the Nuyakuk system. Sockeye salmon in Lake Chauekuktuli spawn almost exclusively on beaches; in Tikchik Lake they spawn only in rivers and creeks. The escapement to the Nuyakuk system has a consistently higher proportion of 3-ocean fish than that to the Wood system.[7]

Kvichak system. — Sockeye salmon of the Kvichak system spawn in streams tributary to lakes, rivers between lakes, beaches of Iliamna Lake, and spring-fed ponds, which are usually located at the heads of small tributaries. They

[7] Burgner, R. L. 1965. Age composition of Nushagak sockeye runs by river system. Univ. Wash., Fish. Res. Inst., Circ. 234, 14 pp.

spawn also in the tributaries to, and on beaches of, small lakes. Some of the fry from these small lakes migrate to nursery areas in Iliamna Lake or Lake Clark.

The distribution of the escapements to large streams, lake beaches, and all other spawning grounds of the Kvichak system in 1959-62 is shown in table 11. When the escapement was extremely large in 1960, the beaches of Iliamna Lake received a larger proportion of the total escapement and the large streams received a smaller proportion than in years when the escapements were smaller. The importance of the other spawning grounds remained nearly constant from 1959 to 1962.

TABLE 11.—*Distribution of sockeye salmon escapements in spawning grounds of the Kvichak system, 1959-62*

Year	Fish in escapement	Fish spawning in—		
		Large streams	Beaches of Iliamna Lake	All others
	Millions	*Percent*	*Percent*	*Percent*
1959	0.7	57.8	25.4	16.8
1960	14.6	26.9	50.0	23.1
1961	3.7	55.0	33.8	11.2
1962	2.6	64.7	19.7	15.6

Escapements to large streams have varied by a factor of 10, whereas those to the system varied by 20 and those to the lake beaches by about 50. Thus, the cyclic nature of the production of sockeye salmon in the Kvichak system could be reinforced or perhaps caused by the cyclic nature of the production from the beaches alone.

We found marked contrasts in age characteristics — both ocean and fresh-water — among spawning groups in the Kvichak system in 1962. Stream spawning groups (except those of the Copper River) had a significantly lower proportion of 3-ocean fish than beach spawning groups.[8] Differences also existed in the average fresh-water age of various spawning groups in the Kvichak system in 1956-58 (Koo and Smith, 1960).

Smith (1964) found little or no difference in the time the various spawning groups entered the Kvichak system in 1957, 1958, and 1959. Adult sockeye salmon were tagged as they entered Iliamna Lake, and the tagged fish were recovered on the spawning grounds. The migration into the lake lasted about 4 weeks. Fish tagged in any one of these weeks were recovered in about the same proportion in large and small streams, on lake beaches, and in spring-fed ponds, regardless of whether spawning in these places occurred early or late in the season.

Naknek system. — The principal spawning grounds of the Naknek system are: (1) Brooks and Grosvenor Rivers (rivers between lakes); (2) American and Hardscrabble Creeks (tributary streams); (3) Naknek River (outlet or trunk river); and (4) beaches of Grosvenor Lake. Some sockeye salmon also spawn on beaches in Iliuk Arm and South Bay of Naknek Lake. The proportions of sockeye salmon that spawn on the several major spawning grounds change markedly from year to year. In some years a single major ground may receive more than 60 percent of the escapement to the system and in other years the same ground may receive less than 10 percent.

Each of the major groups of spawning sockeye salmon in the Naknek system in 1962 was characterized by different proportions of combinations of fresh-water and ocean ages (Straty, 1966). Most major spawning grounds contained a smaller proportion of adults that migrated seaward as age II smolts than did the total escapement to the Naknek River. This anomaly suggests the existence of spawning groups as yet undetected.

Tagging in the Naknek River in 1961 and 1962 demonstrated that all major spawning areas within the system received fish from all parts of the run about in proportion to the sizes of the spawning groups (Straty, 1966). Some slight indication appeared, however, that Brooks Lake and Brooks River received more of the earlier fish than the other areas.

Chignik system. — Sockeye salmon in runs to the Chignik system are predominantly 3-ocean fish. The greatest contrast in age composition in this system is in the time the young live in fresh water: most of the smolts migrate at age I from Black Lake and at age II from Chignik Lake.

Tagging and studies of scales have established that adults returning to Chignik and Black Lakes pass through the fishery at different times (Narver, 1963). The early run (in June) has primarily sockeye salmon bound for Black Lake,

[8] Kim, Wan Soo, and Robert L. Demory. 1963. Kvichak salmon studies, 1962 spawning ground studies. Univ. Wash., Fish. Res. Inst., Circ. 195, 26 pp.

and the late run (in July and August) has primarily fish bound for Chignik Lake.

Karluk system. — The distribution of sockeye salmon on the spawning grounds in the Karluk system has been well documented from data collected on weekly surveys carried out on foot each summer in 1947-62. Salmon that enter the system during May, June, and July tend to occupy all tributaries; those entering during August and September tend to occupy only the large tributaries at the south end of the lake, the lake beaches, and the outlet river.[9]

Sockeye salmon in Karluk Lake have a marked temporal as well as spatial segregation by age group (Rounsefell, 1958; also see footnote 9). In general, salmon that spend the longest time in the ocean (3 years or more) return early in the spawning season and those that spend the least time at sea return late. Since late spawners tend to occupy the large terminal streams, lake beaches, and the upper end of Karluk River, these areas usually receive a disproportionately large number of smaller 2-ocean fish.

The Chignik and Karluk systems contrast sharply with the systems tributary to Bristol Bay in having temporal segregation of spawning units in the trunk river. The absence of marked segregation in Bristol Bay systems may be the result of the short duration of these runs. In general, the Bristol Bay runs last about 4 weeks, and more than 50 percent of each run enters the fishing areas and trunk streams during a few days in early July. In the Chignik and Karluk systems the escapements enter the trunk stream over a 2- to 4-month period.

POTENTIAL SPAWNING POPULATION

The physical capacity of the rivers or beaches to contain adult sockeye salmon imposes a limit on the number of fish that could spawn in each system. It was obvious, however, that a large portion of most of the rivers and beaches was in fact unsuitable for spawning and that the amount of space required for a pair of salmon to spawn varied among different types of spawning grounds. Therefore, to estimate the capacity of each river or beach in terms of numbers of females we determined the area of potential spawning ground and divided this figure by the estimated area required per female.

Estimates of Area of Potential Spawning Grounds

The amount of potential spawning ground for streams and for lake beaches was measured to determine if the area of suitable spawning grounds might limit salmon production in any of the river systems. The data obtained are first approximations because complete and accurate surveys of all spawning grounds could not be completed in 2 years. Estimates of suitable potential spawning area were made for the Wood, Kvichak, Naknek, and Karluk systems (table 12).

During the 2-year study period, catalogs of spawning grounds, which contain descriptions of the physical characteristics and estimates of the area of the potential or utilized spawning grounds and estimates of annual escapements

TABLE 12.—*Estimates of surface area of potential sockeye salmon spawning grounds in streams and lake beaches of Wood, Kvichak, Naknek, and Karluk systems*

System and lake	Streams	Lake beaches	Total
	Hectares	*Hectares*	*Hectares*
Wood system			
Lake Aleknagik	134.6	[1] 86.2	220.8
Lake Nerka	40.9	[1] 1,437.0	1,477.9
Lake Beverley	47.0	[1] 862.6	909.6
Lake Kulik	11.7	[1] 337 9	349.6
Little Togiak Lake	7.2	[1] 108.9	116.1
Total	241.4	2,832.6	3,074.0
Kvichak system			
Iliamna Lake	649.6	[2] 33.0	682.6
Gibraltar Lake	23.0	28 8	51.9
Lake Clark	167.1	49 7	216.8
Total	839.7	111.5	951.3
Naknek system			
Coville Lake	111.0	[3]	
Grosvenor Lake	29.6	[3]	
Naknek Lake [4]	188.3	[3]	
North Arm	7.5	[3]	
Brooks Lake	18.0	[3]	
Total	354.4	[3]	
Karluk system			
Karluk Lake	33.7	[5] 1.2	34.9

[1] Estimates based on gravel types only.
[2] Minimum estimate based on incomplete information.
[3] No estimate made.
[4] Excludes North Arm; North Arm is considered separately because it constitutes a rearing area for juvenile salmon discrete from the rest of Naknek Lake.
[5] Only the beach spawning areas of Thumb and O'Malley Lakes are included here.

[9] Owen, John B., Charles Y. Conkle, and Robert F. Raleigh. 1962. Factors possibly affecting production of sockeye salmon in Karluk River, Alaska. Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska. [Manuscript. 57 pp.]

by stream, were completed for the Kvichak system (Demory, Orrell, and Heinle, 1964) and the Wood system (Marriott, 1964). A catalog for the Naknek system is being prepared.

The amount of potential spawning grounds for streams was estimated as follows: (1) The stream was divided into sections from the mouth to the upper limit of possible spawning, i.e., to the source or to obstructions to the passage of fish, e.g., falls and beaver dams. (2) The total area of each section was determined. (3) The percentage of each section not usable for spawning was estimated on the basis of bottom composition, gradient, and water velocity. Bottom types defined as not usable included silt, bedrock, and large rock. Pools and torrential water were considered unsuitable for spawning. (4) The amount of potential spawning grounds in each section was estimated by subtracting the area unsuitable for spawning from the total area. Spring-fed ponds were treated as streams.

Wood system.—The estimates of the amount of potential spawning grounds in streams of the Wood system (table 12) apply only to streams in which spawning had been observed.

Size of the gravel and depth of the water were used in the lakes of the Wood system as criteria in estimating the area of beach suitable for spawning. The area of lake surface from the shore to 10-m. depth contours (over bottom judged by field observations to be suitable for spawning) was measured on bathymetric maps. Because other factors, such as upwelling ground water, also appear to be important in beach spawning, the estimates based only on size of the gravel and depth of the water exceed the amount of potential beach spawning grounds.

Kvichak system.—The estimates of the amount of spawning grounds in the Kvichak system are minimal. For stream spawning, estimates were made only for streams in which spawning had been seen. For beach spawning in Iliamna Lake, estimates were made only for beaches on which a small escapement of sockeye salmon had spawned (1961). Beaches in the following areas were not examined: Flat Island, Southeast Beaches, Tommy Beach, Lonesome Bay, and Finger Beach.

Observations in Iliamna Lake during the spawning of a large escapement (1960) indicated that beach spawning was much more extensive than was formerly thought, particularly around islands, where it extended to depths of 30 m.

Naknek system. — Estimates of the amount of potential sockeye salmon spawning grounds are available for all streams in the Naknek system, even those in which spawning has never been seen. The reliability of the estimates varies from stream to stream, and the estimates will be modified as more information is obtained.

Sockeye salmon spawn on beaches in Grosvenor Lake and in a lesser amount in other lakes in the Naknek system, but the extent of these spawning grounds has not been estimated.

Karluk system. — Data on the amount of spawning grounds in the Karluk system are from Owen et al. (footnote 9) and are for grounds on which sockeye salmon are known to spawn.

Estimates of Space Requirements of Spawning Females

A spawning female sockeye salmon requires a certain minimum area of gravel bed in which to deposit her eggs. Eggs are buried in about five pockets in an area of disturbed gravel known as the redd. During construction of the redd and spawning and postspawning activities, both the female and male defend a certain territory surrounding the redd.

Wood and Kvichak systems. — Estimates of the minimal space requirements for spawning females in the Wood and Kvichak systems were based on the egg-carrying capacity of the gravel independent of observed spawning density.

Three principal sources of loss of eggs were considered: (1) increased retention of the eggs by the female because of increased density of spawners, (2) dislodgment of eggs from the redds because of repeated excavations of the same gravel by subsequent females (superimposition), and (3) increased egg mortality because of crowding of eggs in the gravel. Data from the Wood and Kvichak systems indicate that as spawning density increases, superimposition of redds limits survival of the eggs. We estimated egg loss from superimposition to be less than 10 percent with a spawning density of one female per 2 m.^{2} This density is low enough to avoid significant egg loss by increased retention or crowding of eggs in the gravel. Calculation of the capacity of streams in the Wood and Kvichak systems to support spawning sockeye salmon is based, therefore, on a density of one female per 2 m.^{2}

Naknek and Karluk systems. — General observations had indicated that the space requirements for spawning female sockeye salmon vary with differences in quality of the gravel and size and stage of the stream and that the space used by a spawning female is elastic — large when escapements are low and small when they are high. We estimated, therefore, the space requirement for a spawning female from maximum observed densities of spawners in measured sections of streams in the Naknek system. Average densities for entire streams were used in the Karluk system.

Our studies confirmed the earlier general observations that space requirements vary among different kinds of streams. For example, in the large and relatively deep rivers between lakes and the terminal rivers in the Naknek system, the space requirements are between 4 and 9 m.² per female. In the smaller streams the requirements are much less — 2 to 3 m.² In the open-water beach areas the requirements are probably similar to or perhaps larger than those in the large rivers. In the shallow torrential lateral streams in the Karluk system, space requirements were often substantially less than 2 m.² (table 13), but 2 m.² would appear typical for the system as a whole on the basis of stream survey data from many areas (Richard Gard, personal communication).

Our calculations of the potential capacity of the streams in the Naknek and Karluk systems to support spawning sockeye salmon are based on the estimate of maximum density for each type of stream.

TABLE 13.—*Estimated numbers of potential redd sites in various types of spawning grounds of the Naknek and Karluk systems*

System and type of spawning ground	Area of potential spawning ground	Area required per female	Redd sites
	Hectares	*M.²*	*Number*
Naknek system			
Terminal streams	124.9	4.1	302,000
Small lateral streams	12.3	2.6	47,000
Large lateral streams	62.7	7.6	83,000
Rivers between lakes	7.2	[1] 8.8	8,000
Outlet river	147.3	8.0	184,000
Lake beaches			[2]
Total	354.4		624,000
Karluk system			
Terminal streams	1.67	2	8,000
Lateral streams	6.71	2	34,000
Lake beaches	1.25	2	6,000
Outlet river	25.28	2	126,000
Total	34.91		174,000

[1] Does not take into consideration successive waves of spawners.

[2] An estimate of 20,000 redd sites is based on number of fish seen using the beaches of Grosvenor Lake. Other beach spawning areas exist.

TABLE 14.—*Estimated maximum populations of adult sockeye salmon in streams and lake beaches of Wood system in any year between 1946 and 1962*

Lake	Fish in—		
	Streams	Lake beaches	Total
	Number	*Number*	*Number*
Aleknagik	622,000	15,000	637,000
Nerka	929,000	392,000	1,321,000
Beverley	98,000	487,000	585,000
Kulik	94,000	144,000	238,000
Little Togiak	16,000	47,000	63,000
Total	1,759,000	1,085,000	2,844,000

Estimates of Potential Spawning Capacity by System

The potential capacity for the streams in each system to support spawning adults was based on the amount of potential spawning grounds and the space required per spawning female. The potential spawning capacities of the beach areas were estimated from escapement surveys and various other data.

Wood system. — The potential spawning area of rivers and streams (including connected ponds) of the Wood system was estimated to be 241.4 hectares (table 12), and the area required per spawning female was estimated to be 2 m.² By dividing the spawning area by the area required per female and assuming a 1 : 1 sex ratio, we calculate that the maximum spawning population in streams in the Wood system is 2,414,000 sockeye salmon.

The maximum numbers of sockeye salmon observed on each spawning ground in 1946-62 were summed by lake for stream spawning and for beach spawning. Since only about 43 percent of the fish that enter the system (estimated by counts from towers) are seen during spawning surveys, the summed maxima have been increased to produce the estimate of the maximum populations for streams and for lake beaches (table 14).

Maximum populations and the estimated potential capacity of the spawning grounds in streams are thought to be in reasonable agreement, because use of the spawning grounds is highly variable and some of the larger streams

have very small populations. Because the maximum number of spawners estimated on beaches is less than the maximum estimated in streams (table 14), the spawning ground potential of the beaches is probably not in excess of that of the streams.

The largest escapement of sockeye salmon to the Wood system since counting from towers began in 1953 was 2,209,000 in 1959 (table 8). Although some spawning grounds were overcrowded in 1959, as evidenced by a large mortality of eggs, most were greatly underutilized. Escapements in 1955-62 varied between 289,000 and 2,209,000 sockeye salmon. Thus, the potential capacity of the spawning grounds in the Wood system greatly exceeds the normal escapements.

Kvichak system. — The area of potential spawning grounds in rivers, streams, and ponds in the Kvichak system was estimated to be 839.7 hectares (table 12), and the space required per spawning female was estimated to be 2 m.^{2} A capacity of 4,199,500 spawning females is calculated from these data; on the basis of 1:1 sex ratio, the potential capacity of the nonlake spawning grounds in the Kvichak system is about 8,399,000 spawners.

We do not have enough data to make a direct estimate of the area of the potential beach spawning grounds in the Kvichak system, but we can estimate it indirectly. The area used by 3,706,000 spawners in 1961 on 16 of 21 recognized spawning beaches was 111.5 hectares (table 12). The area used by the 14,630,000 spawners of 1960 would have been 435 hectares if we assume a constant relation between numbers of spawners and area used (the ratio of spawners in 1961 and 1960 was 1:3.9). Because only 75 percent of the beaches known to be used have been surveyed, the estimate of 435 hectares is further expanded by 4/3, to give 579.9 hectares of beach actually used in 1960. Because only beach areas used for spawning have been considered and the average use of potential spawning grounds in the streams has been 48 percent, the amount of potential beach spawning grounds was calculated by assuming the same rate. This computation gives an estimate of 1,208 hectares of potential beach spawning grounds with a capacity of 12,080,000 spawners.

On the basis of the above information, we postulate a potential spawning population of about 20,500,000 sockeye salmon for the Kvichak system. This figure is greater than the maximum observed escapement through 1962. Escapements since 1955 have varied between 251,000 and 14,630,000 (table 8).[10]

Naknek system. — The amount of potential spawning ground in the Naknek system, the space required per female, and the capacity of the spawning ground were calculated for each of several types of streams. We made estimates of the total potential of the beach spawning grounds.

The total number of potential redd sites — calculated from estimates of the amount of spawning ground available and the size of redd sites—is 624,000 for the streams of the Naknek system (table 13). An estimate of 20,000 redd sites for the beach spawning grounds of Grosvenor Lake is based on past spawning ground surveys. Other beach spawning grounds exist, but their capacity is unknown.

Since estimates of the size of redd sites were based on observations of spawning density on single days, the effect of spawning in waves or surges must be considered. Three waves of fish commonly enter the Brooks River (Hartman, Merrell, and Painter, 1964), which is the major interconnecting stream that produces sockeye salmon. The number of redd sites in the interconnecting streams has been expanded, therefore, by a factor of 3 to produce a more realistic estimate of the capacity of these areas to receive spawning salmon.

If all of these factors are considered and a 1:1 sex ratio is assumed, the estimated spawning capacity of the Naknek system is about 670,000 females, or 1,340,000 fish of both sexes. Escapements in recent years varied between 273,000 and 2,232,000 salmon (table 8). Escapements exceeded 1,260,000 twice in the 14 years from 1949 to 1962.

Karluk system. — Estimates of the size of a redd site for several tributaries in the Karluk system are about 2 m.^{2}, and because estimates are not available for other areas, 2 m.^{2} is used for all. The estimated number of redd sites for streams and lake beaches is 174,000 (table 13), and (assuming a 1:1 sex ratio) the capacity is

[10] The escapement in 1965 was 24.3 million. Some of the spawning grounds had few adult fish; others were so densely occupied that superimposition of redds and retention of eggs caused a great loss of eggs. On most spawning grounds, however, density appeared to be optimal and confirmed the figure given above.

348,000 adults. This estimate is only approximate — the situation in the Karluk system is complicated by the occurrence of successive waves of spawners in most streams and incomplete information on the amount of potential spawning ground, especially on lake beaches. Escapements to Karluk neared or exceeded 1 million fish for many years during the early 1900's.

SPAWNING AREA AS THE LIMITING FACTOR IN PRODUCTION

An excessive density of spawners may cause increased retention of eggs, loss of eggs because of dislodgment from gravel during spawning, and increased mortality of eggs because of crowding of eggs in the gravel. We do not know the relation between these variables and density of spawners.

With the possible exception of the Karluk system, the tentative data on potential spawning areas indicate that the major lake systems could accommodate spawning populations considerably in excess of average present-day escapements. Full use of potential spawning grounds would, however, require a distribution of spawners strictly in proportion to the capacity of each ground. Such a distribution has never been observed.

CAPACITY OF REARING AREAS

Young sockeye salmon usually emerge from the spawning gravels in the spring to begin their stay in the rearing areas of the lakes. Here they remain 1 or 2 years (occasionally 3, as at Karluk) before they migrate seaward in May, June, and July as smolts. The abundance and growth of juvenile sockeye salmon and the age and size of smolts produced in each system were determined and were examined in relation to several physical and biological factors of the rearing areas: (1) number of spawning sockeye salmon per unit of rearing area; (2) relative numbers of other fish species in each system, both possible competitors and predators; (3) movement of presmolt sockeye salmon within and between lakes of a system; (4) basic biological productivity of the waters; and (5) innate characteristics of the various stocks of sockeye salmon.

Because long-term observations were not available for most individual systems, the carrying capacity of each system was judged by means of comparisons among the several systems of the biological and physical characteristics of the rearing areas.

RELATION BETWEEN NUMBERS OF SPAWNERS AND SIZE OF REARING AREAS

In the systems of southwestern Alaska the capacity of the rearing areas to support sockeye salmon is, in general, reflected in the number of adults returning to each system. The most extensive data on the comparative numbers of fish in the returns are found in the escapement records; the escapement is also generally a good indicator of the magnitude of the total return. Because the size of the lakes and systems considered varies widely, the escapements and other measures of productivity are frequently expressed as numbers per square kilometer of lake area. Table 15 gives the average number of adults in the escapements in 1955-62, the area of the lakes, and the numbers of spawners per square kilometer of lake for the major systems in southwestern Alaska.

The systems fall into four general levels of escapement per unit area (table 15): (1) escapements that averaged about 8,000 spawners per square kilometer (Karluk and Chignik); (2) escapements of about 2,300 to 4,400 spawners per square kilometer (Igushik and Wood); (3) escapements between 1,100 and 1,500 spawners per square kilometer (Kvichak, Alagnak, Naknek, and Ugashik); and (4) escapements less than 800 spawners per square kilometer (Egegik, Snake, and Nuyakuk).

For some systems data are available for examining variation in productivity between lakes (in terms of numbers of adults in the escapements to individual lakes) and between years within lakes.

TABLE 15.—*Average sockeye salmon escapements, area of lakes, and spawners per square kilometer of lake by system in southwestern Alaska, 1955-62*

System	Fish in escapement	Lake area	Spawners per square kilometer
	Thousands	*Km.²*	*Number*
Igushik	323	74	4,360
Snake	26	89	290
Wood	996	425	2,340
Nuyakuk (Tikchik)	78	279	280
Kvichak	4,334	2,889	1,500
Alagnak (Branch)	428	297	1,441
Naknek	886	790	1,122
Egegik	826	1,132	730
Ugashik	515	385	1,335
Chignik	492	61	8,070
Karluk	334	40	8,350

Igushik System

In the Igushik system, in 1955-62 the number of spawners per square kilometer of lake in Ualik Lake was only slightly larger than in Amanka Lake if we assign the adults spawning in the interconnecting river and its branch (Ongoke River) to Amanka Lake.

Snake System

Nunavaugaluk Lake is the only lake in the Snake system that produces significant numbers of salmon.

Wood System

The average numbers of spawners per square kilometer in each of the four main lakes of the Wood system in 1955-62 were: Aleknagik, 2,090; Nerka, 2,430; Beverley, 2,490; and Kulik, 2,040. Little Togiak Lake, tributary to Lake Nerka, had a slightly higher density of spawners than the main lakes.

Nuyakuk System

The low average number of spawners per unit lake area in the Nuyakuk system (table 15) is largely due to the low densities in Nuyakuk Lake, the largest lake in the system, where the figure was only 50 spawners per square kilometer from 1959 through 1962.

Kvichak System

The Kvichak is the only major sockeye salmon system in Bristol Bay that has a pronounced cyclic variation in number of adults in the escapement. The effects of this cycle overshadow problems of distribution of the spawners within each year. Over the years 1955-63, the number of spawners per square kilometer of lake varied from 84 — among the lowest numbers observed in Bristol Bay — to 4,890 (table 16). Peak years modify the reproductive potential in subsequent off years. This problem is discussed later.

Naknek System

Many nursery areas of the Naknek system receive juvenile sockeye salmon from upsystem areas; that is, from other than adjacent beaches and tributary streams. Coville Lake represents about 3 percent of the rearing area of the Naknek system but has received as much as 65 percent of the escapement in a given year. This lake is at the upper end of the system, and many of the juvenile sockeye salmon that originate in its tributaries spend some growing time in downsystem lakes. North Arm basin and Brooks Lake make up about 35 percent of the area of the system but receive less than 10 percent of the escapement, and they do not receive fry produced in other areas. The distribution of escapement and subsequently the distribution of the juveniles are considered later.

TABLE 16.—*Numbers of sockeye salmon in escapements and spawners per square kilometer of lake, Kvichak system, 1955-63*

Year	Fish in escapement	Spawners per square kilometer
	Thousands	*Number*
1955	251	84
1956	9,443	3,156
1957	2,843	950
1958	535	179
1959	680	227
1960	14,630	4,890
1961	3,706	1,239
1962	2,581	863
1963	339	113

Chignik System

Chignik Lake had the greatest average concentration of spawners in the Chignik system — about 14,000 per square kilometer of lake in 1956-62. The average for Black Lake during the same period was slightly more than 4,600, about the same as for the Igushik lakes.

Karluk System

Recently emerged fry behave in such a way in the Karluk system that the total escapement is assignable to Karluk Lake for consideration of rearing areas. The progeny of spawners that use the outlet (Karluk River) move upstream into the lake, and progeny of spawners from areas above O'Malley and Thumb Lakes move down into Karluk Lake early in their first summer of life.

SPECIES OF FISH IN THE LAKES

Knowledge of the abundance of species of fish associated with juvenile sockeye salmon in the lakes is essential to understand the factors that may affect the survival and growth of sockeye salmon. Differences in behavior and the distribution of the habitat of the many species required the use of several types of collecting gear: tow nets, beach seines, trap nets, gill nets, and bottom and midwater trawls.

Although as many as 25 species of fish were found in a system, the abundance of most was low. Species of salmon other than sockeye were not sufficiently abundant to compete seriously for rearing area. Juvenile sockeye salmon and one other species of fish constituted 75 to 95 percent of the catches.

Of the species that may be competitors with juvenile sockeye salmon, the threespine stickleback *(Gasterosteus aculeatus)* is most important in the Igushik, Snake, Wood, Kvichak, Nuyakuk, Chignik, and Karluk systems and part of the Naknek system. In other parts of the Naknek system the ninespine stickleback *(Pungitius pungitius)*, pond smelt *(Hypomesus olidus)*, or pygmy whitefish *(Prosopium coulteri)* seem to be of greatest significance. Species of fish in most systems that have varying degrees of importance as predators on juvenile sockeye salmon include Arctic char *(Salvelinus alpinus)*, lake trout *(S. namaycush)*, northern pike *(Esox lucius)*, juvenile coho salmon *(O. kisutch)*, and Dolly Varden *(S. malma)*.

The data on the species in the other systems of southwestern Alaska are too few to permit generalizations.

MIGRATION OF PRESMOLT SOCKEYE SALMON

To study the relation between density of parent spawners (numbers per unit lake area), growth and abundance of progeny, and capacity of the rearing areas, we had to know how long the young sockeye salmon remain in the lake that they first enter as fry. Fyke nets were fished, therefore, in some interconnecting rivers during the summer to detect possible migrations from various lakes. Changes in length frequencies of juveniles and their abundance in tow net catches supplied indirect information on their movements.

Wood System

Catches of fyke nets fished in the connecting rivers of the Wood system indicated no appreciable migration of young sockeye salmon during the summer between Little Togiak Lake and Lake Nerka in 1961 or between Lake Nerka and Lake Aleknagik in 1962.[11] Two other kinds of observations in the Wood system support the conclusion that these fish do not migrate during the summer: (1) the abundance of young-of-the-year in tow net catches after mid-August is generally proportional to the number of parent spawners for each lake (the density of spawners varies widely between lakes within years); and (2) the growth of young-of-the-year is often reduced in lakes that had high densities of spawners the previous fall. We, therefore, assumed that in the main lakes of the Wood system, juvenile sockeye salmon remain within their lake of origin at least during their first growing season.

Kvichak System

Most of the sockeye salmon in the escapement to the Kvichak system spawn in tributaries or on beaches in Iliamna Lake. The only possible significant presmolt interlake migration would be from Lake Clark to Iliamna Lake, and we have no indication that this movement occurs. We investigated this problem directly only at the time of normal smolt migrations in 1959, 1962, and 1963 when we found that the juveniles leaving Lake Clark are mostly age II.[12] Because no age III smolts have been captured at the outlet of Iliamna Lake and no adults with three freshwater annuli have been captured in the system, we assume that the age II juveniles migrating in June from Lake Clark are smolts that pass directly to the outlet of Iliamna Lake. As indicated elsewhere in this paper, the abundance of spawners within Iliamna Lake is greatest in the east end. This concentration produces a greater abundance of fry in that area. Entire age groups move in the lake toward the outlet in the west end, however; this movement is comparable to interlake migrations in other systems.

Naknek System

Interlake migrations of presmolt (age 0 and age I) sockeye salmon are known in the Naknek system.[13] In one movement fish left an area of high density of juveniles to enter areas of low densities (Coville Lake to downlake areas), and in another the migration was from a low- to a high-density area (Brooks Lake to Naknek

[11] Burgner, R. L., and J. M. Green. 1963. Study of interlake migration of red salmon fry, Agulowak River. Univ. Wash., Fish. Res. Inst., Circ. 182. 13 pp.

[12] Orrell, R. F. 1963. Abundance and age of Lake Clark red salmon smolts, 1962. Univ. Wash. Fish. Res. Inst., Circ. 186. 13 pp.

[13] Ellis, Robert J. 1963. The abundance and distribution of juvenile red salmon and associated species in lakes of the Naknek River system and Karluk Lake. Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska. [Manuscript. 80 pp.]

Lake). The interlake and interbasin migrations of presmolt fish in the Naknek system caused large numbers of fish to accumulate in downsystem lake areas, which have comparatively limited spawning grounds. Fyke net catches from Coville, Grosvenor, and Brooks Rivers and tow net catches from the lakes indicate that Naknek Lake, except for the relatively isolated North Arm basin, serves as a rearing area for fish originating in other lakes.

Chignik System

Interlake migration of age 0 sockeye salmon from Black Lake to Chignik Lake was detected by fishing fyke nets in Black River in 1961 and 1962. Scales of age 0 and age I salmon from Chignik Lake indicate that some Black Lake progeny use Chignik Lake as a rearing area, but scales from spawning populations in Black Lake indicate that most fry remain in Black Lake to age I and then migrate directly to the ocean (Narver, 1963). Extensive sampling of Chignik Lagoon with tow nets and seines in 1962 and 1963 revealed that some of the progeny of spawners of Chignik Lake migrate into Chignik Lagoon soon after they emerge from the gravel and use the lagoon as a rearing area.

Karluk System

Interlake movements of presmolt sockeye salmon have not been investigated in the Karluk system. Because Karluk Lake is the only rearing area of significant size, these movements could not be important.

ABUNDANCE AND GROWTH OF FISH IN PELAGIC AREAS

The capacity of a system to produce juvenile sockeye salmon is measured ultimately in the number of smolts produced. We have discussed our studies of the capacities of the spawning grounds. To locate and define factors that affect production of smolts in the rearing areas, we investigated the relation of the abundance of adult sockeye salmon to the abundance and growth of juveniles and associated species in the lakes.

Sockeye Salmon

The abundance of juvenile sockeye salmon in the lakes was measured with the pelagic tow net developed by Johnson (1956) and improved by Burgner (1958; footnote 9). In this study the standard unit of gear was a conical tow net 10 feet (3.1 m.) in diameter and 25 feet (8.3 m.) long. This net was pulled behind a pair of boats at night and fished with the center of the opening at two depths — 1.6 and 5 m. Modifications of the standard tow net were (1) a square opening of 9 feet (2.7 m.) and a length of about 25 feet (8.3 m.), used in the Wood and Kvichak systems; and (2) a square opening of 6 feet (1.8 m.) and a length of about 19 feet (5.8 m.), used in the Chignik system. The rate of catch is expressed in terms of the standard round opening 3.1-m. net pulled 1,500 feet (457 m.) in about 6 minutes.

Because we expected the abundance and growth of juvenile sockeye salmon and associated fishes would vary within lakes, we divided each lake into several sampling areas. The areas were not generally of uniform size, even within a lake. When we wish to discuss the average abundance or size of fish in a lake we must consider the relative contribution of each sampling area to the total population. We do this by a process of weighting in which we consider the portion of the total lake area in each sampling area and the relative abundance and size of the fish in the sampling area.[14] This process is repeated to compile an average for a system of more than one lake.

The mean catches of age 0 and age I and older sockeye salmon in tow nets (surface and deep tows combined) in the Wood, Kvichak, Naknek, Chignik, and Karluk systems, August 16 to September 15, are given in tables 17 and 18. Differences in abundance between systems within years were large (for example, 1961) as were

[14] The following formulas yield the weighted average catch per tow and the weighted average length of fish.

$$C_W = \sum_{i=1}^{n} \left(\frac{a_i}{A}\right) c_i$$

$$L_W = \frac{\sum_{i=1}^{n} (c_i a_i)\, l_i}{\sum_{i=1}^{n} (c_i a_i)}$$

where C_W = weighted catch per tow for entire lake
c_i = average catch per tow for sampling area i
A = surface area of entire lake
a_i = surface area of sampling area i
L_W = weighted average length of fish in the lake
l_i = average length of fish in sampling area i

TABLE 17.—*Weighted mean catches of age 0 sockeye salmon per standard tow (surface and deep tows combined), August 16 to September 15, by lake and year, in lakes of the Wood, Kvichak, Naknek, Chignik, and Karluk systems, 1958-62*

System and lake	Surface area	Fish per tow				
		1958	1959	1960	1961	1962
	Km.²	*Number*	*Number*	*Number*	*Number*	*Number*
Wood system						
Lake Aleknagik	83	31.5	25.5	183.2	215.6	92.2
Lake Nerka	201	26.7	12.2	80.4	98.0	31.0
Lake Beverley	90	3.7	61.3	56.4	94.2	2.8
Lake Kulik	45	4.3	63.1	274.4	92.2	27.0
Little Togiak Lake	6	60.0	240.5	153.5	223.7	39.6
Kvichak system						
Iliamna Lake	2,622					5.0
Lake Clark	267					6.3
Naknek system (all lakes combined)	790				9.5	11.6
Chignik system						
Chignik Lake	22					28.9
					[1] 180.0	[1] 36.0
Black Lake	39					35.7
					[1] 290.0	[1] 56.0
Karluk system						
Karluk Lake	40				10.5	4.3

[1] Surface tows only.

TABLE 18.—*Weighted mean catches of age I and older sockeye salmon per standard tow (surface and deep tows combined), August 16 to September 15, by lake and year, in lakes of the Wood, Kvichak, Naknek, Chignik, and Karluk systems, 1958-62*

System and lake	Surface area	Fish per tow				
		1958	1959	1960	1961	1962
	Km.²	*Number*	*Number*	*Number*	*Number*	*Number*
Wood system						
Lake Aleknagik	83	1.9	0.4	0.3	17.2	3.8
Lake Nerka	201	1.2	.2	1.3	7.0	2.6
Lake Beverley	90	.2	.2	11.2	7.1	2.1
Lake Kulik	45	.8	.4	4.3	31.4	6.9
Little Togiak Lake	6	2.3	2.5	3.1	25.4	18.7
Kvichak system						
Iliamna Lake	2,622					20.2
Lake Clark	267					.0
Naknek system (all lakes combined)	790				2.0	5.5
Chignik system						
Chignik Lake	22					118.2
					[1] 86.4	[1] 125.9
Black Lake	39				.0	.0
						[1] .0
Karluk system						
Karluk Lake	40				.9	1.2

[1] Surface tows only.

differences within systems between years (1961 and 1962 for all lakes of the Wood system). Some of these differences are examined in the following analyses for individual systems.

Wood system.—Preliminary use of the tow net to sample young sockeye salmon was started in lakes of the Wood system in 1957, and full-scale sampling began there in 1958. The relation between numbers of parent spawners per unit lake area and the production of age 0 sockeye salmon as measured by the geometric mean catch per standard tow (mid-August to mid-September) in each of the five Wood system lakes is presented for 1958-62 in figure 4. The relation between catch per tow of age 0 sockeye salmon and density of parent spawners seems to differ among lakes; hence, the data must be examined separately for each lake. A curve describing the relation between abundance of juveniles in the lake and density of parent spawners might be expected to start at zero, reach a maximum, and level off or decline as a result of increased mortality due to overcrowding of adults or eggs and larvae in the spawning areas or of young in the rearing areas. The relatively low catch of juveniles per tow in Little Togiak Lake and Lake

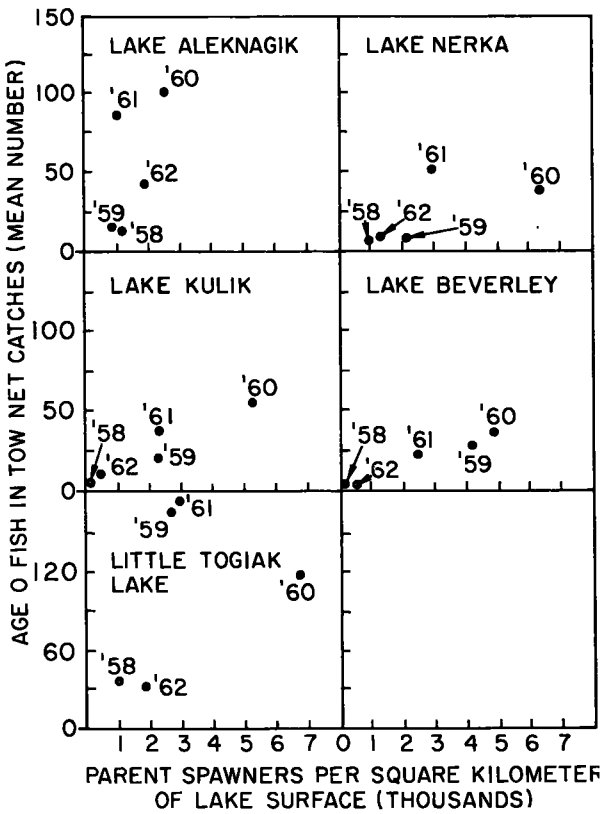

FIGURE 4.—Relation between abundance of age 0 sockeye salmon and numbers of parent spawners per unit lake area in each of the major lakes of the Wood system, 1958-62. The abundance of age 0 fish is the geometric mean of the abundance in tow net catches (mid-August to mid-September) weighted by depth and sampling area. The figure beside each point indicates the year of sampling.

Nerka at parent population densities approaching 7,000 spawners per square kilometer of nursery area (fig. 4) suggests decreased spawning efficiency or increased mortality of young at high population densities. There is some evidence of both.

The variation in the relations of abundance of juveniles to number of parent spawners per unit lake area in lakes of the Wood system is probably due to a combination of several factors: (1) errors in estimating numbers of spawners, (2) changes in survival from egg to juveniles available to the tow nets, and (3) random error in tow net sampling. Catches with the tow net indicate the same general abundance of juvenile salmon as do echo soundings recorded at the time of towing.

Evidence that the capacity of the nursery area may control the growth of fish in the Wood system is provided by data on growth of age 0 sockeye salmon in each of the four main Wood system lakes in 1958-62. The mean length of age 0 juveniles on September 1 is plotted against numbers of parent spawners per unit lake area for each lake (fig. 5). The inverse relation indicates that

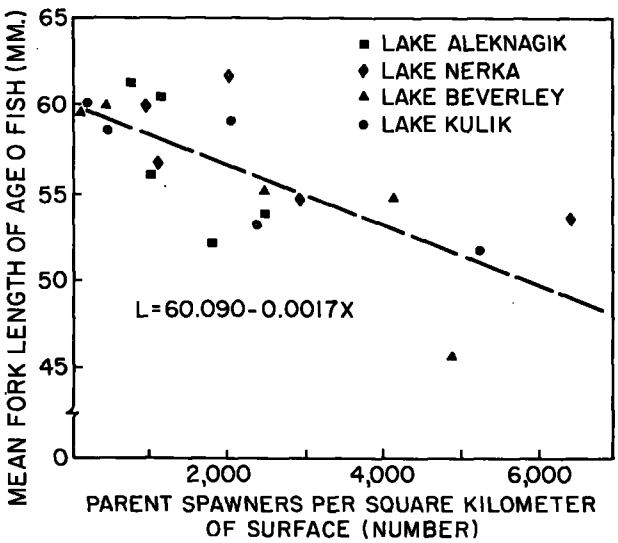

FIGURE 5.—Relation between mean fork length of age 0 sockeye salmon captured in tow nets, 1958-62, and abundance of parent spawners in lakes of the Wood system. The weighted mean fork length of the age 0 fish in each sample was adjusted to September 1 by applying a mean growth of 0.33 mm. per day, computed from growth data. The fish were measured after at least 24 hours in 10 percent Formalin.[15]

[15] Trade names referred to in this publication do not imply endorsement of commercial products.

the progeny of large spawning populations grow slowly. Although the trend of the relation is obvious, the true shape of the line is probably obscured by five factors: (1) minor differences in growth potential (factors such as food availability and temperature) between lakes, (2) competition with variable numbers of yearling sockeye salmon from the previous year, (3) variability in the abundance of competitor species, (4) annual differences in climate that could affect the time of emergence, the length of growing season, and food supply, and (5) inaccuracies in estimates of numbers of spawners.

Differences are frequently observed in size of juvenile sockeye salmon between various parts of nursery lakes. These differences may be due to many factors including (1) real differences in growth rates, (2) differences in length of time the young have been in the lake, (3) differences in size of fry at hatching, and (4) differential rates of dispersion of faster and slower growing individuals. We have, therefore, used the term "apparent growth rate" in discussions of differences in size of juvenile sockeye salmon.

The apparent growth of young sockeye salmon in each of the three single-basin lakes in the Wood system is greatest in the east third and least in the west third of each lake (table 19). This relation holds for years of high and low population densities. Although the difference in apparent growth suggests basic differences in the growth potential of lake areas, progeny are smaller in the end of the lake that is closer to the major spawning grounds; and the differences in size within each lake may be the combined result of the longer lake residence of the early emerging fry and a more rapid dispersion of the larger fish.

TABLE 19.—*Mean fork lengths*[1] *of age 0 sockeye salmon on September 1*[2] *in three single-basin lakes of the Wood system, 1958-62*

Year	Lake Aleknagik			Lake Beverley			Lake Kulik		
	West third	Middle third	East third	West third	Middle third	East third	West third	Middle third	East third
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1958	59.0	59.0	63.4	59.0	60.0	----	58.8	59.8	60.0
1959	57.5	62.7	60.8	50.5	57.3	61.2	61.5	60.6	58.8
1960	53.3	53.7	54.3	42.0	44.5	46.4	50.3	51.7	52.3
1961	52.2	57.5	57.5	51.1	52.2	59.2	51.7	52.8	55.1
1962	47.8	54.2	55.2	58.6	58.9	67.3	57.6	59.5	60.1
Mean	54.0	57.4	58.2	52.2	54.6	59.8	56.0	56.9	57.3

[1] After at least 24 hours in 10 percent Formalin.

[2] Lengths were adjusted to September 1 by applying a mean growth of 0.33 mm. per day computed from growth data.

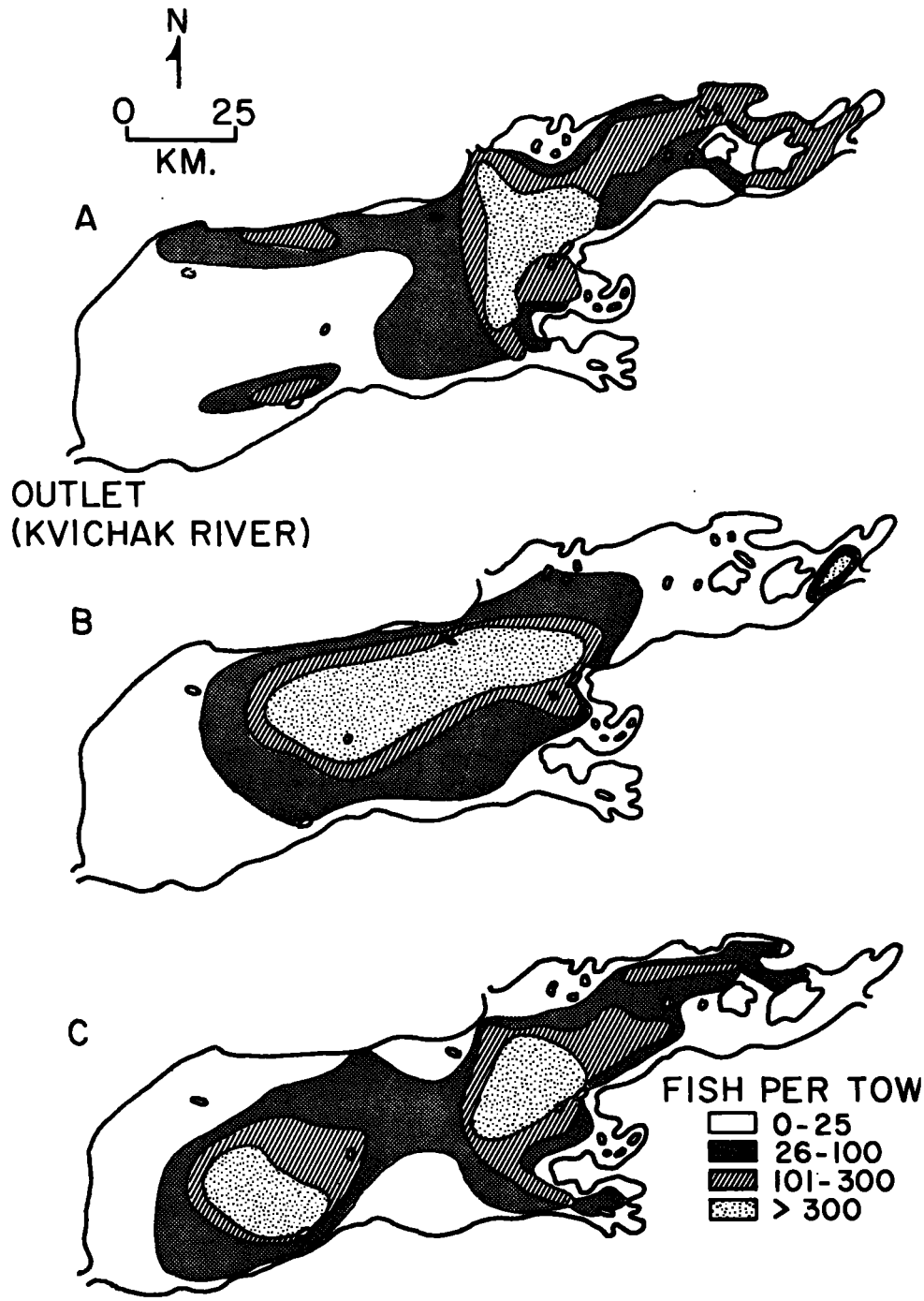

FIGURE 6.—Spatial distribution of juvenile sockeye salmon as indicated by the average catch per tow in Iliamna Lake, 1962. Catches in A (upper) are of age 0 fish caught between August 1 and September 15; in B (middle) are of age I fish caught between June 15 and July 31; and in C (lower) are of age I fish caught between August 1 and September 15.

Kvichak system.—Our most complete measure of the distribution and abundance of juvenile sockeye salmon in the Kvichak system is from tow net samples from Iliamna Lake in 1962 (fig. 6). The contour lines of density in the figure were determined by interpolation of the data on rate of catch between stations sampled and are not precise, but they illustrate the general distribution of the two age classes. The distribution and abundance changed during the summer and was different for age 0 and age I sockeye (fig. 6).

Most of the age 0 fish were in the eastern two-thirds of the lake from August 1 to September 15 —fig. 6A (the major spawning areas are in the eastern half of the lake).

Comparison of the distribution and abundance of age I sockeye salmon in early and late summer indicates a westerly movement, away from the principal spawning areas (fig. 6B and 6C). Age I juveniles had two centers of maximum concentration near the end of August—one in the west third and one in the middle third of the lake. These progeny of the 1960 escapement, therefore, occupied an area of the lake during their second summer (1962) that is probably not heavily used when most of the juveniles migrate to sea as age I smolts in early summer.

We found gradients in proportion of young-of-the-year and yearling sockeye salmon in the tow net catches in 1962 and in the average length of each age group from the outlet of the system to distant points in the system in catches made with an Isaacs-Kidd midwater trawl in 1961 and tow nets in 1962 (table 20). Yearling sockeye salmon were essentially absent from catches in 1961, but in 1962 they made up about 90 percent of the catches in the third of the lake closest to the outlet, about 85 percent in the middle third, and 45 percent in the most distant third. None were taken in Lake Clark. The average lengths of both age classes were greater nearer the outlet and less at the more distant points both years.

A strong gradient was found at the end of August 1962 in the mean length of age I sockeye salmon from three areas of Iliamna Lake. The average lengths in the east, middle, and west thirds of the lake were 81.5, 88.1, and 99.6 mm., respectively. Since spawning is most limited in the west end of the lake, the gradient is thought to be due to the more rapid or earlier migration of the larger and possibly older fish. By the following spring (1963) the westward movement of these fish (now age II smolts) must have been completed because most of them migrated in the first few days after the ice in the lake broke up.

TABLE 20.—*Age class composition and mean fork length of juvenile sockeye salmon on September 1 in various areas of the Kvichak system, 1961-62. The fish were captured with an Isaacs-Kidd midwater trawl in 1961 and in a 6-foot-square opening tow net in 1962. Original measurements were made of live fish and these data converted to preserved fish equivalents*

Area	1961				1962			
	Young-of-the-year		Yearlings		Young-of-the-year		Yearlings	
	Frequency	Average length	Frequency	Average length	Frequency	Average length	Frequency	Average length
	Percent	*Mm.*	*Percent*	*Mm.*	*Percent*	*Mm.*	*Percent*	*Mm.*
Iliamna Lake								
Igiugig					0	----	100	98.6
Shoulderblade					0	----	100	96.3
Grassy					81	56.6	19	90.5
Middle Talarik					24	56.1	76	91.5
Chekok					0	----	100	93.1
Dennis					20	57.8	80	80.2
Upper Talarik	100	59.7	0	----	18	54.7	82	85.3
Ten-Mile Island					15	50.6	85	77.9
Middle Island					8	53.6	92	81.9
Gibraltar					26	52.7	74	88.4
Kakhonak Bay					3	----	97	89.1
Intricate Bay					22	53.6	78	83.8
Tommy Point	100	54.3	0	----	25	50.7	75	79.2
Iliamna	100	53.9	0	----	56	50.2	44	79.5
Triangle Island	100	52.4	0	----	30	52.9	70	77.0
Knutson Bay	100	46.2	0	----	66	52.5	34	76.7
Pedro Bay	100	51.7	0	----	78	48.8	22	76.7
Pile Bay	100	50.2	0	----	75	48.4	25	74.6
Lake Clark								
Lower lake					100	51.3	0	----
Middle lake					100	46.3	0	----

Naknek system.—The interlake migration of sockeye salmon in the Naknek system during their first summer influences the relation between the abundance of young salmon in each lake at the end of the summer and the number of adults in the parent escapement to each lake. Data collected with tow nets in 1962 have been used to estimate a systemwide average catch per tow by day, weighted by area of each lake, for July 11 to August 29. Sampling was not daily. Missing data for an area were derived by averaging the figures of the most recent preceding and the first following sampling in that area. These weighted figures were combined for all areas each date to find the hypothetical catch per tow for the entire system and were smoothed by a moving average of three. The data (fig. 7) show a gradual increase in abundance of age 0 fish while recruitment from the spawning grounds exceeds mortality, a general leveling of the curve from July 20 to August 10, and a decline in rate of catch per tow after August 10. The curve

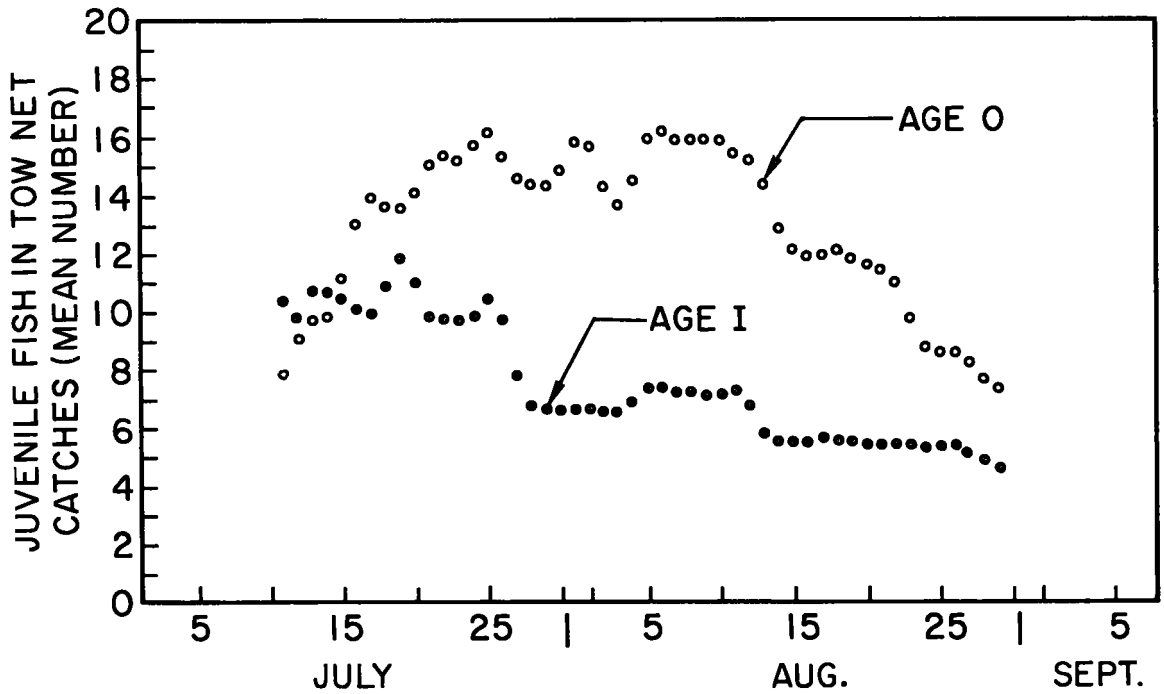

FIGURE 7.—Weighted daily mean catch of juvenile sockeye salmon per tow in Naknek system, all lakes combined, 1962. The mean catch for the system has been weighted by the size of each sampling area, and the daily estimates have been smoothed by a moving average of three—(A + 2B + C) ÷ 4.

would be somewhat higher if data from North Arm, which is not involved in the interlake movement, were omitted. The weighted mean catch of age I juveniles for the system was greatest in the earliest tows, July 11 to 20, and declined gradually during the summer.

Within lakes of the Naknek system we found a wide range in numbers of adult spawners per unit area of lake and also in the abundance of their progeny. Coville Lake had an escapement of about 6,600 adults per square kilometer in 1961; Brooks Lake had 267; and North Arm had 55. In July 1962 (before the presmolt interlake migrations) the average number of age 0 sockeye salmon in tow net catches was 150 in Coville Lake, 2 in Brooks Lake, and 0.5 in North Arm. The abundance of spawning adults (table 15) and of age 0 juveniles in these three lakes nearly cover the range found in southwestern Alaska.

Studies of juvenile salmon in the Naknek system have run too few years to determine the relation between the abundance of age 0 sockeye salmon and the size of the parent population. The escapement to the Naknek system in 1960 was 828,000 spawners, and the average catch of age 0 sockeye per tow in 1961 (in late August) was about 9.5. The escapement in 1961 was about 350,000, and the average catch per tow in 1962 was about 11.6.

The age composition and mean fork lengths of juvenile sockeye salmon on September 1 are presented for the Naknek and Karluk systems in table 21 by lake or sampling area. The average lengths of age 0 sockeye salmon in the Naknek system were greater in 1962 than in 1961, although the numbers of age 0 and age I fish in the system were essentially the same, as indicated by tow net catches in 1961 and 1962 and the smolt emigration in 1962 and 1963. The average catches per tow were 9.5 and 11.6 age 0 fish on August 20, and the smolt migrations were 8 million age I and 8 million age II in 1962 and 6 million age I and 8 million age II in 1963.

The year-to-year variation in basic productivity of the lakes of the Naknek system may cause marked differences in growth of juvenile sockeye salmon independent of their abundance. As was shown earlier in this report, basic productivity was comparatively low in 1961 and high in 1962. The resulting apparent growth of juvenile sockeye salmon reflected these differences.

The variation among mean lengths of age 0 sockeye salmon in the several basins of the Nak-

TABLE 21.—*Age composition and calculated*[1] *mean fork lengths*[2] *on September 1 of age 0 and age I sockeye salmon captured in tow nets in lakes of the Naknek and Karluk systems, weighted by surface area and catch per tow, 1961-62*

System, lake, and year	Age 0 fish		Age I fish	
	Frequency	Mean fork length	Frequency	Mean fork length
	Percent	*Mm.*	*Percent*	*Mm.*
Naknek system				
Coville Lake				
1961	100.0	54	0	----
1962	100.0	60	0	----
Grosvenor Lake				
1961	100.0	46	0	----
1962	100.0	52	0	----
Naknek Lake				
North Arm				
1961				
1962	62.5	56	37.5	98
Iliuk Arm				
1961	84.1	57	15.9	78
1962	69.2	61	30.8	91
South Bay				
1961	64.3	47	35.7	86
1962	26.0	63	74.0	85
West End				
1961	75.1	65	24.9	89
1962	91.8	69	8.2	---
Brooks Lake				
1961	96.3	51	3.7	----
1962	97.1	60	2.9	----
Karluk system				
Karluk Lake				
1961	88.7	40	11.3	83
1962	81.9	49	18.1	76

[1] Curves describing the average length were calculated for each lake each summer; only those data involving 10 or more fish were used.

[2] After at least 48 hours, preservation in 10 percent Formalin.

TABLE 22.—*Calculated mean fork length of age 0 sockeye salmon from the upper end of Naknek system to outlet on September 1, 1962*

Sampling area	Fork length
	Mm.
Coville Lake	
Upper half	56
Lower half	60
Coville River	61
Grosvenor Lake	52
Grosvenor River	63
Naknek Lake	
Iliuk Arm	
Upper third	57
Middle third	63
Lower third	61
South Bay	
Upper third	61
Middle third	66
Lower third	--
West End [1]	69

[1] Does not include samples from the small basin in the northwest corner of Naknek Lake.

nek system (table 22) seems to reflect the results of a combination of at least three factors: (1) movement of the large fish first in the interlake migrations, (2) midseason recruitment of recently emerged fry (especially evident in Grosvenor Lake), and (3) differences in productivity of waters. The average size of juveniles taken in tow nets in Coville Lake increased from the upper to the lower end and increased again in juveniles taken in fyke nets as they migrated from Coville Lake to Grosvenor Lake. The juveniles captured in fyke nets in Grosvenor River were larger than those taken in tow nets in the lake. In the next basin downsystem, Iliuk Arm, smaller fish were more abundant at the inlet (upper third) even though the larger juveniles that migrated from Grosvenor Lake enter this end. The average size was the same in the upper third of South Bay and the adjacent area of Iliuk Arm but increased toward the outlet of the lake.

Chignik system.—The number of parent spawners per unit lake area in the Chignik system was greater in 1960 than in 1961, and, correspondingly, age 0 progeny were more abundant in 1961 than in 1962. The mean lengths of the age 0 progeny on September 1 were less in the year of greater abundance (table 23). The relations are similar to those in the Wood system. In the Chignik lakes, however, the apparent growth of progeny at similar densities of spawners and progeny is better than in the lakes of the Wood system; this difference may be due to a combination of richer nursery areas and fewer competitors in the Chignik lakes.

Karluk system.—The escapement of sockeye salmon in Karluk Lake was greater in 1960 than in 1961, and, correspondingly, age 0 progeny were more abundant in 1961 than in 1962. In 1960 about 349,000 adults entered the system and the average catch per tow of age 0 fish in 1961 was 8.9 from August 16 to September 15. The escapement in 1961 was about 297,000, and the average catch per tow in 1962 was 4.3.

The average length of age 0 sockeye salmon in Karluk Lake was greater in 1962 than in 1961 (table 21). The juveniles were larger in the year of lesser abundance (1962), so it might be assumed that the size of age 0 fish is density-dependent. But because of the long period of recruitment of recently emerged fry into the lake —caused by the extended spawning period (4-5 months)—the mean size of young-of-the-year at the end of the summer is based on fish that may differ in age by many weeks. Differences in the abundance of early- and late-spawning stocks might result, therefore, in apparent but non-

TABLE 23.—*Parent escapement of sockeye salmon, as numbers per square kilometer of lake, average catch of age 0 progeny per standard tow, and average length of age 0 progeny in Black and Chignik Lakes, 1960-61*

Lake and year of spawning	Parent spawners per square kilometer	Age 0 progeny	
		Average catch per tow	Average fork length
	Number	*Number*	*Mm.*
Black Lake			
1960	6,128	180	58.9
1961	3,359	36	69.0
Chignik Lake			
1960	16,773	90	46.9
1961	12,545	56	47.2

existent differences in growth rates between seasons.

For Karluk Lake, both the average catches of juvenile sockeye salmon in tow nets (tables 17 and 18) and the average lengths for each age group (adjusted to September 1) were among the lowest recorded in this study (tables 19, 20, 21).

Associated Species

Several species of fish are captured frequently with juvenile sockeye salmon in the tow nets. The species and abundance vary from system to system. The most common in order of general abundance are threespine stickleback, ninespine stickleback, pond smelt, and pygmy whitefish.

The threespine stickleback is the most abundant species associated with young sockeye salmon in the Wood, Kvichak, Naknek, Chignik, and Karluk systems (table 24). Both species tend to concentrate near shore in the spring and spread toward the pelagic area of the lake as the season advances. Similarities in the food habits of these two species have been well established (Rogers, 1961).

Wood system.—The average abundance of threespine sticklebacks in tow net catches in the Wood system varied in 1958-62 (table 24) almost as much as, but seemingly independently of, that of juvenile sockeye salmon. In some years the biomass of the sticklebacks, as indicated by abundance in tow net catches, has approached or exceeded that of the juvenile salmon.

The average rate of growth of threespine sticklebacks varies from year to year and usually in the same direction as that of the juvenile sockeye salmon (fig. 8). The slowest growth of threespine sticklebacks (and of juvenile sockeye) generally is in years of greatest abundance

TABLE 24.—*Weighted mean catch of sticklebacks per standard tow (surface and deep tows combined), August 16 to September 15 in lakes of the Wood, Kvichak, and Chignik systems, 1958-62*

Species, system, and lake	Fish per tow				
	1958	1959	1960	1961	1962
	Number	*Number*	*Number*	*Number*	*Number*
Threespine sticklebacks					
Wood system					
Lake Aleknagik	81.4	310.2	85.2	62.4	188.0
Lake Nerka	51.5	53.4	26.4	24.0	30.2
Lake Beverley	133.0	51.2	53.7	22.0	3.0
Lake Kulik	285.6	21.9	14.8	13.2	14.1
Little Togiak Lake	113.4	106.3	25.2	51.0	65.6
Kvichak system					
Iliamna Lake					27.8
Lake Clark					.0
Chignik system					
Chignik Lake					3.8
				[1] 4.1	[1] 5.0
Black Lake					170.3
				[1] 196.4	[1] 162.4
Ninespine sticklebacks					
Chignik system					
Chignik Lake					7.2
				[1] 6.6	[1] 7.0
Black Lake					32.2
				[1] 7.2	[1] 28.9

[1] Surface tows only.

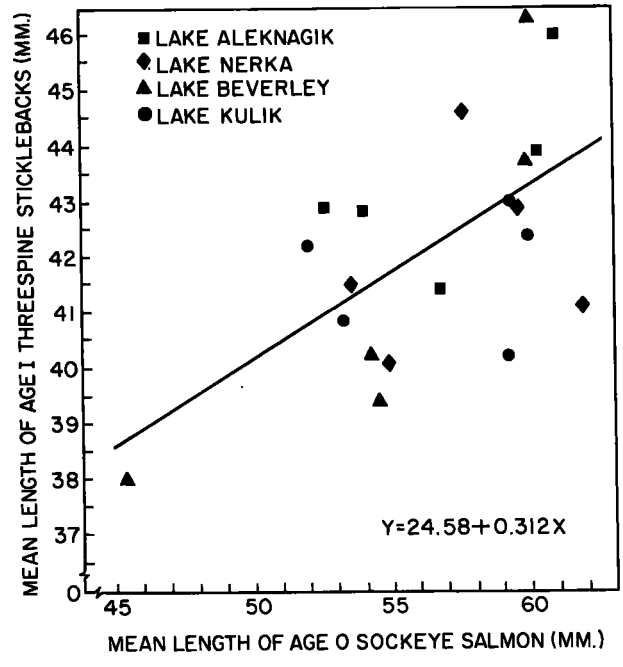

FIGURE 8.—Relation between mean length of age I threespine sticklebacks and mean length of age 0 sockeye salmon taken in tow nets each year, 1958-62, in each of four lakes of the Wood system. The mean lengths of both species have been weighted and adjusted to September 1.

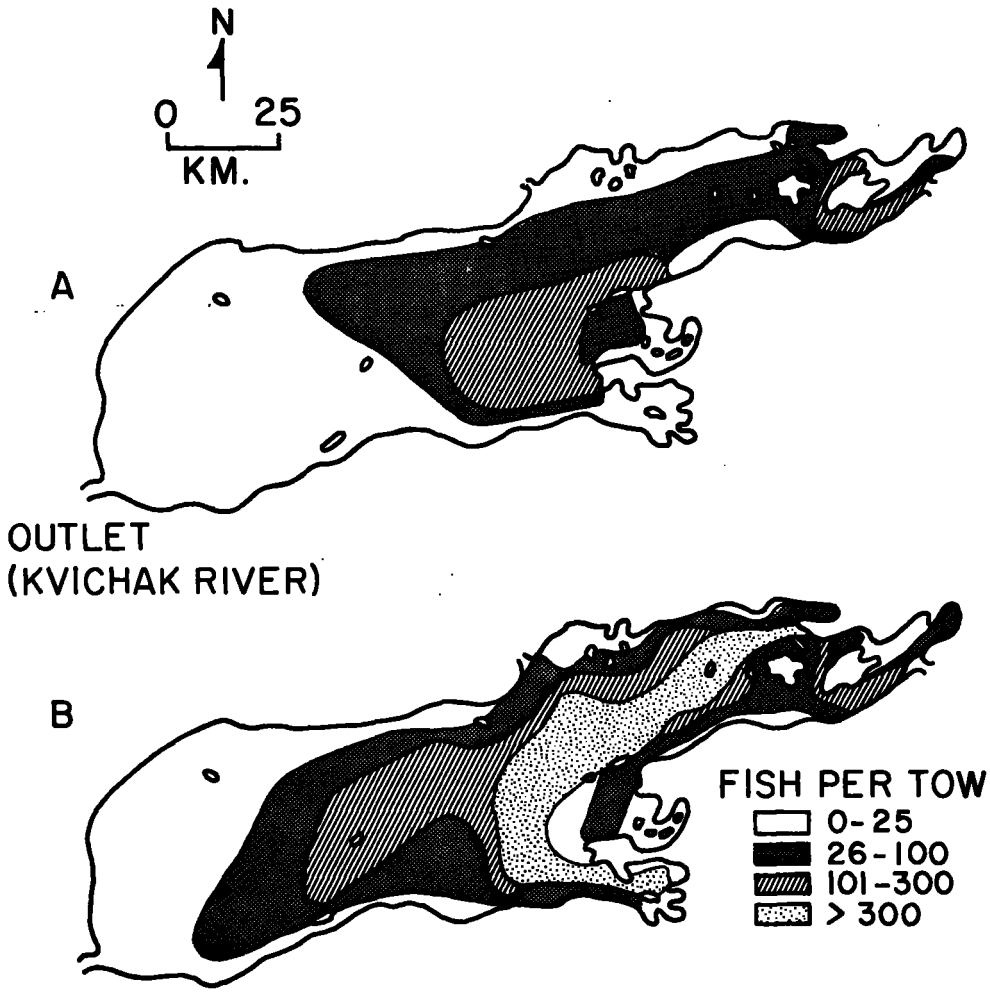

FIGURE 9.—Abundance and distribution of threespine sticklebacks in Iliamna Lake, 1962, as indicated by average catches in tow nets. Catches in A (upper) made June 15 to July 31; in B (lower) August 1 to September 15.

of juvenile salmon. The smaller size of threespine sticklebacks and the juvenile sockeye salmon in the western ends of the lakes of the Wood system suggests that the same factors influence the growth of both species.

Kvichak system.—The abundance and distribution of threespine sticklebacks in Iliamna Lake in tow net catches in 1962 before and after August 1 are shown in figure 9. The abundance contours of figure 9 are intended only to indicate the general situation in the pelagic areas.

Threespine sticklebacks were most abundant in the pelagic areas before August 1 in the upper bays of Iliamna Lake and in an area west of but adjacent to the Kakhonak-Intricate Bay complex (fig. 9A). After August 1, threespine sticklebacks were abundant over a much larger area (fig. 9B). The increased abundance in a larger area must be caused by a seasonal movement of sticklebacks from the littoral zone. Comparisons of the seasonal distribution of threespine sticklebacks and of age 0 and age I sockeye salmon suggest that competition could be greater between sticklebacks and age 0 salmon than between sticklebacks and age I salmon.

No threespine sticklebacks were caught in the limited tow net sampling in Lake Clark in 1962 or 1963.

Naknek system.—The species and abundance of fish caught in the Naknek system in tow nets with juvenile sockeye salmon varied among the lakes (table 25). Threespine sticklebacks were caught in tow nets in all of the lakes and were more abundant than all of the other species,

TABLE 25.—*Weighted mean catch per standard tow (surface and deep tows combined) of species associated with juvenile sockeye salmon, August 16-31, in lakes of the Naknek and Karluk systems, 1961-62*

Species, system, and lake	Fish per tow	
	1961	1962
	Number	*Number*
Threespine sticklebacks		
Naknek system		
Coville Lake	8.0	85.5
Grosvenor Lake	.2	.0
Naknek Lake		
North Arm	.1	3.6
Iliuk Arm	3.4	6.1
South Bay	9.3	12.0
West End	647.8	54.8
Brooks Lake	[1].0	.1
Karluk system		
Karluk Lake	63.9	115.1
Ninespine sticklebacks		
Naknek system		
Coville Lake	8.8	34.4
Grosvenor Lake	.1	.0
Naknek Lake		
North Arm	.0	.2
Iliuk Arm	.2	.8
South Bay	.9	15.0
West End	65.0	29.3
Brooks Lake	.1	.2
Karluk system		
Karluk Lake	.0	.0
Pond smelt		
Naknek system		
Coville Lake	91.0	49.5
Grosvenor Lake	.2	.0
Naknek Lake		
North Arm	.0	.1
Iliuk Arm	.0	.4
South Bay	.1	.1
West End	.1	.6
Brooks Lake	.0	.0
Karluk system		
Karluk Lake	.0	.0
Pygmy whitefish		
Naknek system		
Coville Lake	.0	.2
Grosvenor Lake	.0	.0
Naknek Lake		
North Arm	.0	.1
Iliuk Arm	.0	.1
South Bay	.5	.0
West End	.0	.0
Brooks Lake	.3	.2
Karluk system		
Karluk Lake	.0	.0

[1] Less than 0.05.

except pond smelt in Coville Lake. Although ninespine sticklebacks were distributed the same as threespine sticklebacks, they were generally less abundant. Pond smelt were taken in tow nets in all basins of the Naknek system except Brooks Lake but were abundant only in Coville Lake. Pygmy whitefish, which are basically benthic, were rarely taken in the tow net catches but were highly abundant in trawl catches from Brooks Lake. Areas of the Naknek system that yielded the largest catches of juvenile sockeye salmon or the fastest growing juveniles or both also yielded the largest catches of associated species.

Chignik system.—In the Chignik system, threespine sticklebacks were about 30 times as abundant in tow net catches in Black Lake as in Chignik Lake (table 24). The sticklebacks may be unable to compete successfully with the large populations of young sockeye salmon that often occur in Chignik Lake. Ninespine sticklebacks were slightly more abundant than threespine sticklebacks in Chignik Lake but were less abundant in Black Lake (table 24). Pond smelt were not as abundant as sticklebacks but occurred frequently in tow net catches in both lakes. Other species were seldom taken.

Karluk system.—The threespine stickleback was the only species other than juvenile sockeye salmon captured in tow nets at Karluk Lake (table 25), and sticklebacks were much more abundant than juvenile salmon in all sampling with all gear.

PREDATION ON JUVENILE SOCKEYE SALMON

Predation on juvenile sockeye salmon in fresh water occurs during their emergence, migration from the spawning areas, and residence in and migration from the nursery lakes. Predation by birds and fish is often very obvious and dramatic in southwestern Alaska.

A few studies and many general observations have been made of the relative intensity of predation by various animals in several systems. Most of the predators to be mentioned are present in all the sockeye salmon systems in southwestern Alaska.

In the Mainland Systems the Arctic char is the most significant predator on sockeye salmon, but many others do occur.

In the Igushik, Snake, Wood, and Kvichak systems the Arctic char is the fish that eats the most sockeye salmon juveniles—as migrating fry, as residents in the lakes, and as migrating smolts. In the Nuyakuk system, lake trout are more abundant than Arctic char and consume more young sockeye salmon. Other fish predators observed to eat young sockeye salmon in these lake systems are juvenile coho salmon, northern pike, grayling, and rainbow trout. During the smolt migrations, Arctic Terns *(Sterna paradisaea)* and Bonaparte's Gulls *(Larus philadelphia)* prey on sockeye salmon in the rivers connecting lakes and in the trunk river.

Several species prey on juvenile sockeye salmon at different stages in the Naknek system. Dolly Varden are abundant and in several areas feed actively on sockeye salmon fry during their emergence and migration. Juvenile coho salmon, present throughout the system, have been observed feeding on sockeye salmon fry in Brooks Lake. Presmolt sockeye salmon migrate out of Coville Lake in late summer day and night; at that time predation by lake trout, Arctic Terns, and Bonaparte's Gulls is very obvious.

Dolly Varden and rainbow trout prey on migrating smolts in the Naknek River. Other possible fish predators in the Naknek system are Arctic char, northern pike, Arctic grayling (*Thymallus arcticus*), and sculpins (*Cottus* spp.).

Dolly Varden and juvenile coho salmon both prey on juvenile sockeye salmon in the Chignik system (Roos, 1960), but the predation by coho salmon seems to be the more significant (Roos, 1959).

The Karluk system has large numbers of Dolly Varden and Arctic char (DeLacy and Morton, 1943), which may be serious predators of juvenile sockeye salmon.

The effectiveness of predators in keeping competitors of sockeye salmon in check is unknown but may be important. In the Wood system, for example, threespine sticklebacks are an important item in the diet of Arctic char.

The destruction of a constant number of juvenile sockeye salmon by predators each year would help sustain and perhaps reinforce the cyclic nature of some runs to the Bristol Bay systems. A constant annual demand would have a greater effect in years of low abundance of juvenile sockeye salmon. Such an effect is suggested for the sockeye salmon of Shuswap Lake of the Fraser system (Ward and Larkin, 1964).

REPRODUCTIVE RELATIONS OF POPULATIONS IN FRESH AND SALT WATER

The relations between numbers of smolts produced and numbers of adults in the parent escapements (described by the reproductive curve) are highly variable, even within a system, because they are determined by the interaction of many physical and biological factors. In this section we consider the relations between numbers of adults in the parent escapement and their progeny in terms of numbers, size, and age of smolts migrating to sea, and numbers of adults returning from the sea (catch and escapement).

RELATION BETWEEN NUMBERS OF SMOLTS AND NUMBERS OF ADULTS IN PARENT ESCAPEMENT

The major purpose of studies of the numbers of smolts produced by various numbers of spawners is to define the relation and interpret it to make estimates of optimum escapement (in terms of numbers of smolts) either directly or with the aid of ancillary information.

Smolt migrations were sampled with fyke nets in the trunk rivers. The abundance is expressed in index points for the Wood and Kvichak Rivers and in numbers of fish for the Naknek, Ugashik, and Karluk Rivers. The methods of counting the escapement of adults were described earlier in this report.

The index method of estimating production of smolts requires the use of standard fishing gear, site, and effort. The numbers of smolts captured are then given value in relation to the catches of a base year which has an arbitrary value of 100 index points. This method is used in the Kvichak system (Kerns, 1961) and the Wood system (Burgner, 1962). It yields data comparable between years within a system but not between systems.

The estimates of numbers of smolts produced by a system were based on a regular system of sampling. Many fishing sites were set up across the width of the river, and fyke nets were fished for a fixed period of time once a day in each site in random order. The sequence of fishing sites and times of day was a modified Latin-square design (Cochran and Cox, 1957). Catches were classified according to site, time of day, and date —factors considered to have the greatest influence on variability of the individual catches. Estimates of the total numbers of smolts in the annual migrations were obtained by expanding the mean catch per standard fishing period according to the number of potential fishing sites in the width of the river and the number of fishing periods in the season. We used this method to estimate the numbers of smolts migrating in the Naknek and Ugashik systems.

The age composition of the smolts in each migration was estimated from length-frequency measurements or scale samples taken during the season and weighted by magnitude of fyke net

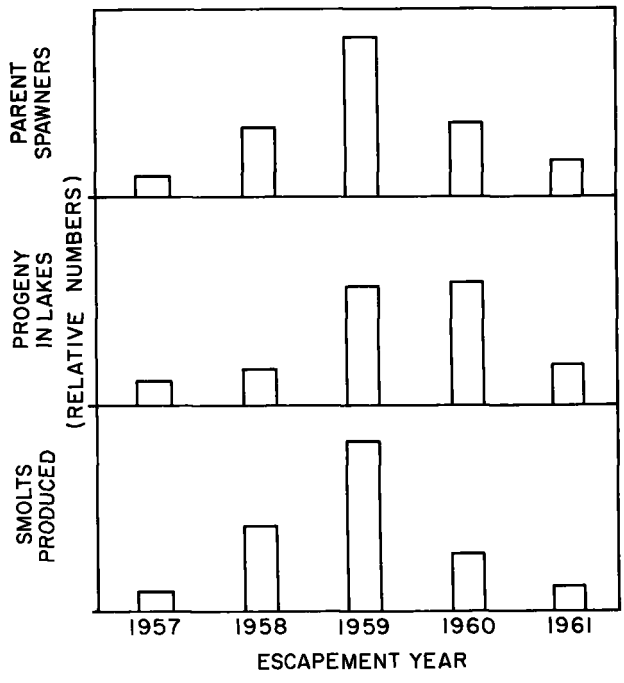

FIGURE 10.—Comparison of relative size of sockeye salmon escapement, abundance of progeny in lakes (based on tow net catches), and smolts in Wood River (based on fyke net catches), Wood system, parent escapement years of 1957-61.

catches for the day (or days) on which the samples were taken. Smolts were measured in the fresh state soon after capture.

Wood System

The Wood system showed two general levels of production of smolts (index points) per 1,000 adults in the escapement, the high level (1951 to 1954) was 0.50 to 1.87 index points (base of 1.00), and the low level (all other years from 1949 to 1961) was 0.10 to 0.27 (table 26). The cause of the considerable difference between the two levels is not known—it might be due to unusually good conditions for survival in the lakes or to a consistent error in indexing smolt abundance from 1951 to 1954.

The index estimates of smolt abundance in the Wood system for later years, 1957-61, can be checked against estimates of abundance at two other stages of fresh-water residence—the relative size of escapements and the abundance of progeny in the lakes (based on tow net samples in late August). The three estimates of abundance had the same general changes from 1957 through 1961 (fig. 10).

TABLE 26.—*Number of sockeye salmon in escapements and abundance, age composition, and mean length of smolts produced, by year of spawning, Wood system, 1949-61*

[Size of escapements for years 1949-52 based on stream surveys only]

Year of spawning	Adults in escapement	Smolts produced	Smolts produced per 1,000 spawners	Age composition of smolts		Mean length [1] of smolts	
				Age I	Age II	Age I	Age II
	Thousands	*Index points*	*Index points*	*Percent*	*Percent*	*Mm.*	*Mm.*
1949	101	10	0.10	----	----	[2] 91	----
1950	452	115	.25	87	13	[2] 87	[2] 103
1951	458	299	.65	94	6	[2] 86	107
1952	227	425	1.87	99	1	87	102
1953	516	290	.56	75	25	85	95
1954	571	286	.50	89	11	82	93
1955	1,383	215	.16	62	38	77	102
1956	773	154	.20	97	3	82	105
1957	289	59	.20	97	3	88	114
1958 [3]	960	255	.27	86	14	88	102
1959 [4]	2,209	508	.23	95	5	82	98
1960 [4]	1,016	167	.16	92	8	80	102
1961 [4]	461	82	.18	92	8	83	104

[1] Fork length of live anesthetized fish.

[2] Based on several samples taken during the main migration season but not weighted by catch.

[3] Age composition and mean length approximated in 1958 because of difficulty in determining age of smolts.

[4] Smolt data furnished by Alaska Department of Fish and Game for 1961-63.

The relation between numbers of smolts produced and numbers of adults in the parent escapement in the Wood system (fig. 11) is nearly linear in years when production per spawner was low (years other than 1951-54). Since the cause of the high rate of smolt production from 1951-54 is unknown, all points on figure 11 must be given equal weight, and, therefore, optimum escapement in terms of smolt production cannot be determined from these data.

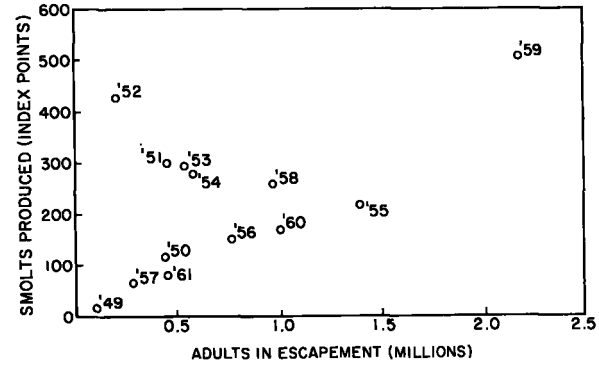

FIGURE 11.—Relation between smolt production (indexed by catches made in fyke nets in Wood River) and number of sockeye salmon in parent escapement, 1949-61, Wood system. The figure beside each point is the year of the parent escapement.

TABLE 27.—*Number of sockeye salmon in escapements and abundance, age composition, and mean length of smolts produced, by year of spawning, Kvichak system, 1952-60* [1]

[Size of escapements for 1952-54 based on stream surveys]

Year of spawning	Fish in escapement	Smolts produced	Smolts produced per 1 million spawners	Age composition of smolts		Mean length [2] of smolts	
				Age I	Age II	Age I	Age II
	Thousands	*Index points* [3]	*Index points* [3]	*Percent*	*Percent*	*Mm.*	*Mm.*
1952	5,970	----	----	----	----	----	109
1953	321	1.95	6.1	28	72	89	116
1954	241	1.15	4.8	78	22	92	120
1955	251	2.65	10.6	23	77	96	114
1956	9,443	181.32	19.2	54	46	84	99
1957	2,843	19.14	6.7	13	87	80	108
1958	535	2.15	4.0	86	14	91	118
1959	680	2.96	4.4	27	73	93	110
1960	14,630	[4] 157.38	10.8	22	78	82	98

[1] Abundance and length data for age II smolts from the 1958 escapement and age I smolts from the 1959 escapement supplied by Alaska Department of Fish and Game.

[2] Fork length of live anesthetized fish.

[3] Based on 24-hour catches.

[4] Marriott (1965).

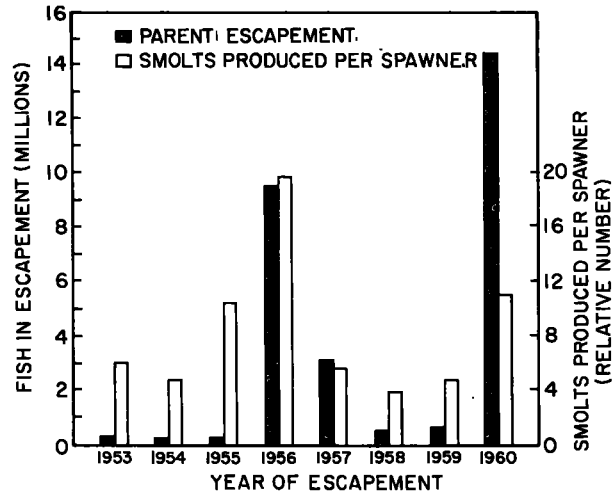

FIGURE 12.—Number of sockeye salmon in parent escapement and relative numbers of smolts produced per spawner, by year of escapement, in the Kvichak system, 1953-60.

Kvichak System

Data on smolts produced (index points) and the numbers of adults in the parent escapement in the Kvichak system are presented in table 27 for 1953-60.

The production of smolts per spawner in the Kvichak system does not follow the classic reproduction curves described by Schaefer (1954), Beverton and Holt (1957), and Ricker (1958). Reproduction curves are based on the assumption that the return per spawner is inversely related to the numbers of spawners, but in the Kvichak system the maximum production of smolts per spawner was produced by the relatively large escapement of 9.4 million in 1956 (table 27, fig. 12). The escapement of 14.6 million adults in 1960 apparently produced smolts at a lower rate per spawner[16] than that of 1956 but still greater than in most years of low escapement.

We assume that two reproduction curves are applicable in the Kvichak system—one for large escapements or "peak" years (over 5 million fish) and one for small escapements or "low" years (5 million fish or fewer). Two derived points are available for calculating the relation between smolt production and large escapements, namely the most recent peak years of the cycle, 1956 and 1960. Axiomatically, the reproduction curve includes the origin. A compound exponential curve of a type suggested by Ricker (1958) fitted to these three points necessarily produces a flat dome. These data indicate that the optimum escapement is less than the 1956 escapement, i.e., less than 9.4 million spawners (footnote 16).

We conclude that our estimate of the number of smolts produced by the 1960 escapement was too low, and, consequently, our estimate of the optimum escapement for peak years is also too low and will be raised as more data become available.

Naknek System

Estimates were made of the number of smolts produced in the Naknek system from each escapement in 1954-61 (table 28). Within these years the escapements ranged from 0.28 to 2.23 million.

The number of smolts produced increased as the escapement increased, up to an escapement of about 1 million (fig. 13). Beyond this point the number of smolts tended to level off (at about 14 million smolts) or decline.

[16] The extraordinarily large return of sockeye salmon to the Kvichak system in 1965 from the 1963 smolt run was unexpected. The smolt production from the 1960 escapement must have been greater than that indicated by the fyke net catches (shown as index points in table 27 and figure 12) because the return was disproportionately large, and ocean survival was not unusually high for sockeye salmon from other systems during this period. Intermittently occurring ice floes in the Kvichak River between May 15 and June 1, 1963, made it difficult to fish the fyke nets properly (footnote 4, table 27).

TABLE 28.—*Number of sockeye salmon in each escapement and number of smolts produced, by year of spawning, Naknek system, 1954-61*

Year of spawning	Fish in escapement	Smolts			
		Age I	Age II	Age III	Total
	Thousands	*Millions*	*Millions*	*Millions*	*Millions*
1954	804	5.06	1.28	----	6.34
1955	279	1.76	.36	----	2.12
1956	1,773	9.70	2.43	0.02	12.15
1957	635	10.03	3.12	----	13.15
1958	278	3.55	1.25	Trace	4.80
1959	2,232	4.37	8.46	.13	12.96
1960	828	8.00	8.72	Trace	16.72
1961	351	6.05	4.97	----	11.02

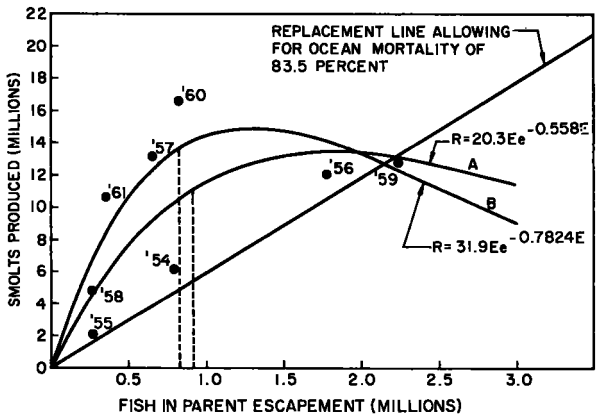

FIGURE 13.—Relations between numbers of smolts produced and number of sockeye salmon in parent escapement in the Naknek system for the escapements in 1954-61. The number beside each point indicates the escapement year. The dashed line indicates the optimum escapement for each curve. R=number of smolts in millions, and E=number in escapement in millions. Curve A fitted to all points; curve B fitted to 1956-61 points (see text).

Ricker-type reproduction curves have been fitted to the smolt-escapement data from the Naknek systems for the escapements of 1954-61 (fig. 13). Curve A was fitted to all points and curve B to the escapements of 1956-61. Smolt production from the 1954 and 1955 escapements may have been underestimated by a substantial amount (because of problems in establishing the procedures for sampling smolts). Curve B is assumed, therefore, to describe the smolt-escapement relation better.

For the Naknek system, estimates of total ocean mortality for sockeye salmon from 3 years of smolt migration ranged from 77.6 to 95.2 percent and averaged 83.5 percent. No attempt was made to correct these estimates for the take of salmon by the high seas fishery.

The replacement line in figure 13 is straight—it is based on the assumption that the average total mortality (83.5 percent) applies to all levels of smolt migrations; i.e., ocean mortality is largely independent of numbers of smolts. If ocean mortality tended to increase with increasing numbers of smolts in the seaward migrations, the replacement line would not be straight but would curve upward. Conversely, if ocean mortality tended to decrease with increasing numbers of smolts, the slope of the replacement line would decrease toward the right. Not enough information is available to determine the nature of ocean mortality, and the safest assumption seems to be that its effects are mostly independent of numbers of smolts entering the ocean.

As indicated in figure 13, maximum yield to the inshore fishery may be realized with escapements ranging from 600,000 to 1 million spawners. If the high-seas catches of Naknek River sockeye salmon were taken into account (i.e., if they were included among the survivors), the total ocean mortality would be lower, the slope of the replacement line correspondingly less, and the apparent optimum escapement range somewhat higher. Thus, we encounter a paradox. If reproduction curves of the kind shown were used to maximize the inshore catch, the total catch (inshore plus high seas) would be less than is biologically possible.

Additional observations are required to define more precisely the form of the smolt-escapement relation and ocean mortality rate.

Ugashik System

Estimates of the numbers of smolts produced in the Ugashik system are available each escapement year, 1956-60 (table 29). These estimates have been used to construct a figure showing the smolt-escapement relation for the system (fig. 14). Escapements of fewer than one-half million fish in 4 of the 5 years caused a crowding of points at the lower end of the scale; interpretation of the form of the smolt-escapement relation is, accordingly, difficult. Smolt production appears nevertheless to increase as the size of the escapement increases. The greatest number of smolts (31.6 million) was produced by the greatest number of adults—2.3 million spawners in 1960. Because we lack observations on escapements of intermediate size, the best that can be determined is that target escapements for the

TABLE 29.—*Number of sockeye salmon in each escapement and number of smolts produced, by year of spawning, Ugashik system, 1956-60*

Year of spawning	Fish in escapement	Smolts			
		Age I	Age II	Age III	Total
	Thousands	*Millions*	*Millions*	*Millions*	*Millions*
1956	425	11.43	0.37	0.06	11.86
1957	215	2.52	2.16	Trace	4.68
1958	280	3.28	3.03	----	6.31
1959	219	.78	3.22	Trace	4.00
1960	2,294	13.47	18.12	(1)	31.59

[1] Age III smolts will migrate seaward in the spring of 1964.

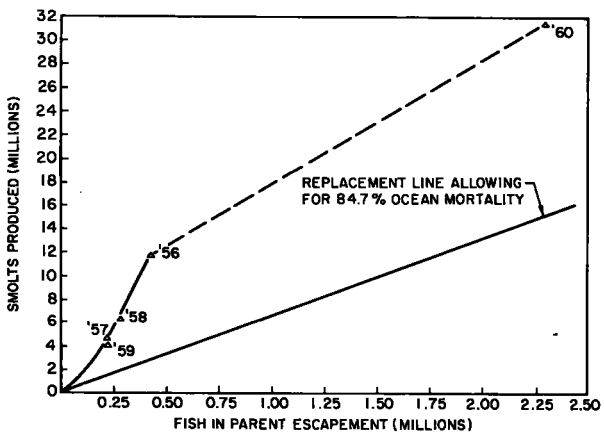

FIGURE 14.—Relation between numbers of smolts produced and number of sockeye salmon in parent escapement in the Ugashik system for the escapements of 1956-60. The number beside each point indicates the escapement year. A broken line is used to connect the values for 1956 and 1960 because the escapements were so different that the probable shape of the curve between them is not apparent.

Ugashik system should probably be greater than one-half million.

Karluk System

Estimates have been made of the numbers of sockeye salmon smolts produced by the Karluk River system for 3 years (1961-63). About 1.5 million smolts were produced each year, although parent escapements varied from 210,000 to 435,000. Within this range of escapements, the relation between numbers of smolts produced and numbers of parents is not definable.

RELATION BETWEEN LENGTH OF SMOLTS AND NUMBERS OF ADULTS IN PARENT ESCAPEMENT

Small smolts would be expected to have greater ocean mortality than large smolts. Indeed, Ricker's (1962) compilation and analysis of return-per-smolt data from six sockeye salmon systems outside Bristol Bay confirmed this general relation. Burgner (1962) determined that a group of age I smolts that migrated from Wood River in 1955 at an average length of about 72 mm. suffered about twice the ocean mortality of a group of age I smolts 90 mm. long that migrated in the same year. This influence of size on survival agrees well with the data shown in Ricker's figure 1 (1962). We, therefore, consider the relation of length of smolts to numbers of adults in the parent escapement and discuss the effects of size of smolts on their survival in the ocean.

Wood System

The relation between the mean length of age I smolts and numbers of adults in the parent escapements in the Wood system is presented in figure 15, where a regression line has been fitted. The equation for the regression of length of age I smolts on number of spawners in the parent escapement is

$$L_l = 87.86 - 4.4X$$

where L_l is the average fork length in millimeters of age I smolts, and X is the parent escapement in millions of spawners. The correlation is significant at the 98-percent level. Thus, the mean length of age I smolts (the dominant age group) is inversely related to the number of parent spawners.

On the basis of this equation, age I smolts from an escapement of 2 million spawners would be expected to have an average length of about 79 mm. and those from 500,000 spawners, about 86 mm.

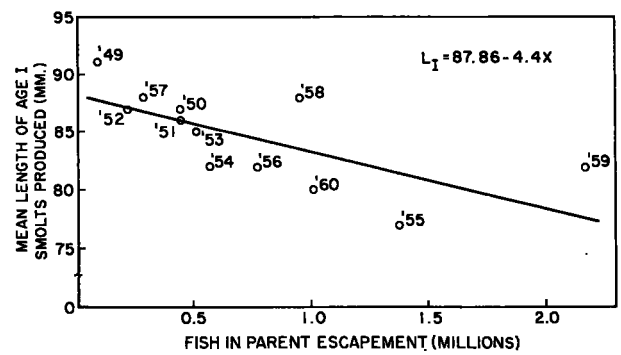

FIGURE 15.—Relation between growth of progeny (as indicated by mean length of age I smolts) and number of adults in the parent escapement, 1949-60, Wood system. The number beside each point indicates the escapement year.

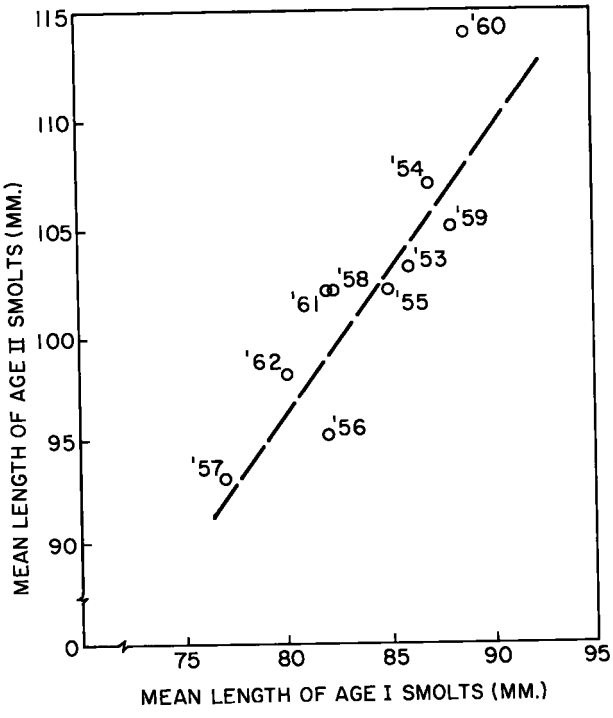

FIGURE 16.—Relation between mean lengths of age II and age I sockeye salmon smolts in the same year of seaward migration, 1953-61, Wood system. The number beside each point indicates the year of smolt migration.

The individual points in the relation between the length of smolts and numbers of adults in the escapement do not fit the regression closely, and, in addition, exact data on natural mortality in the ocean are lacking for the Wood system. Hence, the illustration from the Wood River smolt migration of 1955 given above can only suggest the effect of the size of smolts on ocean survival. It is probable, however, that ocean mortality related to size attained by age I sockeye salmon in fresh water is an important factor in the determination of the numbers of adults in the returns to the Wood system.

The average length of age II smolts was better correlated with the mean length of age I smolts of the following year class than with the number of fish in the parent escapement (fig. 16). This relation suggests the presence of competition for food between age classes of juvenile sockeye salmon.

A lack of significant competition for food among individuals of an age class after their first year in the lake is due to their comparatively small numbers—most sockeye salmon smolts of the Wood River are age I (table 26).

Kvichak System

The data on mean lengths of age I and age II smolts produced by each escapement to the Kvichak system in 1952-60 (table 27) were used to calculate a straight-line regression of smolt length on numbers of adults in the parent escapement for these years. The relation for age I smolts is

$$L_I = 90.64 - 0.7X$$

and for age II smolts

$$L_{II} = 115.51 - 1.4X$$

where L is the length of smolts in millimeters and X is the number of fish (millions) in the parent escapement (fig. 17). The correlation coefficient for age I smolts was $r = -0.73$ and for age II smolts, $r = -0.93$.

The slope of the regression line of smolt size on escapement for age II smolts of the Kvichak system is almost twice that of the age I; the growth retardation caused by competition for food among the progeny of each escapement seems to continue during their second year in fresh water. The contrast to the Wood system in this regard may be the result of the proportionately greater holdover of young to age II smolts in the Kvichak system.

The regression of length of age I smolts on numbers of adults in the parent escapement for the Wood system has a slope six times that derived for age I smolts in the Kvichak system.

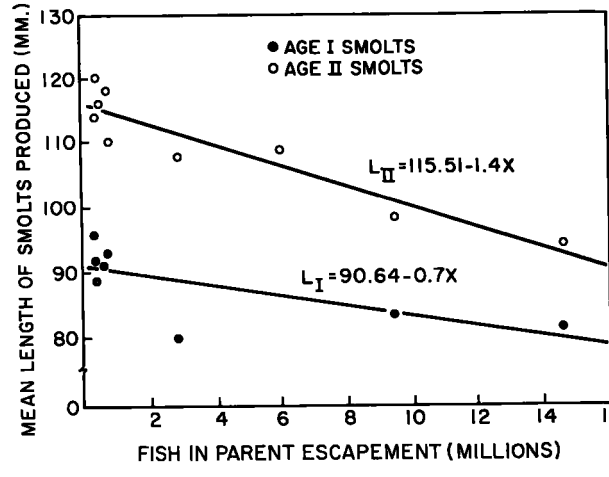

FIGURE 17.—Relation between mean lengths of age I and II sockeye salmon smolts by age class and numbers of adults in the parent escapements, Kvichak system.

This difference may be caused by the relative sizes of the rearing areas of the two systems, because the slopes of the regressions of smolt size on numbers of parent spawners per square kilometer of nursery area are similar for the two systems.

A regression of ocean survival on smolt size with a positive slope of about 0.25 can be calculated from data compiled by Ricker (1962). Thus, although it appears that in the Kvichak system an escapement of about 10 million spawners will produce the greatest number of smolts (age groups I and II combined),[17] the survival of these smolts after they leave the lake will be reduced because the average size of fish in each age group is less than the size of the fewer smolts produced by a smaller escapement. Clearly, the optimum escapement for peak years in the Kvichak system must be determined by maximizing the return as it is influenced by numbers and quality of smolts produced. The optimum escapement must be less, therefore, than that which produces the largest number of smolts.

Another factor also indicates a need for a lower escapement. The regression line in figure 17 has one aberrant point, namely, the length of age I smolts from the 1957 escapement (2,843,000) which followed the large escapement of 1956 (9,443,000). Although the escapement in 1957 was comparatively small, the mean length of age I smolts from the 1957 escapement was less than that of age I smolts from the large 1956 escapement. This discrepancy is interpreted to mean that as young-of-the-year, the age I smolts of the 1957 escapement competed for food with the abundant yearling fish from the 1956 escapement which migrated as age II smolts. Optimum escapement cannot be determined, therefore, by considering one year alone—possible effects of competition between progeny of successive escapements must be carefully considered.

Naknek and Ugashik Systems

Little indication exists for the Naknek and Ugashik systems that the average size of age I smolts is correlated with the number of adults in the parent escapement (figs. 18 and 19). The age II smolts show a similar lack of correlation (data not shown). Scales from smolts indicate that the variations in size of age I fish at the time of seaward migration are caused to a great extent by variations in growing conditions in the lakes just before the smolts leave.

Mortality of sockeye salmon in the ocean is

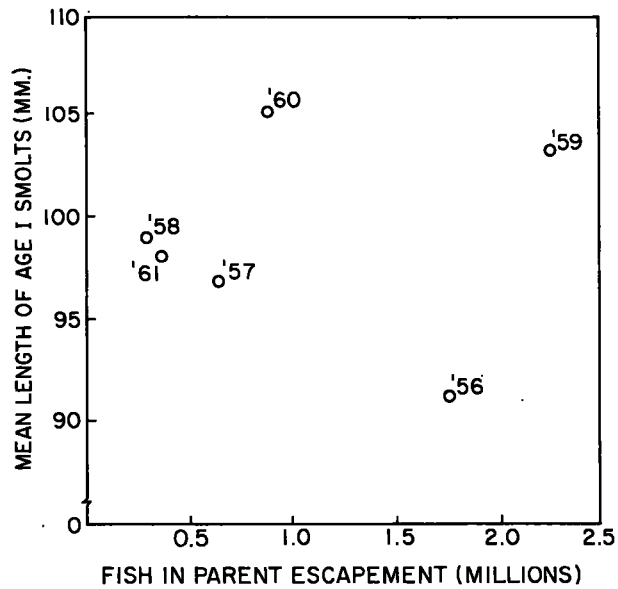

FIGURE 18.—Relation between mean lengths of age I sockeye salmon smolts and number of adults in parent escapements, Naknek system, 1956–61. The number beside each point indicates the parent escapement year.

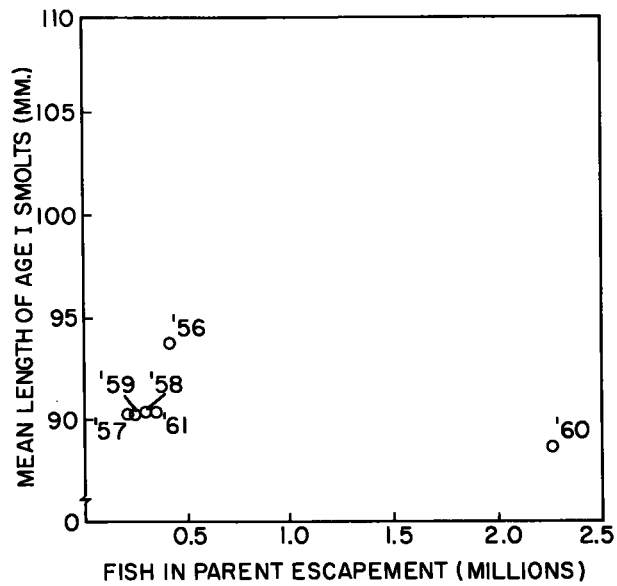

FIGURE 19.—Relation between mean lengths of age I sockeye salmon smolts and number of adults in parent escapements, Ugashik system, 1956-61. The number beside each point indicates the parent escapement year.

[17] This estimate is based on data collected through 1963 (see footnote 16).

influenced by oceanic conditions, the high seas fishery, and the amount of time the salmon spend in the ocean—factors that may mask the effects of the size of smolts on mortality. Estimates of ocean mortality of Bristol Bay sockeye salmon are available for only the Naknek and Ugashik systems (table 30). Age I smolts in the seaward migration from the Naknek system in 1958 were smaller (91 mm.) than smolts of the same age in 1959 (97 mm.) and 1960 (99 mm.). Yet the 1958 group suffered the lowest total ocean mortality (from smolt to return—table 30). Age I smolts of the same year class also had the lowest total ocean mortality for the Ugashik system. The age I smolts in the 1958 Ugashik migration were larger, however, than those of 1959 and 1960. Any effect that smolt size in 1958 might have had on ocean mortality may have been masked by effects of environmental conditions especially conducive to good survival. Valid comparisons can be made only if groups of smolts of different sizes encounter conditions that are similar. Obviously, this situation is rare.

The data in table 30 afford an opportunity for comparison of ocean mortality for age I and age II smolts. Age II smolts without exception suffered a lower total mortality. How much of this difference can be attributed to their larger size rather than time of entry into the estuary cannot be determined, for age II smolts generally enter the sea at least 1 or 2 weeks before age I smolts.

TABLE 30.—*Ocean mortality of sockeye salmon by fresh-water age, Naknek and Ugashik systems*

System, year of seaward migration, and fresh-water age	Smolts in seaward migration	Average length	Average time in ocean	Total mortality
	Millions	*Mm.*	*Years*	*Percent*
Naknek system				
1958				
Age I	9.698	91	2.74	82.8
Age II	.362	114	2.25	28.7
Total	10.060	----	2.68	80.8
1959				
Age I	10.035	97	2.88	96.8
Age II	2.431	106	2.99	89.0
Total	12.466	----	2.93	95.2
1960				
Age I	3.553	99	2.64	92.2
Age II	3.118	109	2.56	67.2
Total	[1] 6.691	----	2.57	80.5
1961				
Age I	4.367	103	2.52	85.6
Age II	1.246	113	2.25	50.1
Total	5.613	----	2.39	77.6
Ugashik system				
1958				
Age I	11.438	93	2.17	69.7
Age II	.222	112	2.04	49.7
Total	11.660	----	2.17	69.3
1959				
Age I	2.520	90	2.78	95.4
Age II	.367	120	2.34	75.5
Total	2.887	----	2.59	92.8
1960				
Age I	3.286	90	2.61	95.6
Age II	2.163	108	2.21	81.4
Total	[1] 5.504	----	2.32	90.0
1961				
Age I	.776	90	2.70	93.5
Age II	3.026	112	2.14	85.3
Total	3.802	----	2.20	86.6

[1] The 1960 totals include age III smolts; none were recorded in other years.

RELATION BETWEEN FRESH-WATER AGE OF SMOLTS AND NUMBER OF ADULTS IN PARENT ESCAPEMENT

The tendency for slow-growing sockeye salmon juveniles to remain an additional year in fresh water before they migrate seaward has been documented (Foerster, 1937; Barnaby, 1944; Krogius and Krokhin, 1956; Koo, 1962). Data presented by Foerster (1944) suggest that in some studies, however, the tendency is reversed, and slow-growing sockeye salmon go to sea at age I. Also, an increase of a year or more in length of residence in fresh water accompanied an increase in growth rate that resulted from reduction of populations (Krogius, 1961). Little is known regarding the factors that cause juvenile sockeye salmon to migrate to sea.

Wood System

We might anticipate in this system a higher percentage of age II smolts from the larger spawning populations than from the smaller because of the inverse relation between number of parents and growth of progeny during their initial year of lake residence. This tendency is suggested by the data (fig. 20), but the progeny of the large escapement year, 1959, are an outstanding exception to the theory that slowly

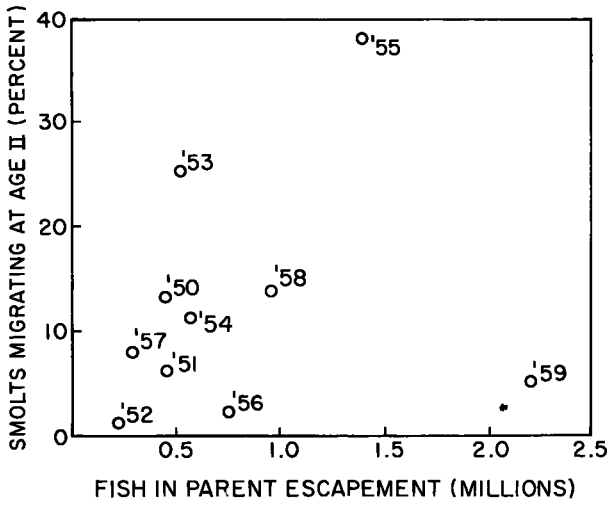

FIGURE 20.—Relation between proportion of total smolt production migrating at age II and number of sockeye salmon in parent escapement, Wood system, 1951-59. The number beside each point indicates the parent escapement year.

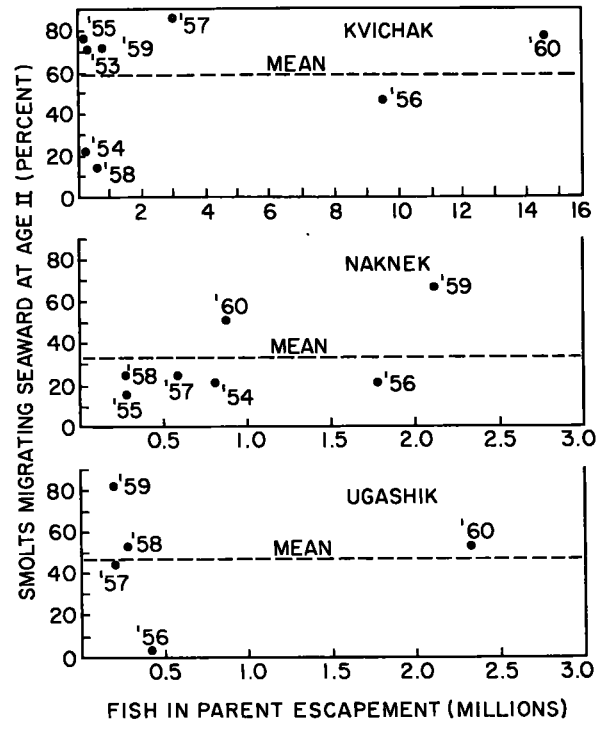

FIGURE 21.—Relation between proportion of progeny migrating as age II smolts and number of sockeye salmon in parent escapement, Kvichak system, 1953–60, Naknek system, 1954-60, and Ugashik system, 1958-60. Figure beside each point indicates year of parent escapement.

growing juveniles go to sea as age II smolts—these progeny grew slowly, but most went to sea at age I. The tow net indices of abundance of this year class as yearlings residing in the lake indicated a considerably higher percentage holdover than was indicated in the index sampling of smolts; some question exists, therefore, as to the accuracy of the index of abundance of age II smolts in the Wood River.

Kvichak System

The lowest recent escapements of sockeye salmon in the Kvichak system (1954 and 1958) produced mostly age I smolts, whereas the intermediate escapements (1953, 1955, 1957, 1959) produced mostly age II smolts. More of the progeny of the largest escapements (1952, 1956, 1960) tended to hold over to age II smolts as the escapement levels increased. The escapement of about 6 million fish in 1952 produced mostly age I smolts (or at least only fish of this age returned in large numbers). The only information we have on the smolt migration in the Kvichak River in 1954 (age I smolts from the 1952 escapement and age II from 1951) is that local residents in Levelock observed it to be "heavy." The 1956 escapement of 9.4 million produced 46 percent age II smolts, and the 1960 escapement of 14.6 million produced at least 78 percent age II smolts (fig. 21, table 27).

Naknek and Ugashik Systems

Data for the Naknek and Ugashik systems do not indicate that the percentage of sockeye salmon progeny migrating seaward as age II smolts is correlated with the number of fish in the parent escapement (fig. 21). The escapements in the Naknek system in 1954-58 ranged from 0.278 to 1.77 million, but the portion of age II smolts remained nearly constant between 16 and 25 percent.

The amount of growth added in the spring before the juveniles migrate as smolts is influenced by climate (Burgner, 1962). In years of favorable growing conditions early in the season, a higher percentage of yearlings may attain some size threshold for migration and leave as age I smolts. Thus, the influence of climate may tend to mask the relation between percentage holdover of progeny in the lakes and the number of parent spawners.

The major sockeye salmon systems on the east side of Bristol Bay tend to have concurrent fluc-

tuations in the percentages of smolts migrating at age II, although the escapement levels vary somewhat independently. The proportions of age II smolts were at or below average for the escapement years 1954, 1956, and 1958 in the Naknek and Kvichak systems and for 1956 and 1958 in the Ugashik system (no data are available for Ugashik in 1954 and 1955). The percentages were above average in the three systems for the escapement years 1959 and 1960 (fig. 21). These concurrent fluctuations suggest the influence of general climatic factors.

RELATION BETWEEN RETURN AND ESCAPEMENT FOR THE NUSHAGAK FISHING DISTRICT

The relation between the numbers of adults returning (catch plus escapement) and the numbers in the parent escapement is of general interest, though frequently the intermediate statistic—numbers of smolts produced—is now available. The longest series of return-escapement data available is for the Nushagak fishing district (Igushik, Snake, Wood, and Nuyakuk Rivers combined) for the escapements of 1946-57 and the resulting returns (table 31).

TABLE 31.—*Number of sockeye salmon in parent escapements and resulting returns, Nushagak district, 1946-57*

Year of spawning	Fish in parent escapement	Fish in resulting return
	Thousands	*Thousands*
1946	4,719	1,207
1947	2,507	953
1948	2,091	1,484
1949	138	376
1950	573	1,751
1951	540	3,749
1952	434	1,574
1953	829	1,431
1954	692	3,122
1955	1,934	5,056
1956	1,212	2,129
1957	499	520

The return-escapement data from the Nushagak district were used to calculate the recruit-spawner relation (reproductive curves) of Schaefer (1954), Beverton and Holt (1957), and Ricker (1958). When the weighted sums of squared deviations of the observed data from each of the predicted curves were calculated, the deviations were least from the curve derived from Ricker's formula:

$$R = aEe^{-bE}$$

where R = number of sockeye salmon in the return, E = number in the parent escapement, and a and b are constants. For the Nushagak district return-escapement data, a = 3.951 and b = 0.6269. The calculated curve and original data for the Nushagak system are presented in figure 22. The estimated maximum yield is at the point where a line parallel to the replacement line is tangent to the curve—for the Nushagak district this point corresponds to an escapement of about 900,000 fish.

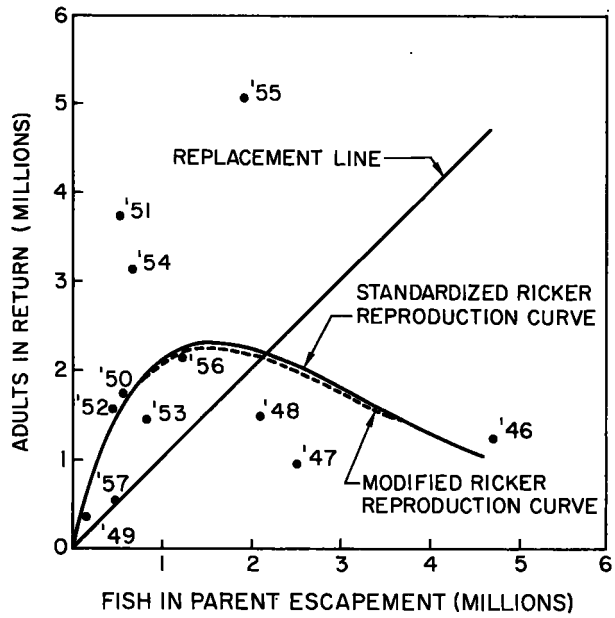

FIGURE 22.—Relation between number of sockeye salmon in return (catch plus escapement) and number in parent escapement, Nushagak fishing district, 1946-57. The number beside each point indicates the parent escapement year.

Addition of another parameter (n) to Ricker's formula as follows

$$R = aEe^{-bE^n}$$

gives greater flexibility in fitting the data. This modified version of Ricker's curve permits more exact fitting of a reproduction curve to observed data.

For the Nushagak data the relation was

$$R = 4.191Ee^{-0.699E^{0.936}}$$

The modification also gives an estimated optimum escapement of about 900,000. This curve is essentially the same as the standardized curve produced by the unmodified Ricker formula.

Ricker's formula can also be used to study the relation of return to potential egg deposition.

The numbers of 2- and 3-ocean female sockeye salmon in the escapements to the Nushagak district are known for 1946-57, and the potential egg deposition by each age group has been estimated (table 32). With potential egg deposition in billions as the independent variable (E), the formula which describes the relation between return and potential egg deposition is

$$R = 1.7456Ee^{-0.2699E}$$

The curves describing this relation permit the estimation of the optimum number of eggs on the spawning grounds. To convert number of eggs to number of spawners, an average fecundity of 4,000 eggs per female and a sex ratio of 1:1 are assumed. This calculation also yields an estimated optimum escapement of about 900,000 fish.

Since 1956 the high seas fishery has taken a substantial portion of the Bristol Bay sockeye salmon run each year. We approximated the high seas catch of fish from the Nushagak fishing district by prorating a portion of the estimated high seas catch of each ocean age group of Bristol Bay sockeye salmon according to the ratio of Nushagak district returns to the total Bristol Bay returns. The optimum escapement was then computed with these corrected returns; it was again found to be between 0.9 and 1.0 million fish.

TABLE 32.—*Number of 2-ocean and 3-ocean females in sockeye salmon escapements and estimated potential egg deposition, Nushagak district, 1946-57*

Year	Two-ocean females [1]		Three-ocean females [1]		Potential egg deposition
	Fish	Eggs	Fish	Eggs	
	Thousands	*Millions*	*Thousands*	*Millions*	*Millions*
1946	2,638	9,600	429	1,840	11,440
1947	850	3,093	704	3,020	6,113
1948	109	397	958	4,110	4,507
1949	32	116	50	215	331
1950	163	593	158	678	1,271
1951	110	400	187	802	1,202
1952	123	448	116	498	946
1953	126	459	338	1,450	1,909
1954	321	1,168	60	257	1,425
1955	836	3,042	228	978	4,020
1956	358	1,303	248	1,064	2,367
1957	115	418	164	704	1,122

[1] The average fecundities of 2- and 3-ocean females are 3,639 and 4,290 eggs on the assumption of mean lengths of 490 and 560 mm., respectively (Mathisen, 1962).

The four reproductive curves, all similar, indicate that an escapement of about 0.9 million sockeye salmon to the Nushagak district will yield the highest surplus of return over parent escapement. Escapements ranging from 0.6 to 1.2 million would theoretically produce about the same surplus because the curve is nearly flat in this area (fig. 22).

A drastic decline in the returns to the Nushagak district occurred in 1946-54. In fact, the returns did not equal the parent escapements in 1946-48. The returns from the relatively large escapements of these 3 years may have been abnormally low. If data from additional years indicate that it is more common for relatively large escapements to produce large returns, the calculated optimum escapement will be higher than 0.9 million.

The escapements of sockeye salmon to the Wood system have averaged about 70 percent of the total for the Nushagak district in recent years; this fact suggests an optimum escapement for the Wood system of about 630,000 sockeye (70 percent of 900,000). The only other period when escapements were counted for the Wood system was in 1908-19, when adults were counted at a weir on Wood River by the U.S. Bureau of Fisheries (no estimates of escapements were made for the other systems of the Nushagak district during these years). Although the average catch in the Nushagak district approached 5 million fish in 1908-19, escapements to the Wood system averaged only 750,000 sockeye salmon (Bower, 1920). The escapements to the Wood system from 1908 to 1919, therefore, averaged only slightly higher than our calculated optimum based on recent data. After 1919, the average catch in the Nushagak district dropped and remained at about 3 million until 1946—we have no satisfactory explanation for the higher production in 1908-19.

INTERPRETATION OF FINDINGS AND APPLICATION TO MANAGEMENT

In this final section we consider those characteristics of the sockeye salmon populations, the spawning grounds, and the nursery lakes that bear on carrying capacity and optimum escapement and, finally, give our best estimate of the optimum escapement for each system. The Mainland Systems tributary to Nushagak Bay—Igushik, Snake, Wood, and Nuyakuk—are discussed together. The Kvichak system of the Mainland group and the Peninsula Systems are discussed individually. The Alagnak and Egegik systems are not discussed.

Igushik, Snake, Wood, and Nuyakuk Systems

The Igushik, Snake, Wood, and Nuyakuk systems are all tributary to Nushagak Bay, the source of most of the fish taken in the Nushagak fishing district. These systems have a combined area of 867 km.^{2} distributed as follows: Igushik system, two lakes and 74 km.^{2}; Snake system, one lake and 89 km.^{2}; Wood system, five main lakes and 425 km.^{2}; and Nuyakuk system, three lakes and 279 km.^{2} The Nushagak fishery operates on a mixture of stocks from the four systems, and the catch for the district is assigned to each system on the basis of age composition and escapement levels. Therefore, the several systems of the district are evaluated in part as a unit.

In the early 1900's the annual commercial catch of sockeye salmon in the Nushagak district averaged about 5 million fish. It declined to an annual average of about 3 million in 1920-45 and suffered another marked decline in the next 10 years. Since 1955 the annual catch has been generally increasing but has not yet reached the pre-1945 levels.

The recent annual escapements to systems of Nushagak Bay have been distributed about as follows: Wood system, 70 percent; Igushik system, 23 percent; Nuyakuk system, 5 percent; and the Snake and several minor systems, 2 percent. The Nuyakuk and Snake systems historically may have produced at much higher levels.

Because of the selective action of the commercial fishery (larger fish are more susceptible to capture, and the time and route of migration and, therefore, exposure to the fishery may vary among the stocks), fishing mortality has not been uniform among the stocks in the Nushagak district. In 1948-60 the percentages of the large 3-ocean adults returning to the Wood, Igushik, and Nuyakuk systems were about 30, 60, and 70 percent, respectively (from data compiled by Burgner, footnote 7).

Studies of migration routes and timing of adult sockeye salmon in Nushagak Bay have shown that runs to the Wood and Igushik systems are partially segregated in the fishing areas (unpublished data of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska). There is evidence that in the past, runs to the Igushik system may have been subject to lower fishing intensity than those from the Wood system. Were the intensity of fishing the same on the two runs, a higher percentage of the fish going to the Igushik system would be captured because of the predominance of the 3-ocean fish.

Since sockeye salmon in the escapement to the Nuyakuk system are primarily 3-ocean fish, and this run of larger fish is presumably fished as intensively as the run of smaller fish in the Wood system, the run to the Nuyakuk system probably suffers a consistently heavier fishing mortality than the run to the Wood system. Over the years this heavier mortality could have caused a decline in the relative contribution of the Nuyakuk system to the Nushagak fishery.

Certain spawning areas within the Wood system consistently contain more 3-ocean than 2-ocean fish. Thus, fishing mortality may vary between groups within a system as well as between systems.

Estimates of the capacities of the potential spawning areas in each system in the Nushagak district indicate that the potential area greatly exceeds that used at the current levels of escapement.

The factors that limit production of juvenile sockeye salmon in systems tributary to Nushagak Bay appear to lie in the rearing areas of the lakes rather than in the spawning areas. Our studies of the limnology of the lakes of these Mainland Systems indicate that they are generally poorer in minerals than lakes of the Peninsula Systems and have a higher calcium-to-sodium ratio. The watersheds in Nushagak Bay have mostly sedimentary rocks, which contribute smaller amounts of minerals to the lake waters than do the igneous rocks common in the watersheds on the peninsula—an area of recent volcanism. Lakes of the Igushik and Wood systems nevertheless ranked fairly high in primary productivity. Lakes in the Nuyakuk system had the highest mineral content of lakes tested in the Nushagak district, but rates of carbon fixation were low. Lakes of the Nushagak Bay area have less of an oceanic climate than the other lakes studied—ice covers the lakes longer, and thermal stratification during the summer is more pronounced.

Although the four main lakes in the Wood system have similar limnological characteristics and similar numbers of sockeye salmon per square kilometer of lake in the escapements, they contrast sharply in the proportion of kinds of spawning grounds. The similarities in numbers per unit of lake area in the average escapements

indicate that the population level is controlled by the capacity of the nursery areas in each lake.

The production of juvenile sockeye salmon in the lakes of the Wood system increases linearly as the escapement increases, up to a density of 5,000 spawners per square kilometer of lake. Above this density the relation is no longer linear, and the production of juveniles per spawner declines when escapements exceed 6,000 per square kilometer. To have 5,000 spawners per square kilometer in all lakes of the system would require an escapement of 2,125,000 fish. At this density, however, the growth of juvenile salmon is considerably reduced. The mean length of age 0 fish in September is inversely related to the size of the parent escapement in each of the lakes of the Wood system. The mean length of age I smolts leaving the system also is inversely related to numbers in the parent escapement.

The combined effect of large populations of juveniles is to increase total mortality (freshwater and ocean) by causing many juveniles to remain an extra year in fresh water and to be of smaller average size for their age when they reach the ocean. This increase in mortality tends to make the population self limiting.

Threespine sticklebacks and Arctic char are the species of fish thought to have the most important effects on juvenile sockeye salmon in the Igushik, Snake, and Wood systems. In the Wood system, threespine sticklebacks and juvenile salmon use the same food supply, and, therefore, the growth of sticklebacks and age I salmon is reduced when large numbers of age 0 salmon are present. In all three systems Arctic char is the chief predator on small fish and probably eats substantial numbers of sticklebacks and juvenile salmon. The role of sticklebacks as a competitor for food and as a buffer between Arctic char and sockeye salmon and the effect of the Arctic char in keeping stickleback populations in check are not understood.

The recent average escapement of sockeye salmon per unit area of lake has been higher in the Igushik than in the Wood system. Juveniles from the larger escapements in the Igushik system have not grown as well (the smolts have not been as long) as those from the smaller escapements, so that here also the food supply apparently limits growth. Preliminary limnological studies show no marked difference in richness between the waters of the Igushik and Wood Lakes, and the greater concentration of spawners in the Igushik system appears to be caused by differences in the intensity of fishing on the two stocks.

Although primary productivity is low in the Nuyakuk system, escapement densities are probably too low to produce enough juvenile salmon to tax the food supply. Spawning areas appear to be far in excess of the present need. Relatively heavy fishing pressure probably has contributed to the present low level of the runs. Lake trout are more plentiful than Arctic char in the Nuyakuk system; the lake trout may be the primary predator on young salmon and sticklebacks.

The return-escapement relations of sockeye salmon in the Nushagak district in 1946-62 indicate that the optimum escapement is about 1 million fish, but that escapements between 600,000 and 1.2 million will produce near-optimum results.

If spawners were properly distributed, production in the Nushagak fishery could probably be increased by increasing the escapements. In an escapement of 1 million, for instance, if 70 percent of the fish went to the Wood system the lakes of the system would have an average density of 1,650 spawners per square kilometer. If distribution of spawners among the lakes were even, this density could be profitably exceeded. In years of uneven distribution of spawners, escapements should be held at a lower level to avoid overstocking of some rearing areas. Further, the mesh size of the gill nets used in the fishery could be regulated so as to obtain escapements of the two primary ocean-age groups in proportions that would more fully use all of the lakes of the Wood system and would give more protection to the populations of the Nuyakuk system. All the consequences of changes in the size of the mesh must be carefully studied, however, before this change is initiated.

Kvichak System

The Kvichak, the largest sockeye salmon system in Alaska, consists principally of two lakes, Iliamna and Clark, which total 2,889 km.^{2} The sizes of the runs in this system are cyclic. The range of the escapement in 1955-63 was 250,000 to 14.6 million. In 1931-61 the annual catch of the Naknek-Kvichak fishery averaged about 7.5 million fish. During the years of very large returns the Bristol Bay catch is dominated by salmon returning to the Kvichak system.

Within the Kvichak system there are many spawning groups of sockeye salmon. Adult fish of the different spawning groups are not segregated by time of passage into Iliamna Lake. The returnees generally have spent 1 or 2 years in fresh water and 2 or 3 years in the ocean; four principal age groups result. The age composition of the adults differs among the spawning grounds. In 1962, streams, with one major exception, contained significantly higher proportions of 2-ocean spawners than did beaches. It is not known if the relative proportion of 2- and 3-ocean fish is genetic. Fresh-water age, however, is probably determined more by the environment than by genetic factors.

Sockeye salmon generally spawn within the Kvichak system from early August to mid-October—a time span that probably reflects the adaptation of the various spawning populations to the different types of environments. Fry also emerge over an extended period. An indirect measure of the relative time of emergence is the size of juveniles during their first summer. The greatest range in time of emergence in the Kvichak system is in Lake Clark, where age 0 sockeye salmon in August range from 32 to more than 60 mm.

Although estimates of the amount of potential spawning area in the Kvichak system are incomplete, the available data indicate that the carrying capacity for this system is about 20.5 million spawners. Even the largest recorded escapement —14.6 million spawners in 1960—did not approach this figure (footnote 10). Between 1955 and 1963, the escapements in terms of number of adults per square kilometer of lake ranged from 84 in 1955 to 11,890 in 1960. The escapements to Lake Clark have not been well documented but are thought to be somewhat less than 10 percent of the total for the Kvichak system.

The greatest abundance of age 0 sockeye salmon in Iliamna Lake is in the vicinity of the heaviest spawning—in the east half of the lake. As the age and size of young fish increase they spread over the whole lake, and the largest fish are found in the western part.

Our knowledge of predators and potential food competitors in the Kvichak system is scanty. We do know that the distribution of threespine sticklebacks, the main potential competitor with juvenile sockeye salmon for food, is similar to that of age 0 salmon. Large populations of lake trout, Dolly Varden, Arctic char, and rainbow trout are also present. We suspect that competition for food and predation are important factors in the production of juvenile sockeye salmon in Iliamna Lake. The effect of predation would be much heavier in years of low abundance of juveniles and, thus, would tend to maintain the cyclic pattern of the Kvichak run.

Lakes of the Kvichak system are generally similar limnologically to lakes of the other Mainland Systems. The values for pH and concentrations of total dissolved solids and total alkalinity are intermediate among all systems. The rates of carbon fixation in Iliamna Lake were near the lower end of the range for mainland lakes, but in Lake Clark the rates were much reduced, probably because of the opacity of the water. The Kvichak system ranks in the same general position in numbers of spawners per lake area and in rate of carbon fixation per square meter, i.e., in the low range of the intermediate values.

Limnological studies in the Kvichak system span too short a time to permit comparisons between years. Future studies will determine whether dissolved minerals differ between off and peak years of the cycle; such differences could cause cyclic manifestations or, conversely, be caused by them.

Observations span too few years to indicate the relation between production of fry and parent escapement.

The relation between production of smolts and parent escapement varies, depending on whether we consider peak years or low years. The progeny of the 2 peak years studied, 1956 and 1960, had production indices of smolts of 181 and 150, respectively, although the escapement was almost 50 percent greater in 1960 than 1956. In both years, 2-ocean fish were dominant in the escapement—98 percent in 1956 and 99 percent in 1960. The maximum number of smolts is apparently produced at escapements below the 1960 level of 14.6 million (based on data collected through 1963). A reproduction curve based on the data of the 2 peak years 1956 and 1960 indicates that a range of escapements of 5 to 12 million will not drastically change the number of smolts produced.

A target escapement for peak years must be based on several factors in addition to the number of smolts produced. The data clearly show a

negative linear relation between the average length of smolts produced and the escapement level—that is, growth is retarded through intraspecific competition for food when the population of juvenile salmon is too great. It is known that ocean survival is generally positively correlated with size of smolts at migration, although data do not exist to calculate the differences in survival rates for the Kvichak system.

Whether the progeny of large escapements migrate at age I or age II in the Kvichak system is probably determined by the size they attain during their first year in fresh water. The percentage of young salmon that migrate as age II increases as the population of young salmon in the nursery areas increases, although the percentage holdover to age II can be modified by the environment. Any extension of the average length of the fresh-water life in the Kvichak system will also extend the length of the reproductive cycle.

In assessing the optimum escapement for the Kvichak system, we must consider production in an entire cycle and not for just one outstanding year such as 1956. Before 1942, the returns of the peak years contained progeny of at least two (and usually three) escapements.

If we accept the thesis that the carrying capacity of the nursery areas limits the production of sockeye salmon in the Kvichak system, a rational approach to regulation would be to utilize the nursery areas to the fullest every year. This approach would require the presence of age I juveniles (fish that will migrate as age II smolts) in addition to the young-of-the-year, because only age I and older fish use the larger downlake portion of the nursery area. Historically, fish that went to the ocean as age II smolts made up almost 60 percent of the catches in the Naknek-Kvichak district (fish from the Kvichak system constituted the greater share of the catch in peak years).

If we also assume that the historical sequence of large and small escapements of the Kvichak cycle is the one which will yield the greatest return over many years, the following conclusion is unavoidable. The Kvichak system must be managed so as to provide at least two, and preferably three, successive large escapements preceded and followed by smaller escapements. The relative abundance of fish in the successive years of large escapements may be manipulated in such a manner as to provide about the same potential egg deposition each year. Because of the present conditions of the stocks, it may take two or more cycles to reestablish this pattern. Only after the historical pattern has been restored will it be possible to define an optimum escapement for the peak years, which may well be higher than that desirable during the present transition period.

Collection of vital statistics must be improved substantially to define the optimum escapement of sockeye salmon for the Kvichak system. To clarify the known vagaries of cycles of abundance and reproductive capacity, not only must better methods be devised to assess the escapement, the standing crop of young salmon in the lakes, and the smolt migration but many other factors must be evaluated.

Naknek System

The Naknek system consists of a series of interconnected lakes totaling 790 km.^{2} Drainage to Bristol Bay is via the Naknek River into the Naknek-Kvichak fishing district. Adult sockeye salmon returning to the Naknek system mingle in the fishing area in Bristol Bay with others bound for the Kvichak and Alagnak systems. Catches were reported for the Naknek-Kvichak district as a whole until recent years, when portions of the catch were assigned to the respective river systems of the district on the basis of age composition and escapement. Since 1957 the run to the Naknek River has averaged 1.6 million fish—the commercial catch averaged 760,000 and the escapement 840,000.

The escapement of sockeye salmon to the Naknek system is composed mainly of 2- and 3-ocean fish, the relative strength of the groups varies widely from year to year. Fresh-water and ocean ages and numerical strength of the various spawning units within the system fluctuate somewhat independently of each other. The various spawning units seem to pass through the trunk river at about the same time.

Estimates of the total capacity of the potential spawning areas of the system are in excess of the average escapement for the past 10 years. Only limited data are available on the escapement of sockeye salmon per unit lake area for each lake, but great variations are known to exist among the lakes of the system. In 1961 Coville Lake received 6,600 spawners per square kilometer of lake. This density of spawners produced a catch

of 150 age 0 fish per tow in 1962. North Arm had a spawner density of 55 per square kilometer of lake in 1961 and a catch of age 0 fish of 0.5 per tow in 1962. Migration of presmolt juveniles, however, results in the accumulation of young in the rearing areas of Naknek Lake regardless of the distribution of spawners. The studies have run too few years to determine the relation between the abundance of age 0 fish and various levels of the parent population.

The abundance and growth of juvenile sockeye salmon and other species and the primary productivity of the lakes varied between years and among the lakes. Differences in primary productivity between years were accompanied by marked differences in growth of juvenile sockeye salmon, independent of their abundance. The abundance of juveniles was greater in 1962 than in 1961, but the rate of growth was greater in 1962. The primary productivity, on the other hand, was greater in 1962 than in 1961 because of differences in climate. The species and abundance of fish associated with the juvenile sockeye salmon vary among the lakes and among areas within the lakes. Threespine sticklebacks were universally present, and their abundance was matched only by pond smelt in Lake Coville and pygmy whitefish in Brooks Lake. The areas of the Naknek system that yielded the largest catches of juvenile sockeye salmon or the fastest growing juveniles also yielded the largest catches of associated species. The role of the associated species as competitors or predators, or as buffers between predators and juvenile sockeye salmon, is unknown. Several potentially important predator fish are present in the Naknek system, but their significance is not known.

Lakes of the Naknek system have limnological characteristics that fall between those that are characteristic of lakes of the Mainland Systems and also the other lakes of the Peninsula Systems. Lakes of the Naknek system are richer than the mainland lakes in total dissolved solids, total alkalinity, sodium, silica, iron, and manganese and generally richer in many of the other items measured. The large quantities of igneous materials in the watershed and wind-borne materials from the ocean apparently contribute substantially to this richness. These lakes are influenced by the oceanic climate; their ice covers break up relatively early in the spring. Thermal stratification is seldom pronounced, and strong wind action mixes surface waters with deeper waters from time to time during the summer. Rates of carbon fixation by photosynthesis are relatively high, and the standing crops of phytoplankton are similar to those of other peninsula lakes. Because of differences in drainage and basin types, lakes in the Naknek system nearly encompass the range of types of sockeye salmon nursery lakes along the Alaska Peninsula, although Chignik and Black Lakes rank higher than any Naknek lakes in photosynthetic rates and chlorophyll values.

Data on the relation of smolt production to escapement in the Naknek system in 1954-60 show an increase in numbers of smolts produced with increased escapement up to about 1 million fish. Accurate determination of optimum escapement from reproduction curves based on smolt-escapement relations is dependent on knowledge of mortality rates in the ocean. For the Naknek system, estimates of total ocean mortality for sockeye salmon from 3 years of smolt migration ranged from 77.6 percent to 95.2 percent and averaged 83.5 percent (no correction for a high seas fishery).

If total ocean mortalities range around 83.5 percent, maximum yields may be realized with escapements of 0.6 to 1.0 million. The presently known spawning areas have a capacity of about 1.3 million spawners. Escapement levels do not appear to have any effect on the size of age I smolts or the percentage of the progeny that migrates seaward as age II smolts. The Naknek lakes are richer in basic nutrients and generally have higher rates of phytoplankton production than the mainland lakes. Major differences in climate between years probably influence the growth of young sockeye salmon more strongly than do differences in their density. At present we do not know whether the upper limit on the production of smolts is imposed by the capacities of the spawning areas, the capacities of the nursery areas, or a combination of several factors that may or may not include these two.

Ugashik System

The Ugashik system on the Alaska Peninsula is the southernmost of the major river systems that drain into Bristol Bay. The system consists of two lakes, Upper and Lower Ugashik, which total 385 km.[2] Our studies in the Ugashik system included limnological observations, con-

tinuation of studies of smolts, catch, and escapement, and analysis of data previously collected.

Commercial fishing began in the Ugashik district in 1889 when several small salteries were established. Unlike the other districts of Bristol Bay, the Ugashik fishery developed rapidly and experienced a decline in the catch several years before peak production was achieved in the Egegik and Naknek-Kvichak districts.

The Ugashik also differs from the other Bristol Bay systems in that it has had several periods of peak production of sockeye salmon. The first was early—from 1899 to 1903—when the annual catch averaged 1,114,400 fish. A period of gradual decline followed, and in 1911 the catch reached its lowest point—about 113,000 fish. Between 1904 and 1916 the annual catch averaged 368,400; from 1917 to 1923, it rose to about 882,000. The 1924-42 period was characterized by generally low catches. A regulatory closure of the fishery occurred in 1935. Fishing effort in the district was greatly curtailed in 1940 and 1941 because of the war. Annual catches in 1942-48 averaged nearly 1 million fish. Since 1949, with a few exceptions (1953, 1954, and 1960) the annual catch has averaged less than 500,000.

Escapement counts were obtained for the Ugashik system in 1925-32 and 1949-63. Escapements during the earlier period ranged from 149,000 in 1929 to 1,380,000 in 1931 and averaged about 533,000 fish; escapements in the later period varied from 77,000 to 2,294,000 and averaged about 574,000.

The Ugashik system, in common with other Peninsula Systems, is currently supporting escapement densities that average about 1,300 sockeye salmon per square kilometer of lake. This density is about one-sixth of that observed in the Chignik and Karluk systems and about one-half of that of the Wood system. Most of the sockeye salmon of the Ugashik system spawn in tributary streams that drain the foothills of the Aleutian Range.

Limnological observations, though not as extensive as those made in other systems, indicate that the Ugashik lakes rank low in total dissolved solids, phytoplankton abundance, and primary productivity.

Estimates of the numbers, ages, and sizes of smolts have been obtained annually since 1958. We cannot see a relation between the size of smolts and parent escapement nor between the proportions of each year's progeny that migrate seaward at age II and escapement. It is possible that relationships are masked by year-to-year variations in environmental conditions.

Although the size of smolts in the Ugashik system apparently is not related to escapement, the number of smolts produced is. The greatest recorded escapement (2.3 million fish in 1960) produced the greatest recorded smolt migration (31.40 million). Low escapements of 215,000 in 1957 and 219,000 in 1959 resulted in 4.33 million and 4.08 million smolts, respectively. The escapement of 425,000 fish in 1956 produced about 12 million smolts. Because no escapements have been of intermediate size, it is not possible to define precisely the smolt-escapement relation over the entire range. All that can be determined now is that smolt production increases markedly with increasing escapement up to about one-half million. The results from the large 1960 escapement show only that increases in numbers of smolts can be realized from escapements greater than one-half million.

The best that can be inferred from the suggested form of the smolt-escapement relation is that the target escapement should be at least 500,000.

Chignik System

The history of the fishery on sockeye salmon runs of the Chignik system is similar to that of the Nushagak district in that the catch remained high until the 1920's, then dropped to a lower level from which it has never recovered.

The two lakes in the Chignik system—Black and Chignik—have dissimilar physical characteristics. Black Lake (mean depth, 3 m.) is the shallowest of the lakes we studied. Chignik Lake has less area than Black Lake but has six times the volume. The total area of the two lakes is 61 km.^{2}

Chignik Lake supports an unusually large escapement of sockeye salmon per unit lake area. The average escapement of 14,000 per square kilometer of lake for 1955-62 is the highest for the lakes studied. Black Lake had an average escapement of about 4,600 per square kilometer over the same period.

Chignik and Black Lakes had the highest primary productivity and chlorophyll *a* concentrations of the lakes studied. The richness of the lakes is undoubtedly the main reason that the

Chignik system has been able to produce large numbers of sockeye salmon per unit lake area.

Although spawning in the Chignik system is primarily in streams, about one-third of the spawning in Chignik Lake is on the beaches. Most of the stream spawning is in the longer streams. No estimates have been made of potential spawning area, but the level of sockeye salmon production by the Chignik system does not appear to be controlled by the capacity of the spawning grounds.

The runs to Black and Chignik Lakes are segregated in time of passage through the fishery. This segregation is significant because it permits control of the escapement to each lake by regulation of the fishery.

The adults returning to the Chignik system are predominantly 3-ocean fish.

The average time juvenile sockeye salmon remain in fresh water is different in the two lakes; the smolts from Black Lake are mostly age I, and those from Chignik Lake are mostly age II.

Age 0 sockeye salmon are reared in three major areas in the Chignik system—Black Lake, Chignik Lake, and Chignik Lagoon. Most of the juvenile sockeye salmon that originate in Black Lake remain there to the smolt stage, although some age 0 fish migrate into Chignik Lake. The brackish water of Chignik Lagoon is the rearing area for a significant part of the Chignik Lake progeny.

The growth of juvenile sockeye salmon is inversely related to the density of the parent population within each of the two lakes. Accurate indexing of the abundance of migrating smolts has not been achieved in the Chignik system, but studies of the size and age composition of the smolts and of abundance and growth of juveniles in the lakes are in agreement. Both studies indicate an increase in abundance, a reduction in growth rate, and an increase in average length of fresh-water residence for progeny of larger escapements. Also, the density of spawners is generally lower, and the juveniles grow faster in Black Lake than in Chignik Lake.

The juvenile sockeye salmon produced by the Chignik system are larger than those of the Wood system at comparable parent population densities—an indication that growing conditions are more favorable in the Chignik system.

Several species of fish other than sockeye salmon are also present in the system. Threespine and ninespine sticklebacks and pond smelt are present and are potential competitors of sockeye salmon for food; they also may act as buffer species between sockeye salmon and predators. The potential competitors are much more abundant in Black than in Chignik Lake; possibly they are held in check in Chignik Lake by the great abundance of young sockeye salmon. Young coho salmon and Dolly Varden, also present, are the system's principal predators on juvenile sockeye salmon. Arctic char and lake trout are not present.

The abundance of associated species and the growth of juvenile sockeye salmon indicate that recent escapements in the Chignik system as a whole have been adequate, but apportionment of the escapement to the two lakes must be considered. Low escapements to Black Lake and the resultant underutilization of its nursery areas by juvenile sockeye salmon may be one reason for the large populations of potential competitors in this lake. In contrast, the relatively high escapements to Chignik Lake have resulted in a shortage of food that has undoubtedly led to the reduced growth and survival of juvenile sockeye salmon and perhaps kept the populations of potential competitors low. The optimum escapement to Black Lake, therefore, is greater than the present level of escapement; to Chignik Lake it is considerably less than the larger escapements of recent years.

Suggested target escapements for each lake are based on the relative success of recent escapements and the effective rearing areas of the lakes. Although the total area of Black Lake is 39 km.^{2}, the effective rearing area is only about 30 km.^{2} because of extensive shoals not utilized by juvenile salmon. We recommend that escapements to Black Lake should be increased from the recent average of 4,600 per square kilometer of effective rearing area to 6,000 to 8,000, or a total of 180,000 to 240,000 fish.[18] The effective rearing area of Chignik Lake as determined from tow net catches includes the entire surface area of 22 km.^{2} The suggested escapement to Chignik Lake is 8,000 to 10,000 per square kilometer or a total of 180,000 to 220,000 fish. This escapement is a reduction from the average in

[18] Recent studies of distribution and growth of species which compete with juvenile sockeye salmon for food and space in the Chignik system suggest that the populations of competitors would be reduced by larger populations of juvenile salmon. Therefore, the attainment of the recommended escapements might make it possible to increase escapements considerably above 240,000.

recent years of 14,000 adults per square kilometer.

Karluk System

The Karluk River sockeye salmon run has been historically among the more valuable in Alaska. Commercial fishing began at Karluk in 1882. Several million fish were harvested annually in the early years of the fishery (1885-95), but a long-term decline began after the turn of the century. This declining trend continued in spite of attempts to maintain escapement levels; in recent years, the total run seldom has exceeded 1 million fish.

The timing of the run of adult sockeye salmon to the Karluk system is similar to that of the Chignik system in that it extends 4 to 5 months. The Karluk run has late spring and fall peaks. Beach spawning is insignificant in most years, and most of the spawners are dispersed over the lateral and terminal tributaries and the outlet, Karluk River. Occasionally, however, as much as 25 percent of the escapement may use beach areas. Certain terminal streams and beach areas are used by both spring and fall spawners. The lateral tributaries, however, are used almost exclusively by spring spawners.

The individual spawning areas in the Karluk system are occupied continuously for about 5 weeks to 5 months by a succession of spawners, with the result that many more spawners are accommodated than could be if they all spawned in 2 or 3 weeks. This occupation by successive waves of spawners introduces questions as to the effect of superimposition of redd sites on the success of spawning. We do not know the answers.

The Karluk Lake watershed is composed of sedimentary rock and is so situated as to be strongly influenced by the oceanic climate. The lake waters originate from snowmelt and surface runoff. Two small lakes, Thumb and O'Malley, drain into separate arms of Karluk Lake.

The concentrations of most of the chemical constituents in Karluk Lake are similar to those of lakes of the Alaska Peninsula, particularly the high concentration of sodium and the low levels of nitrate nitrogen and total alkalinity. Of all the lakes studied, however, Karluk Lake is second only to those of the Chignik system in productivity as measured by rate of carbon fixation and content of chlorophyll *a*. The very high productivity is paralleled by the rank of the Karluk system as first in density of spawners per unit lake area.

The growth of juvenile sockeye salmon was correlated positively with changes in lake productivity and negatively with the abundance of juveniles in 1961 and 1962. Because of varying numerical strength of young from a protracted period of fry emergence and migration, growth data are difficult to interpret.

The only abundant potential competitor with juvenile sockeye salmon for food in Karluk Lake is the threespine stickleback. Arctic char and Dolly Varden are the most abundant predators.

The estimate of numbers of smolts produced in Karluk Lake each year in 1961-63 was about 1.5 million. Numbers of smolts and numbers of adults in the parent escapements were not related; the parent escapements ranged from 210,000 to 435,000 fish.

Data on fluctuations in abundance of sockeye salmon in Karluk Lake have been analyzed in some detail by Barnaby (1944) and Rounsefell (1958). Portions of these data that deal specifically with the return-escapement relation have been reported in a bulletin of the International North Pacific Fisheries Commission (1962), where it is concluded that in the past, escapements of about 750,000 fish have produced the largest surplus of return over escapement. The expanded research in 1961 and 1962 did not yield new information that would alter this conclusion. Recent work serves, however, to emphasize that restoration of the Karluk runs to former high levels will require considerably more than mere manipulation of numbers of spawners in the escapement. Evidence suggests that the average reproductive capacity of the sockeye salmon in the Karluk system was reduced while the run was in decline. Current research at Karluk is directed toward determination of the cause of this reduction.

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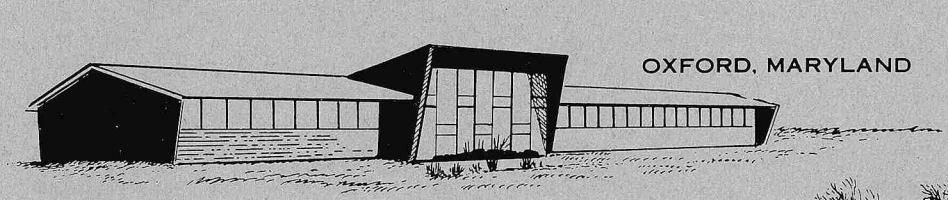

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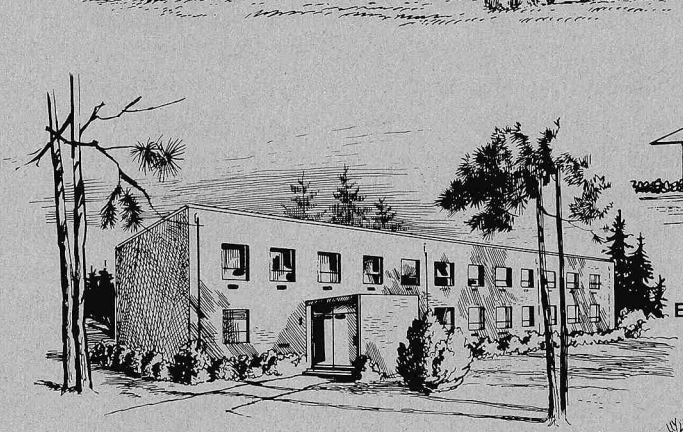

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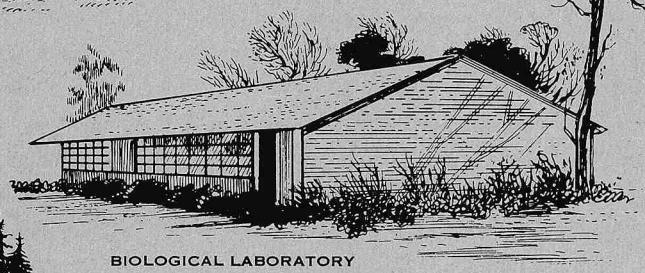

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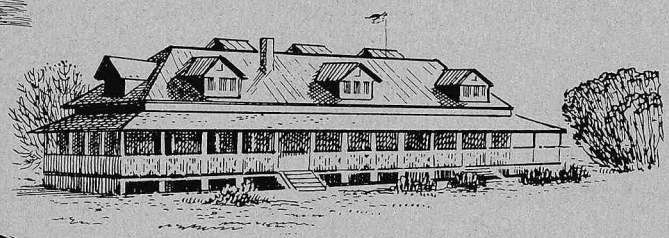

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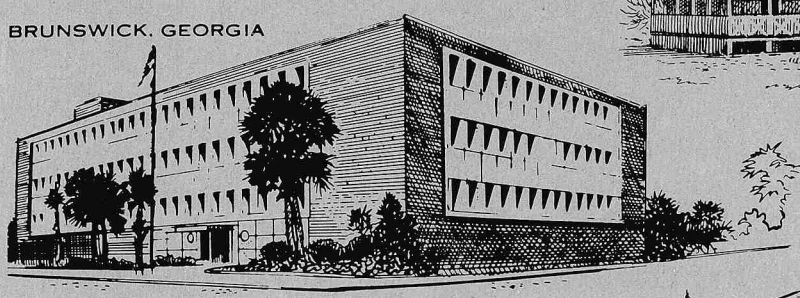

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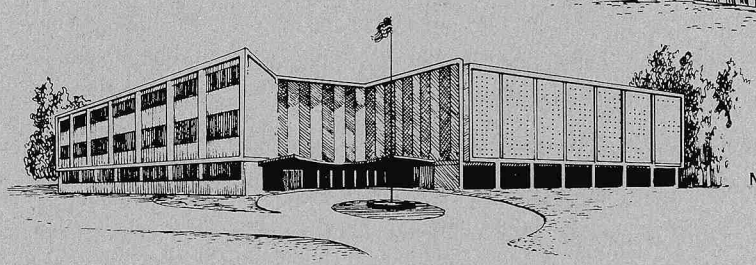

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María M. Diéguez was the illustrator.

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WESTERN ATLANTIC SHRIMPS OF THE GENUS *PENAEUS*

BY ISABEL PÉREZ FARFANTE, SYSTEMATIC ZOOLOGIST [1]

BUREAU OF COMMERCIAL FISHERIES SYSTEMATICS LABORATORY
WASHINGTON, D.C. 20560

ABSTRACT

Four subgenera of the genus *Penaeus* are described (*Litopenaeus*, *Penaeus* s.s., *Fenneropenaeus*, and *Melicertus*). Eight species and subspecies (*P. setiferus*, *P. schmitti*, *P. duorarum duorarum*, *P. duorarum notialis*, *P. aztecus aztecus*, *P. aztecus subtilis*, *P. paulensis*, and *P. brasiliensis*) are recognized as occurring in the western Atlantic. Synonymies are given. Lectotypes have been designated for two species, and the disposition of all types is shown. Diagnoses, detailed descriptions, and illustrations are presented for each species and subspecies. Geographic and bathymetric distributions are given. Affinities are discussed, and conclusions concerning ranges of variation and their spatial distribution are based on morphometric studies and other characters. The development of the external genitalia through the juvenile stage and the size range at which each taxon reaches the subadult stage are presented. Many details of ecology and life history are critically summarized and reviewed. A brief appraisal of the commercial importance of each form is also given.

The economic importance of the shrimp industry in eastern America becomes abundantly clear when one realizes that in 1965 the United States produced over 100 million kg. of *Penaeus* shrimp, and Latin America together with the Guianas harvested no less than 57 million kg. The fact that these animals are of such value has undoubtedly been largely responsible for the extensive research that has been devoted to the many aspects of the biology of the members of the genus *Penaeus*. Even so, there has been a long-felt need for a comprehensive treatment of the systematics of the group. This need has been emphasized by the fact that, although much valuable information exists for the group as a whole, misidentifications of individuals and of populations have led to confusing and sometimes conflicting conclusions.

The extensive collections of *Penaeus* available for this study have enabled me to evaluate the interrelationships of the western Atlantic members of the genus and, in turn, their affinities with those occurring elsewhere. To express the supraspecific relationships that have been recognized, I propose four subgenera and provide a key to facilitate their recognition. This key, as well as that which follows, is arranged solely for convenience and no phylogenetic inferences should be drawn from it.

Because species descriptions are widely scattered in literature that is not readily available and because most of these descriptions do not take into account many of the characters that have been found to be of considerable taxonomic importance, each taxon occurring in eastern American waters has been redescribed and figured.

As nearly as possible, a complete synonymy and list of references (including misidentifications) are indicated for each species and subspecies, and the page citations are included. All references listed were consulted in the original. Every attempt has been made to correlate earlier findings with the taxa recognized here, but, as might be expected, I was not always successful. In listing the types and their dispositions, some modifications of the original designations have been made. A list of the material examined precedes a brief diagnosis and a detailed description of morphological characters.

In addition, for each species and subspecies, the range of variation of these characters is included

[1] Also Associate in Invertebrate Zoology, Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138.

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and, insofar as possible, they are correlated with the geographical distribution of each animal. In the study of variation, I considered 40 characters other than those of the external genitalia. Those characters found to be of value are treated in the text and in figures and graphs. Data on color, size, and sex differences in size are presented. A survey of work on the biology and systematics of each taxon is also included. Until 1936–39 only five species were known to occur in the region. In 1967, I described one new species and two new subspecies from the western Atlantic.

Particular attention has been accorded the development of the systematic characters of the juveniles of each taxon. A description is given of the progressive changes in the development of the external genitalia which will aid in the identification of juveniles. The size range at which each taxon reaches the subadult stage, or at which the external genitalia attain adult form, has been determined.

Geographic and bathymetric ranges are derived from published data as well as material I examined. The commercial importance of each kind of shrimp is summarized. Comments on the systematics, interrelationships of the various taxa, items of special interest, and discussion of specific problems conclude the presentation.

The morphological nomenclature I adopted is, for the most part, that of Kubo (1949). A few slight modifications were made for the sake of brevity and clarity. For example, the lobules of the petasma are given single names—dorsomedian ventromedian, dorsolateral, and ventrolateral—to avoid such unnecessarily long wording, as, for instance, "ventral lobule of lateral lobe"; the "thickened ventral margin of the petasma" is called the ventral costa; and the two parts of the median protuberance of the thelycum are called the anterior and posterior processes. Whereas most previous investigators recognize "proximal" and "distal" pieces of the appendix masculina, it seems to me that the so-called proximal piece is only a modification of the endopod of the second pleopod; therefore, the "distal piece" appears to be equivalent to what in other decapods is called the appendix masculina. For this reason "appendix masculina" as used herein is the "distal piece" of other authors. A definitive terminology for the external genitalia, however, must await further study of their development and a demonstration of their homologies.

The measurement of total length is the distance from the tip of the rostrum to the posterior end of the telson, and that of the carapace is the distance from the dorsal portion of the postorbital margin to the midposterodorsal margin of the carapace. The latter dimension is accurate to 0.5 mm. In the text total length, carapace length, and rostrum length are often abbreviated t.l., c.l., and r.l., respectively. The citations to figures in the references listed for each taxon have been restricted to those illustrating morphological characters; other figures appear in the pages cited.

GENUS *PENAEUS* FABRICIUS

Penaeus Fabricius, 1798: 408 (type species, by subsequent designation of Latreille, 1810, *Penaeus monodon* Fabricius; neotype for *Penaeus monodon*, designated by Holthuis, 1949, ♂, Leiden Museum); Latreille, 1802: 246–250; Latreille, 1806: 53, 54; Latreille, 1810: 102, 422; Heller, 1863: 292, 293; Smith, 1882: 92–95; Smith, 1885 (not 1886 as is commonly stated): 170, 171; Bate, 1888: xii, 229–230 [part]; de Man, 1911: 95–97; Balss, 1914: 13; Burkenroad, 1934: 73–77; Anderson and Lindner, 1945: 302; Kubo, 1949: 268–270; Dall, 1957: 140–142; Gunter, 1957: 98.

Peneus Weber, 1795: 94 (nomen nudum, Opinion 104, International Commission on Zoological Nomenclature); Philippi, 1840: 190; Smith, 1869a: 27; Smith, 1869b: 390; Alcock, 1901: 12–14; Alcock, 1905: 510–515.

Melicertus Rafinesque, 1814: 22.

Penecus H. Milne Edwards, 1837: 414.

Penoeus Lucas, 1840: 195, 196.

Paneus Collins and Smith, 1892: 102.

Panaeus Thallwitz, 1892: 3.

DIAGNOSIS

Rostrum usually with ventral teeth. Carapace without longitudinal or transverse sutures; cervical and orbito-antennal sulci and antennal carinae always present. Hepatic and antennal spines pronounced, pterigostomial angle rounded. Longitudinal ridge of side of sixth abdominal somite interrupted. Telson with deep median sulcus, without fixed subapical spines, with or without lateral movable spines. First antennular segment without spine on ventral distomedian border. Antennular flagella usually shorter than carapace. Palp of first maxilla with two or three segments, usually three.

Basial spines on first and second pereopods, exopods on first four pereopods and usually on fifth. Petasma symmetrical, podlike, with or without distomedian projections, and with lateral lobes usually armed with long ventral costae. Appendix masculina subtriangular to ovoid, bearing spines. Thelycum often with median protuberance at posterior margin of sternite XIII, open or usually with two lateral plates covering or almost covering sternite XIV. Zygocardiac ossicle consisting of principal tooth followed by longitudinal row of smaller teeth often ending in cluster of minute teeth. Pleurobranchiae on somites IX to XIV; rudimentary arthrobranch on VII, and posterior arthrobranch on XIII somites; mastigobranchiae on VII to XII somites. Body glabrous (after Dall, 1957, modified). Figures 1 to 3 illustrate characters used in *Penaeus* taxonomy.

Two divisions of the genus *Penaeus* were recognized by Burkenroad (1934): in Division 1 he placed the species with a short adrostral carina (not approaching the posterior margin of the carapace) and lacking a gastrofrontal carina, and in Division 2 the species with a long adrostral carina (almost reaching the posterior margin of the carapace) and possessing a gastrofrontal carina. Kubo (1949) recognized Burkenroad's Division 2, although he used the adrostral sulcus instead of the

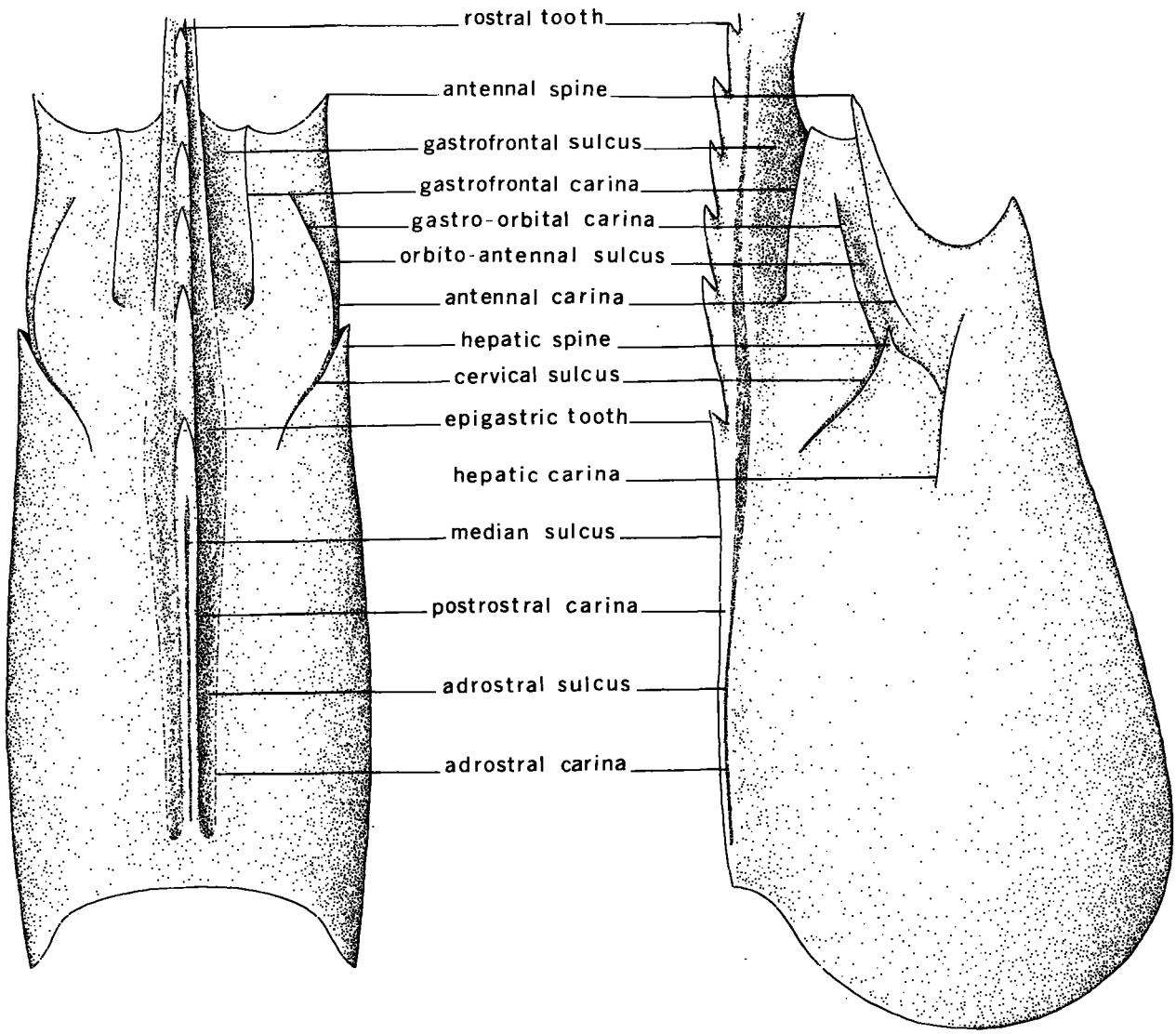

FIGURE 1.—Dorsal and lateral views of carapace showing features used in *Penaeus* taxonomy.

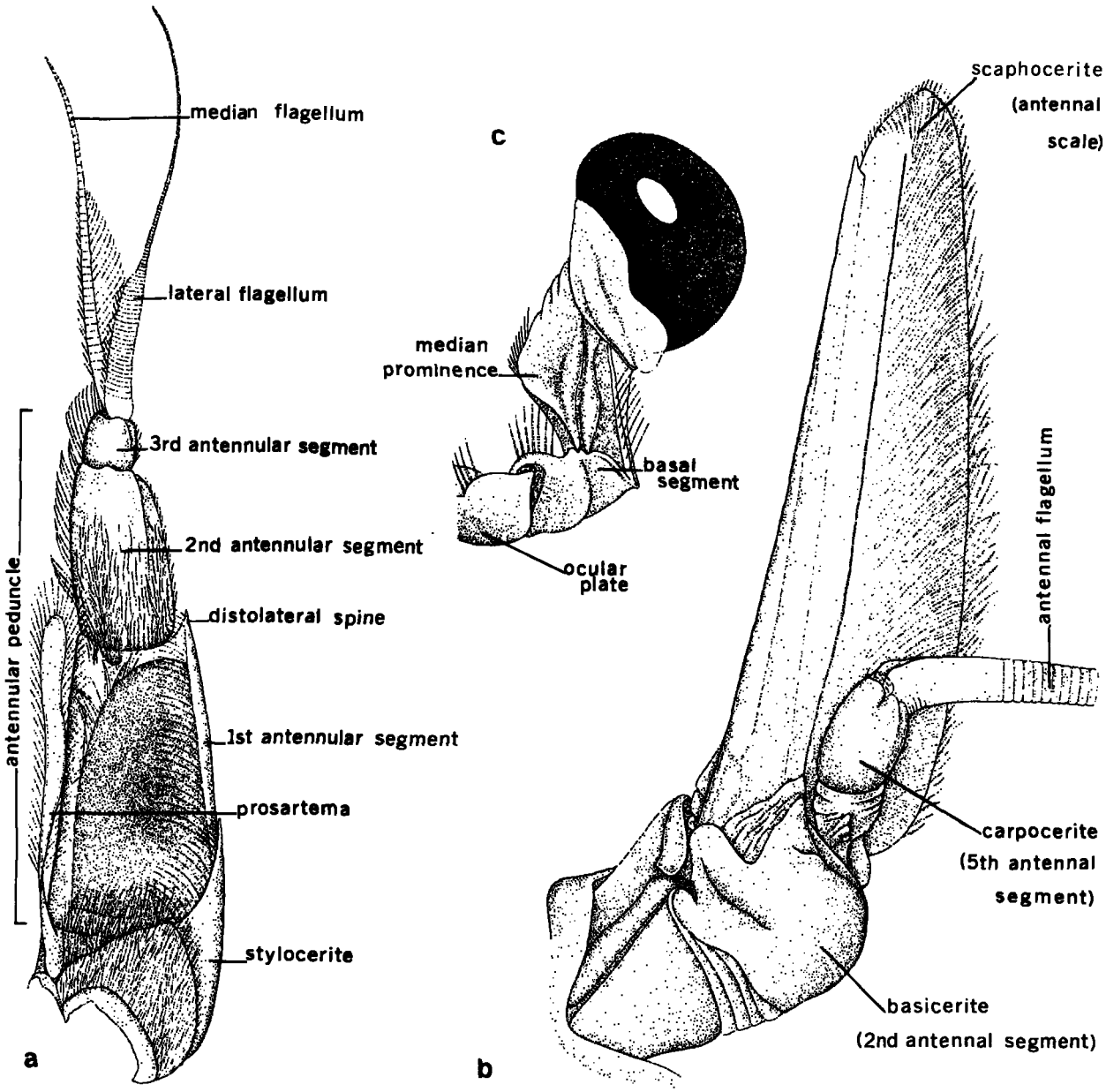

FIGURE 2.—Cephalic appendages and eye of a member of the genus *Penaeus*. a. Dorsal view of right antennule. b. Ventrolateral view of right antenna. c. Dorsal view of right eye.

adjacent adrostral carina. He also called attention to another character, a well-defined hepatic carina. Kubo grouped the nongrooved *Penaeus*, Division 1, into two subdivisions, characterized by the presence or absence of a hepatic carina, the depth of the adrostral sulcus, and the development of the adrostral carina.

I consider that within the genus *Penaeus* are four different groups which are here designated as subgenera.

KEY TO THE SUBGENERA OF THE GENUS *PENAEUS*

1. Adrostral sulcus and carina short, not reaching posteriorly beyond midlength of carapace; gastrofrontal carina absent_____ 2

Adrostral sulcus and carina long, reaching posteriorly much beyond midlength, usually almost to posterior margin of carapace; gastrofrontal carina present_____ *Melicertus*

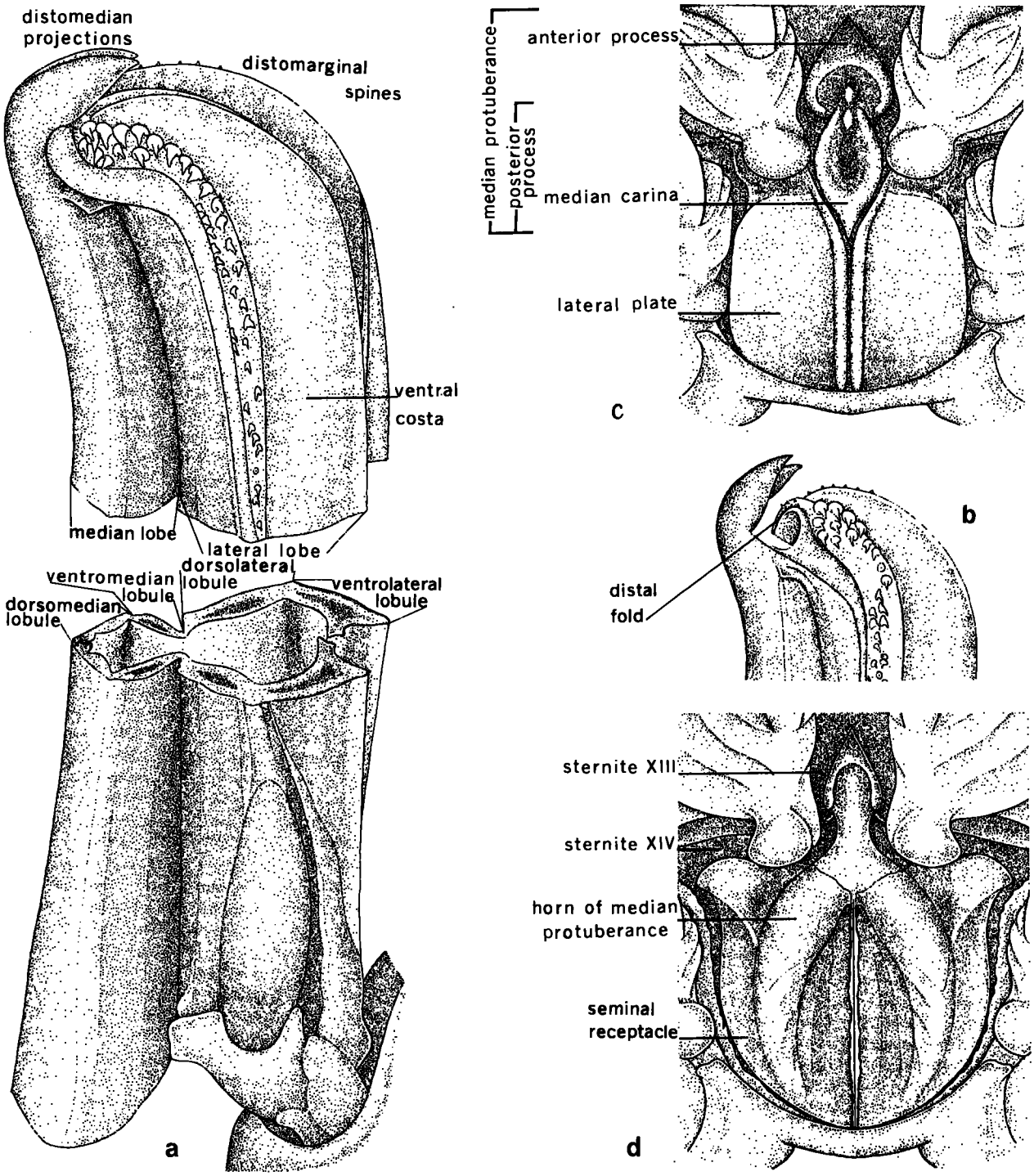

FIGURE 3.—Features of the external genitalia used in *Penaeus* taxonomy. Petasma: a. Cross section with arrangement of lobes. b. Distal portion. c. Thelycum. d. Thelycum with lateral plates removed showing seminal receptacle and position of horns of median protuberance.

2. Hepatic carina prominent 3
Hepatic carina absent or ill defined ..... *Fenneropenaeus*

3. Thelycum open type. Petasma with ventral costa short, not reaching distal margin of lateral lobe ..... *Litopenaeus*
Thelycum closed type. Petasma with ventral costa long, reaching distal margin of lateral lobe ..... *Penaeus* s.s.

SUBGENUS *Litopenaeus* NEW SUBGENUS

Type species, *Penaeus* (*Litopenaeus*) *vannamei* Boone, here designated.

Diagnosis

Thelycum of open type, lacking sperm receptacle. Petasma formed by relatively simple petasmal endopods, with short ventral costae; median lobes of petasma not extended distally, not or just barely reaching distal margin of lateral lobes. Carapace with adrostral carina and sulcus short, extending to, or only slightly posterior to, epigastric tooth; gastrofrontal carina absent; hepatic carina well developed; gastro-orbital carina short, extending anteriorly not more than three-quarters, usually two-thirds, of the distance from hepatic spine to postorbital margin.

Etymology

Litopenaeus, from the Greek litos, meaning plain.

List of Species

P. (*L.*) *vannamei* Boone, *P.* (*L.*) *stylirostris* Stimpson, and *P.* (*L.*) *occidentalis* Streets in the eastern Pacific; *P.* (*L.*) *setiferus* (L.), and *P.* (*L.*) *schmitti* Burkenroad in the western Atlantic.

SUBGENUS *Penaeus* s.s.

Type species, *Penaeus* (*Penaeus*) *monodon* Fabricius.

Diagnosis

Thelycum of closed type. Petasma with ventral costae long, strongly curved distally, and with median lobes only slightly prolonged distally. Carapace with adrostral carina and adrostral sulcus short, extending about to level of epigastric tooth; gastrofrontal carina absent; hepatic carina well defined and gastro-orbital carina short, extending anteriorly not more than two-thirds of the distance from hepatic spine to postorbital margin.

List of Species

P. (*P.*) *monodon* Fabricius and *P.* (*P.*) *esculentus* Haswell in the Indo-Pacific; and *P.* (*P.*) *semisulcatus* de Haan in the Indo-Pacific and eastern Mediterranean Sea.

SUBGENUS *Fenneropenaeus* NEW SUBGENUS

Type species, *Penaeus* (*Fenneropenaeus*) *indicus* H. Milne Edwards, here designated.

Diagnosis

Thelycum of closed type. Petasma with ventral costae long, strongly curved distally, and with median lobes only slightly projected distally. Adrostral sulcus and carina short, extending about to level of epigastric tooth, sulcus shallow and carina attenuated posteriorly; gastrofrontal carina absent; hepatic carina absent or ill defined; gastro-orbital carina short or absent, if present extending anteriorly not more than two-thirds, or occupying middle one-third of the distance from hepatic spine to postorbital margin.

Etymology

Fenneropenaeus for Fenner A. Chace, Jr., whose advice through the years has been very helpful to me in my studies.

List of Species

P. (*F.*) *indicus* H. Milne Edwards, *P.* (*F.*) *merguiensis* de Man, *P.* (*F.*) *penicillatus* Alcock, and *P.* (*F.*) *orientalis* Kishinouye. The four species are Indo-Pacific.

SUBGENUS *Melicertus*

Type species, by monotypy, *Melicertus tigrinus* Rafinesque, 1814: 22 (=*Cancer kerathurus* Forskål, 1775).
Salambria "Burkenroad" Balss, 1957: 1518 (nomen nudum).

Diagnosis

Thelycum of closed type. Petasma with ventral costae long, strongly curved or almost straight distally, and with distomedian projections usually prominent. Carapace with adrostral carina and sulcus long, extending posteriorly considerably beyond epigastric tooth, usually almost reaching posterior margin of carapace; gastrofrontal carina present; hepatic carina prominent; gastro-orbital carina long, extending anteriorly at least, usually more than three-quarters of the distance from hepatic spine to postorbital margin.

List of Species

P. (*M.*) *brevirostris* Kingsley and *P.* (*M.*) *californiensis* Holmes from the eastern Pacific; *P.* (*M.*) *aztecus aztecus* Ives, *P.* (*M.*) *aztecus subtilis* Pérez Farfante, *P.* (*M.*) *paulensis* Pérez Farfante, *P.* (*M.*) *brasiliensis* Lat., *P.* (*M.*) *duorarum duorarum* Burkenroad, and *P.* (*M.*) *duorarum notialis* Pérez Farfante from the western Atlantic—the last-named subspecies from the eastern Atlantic (West Africa) also; *P.* (*M.*) *kerathurus* (Forskål) from the Mediterranean Sea and eastern Atlantic; *P.* (*M.*) *latisulcatus* Kishinouye, *P.* (*M.*) *longistylus* Kubo, *P.* (*M.*) *marginatus* Randall, *P.* (*M.*) *plebejus* Hess, and *P.* (*M.*) *teraoi* Kubo from the Indo-Pacific; and *P.* (*M.*) *japonicus* Bate (?=*P.* (*M.*) *canaliculatus* Olivier) from the Indo-Pacific and eastern Mediterranean Sea.

The list of Indo-Pacific species follows the conclusions of Hall (1962) and Racek and Dall (1965), as well as previous opinions by Kubo (1949), Holthuis (1949), and Dall (1957).

Remarks on Subgenera

The five species of the subgenus *Litopenaeus* are restricted to American waters and differ markedly from other members of the genus in characters of the external genitalia which neither Burkenroad (1934) nor Kubo (1949) took into account when they recognized species groups of the genus *Penaeus*. In respect to both the thelycum and the petasma, these species are more primitive than the species of the other subgenera. The open thelycum, which is obviously less specialized than the closed type, has only ridges and protuberances for the fastening of the spermatophores, which are left exposed. In *Litopenaeus* the spermatophores have strong structures for attachment to the thelycum, whereas in the remaining species these structures seem to be represented—as suggested by Burkenroad (1934)—by vestigial processes. Only one species with a closed thelycum (*P. japonicus*) has spermatophores with large processes (Tirmizi, 1958), but the processes differ from those in the species with an open thelycum. The lack of a gastrofrontal carina and the possession of a hepatic carina seem to be primitive.

Since the species of the genus *Litopenaeus* appear to be more primitive and are restricted to American waters, I agree with Burkenroad (1934) that the genus could well have originated in the Western Hemisphere.

The remaining species of *Penaeus* have a closed thelycum, which possesses two flaps that occur as "lateral plates" on the ventral surface of sternite XIV; the lateral plates are separated by a median slit that opens into a seminal receptacle dorsal to and continuous with the lateral plates. *P. japonicus* provides an exception in having a pouchlike thelycum with an anterior opening on sternite XIV.

Penaeus s.s. is apparently the more primitive of the groups of species with a thelycum of the closed type, sharing with *Litopenaeus* the sculpture of the carapace, including a well-developed hepatic carina. Kubo placed the species of *Litopenaeus* and *Penaeus* s.s. together in his subdivision 2.

Fenneropenaeus differs from *Penaeus* s.s. in lacking a hepatic carina or, in one species (*P. penicillatus*), having only a barely noticeable one; the character seems to have been secondarily lost. The absence of this carina in most species of *Penaeus* s.s., and the shallow adrostral sulcus and posteriorly attenuated adrostral carina indicate a tendency for the carapace to become smoother.

There is little doubt that *Melicertus* includes the most advanced group of species; the long adrostral sulcus and carina appear late in development, at the beginning of the juvenile stage.

Key to the Western Atlantic Species of *Penaeus*

1. Adrostral sulcus short, extending to epigastric tooth; gastrofrontal carina absent ("non-grooved shrimps") ---------- 2
   Adrostral sulcus long, extending posteriorly beyond epigastric tooth; gastrofrontal carina present ("grooved shrimps") ---------- 3
2. Petasma with distal portion of lateral lobe bearing diagonal ridge on inner surface, and distal ventromedial corner rounded. Thelycum with anterolateral ridges turned mesially and pair of fleshy protuberances on sternite XIV---- ----------*P.* (*L.*) *setiferus* (L.) (p. 468)
   Petasma with distal portion of lateral lobe lacking diagonal ridge on inner surface, and distal ventromedial corner produced in subrectangular projection. Thelycum with subparallel anterolateral ridges, never turned mesially, and pair of rounded and rigid protuberances on sternite XIV---------- -----*P.* (*L.*) *schmitti* Burkenroad (p. 487)
3. Petasma with distomedian projection long; distal fold intruding considerably inside petasma

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forming large auricle; ventral costa with apex free. Lateral plates of thelycum with anteromedial corners extended anteriorly forming two projections which cover posterior process ----------*P.* (*M.*) *brasiliensis* Lat. (p. 562)

Petasma with distomedian projection relatively short, distal fold not forming auricle; ventral costa with apex attached to adjacent membranous portion. Lateral plates of thelycum with anteromedial corners not extended; posterior process exposed----------4

4. Petasma with distal portion of ventral costa armed along free border with minute spines, broadening and turning proximally rather abruptly. Lateral plates of thelycum with anteromedial corners slightly divergent; posterior process with undivided median carina ----------5

Petasma with distal portion of ventral costa unarmed along free border, almost straight or arc-shaped, gradually broadening and gradually turning proximally. Lateral plates of thelycum with anteromedian corners widely divergent; posterior process with median carina bifurcate anteriorly----------6

5. Dorsolateral sulcus narrow, ratio between keel height and sulcus width (measured at about one-third of somite length from posterior margin) usually more than three, sulcus often almost closed----------*P.* (*M.*) *duorarum duorarum* Burkenroad (p. 499)

Dorsolateral sulcus broad, ratio between keel height and sulcus width usually less than three----------*P.* (*M.*) *duorarum notialis* Pérez Farfante (p. 520)

6. Adrostral sulcus long, almost reaching posterior margin of carapace, deep and broad posteriorly, ⅕ to 2 times width of postrostral carina (measured at posterior one-eighth of distance from posterior end of adrostral sulcus to epigastric tooth)----------7

Adrostral sulcus relatively short, never approaching posterior margin of carapace, shallow and narrow posteriorly, ⅕ to ¾ times width of postrostral carina----------*P.* (*M.*) *aztecus subtilis* Pérez Farfante (p. 546)

7. Median sulcus long and deep along entire length. Dorsolateral sulcus broad, ratio between height of keel and sulcus width usually less than three. Petasma with distal portion of ventral costa tapering to point, arc shaped, and armed with elongated group of closely set teeth on attached border. Thelycum with anterior and posterior processes broad----------*P.* (*M.*) *aztecus aztecus* Ives (p. 527)

Median sulcus short, shallow and often interrupted. Dorsolateral sulcus narrow, ratio between height of keel and sulcus width usually more than three, sulcus often almost closed. Petasma with distal portion of ventral costa blunt, almost straight, and armed with irregularly arranged teeth. Thelycum with anterior and posterior processes narrow ----------*P.* (*M.*) *paulensis* Pérez Farfante (p. 555)

Penaeus (*Litopenaeus*) *setiferus* (LINNAEUS)

Figures 4 to 13

United States: white shrimp, grey shrimp, lake shrimp, green shrimp, green-tailed shrimp, blue-tailed shrimp, rainbow shrimp, Daytona shrimp, common shrimp, and southern shrimp. Mexico: camarón blanco.

Astacus fluviatilis, Americanus Seba, 1759: 41, pl. 17, fig. 2; [fide] Holthuis, 1962: 115, 116; [fide] Holthuis, 1964a: 227, 228; [fide] Holthuis, 1964b: 233.

Cancer setiferus Linnaeus, 1767: 1054, 1055 (neotype, designated by Burkenroad, 1939, ♂, YPM 4385—BOC 237 [2]—off Matanzas Inlet, Fla., 8 to 10 fm., April 2, 1934, M.B. Bishop); Houttuyn, 1769: 434, 435; Müller, 1775: 1133; [fide] Holthuis, 1962: 115, 116; [fide] Holthuis, 1964a: 227–229; [fide] Holthuis, 1964b: 232–234; International Commission on Zoological Nomenclature, 1967: 151, 152.

?Cancer (*Gammarellus*) *setiferus:* Herbst, 1793: 106, 107, pl. 34, fig. 3.

?Penaeus orbignyanus Latreille, 1817: 155.

Penaeus fluviatilis Say, 1818: 236, 238; Gunter, 1962a: 109–112; Gunter, 1962b: 121; Gunter, 1962c: 216–224, 226; Gunter, 1963: 103–108; Gunter and Hall, 1963: 295, 297, 304; Gunter, 1964: 229; Gunter, Christmas, and Killebrew, 1964: 181–185; [fide] Holthuis, 1964a: 227; [fide] Holthuis, 1964b: 233, 234; Ingle, 1964:

[2] The references made to specimens in the literature under the Bingham Oceanographic Collection catalog numbers are mentioned here with the initials BOC. This collection is in the Peabody Museum of Natural History, Yale University.

232; Hutton, 1964: 439; Joyce, 1965: 14–16, 24–26, 34–36, 44–46, 53–55, 62–64, 70–72, 79, 80, 88, 89, 93, 94, 99, 100, 103–112, 114–116, 121, 123, 128, 132, 136–146, 154, 171–173, 175, 178–180, 183, 184, 186–192, 220, 221; Loesch, 1965: 41, 42, 48, 49, 52, 54–56; Christmas, Gunter, and Musgrave, 1966: 196, 197, 199, 203, 205, 208–212, fig. 4; Joyce and Eldred, 1966: 9, 10, 11, 13, 16, 22, 23, 31, 32, 34–36.

Penaeus setiferus: H. Milne Edwards, 1837: 414, 415 [part]; De Kay, 1844: 30; Gibbes, 1850: 199; de Saussure, 1858: 471 [part]; Stimpson, 1871: 133; Kingsley, 1882: 107 [part]; Rathbun, 1884: 821–823, pl. 273; Smith, 1885: 170; Herrick, 1887: 46, 47, 55, pl. 5, fig. 6; Ives, 1891: 196; Evermann, 1892: 90; Rathbun, 1893: 821–823, pl. 273; Sharp, 1893: 110 [part]; Spaulding, 1908: 3–21, pls. 1–4; Andrews, 1911: 420–423, figs. 1, 2; de Man, 1911: 95; Fowler, 1913: 314, 316–318, 542, pl. 92; Tulian, 1920a: 104, 105; Tulian, 1920b: 106–114; Viosca, 1920: 121–124, 1 fig.; Viosca, 1924: 90–93; Weymouth, 1931: 11–13, 1 fig.; Weymouth, Lindner, and Anderson, 1932: 108–110; Lindner, 1933: 51–53; Weymouth, Lindner, and Anderson, 1933: 1–24, figs. 3a, 4a; Burkenroad, 1934: 61, 74, 77–91, 112, 134, 138, figs. 5–7; Johnson and Lindner, 1934: 4, 56, 57; Myers and Gowanloch, 1934: 9–12, 14–21; Pearson, 1935: 172; Burkenroad, 1936: 315–318, fig. 1b; Lindner, 1936: 155–158, 160–167, figs. 1, 2 (top); Viosca, 1938: 52; Burkenroad, 1939: 5, 17–25, 27, 48, 51, 52; Collier, 1939: 32, 33; Pearson, 1939: 2, 3, 5–30, 33, 35–43, 45–51, 53–56, 59, 61–63, 65–68, 70–72, figs. 1–20, 22–30, 36–39; Rioja, 1939: 316, 318, figs. 6–9; Rioja, 1940a: 261, 262, 266; Rioja, 1940b: 267, 268, 273; Viosca, 1940: 33, 34, 36; Gunter, 1941: 203, 204; Rioja, 1941a: 200, 206, 207, 213–215, figs. 10–12, 22; Rioja, 1941b: 225, 226; Anderson and Lindner, 1945: 303; Gunter, 1945: 25, 69, 77, 87, 90, 94, 100, 101, 105, 106, 113, 115, 119, 178, 179; Viosca, 1945: 276; Anderson, 1948: 1–4, 1 fig.; King, 1948: 244–262, pls. A–G; U.S. Fish and Wildlife Service, 1948: 1–5; Anderson, King, and Lindner, 1949: 168–171; Anderson, Lindner, and King, 1949: 16; Burkenroad, 1949: 688–689; Broad, 1950: 1–4, 4 figs.; Gunter, 1950: 13–24, 26, 40–49; Hedgpeth, 1950: 106, 107, 113; Idyll, 1950: 7, 9–15, 17, 19, 23, 25, fig. 1; Rioja, 1950: 149–150, pl. 1, figs. 2–5; Sprague, 1950: 4; Whitten, Rosene, and Hedgpeth, 1950: 78; Broad, 1951: 27, 30, 31, 33, 34, fig. 2; Sánchez Roig and Gómez de la Maza, 1951: 113–118; Gômez de la Maza, 1952: 167, 168, 171, fig. 2 b, c; Leone and Pryor, 1952: 27–31; Springer and Bullis, 1952: 7–12; Carlson, 1953: 32; Heegaard, 1953: 75–105, 12 pls.; Hedgpeth, 1953: 159–161, 210; Hildebrand and Gunter, 1953: 151–155; Lindner, 1953: 65–69; Pérez Farfante, 1953: 229, 232–235, 241; Williams, 1953: 156, 158–160, figs. 1, 2; Anderson, 1954: 98, 99; De Sylva, 1954: 10, 18, 19, 21, 23, 26, 33, 34, fig. 4; Gunter and Hildebrand, 1954: 95–102; Hildebrand, 1954: 233, 238–241, 243, 246, 261–263, 265, 324–326, 349, 350, 360, 362; Sprague, 1954: 248, 251; Springer and Bullis, 1954: 4, 5, 13–16; Hildebrand, 1955: 171–173, 176, 177, 190, 191, 220, 226, 227; Parker, 1955: 204, 205, 210; Voss, 1955: 5, 8, 10, figs. 9, 9 a, b; Williams, 1955a: 116–118, 127, 129–135, 140, 141, 143–145; Williams, 1955b: 200, 203, 204, 206; Anderson, 1956: 1, 2, 4, 5, 8, 11–13; Guest, 1956: 6, 10, 13, 14, 18, figs. 2, 3; Gunter, 1956: 99–105; Johnson and Fielding, 1956: 175–189; Lindner and Anderson, 1956: 555–645, figs. 1–46; Springer and Bullis, 1956: 9; Anderson, 1957: 399–403; Carranza, 1957: 147; Dall, 1957: 142; Dawson, 1957: 1068, fig. 1; Ingle, 1957: 10–12, 16, 17; Lindner, 1957: 69, 72, 83, 84, 129; Pearse and Gunter, 1957: 139, 147, 151; Simmons, 1957: 178, 191, 199; Viosca, 1957: 12, 13, 20, 2 figs.; Woodburn, Eldred, Clark, Hutton, and Ingle, 1957: 6–12, fig. 2; Anderson, 1958a: 1, 2, fig. 1; Anderson, 1958b: 1–7, 1 fig.; Anderson and Lindner, 1958: 1–13; Darnell, 1958: 385, 400, 405, 407, 408; Eldred, 1958: 6, 9, 11, 12, 20–24; Gunter and Shell, 1958: 16, 17, 19, 22, 23, 32; Hildebrand, 1958: 158, 159, 170; U.S. Fish and Wildlife Service, 1958b: 1, 6, 8, 12, 13, 16, 18, 22, 24–28, 30, 32, fig. I–5a; Williams, 1958: 283–286, 288–290; Collier, Gunter, Ingle, and Viosca, 1959: 1–5; Costello, 1959: 1; Eldred, 1959a: 75; Holthuis, 1959: 62; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959: 6, 7, 9, 10, 12, 16, 19–22, 24; Iversen and Manning, 1959: 130, 131; Kruse, 1959: 123, 126, 128, 130, 132, 134, 136, 137, 141, 142; Williams, 1959: 281, 282, 285, 289; Young, 1959: 1–168, 89 figs.; Chin, 1960: 135–141, figs. 1–5; Eldred and Hutton, 1960: 91, 97, 99, 101, 103, 108, fig. 10 a–d; Hoese, 1960a: 592, 593; Hoese, 1960b: 330, 331; Iversen and Idyll, 1960: 4, 6; Williams, 1960: 560; Bearden, 1961: 3–8; Dobkin, 1961: 321, 325, 327, 345–348; Eldred, Ingle, Woodburn, Hutton, and

Jones, 1961: 80, 86, 88, 89, 97, 98, 109; Gunter, 1961a: 599; Gunter, 1961b: 183, 184; Iversen and Jones, 1961: 16; Renfro, 1961: 10, 12; Anderson, 1962: 1, 2, fig. 1; George, 1962: 160, 162; Holthuis, 1962: 115, 118; Hutton, Ball, and Eldred, 1962: 327, 330, 331; Kutkuhn, 1962: 343, 355, 361, 369–388, 397, 401; Boschi, 1963: 5, 6, 19, 20; Kutkuhn, 1963: 66–77; McFarland and Lee, 1963: 391, 393–397, 399, 400, 402–415; Renfro and Brusher, 1963: 13–17; Zein-Eldin, 1963a: 188–196; Holthuis, 1964a: 227–229; Hutton, 1964: 439, 440, 444, 445; Klima, 1964: 60, 63, 64, fig. 3; Aldrich, 1965: 370–375; Anderson and Lunz, 1965: 1–5; Broad, 1965: 86–90; Bullis and Thompson, 1965: 6; Copeland, 1965: 19; Ewald, 1965c: 103, 107, 109, 113, 114, 2 figs.; Holthuis and Rosa, 1965: 6; Temple and Fischer, 1965a: 59, 61; Temple and Fischer, 1965b: 16; Williams, 1965: 18–21, 23, 24, 26, 27, figs. 8, 9; Van Engel, 1965: 38; Zein-Eldin and Aldrich, 1965: 210–213; Anderson, 1966: 1, 3–7, figs. 3–9; Copeland and Truitt, 1966: 68, 69, 72, 73; Kutkuhn, 1966a: 19, 20, 27, 28, fig. 2; St. Amant, Broom, and Ford, 1966: 4; Sykes and Finucane, 1966: 374; Aldrich, Wood, and Baxter, 1967: 80; Baxter and Renfro, 1967: 149, 151–158; fig. 3; Lyles, 1967: 315–317, 371–376; McCoy and Brown, 1967: 1–3, 8–10, 13, 14, 17, 20, 21, 24–27; Temple and Fischer, 1967: 323–325, 328, 331–333; Zamora and Trent, 1968: 17–19.

Peneus setiferus: Gibbes, 1848: xiv; Kingsley, 1878: 69; de Saussure, 1858: 421; Kingsley, 1879: 330; Hay and Shore, 1918: 378, pl. 25, fig. 5; Boone, 1930: 15, 105, 106, pl. 31.

Penaeus setifer: Agassiz, 1849: 63, fig. 17c; Doflein, 1900: 126, 127 [part], fig. 1.

Paneus setiferus: Collins and Smith, 1892: 102.

Panaeus gracilirostris Thallwitz, 1892: 3, fig. 5. (According to Burkenroad, 1939).

Penaeus gracilirostris: de Man, 1911: 100, 101.

Penaeus setifera: Cowles, 1930: 355, 356, 358.

Palaemonetes setiferus: Lunz, 1956: 93.

Penaeus sertiferus: Aldrich, Wood, and Baxter, 1967: 80.

White shrimp: Lunz, 1956: 93; Loesch, 1957: 39, 41; Lunz, 1958: 47; Baxter and Furr, 1964: 29; Renfro and Brusher, 1964: 13–15; Zein-Eldin, 1964: 65–67; Klima and Benigno, 1965: 38, 39; Renfro and Brusher, 1965: 10; Zein-Eldin and Griffith, 1965: 77, 78; Zein-Eldin, 1966: 41–43, fig. 39.

?Shrimp: Flint, 1956: 11, 12.

Taxonomic Remarks

The International Commission on Zoological Nomenclature has used its plenary powers (Opinion 817, 1967) to validate the selection of Burkenroad's neotype of *Cancer setiferus* Linnaeus, and, thus, the white shrimp from the Atlantic Coast of the United States and the Gulf of Mexico is *Penaeus setiferus* (L.). Consequently, the white shrimp from the Caribbean Sea and the Atlantic Coast of South America are referable to *P. schmitti* Burkenroad. Both names—*Cancer setiferus* Linnaeus and *Penaeus schmitti* Burkenroad—have been placed on the Official List of Specific Names.

Holthuis (1962) selected as lectotype of *Astacus fluviatilis, Americanus* Seba, 1759, the figure No. 2 of plate 17, given by Seba to illustrate his description.

Gunter's (1962a) suggestion that *Penaeus orbignyanus* Lat. should be considered a nomen dubium seems logical. Latreille (1817) stated that the type specimen was sent to him by "Dr. d'Orbigny" from the Département de la Vendée in western France. Burkenroad (1939) failed in his attempt to locate the type, which, according to H. Milne Edwards (1837), could not be differentiated from *P. setiferus*. The specimen could have been a stray from the western Atlantic actually collected in that improbable locality, or it could have been collected in America and given to Dr. d'Orbigny. In either case, it does not seem probable that it will ever be determined if the name corresponds to *P. setiferus* or *P. schmitti*.

Study Material

UNITED STATES

New Jersey: 1 ♂, USNM, off Long Branch, August 1887, T. Steelman and G. H. Bean. 1 ♂, USNM, off New England Creek, 1 fm., October 19, 1929, H. G. Richards. 1 ♀, PANS, Atlantic City, Ch. Buvinger. 1 ♂ PANS, Ocean City, July 6, 1913, D. McCadden. 1 ♂, PANS, Ventnor, summer 1949, C. B. Atkinson. 1 ♀, YPM, Dennis Cove, August 27, 1932.

Maryland: 1 ♂, USNM, Saint Jeromes, September 17, 1889, USFC.

Virginia: 1 ♂, USNM, off Plantation Light, Chesapeake Bay, July 8, 1920, 25 fm., *Fish Hawk* Sta. 8826. 1 ♂, USNM, Chesapeake Bay, R. E. Earll and E. McDonald, 1880. 1 ♂, USNM, Rappahannock River, 12 to 15 fm., October 19, 1921, W. C. Schroeder. 13 ♂ 14 ♀, USNM, Pagan Creek, James River, October 31, 1930, J. C. Pearson. 1 ♂,

CBL, Silver Beach, Chesapeake Bay, October 28, 1953. 2 ♂, USNM, Willoughby Point, May 1880, R. E. Earll and E. McDonald. 1 ♂, USNM, off mouth Chesapeake Bay, 18 fm., November 16, 1880, *Fish Hawk* Sta. 901.

North Carolina: 3 ♂ 3 ♀, USNM, off Beaufort Inlet, 40 to 50 fm., October 6, 1949, A. B. Williams. 3 ♂ 1 ♀, USNM, Beaufort, H. L. Osborn. 1 ♂, YPM, Fort Macon, H. C. Yarrow. 1 ♂, YPM, Fort Macon, J. E. Coues. 6 ♂ 8 ♀, AMNH, Morehead City.

South Carolina: 5 ♀, USNM, Stono Inlet, June 5, 1935, J. C. Pearson. 1 ♂ 6 ♀, USNM, Folly Beach, H. T. Ebner. 1 ♂ 2 ♀, USNM, off Hilton Head, October 11, 1941, *Madelena*.

Georgia: 1 ♀, USNM, Savannah, October 9, 1930, I. R. Tomkins. 1 ♂ 1♀, USNM, Savannah, 1930, I. R. Tomkins. 76 ♂ 75 ♀, YPM, mouth of Wilmington River, 6 to 8 fm., April 5, 1934. 89 ♂ 67 ♀, YPM, St. Simons Sound, April 4, 1934. 13 ♂ 10 ♀, USNM off Brunswick, 3 to 4 fm., August 26, 1965, W. W. Anderson. 5 ♂ 12 ♀, USNM, Jekyll Creek, March 25, 1940, 8 fm., *Pelican* Sta. 199–201.

Florida: 1 ♂, USNM, off Jacksonville, 6 to 8 fm., October 2, 1957, *Combat* Sta. 504. 28 ♂ 24 ♀, YPM, off Matanzas Inlet, 8 to 10 fm., April 2, 1934. 1 ♂ 1 ♀, USNM, off Matanzas Inlet, 8 fm., November 19, 1963, *Silver Bay* Sta. 5381. 3 ♂ 3 ♀, USNM, S. of Saint Augustine, 11 fm., April 16, 1940, *Pelican* Sta. 212–213. 8 ♂ 9 ♀, USNM, off Cape Kennedy, 9½ fm., January 26, 1962, *Silver Bay* Sta. 3710. 6 ♂ 3 ♀, USNM, off Cape Kennedy, 7½ fm., October 9, 1934, W. W. Anderson. 15 ♂ 25 ♀, USNM, off Cocoa Beach, 10 to 11 fm., January 13, 1965, *Oregon* Sta. 5181. 22 ♂ 20 ♀, USNM, off Melbourne Beach, 11 fm., January 13, 1965, *Oregon* Sta. 5182. 1 ♂ 1 ♀, USNM, off Melbourne Beach, 20 to 22 fm., January 13, 1965, *Oregon* Sta. 5183. 2 ♂ 3 ♀, USNM, N. of Fort Pierce, 8 fm., January 28, 1962, *Silver Bay* Sta. 3715. 3 ♂ 10 ♀, USNM, Pilot Cove, Apalachicola Bay, November 12, 1958, R. M. Ingle. 6 ♂ 5 ♀, SW. of Apalachicola Bay, 6 fm., October 31, 1953, *Oregon* Sta. 863. 15 ♂ 12 ♀, USNM, Apalachicola Bay, July 17, 1961, SPML.

Alabama: 1 ♀, YPM, off Mobile Bay, March 20, 1937, 12 fm., *Atlantis* Sta. 2812. 1 ♂ 1 ♀, USNM, off Mobile Bay, 7 fm., December 14, 1950, *Oregon* Sta. 185. 3 ♂ 5 ♀, USNM, off Mobile Bay, 7 fm., January 28, 1962, *Oregon* Sta. 3475. 2 ♀, USNM, off Alabama, 19 fm., December 14, 1950, *Oregon* Sta. 188.

Mississippi: 23 ♂ 25 ♀, GCRL, Mississippi Sound, September 5, 1963, J. Y. Christmas. 11 ♂ 10 ♀, GCRL, Mississippi Sound, September 25, 1963, J. Y. Christmas. 16 ♂ 14 ♀, GCRL, Mississippi Sound, October 30, 1963, J. Y. Christmas. 2 ♂ 5 ♀, USNM, Biloxi Bay, June 18, 1965, GCRL. 7 ♀, USNM, Biloxi Bay, March 1965, GCRL.

Louisiana: 2 ♂ 3 ♀, USNM, New Orleans, Louisiana Conserv. Comm. 1 ♂, YPM, New Orleans, R. W. Shuffeldt. 12 ♂ 7 ♀, USNM, Lake Pontchartrain, 2⅓ fm., November 25, 1953, R. M. Darnell. 24 ♂, AMNH, off Bayou Scofield, January 3, 1931, M. D. Burkenroad. 1 ♀, USNM, Breton Island, S. Springer. 1 ♂ 2 ♀, YPM, Grande Isle, 6 fm., July 21, 1930. 2 ♂ 1 ♀, USNM, Grande Isle, July 14, 1928, E. H. Behre. 25 ♂ 25 ♀, USNM, Puffer Point, Barataria Bay, July 22, 1932, J. C. Pearson.

Texas: 4 ♂ 1 ♀, USNM, off mouth of Sabine River, 10 fm., May 19, 1965, BCFBLG. 7 ♂ 4 ♀, USNM, off mouth of Sabine River, 10 fm., May 19, 1965, BCFBLG. 3 ♂, USNM, Swan Lake, Galveston, August 19, 1965, BCFBLG. 2 ♂ 1 ♀, USNM, Swan Lake, Galveston, June 24, 1965, BCFBLG. 3 ♂ 3 ♀, USNM, S. of Galveston Island, 5 fm., August 10, 1960, *Oregon* Sta. 2884. 9 ♂ 4 ♀, USNM, off Galveston, April 1965, BCFBLG. 2 ♂, USNM, off Port Aransas, 9 fm., November 26, 1950, *Oregon* Sta. 149. 2 ♂ 1 ♀, USNM, Corpus Christi, H. B. Parks. 2 ♂ 3 ♀, USNM, off Padre Island, 7½ fm., January 27, 1964, *Oregon* Sta. 4641.

MEXICO

Tamaulipas: 5 ♂ 2 ♀, INIBP–USNM, Tampico, May 14, 1963, S. García.

Veracruz: 1 ♀, USNM, Bocaina, Laguna de Tamiahua, June 9, 1964, R. Márquez and C. Tovar. 1 ♂ 1 ♀, INIBP, Villa Cuauhtémoc, April 8, 1962, S. García. 1 ♂ 1 ♀, USNM, Laguna de Pueblo Viejo, Villa Cuauhtémoc, June 20, 1963, S. García. 1 ♂ 1 ♀, INIBP, Laguna de Pueblo Viejo, Villa Cuauhtémoc, October 17, 1964, S. García. 1 ♂ 2 ♀, USNM, La Bocana, Tuxpan, March 7, 1964, A. Mendoza and R. Márquez. 14 ♂ 2 ♀, INIBP–USNM, Tuxpan, August 29, 1963, S. Basulto. 2 ♂ 3 ♀, INIBP–USNM, Estero Tabasco, Tuxpan, March 3, 1964, A. Mendoza. 6 ♂ 9 ♀, INIBP–USNM, Estero Jacome, Tuxpan, December 18, 1963, S. García. 3 ♀, USNM, Río Pantepec, Tuxpan. 5 ♀, INIBP–

USNM, Río Pantepec, Tuxpan, April 10, 1963, S. Basulto and M. C. Rodríguez de la Cruz. 2 ♀, USNM, Río Pantepec, Tuxpan, February 11, 1964, members Sociedad Cooperativa Río Pantepec. 3 ♂ 5 ♀, INIBP–USNM, mouth of Río Pantepec, Tuxpan, June 7, 1964, C. Tovar and R. Márquez. 6 ♂ 4 ♀, INIBP–USNM, Laguna La Tapada, November 28, 1963, A. Macías and U. Barron. 1 ♂, INIBP, Laguna de Buen País, 12 km. W. of Alvarado, F. Lachica and F. Carmona, April 1965.

Tabasco: 5 ♂ 5 ♀, INIBP–USNM, Laguna Pajonal, July 4, 1963, D. Fuentes.

Campeche: 2 ♀, INIBP–USNM, Golfo de Campeche, 26 fm., April 30, 1959, R. Ramírez and M. Flores. 5 ♂ 3 ♀, INIBP–USNM, Boca Nueva, Los Pinos, April 28, 1959, R. Ramírez and M. Flores. 3 ♂ 1 ♀, INIBP–USNM, N. of Isla del Carmen, 3 fm., May 5, 1959, R. Ramírez and M. Flores.

Diagnosis

Adrostral carina and sulcus short, ending at epigastric tooth. Petasma with inner surface of distal portion of lateral lobe with diagonal ridge and prominent fold near rounded distoventral corner; emargination median to inner lappet shallow. Thelycum with pair of anterolateral, sharp ridges, posterior portions of which bend mesially, and pair of posterior, fleshy, closely set lobes on sternite XIV; posterior margin of sternite XII bearing pair of relatively small scalloplike projections.

Description

ROSTRUM (fig. 4)

Teeth $\frac{4\text{–}10}{0\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—70, 9/2—12, 7/2—13, 8/3—1.50, 9/3—1.25, 8/1—0.75, 10/2—0.50, 6/2—0.50, 7/0—0.25, 4/1—0.25; N=400) + epigastric; ventral teeth relatively far apart, first tooth usually opposite or anterior to last dorsal tooth; rostrum slender and long, in juveniles extending to base of distal one-fifth of thickened portion of lateral antennular flagellum; maximum length in relation to c.l. (carapace length) obtained at 10 to 16 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ (rostrum length) as high as 1.10); decreasing progressively with increasing length of shrimp, reaching midlength of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.55); rostrum straight, slightly concave posteroventrally; highest portion of blade usually at level of second, occasionally of third dorsal tooth, and at level of first tooth in some young; third dorsal tooth level with anterior margin of carapace; tip slender and long, almost one-half of length of rostrum. Postrostral carina narrow and relatively short, ending $\frac{1}{5}$ to $\frac{1}{13}$ c.l. from posterior margin of carapace, shorter in larger individuals. Median sulcus shallow, interrupted and variable in shape: consisting of anterior elongated concavity in wider portion of postrostral carina, either blunt or continuing as line toward epigastric tooth, and leading posteriorly by a groove to a narrower concavity; sometimes both concavities separated by constriction, and often median sulcus consisting of a single blunt anterior concavity; median sulcus represented posteriorly by few minute pits. In small specimens median sulcus consisting of three or four pits. Adrostral carina rounded and short, ending at level of epigastric tooth. Adrostral sulcus shallow and short, same length as adrostral carina.

CARAPACE (fig. 5)

Length in proportion to total length smaller in juveniles; according to my data increasing suddenly at subadult stage. Gastrofrontal sulcus absent; gastrofrontal carina absent except for a short, almost imperceptible rib present sometimes at level of first two dorsal teeth. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening into base of spine. Gastro-orbital carina pronounced, sharp, and relatively short, occupying posterior $\frac{3}{5}$ to $\frac{2}{3}$ distance between postorbital margin and hepatic spine. Cervical sulcus short and shallow extending dorsally to two-fifths c.l. from postorbital margin of carapace; in small individuals extending farther posteriorly as line. Hepatic carina $\frac{1}{6}$ to $\frac{1}{5}$ c.l., sharp, sloping anteroventrally to end $\frac{1}{18}$ to $\frac{1}{13}$ c.l. from anterior margin of carapace; hepatic sulcus shallow. Antennal spine acute and relatively short; hepatic spine prominent.

ANTENNULES

Lateral flagellum long, seven-tenths to almost same length as antennular peduncle, slightly longer and with articles shorter than median flagellum. Median flagellum exhibiting sexual dimorphism: in adult males markedly flattened dorsoventrally, with two closely set rows of stout processes of unequal sizes along midportion of

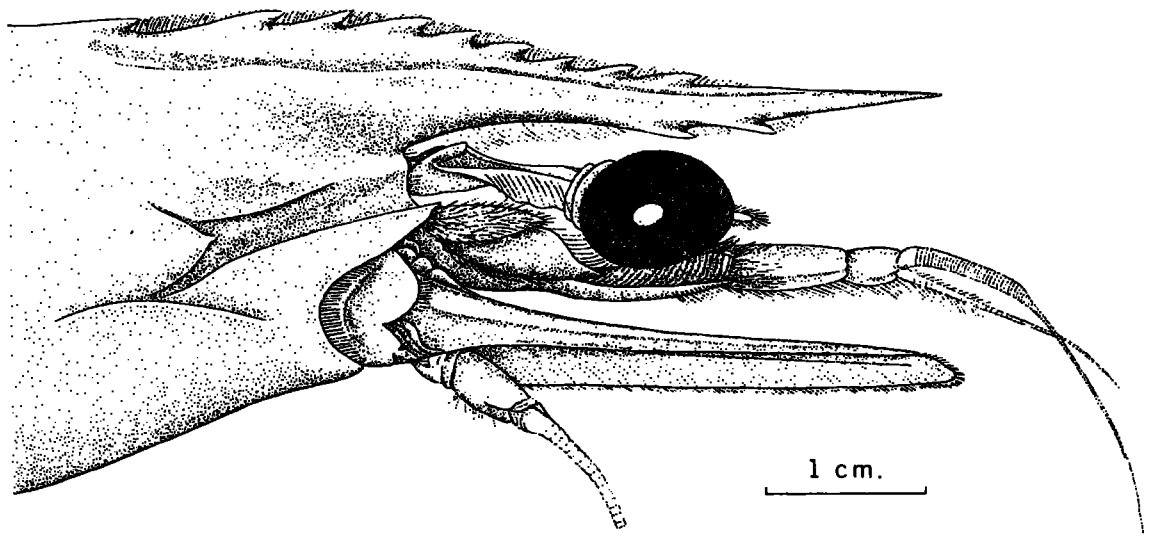

FIGURE 4.—*Penaeus (L.) setiferus (L)*. Rostrum, ♀ 36 mm. c.l., off Cocoa Beach, Fla.

internal margin, and with long setae along proximal one-fourth of external margin; in females processes lacking but long setae present along proximal two-fifths of external margin. Those processes were described by Rioja (1939) and Young (1959); the latter worker stated that "Since the antennular flagella are olfactory, the sexually dimorphic medial flagellum of the male *Penaeus setiferus* probably functions to enable the male to find the sexually mature female during the time of mating." Anterolateral spine small, sharp. Stylocerite reaching slightly beyond midlength of first antennular segment. Prosartema extending to proximal fourth of second antennular segment.

ANTENNAE

Scaphocerite length 2½ times maximum width; spine reaching or slightly surpassing distal end of third antennular segment. Carpocerite about 1¼ times longer than wide, its distal end reaching base of eye. Antennal flagellum very long, 2½ to 3 times body length (fig. 6).

THORACIC APPENDAGES

Third maxilliped reaching at least distal end of first, and at most distal end of proximal ⅔ of second antennular segment; length of dactyl ⅜ to ¾ of propodus. First pereopod extending to distal end of carpocerite or surpassing it by as much as four-fifths length of dactyl. Second pereopod reaching distal end of first and, at most, distal end of proximal three-quarters of second antennular segment. Third pereopod extending to distal end of antennular peduncle or surpassing it by length of entire propodus. Fourth pereopod exceeding carpocerite by ⅓ to ¾ length of propodus. Fifth pereopod surpassing fourth by one-half to entire length of dactyl. Exopods on all pereopods; long ischial and basial spines on first pereopod, and rather long basial spine on second pereopod.

ABDOMEN

Carinate dorsally from one-quarter of third or from fourth somite posteriorly, carina gradually increasing in height posteriorly forming keel on sixth somite, and ending in sharp spine on posterior margin of somite. Dorsolateral sulcus (fig. 7) very shallow and narrow, without lips; in young individuals running almost entire length of somite, in adults extending only from slightly anterior of midlength of somite to near posterior margin. Sixth abdominal somite with three cicatrices on each side, anterior one longest; fifth somite with one cicatrix and diagonal series of minute pits anterior to sinus on posterior margin of somite situated on rib in large specimens; fourth somite with similar series of pits dorsal to sinus on posterior margin of somite. Ventral margin of pleuron of first somite slightly to moderately indented. Telson (fig. 8) with deep median sulcus and acuminate tip. Dorsoventral axis of larger males much shorter than that of females of corresponding lengths.

PETASMA (fig. 9 a–c)

Lateral lobe with distal portion of inner surface bearing conspicuous rounded fold and diagonal ridge, which undulates proximally to near mid-

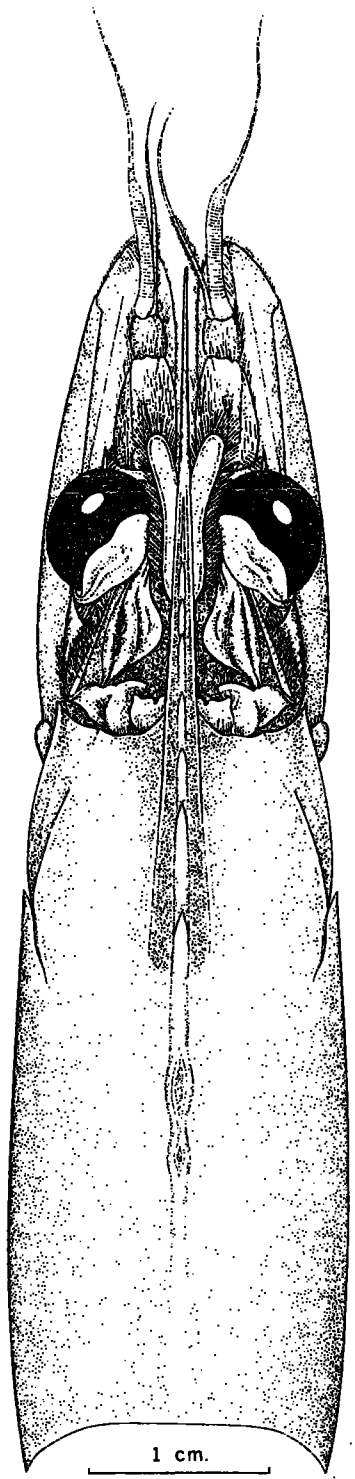

FIGURE 5.—*Penaeus (L.) setiferus* (L.). Cephalothorax, ♀ 41.5 mm. c.l., off Cocoa Beach, Fla.

length of petasma. Distoventral corner of lateral lobe rounded and with nearly symmetrical S-shaped ridge on free border; anterior half of ventral border with two narrow ribs joined at both ends. Emargination median to inner lappet shallow. Outer surface of lateral lobe with relatively narrow band of spines, three to four, rarely five, rows abreast distally and decreasing to one or two proximally. Pair of crests flanking band of spines distally, crest close to median lobe more prominent and sharp than crest near free ventral margin; latter crest plain, not bifurcated. Lateral lobe at almost same level as median lobe, extended only slightly anteriorly.

APPENDIX MASCULINA (fig. 9 d, e)

Subtriangular, its length almost twice width at base, and armed with short spines along distal portion of median margin and with long spines on distal portion; distal spines slightly less than half length of appendix. Anterior surface subplane, posterior surface strongly concave, concavity bordered by strong arch-shaped ridge.

SPERMATOPHORE

Elongate, podlike, actually consisting of two spermatophores; in mature males each lying completely formed in paired terminal ampullae and joined when discharged. Anterior end, when attached to female, bearing pair of winglike lateral processes, each armed with short triangular projection at posterior edge. Posterodorsal portion extended into horizontal plate.

THELYCUM (figs. 10 and 11)

Open type. Sternite XIV with two anterolateral, prominent and sharp ridges; posterior portions of ridges converging mesially but not meeting near middle of sternite; occasional sharp, short rib present between converging ridges. Posterior portion of sternite XIV with pair of conspicuous, closely set, anteriorly produced, fleshy, usually light-colored lobes, separated in large individuals by low median rib. Sternite XIII with strong median plate extending posteriorly as fleshy, emarginated, shelflike projection overhanging sternite XIV; ridge on posterior margin of plate moderately strong; on anterior portion of sternite XIII, fleshy tonguelike lamella bordered by minute setae forming floor of cavity roofed by strong transverse ridge on posterior margin of

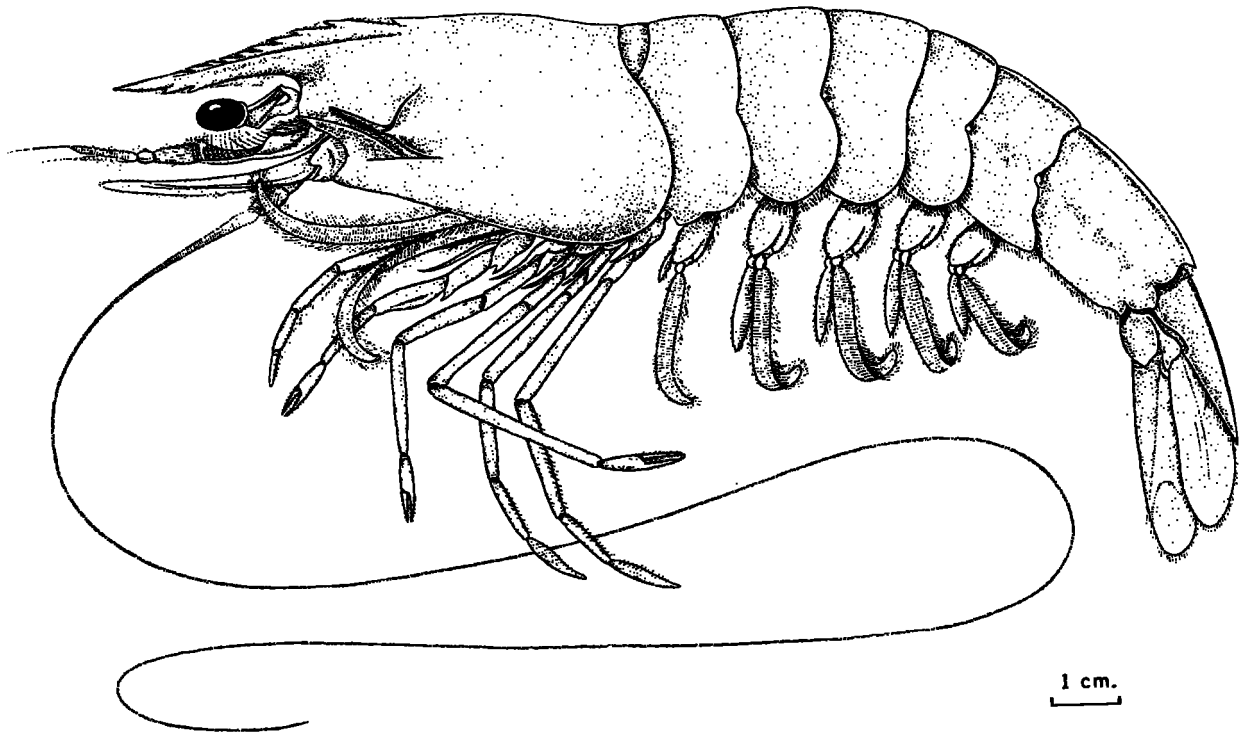

FIGURE 6.—*Penaeus* (*L.*) *setiferus* (L.). Lateral view, ♀ 49 mm. c.l., off Cape Kennedy, Fla.

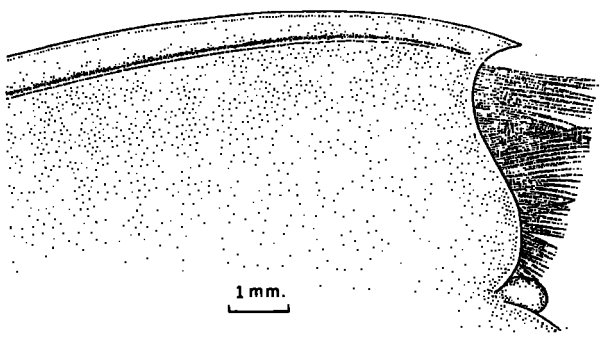

FIGURE 7.—*Penaeus* (*L.*) *setiferus* (L.). Sixth abdominal somite, posterodorsal portion, ♀ 38 mm. c.l., Biloxi, Miss.

sternite XII; ridge of sternite XII (hidden by structures surrounding gonopores and coxae of third pair of pereopods) with pair of relatively small, lateral scalloplike projections.

COLOR

Penaeus setiferus has a translucent white, almost glasslike appearance and, thus, it is most commonly known as the "white shrimp." It is also often termed the "gray shrimp," and in some localities, because it is greenish, it is given the name

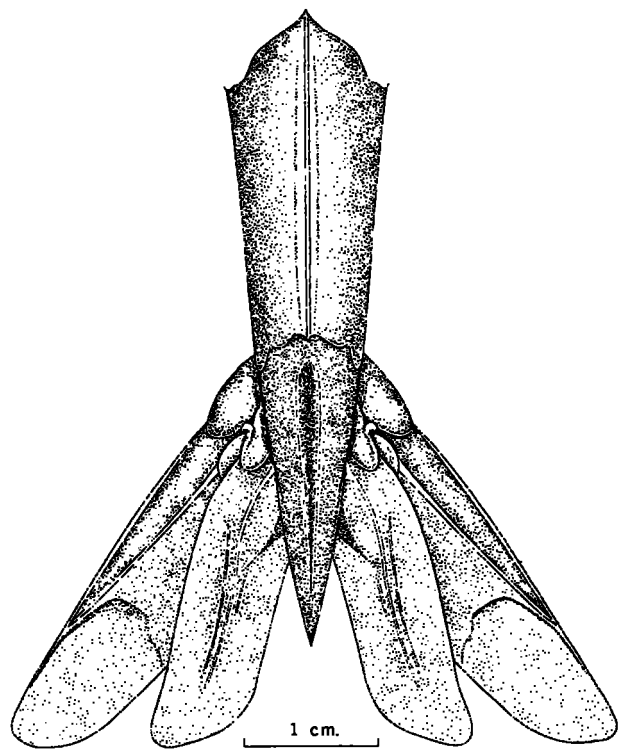

FIGURE 8.—*Penaeus* (*L.*) *setiferus* (L.). Dorsal view of sixth abdominal somite, telson and uropods. ♀ 36.5 mm. c.l., off Cocoa Beach, Fla.

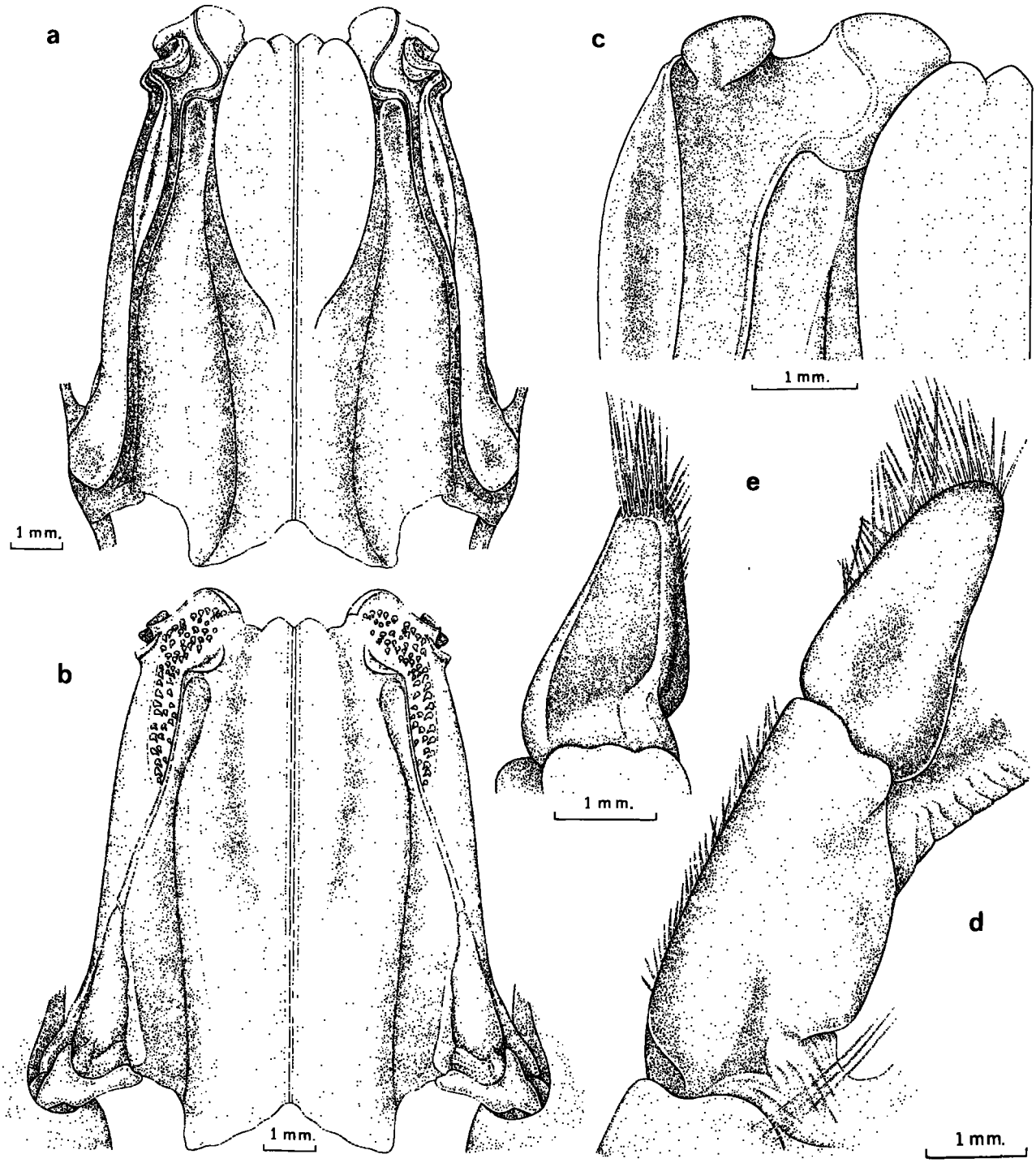

FIGURE 9.—*Penaeus* (*L.*) *setiferus* (L.). a. Petasma, interior surface, ♂ 39.5 mm. c.l., off Melbourne Beach, Fla. b. Petasma, exterior surface, ♂ 39.5 mm. c.l., off Melbourne Beach, Fla. c. Petasma, interior surface of distal portion of left half, ♂ 35 mm. c.l., Biloxi Bay, Miss. d. Appendix masculina, right. ♂ 35 mm. c.l., Biloxi Bay, Miss. e. Appendix masculina, posterior surface, ♂ 35 mm. c.l., Biloxi Bay, Miss.

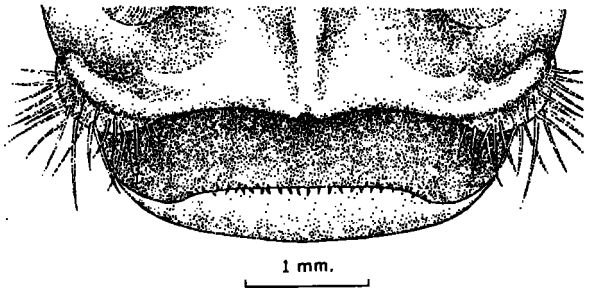

FIGURE 10.—*Penaeus* (*L.*) *setiferus* (L.). Posterior portion of sternite XII and tonguelike lamella of sternite XIII, ♀ 45 mm. c.l., off Cocoa Beach, Fla.

"green shrimp." The entire body of this species often has a bluish hue that is due to a predominance of blue chromatophores which are concentrated near the margins of the telson and uropods. Intermingled with the blue are red chromatophores in the distal portion of uropods that form a brownish-purple blotch; the uropods also bear a narrow yellowish marginal band. A dark band of black specks occurs close and parallel to the posterior margins of the carapace and the abdominal somites. The sides of the body are often pinkish and the pleopods as well as the tips of the pereopods are dark red.

Distribution and Morphological Variations

Penaeus setiferus ranges along the Atlantic Coast of the United States from Fire Island, N.Y. (Burkenroad, 1934), to Saint Lucie Inlet in east Florida (Gunter and Hall, 1963); its center of abundance is in Georgia and northeast Florida (Anderson and Lunz, 1965). Its range along the coast of Florida is discontinuous; the species is absent around the southernmost portion of the peninsula and along the Gulf Coast to the mouth of the Ochlockonee River in the west portion of Apalachee Bay. The white shrimp appears again in the mouth of the Ochlockonee River (Eldred, *In* Joyce, 1965) and its range extends along the north coast of the Gulf and the northeastern Mexican Coast—with a center of abundance in Louisiana—and continues uninterrupted southward around the Golfo de Campeche to the vicinity of Ciudad Campeche—with another center of abundance in northeast Tabasco and the adjacent waters of Campeche.

Bullis and Thompson (1965) took this species at lat. 20° 17′ N., long. 91° 35′ W., which is the northernmost record on the Continental Shelf of Yucatán and is probably very close to the northern limit of its range along this Coast (fig. 12).

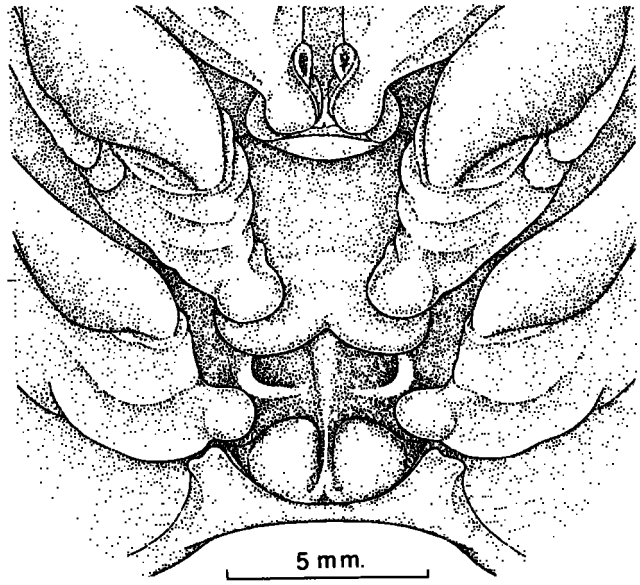

FIGURE 11.—*Penaeus* (*L.*) *setiferus* (L.). Thelycum, ♀ 44 mm., c.l., off Sabine River, Tex.

The white shrimp also has been recorded three times from near the Tortugas Islands. Springer and Bullis (1952) found a single specimen north of those islands in 25 fm. Boone (1930) described and illustrated a male which she stated had been taken in the Marquesas Keys in 30 fm. Thanks to the cooperation of Woodhull B. Young, I had the opportunity to examine *Penaeus* in the Vanderbilt Museum, where the specimen recorded by Boone was supposed to have been deposited, but I failed to locate it. Finally, Kutkuhn (1962) reported white shrimp from the Sanibel-Tortugas area on the basis of a processing plant's report. Because this species has not been found in the enormous amount of material examined in the many investigations carried out in southwestern Florida, the records of Boone and Kutkuhn may have been erroneous.

Formerly, white shrimp were believed to be absent from south of Cabo Rojo, along the coast of Veracruz to Tupilco, Tabasco. Recently, however, I examined a number of specimens from Tuxpan, and a single male from Laguna de Buen País, near Alvarado, Veracruz, so the species is present along that coast even though it may be scarce.

P. setiferus has a more localized distribution within its range than do the sympatric species of *Penaeus*. Its range not only has a wide gap but also has interruptions within restricted areas. A number of factors—salinity, temperature, substrate,

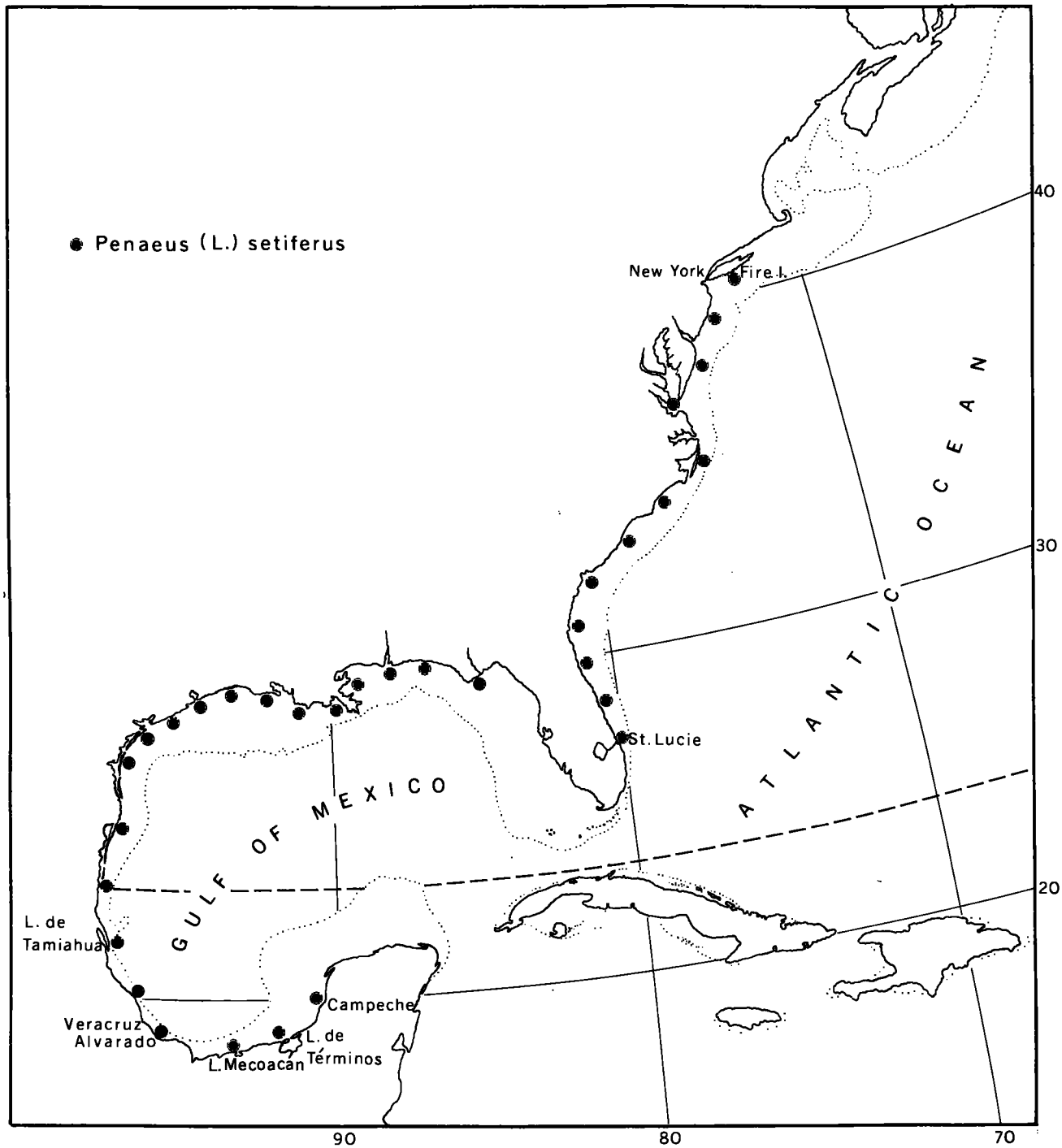

FIGURE 12.—Distribution of *Penaeus* (*L.*) *setiferus* (L.).

food, and cover—have been mentioned as responsible for these discontinuities, but no adequate explanation has been advanced.

The reported occurrence of *P. setiferus* in the waters of Cuba and Jamaica by Burkenroad (1936, 1939) was probably an error. In the many years of field work in Cuba, during which I have identified thousands of specimens, not a single *P. setiferus* was found, nor have specimens been encountered in the extensive collections from the Antilles that I have studied more recently. I have stated (Pérez Farfante, 1953) that it seems very

unlikely this species could ever have reached Cuban waters, much less farther south, since it does not seem to live off the southernmost end of Florida.

Large concentrations of white shrimp are found in less than 20 fm.; it is rare at greater depths where brown shrimp (*P. a. aztecus*) and, in some areas, pink shrimp (*P. d. duorarum*) occur in quantities sufficient to sustain profitable fishing. Nevertheless, white shrimp do invade water deeper than 20 fm. Springer and Bullis (1952) reported them at 43 fm. off Alabama and Louisiana, and later Bullis and Thompson (1965) caught *P. setiferus* in 45 fm. off Louisiana. This latter depth is considered very close to the lower bathymetric limit of the species.

Extensive biometric studies that took into account 45 different characters have failed to show any significant morphological differences between the white shrimp from the Atlantic and those from the Gulf of Mexico.

Some time during the past, the range of *P. setiferus* became discontinuous—probably toward the close of the Pleistocene with the consolidation of the Florida Peninsula. The Pleistocene range of the white shrimp probably extended from the Carolina Coast southward across the Suwannee straits into the Gulf, and with the elevation of the peninsula and the closing of the straits, the population was divided. The northern segment has succeeded in moving south to middle Florida, as far as the Saint Lucie estuary. For some reason, perhaps ecological, however, the Gulf population has not become established beyond the eastern portion of Apalachee Bay along the west coast of the peninsula.

Although recent genetic interchange between the Atlantic population and the Gulf population seems unlikely, the two, as stated above, cannot be distinguished. The three characters—relative lengths of the rostrum, petasma, and third pereopod—which Burkenroad (1934) indicated might prove to be different in the two stocks, vary with increasing size, and the first also with attainment of sexual maturity in the female. The proportional length of the rostrum $\frac{(r.l.)}{(c.l.)}$ is variable and decreases as the adult shrimp grow longer; but it

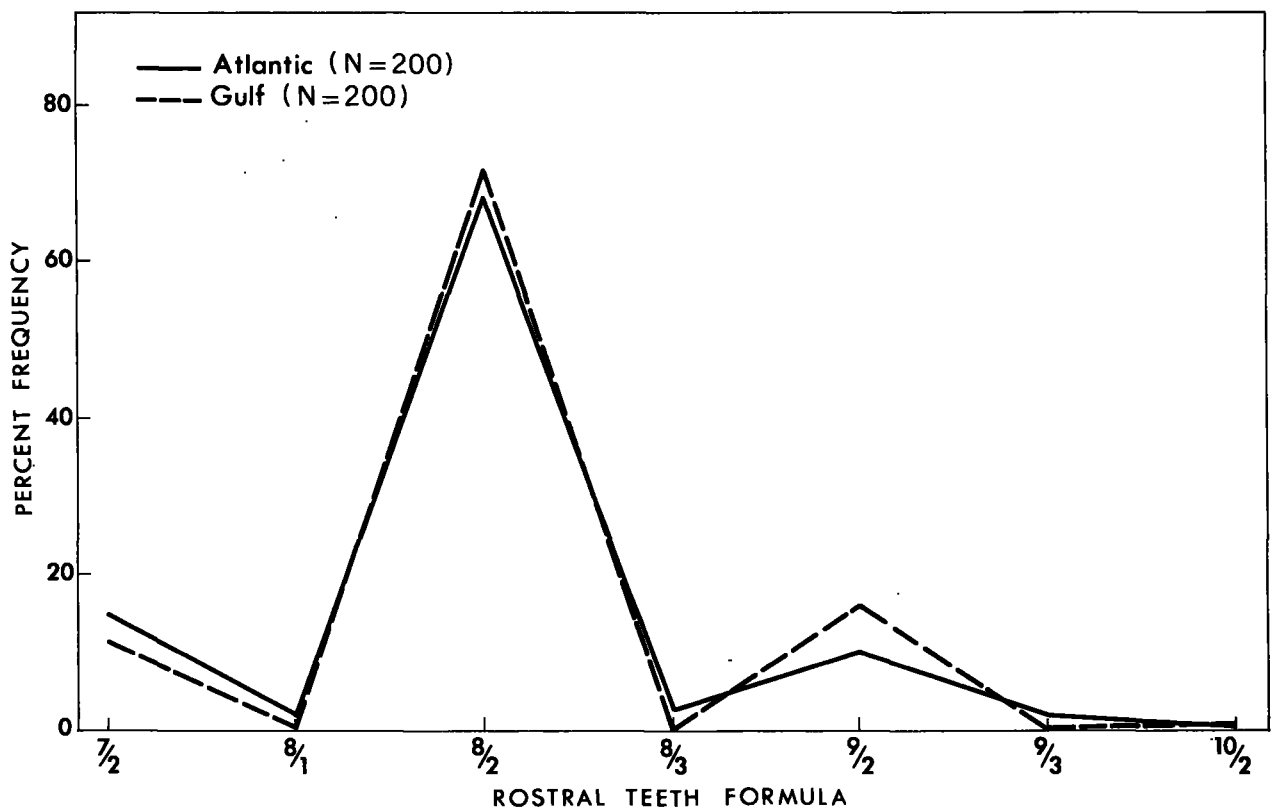

FIGURE 13.—Percentage frequency of the different combinations of rostral teeth in *Penaeus* (*L.*) *setiferus* (L.) from the Atlantic Ocean and the Gulf of Mexico.

exhibits a range of variation that is about the same in both stocks. The range of relative length of the petasma in shrimp with the same total length in the two areas also overlaps. In both stocks the third pereopod, believed to be shorter in the Atlantic individuals, increases with increasing size, and, thus, its relative length depends on the size of the shrimp; no significant difference has been observed among shrimp of the same length in the two populations. To be sure, the largest females examined in this study came from the Gulf of Mexico, and their third pereopods were comparatively longer than those of the largest females that were available from the Atlantic; however, the Atlantic females were smaller than the Gulf females. It now seems clear that the apparent differences in the two populations are not real if shrimp of the same size are compared.

Burkenroad (1934) mentioned that the median sulcus might be used to distinguish the two stocks. The median sulcus of *P. setiferus* from the Atlantic Coast usually consists of two shallow depressions joined by a groove—the anterior one attenuated anteriorly as a line—but this type of median sulcus also occurs in some specimens from several localities in the northern Gulf of Mexico and in many from Campeche. White shrimp from the Gulf often have a median sulcus consisting of two isolated shallow concavities, the anterior one blunt. The rostral tooth formula is almost the same in the two populations as is indicated in figure 13.

Rioja (1939) described the median flagellum of this species as having "16 articles bearing one long central and two small lateral spines [processes]." In contrast, I found that the number of articles armed with processes varies, and that each article almost always has two processes, one long and one short; only in one instance was an article observed to bear three processes. Articles bearing two processes are typical throughout the range of the species—in the Atlantic as well as in the Gulf of Mexico.

Relationships

P. setiferus closely resembles *P. schmitti*, the white shrimp from the Antilles, Central America, and South America; the external genitalia, however, allow the two species to be separated readily. The pair of fleshy, closely set, anteriorly produced posterior lobes and the medially turned anterolateral ridges on sternite XIV set female *P. setiferus* apart from females of *P. schmitti*. Also, the posterior ridge of sternite XII has only two small lateral convexities. The diagonal ridge and conspicuous fold on the interior surface of the distal portion of the lateral lobe of the petasma are typical of *P. setiferus* males.

Serological tests by Leone and Pryor (1952) indicated that, although *P. setiferus* is more closely related to *P. d. duorarum* than to *P. a. aztecus*, the latter two are more closely allied than either is to *P. setiferus*. Their results, thus, confirm conclusions reached through a study of the external morphology of the three shrimps.

Reproduction

SUBADULT STAGE-SEXUAL MATURITY

Males have been found with petasmal endopods joined (animals in subadult stage) at a minimum size of 22 mm. c.l., 105 mm. t.l. The joining of the petasmal endopods occurs within the size range 22 to 27 mm. c.l., 105 to 127 mm. t.l. The minimum size at which females are impregnated is not known.

According to Burkenroad (1934), males have spermatophores fully developed, of maximum dimensions they will attain throughout the life of the shrimp, at a minimum of about 35 mm. c.l., about 155 mm. t.l., but ripe sperm first appear at 25 mm. c.l., about 118 mm. t.l. The smallest ripe females recorded (Burkenroad, 1939) had a carapace length of 30 mm. (about 135 mm. t.l.).

COPULATION

Copulation in *P. setiferus* is believed to take place between hard-shelled individuals (Burkenroad, 1939). Mating in this condition is contrary to that in the species of *Penaeus* with a closed thelycum, in which females are impregnated immediately after molting.

During copulation the male attaches the spermatophore to the female. The spermatophore remains anchored on the thelycum by various attachment structures and a glutinous material that accompanies it when it is extruded. The coxae of the fourth and fifth pereopods of the female are produced into platelike projections bearing long bristles directed medially which press the spermatophore against the thelycum and also help it to adhere to the thelycum. Despite the various devices that help to hold the spermatophore anchored, it seems to be rather easily dislodged because few females are found with spermatophores. The spermatozoa have generally been thought to be released from the spermatophore simultaneously with the expulsion of the ova. Harry L. Cook (per-

sonal communication), however, observed in the laboratory that mature females that did not bear a spermatophore spawned eggs that developed normally; the eggs were reared to subadult stages.

OVARY DEVELOPMENT

The female reproductive system consists, as in other *Penaeus*, of two partly fused ovaries, which in mature animals extend for much of the length of the body. Each ovary has a long, slender anterior lobe that extends to the level of the anterior portion of the gastric mill and bears lateral projections (usually 6–8) in the cephalothorax, and a posterior lobe running the length of the abdomen dorsolateral to the midgut.

The five ovary stages recognized by King (1948) and now generally accepted are:

1. Undeveloped. Found in young shrimp; ovaries are small and translucent.

2. Developing. Ovaries larger, opaque, and yellowish, with scattered melanophores over surface.

3. Nearly ripe or yellow. Ovaries are still larger than in previous stage and are yellow to yellowish-orange.

4. Ripe. Ovaries reach maximum size, occupy practically all space among other organs, and are drab olive-brown. Diameters of ova range from 0.192 to 0.300 mm. (Gutsell MS.[3]). According to Pearson (1939), eggs measure 0.28 mm.

5. Spent. Recently spawned ovaries are flaccid, muddy green, not so deeply colored as in the ripe stage. As they regress the ovaries become yellowish or milky and resemble the "developing" stage. Only through microscopical examination can the stage of the opaque ovary be accurately determined, although the length and weight of the gland often permit a distinction between the two stages.

The eggs are spherical and opaque, and possess a chorion with purplish-blue coloration in reflected light under a microscope (Pearson, 1939). The spermatozoa have a large, subspherical head, a short and narrow middle piece, and a relatively thick, short tail (King, 1948).

The number of eggs produced by a female is not known with certainty. Burkenroad (1934) indicated that a female white shrimp produces an average of about 500,000 eggs, whereas Anderson, King, and Lindner (1949) stated that the ovary of a 172-mm. female contained about 860,000 eggs and that a female could be expected to lay between 500,000 and a million eggs at a single spawning. For the present, this range of fecundity of one-half to almost a million eggs in a single spawning must be accepted.

SPAWNING

Spawning is in oceanic waters. On the basis of the presence of ripe and recently spent females, Lindner and Anderson (1956) concluded that in Louisiana waters most spawning takes place in depths of 4.5 to 17 fm. Their finding has been confirmed by a number of authors for the entire northern Gulf of Mexico. Pearson (1939) and Lindner and Anderson (1956) indicated that in some areas of the Atlantic Coast spawning may occur near shore.

The beginning of spawning varies slightly in different areas, but even within an area it seems to vary from year to year and with depth. Lindner and Anderson (1956) stated that spawning probably begins late in March or early in April and may extend into November, though probably it is completed by the end of September. Renfro and Brusher (1964) concluded that in the northern Gulf of Mexico the onset of spawning is in mid-April or early in May at 7½ fm., but takes place several weeks earlier at 15 fm. Recently, Temple and Fischer (1967), as a result of their studies in the Gulf of Mexico, near Galveston, Tex., stated that "The occurrence of larvae at 14 m. (about 7¾ fm.) stations in April to August reflects, we believe, the spawning of white shrimp in shallow waters." In northeast Florida spawning seems to begin at about the same time as in Texas; Joyce (1965) suggested that spawning probably begins in April and lasts until October. In South Carolina and North Carolina it apparently starts later. Lindner and Anderson (1956) stated that in South Carolina they found spawning to start in May and extend into September; they believed that no more than 2 weeks separated the onset of spawning in South Carolina and Texas. Williams (1955a) gathered evidence that spawning starts in May in North Carolina.

Lindner and Anderson (1956) concluded that in the northern Gulf of Mexico, spawning appears to increase to a single peak in June or July, but the number of shrimp in inshore waters did not follow this trend. On the basis of frequency distribution of the catches, two main broods appeared annually in certain localities and three in others.

[3] Gutsell, James S. A study of the ovaries of the common shrimp *Penaeus setiferus* with reference to the life history. In the files of the Gulf Investigations, U.S. Fish and Wildlife Service, New Orleans, La. (Unpublished manuscript, 1936).

Gunter (1950) and Kutkuhn (1962) in the same region and Joyce (1965) in northeast Florida found two main broods annually.

Temperature is a major factor controlling spawning. Lindner and Anderson (1956) stated that spawning seems to be started more by rapid changes in temperature than by attainment of an optimum temperature; sudden warming in the spring apparently triggers spawning, which appears to end when the temperature declines abruptly in the fall, even though the water is warmer at this time than at the beginning of the spawning season.

Evidence is considerable that *P. setiferus* may spawn more than once during its life span. King (1948) found that immediately after the first spawning the spent ovaries grow considerably. He suggested that females which spawn early in the season may develop a second crop of eggs and spawn again the same season. Studies of ovary development in the northwestern Gulf by William C. Renfro and Robert F. Temple (personal communication) indicate that recovery and redevelopment are fairly rapid, at least during the summer; recently spent ovaries contained large numbers of rapidly developing ova together with ripe ova in the process of being absorbed. According to Lindner and Anderson (1956), the percentage of females with spent ovaries is very low in Louisiana waters from June through August. They suggested shrimp could spawn four times in a season.

SEX RATIO

The general male-female ratio appears to be about 1:1; considerable variation has been observed, however. I have examined many offshore samples that contained but one sex, so some segregation by sexes may occur.

Postembryonic Development

LARVAE, POSTLARVAE, AND JUVENILES

Eggs hatch within a few hours after spawning, and the young emerge as nauplii, the first of 11 larval stages. Pearson (1939) was the first to study the larval development of white shrimp through material found in plankton samples and by rearing experiments. So accurate were his observations that subsequent studies by Heegaard (1953) and Johnson and Fielding (1956) have proved his series of stages almost faultless, except that one mysis stage was not recognized. Harry L. Cook (personal communication) observed in the laboratory that *P. setiferus* has five nauplial, three protozoeal, and three mysis stages. After the last mysis comes the first mastigopus or first postlarva.

Some investigators doubt the existence of diagnostic characters that distinguish the larvae of western Atlantic *Penaeus*, whereas others maintain that they can be separated. Pearson (1939) and Heegaard (1953) described the main characteristics of various larvae of *P. setiferus*.

The whole larval cycle of the white shrimp was found by Johnson and Fielding (1956) to extend 10 to 12 days, but these authors stated that "the duration of the metamorphic period is not fixed, but depends to some extent on local conditions of food and habitat." At the end of this period the planktonic larvae have reached the postlarval stage. Early postlarvae are planktonic and live offshore. As they grow they move toward and finally enter inshore waters.

Williams (1959) distinguished postlarvae under 12 mm. t.l. of *P. setiferus*, *P. a. aztecus*, and *P. d. duorarum* on the basis of two characters recognized by Pearson (1939)—the relative lengths of the rostrum and third pereopod—as well as by body size and shape of the distal end of the antennal scale. These characters have proved to be helpful, although it seems that sometimes their range of variation in the various species overlaps. According to Baxter and Renfro (1967), those features allow the identification of white shrimp postlarvae up to 10 mm. t.l. in the Galveston area.

Recently, Zamora and Trent (1968) reported that in postlarval white shrimp the keel of the sixth abdominal somite is smooth, lacking setae, whereas that of postlarval brown and pink shrimps bears setae. The presence or absence of setae on the keel considerably facilitates the separation of the postlarvae of white shrimp from those of the pink and brown shrimps.

Small *Penaeus* are considered juveniles when they have attained the ultimate rostral tooth formula. Freshly caught juveniles of the white shrimp often have widely spaced body chromatophores and, thus, have a lighter color than those of sympatric pink and brown shrimps; this character, however, has only limited diagnostic value since shrimp collected from dark substrates tend to be dark. Juveniles 18 mm. t.l. have no long adrostral sulci and so are easily separated from the grooved *Penaeus*.

In the development of individuals sex can be determined easily when they reach 6 mm. c.l., 28 mm. t.l. At this length females can be distinguished from males by the endopods of the first pair of pleopods, which are relatively shorter and narrower, and by the presence of two protuberances on sternite XIV, which are minute but clearly distinct. At 18 mm. c.l., 86 mm. t.l., the median flagellum of the male bears a few long processes, at 21 mm. c.l., 96 mm. t.l., it has small processes, and at 23 mm. c.l., 109 mm. t.l., its longer and shorter processes are well developed. The sizes given above are the minimum at which the antennular processes, in males, have attained the respective stages of development.

GROWTH

Growth studies in *Penaeus* shrimps are difficult because of the variation in rate of increase according to size and sex of individuals as well as during the different seasons of the year. After rearing shrimp in ponds, Johnson and Fielding (1956) estimated that white shrimp attain a total length of about 80 mm. 2 months after hatching. Gunter (1950) had previously reported a growth rate of 25 to 40 mm. per month from 28 to 100 mm. t.l. in inshore water adjacent to the Gulf of Mexico, and Viosca (1920) estimated a monthly growth of about 25 mm. for shrimp with 30 to 150 mm. t.l. In Mobile Bay, Ala., Loesch (1965) found that white shrimp increase 12 to 27 mm. a month in winter, 18 to 31 mm. in summer, and the "very young" may grow as much as 65 mm. per month in summer. Williams (1955a) calculated that inshore white shrimp in North Carolina grow about 36 mm. per month during the summer, and Joyce (1965) estimated that white shrimp in northeast Florida grow an average of 35 mm. per month. Lindner and Anderson (1956) concluded that individuals 100 mm. long reached 141 mm. in 2 months—an average increase of 20.5 mm. per month. Lindner and Anderson (1956) also showed that shrimp grow rapidly through the spring to early fall. Klima (1964) estimated that in Louisiana waters during the fall white shrimp grow from 120 mm. to 159 mm. in 2 months, an average of about 19.5 mm. per month, whereas larger shrimp grow very little. Growth is negligible during the winter, a conclusion reached by Lindner and Anderson (1956) for all populations, by Kutkuhn (1962) for the Louisiana offshore population, and by Joyce (1965) for the northeast Florida population.

Kutkuhn (1962) estimated that the rate of weight increase is relatively low in small shrimp, reaches a maximum in the middle of the size range, and then decreases progressively with further increase in size. He found that growth also varies considerably from year to year; one age class showed a 30-percent increase from November through April, whereas the corresponding age class in the previous year showed a 150-percent increase during the same period.

SEX DIFFERENCES IN SIZE

The largest female examined, collected off mouth of Sabine River, Tex., is 60 mm. c.l., 200 mm. t.l.; the largest male, collected off Bayou Scolfield, La., is 41 mm. c.l., 175 mm. t.l.

Sizes of females and males differ little inshore, as shown in the length frequency distribution of the shrimp in North Carolina (Williams, 1955a) and in northeast Florida (Joyce, 1965). A sex-size disparity occurs offshore, where females are larger than males (Weymouth et al., 1933). In my samples the differences in length between sexes do not appear to be so pronounced as those shown by the grooved shrimps.

Ecology

FOOD

Juvenile and adult white shrimp were reported to be omnivorous by Viosca (1920), Weymouth et al. (1933), Darnell (1958), and Broad (1965). Their digestive tracts have been found to contain, in addition to inorganic detritus and organic debris, fragments of many different animals, particles of higher plants, and a variety of diatoms and other algae.

Studies by Flint (1956) of the stomach contents of "shrimp" (some of which were probably white shrimp) from Louisiana showed they were scavengers. He found a great variety of fragments of bryozoa, sponges, and corals and also sand grains. He stated that filaments of blue-green algae, lithophytic algae, and diatoms were present in such quantities as to indicate that algae may often serve as an important element of their diet. This worker assumed that the presence of diatoms "was incidental to the intake of other structures to which they were adherent or attached." Flint also noted that the contents of the intestinal tract of small shrimp about 10 mm. t.l. "consisted almost

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entirely of cropped filaments of blue-green algae and such diatoms as ordinarily in the natural habitat would have been found adherent to them."

Studies by Zein-Eldin (1964) emphasized the importance of an abundance of food during the postlarval–juvenile period in the life of the shrimp and indicated the ultimate value of the estuarine waters in providing the vast amount of food required for the rapid growth of the shrimp before it returned to the sea.

SUBSTRATE

P. setiferus inshore live mostly on muddy or peaty bottoms that have large quantities of decaying organic matter or vegetation for protection. Occasionally they occur on bottoms of sand or clay (Williams, 1955a, 1955b). Laboratory experiments by Williams (1958) indicated that the young white shrimp prefer softer substrates than do the young pink or brown shrimps.

Adult white shrimp are most abundant in offshore waters on soft muddy and silt bottoms. They also live on bottoms of clay or sand with fragments of shells (Springer and Bullis, 1954; Hildebrand, 1954, 1955).

P. setiferus burrows in the bottom but apparently not as regularly as do the brown or pink shrimps. Williams (1958) observed that it leaves the long antennae lying on the surface of the bottom, whereas the other two shrimps often bury their antennae (which are shorter than those of the white shrimp).

DIEL CYCLE

Although *P. setiferus* has been thought to be a diurnal species, Williams (1958) found that in the laboratory it is also active at night. Fishing for white shrimp, inshore as well as offshore, is usually carried out during the day, but some successful catches are made at night. Joyce (1965) considered white shrimp to be diurnal, but stated that in certain inshore localities during the summer, sample catches at night equaled or even exceeded those made during the day. He suggested that migration could have been a factor in the abundance of shrimp in these instances.

MOVEMENTS

Most scientists believe that favorable currents transport the larvae and early postlarvae toward inshore waters.

Many studies have been made on the movements of the postlarvae of white shrimp. As stated earlier, shrimp reach the nursery grounds as postlarvae, 6 to 7 mm. long (Weymouth et al., 1933; Anderson, King, and Lindner, 1949; Bearden, 1961; Baxter and Renfro, 1967). There they adopt a benthic existence (Anderson, King, and Lindner, 1949; Williams, 1955a) either immediately or, as indicated by Joyce (1965), after having traveled some distance inland. Williams (1955a) also stated that postlarvae, as well as juveniles, are able to move many miles before finding a suitable nursery area. In the northern Gulf of Mexico they arrive in coastal waters from May to November (Christmas et al., 1966; Baxter and Renfro, 1967). According to Baxter and Renfro (1967), peak postlarval immigration into Galveston Bay, Tex., occurs in the summer. In South Carolina (Bearden, 1961) and in North Carolina (Williams, 1955a) postlarvae begin to arrive in early June, and the period of influx extends throughout the summer to mid-August or September. Postlarval abundance appears to show two peaks in the area, one in early June and the other in mid-August.

In the nursery grounds, the size of juveniles often shows a gradient; the smaller individuals are farther inland. White shrimp may be found in rivers as far from the coast as about 160 km. (Burkenroad, 1934) and 210 km. (Joyce, 1965)—farther than the brown or pink shrimps. Shrimp grow rapidly, and as they grow they move back to water nearer the sea and shrimp return to the sea when they have attained a modal length between 100 and 120 mm. t.l. (Weymouth et al., 1933; Gunter, 1950; Lindner and Anderson, 1956). The seaward migration takes place from spring through summer and early winter. In some areas two migrations are typical, one in spring and the other at the onset of winter. The first seems to be undertaken by shrimp hatched late in the previous spawning season, and the second migration is by shrimp spawned early in spring. Lindner and Anderson (1956) and Joyce (1965) believe that the stage of maturation of the gonads is the main determinant of this migration, although fall and winter temperatures also influence it.

Adult shrimp may migrate long distances parallel to the shoreline. On the Atlantic Coast, the tagging experiments by Lindner and Anderson (1956) indicated that white shrimp move south during the fall and early winter and northward in late winter and early spring. The longest migration recorded was made by a shrimp that moved

south from near Beaufort, N.C., where it was tagged, to the east coast of Florida, covering a distance of about 580 km. in 95 days. The longest northward migration was made by a shrimp that moved from south of Cape Kennedy, Fla., north to the coast of South Carolina, a distance of about 419 km. in 168 days.

McCoy and Brown (1967) also reported that some shrimp migrate southward from North Carolina. The greatest distance known to have been traveled by the animals they released was 555 km.; two individuals were recaptured off St. Augustine, Fla. That all of the North Carolina population does not leave the area during the winter, however, is attested by the limited white shrimp fishery off Cape Fear during the coldest months of the year (Williams, 1955a).

The limited information gathered by Lindner and Anderson (1956) through tagging in the northeastern Gulf indicated that during the fall and winter white shrimp tend to move into deeper water and toward the mouth of the Mississippi River. The population from the northwestern Gulf, west of the Mississippi River to central Texas, also exhibits only offshore and inshore movements associated with temperature changes and spawning. The marine shelf off the mouth of the Mississippi River seems to be a natural barrier because this area was not crossed apparently in either direction.

Along the coast from south-central Texas to northern Mexico, white shrimp seem to move southward during the fall and early winter and northward in the spring. These coastwise movements compare with those observed for white shrimp on the Atlantic Coast and were first documented by Lindner and Anderson (1956) and later by Gunter (1962c), who based his conclusions on evidence that catches of white shrimp increased during the winter southward along the Coast.

EFFECTS OF TEMPERATURE

As stated earlier, spawning seems to be greatly influenced by temperature, which by its sudden changes apparently initiates and later terminates the ovulation. Temple and Fischer (1967) found that along the coast of Texas white shrimp larvae were present from May through September and that a close correlation appears to exist between temperature and abundance of larvae.

The rate of growth is directly related to temperature, for it reaches its maximum during the warmer months, becomes very slow or negligible during winter, and resumes or increases with the advent of higher temperatures in late winter or early spring.

Laboratory experiments by Zein-Eldin and Griffith (1965) indicated that temperature affected the growth and molting of postlarvae. Animals tested at 18°, 25°, and 32° C., at a salinity of 25 p.p.t., showed that molting frequency and growth increased with temperature, although the increase in total length per molt was independent of temperature. This finding suggests that temperature influences growth through a change in molting rate but has no effect on the increase in size per molting. Their studies indicated further that, at a given salinity, postlarval white shrimp are more sensitive to low temperatures than are postlarval brown shrimp, but that, conversely, white shrimp postlarvae can better withstand high temperatures. Another experiment by Zein-Eldin (1966) confirmed this result.

Lindner and Anderson (1956) gathered evidence that white shrimp moved from shallow to deeper water during cold periods and that the smaller shrimp returned to shallower water when the temperature of the water increased.

There is also some information on how extremes of temperature affect white shrimp. Lunz (1956) reported that *P. setiferus*, 51 to 95 mm. t.l., had survived 36° C. in a pond in South Carolina. Reports of mortality of white shrimp during cold waves have been given by Gunter (1941), Gunter and Hildebrand (1951), Lunz (1958), and Joyce (1965), all of whom have found white shrimp dead after near freezing (4° and 4.5° C.) or freezing temperatures. Joyce found shrimps in a state of decay, which suggested that they had died during the first days of freezing temperatures. Sudden changes of temperature often may be responsible for the mortality of the shrimp rather than the temperature itself, although both the rate of change and the duration of high or low temperatures doubtlessly affect mortality.

EFFECTS OF SALINITY

Conclusions about the influence of salinity on the life and distribution of white shrimp inshore vary widely. High concentrations of young individuals in low-salinity waters (less than 10 p.p.t.) have been reported by a number of authors—Gunter (1950), Gunter and Shell (1958), Gunter (1961a), Gunter et al. (1964), and H. Loesch (in

unpublished data, the conclusions of which were included in the paper by Gunter et al., 1964). Williams (1955a) pointed out that in North Carolina young white shrimp are most abundant in the areas of lowest salinity and that in general they live in waters of lower salinity than do the brown or pink shrimps. Gunter (1961a) suggested that the low salinity of Louisiana nursery grounds may be optimal for juvenile white shrimp. Joyce (1965) reported that white shrimp made up by far the largest percentage of shrimp in localities of lower salinities and that no white shrimp were caught in the high-salinity waters of the Edgewater-Oak Hill (Fla.) area. The fact that white shrimp move farther upriver and grow to a greater size in inshore waters seems to indicate that the young have a higher tolerance to low salinity over a longer period of their development than the sympatric *Penaeus*.

Gunter and Hildebrand (1954) are of the opinion that in Texas there is a direct correspondence between rainfall of the State and production of white shrimp. Gunter et al. (1964) pointed out that the drought from 1947 to 1957 was accompanied by a remarkable decline in production of white shrimp, and when the long drought was over the annual production increased 331 percent from 1957 to 1958.

The lowest salinities at which the young of *P. setiferus* have been recorded are 0.42 p.p.t. in the northern Gulf of Mexico (Gunter and Shell, 1958) and 0.26 p.p.t. in northeast Florida (Joyce, 1965).

Although the field studies mentioned above indicate that white shrimp prefer low-salinity water, other studies show that they are not affected adversely by high salinity and are rather insensitive to large fluctuations in salinity. Lindner and Anderson (1956), as a result of their investigation in the waters of Louisiana, and Hoese (1960a, 1960b) who worked in various localities along the coast of Texas, concluded that within certain areas at least, young shrimp are indifferent to varying salinity. In Laguna Madre small white shrimp have been found at salinities of 47.96 p.p.t. (Hildebrand, 1958) and 41.3 p.p.t. (Gunter, 1961a). Lunz (1956) reared juveniles at 17.6 to 33.2 p.p.t., and Johnson and Fielding (1956) found that white shrimp could be reared successfully in ponds at salinities of 18.5 to 34 p.p.t. Laboratory experiments by Zein-Eldin (1963a) showed that, under constant temperature and rather restricted diet, postlarval shrimp can survive and grow within a wide range of salinity. She stated that "it would appear that salinity tolerance *per se* may not play a direct role in the growth and survival of postlarval and juvenile shrimp in the estuarine environment." Joyce (1965) observed a temperature-salinity relation in the distribution of inshore shrimp and stated that apparently these shrimp remained away from areas of low salinity during cold weather. This finding agrees with the laboratory findings of Zein-Eldin and Aldrich (1965), who observed that postlarvae of *P. a. aztecus*, at temperatures below 15° C., exhibited decreased tolerance to low salinity. Burkenroad (1939) suggested that the general geographic distribution of the species possibly depends on a temperature-salinity correlation and that temperature might limit the occurrence of white shrimp within an extreme range of salinity.

ENEMIES AND DISEASES

P. setiferus, like *Penaeus* in general, constitute part of the diet of many carnivorous teleost and some elasmobranch fishes (Gunter, 1945; Darnell, 1958). Cannibalism, common among *Penaeus* as soon as they reach the postlarval stage, makes their maintenance in aquariums difficult for laboratory experiments if they are not well fed.

White shrimp appear to suffer from a number of diseases, some of them caused by parasites. Telosporidians, cnidosporidians, trematodes, cestodes, and nematodes have been recorded from white shrimp (Sprague, 1950, 1954; Kruse, 1959; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959; Hutton et al., 1962; Hutton, 1964; Aldrich, 1965). Dawson (1957) and Joyce (1965) reported *Balanus* on white shrimp.

HARDINESS

According to De Sylva (1954), *P. setiferus* is more delicate and short lived than *P. d. duorarum* and *P. a. aztecus*. Apparently, it is also the most susceptible to low temperatures. Broad (1965) too considers *P. setiferus* less hardy than *P. a. aztecus*.

Commercial Importance

This species is fished in several areas along the eastern coast of the United States, the most important of which are Georgia and the northeast coast of Florida. The most northern fishery is in the vicinity of Pamlico Sound, North Carolina.

The largest production by far is in the Gulf of Mexico, where the waters of Louisiana and eastern

Texas yield the highest catches. This species was the only shrimp fished in the estuarine waters along the northern coast of the Gulf of Mexico until about 1937–38, when offshore stocks began to be fished. The resource then declined while landings of brown and pink shrimps increased. By mid-1950, catches of those two species far exceeded catches of white shrimp. During 1956–59, white shrimp constituted only 20 percent of all Gulf shrimp produced by U.S. fishermen, but landings in recent years have risen again. According to Lyles (1967), annual landings of white shrimp in the United States during 1965 were 30,865,840 kg. (whole weight), or about 31 percent of all shrimp landed.

Along the Gulf coast of Mexico the white shrimp is caught commercially on the northeast coast of Tamaulipas and off Cabo Rojo, Veracruz, where it is fished in small quantities. The most important white shrimp grounds in Mexico are between Laguna Mecoacán and Paso Real, in Golfo (Bahía) de Campeche. *P. setiferus* contributes substantially to the shrimp landings from the Gulf coast of Mexico—20,224,000 kg. in 1966 (Croker, 1968)—but the actual composition of the landings, which also include *P. d. duorarum* and *P. a. aztecus*, is not known.

Penaeus (Litopenaeus) schmitti BURKENROAD

Figures 14 to 19

Cuba, Honduras, Nicaragua, Venezuela: camarón blanco. Cuba: camarón casquiazul. Venezuela: longostino blanco. Brazil: camarão legítimo, camarão verdadeiro, camarão branco, camarão lixo, vilafranca, caboclo. United States: white shrimp, blue shrimp, green shrimp. British Honduras: white shrimp.

Cancer setiferus: Gmelin, 1790: 2990 [part]; [fide] Gunter, 1962a: 108; Gunter, 1962b: 119; Gunter, 1963: 104, 105, 107, 108; Gunter, 1964: 229–231. Not *Cancer setiferus* L., 1767.

Astacus setiferus: Olivier, 1791: 343. Not *C. setiferus* L., 1767.

Palaemon setiferus: Olivier, 1811: 660; [fide] Gunter, 1962a: 108. Not *C. setiferus* L., 1767.

Penaeus setiferus: H. Milne Edwards, 1837: 414, 415 [part]; de Saussure, 1858: 471 [part]; Heller, 1865: 121; Bate, 1881: 176–178, pl. 11, fig. 1; Kingsley, 1882: 107 [part]; Sharp, 1893: 110 [part]; Guppy, 1894: 115; Rathbun, 1897: 45, 46; Rathbun, 1900: 151; Moreira, 1901: 7, 72, 73; Johnson and Lindner, 1934: 68; Burkenroad, 1934: 77, 86 [part]; Burkenroad, 1939: 19, 20 [part]; von Ihering, 1940: 194, 871, fig.; de Oliveira, 1940: 141; Magalhães Filho, 1943: 12, 24; Magalhães Filho, 1944: 100, 101; de Oliveira, 1944: 133; de Oliveira, 1950: 371, 386; Sánchez Roig and Gómez de la Maza, 1952: 162, 163, fig. 5; Devold, 1958: 20; Gunter, 1962a: 107–112; Gunter, 1962b: 119–121; Gunter, 1963: 103, 105–108; Gunter, 1964: 229, 230; Gunter, 1966: 78. Not *P. setiferus* (L.), 1767.

Penaeus setifer: von Martens, 1872: 141, 142; von Martens, 1876: 38; Doflein, 1900: 126, 127 [part].

Peneus setiferus: von Ihering, 1897: 156. Not *P. setiferus* (L.), 1767.

Penaeus schmitti Burkenroad, 1936: 313–318, figs. 1a, 2, 3 (lectotype, here designated, ♂, YPM 4396–BOC 128–Kingston, Jamaica, February 1, 1934; paralectotypes, YPM); Burkenroad, 1939, 19, 20; Anderson and Lindner, 1945: 304; Whiteleather and Brown, 1945: 25, 27; Carlson, 1953: 34; Pérez Farfante, 1953: 232–235, 238, 241; Pérez Farfante, 1954a: 97; Voss, 1955: 8, 10, fig. 10a, b; Gunter, 1956: 100; Dall, 1957: 142; Lindner, 1957: 11–14, 16, 21–23, 34–36, 65–67, 69, 70, 129–131, 153, 154, 160–165; Suárez Caabro, 1957: 137; U.S. Fish and Wildlife Service, 1958a: 11, 13; Lindner, 1858: 31–33; Suárez Caabro, 1958: 5, 7; Bullis and Thompson, 1959a: 41; Bullis and Thompson, 1959b: 7, 9; Higman, 1959: 8, 10, 13; Holthuis, 1959: 42–44, 61–63, 66, fig. 6a; Eldred and Hutton, 1960: 91, 98, 99, 101, 104, 108; Sadowski and Radasewski, 1960: 1–5; Anonymous, 1961: 34; Pérez Farfante, Acosta, and Alemany, 1961: 33, 36–38, 50; Gunter, 1962a: 110, 111; Holthuis, 1962: 115, 117, 118; Idyll, 1962: 184; Kutkuhn, 1962: 343; Loesch, 1962: 172–177; Miles, 1962: 189, 193; Boschi, 1963: 5, 6, 13, 17–20, 29, figs. 5 (1–7), 11; Davant, 1963: 9–11, 26–29, 34, 35, 66, 67, 82–85, 87, 88, 90, 91, figs. 4, 5, and 4, 5, bis; Gunter, 1963: 103, 104, 106; Simpson, 1963: 22, 23; Boschi, 1964: 39, 41; Ewald, 1964: 20, 22, 24, 25, table, figs. 10, 11; Gunter, 1964: 230, 231; Holthuis, 1964a: 227–229; Neiva and Wise, 1964: 132, 133; Tremel, Wise, Mistakidis, and Jonsson, 1964: 6, 7, 12, 20, 24; Ewald, 1965a: 26, 29, 30; Ewald, 1965c, 51, 52, 59, 65, 69, 72–74, 80, 81, 83, 84, 86, 88–99, 103–114, 5 figs., pls. 3–5; García Pinto, 1965: 131–134; Holthuis and Rosa, 1965: 6; Mistakidis, 1965: 9, 11, 18, 28; Pericchi López, 1965: 23; da

Silva, 1965: 1, 3; Simpson, Griffiths, and Atilano, 1965: 77; Tremel and Mistakidis, 1965: 2, 4; Alves Coelho, 1966: 162, 168; Mistakidis and Neiva, 1966: 434; Neiva and Mistakidis, 1966: 1, 2, 5, 6, figs. 9a, b; Croker, 1967: 63, 67, 68, 73–75, 78–80, 84, 86, 87, 89, 94, 95, 98, 106; International Commission on Zoological Nomenclature, 1967: 151, 152; Instituto de Fomento Nacional, 1967: 5, 8.

Penaeus setilerus: Magalhães Filho, 1944: 101, fig. 4B.

Penaeid schmitti: Anonymous, 1962: 56.

Penaeus schimitti: Boschi, 1964: 40.

Penaeus schmitt: Gunter, 1964: 230.

White shrimp: Carlson, 1953: 34.

Camarão legítimo: Richardson and Moraes, 1960: 8, 9, 18, 34, 36, 42, 43, 48; Braga, 1962: tables 1, 2.

Taxonomic Remarks

Burkenroad (1936), in his description, cited two "types," one a male and the other a female. I here designate the male as the lectotype of *Penaeus schmitti* Burkenroad; the remaining specimens in the type series are paralectotypes.

Study Material

CUBA

4 ♂ 3 ♀, CIP, Cojímar, La Habana, 1954, J. A. Suárez Caabro. 3 ♂ 2 ♀, CIP, Jaruco, La Habana, 1954, A. de la Torre. 1 ♂ 2 ♀, USNM, Bahía de Matanzas, 1954, C. Sánchez. 5 ♂ 6 ♀, CIP, Nuevitas, Camagüey, 1953, J. A. Suárez Caabro. 1 ♂ 1 ♀, USNM, estuary Río Cacoyugüín, Bahía de Gibara, Oriente, C. G. Aguayo. 2 ♂ 3 ♀, CIP, Banes, Oriente, 1953, A. R. Quiñones. 6 ♂ 4 ♀, CIP, Antilla, Oriente, 1953, H. Martínez. 5 ♂ 5 ♀, CIP, Bahía de Nipe, Oriente, 1953, J. Fernández Pardo. 12 ♂ 1 ♀, CIP, Niquero, Oriente, T. Sánchez. 5 ♂ 2 ♀, USNM, Manzanillo, Oriente, J. Saavedra. 22 ♂ 19 ♀, CIP, Manzanillo, Oriente, 1954, T. Sánchez. 50 ♂ 50 ♀, CIP, Golfo de Guacanayabo, Oriente, 1959, I. Pérez Farfante. 42 ♂ 38 ♀, CIP, off Santa Cruz del Sur, Camagüey, 1954, I. Pérez Farfante and G. Canet. 18 ♂ 15 ♀, CIP, Júcaro, Las Villas, 1954, G. Canet and T. Sánchez. 20 ♂ 22 ♀, CIP, Tunas de Zaza, Las Villas, 1954, G. Canet and T. Sánchez. 3 ♂ 5 ♀, CIP, Casilda, Las Villas, 1954, G. Canet and T. Sánchez. 1 ♂ 1 ♀, USNM, Bahía de Cienfuegos, Las Villas, 1954, G. Muñoz.

JAMAICA

29 ♂ 29 ♀, USNM, March 1–11, 1884, *Albatross.* 10 ♂ 15 ♀, YPM, Kingston market, February 26, 1937, *Atlantis* in port.

HAITI

3 ♀, USNM, Port au Prince, March 10, 1944, A. Curtis. 1 ♂, USNM, Port au Prince, August 22, 1945, A. Curtis. 1 ♂, USNM, Port au Prince, September 14, 1945, A. Curtis. 1 ♀, USNM, Port au Prince, 1946, A. Curtis. 1 ♂ 1 ♀, USNM, Montet, May 17, 1930, W. Parish.

BRITISH HONDURAS

1 ♀, UMML, Belize, April 15, 1954, E. P. Bradley.

NICARAGUA

1 ♀, UMML, off Nicaragua, 1959. 2 ♂ 2 ♀, UMML, S. of Puerto Cabezas, August 8, 1958. 2 ♂ 1 ♀, USNM, Bluefields, 1965, A. Flores.

COSTA RICA

4 ♂ 1 ♀, USNM, Puerto Limón, November 1966, Ex. M. C. Filippi.

PANAMA

1 ♀, USNM, Fox Bay, Colón, March 31, 1911, S. E. Meek and S. F. Hildebrand. 1 ♀, USNM, Fox Bay, Colón, February 23, 1935, S. F. Hildebrand. 2 ♀, USNM, Mindi Cut, Canal Zone, February 3–4, 1911, S. E. Meek and S. F. Hildebrand. 15 ♂ 8 ♀, USNM, Colón, January 27, 1912, S. E. Meek and S. F. Hildebrand. 2 ♂ 2 ♀, YPM, Limón Bay, Canal Zone, October 1934, *Atlantis* in port.

COLOMBIA

6 ♂ 10 ♀, USNM, off Tucuracas, Departamento de la Guajira, 12 fm., October 6, 1965, *Oregon* Sta. 5674.

VENEZUELA

3 ♂ 2 ♀, UMML, Lake Maracaibo, December 1963, J. J. Ewald. 9 ♂ 15 ♀, USNM, Curarire, Lake Maracaibo, July 9, 1964, J. J. Ewald. 12 ♂ 3 ♀, USNM, Barranquita, Lake Maracaibo, April 23, 1964, J. J. Ewald. 2 ♀, USNM, Tacarigua de la Laguna, Miranda, March 1, 1949, Hno. Ginés. 4 ♂ 2 ♀, USNM, Gulf of Venezuela, May 3, 1964, J. J. Ewald. 1 ♀, USNM, Castilletes, Gulf of Venezuela, 10 fm., October 6, 1965, *Oregon* Sta. 5669. 1 ♀, UMML, Carenero, 1962, Tovar. 1 ♂, USNM, off Isla Mariusa 13 to 15 fm., August 26, 1958, *Oregon* Sta. 2211. 1 ♂ 1 ♀, USNM, off Punta

Araguapiche, 15 fm., August 26, 1958, *Oregon* Sta. 2210. 2 ♀, USNM, off Boca Araguao, 9 to 10 fm., August 27, 1958, *Oregon* Sta. 2215.

TRINIDAD

1 ♀, UWI, Caroni Swamp, October 1965, P. R. Bacon. 1 ♀, USNM, Cocorite Swamp, August 31, 1966, P. R. Bacon. 1 ♂ 2 ♀, USNM, Maturin Bar, Gulf of Paria, 6 fm., April 26, 1944, R. J. Whiteleather and H. H. Brown.

GUYANA

2 ♂ 2 ♀, USNM, pond of Fisheries Laboratory, Department of Agriculture, 1960, W. H. L. Allsop. 1 ♀, USNM, off Guyana, 12 fm., May 30, 1957, *Coquette* Sta. 155. 5 ♂ 3 ♀, USNM, off Guyana, 10 fm., March 25, 1963, *Oregon* Sta. 4306.

SURINAM

1 ♂, USNM, NE. of mouth of Surinam River, 13 1/5 fm., June 11, 1957, *Coquette* Sta. 203. 1 ♀, USNM, off mouth of Surinam River, 13⅕ fm., June 11, 1957, *Coquette* Sta. 208. 1 ♂, USNM, off mouth of Surinam River, 14⅗ fm., June 28, 1957, *Coquette* Sta. 293. 5 ♀, UMML, off Surinam, summer 1960, H. Lijding.

BRAZIL

Pará-Maranhão: 1 ♂ 2 ♀, USNM, June–July 1965, P. Paiva.

Maranhão: 1 ♂ 2 ♀, USNM, June 30, 1965, J. Fausto Filho.

Ceará: 2 ♂ 1 ♀, USNM, Fortaleza, April 6, 1965, J. Fausto Filho.

Pernambuco: 2 ♂ 2 ♀, USNM, Recife, August 10, 1964, P. Alves Coelho. 2 ♂ 1 ♀, USNM, Recife, H. von Ihering.

Alagoas: 1 ♂, USNM, Maceió, July 22, 1899, Branner-Agassiz Exped.

Bahia: 1 ♂ 2 ♀, USNM, Mapelle, Hartt Exped. 1 ♂, YPM, Lagoon in Caravelas, Hartt Exped. 17 ♂ 14 ♀, USNM, Taperoá, March 3, 1966, E. Luz. 14 ♂ 1 ♀, USNM, Maragogipe, 1966, A. Barbosa de Oliveira.

Sergipe: 4 ♂ 5 ♀, USNM, mouth of Agua Azeda River, Nossa Senhora do Socorro, March 9, 1966, do Condese.

Espírito Santo: 1 ♂ 1 ♀, MNHNP, Villa d'Anchieta, November 30, 1961, *Calypso* Sta. 92.

Rio de Janeiro: 2 ♂ 2 ♀, USNM, Baía de Sepetiba, 1 fm., SUDEPE. 2 ♂ 1 ♀, USNM, Rio de Janeiro, Ex. Museo Paulista. 1 ♂, USNM, Rio de Janeiro, H. von Ihering.

São Paulo: 1 ♂, USNM, Santos, 1949, J. de P. Carvalho. 1 ♀, USNM, Santos, September 12, 1925, W. L. Schmitt. 7 ♂ 12 ♀, USNM, Santos, September 6, 1964, G. Vazzoler. 1 ♂, USNM, Santos, June 1913, H. Leuderwaldt. 2 ♂ 2 ♀, USNM, Farol de Moela, October 29, 1964, G. Vazzoler. 5 ♂ 4 ♀, USNM, Cananéia, September 1965, V. Sadowsky. 1 ♀, USNM, Cananéia, November 1955, E. E. Boschi. 1 ♂, USNM, Cananéia, Mar do Cubatas, 1950, J. de P. Carvalho.

Paraná: 2 ♀, USNM, Paranaguá, 1965, W. Romanzini.

Santa Catarina: 1 ♀, CPPSC, Armação da Piedade, January 3, 1965, E. Tremel.

Diagnosis

Adrostral carina and sulcus short, ending at epigastric tooth. Petasma with inner surface of distal portion of lateral lobe smooth, lacking diagonal ridge and fold, and with distoventral corner produced, forming subrectangular projection; emargination median to inner lappet deep. Thelycum with pair of subparallel anterolateral almost straight ridges followed posteriorly by two rounded and rigid protuberances on sternite XIV; posterior margin of sternite XII bearing two pairs of rather large projections.

Description

ROSTRUM (fig. 14)

Teeth $\frac{7\text{–}10}{1\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—55, 9/2—26, 7/2—15, 7/1—2, 8/1—1, 10/2—0.66, 9/3—0.33; N=300) + epigastric; ventral teeth relatively far apart, first tooth usually opposite or anterior to last dorsal tooth; rostrum slender and long, in juveniles extending to base of distal ¼ of thickened portion of lateral antennular flagellum; maximum length in relation to carapace length obtained at 13 to 16 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.95); decreasing progressively with increasing length of shrimp, reaching distal end of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.54); rostrum straight, slightly concave posteroventrally; highest portion of blade usually at level of second, occasionally of third dorsal tooth, and at level of first tooth in some young; third dorsal tooth level with anterior margin of carapace; tip slender and long, almost one-half of length of rostrum.

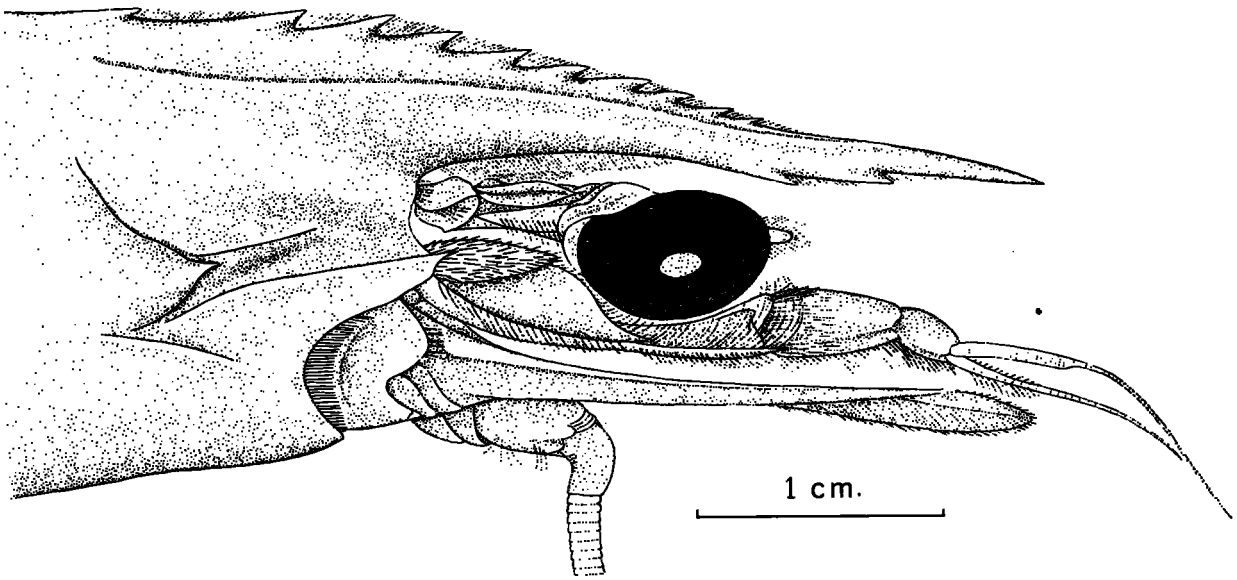

FIGURE 14.—*Penaeus* (*L.*) *schmitti* Burkenroad. Rostrum, ♀ 39 mm. c. l., Santos, Brazil.

Postrostral carina narrow and relatively short, ending 1/7 to 1/13 c.l. from posterior margin of carapace, shorter in larger individuals. Median sulcus shallow, sometimes extremely so, interrupted, often appearing as two elongated depressions followed posteriorly by series of three to six minute pits. Adrostral carina rounded and short, ending at level of epigastric tooth. Adrostral sulcus shallow, and short, same length as adrostral carina.

CARAPACE (fig. 15)

Length in proportion to total length smaller in juveniles, according to my data increasing suddenly at about the size at which subadult stage is reached. Gastrofrontal sulcus and carina absent, except for a short, almost imperceptible rib subparallel to first two rostral teeth. Orbito-antennal sulcus wide anteriorly and narrowing posteriorly to below apex of hepatic spine, there widening into base of spine. Gastro-orbital carina pronounced, sharp and relatively short, occupying posterior 3/5 to 2/3 distance between postorbital margin of carapace and hepatic spine. Antennal carina very prominent. Cervical sulcus deeper at its lower half and extremely shallow above, ending at about two-fifths c.l. from postorbital margin of carapace. Hepatic carina 1/6 to 1/5 c.l., sharp, sloping slightly anteroventrally to end 1/11 to 1/14 c.l. from anterior margin of carapace. Antennal spine acute and relatively short; hepatic spine prominent.

ANTENNULES

Lateral flagellum long, its length seven-tenths to almost same length as antennular peduncle, slightly longer than median flagellum, with articles shorter than those of median flagellum. Median flagellum exhibiting sexual dimorphism: in adult males markedly flattened dorsoventrally, with two closely set rows of stout processes of unequal sizes along midportion of internal margin, and with long setae along proximal one-fifth of external margin; in females processes lacking but long setae present along proximal two-fifths of external margin. Anterolateral spine small, sharp. Stylocerite reaching slightly beyond midlength of first antennular segment. Prosartema extending to proximal fifth of second antennular segment.

ANTENNAE

Scaphocerite 2½ to 2⅔ times maximum width; spine reaching three-quarters of length of third antennular segment to one-fifth of length of thickened portion of antennular flagellum. Carpocerite about 1¼ times longer than wide, its distal end reaching base of eye. Antennal flagellum very long, 2½ to 2⅔ times body length.

THORACIC APPENDAGES

Third maxilliped reaching at least distal end of proximal five-sixths of first antennular segment, and at most distal end of proximal five-sixths of second antennular segment; length of dactyl 2/3 to 3/4 of propodus. First pereopod extending to distal

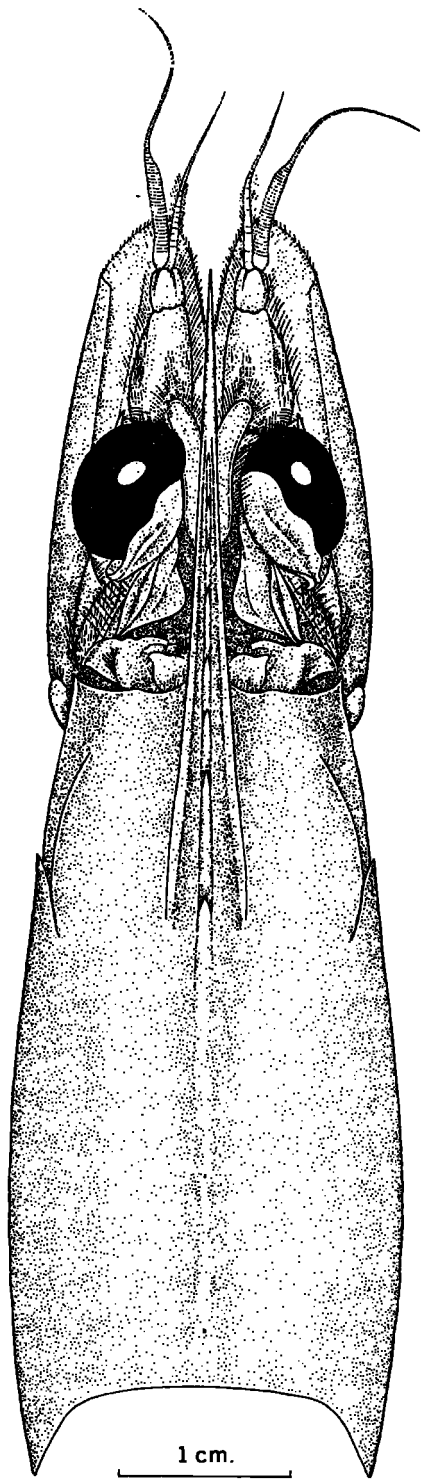

FIGURE 15.—*Penaeus* (*L.*) *schmitti* Burkenroad. Cephalothorax, ♀ 42 mm. c.l., Farol de Moela, Santos, Brazil.

end of carpocerite or surpassing it as much as five-sixths length of dactyl. Second pereopod reaching from seven-ninths of first antennular segment to one-third of second antennular segment. Third pereopod exceeding antennular peduncle from 2/3 to 7/8 of propodus. Fourth pereopod exceeding carpocerite from one-fifth to entire length of dactyl. Fifth pereopod surpassing fourth pereopod only by about one-half length of dactyl. Exopods on all pereopods; long ischial and basial spines on first pereopod; and rather long basial spine on second pereopod.

ABDOMEN

Carinate dorsally from midlength of third or from fourth somite posteriorly, carina gradually increasing in height forming keel on sixth somite, and ending in sharp spine on posterior margin of somite. Dorsolateral sulcus very narrow, shallow, and without lips. Sixth abdominal somite with three cicatrices on each side, anterior one longest; fifth somite with one cicatrix and diagonal series of minute pits anterior to sinus on posterior margin of somite; fourth somite with similar series of pits dorsal to sinus on posterior margin of somite. Ventral margin of pleuron of first somite moderately to deeply indented. Telson unarmed, with deep median sulcus and acuminate tip.

PETASMA (fig.16 a–c)

Lateral lobe with distal portion of inner surface smooth, lacking diagonal ridge and fold; distoventral corner of lateral lobe typically produced medially in subrectangular projection; anterior half of ventral border with two narrow ribs joined at both ends. Emargination median to inner lateral lappet relatively deep. Outer surface of lateral lobe armed with broad band of very closely set spines, as many as seven rows abreast distally and decreasing to two proximally. Crests distally on each side of band of spines, the one close to median lobe more prominent and sharp than that near free ventral margin, latter crest bifurcate. Lateral lobe often extending conspicuously beyond median lobe.

APPENDIX MASCULINA (fig. 16 d, e)

Subtriangular, its length twice or slightly greater than width at base, armed with short spines along median margin and with long ones on distal portion; distal spines slightly less than half length of appendix. Anterior surface subplane, posterior surface strongly concave, concavity bordered by arch-shaped ridge.

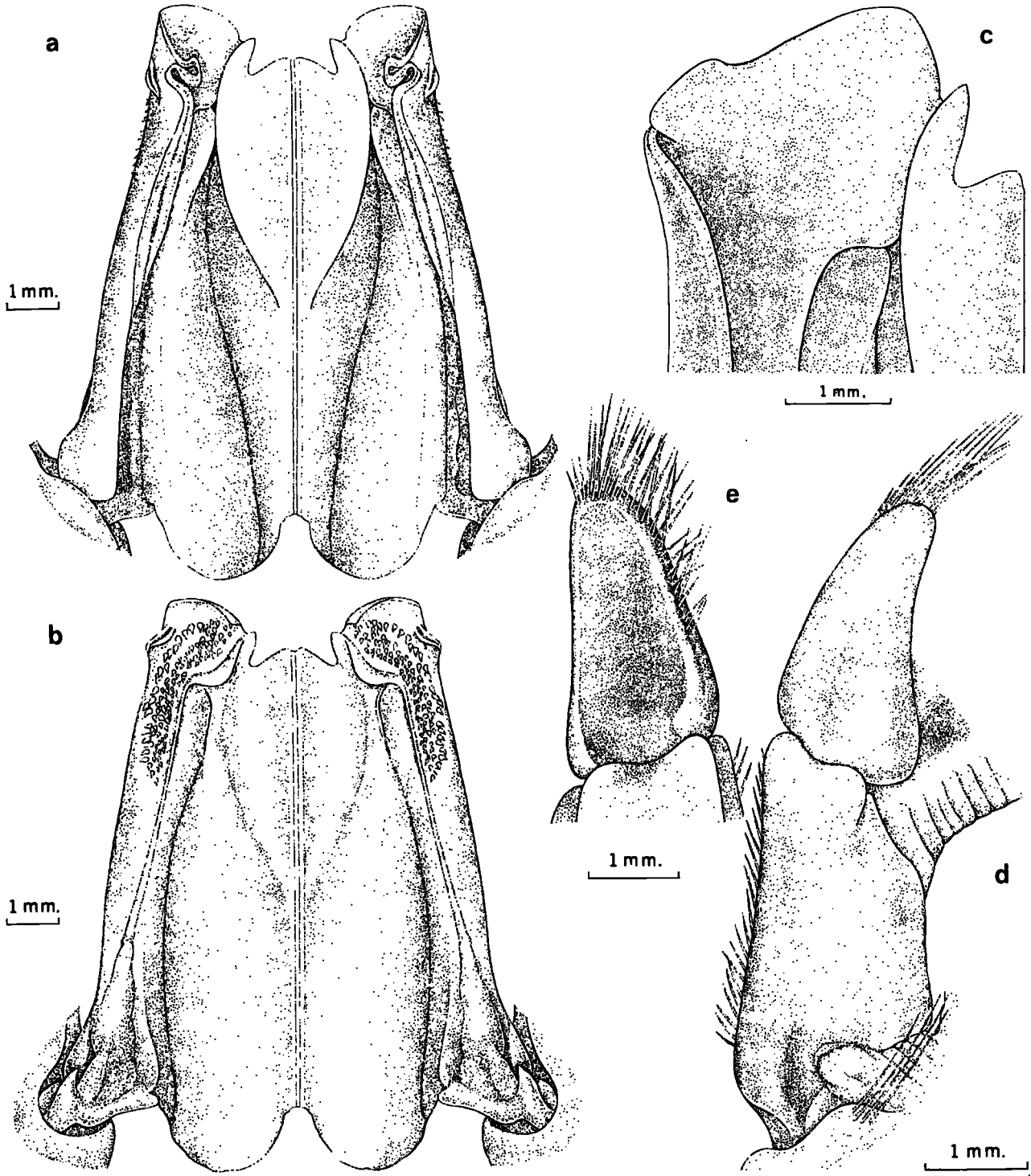

FIGURE 16.—*Penaeus* (*L.*) *schmitti Burkenroad.* a. Petasma, interior surface, ♂ 33 mm. c.l., off Tucuracas, Colombia. b. Petasma, exterior surface, ♂ 33 mm. c.l., off Tucuracas, Colombia. c. Petasma, interior surface of distal portion of left half, ♂ 36 mm. c.l., Punta Araguapiche, Venezuela. d. Appendix masculina, ♂ 36 mm c.l., Farol de Moela. Santos, Brazil. e. Appendix masculina, posterior surface, ♂ 36 mm. c.l., Farol de Moela, Santos, Brazil.

SPERMATOPHORE

Elongate and podlike, actually consisting of two spermatophores; in mature males each lying completely formed in paired terminal ampullae and joined when discharged. Anterior end, when attached to female, bearing pair of winglike lateral processes, each armed with short triangular projection at posterior edge. Posterodorsal portion extended into horizontal plate.

THELYCUM (figs. 17 and 18)

Open type. Sternite XIV with two subparallel anterolateral ridges running posteriorly without turning medially; ridges followed posteriorly by two protuberances, either rounded or subconical with rather inconspicuous apices; very narrow groove bordered by ribs, running along midline of sternite between anterior portion of protuberances. Strong median plate of sternite XIII with emarginated, shelflike projection overhanging sternite XIV; ridge on posterior margin of plate prominent; on anterior portion of sternite XIII fleshy tonguelike lamella bordered by minute setae forming the floor of cavity roofed by strong transverse ridge on posterior margin of sternite XII; ridge of sternite XII (hidden by the structures surrounding the gonopores and coxae of third pair of pereopods) with two pairs of strong projections, lateral pair often more prominent.

COLOR

P. schmitti is most frequently translucent white, having an almost glasslike appearance, with predominantly dark blue chromatophores and a bluish, grayish, greenish, or yellowish cast. Freshly caught juveniles are variable in color but most often light, with blue chromatophores rather sparsely distributed over the body and tail-fan; however, brownish or reddish-brown animals are not uncommon inshore.

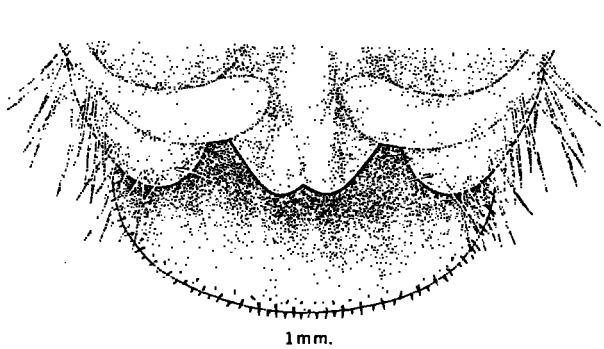

FIGURE 17.—*Penaeus* (*L.*) *schmitti* Burkenroad. Posterior portion of sternite XII and tonguelike lamella of sternite XIII, ♀ 50.5 mm. c.l., off Guyana.

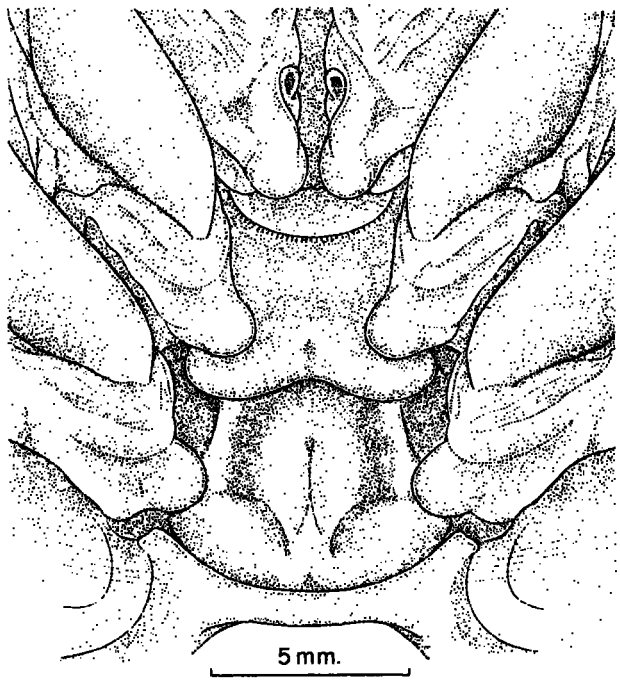

FIGURE 18.—*Penaeus* (*L.*) *schmitti* Burkenroad. Thelycum, ♀ 43.5 mm. c.l., off Guyana.

Distribution and Morphological Variations

P. schmitti ranges from Cuba throughout the Greater Antilles and the Virgin Islands, apparently reaching the Lesser Antilles; it is also found in Trinidad. On the Continental Shelf, white shrimp are found from Belize, British Honduras, along the Caribbean Coast of Central America and northern South America and throughout the Atlantic Coast of South America to Laguna (lat. 28°29′ S.), Brazil (fig. 19). *P. schmitti* vicariates, or occupies the same kind of habitat, as the allopatric northern white shrimp *P. setiferus*.

Eldred and Hutton (1960) reported *P. schmitti* from off Cape Kennedy, Fla. This record is based on the statement by Harvey R. Bullis that during exploratory trips aboard the *Oregon* in 1956 and 1957, a number of specimens of this species were caught but not preserved. I have examined collections of *Penaeus* from the same area and found no *P. schmitti*.

The Lesser Antilles have a single record of white shrimp. According to Bate (1881), the description of "*P. setiferus*" by H. Milne Edwards (1837) was based on one specimen from the Island of

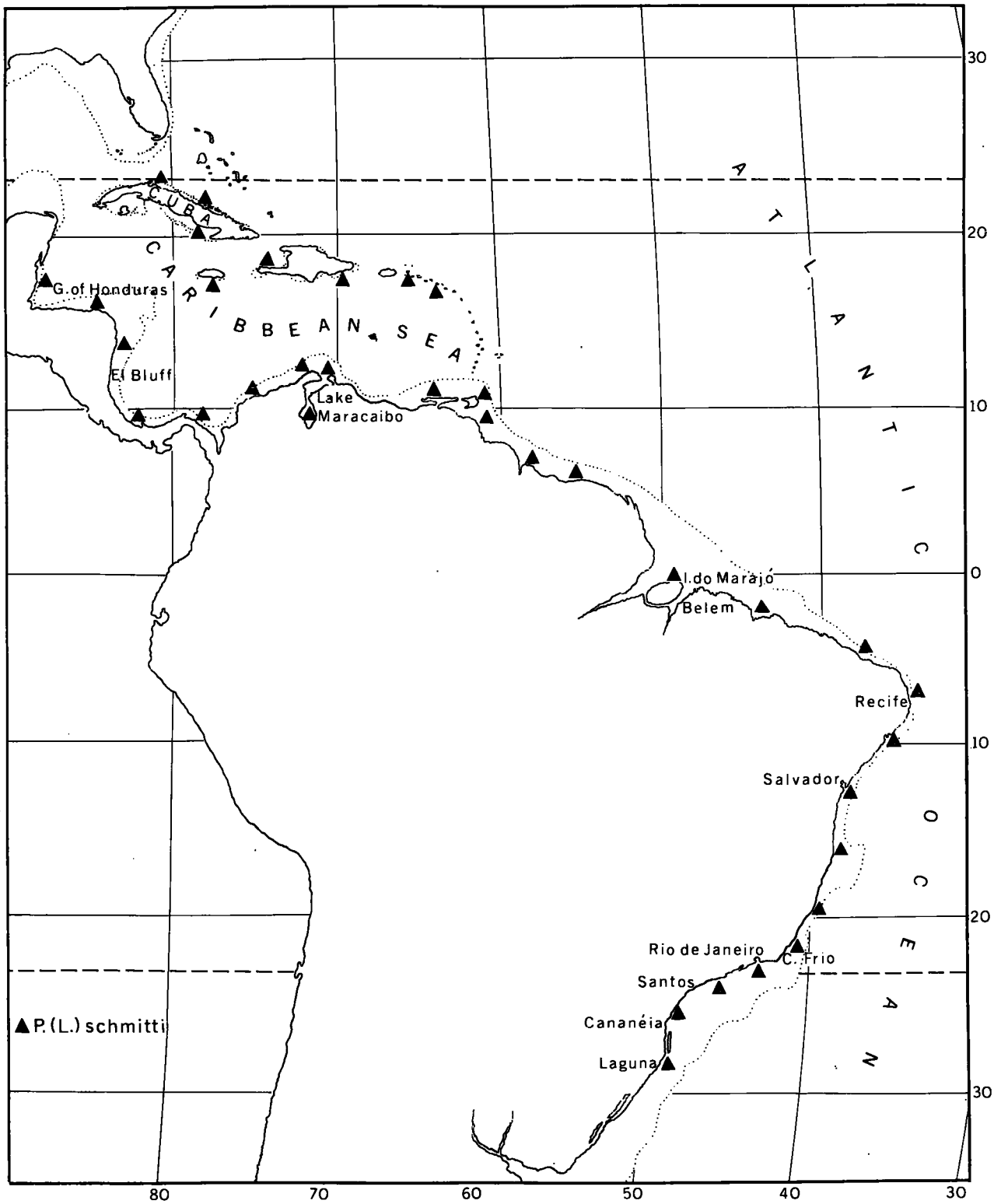

FIGURE 19.—Distribution of *Penaeus* (*L.*) *schmitti* Burkenroad.

Guadeloupe. The white shrimp is extremely rare in that general area; scarcity of brackish waters, or high salinity and unsuitable bottom may be responsible for the failure of the species to establish around those islands, where *P. a. subtilis* and *P. brasiliensis* are common.

This white shrimp is rather restricted within its range. Not only are there broad stretches where it seems to be absent; it also exhibits a disjunct distribution within rather small areas. In my intensive sampling for *Penaeus* in the waters around Cuba, both *P. schmitti* and *P. duorarum notialis* were found to be rather abundant. The latter lives in many localities around Cuba, but the white shrimp is restricted to certain areas. On the south shore, for instance, white shrimp is absent west of Bahía de Cienfuegos, and from the entire Golfo de Batabanó to the westernmost tip of Cuba. The dense concentrations of this species that are fished intensively are in relatively shallow water. In Cuba, white shrimp are found in large numbers to depths of 12 fm., and in the waters of the Gulf of Venezuela, they are abundant as deep as 10 to 14 fm. Although *P. schmitti* in most areas is found in water not deeper than 15 fm., off the coast of Honduras it is fished in depths between 11 and 20 fm. (Loesch, 1962), and Bullis and Thompson (1959b) caught a few specimens in water 15 to 26 fm. deep, off the northeast coast of South America. The reported (Anonymous, 1961) catches in 150 to 200 fm. off the western edge of Great Bahama Bank have not been authenticated; if this species does live in that area it is likely that the shrimp that appeared in this deepwater haul entered the net as it approached the surface.

My detailed studies of representative samples from many areas indicate little geographic variation in the diagnostic characters of *P. schmitti* throughout its range. I have been unable to recognize any significant differences between the population of the Caribbean Sea and that of the Atlantic, or throughout the latter population.

Although my data (fig. 19) and those of Ewald (1965c) seem to indicate that a change in the relation between carapace length and total length occurs at the time the white shrimp reaches about 21 to 22 mm. c.l., García Pinto (1965) found two discontinuities instead of one in that relation—one at a smaller and the other at a larger size.

Relationships

P. schmitti has close affinities with *P. setiferus*. Females, however, may be distinguished by the two rigid, rounded posterior protuberances on somite XIV and the two anterolateral ridges that are almost parallel. The ridge at the posterior margin of somite XII also has typical shape, bearing two pairs of large convexities on each side, the lateral being the larger. Males of *P. schmitti* have the distomedian corner of the lateral lobe of the petasma produced in a characteristic subrectangular projection, with the inner surface lacking a diagonal ridge. The crest located nearer the ventral margin on the outer surface of the lateral lobe is also typically bifurcate instead of plain. In the original description of *P. schmitti*, Burkenroad considered the contour of the margin of the pleuron of the first pleonic somite a diagnostic character, but I have found the contour unreliable, for its shape varies over a wide range.

Reproduction

SUBADULT STAGE-SEXUAL MATURITY

The minimum size of males with joined petasmal endopods is 21 mm. c.l., 100 mm. t.l.—apparently the smallest size at which males reach the subadult stage. The joining of the petasmal endopods occurs, however, within the size range 21 to 27 mm. c.l., 100 to 126 mm. t.l. In both *P. schmitti* and *P. setiferus* the petasmal endopods join at a larger size than in the grooved *Penaeus*.

Thus far, it has not been possible to determine accurately the minimum size at which females are capable of being impregnated, although, according to my observations, the thelycum seems fully developed at 21 mm. c.l., 100 mm. t.l. The minimum size at which females of this species reach sexual maturity is not known.

COPULATION

As it seems to be true in other *Penaeus* with an open thelycum, copulation in *P. schmitti* is believed to take place between hard-shelled individuals. The smallest females that have been found impregnated were 30 mm. c.l. The spermatophores are attached to the thelycum by means of the anterolateral wings, the triangular structure on the posterior margin of each wing, and the posterodorsal extensions. The glutinous material that surrounds the spermatophores when extruded aids in holding them temporarily to the thelycum. The coxae of the fourth and fifth pereopods of the

female are produced into a platelike projection bearing long bristles directed medially which press the spermatophore against the thelycum, and help it adhere to the thelycum.

Few females have been found carrying spermatophores. I caught impregnated females in southern Cuba from February to June. In western Venezuela, between April and September Ewald (1965c) found a number of females with spermatophores attached, and off Tucuracas, Departamento de la Guajira, Colombia, at *Oregon* Sta. 5674, a female with a spermatophore attached was caught in October.

OVARY DEVELOPMENT

The reproductive system of *P. schmitti* is similar to that of *P. setiferus*. In mature females two partly fused ovaries extend almost the entire length of the body, from the cardiac region of the stomach to the posterior end of the abdomen. The development of the ovary in *P. schmitti* has not been studied in detail. Five stages have been recognized by external characters similar to those described for *P. setiferus:*

1. Undeveloped. Ovaries very narrow and translucent.
2. Developing. Ovaries rather opaque and yellowish with chromatophores on the surface.
3. Nearly ripe or yellow. Ovaries larger than in the previous stages, and yellow-orange.
4. Ripe. Ovaries greatly distended, and drab olive or brownish.
5. Spent. Ovaries flaccid, from light green to whitish.

SPAWNING

Spawning is in oceanic waters. Ewald (1965c) reported sexually mature females from water about 10 to 15 fm. deep in the Ensenada de Calabozo, Gulf of Venezuela, where maximum spawning occurs in April through June. In southern Cuba I found ripe females in March through June and in water 8 to 12 fm. deep.

The presence of white shrimp 20 mm. t.l. in Cuban waters during March seems to indicate that *P. schmitti* may spawn there also in late February. Da Silva (1965) in Baía de Sepetiba, Brazil, took advanced larvae and juveniles in March and April, which suggests that spawning takes place until late summer in those waters.

SEX RATIO

The general male-female ratio is about 1:1. Ewald (1964) reported that in samples of sizes larger than 20 to 25 mm. c.l. from commercial catches, the percentage of females was slightly higher than that of males, but these samples were from areas where females seemed to be larger than males and, thus, more easily caught by the nets employed.

Postembryonic Development

LARVAE, POSTLARVAE, AND JUVENILES

To date, the larvae and postlarvae of this species have not been studied. Juveniles 18 mm. t.l. have short adrostral sulci, and, thus, may be separated from those of the grooved *Penaeus*. Juvenile *P. schmitti* frequently can be separated also by their light coloration.

In the development of individuals sex can be determined easily when they reach 6 mm. c.l., 28 mm. t.l. At this length the endopods of the first pair of pleopods in males are much wider than those in females, and the appendix masculina, although minute, is well formed.

Development of the petasma and median antennular flagellum in the males proceeds as follows: at 16 mm. c.l., 80 mm. t.l., the petasma has two rows of spines but lacks crests in the outer surface. At 17 mm. c.l., 83 mm. t.l., the petasma is still unjoined and the median flagellum bears long processes. At 21 mm. c.l., 100 mm. t.l., the petasmal endopods first join, the lateral lobes have three or four rows of spines, and the median flagellum has good numbers of long and a few short processes. Shrimp as small as 23 mm. c.l., 108 mm. t.l., have the petasma with the outer bands of spines fully developed and the median flagellum with both series of processes in large numbers.

Progressive changes in the thelycum occurs as follows: in females 10 mm. c.l., 48 mm. t.l., the thelycum bears low but distinct anterolateral ridges on sternite XIV. At 17 mm. c.l., 83 mm. t.l., the posterior protuberances, as well as the shelf overhanging from sternite XIII, are clearly formed and the ridges are prominent. At 21 mm. c.l., 100 mm. t.l., the thelycum seems to be fully developed and capable of holding the spermatophores in place; only females with a carapace length greater than 29 mm., however, have been found bearing spermatophores.

An incomplete investigation on the southern shores of Camagüey Province, Cuba, by Pérez Farfante et al. (1961) provided some data on juveniles of *P. schmitti*. Individuals 20 to 50 mm. t.l. were taken in estuarine water ⅓ to ½ fm.

deep from March to July, but were absent in August, scarce in September, and absent again in October and December. According to de Oliveira (1950), juveniles are abundant in Baía de Guanabara, Brazil, in January and February (during the summer) and da Silva (1965) collected larvae and juveniles in Baía de Sepetiba, Brazil, in March and April, or in late summer and early fall.

GROWTH

Little information is available on growth of this species. It has been stated (Anonymous, 1962) that in Guyana individuals kept in ponds grew from 25 mm. t.l. to 200 to 225 mm. t.l. through a period of 7 to 8 months. Ewald (1965c) estimated that in Lake Maracaibo—where juveniles and subadults live—shrimp increase up to 50 mm. monthly. Finally, Khandker (in press) found that in Laguna de Unare, Venezuela, *P. schmitti* grew an average of 1 mm. per day from July through October.

SEX DIFFERENCES IN SIZE

Females attain a greater length than males. The maximum reported female length is 235 mm. t.l. (Davant, 1963). The largest male measured was 43 mm. c.l. (about 175 mm. t.l.); it was taken in the Gulf of Venezuela by Ewald (1965c).

In inshore samples males and females are about the same size, whereas in the offshore material some of the females are larger than the largest males. This sex-size disparity in the white shrimp was noticed in material obtained by Loesch (1962) and in the material I examined.

Ecology

FOOD

White shrimp are omnivorous. They ingest algae, organic debris and sand, as well as a variety of animals. Among the animal remains found in their digestive tract are those of nematodes, annelids, mollusks, and crustaceans.

SUBSTRATE

P. schmitti offshore lives on soft bottoms of mud and silt, often mixed with coral sand and small fragments of mollusk shells. Although not numerous, these shrimp also occur in patches predominantly of sand on rock bottoms. In estuarine water, late postlarvae and juveniles live on muddy bottoms where there is abundant vegetation or organic debris.

DIEL CYCLE

In some areas—Gulf of Venezuela (Ewald, 1965c) and southern Cuba (Pérez Farfante, 1954b; Pérez Farfante et al., 1961)—the capture of adults day and night indicates that they are active at all hours, but in Honduras and Nicaragua they are caught almost exclusively during the day. In Cuba, juveniles and subadults of *P. schmitti* are fished in estuarine waters mostly at dawn or during the morning. According to Ewald (1964), white shrimp are fished commercially in Lake Maracaibo during the last hours of the night, and Boschi (1963) stated that they are taken in the lagoons of Cananéia, Brazil, in the first hours of the morning. It, thus, seems as if the young shrimp are more active at dawn and the hours immediately after.

MOVEMENTS

The larvae of *P. schmitti* move from the sea, where hatching occurs, to brackish waters where they arrive as postlarvae. Khandker (in press) reported that postlarvae appear at the seashore near Laguna de Unare, Venezuela, in June and July and begin to enter the Laguna in July at an average length of 8.5 mm. t.l. Ewald (1965c) collected thousands of postlarvae up to 10 mm. t.l. in the Estrecho de Maracaibo, and the occurrence of these postlarvae indicates a movement from the Ensenada de Calabozo, where mature females are found, toward Lake Maracaibo, one of the most important nursery grounds of the white shrimp.

The juveniles grow rapidly in the rich estuarine waters, reaching a size and abundance that makes commercial fishing highly profitable. At the end of a few months—6 to 9 in Lake Maracaibo (Ewald, 1965c)—they move back to sea where the life cycle is completed. An indication of the seaward migration of *P. schmitti* was given by Ewald (1965c), who found that the largest as well as the average sizes of both males and females in Lake Maracaibo were smaller than those in the Gulf of Venezuela. This observation suggests that as the shrimp grow they move from the almost fresh waters of the lake to waters of higher salinity in the Gulf. With regard to size distribution in sea waters, Pérez Farfante (in press) in Cuba found a gradient from shallow to deep water; the largest specimens were farthest from shore and in the deepest water.

EFFECTS OF TEMPERATURE

No studies have been made on the influence of temperature on the life and distribution of this white shrimp. The geographical distribution and the fact that the densest population is in the Gulf of Venezuela-Lake Maracaibo complex indicate that *P. schmitti* is a warm-water species. White shrimp, however, are found as far south as Laguna (lat. 28°29′ S.), Brazil, in water influenced by the Falkland Current.

EFFECTS OF SALINITY

Among the sympatric *Penaeus*, the young *P. schmitti* seems to have the greatest preference for low-salinity water. Da Silva (1965) stated that the white shrimp is by far the most abundant species in Baía de Sepetiba, Brazil, where the salinity is very low because about a dozen rivers flow into it. In western Venezuela, white shrimp are most abundant in the low-salinity water of Lake Maracaibo and in the southwestern part of the Gulf of Venezuela, which has the lowest salinity in the area. In contrast, white shrimp within the Gulf of Venezuela are absent from the Golfete de Coro, where the salinity is extremely high because of intense evaporation.

ENEMIES AND DISEASES

No detailed study of *P. schmitti* predators has been undertaken. It is, however, well established that *Penaeus* shrimp in general are an important food of various species of carnivorous fishes and various other animals. My examination of the stomach contents of different snappers (Lutjanidae) showed that white shrimp made up a high percentage of their food. Nikolić and Ruíz (in press) reported white shrimp in the stomach of a stingray "lebisa," and also in stomachs of porpoises. White shrimp are also cannibalistic, like other *Penaeus*.

Specimens have been found with black coloration, apparently suffering from "black spot" caused by a microsporidian sporozoan (Ewald, 1964, 1965c).

Commercial Importance

P. schmitti is commercially important in Cuba, the Caribbean waters of Central America, Colombia, and especially in Venezuela. It is also extensively fished commercially along the coast of Brazil. Cuba has a fishery for white shrimp in the Gulf de Guacanayabo and along the southern coast of Camagüey and Las Villas to Bahía de Cienfuegos. In Guatemala, small quantities of white shrimp are caught at Lago Izabal (Lindner, 1957) and in the western portion of Bahía de Amatique (Croker, 1967). The only important fisheries for white shrimp in Central America are in Honduras and Nicaragua. In 1965, Honduras shrimp exports to the United States (which represent almost the entire production) amounted to 740,270 kg. (heads-off);[4] practically all shrimp in Honduras are caught on the Caribbean Coast, and Loesch (1962) estimated that *P. schmitti* accounts for about half of the catches made there. In Nicaragua fishing for white shrimp, although seasonal, is highly productive; the composition of the production is not known. In Colombia the young are taken commercially in the lagoons near the mouth of the Río Magdalena, and adults are caught in the vicinity of Cartagena (Alejandro Londoño, personal communication).

The greatest fishery by far is in western Venezuela. According to Ewald (1965c), in 1964 the total shrimp production in Lake Maracaibo-Bahía de Tablazo, Gulf of Venezuela, amounted to 4,249,531 kg., and white shrimp made up 70 percent of the shrimp caught in Lake Maracaibo and 50 percent of that caught in Bahía de Tablazo. In 1965 catches in this area amounted to 7,242,130 kg. (according to Croker, 1967, "weights are mostly in heads-off equivalents although shrimp for the domestic market are probably recorded as heads-on"). In the coastal lagoons to the east, white shrimp support several small fisheries (Davant, 1963; Khandker, in press) and appear to be scarce in the shallow waters of Guyana, Surinam, and French Guiana, where only small quantities are caught.

P. schmitti, as stated earlier, is abundant in the waters of Brazil. It is taken commercially in or when leaving the estuarine nursery grounds from Belém along the coast to São Luis, and also at Parnaiba, Natal, Recife, and in Salvador. In eastern Brazil, camarão legítimo makes up part of the commercial catches from Rio Doce to Cabo Frio and Baía de Guanabara. The most important fisheries for this shrimp in Brazil are those in Baía de Sepetiba (da Silva, 1965) and in the lagoons along the coast of the States of São Paulo (Sadowski and Radasewski, 1960; Braga, 1962), Paraná and Santa Catarina (Richardson and Moraes, 1960; Tremel et al., 1964; Tremel and Mis-

[4] All exports figures cited here for Latin America should be understood to include only "heads-off" estimates.

takidis, 1965). In Rio de Janeiro landings of camarão legítimo during 1965–66 reached an all-time high, averaging 754,200 kg. (SUDEPE). At São Paulo landings averaged 119,900 kg. (Instituto de Pesca Marítima) during the same two-year period and in Santa Catarina they increased sharply in 1966, to 69,700 kg., after extremely poor landings during 1965, when only 4,500 kg. were reported (Centro de Pesquisas de Pesca).

Penaeus (Melicertus) duorarum duorarum BURKENROAD

Figures 20 to 31

United States: pink shrimp, spotted shrimp, pink-spotted shrimp, brown-spotted shrimp, grooved shrimp, green shrimp, pink night shrimp, red shrimp, hopper, skipper, pushed shrimp. Mexico: camarón rosado.

Penaeus brasiliensis: Gibbes, 1850: 198 [part]; Stimpson, 1871: 132 [part]; ? Smith, 1874: 642; Rathbun, 1884: 821–823 [part]; Ives, 1891: 194, 200 [part]; Evermann, 1892: 90 [part]; Rathbun, 1893: 821–823 [part]; Sharp, 1893: 108, 109 [part]; A. Milne Edwards and Bouvier, 1909: 235–238, figs. 64–67, pl. 6, figs. 11, 12; Andrews, 1911: 420, 422–424, figs. 3, 4; de Man, 1911: 96; Boone, 1927: 78 [part]; Cowles, 1930: 355, 356, 358 [part?]; Weymouth, 1931: 11 [part?]; Burkenroad, 1934: 61, 75, 77, 78, 93, 94 [part]; Johnson and Lindner, 1934: 4, 5 [part]; Myers and Gowanloch, 1934: 12 [part?]; Pearson, 1935: 172 [part]; Lindner, 1936: 155 [part?]; Pearson, 1939: 2, 30–39, 50, 51, 53, 59, 71, 72 [part]; Anderson, 1948: 1 [part]. Not *P. brasiliensis* Lat., 1817.

Peneus braziliensis: Coues, 1871: 124 [part?]; Kingsley, 1878: 69 [part]; Kingsley, 1879: 330 [part?]; Kingsley, 1880: 427 [part].

Penaeus braziliensis: Kingsley, 1882: 106 [part]; Verrill, 1922: 41–43 [part], pl. 13, figs. 1, 2 (?), pl. 16, figs. 1, 2, 2a (?), pl. 17, fig. 10d–f; Williams, 1959: 281, 285, 286, 288 [part].

Paneus brasiliensis: Collins and Smith, 1892: 102 [part].

Peneus brasiliensis: Faxon, 1896: 162 [part]; Hay and Shore, 1918: 377, 378 [part], pl. 26, fig. 6 (?); Boone, 1930: 14, 15, 101–105 [part], pl. 30.

Penaeus duorarum Burkenroad, 1939 [part, "Form A"]: 4, 21, 27, 30, 31–34, 36, 39–45, 51, figs. 23, 25 ("holotype and cotypes", 1 ♂ 2 ♀, YPM 4806–BOC 255 and 256, off Mobile Bay, Ala., 20 fm., March 20, 1937, *Atlantis* Sta. 2813, lat. 29°45′ N., long. 88°11′ W. [1 of the ♂ types "taken abroad," see below]); Anderson, Lindner, and King, 1949: 16; Burkenroad, 1949: 688; Broad, 1950: 1–4, 2 figs.; Gunter, 1950: 22–27, 40, 46, 47, 49; Holthuis, 1950: 27; Idyll, 1950: 7, 9, 10, 14, 15, 17, 19, 22, fig. 1; Broad, 1951: 27, 28, 30–32, 34, 35; Burkenroad, 1951: 26; Sánchez Roig and Gómez de la Maza, 1951: 113; Gómez de la Maza, 1952: 167, 169–171, fig. 1b; Leone and Pryor, 1952: 27–31; Springer and Bullis, 1952: 9, 10, 12, fig. 9; Hedgpeth, 1953: 159, 160, 210; Hildebrand and Gunter, 1953: 152, 155; Pérez Farfante, 1953: 229, (238, 241 [part]); Williams, 1953: 156–160, figs. 1, 2; De Sylva, 1954: 10, 18, 19, 23, 24, 26, 29, 33, fig. 1; Hildebrand, 1954: 233, 241, 245, 247, 266, 267, 350; Springer and Bullis, 1954: 3, 4, 6–8, 12, 16, fig. 10c; Hildebrand, 1955: 172, 174–179, 220, 224–227; Parker, 1955: 205; Voss, 1955: 5, 8, 10, figs. 11, 14, 15; Williams, 1955a: 116–118, 129, 133–136, 137, 140–142, 144; Williams, 1955b: 200, 204, 206, fig. 2; Anderson, 1956: 2, 4; Darnell and Williams, 1956: 844–846; Guest, 1956: 6, 12, 14, 18, figs. 2, 3; Gunter, 1956: 99–105; Springer and Bullis, 1956: 9; Anderson, 1957: 399; Carranza, 1957: 147; Ingle, 1957: 10, 13, 16, 17; Lindner, 1957: 83, 84, 92; Simmons, 1957: 178, 191, 199; Viosca, 1957: 12, 20, 1 fig.; Woodburn et al., 1957: 5–7, 12–14, 18, 20–24, 31, fig. 1; Anderson, 1958a: 1–3, fig. 3; Anderson, 1958b: 2; Darnell, 1958: 385, 388; Eldred, 1958: 2–13, 15–21, 23–25, figs. 2–15; Hildebrand, 1958: 159; Hutton and Eldred, 1958: 27; Lindner, 1958: 29–33; U.S. Fish and Wildlife Service, 1958b: 1, 6, 8, 12, 15, 18, 20–22, 24–26, 33, 34, fig. I–5b; Williams, 1958: 283–290; Collier, Gunter, Ingle, and Viosca, 1959: 1; Costello, 1959: 1–5; Costello and Allen, 1959: 13–18; Eldred, 1959a: 75, 76; Eldred, 1959b: 2–6; Hutton, Sogandares-Bernal, and Eldred, 1959: 490; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959: 6–13, 15–17, 19–25, 27, fig. 22; Ingle, Eldred, Jones, and Hutton, 1959: 1–45; Iversen and Manning, 1959: 130–132; Kruse, 1959: 123, 124, 126, 128, 130–132, 134, 136, 137, 139, 142, 144; Sogandares-Bernal and Hutton, 1959: 362; Williams, 1959: 282, 288, 289, figs. 1–3, 5–7; Chin, 1960: 135, 136, 140; Costello and Allen, 1960: 5–9; Eldred, 1960: 164, 165; Eldred and Hutton, 1960: 91, 97–99, 101, 103, 104, 106, 108, figs. 3, 4, 8; Hoese, 1960a: 592, 593; Hoese, 1960b: 330, 331; Hutton

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and Sogandares-Bernal, 1960: 290; Iversen and Idyll, 1960: 1–8; Iversen, Jones, and Idyll, 1960: 1–62; Kutkuhn, 1960: 11–15; Renfro, 1960b: 63, 64, 1 fig.; Williams, 1960: 560, 561, 565, 567, 569, 570; Anonymous, 1961: 34; Bearden, 1961: 3, 4, 6–8; Costello and Allen, 1961: 18–21; Cummings, 1961: 462–468, figs. 3, 5a, b; Dobkin, 1961: 321–348, figs. 2–20; Eldred, Ingle, Woodburn, Hutton, and Jones, 1961: 5–136; Gunter, 1961a: 599; Ingle, 1961: 22–27; Iversen and Jones, 1961: 1–28; Renfro, 1961: 11; Tabb and Manning, 1961: 594; Anderson, 1962: 1, 2, fig. 3; Gunter, 1962a: 107, 108; Gunter, 1962c: 216–223, 226; Hutton, Ball, and Eldred, 1962: 327–332, fig. 4; Kutkuhn, 1962: 343, 355, 369–378, 383, 388, 397, 398, 401; Tabb, Dubrow, and Jones, 1962: 6–28; Tabb, Dubrow, and Manning, 1962: 12, 42, 44, 52, 60, 61, 63, 74; Baxter, 1963: 80; Boschi, 1963: 5, 6, 13, 20–23, 26, 29, 35, fig. 6 (1–5); Gunter, 1963: 108; Gunter and Hall, 1963: 295, 297, 304; Kutkuhn, 1963: 66–77; McFarland and Lee, 1963: 391, 392, 394, 406, 408–410; Renfro and Brusher, 1963: 15, 16; Zein-Eldin, 1963a: 188–196 [part]; Aaron and Wisby, 1964: 121–130; Costello and Allen, 1964: 30, 31; Fuss, 1964: 62–73, figs. 1, 3; Gunter et al., 1964: 182, 184; Hutton, 1964: 440, 444, 445; Jones, Dimitriou, Ewald, and Tweedy, 1964: 1–3, 9, 10, 16–75; Renfro, 1964: 95; Anderson and Lunz, 1965: 1, 4–6; Broad, 1965: 86–89; Bullis and Thompson, 1965: 6; Copeland, 1965: 11, 13, 14, figs. 2, 3; Eldred, Williams, Martin, and Joyce, 1965: 1–4, 7–25; Ewald, 1965b: 436–448; Holthuis and Rosa, 1965: 4 [part]; Idyll and Jones, 1965: 25–27; Joyce, 1965: 14, 19, 20, 24, 29, 30, 34, 39, 40, 44, 49, 50, 53, 58, 59, 62, 67, 68, 70, 75, 76, 79, 80, 83, 84, 88, 91, 93, 96, 98, 99, 102–104, 115, 121–128, 132, 134, 154–161, 170, 173, 177–192, 219, 221; Loesch, 1965: 42–56; Saloman, 1965: 1–13; Simpson et al., 1965: 77; Temple and Fischer, 1965a: 59; Van Engel, 1965: 38; Williams, 1965: 21–24, 26, 27, figs. 10, 11; Zein-Eldin and Aldrich, 1965: 199, 212; Christmas et al., 1966: 196, 197, 200, 201, 204–206, 209, 211, 212, fig. 5; Cook, 1966: 438; Copeland and Truitt, 1966: 65, 68–70, 72, 73; Costello and Allen, 1966: 449–459; Fuss and Ogren, 1966: 170–189; Hughes, 1966: 504; Joyce and Eldred, 1966: 8, 9, 11–13, 16, 19–21, 23, 25, 32–34; Kutkuhn, 1966a: 19, 20, 26; Kutkuhn, 1966b: 313–338; Sykes and Finucane, 1966: 372–376; Baxter and Renfro, 1967: 151, 152; Lyles, 1967: 315–317, 371–376; McCoy and Brown, 1967: 1–3, 8–11, 14, 15, 18, 21, 22, 25–27; Temple and Fischer, 1967: 323, 325; Saloman, 1968: 1–5; Zamora and Trent, 1968: 17, 19.

Penaeus duoarum: Anderson and Lindner, 1945: 306 [part]; Gunter, 1945: 77; Dall, 1957: 142, 226 [part].

Penaeus ducrarum: Viosca, 1957: 10.

Penaeus duorarium: Broad, 1965: 87.

Penaeus duorarum duorarum: Pérez Farfante, 1967: 98.

Pink shrimp: Renfro and Brusher, 1964: 13; Cook, 1965: 11; Idyll, Iversen, and Yokel, 1965: 28, 29; Idyll and Jones, 1965: 25, 27; Idyll, Iversen, and Yokel, 1966: 19, 20; Lindner, 1966: 18–26.

Shrimp: Higman, 1952: 1–4; ?Flint, 1956: 11, 12.

Taxonomic Remarks

I have examined 1 ♂ and 2 ♀ of the 2 ♂ 2 ♀ BOC "301" ("Holotype and Cotypes") mentioned by Burkenroad (1939) in the original description. They are together in a single bottle accompanied by two labels, on one of which is written "Holotype" and on the other "Cotypes," both with complete information on locality, depth, and date they were caught by the *Atlantis*. Neither label, however, shows the sex of the specimens. The label for the holotype is numbered 255 and the other 256; neither is numbered 301, the BOC catalog number given by Burkenroad. In addition to the two labels, there is in the bottle a slip of paper on which is written "smaller ♂ taken abroad" in Burkenroad's handwriting. It was not possible for me to determine which of these specimens is the holotype.

Several erroneous records for this subspecies occur in the literature. I have examined the male of "*P. brasiliensis*" from west of Whale Rock, northwest end of Arrecife Alacrán, MCZ 7211, described and illustrated by Milne Edwards and Bouvier (1909). I found it to be *P. d. duorarum*. Burkenroad (1934) pointed out that their illustrations show unusual features of the rostrum, carapace, and fifth and sixth abdominal somites. I believe that the first maxilla is not shown correctly either. These structures were undoubtedly misrepresented by the artist. I also examined material from Turtle Harbor, Fla., described by Boone (1930) and deposited in the Vanderbilt Marine Museum, Long Island, N.Y. The specimen figured in her plate 30 under the name "*P. brasiliensis*" is a

female of *P. d. duorarum*, and although it is in a jar with a male of the same species (from the Marquesas Keys), it was easily identified because the object—a spermatophore—which appears in the photograph between the fifth pair of pereopods and the first pair of pleopods still remains attached.

Study Material

UNITED STATES

Maryland: 1 ♂ 1 ♀, CBL, Holland Strait to Smith Island, July–September 1964, E. Harrison. 3 ♂ 3 ♀, CBL, around Smith and Bloodsworth Islands, summer 1965, E. Harrison.

Virginia: 1 ♂, USNM, Cape Charles, August 18, 1897, W. H. Stirling. 2 ♂ 6 ♀, USNM, Cape Charles, September 1890, W. P. Seal. 3 ♂, USNM, Cape Charles, October 25, 1897, W. H. Stirling. 1 ♂, USNM, James Fishery, Norfolk, September 30, 1921, W. C. Schroeder.

North Carolina: 1 ♂, USNM, off Cape Hatteras, 14 fm., October 19, 1884, *Albatross* Sta. 2283. 1 ♂ 2 ♀, USNM, off NE. Cape Hatteras, 13 fm., October 19, 1884, *Albatross* Sta. 2285. 1 ♀, YPM, off Cape Hatteras, 11 fm., October 19, 1884, *Albatross* Sta. 2286. 1 ♀, USNM, off Cape Lookout, 15 to 16 fm., February 18, 1950, *Albatross III* Sta. 1. 2 ♂ 3 ♀, USNM, off Cape Lookout, 8 to 7 fm., August 27, 1959, *Silver Bay* Sta. 1312. 4 ♀, USNM, SE. of Lookout Lighthouse, 17 fm., January 25, 1949, *Willi Bross*. 4 ♂ 10 ♀, USNM, Beaufort Bar, 7 to 8 fm., October 6, 1949, A. Williams. 2 ♂ 1 ♀, USNM, off Beaufort, October 11, 1941, *Madelena*, W. W. Anderson. 14 ♂ 20 ♀, USNM, Bogue Sound, Morehead City, September 5, 1964, B. B. Collette and D. M. Cohen. 1 ♂, USNM, Middle Sound, Wilmington, April 18, 1880, R. E. Earll. 12 ♂ 21 ♀, USNM, Bogue Inlet Sea Buoy, 7 fm., June 7, 1949, *Perry E. Meyers*, W. W. Anderson. 7 ♂ 2 ♀, YPM, Fort Macon. 1 ♂, YPM, Fort Macon, H. C. Yarrow. 1 ♀, YPM, Fort Macon, J. E. Coues.

Georgia: 1 ♂, USNM, Doboy Sea Buoy, October 3, 1941, *Perry E. Meyers*, W. W. Anderson.

Florida: 1 ♂, YPM, off Matanzas Inlet, 8 to 10 fm., April 2, 1934, M. B. Bishop. 1 ♀, USNM, off Flagler Beach, 35 to 38 fm., June 2, 1957, *Combat* Stas. 345, 346. 1 ♂, USNM, off New Smyrna Beach, 27 fm., November 8, 1963, *Silver Bay* Sta. 5228. 1 ♂ 1 ♀, USNM, off Edgewater, 9 fm., January 21, 1960, *Silver Bay* Sta. 1562. 1 ♂, USNM, off Cape Kennedy, 20 fm., September 20, 1961, *Silver Bay* Sta. 3360. 1 ♀, off Cape Kennedy, 180 fm., January 26, 1962, *Silver Bay* Sta. 3710. 1 ♂ 1 ♀, USNM, off Cape Kennedy, 30 fm., November 8, 1963, *Silver Bay* Sta. 5231. 2 ♂, USNM, off Cape Kennedy, 20 fm., November 9, 1963, *Silver Bay* Sta. 5241. 2 ♂ 5 ♀, USNM, off Cocoa Beach, 10 to 11 fm., January 13, 1965, *Oregon* Sta. 5181. 5 ♂ 3 ♀, USNM, off Melbourne Beach, 11 fm., January 13, 1965, *Oregon* Sta. 5182. 7 ♂ 4 ♀, USNM, off Melbourne Beach, 30 fm., January 14, 1965, *Oregon* Sta. 5200. 7 ♂ 8 ♀, USNM, off Melbourne Beach, 30 to 29 fm., January 14, 1965, *Oregon* Sta. 5201. 5 ♂ 6 ♀, USNM, off Melbourne Beach, 30 to 31 fm., January 15, 1965, *Oregon* Sta. 5202. 4 ♂ 5 ♀, USNM, off Sebastian, 31 to 28 fm., January 15, 1965, *Oregon* Sta. 5203. 1 ♂ 1 ♀, USNM, Lantana, February 12, 1892, H. M. Smith. 1 ♀, USNM, Lemon City, E. J. Brown. 3 ♂ 2 ♀, YPM, mouth of Indian River, March 21, 1874, E. Palmer. 2 ♂ 2 ♀, YPM, off Miami Beach, February 21, 1927, *Pawnee* II. 23 ♂ 24 ♀, USNM, Biscayne Bay, February 2, 1966, D. M. Allen. 1 ♂ 1 ♀, USNM, off Elliott Key, 36 fm., October 24, 1960, *Silver Bay* Sta. 2351. 1 ♂, USNM, off Key Largo, Florida Keys, 40 fm., November 10, 1961, *Silver Bay* Sta. 3523. 5 ♂ 10 ♀, USNM, off Key Largo, 30 fm., October 26, 1960, *Silver Bay* Sta. 2380. 14 ♂ 4 ♀, USNM, off Key Largo, 40 fm., November 10, 1961, *Silver Bay* Sta. 3523. 8 ♂ 4 ♀, USNM, off Key Largo, 40 to 45 fm., November 9, 1961, *Silver Bay* Sta. 3521. 2 ♂ 2 ♀, USNM, Card Sound, February 13, 1889, USFC. 1 ♂ 1 ♀, USNM, Upper Jewfish, Bush Lake, 1½ fm., January 30, 1903, *Fish Hawk*. 13 ♂ 6 ♀, USNM, off Sombrero Key, Florida Keys, 32 to 30 fm., October 28, 1960. 4 ♂, USNM, Newfound Harbor Key, December 7, 1906, *Arian*, B. A. Bean. 57 ♂ 57 ♀, USNM, Florida Bay, February 1962, D. C. Tabb and D. Dubrow. 1 ♂ 2 ♀, USNM, Key West, 1884, *Albatross*, W. Nye. 17 ♂ 19 ♀, USNM, Key West, 1886, *Albatross*. 18 ♂ 29 ♀, USNM, off Marquesas Keys, 9 to 7 fm., July 19, 1957, *Silver Bay* Sta. 78. 1 ♂, VMM, Marquesas Keys. 20 ♂ 15 ♀, USNM, Tortugas grounds, 11 fm., September 18–23, 1961, *George Bowers*, C. H. Saloman. 11 ♂ 10 ♀, USNM, Tortugas grounds, February 1966, R. Benton. 4 ♂ 3 ♀, USNM, off Tortugas, 37 fm., April 13, 1954, *Oregon* Sta. 1004. 1 ♀, VMM, Turtle Harbor, January 10, 1923, *Ara*. 1 ♀, VMM, Turtle Harbor, April 10, 1923, *Ara*.

2 ♂ 1 ♀, USNM, 48 km. NE. of Loggerhead Key, Tortugas, 19 fm., December 3, 1954, G. H. Eubank. 1 ♀, YPM, Double Headed Shot Cays, 3 fm., March 7, 1925, *Pawnee II.* 3 ♂, USNM, off Cape Sable, 3 fm., December 18, 1902, *Fish Hawk* Sta. 7358. 1 ♀, USNM, Cape Romano, 6 fm., April 7, 1954, *Oregon* Sta. 993. 1 ♂ 3 ♀, USNM, Marco, February 25, 1889, USFC. 16 ♂ 12 ♀, USNM, SW. of Naples, July 18, 1957, *Silver Bay* Sta. 67. 4 ♂ 8 ♀, USNM, Sanibel grounds, 6 fm., March 19, 1962, D. M. Allen. 3 ♂ 8 ♀, USNM, Sanibel grounds, 6 fm., March 19, 1962, *Silver Bay*, D. M. Allen. 20 ♂ 5 ♀, YPM, Sanibel Island, shore, June 1935, M. Storey. 1 ♂ 2 ♀, USNM, Charlotte Harbor, March 1887, W. H. Dall. 6 ♂ 10 ♀, YPM, off Englewood, 4 fm., January 7, 1936, Bass Biol. Station. 76 ♂, USNM, St. Petersburg, Tampa Bay, October 3, 1938, V. E. Springer and K. D. Woodburn. 13 ♂ 11 ♀, USNM, Tampa Bay, March 29, 1901, *Fish Hawk* Sta. 7109. 4 ♂ 3 ♀, USNM, Tarpon Springs, November 5, 1896, USFC. 2 ♀, USNM, Anclote Keys, 6¼ fm., January 24, 1902, *Fish Hawk* Sta. 7239. 1 ♂ 3 ♀, USNM, Cedar Keys, October 6, 1949, G. K. Reid. 3 ♂ 1 ♀, USNM, Pensacola, February 9, 1885, *Albatross*. 2 ♂ 1 ♀, USNM, Pensacola Bay, 2½ fm., September 1929, W. C. Schroeder.

Alabama: 2 ♀, USNM, off Mobile, 7 fm., January 28, 1962, *Oregon* Sta. 3475. 1 ♂ 2 ♀, YPM, off Alabama, 19 fm., March 20, 1937, *Atlantis* Sta. 2813.

Mississippi: 7 ♂ 5 ♀, GCRL, Mississippi Sound, off Horn Island, May 13, 1964, J. Y. Christmas. 16 ♀, USNM, off Pascagoula, 17 to 18 fm., January 23, 1958, *Oregon* Sta. 2374.

Louisiana: 3 ♂, USNM, off Louisiana, 12 fm., February 6, 1938, *Pelican*. 33 ♂, USNM, Cat Island, November 15, 1931, J. C. Pearson.

Texas: 4 ♂ 5 ♀, USNM, off Texas, 12 fm., April 28, 1938, *Pelican* Sta. 49–5. 4 ♂ 8 ♀, USNM, off mouth of Sabine River, 10 fm., May 19, 1965, BCFBLG. 4 ♂ 6 ♀, USNM, off Galveston, 15 fm., March 26 to April 2, 1966, BCFBLG. 4 ♂ 4 ♀, USNM, off Freeport, 15 fm., September 22, 1966, BCFBLG. 3 ♀, USNM, off western Texas, Gulf of Mexico, April 1965, BCFBLG. 2 ♀, USNM, off western Texas, Gulf of Mexico, April 1965, BCFBLG. 2 ♂ 3 ♀, USNM, S. of Padre Island 12 fm., January 27, 1964.

MEXICO

Tamaulipas: 7 ♂ 4 ♀, USNM, N. of Hut's Bayou, 8 to 10 fm., March 17, 1947, *Pelican* hauls 7 to 12, Mexican tagging trip. 4 ♂ 4 ♀, INIBP–USNM, Tampico, May 14, 1963, S. García. 3 ♀, INIBP, off Tampico, June 30, 1959, E. Ramírez and G. Aguilar.

Veracruz: 1 ♂ 2 ♀, INIBP–USNM, Bocaina, Laguna de Tamiahua, June 9, 1964, R. Márquez and C. Tovar. 4 ♂ 3 ♀, INIBP–USNM, Tuxpan, August 29, 1963, S. Basulto. 1 ♂ 1 ♀, INIBP–USNM, Tuxpan, off La Bocana, March 7, 1964, A. Mendoza and R. Márquez.

Campeche: 8 ♂ 5 ♀, INIBP–USNM, shore, Campeche, November 1963, fishermen. 2 ♀, INIBP–USNM, Golfo de Campeche, 7 fm., May 2, 1959, R. Ramírez and M. Flores. 2 ♂, USNM, off Campeche, 26 fm., November 21, 1958, *Silver Bay* Sta. 846. 3 ♂ 2 ♀, INIBP–USNM, NW. of Campeche, 26 fm., April 30, 1959, R. Ramírez and M. Flores. 5 ♀, INIBP–USNM, Morro to Ceybaplaya, 7 fm., May 3, 1959, R. Ramírez and M. Flores. 2 ♂ 5 ♀, USNM, off Cayo Arcos, 20 fm., December 11, 1952, *Oregon* Sta. 720.

Yucatán: 8 ♂ 10 ♀, INIBP–USNM, between Dzilam de Bravo and Yalkubul, October 10, 1961, M. Solís. 2 ♂ 1 ♀, MCZ, NW. of Arrecife Alacrán, 6 km. off Whale Rock, 35 fm., *Blake* Sta. 37.

Quintana Roo: 1 ♂, INIBP, 90° NNW. of Isla Mujeres, 21 fm., July 17, 1967, H. Chapa Saldaña, D. Fuentes, and J. M. de la Garza.

BERMUDA ISLANDS

1 ♂, YPM, Mullet Bay, ½ fm., January 27–29, 1935. 1 ♂, YPM, Gibbet Island Bay, September 19, 1905. 1 ♀, YPM, Fairyland Creek, September 30, 1915. 2 ♀, YPM, Ferry Beach, 1936.

Diagnosis

Adrostral sulcus broad posteriorly and long, almost reaching posterior margin of carapace. Median sulcus long, ending immediately anterior to posterior end of adrostral sulcus, and deep along its entire length. Dorsolateral sulcus narrow, sometimes almost closed. Petasma with distal portion of ventral costa broadening and turning proximally rather abruptly, armed with minute spines along free border and with compact group of large teeth on attached border; apex of ventral costa adnate to adjacent wall; distal fold small, unarmed or with few submarginal spinules. Thelycum with anterior process relatively large, and

with prominent undivided median carina on posterior process; carina exposed owing to slight divergence of anteromedian corners of lateral plates.

Description

ROSTRUM (fig. 20 a, b)

Teeth $\frac{7\text{–}10}{1\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—67, 9/2—21, 8/3—5, 7/2—4, 9/3—2, 7/1—1; N=300)+epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to distal dorsal tooth; rostrum relatively short in larger juveniles, reaching at most to base of lateral antennular flagellum; attaining maximum length in relation to carapace length at 8 to 13 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.75); decreasing progressively with increasing length of shrimp, rostrum reaching distal end of first antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.35); rostrum straight apically or directed downward, occasionally upturned, convex proximally; highest portion of blade at level of third dorsal tooth; latter level with anterior margin of carapace; rostrum tip 1/5 to 1/4 r.l. Postrostral carina strong, prominent, uniform in width or slightly wider in anterior half, and long, extending almost to posterior margin of carapace. Median sulcus deep throughout, long, ending near posterior margin of cara-

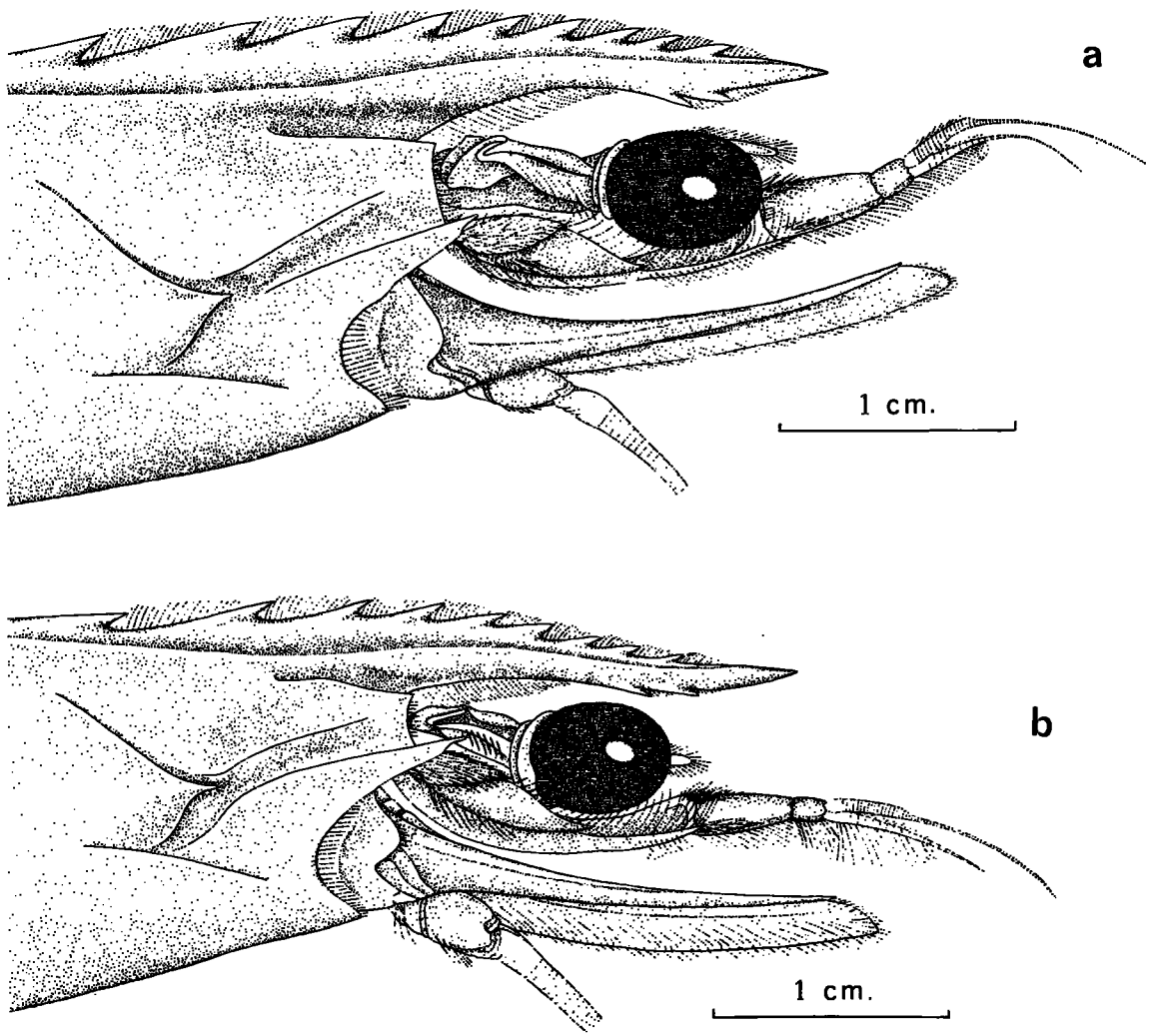

FIGURE 20.—*Penaeus* (*M.*) *duorarum duorarum* Burkenroad. a. Rostrum, ♀ 37 mm. c.l., off Sebastian, Fla. b. Rostrum, ♂ 35 mm. c.l., off Melbourne Beach, Fla.

pace. Adrostral sulcus deep, broad posteriorly, 3/5 to 1½ width of postrostral carina, measured at level of one-eighth distance from its posterior end to epigastric tooth, and long, ending 1/13 to 1/20 c.l. from posterior margin of carapace. Adrostral carina prominent, sharp along carapace, and long, same length as adrostral sulcus.

CARAPACE (fig. 21)

Length in proportion to total length smaller in juveniles, according to my data increasing slightly at subadult stage. Gastrofrontal sulcus broad, extending to about one-fifth c.l.; gastrofrontal carina sharp, turning slightly toward dorsal margin posteriorly, ending in acute orbital angle anteriorly. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine. Gastro-orbital carina high and sharp, occupying approximately posterior four-fifths of distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus 1/5 to 1/4 c.l., ending slightly anterior to midlength of carapace. Hepatic carina 1/5 to 1/4 c.l., sharp, sloping slightly anteroventrally to end 1/13 to 1/20 c.l. from anterior margin of carapace. Antennal spine prominent and acute; hepatic spine pronounced.

ANTENNULES

Lateral flagellum ½ to 3/5 length antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum. Anterolateral spine small, sharp. Stylocerite acuminate, reaching slightly beyond midlength of first antennular segment. Prosartema extending to distal end of proximal fifth of second antennular segment.

ANTENNAE

Length of scaphocerite 2½ times maximum width, its length relative to carapace length decreasing slightly with growth; spine reaching at least distal end of antennular peduncle and at most distal end of proximal one-fourth of thickened portion of lateral flagellum. Carpocerite length 1¼ width, reaching distal end of optic peduncle. Antennal flagellum relatively short, about 1⅓ body length.

THORACIC APPENDAGES

Third maxilliped reaching at least proximal one-fifth but not beyond distal end of second antennular segment; length of dactyl 3/5 to 2/3 that of propodus. First pereopod reaching base of carpocerite and at most exceeding it by seven-eighths

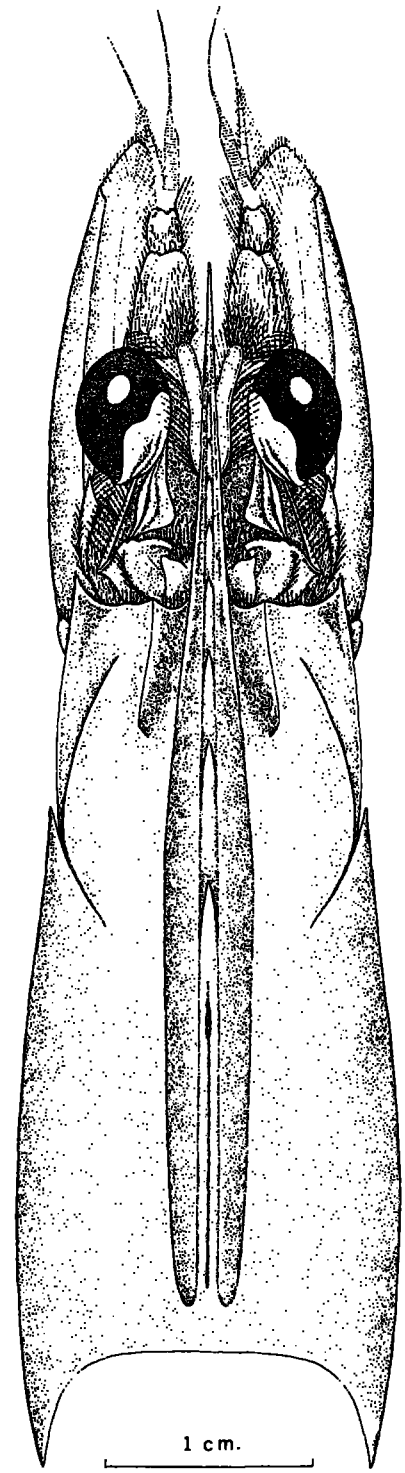

FIGURE 21.—*Penaeus (M.) duorarum duorarum* Burkenroad. Cephalothorax, ♀ 37.5 mm. c.l., off Melbourne Beach, Fla.

of propodus. Second pereopod surpassing carpocerite by one-half of length of dactyl to entire propodus. Third pereopod extending to distal end of second or at most surpassing third antennular segment by entire dactyl. Fourth pereopod reaching base of carpocerite or exceeding it by entire length of dactyl. Length of fifth pereopod subequal to that of fourth. Exopods on all pereopods; long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

ABDOMEN

Carinate dorsally from posterior half of fourth somite, posteriorly carina gradually increasing in height to form keel on sixth somite, ending in sharp spine on posterior margin. Dorsolateral sulcus (fig. 22) very narrow, ratio between height of keel and width of sulcus (at about one-third length from posterior margin of somite) varying from about 2.5 to 15.5 (modally 4.5, fig. 23); in some specimens sulcus almost entirely closed. No significant difference in K/S (ratio of the height of the keel to the width of the sulcus) between males and females at any size. Figure 24 shows K/S also has a modal value of 4.5 in size classes to 22 mm. c.l. and in the largest class, whereas K/S mode increases slightly in intermediate classes. Lips sharp, bordering sulcus to near posterior end, there sulcus widens slightly in nearly oval depression. Sixth abdominal somite with three prominent cicatrices on each side, anterior one longest; fifth somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite; fourth abdominal somite with similar series of pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

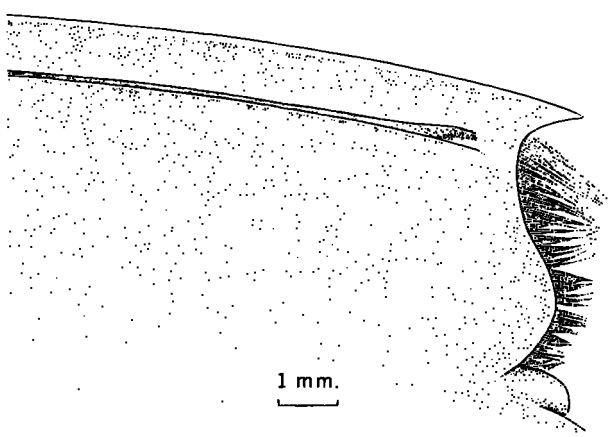

FIGURE 22.—*Penaeus (M.) duorarum duorarum* Burkenroad. Sixth abdominal somite, posterodorsal portion. ♀ 42.5 mm. c.l., off Long Key, Florida Keys.

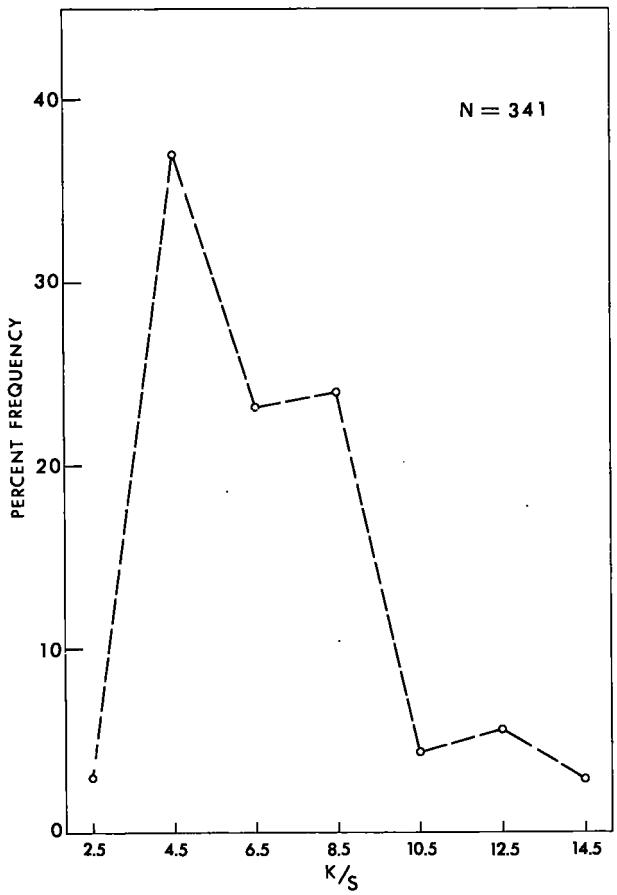

FIGURE 23.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus (M.) duorarum duorarum* Burkenroad.

PETASMA (fig. 25 a–d)

Ventral costa broadening and turning proximally rather abruptly, with apex adnate to membranous side of ventrolateral lobule, distal portion armed along free margin with a series of 1 to 12, usually 4 to 7, minute spines clearly distinct (even in rather small juveniles 9 mm. c.l., about 42 mm. t.l.), and on attached margin with compact group of 6 to 16 prominent, often curved teeth. Ventrolateral lobule with narrow band of minute spines consisting of single series distally, pair of series proximally followed by three or four longer, closely set series. Distal fold of free margin of lateral lobe small, intruding little inside petasma, unarmed or with few spinules near free edge. Distomedian projections rather thick and relatively short, forming hood overhanging distal portion of ventral costae.

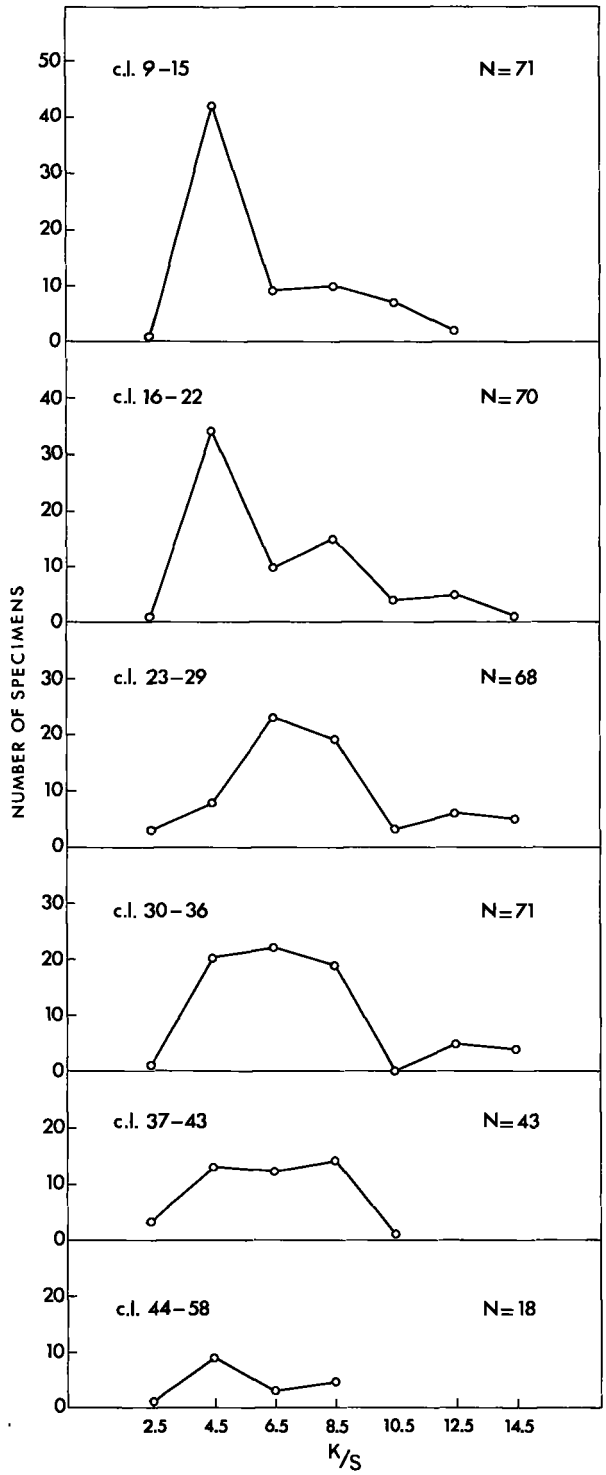

FIGURE 24.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *duorarum duorarum* Burkenroad of different size classes.

APPENDIX MASCULINA (fig. 25 e–f)

Broad, its length 1$\frac{1}{10}$ to 1$\frac{1}{5}$ maximum width, armed with single row of strong spines along distal two-thirds of concave lateral margin, and with three rows of longer spines along distal and median margins. Anterior surface slightly convex, posterior surface strongly concave, with sharp ridge projecting from median margin.

THELYCUM (figs. 26 and 27)

Anterior process relatively large, bordered by strongly convex, sharp ridge, surrounding rather strongly concave ventral surface. Posterior process bearing single, prominent, median carina, extending anteriorly toward anterior process. Lateral plates with median appressed border raised as a ridge or lip; rounded or slightly projecting anteromedian corners diverging, leaving median carina exposed. Seminal receptacle dorsal to lateral plates provided with median slitlike opening; latter corresponding to fissure between plates.

COLOR

Color of *P. d. duorarum* is variable. Specimens from the Tortugas and Campeche commercial grounds are generally pink, and fishermen in those areas refer to this subspecies as "pink shrimp" and "camarón rosado," respectively. Large individuals from the northern Gulf of Mexico frequently have a grayish color, and brownish specimens are also common in inshore waters. Young shrimp are also of a clear gray, whitish, green, or pink coloration, and some are almost colorless. The pink coloration is often deep, and the live-bait shrimp dealers along both coasts of Florida call this subspecies "red shrimp." Williams (1953) described freshly caught juveniles from North Carolina as having the uropods with chromatophores scattered uniformly, reddish brown distally and blue along the creases. The uropods of the subadult are almost transparent, with a light blue margin.

P. d. duorarum very often has a reddish or purplish brown spot on each side at the juncture of the third and fourth abdominal somites—hence, the common names pink-spotted, brown-spotted, or simply spotted shrimp. Many specimens, however, lack abdominal spots, and, when present, the spots usually fade and become invisible after death. This shrimp also shows concentrations of chromatophores that darken certain areas, like narrow bands anterior to the posterior margin of the carapace and abdominal somites, as well as

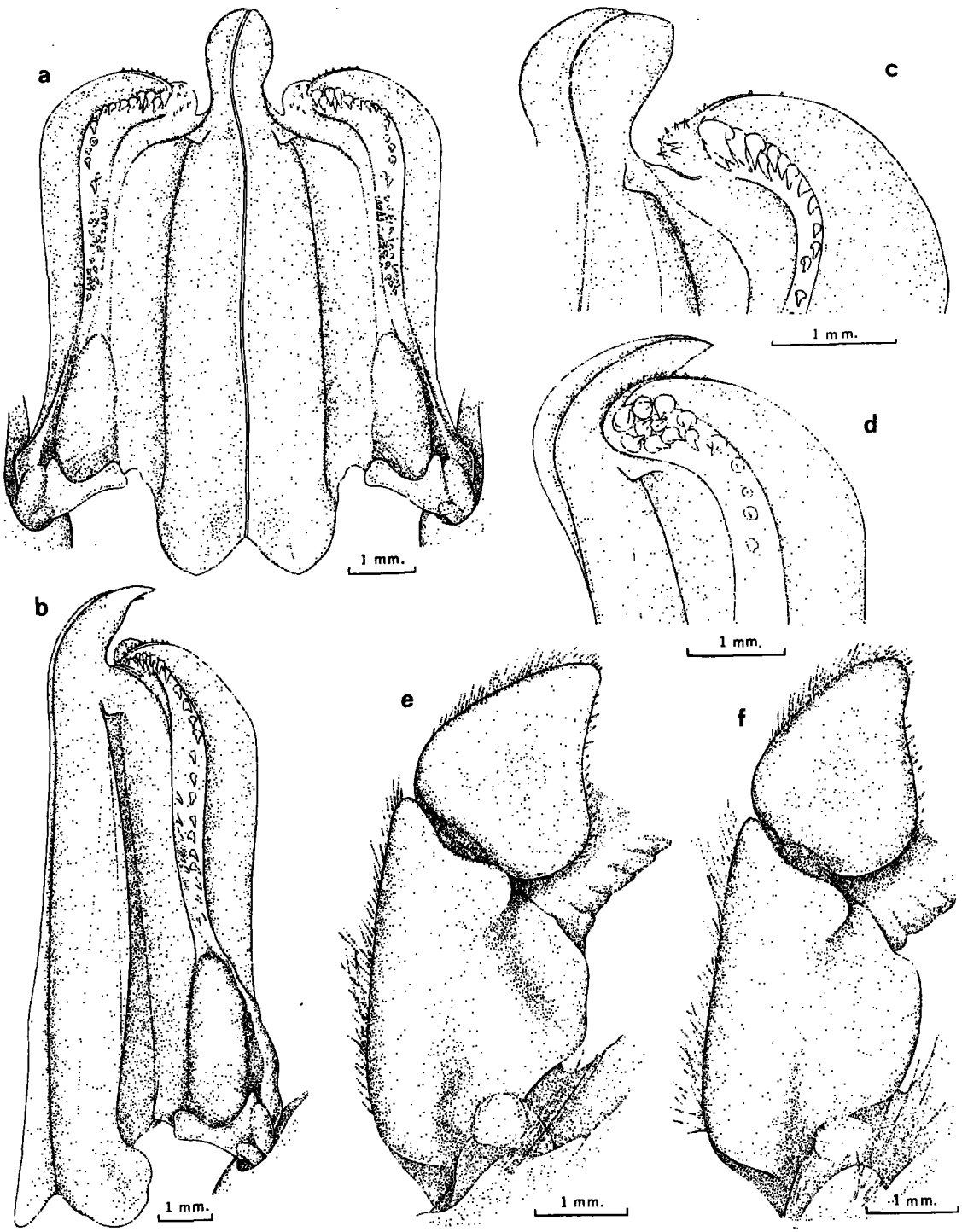

FIGURE 25.—*Penaeus* (*M.*) *duorarum duorarum* Burkenroad. a. Petasma, exterior surface, ♂ 38.5 mm. c.l., off mouth of Sabine River, Tex. b. Petasma, ♂ 25.5 mm. c.l., off mouth of Sabine River, Tex. c. Petasma, distal portion, ♂ 36.50 mm. c.l., off Melbourne Beach, Fla. d. Petasma, distal portion. ♂ 33.5 mm. c.l., off Sebastian, Fla. e. Appendix masculina, ♂ 38.5 mm. c.l., off Edgewater, Fla. f. Appendix masculina, ♂ 39 mm. c.l., off mouth of Sabine River, Tex.

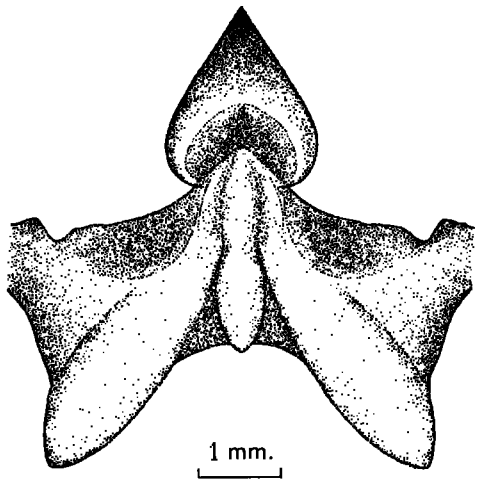

FIGURE 26.—*Penaeus (M.) duorarum duorarum* Burkenroad. Median protuberance with horns on posterior margin of sternite XIII, ♀ 47.5 mm. c.l., northwestern Gulf of Mexico.

roundish patches at the center of each pleuron. Gunter and Hall (1963) described the pink shrimp as having a saddle-shaped mark extending from the prominent abdominal spot forward and diagonally across the second abdominal somite and over the posterior end in the spot on the third somite.

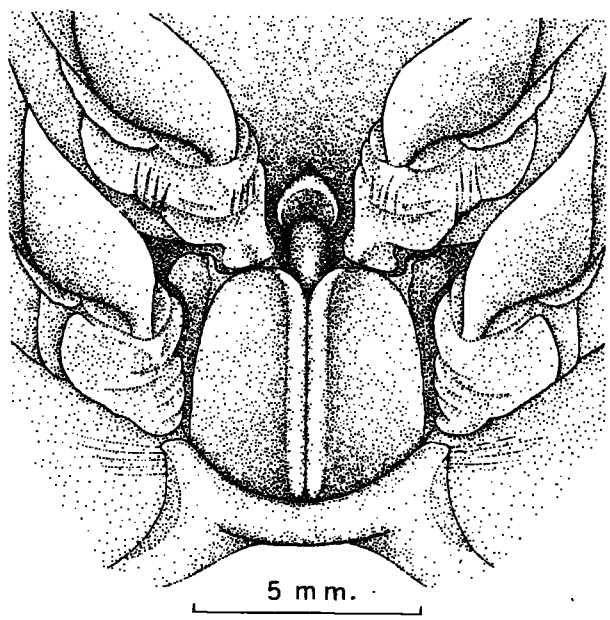

FIGURE 27.—*Penaeus (M.) duorarum duorarum* Burkenroad. Thelycum, ♀ 38 mm. c.l., Sanibel grounds, Fla.

Distribution and Morphological Variations

The range of *P. d. duorarum* extends from lower Chesapeake Bay southward along the Coast to the Florida Keys and Gulf of Mexico. In the Gulf it ranges from the Tortugas Islands along the Gulf Coast of the United States and through the coastal waters of Mexico to Cape Catoche and south to Isla Mujeres. It is also found in the Bermuda Islands (fig. 28). This paper carries the first report of pink shrimp from the northern coast of Yucatán and beyond Cape Catoche.

The densest populations of pink shrimp are off southwestern Florida and in the southeastern portion of Golfo de Campeche. The Gulf of Mexico, thus, is considered the center of distribution of the subspecies.

The greatest concentrations of pink shrimp are between 6 and 20 fm. but in some localities pink shrimp are abundant at depths of as much as 35 fm. A few specimens were collected at 180 fm. (*Silver Bay* Sta. 3710) off Cape Kennedy, Fla., and it has been reported (Anonymous, 1961) that catches of "*P. duorarum*" were taken at 150 to 200 fm. off the western edge of the Great Bahama Bank. These shrimp could have been either *P. d. duorarum* or *P. d. notialis* because which of the two subspecies occupies the area is not known.

P. d. duorarum shows some degree of variation throughout its range: the keel–dorsolateral sulcus ratio ranges rather widely, the breadth of the adrostral sulcus varies, the number of external spines at the distal end of the ventral costa of the petasma varies considerably, and the distal fold of the petasma may or may not be armed with submarginal spinules. None of the variations, however, are restricted to portions of the range.

Relationships

P. duorarum duorarum has the dorsolateral sulcus narrower than *P. duorarum notialis* from the Caribbean Sea, the Atlantic Coast of South America, and Africa. Burkenroad (1939) was the first to point out this difference between the two and called the former "Form A," and the latter "Form B." Biometric studies have indicated a statistically significant difference in the ratio (K/S) of K (height of the keel) to S (width of the sulcus) between those populations. In *P. d. notialis* from the southern region, K/S varies from about 0.25 to 3, modally 1.75 (fig. 34). Overlapping is so

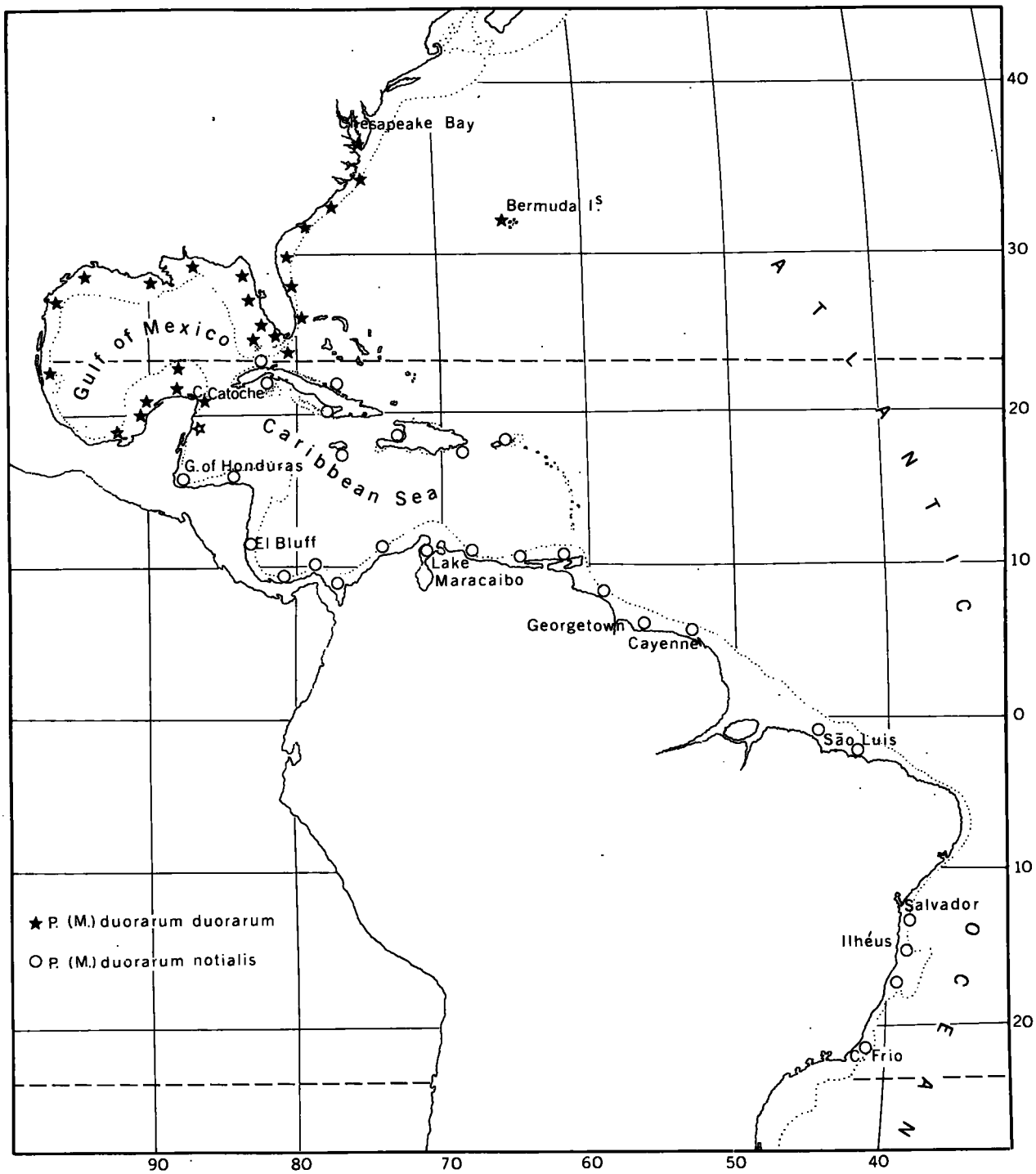

FIGURE 28.—Distribution of *Penaeus* (*M.*) *duorarum duorarum* Burkenroad and *Penaeus* (*M.*) *duorarum notialis* Pérez Farfante.

small that I consider each population to represent a geographical subspecies; thus, the name *P. duorarum duorarum* applies to the typical shrimp (Pérez Farfante, 1967). The two subspecies also differ in the length of the third pereopod, which is proportionately shorter in *P. d. duorarum* than in *P. d. notialis*.

Adult *P. d. duorarum* can be separated readily from the closely related *P. a. aztecus* and *P. brasiliensis*. Females may be recognized by the undivided median carina on the posterior process and the slightly divergent anteromedian corners of the lateral plates. Males may be distinguished by the shape, the external spination, and the compact group of very large, pointed teeth of the ventral costa; the small, and either plain or sparsely armed distal fold of the petasma, and also by the appendix masculina, which is stubby and broader at the base than in *P. a. aztecus* and *P. brasiliensis*. The shape of the ventral costa, which I recognized as a diagnostic character for the first time, is a striking feature by which the grooved species of *Penaeus* from the western Atlantic and the Gulf of Mexico may be distinguished.

P. d. duorarum also can be separated from *P. a. aztecus* by its comparatively higher keel and narrower dorsolateral sulcus; as stated above, the ratio K/S in the former is usually over 3 (fig. 23); in only about 5 percent of my sample was K/S smaller. Pink shrimp also have a higher rostrum which is usually straight rather than sinuous; the shape of the rostrum varies, however, and occasionally specimens of *P. d. duorarum* have the tip of the rostrum upturned (fig. 20b), and some *P. a. aztecus* have a straight rostrum (fig. 39b). In addition, pink shrimp have a proportionately shorter rostrum than *P. a. aztecus*, the ratio $\frac{\text{r.l.}}{\text{c.l.}}$ varying from a maximum of 0.75 in the young to about 0.35 in individuals of 50 mm. c.l.; the rostrum reaching to the base of the thickened portion of the lateral antennular flagellum in the young and to the distal end of the first antennular segment in specimens of 50 mm. c.l. The rostrum provides a useful but not an entirely reliable character for separating the two subspecies.

The third pereopod is stouter and much shorter in *P. d. duorarum* than in *P. a. aztecus*, reaching only to the distal end of the second and at most exceeding the third antennular segment by the entire dactyl. The merus and, particularly, the carpus (fig. 29) are responsible for the shorter length in *P. d. duorarum*, for the differences in the lengths of the other podomeres of the third pereopod are small (table 3). Tables 1 and 2 show the lengths of the five distal podomeres (dactyl to ischium) of the third maxilliped and of the first pereopod for three carapace-length intervals in *P. a. aztecus*, *P. d. duorarum*, and *P. brasiliensis;* no significant differences in these characters are evident. Another difference between the pink and brown shrimps is the ratio between the lengths of the carapace and abdomen, adult *P. d. duorarum* has a shorter abdomen.

The dark-colored spot on each side between the third and fourth abdominal somites is generally characteristic of *P. d. duorarum;* but many specimens lack abdominal spots, and similar spots are present not only in the other subspecies of *P. duorarum* from the Antilles and Central and South America, but also in *P. brasiliensis* and occasionally in *P. a. aztecus*. Throughout much of its range, *P. d. duorarum* lives in close proximity with *P. a. aztecus*, and the presence of abdominal spots cannot be used reliably to separate the two

TABLE 1.—*Ranges of lengths of distal five podomeres of third maxilliped in* P. a. aztecus, P. d. duorarum, *and* P. brasiliensis *of indicated intervals of carapace length*

[Based upon a minimum of 30 specimens for each subspecies and species]

Carapace length in mm.	Dactyl			Propodus			Carpus			Merus			Ischium		
	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
20.0–30.0:															
Minimum	2.0	2.0	2.0	3.0	3.0	3.0	4.5	4.5	4.5	5.0	5.0	5.0	5.5	6.5	5.5
Maximum	3.0	3.0	3.0	4.5	4.5	4.5	6.0	6.0	6.0	6.5	6.5	6.5	8.0	8.0	8.0
30.1–40.0:															
Minimum	3.0	3.0	3.0	4.5	4.5	4.5	6.0	6.0	6.0	6.5	6.5	6.5	8.0	8.0	8.0
Maximum	3.5	3.5	3.5	5.5	5.5	5.5	8.5	8.5	8.5	9.0	8.5	8.5	11.0	11.0	11.0
40.1–50.0:															
Minimum	3.5	3.5	3.5	5.5	5.5	5.5	8.5	8.5	8.5	9.0	8.5	8.5	11.0	11.0	11.0
Maximum	4.0	4.0	4.0	7.0	6.5	6.5	9.5	9.5	9.5	11.5	11.5	10.5	14.5	14.0	14.0

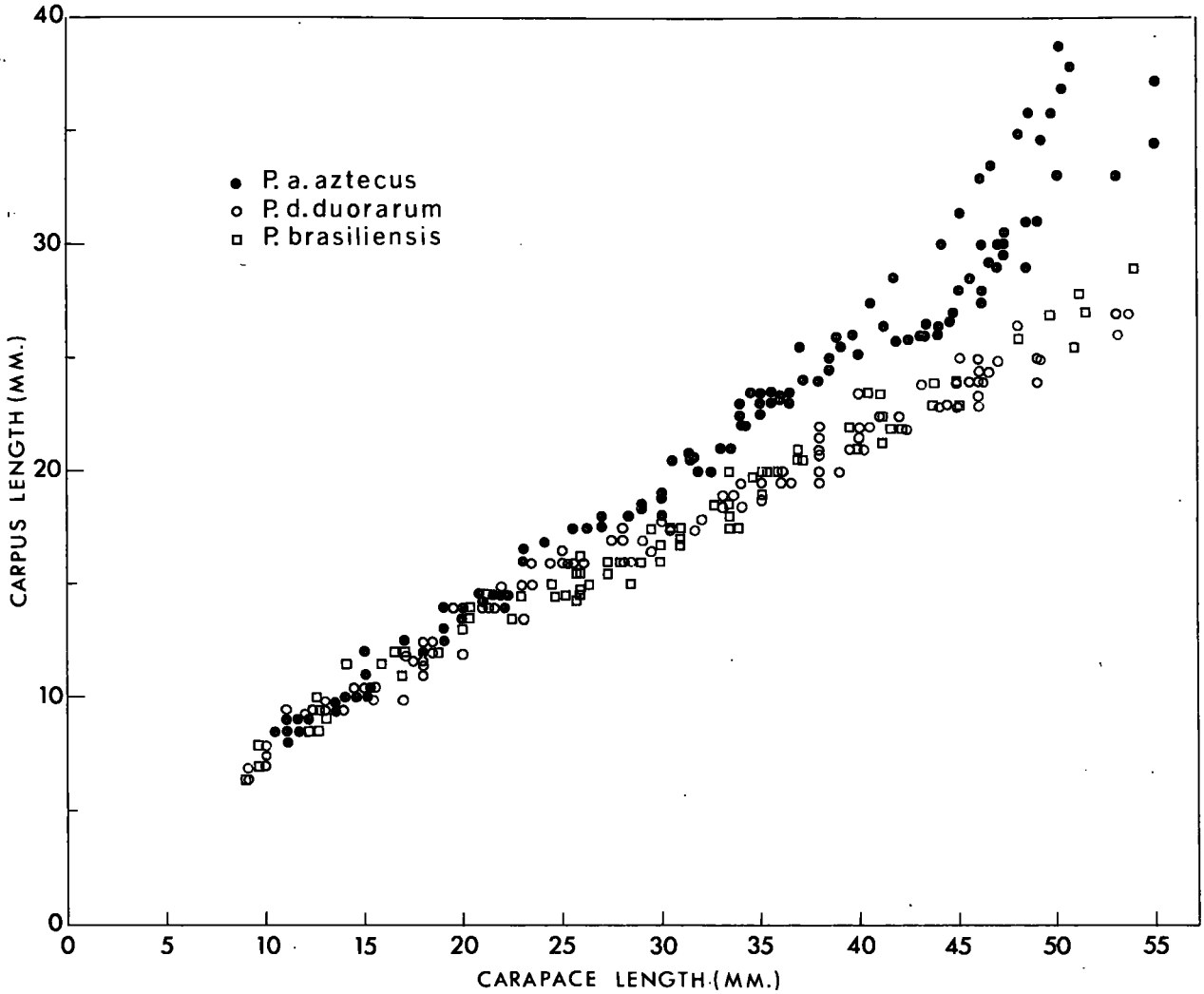

FIGURE 29.—Carpus length-carapace length relation in *Penaeus* (*M.*) *aztecus aztecus* Ives, *Penaeus* (*M.*) *duorarum duorarum* Burkenroad, and *Penaeus* (*M.*) *brasiliensis* Lat.

TABLE 2.—*Ranges of lengths of distal five podomeres of first pereopod in* P. a. aztecus, P. d. duorarum, *and* P. brasiliensis *of indicated intervals of carapace length*

[Based upon a minimum of 30 specimens for each subspecies and species]

Carapace length in mm.	Dactyl			Propodus			Carpus			Merus			Ischium		
	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
20.0–30.0:															
Minimum	3.0	3.0	3.0	5.0	4.5	4.5	5.0	5.0	5.0	5.0	5.0	5.0	3.5	3.5	3.5
Maximum	4.0	4.0	4.0	6.5	6.5	6.0	6.5	6.5	6.0	7.0	7.0	6.5	5.0	5.0	4.5
30.1–40.0:															
Minimum	4.0	4.0	4.0	6.5	6.5	6.0	6.5	6.5	6.0	7.0	7.0	6.5	5.0	5.0	4.5
Maximum	5.5	5.5	5.0	8.5	8.5	7.5	8.5	8.5	8.0	8.5	8.5	8.0	6.0	6.0	5.5
40.1–50.0:															
Minimum	5.5	5.5	5.0	8.5	8.5	7.5	8.5	8.5	8.0	8.5	8.5	8.0	6.0	6.0	5.5
Maximum	7.0	7.0	6.0	11.0	11.0	9.5	11.0	11.0	10.0	11.0	11.0	10.0	8.0	8.0	7.0

TABLE 3.—*Ranges of lengths of distal five podomeres of third pereopod in* P. a. aztecus, P. d. duorarum, *and* P. brasiliensis *of indicated intervals of carapace length*

[Based upon a minimum of 30 specimens for each subspecies and species]

Carapace length in mm.	Dactyl			Propodus			Carpus			Merus			Ischium		
	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.	P.a.a.	P.d.d.	P.b.
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
20.0–30.0:															
Minimum	3.5	3.0	3.0	6.5	6.0	6.0	14.5	12.0	13.5	8.5	7.0	8.0	4.5	4.5	4.5
Maximum	4.5	4.0	4.0	8.5	8.0	8.0	19.0	17.5	17.5	12.0	11.0	11.0	6.0	6.0	6.0
30.1–40.0:															
Minimum	4.5	4.0	4.0	8.5	8.0	8.0	18.0	17.5	16.0	11.5	11.0	10.5	6.0	6.0	6.0
Maximum	5.5	5.0	5.0	10.5	9.5	9.5	26.0	22.0	22.0	15.5	13.0	13.5	8.0	8.0	8.0
40.1–50.0:															
Minimum	5.5	5.0	5.0	10.5	9.5	9.5	25.0	21.0	21.0	15.0	13.0	13.5	8.0	8.0	8.0
Maximum	7.0	6.0	6.0	14.0	13.0	13.0	39.0	26.5	26.5	19.5	16.5	16.5	9.5	9.0	9.0

subspecies, as has been done to identify freshly caught specimens.

Juveniles of the grooved *Penaeus* from the western Atlantic and the Gulf of Mexico are difficult to identify. A number of characters, however, allow the separation of those of *P. d. duorarum* from most of those of *P. a. aztecus*. The former have a narrower dorsolateral sulcus, usually a shorter rostrum, a stouter body, and often external genitalia that are better developed than those of *P. a. aztecus* at the same length. In addition, male juveniles of *P. d. duorarum* may be separated from those of *P. a. aztecus* by the ridge on sternite XIV which is higher and pointed anteriorly (fig. 30). Being usually better developed than males of *P. a. aztecus*, they also have the petasmal endopod larger at the same carapace length. At 11 mm. c.l., 51 mm. t.l.—occasionally at 9 mm. c.l., 42 mm. t.l.—the petasma frequently has spines on the distal margin of the ventral costa. Small females of pink shrimp may be distinguished by characters of the thelycum. At 10 mm. c.l., 47 mm. t.l., they lack a knob on the midline at the posterior margin of sternite XIII, whereas brown shrimp of comparable length possess such a knob; and at 12 mm. c.l., 55 mm. t.l., the posterior margin of sternite XIII in the pink shrimp is smooth, whereas that of the brown shrimp bears a small spine projecting posteriorly. Finally, in *P. d. duorarum* the median carina is simple, whereas in *P. a. aztecus* of at least 14 mm. c.l., 65 mm. t.l., it has two anterior arms.

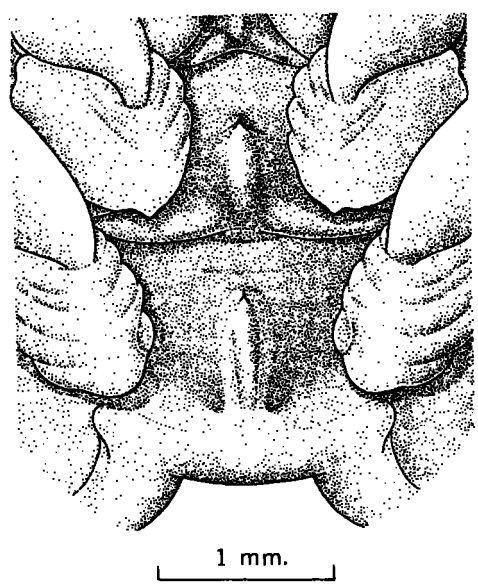

FIGURE 30.—*Penaeus* (*M.*) *duorarum duorarum* Burkenroad. Sternites XIII and XIV, ♂ 10 mm. c.l., Cat Island, La.

Juveniles of *P. d. duorarum* can often be distinguished from those of *P. brasiliensis* by having the adrostral carina markedly convex dorsally on the posterior two-thirds of the rostrum, rather than straight along the entire length of the rostrum. This character varies, however, and the variations in its shape seem to intergrade with those shown by *P. brasiliensis*. Differences in the external genitalia are discussed under the latter species.

Reproduction

SUBADULT STAGE-SEXUAL MATURITY

In males, I found the petasmal endopods to be first joined at 14 mm. c.l., 65 mm. t.l. This length seems to be the smallest at which copulation can be carried out by male pink shrimp. The petasma, however, can remain unjoined to 19 mm. c.l., 86 mm. t.l.; thus, males attain the subadult stage within the range of 14 to 20 mm. c.l. Small males 8 mm. c.l., 34 mm. t.l., were found with developed spermatophores within the terminal ampullae.

Females are considered subadults when the thelycum is sufficiently developed to permit im-

pregnation; in the grooved *Penaeus* this occurs when median borders of lateral plates meet. The minimum length at which I found females with a functional thelycum is 15 mm. c.l., 69 mm. t.l., but in some individuals the lateral plates do not become contiguous until the shrimp attain 20 mm. c.l., 89 mm. t.l. Therefore, pink shrimp females attain the subadult stage within the range of 15 to 20 mm. c.l., 69 to 89 mm. t.l. The minimum length at which they have been found with well-developed ovaries is 92 mm. t.l.; ripe females of this length were reported by Eldred et al. (1961) off Tampa Bay, Fla. This size is larger than that at which females can be first impregnated.

Eldred (1958) discussed the statement by Burkenroad (1939) that the smallest impregnated females of *P. duorarum* he found were 23 mm. c.l. and the smallest males with joined petasmal endopods were 15 mm. c.l. The smallest impregnated females she had found in Florida waters were considerably larger (31 mm. c.l.), and suggested that Burkenroad (who did not mention locality) could have referred to *P. duorarum* from the Caribbean Sea, that is to say, to *P. d. notialis*. Individuals of the latter subspecies, however, do not seem to attain the subadult stage at smaller size than do those of *P. d. duorarum*. Whatever the locality of Burkenroad's specimens, the discrepancy was caused by a difference in technique—Burkenroad measured the length of the carapace from postorbital margin to posterior margin of carapace (see Burkenroad, 1936) while Eldred included the rostrum. Addition of the length of the rostrum to Burkenroad's measurements greatly reduces the discrepancy.

COPULATION

Copulation in *P. d. duorarum* seems to take place (as in all *Penaeus* with a complicated thelycum) between a hard-shelled male and a soft-shelled female soon after the female molts. The reasons for this assumption are many: for transfer of the spermatophores into the thelycum the petasma must have its two valves firmly joined (soft newly molted males have the petasma unjoined or partially joined); only hard-shelled males have been seen with extruding spermatophores; females kept in aquariums were apparently impregnated shortly after molting while in soft-shelled condition, and their exoskeletons carried the spermatophores to the following ecdysis; finally, even in live specimens, it is difficult to open the thelycum of hard-shelled females (Eldred, 1958).

Copulation takes place several times during the growth and development of the females and is not directly associated with maturation and spawning. This conclusion is based on the facts that spermatophores are cast off at each ecdysis and impregnated females are found with ovaries in different stages of development, from undeveloped to ripe.

Impregnated females of *P. d. duorarum* carry the spermatophores inside the seminal receptacle and can usually be detected by the strongly convex shape of the lateral plates of the thelyca. The lateral plates may remain convex after spawning, however, and, thus, their bulging appearance cannot be taken as a certain indication of impregnation.

There seems to be evidence that offshore *P. d. duorarum* mate throughout the year; in the Tortugas area, Ingle et al. (1959) found the largest percentage of impregnated females in May and June, but also some in all months of the year.

OVARY DEVELOPMENT

In *P. d. duorarum*, as in all its congeners, the ovaries extend from the anterior end of the cephalothorax to the posterior end of the abdomen. Each ovary consists of one anterior lobe and six to eight lateral lobes in the cephalothorax and one long lobe in the abdomen. The size, color, and texture of the ovaries vary with the degree of maturity. The development of the ovary in *P. d. duorarum* has been studied by Cummings (1961), who identified the following stages:

1. Undeveloped. Ovaries very slender, translucent, flaccid, and invisible through the exoskeleton. Ova transparent, small, modal size less than 0.137 mm.

2. Developing. Ovaries still flaccid, but larger, opaque, white to pale olive-buff. Modal size of ova 0.137 to 0.274 mm.

3. Nearly ripe. Ovaries larger, relatively light bluish green at the beginning and darker at the end, somewhat turgid, and visible throughout the exoskeleton. Modal size of ova 0.274 to 0.342 mm.

4. Ripe. Ovaries dark grayish green, very similar in appearance to the previous stage from which they can be distinguished only microscopically by the presence around the nucleus of a peripheral layer of rodlike bodies with apices directed toward the center of the ova. According to Cummings, the modal size of the ova is slightly less than 0.37 mm. Dobkin (1961), however, reported that eggs spawned at the laboratory measured 0.31 to 0.33 mm., and Eldred et al. (1965) found that eggs

ranged from about 0.23 to 0.33 mm. in diameter.

5. Spent. Ovaries are flaccid and their color fades, becoming milky as the regression proceeds.

Eggs of pink shrimp, like those of other *Penaeus*, are demersal. According to Dobkin (1961), "eggs are yellow brown in color and opaque, although when light is reflected in a certain way, the chorion shows the blue hue reported by Pearson (1939) for the eggs of *P. setiferus*."

SPAWNING

Spawning takes place in oceanic waters at 2 to 26 fm. and probably at greater depths also. In laboratory experiments by Ewald (1965b) spawning occurred in the early morning.

Field work by Cummings (1961), Tabb, Dubrow, and Jones (1962), and Jones et al. (1964) gave some indications that on the Tortugas grounds spawning continues throughout the year. Evidence is also strong that spawning is more intense during spring, summer, and fall (Ingle et al., 1959; Cummings, 1961; Jones et al., 1964). On the basis of analysis of fishery statistics Kutkhun (1962) indicated two peaks of spawning, one in the spring and the other in the summer. Farther north spawning is thought to be restricted to certain months; Joyce and Eldred (1966) stated that at the St. Petersburg and St. Augustine latitudes in Florida, spawning does not begin until early spring, and Williams (1955a, 1965) reported that in North Carolina postlarvae enter inshore water only from May to November.

The northernmost breeding population of *P. d. duorarum* seems to be that off North Carolina where Burkenroad (1949), Broad (1950), and Williams (1955a) reported mature females.

In regard to the relation of spawning to water temperature in *P. d. duorarum*, Eldred et al. (1965) stated that rising temperatures seem to be the most important factor inducing spawning, whereas Idyll and Jones (1965) indicated that spawning intensity is affected mostly by absolute temperature and changes in temperature. The minimum temperature at which Jones et al. (1964) found hours-old larvae was 19.6° C. Spawning has been recorded up to 30.1° C. (Eldred et al., 1965) and 30.6° C. (Jones et al., 1964).

P. d. duorarum probably spawns more than once as is believed to be true for various other *Penaeus*. This assumption is based on the evidence that large females about 180 mm. t.l. and longer are found with their ovaries in a developing stage, which suggests that preparation for a second spawning was taking place. Cummings (1961) found one ripe female with large ova in addition to a group of undeveloped ova, which also suggests the development of two successive batches of eggs by an individual.

SEX RATIO

The general ratio of males to females is about 1:1 in inshore populations (Tabb, Dubrow, and Jones, 1962; Eldred et al., 1961; Saloman, 1965). The sex ratio in offshore populations has not been definitely established. Studies by Iversen et al. (1960) on the Tortugas grounds showed that the percentage of females does not increase with size. Kutkuhn (personal communication), however, found that the percentage does increase, and Ingle et al. (1959) and Eldred et al. (1961), on the basis of their sampling in a restricted area on the same grounds, also found a predominance of females at greater lengths. Sexes appear to segregate because many samples contain but one sex.

Postembryonic Development

LARVAE, POSTLARVAE, AND JUVENILES

By maintaining eggs that had been spawned in the laboratory, Dobkin (1961) ascertained that *P. d. duorarum* goes through five nauplial stages preceding the first protozoea. He also tried to work out the rest of the larval development by assembling stages obtained in plankton tows. This investigation produced a second and a third protozoea and three mysis stages before the postlarvae developed. The studies by Jones et al. (1964) and the rearing experiment by Ewald (1965b) seem to corroborate that pink shrimp pass through 11 larval stages. The larval cycle in the laboratory occurred in a minimum of 15 days, during which time the animal grew from a first nauplius to first postlarva.

Dobkin (1961) described the larval stages of *P. d. duorarum* and found them slightly larger than, and different from, those of *P. setiferus*. Some larval specialists question the validity of the diagnostic characters given, maintaining that observable distinguishing features between the corresponding larvae of the two shrimps have not been found. First and second postlarvae were closely similar to those of *P. setiferus* and had about the same size range. In *P. d. duorarum* first postlarvae ranged from 3.8 to 4.8 mm. t.l. (Ewald, 1965b, obtained somewhat smaller first postlarvae, 2.9 to 4.6 mm. t.l.), the second 4.7 to 6.6 mm. In the

first postlarva, however, the supra-orbital spine was almost always absent in *P. d. duorarum* but still present, although reduced, in *P. setiferus*. The first ventral teeth appeared when the number of dorsal teeth had increased to 7, at about 10 to 11 mm. t.l.; postlarvae with 8 to 10 dorsal and 2 ventral teeth were 12.5 to 13.7 mm. long. The variation in length of the postlarvae within a single dentition stage has been corroborated by Tabb, Dubrow, and Jones (1962) in the population of Florida Bay. Pink shrimp having six dorsal and no ventral rostral teeth had a carapace from 1.7 to 2.3 mm. long; the relation of length to dentition is most variable in the seven-to-nine tooth stages when the ventral teeth are being formed.

Postlarvae of *P. d. duorarum* under 12 mm. t.l. were distinguished by Williams (1959) from those of *P. setiferus* and *P. a. aztecus* (see under the latter subspecies).

Juvenile *P. d. duorarum* 18 mm. t.l. have shallow but distinctly long adrostral sulci and at 20 mm. t.l. the sulci are well developed. This character allows for a rapid separation of early juveniles of pink shrimp from those of the nongrooved *P. setiferus* and *P. schmitti*.

It is difficult to differentiate between the sexes in small specimens but, at a minimum of about 20 mm. t.l., males and females can be distinguished by the shape and position of the endopods of the first pair of pleopods. In the male the endopod is located more proximally on the basis and is a little longer than in the female. Small males can also be distinguished by the ridge on the midline of sternite XIV (fig. 31a); in females sternite XIV is drawn ventrally to a median point (fig. 31b). Males 11 mm. c.l., 51 mm. t.l., with the petasmal endopods still unjoined, usually have the ventral costa with minute distomarginal spines and a few teeth near the apex. (See also under Relationships.)

GROWTH

A number of studies on growth of *P. d. duorarum* at various phases of its life cycle have been conducted. Among those concerned with larval development, that of Ewald (1965b) is the most complete. In the laboratory the larval phase was completed in 15 to 25 days, during which time the animals grew from a first nauplius (about 0.4 mm. t.l.) to a first postlarva (2.9 to 4.6 mm. t.l.). Ewald also found in the laboratory that specimens from 6.9 to 9.4 mm. t.l. grew from 0.35 to 0.51 mm. t.l. per day for 25 days.

There are various estimates of growth rate in juvenile and subadult pink shrimp. Tabb, Dubrow, and Jones (1962), in length-frequency studies of shrimp of northern Florida Bay, found that individuals of 6 mm. average c.l. increased at a monthly rate of 2 mm. average c.l., and that the rate increased to a maximum of 3 to 4 mm. monthly until an average size of 20 mm. c.l. was reached. Through mark-recapture studies, Costello and Allen (1960) estimated that pink shrimp 16.7 mm. mean c.l. in Florida Bay and adjacent waters grew at a rate of 3.5 mm. mean c.l. per month. Kutkuhn

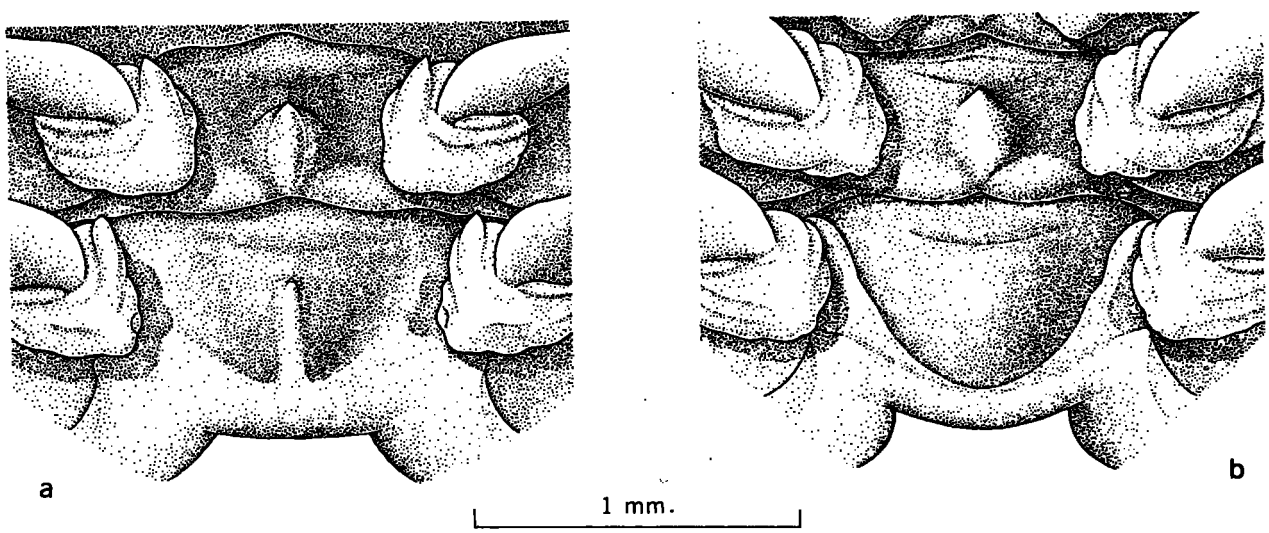

FIGURE 31.—*Penaeus* (*M.*) *duorarum duorarum* Burkenroad. a. Sternites XIII and XIV, ♂ 5.5 mm. c.l., Tampa Bay, Fla. b. Sternites XIII and XIV, ♀ 5 mm. c.l., Tampa Bay, Fla.

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(1966b), on the basis of a mark-recapture experiment, estimated that in the Tortugas area shrimp 17.9 to 20.2 mm. c.l., 84.2 to 94.1 mm. t.l., at the beginning of the experiment grew an average of about 3.4 mm. t.l. per week. He also demonstrated that in shrimp above 30 mm. c.l. weight increases rapidly in relation to increase in carapace length. Williams (1955a), using upper extremes of size distribution, calculated that juvenile shrimp in North Carolina grew at a mean rate of 52 mm. t.l. in July, and 7.5 mm. t.l. per month in winter and early spring.

Growth rate in adult pink shrimp has attracted the attention of a number of investigators. Iversen and Idyll (1960) studied the shrimp on the Tortugas grounds and showed that females 31 mm. c.l. grew an average of about 2 mm. c.l. per month, and males 26 mm. c.l. grew an average of about 1 mm. c.l. per month. Growth studies on the same grounds by Iversen and Jones (1961) indicated, for both sexes combined, an average monthly increase of 1.8 mm. c.l. in "small shrimp" (25 mm. c.l.), 1 mm. c.l. in "medium shrimp" (33 mm. c.l.), and very little (0.5 mm. c.l.) or no growth in "large shrimp" (40 mm. c.l.).

SEX DIFFERENCES IN SIZE

The females of *P. d. duorarum* reach a maximum length of 280 mm. t.l.; a truly giant specimen of this size from the Campeche fishing grounds is in the collection of the St. Petersburg Marine Laboratory, Fla. The males are usually much smaller, although Thomas J. Costello (personal communication) measured one of 269 mm. t.l.

In North Carolina, Williams (1955a) observed that the size disparity between sexes in *P. d. duorarum* is statistically significant at mean total length slightly exceeding 100 mm. [no less than 21 mm. c.l.]. In Tampa Bay, Saloman (1968) found that small females with a mean carapace length of 13.7 mm. were larger than the juvenile males collected with them. The disparity in length between larger females and males has been reported for many localities by various authors. Because the females are larger than the males, a sample containing both sexes produces a bimodal distribution. On the average, the large males and females are found at the greater depths throughout the subspecies range.

Ecology

FOOD

P. d. duorarum is mostly a bottom and a nocturnal feeder. Omnivorous like other penaeids, it ingests algae and fragments of higher plants, as well as sand, mud, and organic debris. It also feeds on a larger variety of animals, including foraminiferans, hydroids, nematodes, mollusks, polychaetes, crustaceans, tunicates, and fish larvae (Williams, 1955a, 1958; Flint, 1956; Woodburn et al., 1957; Eldred et al., 1961).

SUBSTRATE

P. d. duorarum prefers rather firm bottoms of mud and silt with coral sand containing a mixture of mollusk shells, as has been shown by investigations in the Gulf of Mexico by Springer and Bullis (1954), Hildebrand (1954, 1955) and Gunter (1956), and by laboratory experiments by Williams (1958). Pink shrimp also live on hard sand bottoms. The distribution of the subspecies in the northern Gulf of Mexico may be explained by its preference for firm bottoms. Whereas it is scarce on the soft muddy bottoms from Mississippi to middle Texas, it is very abundant on the firmer bottoms off the Tortugas Islands and the southeastern part of the Golfo de Campeche. Its presence north of Ciudad Campeche, Mexico, where *P. setiferus* is absent, also could be attributed to the firm bottoms there.

DIEL CYCLE

Adult pink shrimp are nocturnal and are fished at night in all areas. They seem, however, to be somewhat active on cloudy days and during days when the water is turbid (Hildebrand, 1955; Eldred et al., 1961). Several observations indicate that they normally remain buried during daytime.

Larvae seem to be as nocturnal as adults. Jones et al. (1964) made by far the largest catches after dark and concluded that larvae move vertically, gathering near the surface at night and descending in the water during the day. Postlarvae, however, apparently are active day and night, because Eldred et al. (1965) captured 54 percent of the postlarvae taken over 24 hours in the daytime in Tampa Bay.

Juveniles and subadults seem to be mostly nocturnal but capable of diurnal activity. Higman (1952) and Tabb, Dubrow, and Jones (1962) collected large numbers of specimens leaving estuaries in southern Florida at night but few or none during the day. In Tampa Bay, Saloman (1968) made larger catches during darkness, and Joyce (1965) noted that his sampling in northeast Florida yielded a larger percentage of young *P. d. duorarum* at night, but because of the size composi-

tion of sample catches he concluded that the very small shrimp were mainly nocturnal whereas the larger individuals were more diurnal.

In the laboratory, Williams (1958) noted that several groups of shrimp, with mean total length of 50 to 60 mm., were active at night, and, during the day, remained almost or completely hidden in the substrate. In contrast, Eldred et al. (1961) reported that in aquariums, individuals smaller than 55 mm. t.l. were active during the day or when exposed to bright light, whereas large specimens remained buried in the sand. Aaron and Wisby (1964) stated that in their laboratory experiments, more than half of the shrimp, 55 to 105 mm. t.l. "between the leading edge of the blades and the spine of the telson," showed positive phototaxis when exposed to 3.23 lumens per 1 $m.^2$, those 75 mm. showed the greatest. Studies by Fuss and Ogren (1966) indicated that larger shrimp are more sensitive to light than smaller shrimp, although most individuals within the size ranges (80 to 180 mm. t.l.) observed showed a negative photic response: burrowed in the presence of daylight or artificial light. They are of the opinion that light is apparently the most important single factor in shrimp diel activity.

Availability of pink shrimp offshore seems to vary with the phases of the moon. Fishermen say, and many others have observed, that offshore catches show a sharp decrease during the full moon. The activity of shrimp inshore through the lunar cycle has not been clearly determined. Eldred et al. (1965) recorded a higher percentage of postlarvae during the full-moon spring tides. Idyll et al. (1965) are of the opinion that moon phase and speed of ebbing current are two of the more important factors responsible for the variation in the size of the catch of shrimp at the mouth of the estuaries. At Buttonwood Canal, Fla., they consistently obtained higher numbers of shrimp moving on the ebb tide during or near the new and full moon than during the other moon phases. Copeland (1965) reported peak seaward migrations at the time of the full moon, whereas Saloman (1968) caught greater numbers of shrimp during the dark phases of the lunar cycle than during the full moon.

In the laboratory, Aaron and Wisby (1964) found evidence that the moon phase has a significant effect on the activity of shrimp; they observed that maximum photoactivation occurred during the full moon, and the minimum during the new moon. Fuss and Ogren (1966), in turn, reported that in aquariums, direct correlations between lunar cycles per se and pink shrimp nocturnal activity were not well defined. Size of animals and light intensity—as Fuss and Ogren have suggested—could be responsible for the differences in behavior in relation to lunar changes.

MOVEMENTS

The larvae of *P. d. duorarum* move from the spawning sites toward inshore waters and, thus, have the same migratory pattern as the sympatric *Penaeus*. The larvae are thought to be carried by currents, but, as stated earlier, the larvae probably are not entirely passive during their onshore movement.

Larvae develop at sea and the young shrimp arrive in the nursery grounds usually as postlarvae. Postlarval shrimp are predominantly transported inshore by flood tides (Tabb, Dubrow, and Jones, 1962; Copeland and Truitt, 1966; Hughes, 1966). Hughes (1966) stated that the movement of the postlarvae into the nursery areas is apparently effected largely by their passive displacement by the tide. Although most postlarvae reach estuarine waters, some pink shrimp may complete their entire life cycle in oceanic waters. Ingle et al. (1959) and Eldred et al. (1961) have advanced the view that the extensive shallows from Key West, Fla., west through the Marquesas Keys to Rebecca Shoal, are nursery grounds for pink shrimp.

The studies by Williams (1959) in North Carolina, Bearden (1961) in South Carolina, and Tabb, Dubrow, and Jones (1962) in Florida Bay showed that most postlarvae enter the inshore waters at the six-to-seven-rostral-tooth stages, although in Florida Bay a few were at the four-rostral-tooth stage. In Tampa Bay, Eldred et al. (1965) found that the postlarvae arrive when younger—when the rostrum possesses a minimum of two and a mode of four teeth.

The period of postlarval movement of pink shrimp varies with the range of the subspecies. In North Carolina, Williams (1955a, 1965) reported that influx takes place from late May to November. Bearden (1961) showed similar movement in South Carolina. Joyce (1965) on the basis of the presence of individuals 40 mm. t.l. and smaller, concluded that in northeast Florida major inshore movement appears to take place from June through December.

The extensive sampling data from southwest Florida suggest that postlarvae enter in-

shore water throughout the year, but that peaks of abundance occur, which vary from one year to another. In Florida Bay a large peak was reported from April to June by Tabb, Dubrow, and Jones (1962) and from July through October by Jones et al. (1964). A secondary peak of abundance is known to take place late in the fall or during the winter. In Tampa Bay an extremely large peak was recorded in July by Eldred et al. (1965). In Mississippi, Christmas et al. (1966) found pink shrimp postlarvae from May through December, but only a few before July. In the Aransas Pass, Tex., inlet, Copeland and Truitt (1966) observed a maximum peak of postlarval *P. d. duorarum* in August and September.

Small pink shrimp grow rapidly in the nursery areas and move toward the sea as they approach maturity. They leave mostly on the ebb tides since sample catches are usually much larger then than during flood tides, and largest when the tidal current is strongest. Costello and Allen (1966) estimated that shrimp remain in the estuaries of southwest Florida for a period ranging from about 2 to 6 months.

Hughes (in press) has suggested that the displacement of the postlarvae inshore on flood tides and the emigration of the "juveniles" offshore on ebb tides appear to be effected by the respective responses of the two stages to changes in salinity. Juveniles usually exhibit a positive rheotaxis; however, when the salinity of the water decreases downstream swimming ensues. This ensures that in nature juveniles will swim against the current and, thus, resist displacement in an inshore direction by the flood tide but will swim offshore with the ebb tide. Postlarval shrimp respond to a decrease in salinity by dropping to the substrate; when the salinity increases they become active in the water column. Consequently, postlarvae are moved inshore on the flood tide and evade displacement seaward on the ebb tide.

A number of studies have been carried out in different localities to follow the migration of pink shrimp as they leave the estuaries. Tabb, Dubrow, and Jones (1962) and Idyll et al. (1966) investigated the emigration from the estuaries to Florida Bay. The former authors observed that many shrimp move to the Bay at about 18 to 20 mm. c.l. (about 82 to 90 mm. t.l.) and practically all before attaining a carapace greater than 25 mm. (about 105 mm. t.l.). Idyll et al. (1966) estimated that the monthly mean size of the migrating shrimp ranged from 9.9 mm. c.l. (about 46 mm. t.l.) to 18 mm. c.l., and averaged 14 mm. c.l. (about 65 mm. t.l.). The relative abundance of shrimp moving to Florida Bay fluctuates seasonally. Numbers are greatest in late summer and early fall, and abundance reaches a peak in September. A second peak occurs from January to April. Eldred et al. (1961) in Tampa Bay found that shrimp began their seaward movement at 85 mm. t.l. in April and continued to leave through July. Mass migration to offshore waters did not seem to occur during the fall and winter. Copeland (1965) stated that most shrimp leave through Aransas Pass, Tex., inlet, at 70 to 90 mm. t.l., from April through October. Joyce (1965) gathered evidence that in northeast Florida the young leave the nursery grounds at a length of 85 to 90 mm.

Williams (1955a) in North Carolina observed that pink shrimp that arrive at the nursery grounds in spring grow rapidly and after having reached the subadult stage move back to the ocean, where as young adults they are harvested in late summer and fall. Individuals that overwinter in the estuaries migrate to the sea in May and June and become the object of a spring fishery.

Several investigations have been made to establish the movements of pink shrimp leaving the nursery areas of southwest Florida for the spawning grounds. Costello and Allen (1966) concluded that: (a) some pink shrimp from shallow coastal waters of southwest Florida follow broad migratory routes in moving to offshore grounds; (b) shrimp from each nursery area seem to assume "a distinct pattern of distribution on the offshore grounds," that is, those found in the Tortugas come from shallow waters ranging from northeast to east of the grounds, whereas those taken on the Sanibel grounds are immigrants from the adjacent coastal waters; (c) ranges of the stocks from which the Sanibel and Tortugas populations are derived overlap along the southwest coast of Florida and in the offshore water between the two trawling grounds; (d) shrimp enter the Tortugas grounds from the north, east, and southeast. Furthermore, it seems that the Tortugas shrimp do not migrate to the Sanibel fishing areas, and south Sanibel shrimp seldom migrate to the Tortugas grounds or to the northwest Sanibel grounds. The above conclusions were based on various mark-recapture experiments by Costello and Allen (1960,

1961, 1964, 1966); Iversen and Idyll (1960), Iversen and Jones (1961), and the sampling studies in the area by Ingle et al. (1959), Iversen et al. (1960), and Eldred et al. (1961). The investigation of Iversen et al. (1960) on the size distribution of shrimp suggested that they leave the Tortugas grounds in a northwesterly direction and move toward deeper water.

Evidence suggests that hurricanes markedly influence the movement of shrimp. Massive offshore migration takes place in response to abnormalities brought about by the storms. In 1960 after hurricane "Donna" struck southern Florida, the catches on the Tortugas grounds included a much higher percentage of small individuals, and the average size of shrimp was smaller than in previous years (Eldred et al., 1961). These changes indicated that hurricanes can cause the shrimp to move offshore earlier and at a smaller size than normal. Also, hurricanes in the nursery areas are known to cause high mortality among the young (Tabb, Dubrow, and Jones, 1962).

In contrast to our rather clear understanding of migrations of *P. setiferus*, almost nothing is known about coastal migrations of *P. d. duorarum*. Neither seasonal migrations nor movements in response to temperature changes in the latter have been adequately investigated. Recent data acquired by McCoy and Brown (1967) from release and recapture procedures indicated that pink shrimp migrated southward from Beaufort Inlet, N.C., from May through August; however, the greatest distance traveled was only 193 km. in 5 weeks.

EFFECTS OF TEMPERATURE

P. d. duorarum is the only *Penaeus* that overwinters in the estuaries of North Carolina. There Williams (1955a) found them at 6° C. and suggested that they may survive the severe winter cold by burrowing deeply into the substrate. The laboratory experiments of Williams (1960) showed that *P. d. duorarum* was better able to withstand a combination of low salinity and temperature than *P. a. aztecus*. This discovery may help to explain the occurrence of pink shrimp in the northern inshore waters of North Carolina during the winter and even in those of Virginia, where, according to Van Engel (1965), specimens are taken in almost all months. On the basis of our present knowledge, there is no explanation for the fact that even though the pink shrimp is more tolerant of low temperatures than are white and brown shrimps, the northern limit of its range is some 2°30′ and 3°25′, respectively, south of that of the others; obviously, some factor other than temperature has prevented their spreading farther north.

Local movements of young shrimp in response to sudden changes in temperature have been observed. In southwest Florida, Tabb, Dubrow, and Jones (1962) noted that the shrimp moved out of the shallows to deeper, warmer water during cold periods and returned again as soon as the water began to warm. They indicated that if the descent in temperature occurred gradually, the shrimp seemed to remain in the inshore waters.

Temperature is one of the principal factors governing growth (see above) and survival of pink shrimp as it is known to be for the closely allied *Penaeus*. The maximum temperature at which *P. d. duorarum* has been recorded is 35.5° C., at which Eldred et al. (1961) collected them in Tampa Bay. In general, it seems that the lower temperature limit for pink shrimp activity is about 14° to 16° C. (Williams, 1955a; Fuss and Ogren, 1966). Complete cessation of activity occurs below about 10° C. (Williams, 1955a; Eldred et al., 1961; Fuss and Ogren, 1966). The lowest temperature at which pink shrimp have been found is 3.5° C.; a single specimen was collected in Lower Chesapeake Bay (Thimble Shoal Light) in February (W. A. Van Engel, personal communication).

EFFECTS OF SALINITY

Larval and early postlarval stages, large subadults, and adults abound in oceanic waters of high salinity. On the Tortugas fishing grounds Iversen et al. (1960) reported bottom salinities (10-15 fm.) of 36.15 p.p.t. to 37.73 p.p.t.

Postlarvae, juveniles, and early subadults live in inshore water within a wide range of salinities. Tabb, Dubrow, and Jones (1962) have recorded salinities of zero to 47 p.p.t. in the nursery areas of south Florida. Joyce (1965) found specimens 80.5 km. up the St. Johns River, Fla., in almost fresh water. Gunter et al. (1964) indicated that salinity seems to be a limiting factor in the abundance of *P. d. duorarum* as well as of *P. setiferus* and *P. a. aztecus*. Their investigations in inshore water adjacent to the Gulf of Mexico showed that pink shrimp were more abundant at salinities of 18 p.p.t. and above, whereas brown shrimp were more abundant in water of 10 to 20 p.p.t. and white shrimp in water of salinity lower than 10 p.p.t.

They also pointed out that the greatest abundance of adult pink shrimp occurs in areas where the salinity is high.

ENEMIES AND DISEASES

Predation by fishes is very probably the most important cause of natural mortality among pink shrimp, as it is for most *Penaeus*. Several workers have demonstrated that the pink shrimp is an important food for some fishes. Aquatic birds are also possibly among their enemies.

Parasites of the pink shrimp include protozoans, trematodes, cestodes, and nematodes, and even an insect (Sprague, 1950, 1954; Hutton and Eldred, 1958; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959; Hutton, Sogandares-Bernal, and Eldred, 1959; Kruse, 1959; Hutton et al., 1962). The microsporidian *Thelohania duorara* Iversen and Manning causes what is commonly known as "milk" or "cotton" shrimp, because of the opaque whitish discoloration shown by infected individuals.

Commercial Importance

P. d. duorarum is one of the most valuable species of commercial shrimp in the Gulf of Mexico fisheries. The areas of maximum productivity are the Tortugas-Sanibel and Obregón-Campeche grounds. Annual catches from the former are about 8,000,000 kg. (whole weight) and from the latter are even higher. In the Tortugas-Sanibel grounds at least 80 percent of the catches are made during winter-spring, but in the Obregón-Campeche beds pink shrimp production shows little seasonal variation. Throughout the rest of the Gulf region, pink shrimp are taken in moderate quantities in northern Florida and western Texas, but catches in other areas are rather insignificant.

Pink shrimp make up part of the occasional commercial catches made at the southernmost portion of the range, between Isla Contoy and Isla Mujeres, Mexico. They are fished commercially also along the southeastern coast of the United States. Moderate catches are taken off North Carolina and small ones off the other southern Atlantic States.

Lyles (1967) reported that in 1965 landings of pink shrimp in the United States were 19,760,132 kg. (whole weight) which represents about 20 percent of all *Penaeus* shrimp landed in the Gulf and Atlantic States.

Penaeus (Melicertus) duorarum notialis
PÉREZ FARFANTE

Figures 32 to 38

Cuba: camarón acaramelado, camarón cocinero, camarón carbonero. Nicaragua: camarón rojo. Venezuela: langostino amarillo, langostino rosado, camarón rosado sin mancha.

Penaeus brasiliensis: Miers, 1878: 299, 306 [part]; Ives, 1891: 199 [part]; Rathbun, 1897: 46 [part]; Rathbun, 1901: 100, 101 [part]; Pesta, 1915: 113 [part]; Boone, 1927: 78 [part]; Boone, 1930: 14, 15, 101–105 [part]; Burkenroad, 1934: 88, 93, 94 [part], 109; Schmitt, 1935: 128, 129 [part?]. Not *P. brasiliensis* Lat., 1817.

Penaeus duorarum: Burkenroad, 1939 [part, "Form B"]: 29, 31–34, 40–45, figs. 18, 19, 26, 27; Sánchez Roig and Gómez de la Maza, 1951: 113; Pérez Farfante, 1953: 232–234, 236, 237, (238, 241 [part]); Pérez Farfante, 1954a: 97, 98; Pérez Farfante, 1954b: 9, 13, 20, 26–30; Pérez Farfante, 1955: 180; Lindner, 1957: 11, 14, 25, 66, 69–72, 159, 160, 165; Suárez Caabro, 1957: 137; Eldred, 1958: 5, 23; Suárez Caabro, 1958: 5, 7; U.S. Fish and Wildlife Service, 1958a: 11; Holthuis, 1959: 67, 68; Eldred, 1960: 164, 165; Eldred and Hutton, 1960: 91, 98, 101, 106, 108, fig. 7a; Eldred et al., 1961: 87, 90, 91; Pérez Farfante et al., 1961: 18, 22, 33–55, 60, 63; Anonymous, 1962: 56, 1 fig.; Idyll, 1962: 184; Loesch, 1962: 172–177; Rossignol and Repelin, 1962: 157–174; Davant, 1963: 9, 11, 15–17, 31–35, 65, 67, 71–73, 86–91, figs. 6b, 11–14, and bis; Simpson, 1963: 22, 23; Boschi, 1964: 39–41; Ewald, 1964: 10, 20–23, 24, 28, tables [part]; Ewald, 1965a: 29; Ewald, 1965c: 52, 59, 65, 67, 69, 72–74, 80, 81, 83, 84, 86, 87, 91, 93–96, 114, (80, 88–90, 92, 97–99, 113, fig. 13 [part]); Holthuis and Rosa, 1965: 4 [part]; Joyce, 1965: 132, 135, 220, 221; Pericchi López, 1965: 24; da Silva, 1965: 3, 4; Simpson et al., 1965: 77; Williams, 1965: 22, 23; Neiva and Mistakidis, 1966: 5, 6, fig. 11a, b; Croker, 1967: 63, 67, 68, 72–74, 79–81, 84, 87, 98, 110; Instituto de Fomento Nacional, 1967: 5, 8.

Penaeus duoarum: Anderson and Lindner, 1945: 306 [part]; Dall, 1957: 142, 226 [part].

Penaeus duorarum Burkenroad "var. *cameronensis*" Rossignol and Repelin, 1962: 159.

Penaeus duorarum notialis Pérez Farfante, 1967: 94–98, fig. 4a–d; (holotype, ♂, USNM 119132, off Las Piedras, Gulf of Venezuela, 26 fm., Oc-

tober 5, 1965, *Oregon* Sta. 5664, lat. 11°44′ N., long. 70°22′ W.).

Taxonomic Remarks

Questions have arisen concerning the identity of *P. duorarum* from tropical West Africa. Burkenroad (1939) identified the specimens from that region as *P. duorarum* "Form B," the same as "candied shrimp" from the Caribbean region and the Atlantic Coast of South America. My studies also indicate that the specimens of *P. duorarum* from both regions should be referred to *P. d. notialis*. On the basis of biometric studies Rossignol and Repelin (1962) concluded that there are two different populations of this shrimp in West Africa: one population along the coast of Cameron has shrimp with the third pair of pereopods longer than they are in the other population that ranges along "la côte du Congo et du Sud Gabon." They considered the northern population a different variety and named it "cameronensis." This varietal name does not have priority over *notialis* because under the International Rules of Zoological Nomenclature, a new name published after 1960 as a variety is to be regarded as of infrasubspecific rank. In the eastern Atlantic *P. d. notialis* ranges both west to Cap Blanc and south to Angola beyond the areas considered by Rossignol and Repelin.

Study Material

For a list of records see Pérez Farfante, 1967. Additional records follow.

MEXICO

Quintana Roo: 2 ♂, USNM, Punta Nicchehabin, Bahía de la Ascensión, less than 1/3 fm., April 13, 1960, F. C. Daiber, Smithsonian- Bredin Exped. Sta. 65–60.

COLOMBIA

1 ♂, USNM, off Punta Broqueles, 400 fm., *Oregon* Sta. 4902, May 28, 1964.

Diagnosis

Adrostral sulcus broad posteriorly, and long, reaching almost to posterior margin of carapace. Median sulcus long, ending immediately anterior to posterior end of adrostral sulcus, and deep along its entire length. Dorsolateral sulcus broad. Petasma with distal portion of ventral costa broadening and turning proximally rather abruptly, armed with minute spines along free border and with compact group of large teeth on attached border; apex of ventral costa adnate to adjacent wall; distal fold small, unarmed or with few submarginal spinules. Thelycum with apical process relatively large, and with prominent, short, undivided median carina on broad posterior process; carina exposed owing to slight divergence of anteromedian corners of lateral plates.

Description

ROSTRUM

Teeth $\frac{7–9}{0–2}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—61, 9/2—30, 8/1—4, 7/2—3, 7/1—1, 9/1—0.33, 7/0—0.66; N=300)+epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to last dorsal tooth; rostrum relatively short in larger juveniles and subadults, reaching at most to distal end of antennular peduncle; attaining maximum length in relation to carapace length at 12 to 18 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.75); decreasing progressively with increasing length of shrimp, rostrum reaching distal end of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.40); rostrum straight apically, occasionally upturned, convex proximally; highest portion of blade at level of third dorsal tooth; latter level with anterior margin of carapace; rostrum tip 1/8 to 1/4 r.l. Postrostral carina strong, prominent, and uniform in width or slightly wider in anterior half, and long, extending almost to posterior margin of carapace. Median sulcus deep throughout, long, ending near posterior margin of carapace. Adrostral sulcus deep, broad posteriorly, 1/8 to 1½ width of postrostral carina, and rather long, ending 1 1/11 to 1 1/16 c.l. from posterior margin of carapace. Adrostral carina prominent and long, same length as adrostral sulcus.

CARAPACE (fig. 32)

Length in proportion to total length smaller in juveniles, increasing abruptly at about subadult stage. Gastrofrontal sulcus broad, extending posteriorly to about one-fifth c.l.; gastrofrontal carina sharp, turning slightly posterodorsally and ending in acute orbital angle anteriorly. Orbitoantennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening into base of spine. Gastro-orbital carina high and sharp, occupying posterior 3/4 to 4/5 of dis-

tance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus 1/5 to 1/4 c.l., ending slightly anterior to midlength of carapace. Hepatic carina 1/5 to 1/4 c.l., sharp, sloping anteroventrally to end 1/15 to 1/20 c.l. from anterior margin of carapace. Antennal spine prominent and acute; hepatic spine pronounced.

ANTENNULES

Lateral flagellum about three-quarters of length of antennular peduncle, slightly longer and with articles shorter than median flagellum; anterolateral spine sharp; stylocerite acuminate, reaching slightly beyond midlength of first antennular segment. Prosartema reaching distal end of proximal fifth of second antennular segment.

ANTENNAE

Length of scaphocerite 2½ times maximum width, its length relative to carapace length decreasing slightly with growth; spine reaching distal end of antennular peduncle or to distal end of proximal quarter of thickened portion of dorsal flagellum. Carpocerite 1¼ times longer than wide, reaching distal end of optic peduncle. Antennal flagellum relatively short, about 1⅓ body length.

THORACIC APPENDAGES

Third maxilliped reaching at least distal one-third of second and, at most, distal end of third antennular segment; longer in larger individuals. Length of dactyl 3/5 to 3/4 that of propodus. First pereopod surpassing carpocerite by half length of dactyl or by entire length of propodus. Second pereopod surpassing carpocerite at least by entire length of propodus and, at most, by one-half length of carpus. Third pereopod exceeding antennular peduncle by one-half length of dactyl or by one-eighth length of carpus. Fourth pereopod surpassing carpocerite by one-half length of dactyl to three-quarters length of propodus. Fifth pereopod subequal in length to fourth. Exopods on all pereopods; long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

ABDOMEN

Carinate dorsally from posterior half of fourth somite posteriorly, carina increasing in height progressively from base to keel on sixth somite, there ending in sharp spine on posterior margin. Dorsolateral sulcus characteristically broad (fig. 33), ratio between height of keel and width of sulcus ranging from about 0.25 to 3, modally 1.75 (fig. 34); K/S mode 1.75 in size classes 16 to 36

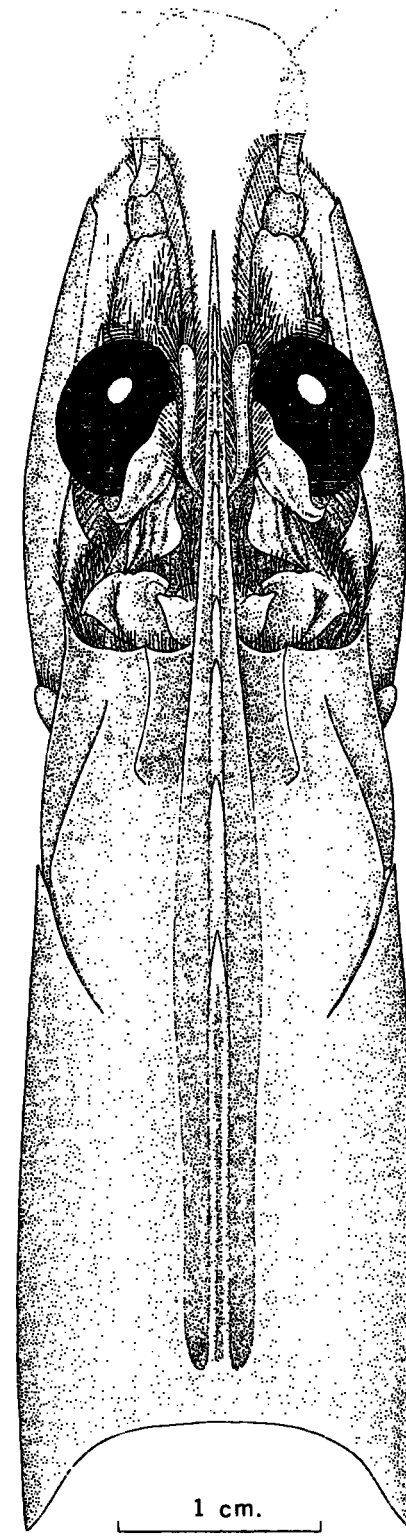

FIGURE 32.—*Penaeus* (*M.*) *duorarum notialis* Pérez Farfante. Cephalothorax, holotype, ♂ 41.5 mm. c.l., off Las Piedras, Gulf of Venezuela.

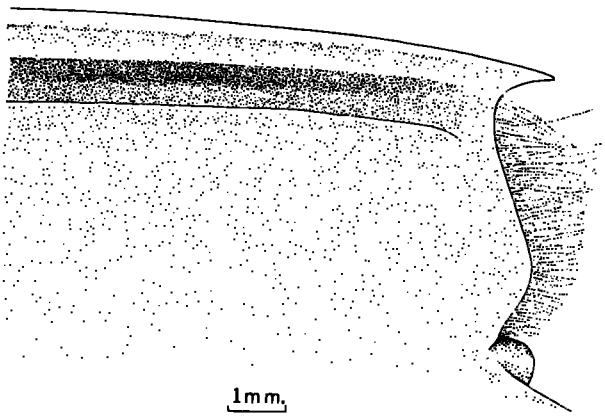

FIGURE 33.—*Penaeus (M.) duorarum notialis* Pérez Farfante. Sixth abdominal somite, posterodorsal portion, ♀ 42 mm. c.l., off Great Pedro Bluff, Jamaica.

mm. c. l., and less in smaller and larger size classes (fig. 35); both lips sharp. Sixth abdominal somite with three prominent cicatrices on each side, anterior the longest; fifth somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite; fourth abdominal somite with similar series of pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

PETASMA (fig. 36)

As in *P. d. duorarum.*

APPENDIX MASCULINA

As in *P. d. duorarum.*

THELYCUM (fig. 37)

Similar to that of *P. d. duorarum.*

COLOR

Although variable, color of *P. d. notialis* is most frequently light brown; thus, the name camarón acaramelado (candied shrimp) in Cuba and langostino amarillo in Venezuela. In certain areas it is pink and is known as camarón rosado (pink shrimp), whereas in other areas it is very dark brown and is called camarón carbonero (coal-carrying shrimp) or camarón cocinero (cook shrimp).

In the Antilles, this subspecies has a large, dark, reddish-brown spot on each side at the junction of the third and fourth abdominal somites, whereas in northern South America, it consistently seems to lack these large spots.

Distribution and Morphological Variations

In American waters, *P. d. notialis* ranges from Cuba through the Greater Antilles to the Virgin Islands and from Bahía de la Ascensión, Quintana

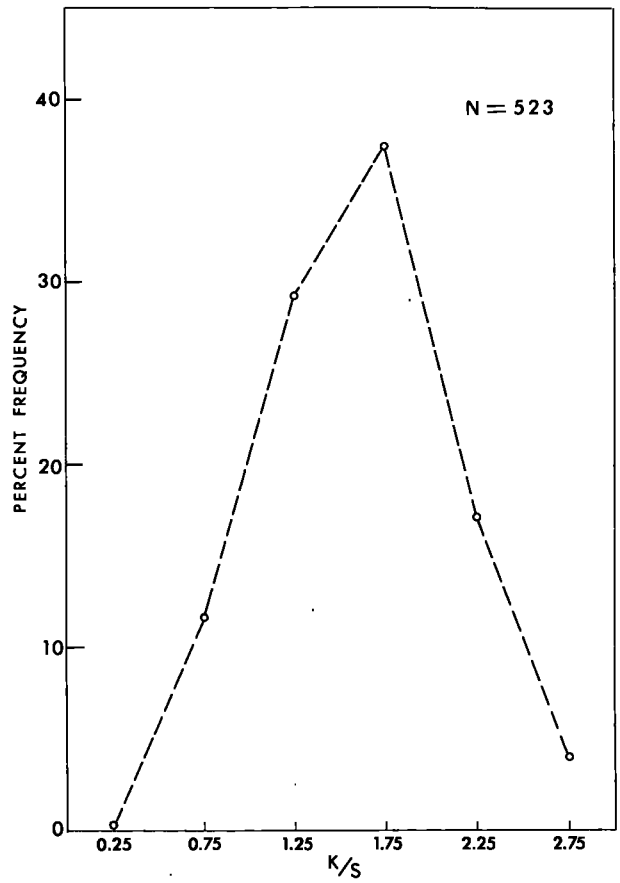

FIGURE 34.—Percentage of distribution of keel-sulcus (K/S) in *Penaeus (M.) duorarum notialis* Pérez Farfante.

Roo, Mexico, along the Caribbean Coast of Central America and South America and the Atlantic Coast of South America to São Luis, Brazil. It is apparently absent from northeastern Brazil, but appears again in Ilhéus and extends south to Cabo Frio (fig. 28). Here, for the first time, *P. d. notialis* is recorded from the Caribbean Coast of Mexico, north of the Gulf of Honduras. It is also found in the eastern Atlantic, along the coast of Africa, from Cap Blanc to Angola.

A few specimens of this subspecies have been reported beyond the northern and southern limits of its range in the western Atlantic as given here. I believe that those from northeast Florida recorded by Joyce (1965) are most likely members of the small percentage of *P. d. duorarum* that have a rather broad dorsolateral sulcus, as figure 23 shows. Although camarón acaramelado has been mentioned from Baía de Guanabara, Brazil (da Silva, 1965), it is doubtful that it reaches so far south. I have examined specimens from that

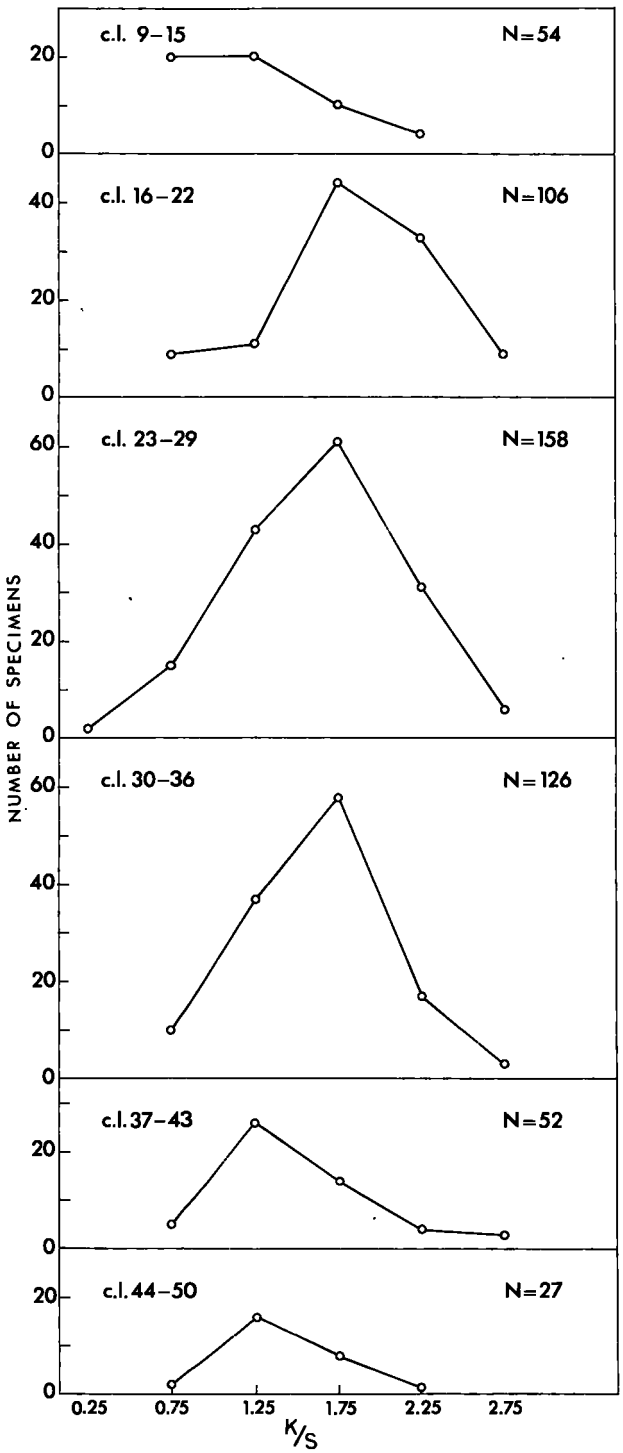

FIGURE 35.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *duorarum notialis* Pérez Farfante.

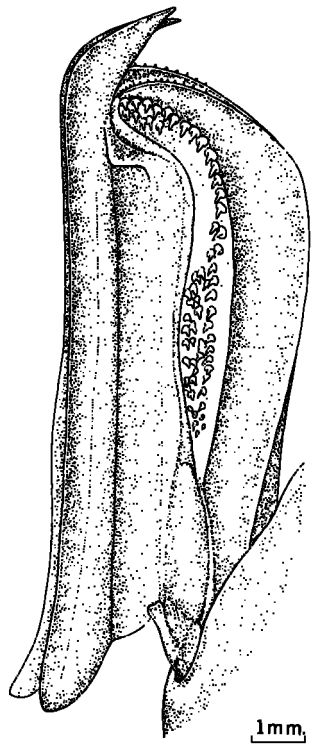

FIGURE 36.—*Penaeus* (*M.*) *duorarum notialis* Pérez Farfante. Petasma, ♂ 34 mm. c.l., off Las Piedras, Gulf of Venezuela.

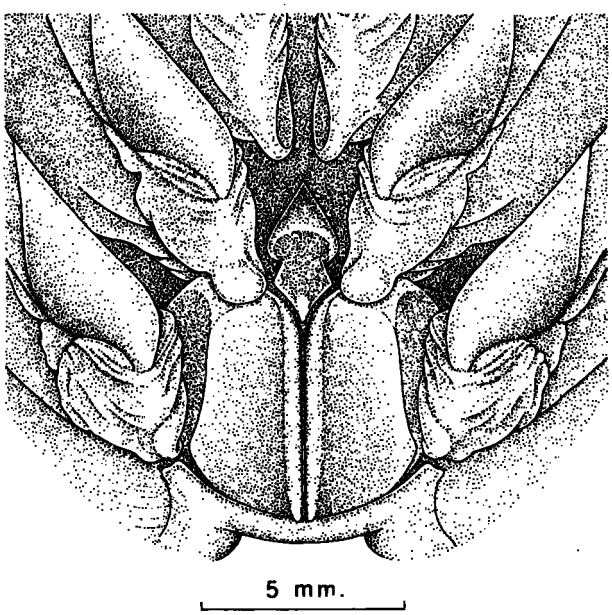

FIGURE 37.—*Penaeus* (*M.*) *duorarum notialis* Pérez Farfante. Thelycum, ♀ 38 mm. c.l., off Las Piedras, Gulf of Venezuela.

locality identified as "*P. duorarum*," but they were actually *P. paulensis*.

The bathymetric distribution of *P. d. notialis* seems to extend to water much deeper than has been previously reported. The greatest depths at which this subspecies was known to live were 60 to 65 fm. (Pérez Farfante, 1967), but a single male was caught at 400 fm. off Punta Broqueles, Colombia, *Oregon* Sta. 4902. It was taken with other penaeids—*Hymenopenaeus robustus* Smith, *Aristaeomorpha foliacea* (Risso), *Plesiopenaeus edwardsianus* (Johnson), and *Aristeus antillensis* Bouvier—which occupy water deeper than that in which *Penaeus* usually live. On the basis of this record, it seems possible that camarón acaramelado occasionally may wander into water as deep as 400 fm. Moderately large concentrations of *P. d. notialis* are found in the Greater Antilles in 2 to 15 fm., in the Gulf of Venezuela in 20 to 25 fm., and off Honduras, Nicaragua, and the northeast coast of South America higher densities are found in deeper water, 34 to 35 fm.

Penaeus d. notialis is remarkably uniform throughout its range in American waters. Among the few variations that exist is the relative length of the third pereopod. Although its length varies rather considerably, it seems to me that little systematic importance can be attached to this character in the western Atlantic. For example, in a single locality I found females with a carapace of 40 mm. in which the length of the carpus—which is indicative of the length of the third pereopod—ranges from 26 to 29 mm.; in turn, females with 36 and 40.5 mm. c.l. have a carpus of 29 mm. (fig. 38). Furthermore, in large females from the Golfo de Darién to Islas San Bernardo, Colombia, the carpus is considerably longer than in the females of the same size from neighboring

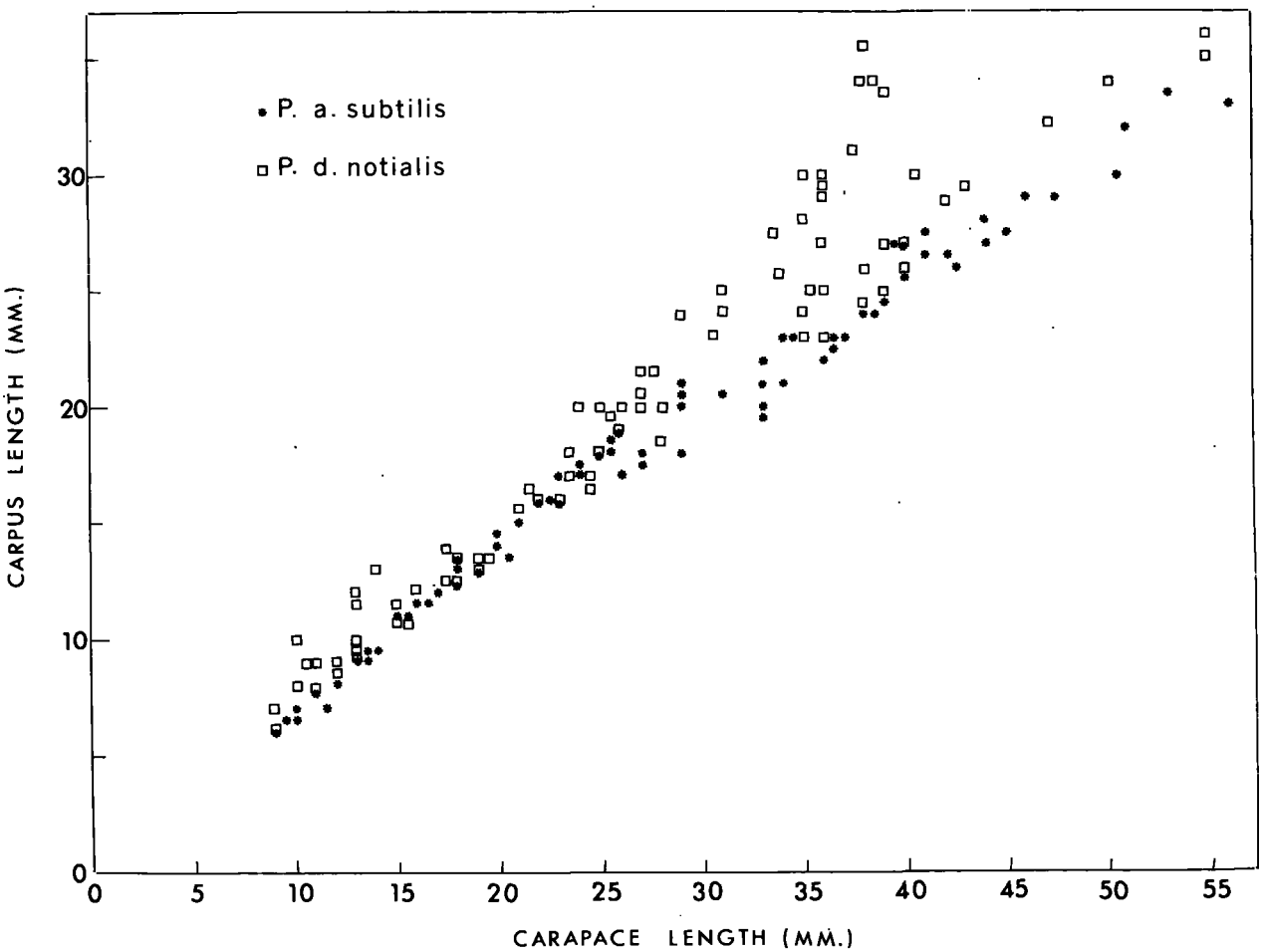

FIGURE 38.—Carpus length-carapace length relation in *Penaeus (M.) aztecus subtilis* Pérez Farfante and *Penaeus (M.) duorarum notialis* Pérez Farfante.

Central America and the Gulf of Venezuela; no other apparent differences exist between the specimens examined. The discontinuity in the range of variation in this character in the western Atlantic is in contrast to the observations by Rossignol and Repelin (1962) who were working with this subspecies along the west coast of Africa (see above).

Relationships

(See under *P. duorarum duorarum.*)

Reproduction

SUBADULT STAGE-SEXUAL MATURITY

The number of small specimens examined was not sufficient to permit a conclusion as to the size range at which they become subadults. Males were found with petasmal endopods first joined at 16 mm. c.l., 73 mm. t.l. The minimum size at which females had the thelycum fully developed was 16 mm. c.l., 73 mm. t.l.

COPULATION

Copulation has not been observed, but it most probably takes place between a soft-shelled female and a hard-shelled male for the same reasons that were mentioned earlier for *P. d. duorarum*. Information on impregnation is too meager to allow conclusions.

OVARY DEVELOPMENT

My observations show that in *P. d. notialis* the ovaries go through five basic stages that are similar to those described for *P. d. duorarum* and can be recognized by the same characters of size and color.

SPAWNING

The presence of very small juveniles in shallow coastal waters of southern Camagüey, Cuba, as well as in Laguna Doctor, Playa de Baracoa, Cuba, throughout most of the year seems to indicate that spawning is probably continuous around the island. The preliminary investigation of specimens from Cuban waters by Pérez Farfante et al. (1961) showed that mature females were present in the waters south of Camagüey from March through May.

SEX RATIO

In inshore waters and coastal waters to 12 fm., the ratio of males to females seems to be approximately 1 : 1. Pérez Farfante et al. (1961) found the entire sample from Laguna Doctor, Playa de Baracoa, Cuba, contained 54 percent males and 46 percent females, and a sample from the southern coast of Cuba had 51 percent males and 49 percent females.

Postembryonic Development

LARVAE, POSTLARVAE, AND JUVENILES

No studies have been conducted on either larval or postlarval stages of this shrimp.

My studies of small shrimp showed that the adrostral sulci are only faintly indicated in juveniles 18 mm. t.l., but are clearly distinct in specimens 19 mm. t.l.

In the development of "candied shrimp" sex can be determined when they reach about 20 mm. t.l. At this length the endopods of the first pair of pleopods in the males are situated more proximally on the bases and are a little longer than in the females. In addition, males have a sharp ridge along the median line of sternite XIV, which increases slightly in height anteriorly and forms a sharp angle at its anteroventral extremity. Females have no ridge along the median line of sternite XIV, which instead is produced to a median point.

The following discussion on the development of juveniles consists largely of a summary of progressive changes occurring in the petasma and the thelycum. In males 9 mm. c.l., 42 mm. t.l., the ventral costae of the petasma may be armed with at least one distomarginal spine, and 12 mm. c.l., 55 mm. t.l., the ventral costae possess several distomarginal spines and relatively strong subapical teeth. At 16 mm. c.l., 73 mm. t.l., males may have the petasma joined.

Progressive changes in the thelycum occur as follows. In females with a 5 mm. c.l., 24 mm. t.l., the lateral plates are distinct, and at 9 mm. c.l., 42 mm. t.l., their anterior margins touch or almost touch the apex of the horns of the median protuberance. At 12 mm. c.l., 55 mm. t.l., the posterior process often bears a small posteromedian carina, which does not project caudally, and the lateral plates partially cover the horns of the median protuberance. Larger females exhibit this typically undivided median carina. As stated earlier, some females 16 mm. c.l., 73 mm. t.l. have the lateral plates contiguous along median borders, and, thus, the thelycum with functional form.

GROWTH

The only information available comes from the laboratory experiment by Pérez Farfante et al. (1961) during which juveniles 25 mm. t.l. grew to

42 mm. t.l. in 48 days, or at an average daily rate of 0.36 mm.; and individuals 75 to 90 mm. t.l. grew 10 mm. t.l. in 30 days—an average daily increase of 0.33 mm.

SEX DIFFERENCES IN SIZE

The largest female I examined was 48 mm. c.l., 192 mm. t.l., and the largest male 41 mm. c.l., 175 mm. t.l., from off Las Piedras, Gulf of Venezuela. Ewald (1965c) reported females 55 mm. c.l. in the lower Gulf of Venezuela. Although the females of *P. d. notialis* attain a much larger size than the males, both increase in length with increasing depth (Pérez Farfante et al., 1961).

Ecology

SUBSTRATE

"Candied shrimp" live on a variety of bottom types—very soft to firm mud, sand and mud, and predominantly sand patches among rocks.

DIEL CYCLE

Juveniles as well as adults are mostly nocturnal in habit. In Cuba, however, they constitute a small percentage of the commercial catches taken during the day.

The only data available on the behavior of "candied shrimp" in relation to moon phases are statements by fishermen that these shrimp become extremely scarce during the full moon.

MOVEMENTS

The sampling by Pérez Farfante et al. (1961) in Cuba showed that the young remain in estuarine waters until they are about 85 mm. t.l., at which length they seem to move seaward. In Laguna Doctor, Playa de Baracoa, Cuba, however, larger specimens were caught (to 130 mm. t.l.).

EFFECTS OF TEMPERATURE

No studies have been made.

ENEMIES AND DISEASES

Only a few enemies and diseases of "candied shrimp" are known. Undoubtedly, this is because so little attention has been accorded them. Carnivorous fishes are probably their most important enemies. They are also victims of their brethren, particularly the young. "Candied shrimp" suffer an infection that causes them to become opaque white, a malady similar to that found in *P. d. duorarum* called "cotton shrimp" or "milk shrimp" in the United States. This condition is rather common in shrimp from southern Cuba.

Commercial Importance

P. d. notialis and *P. schmitti* are the most important commercial shrimps in the Greater Antilles and the Caribbean Coast of Central America. It makes up about half of Honduran shrimp catches (the rest consists mostly of *P. schmitti* and small quantities of *P. a. subtilis*); as stated earlier, practically the entire production is exported to the United States and in 1965, amounted to 740,270 kg. In Nicaragua, *P. d. notialis* and *P. brasiliensis* account for a large percentage of the shrimp taken along the Caribbean Coast; exports to the United States from eastern Nicaragua in 1964 amounted to 1,049,623 kg. (catches by U.S. vessels off Nicaragua are not included). Most of the rather small catches of grooved shrimps in the Gulf of Venezuela (Ewald, 1965c) consist of *P. d. notialis*. This shrimp also occurs in the enormous catches made along the northeastern Atlantic Coast of South America, from Guyana to Baía de Marajó, Brazil. Croker (1967) stated that because it is not distinguished from *P. brasiliensis* by the fisherman, it is not possible to say what proportion of the catches it constitutes. Finally, according to Lindner (1957), *P. d. notialis* is taken commercially along the southernmost portion of its range, from Ilhéus to Cabo Frio, Brazil.

Penaeus (Melicertus) aztecus aztecus IVES

Figures 39 to 50

United States: brown shrimp, brownies, green lake shrimp, red shrimp, redtail shrimp, golden shrimp, native shrimp. Mexico: camarón café, camarón moreno.

Penaeus brasiliensis: Gibbes, 1850: 198 [part]; Stimpson, 1871: 132; Verrill, Smith, and Harger, 1873: 551; Smith, 1874: 642; Smith, 1880: 267; Rathbun, 1884: 821–823 [part]; Herrick, 1887: 47; Ives, 1891: 199 [part]; Evermann, 1892: 90 [part]; Rathbun, 1893: 821–823 [part]; de Man, 1911: 96 [part]; Fowler, 1913: 314–316, 542; Cowles, 1930: 355, 356, 358 [part]; Weymouth, 1931: 11 [part]; Weymouth et al., 1932: 108 [part]; Weymouth et al., 1933: 2, 4, 6, 8, 12, 21, figs. 3b, 4b; Burkenroad, 1934: 81, 82, 89–93, 138, (61, 75, 77, 78, 88, 94, 134 [part]), figs. 8, 9; Johnson and Lindner, 1934: 4, 57 [part]; Myers and Gowanloch, 1934: 12 [part]; Lindner, 1936: 155 [fig. 2 middle?]; Pearson, 1939: 2, 28, 30–39, 50, 51, 53, 59, 71, 72 [part],

figs. 21–31; Anderson, 1948: 1 [part]; U.S. Fish and Wildlife Service, 1958b: 13 [part]. Not *P. brasiliensis* Lat., 1817.

Peneus braziliensis: Coues, 1871: 124 [part]; Kingsley, 1878: 69 [part]; Kingsley, 1879: 330 [part]; Kingsley, 1880: 427 [part].

Penaeus brasiliensis, var. *aztecus* Ives, 1891: 190, 191, 199 [part] (lectotype, here designated, ♀, PANS 4764, Veracruz, Mexico, Heilprin Expedition, 1890; paralectotypes, PANS); de Man, 1911: 95, 96; Burkenroad, 1934: 94.

Paneus brasiliensis: Collins and Smith, 1892: 102 [part].

Penaeus brasiliensis aztecus: Sharp, 1893: 109; Burkenroad, 1939: 27, 34.

Peneus brasiliensis: Faxon, 1896: 162; Sumner, Osburn, and Cole, 1913: 665; Hay and Shore, 1918: 377, 378, fig. 6 [part ?].

Penaeus braziliensis: Tulian, 1920b: 107, 108; Williams, 1959: 281, 282, 285–288 [part]; Dobkin, 1961: 347 [part].

Penaeus aztecus: Burkenroad, 1939 [part, "Form A"]: 5, 20, 21, 23, 25–27, 29, 30, 33, 46, figs. 20, 21, 24, 30, 31; Pearson, 1939: 30; Gunter, 1941: 203; Anderson and Lindner, 1945: 306 [part]; Gunter, 1945: 69, 77, 87, 113, 115, (178?); Anderson et al., 1949: 16; Burkenroad, 1949: 688; Knapp, 1949: 139; Broad, 1950: 1–4, 3 figs.; Gunter, 1950: 13, 15, 20–27, 40, 42, 43, 46–49; Hedgpeth, 1950: 106–108, 110–113, 118; Idyll, 1950: 7, 9, 10, 14, 17, 19, 22, 25, fig. 1; Sprague, 1950: 2; Whitten et al., 1950: 78; Broad, 1951: 27–29, 31–35; Gunter and Hildebrand, 1951: 733; Sánchez Roig and Gómez de la Maza, 1951: 113; Gómez de la Maza, 1952: 167, 170, 171, fig. 1a; Leone and Pryor, 1952: 27–31; Springer and Bullis, 1952: 8–10, 12; Heegaard, 1953: 76, 78, 102; Hedgpeth, 1953: 159–161, 210; Hildebrand and Gunter, 1953: 152, 155; Pérez Farfante, 1953: 229, 230 (238, 241 [part]); Williams, 1953: 156–160, figs. 1, 2; De Sylva, 1954: 10, 18, 19, 23, 24, 26, 27, 29, 31, 33; Hildebrand, 1954: 233, 234, 241–248, 261–267, 324–326, 349–351, 362–366; Sprague, 1954: 248, 251; Springer and Bullis, 1954: 3–6, 13–16; Hildebrand, 1955: 172–179, 190, 220, 224, 226, 227; Parker, 1955: 193, 197, 211; Voss, 1955: 5, 8, 11, figs. 11, 16, 17; Williams, 1955a: 116, 118, 127, 138–141, 144; Williams, 1955b: 200, 203, 204, 206; Guest, 1956: 6, 12, 14, 18, figs. 2, 3; Gunter, 1956: 99, 105; Springer and Bullis, 1956: 9; Anderson, 1957: 399; Carranza, 1957: 147; Dall, 1957: 142, 226, 227; Ingle, 1957: 10–12, 14–17; Lindner, 1957: 72, 73, 83, 84; Pearse and Gunter, 1957: 139; Simmons, 1957: 178, 191, 199; Viosca, 1957: 12, 20, 1 fig.; Woodburn et al., 1957: 6, 7, 11; Anderson, 1958a: 1–3, fig. 2; Anderson, 1958b: 2; Darnell, 1958: 369, 385, 388, 400, 405; Gunter and Shell, 1958: 17, 23; Hildebrand, 1958: 159; Lunz, 1958: 47; U.S. Fish and Wildlife Service, 1958b: 1, 6, 8, 12, 13, 15, 18–22, 24–28, 30, 32, fig. I–5c; Williams, 1958: 283–290; Collier et al., 1959: 1–5; Eldred, 1959a: 75; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959: 6, 7, 9, 10, 12, 14–16, 19–24; Iversen and Manning, 1959: 130; Kruse, 1959: 123, 124, 126, 128, 130, 134, 136, 137, 140–142, 144; Williams, 1959: 281–283, 285–289, figs. 4, 8; Young, 1959: 7, 8; Chin, 1960: 135–141; Eldred, 1960: 164, 165; Eldred and Hutton, 1960: 91, 97, 98, 101, 103, 104, 106, 108, figs. 5–9; Hoese, 1960a: 592, 593; Hoese, 1960b: 330, 331; Inglis, 1960: 66–69; Renfro, 1960a: 9, 10; Renfro, 1960b: 63, 64, 1 fig.; Wheeler, 1960: 7, 8; Williams, 1960: 560–570; Bearden, 1961: 3–8; Costello and Allen, 1961: 21; Eldred et al., 1961: 69, 80, 86–88, 97, 98, 109; Gunter, 1961a: 599; Gunter, 1961b: 184; Renfro, 1961: 11, 12; Tabb and Manning, 1961: 594, 595; Anderson, 1962: 1, 2, fig. 2; George, 1962: 160–163; Gunter, 1962a: 107, 108; Gunter, 1962c: 216–226; Hutton et al., 1962: 327, 330, 331; Kutkuhn, 1962: 343, 355, 361–370, 385, 388, 394–396, 401; Tabb, Dubrow, and Jones, 1962: 7, 11, 12, 28; Baxter, 1963: 79, 80, 82–87; Boschi, 1963: 5, 6, 13, 20, 23, 26–29 [part], fig. 8 (1, 2, 3 [right], 4–6).; Gunter and Hall, 1963: 295, 296, 304; Gunter, 1963: 108; Kutkuhn, 1963: 66–77; McFarland and Lee, 1963: 391, 392, 394–397, 399, 401–415; Renfro and Brusher, 1963: 13–17; St. Amant, Corkum, and Broom, 1963: 14–22, 25; Zein-Eldin, 1963a: 188–196; Costello and Allen, 1964: 31; Gunter et al., 1964: 182–184; Hutton, 1964: 440, 445; Jones et al., 1964: 1; Klima, 1964: 52–60, 63, 64; Renfro, 1964: 94–97; Aldrich, 1965: 370–375; Anderson and Lunz, 1965: 1, 4–6; Broad, 1965: 86–90; Bullis and Thompson, 1965: 6, 7; Cook, 1965; 12, 13; Copeland, 1965: 9, 13, 14; Eldred et al., 1965: 2, 17, 26; Holthuis and Rosa, 1965: 4 [part]; Joyce, 1965: 14, 17, 18, 24, 27, 28, 34, 37, 38, 44, 47, 48, 53, 56, 57, 62, 65, 66, 70, 73, 74, 79–82, 88, 90, 93, 95, 99, 101, 103, 114–121, 128, 132, 134, 145–154, 170–173, 176–180, 184, 185, 191, 192, 220, 221; Loesch, 1965: 42, 45, 47, 49–51, 53, 54, 56, 57; Temple and

Fischer, 1965a: 59, 60; Temple and Fischer, 1965b: 16; Van Engel, 1965: 38; Williams, 1965: 22–27, fig. 12; Zein-Eldin and Aldrich, 1965: 199–216; Zein-Eldin and Griffith, 1965: 77–81; Anderson, 1966: 1, 3; Christmas et al., 1966: 186, 196–198, 201, 202, 205, 212, figs. 2, 3; Cook, 1966: 438; Copeland and Truitt, 1966: 65, 68–70, 72, 73; Joyce and Eldred, 1966: 8, 9, 11–13, 16–19, 22, 25, 31, 32, 34, 35; Kutkuhn, 1966a: 19, 20, 26; Parker, 1966: 32, 34, 35; St. Amant et al., 1966: 1, 2, 4, 5, 7, 8, 10–14, 16; Sykes and Finucane, 1966: 374; Aldrich et al., 1967: 80; Baxter and Renfro, 1967: 149–158, figs. 2, 3; Lyles, 1967: 315–317, 371–376; McCoy and Brown, 1967: 1–3, 8, 10, 12, 14, 16, 19, 21, 23, 25–27; Temple and Fischer, 1967: 323, 325, 328, 329, 332, 333; Trent, 1967: 7–16; Villalobos-Figueroa, Suárez Caabro, Gómez, de la Lanza, Aceves, Manrique, and Cabrera, 1967: 75, 85; Zamora and Trent, 1968: 17–19.

Penaeus axtecus: Gunter, 1950: 40.

Palaemonetes aztecus: Lunz, 1956: 93.

Penaeus aztecus aztecus: Pérez Farfante, 1967: 84, 87.

Brown shrimp: Loesch, 1957: 40, 41; Zein-Eldin, 1963b: 61, 62; Aldrich, 1964: 61–64; Baxter and Furr, 1964: 28, 29; Renfro and Brusher, 1964: 13, 14; Klima and Benigno, 1965: 38–40; Renfro and Brusher, 1965: 10; Ringo, 1965: 68–70; Parker, 1966: 32, 34, 35; Zein-Eldin, 1966: 41, 42.

?Shrimp: Flint, 1956: 11, 12.

Taxonomic Remarks

Burkenroad (1939) cited 11 ♂ and 7 ♀ in Ives' syntypes series, and named them "Holotypes and Cotypes" of *P. aztecus* Ives. He mentioned a "Holotype female, 'Form A,' carapace 11.2 mm." I examined the syntypes, which are in the Academy of Natural Sciences of Philadelphia, and found that Burkenroad had selected a female which he labeled "lectotype" (PANS No. 4764). This female is here designated as lectotype of *Penaeus aztecus* Ives. The specimen actually has 21.2 mm. c.l., and on the label that accompanies it the locality is not given, but since 7 ♀ were cited by Burkenroad, and I found that there are now but 6, I assume that the lectotype was removed from Ives' lot. It should be mentioned, however, that this lot has 12 instead of 11 males.

Study Material

UNITED STATES

Massachusetts: 1 ♀, USNM, Tisbury Pond, Martha's Vineyard, October 18, 1906, V. N. Edwards. 1 ♂, UMML, Great Pond, W. Tisbury, Martha's Vineyard, November 1, 1957, A. J. Provenzano. 1 ♀, USNM, Katama Bay, Martha's Vineyard, September 8, 1900, V. N. Edwards.

New York: 2 ♀, USNM, Shinnecock Bay, Long Island, September–October 1957, F. H. Low. 2 ♂ 2 ♀, NYCD, Harts Cove, Moriches Bay, September 10, 1962, R. L. Wigley.

New Jersey: 1 ♀, USNM, Brigantine Refuge, Oceanville, August 17, 1949, P. F. Springer. 1 ♂, USNM, Beesley's Point, September 9, 1887, T. H. Bean. 6 ♂ 1 ♀, USNM, Beesley's Point, September 10, 1887, T. H. Bean. 1 ♀, USNM, Lousy Harbor, Great Egg Harbor, August 18, 1887, T. H. Bean. 2 ♂ 1 ♀, YPM, Delaware Bay, 4 fm. or less, September 1932, A. E. Parr. 1 ♀, PANS, Ventnor, summer 1949, C. B. Atkinson. 4 ♀, YPM, Mispillion River, 4 fm. or less, August 26, 1932, A. E. Parr.

Maryland: 1 ♂ 10 ♀, CBL, Holland Straits to Smith Island, July–September, 1964, E. Harrison. 1 ♀, USNM, Tred Avon River, 3 km. from Easton, B. E. McHale. 1 ♂, CBL, Drum Point, Chesapeake Bay, 2½ fm., August 8, 1953, R. Robinson. 2 ♂ 1 ♀, CBL, Smith and Bloodsworth Island, summer 1965, E. Harrison.

Virginia: 1 ♂, USNM, Mobjack Bay, July 16, 1892, *Grampus* Sta. 5.

North Carolina: 2 ♀, AMNH, S. of Pamlico Sound. 6 ♂ 10 ♀, USNM, off Beaufort Inlet, October 1964, A. B. Williams. 6 ♂ 8 ♀, USNM, Neuse River at mouth of Adams Creek, August 30, 1949, A. B. Williams.

South Carolina: 1 ♀, YPM, off Charleston Harbor, October 1935, G. R. Lunz and Y. H. Olsen.

Georgia: 2 ♀, USNM, N. end of St. Catherines Island, July 16, 1931, W. W. Anderson. 7 ♂ 12 ♀, USNM, off Brunswick, 3 to 4 fm., August 26, 1965, BCFBL-Brunswick.

Florida: 1 ♂, USNM, N. of Jacksonville, 6 to 8 fm., October 2, 1957, *Combat* Sta. 504. 1 ♂ 3 ♀, USNM, S. of Cape Kennedy, 22 fm., March 23, 1956, *Pelican* Sta. 14. 1 ♂, USNM, off Cape Kennedy 9½ fm., January 26, 1962, *Silver Bay* Sta. 3710. 1 ♂, USNM, off Cape Kennedy, 20 fm., November 9, 1963, *Silver Bay* Sta. 5241. 3 ♂ 2 ♀, USNM, off Cocoa Beach, 10 to 11 fm., January 13,

1965, *Oregon* Sta. 5181. 2 ♂ 2 ♀, USNM, off Melbourne Beach, 11 fm., January 13, 1965, *Oregon* Sta. 5182. 13 ♂ 18 ♀, USNM, off Melbourne Beach, 30 fm., January 14, 1965, *Oregon* Sta. 5200. 7 ♂ 37 ♀, USNM, off Melbourne Beach, 30 to 31 fm., January 15, 1965, *Oregon* Sta. 5202. 7 ♂ 28 ♀, USNM, off Sebastian, 31 to 28 fm., January 15, 1965, *Oregon* Sta. 5203. 4 ♂ 4 ♀, USNM, off Sebastian, 34 to 35 fm., March 14, 1965, *Oregon* Sta. 5350. 1 ♂, USNM, off Fort Pierce, 50 fm., November 11, 1961, *Silver Bay* Sta. 3529. 2 ♀, USNM, off Stuart, 30 fm., November 11, 1963, *Silver Bay* Sta. 5268. 5 ♂ 4 ♀, AMNH, W. side Destin Bridge, Pompano Beach, 2½ fm., July 29, 1948, L. A. Burry. 3 ♂ 3 ♀, USNM, off Key Largo, 50 fm., November 10, 1961, *Silver Bay* Sta. 3524. 2 ♂ 1 ♀, USNM, off Matacumbe Key, 50 fm., November 10, 1961, *Silver Bay* Sta. 3524. 1 ♂, USNM, off Lower Matacumbe Key, 60 fm., October 27, 1960, *Silver Bay* Sta. 2391. 22 ♂ 10 ♀, USNM, Pilot Cove, Apalachicola Bay, November 12, 1958, R. M. Ingle. 1 ♂ 2 ♀, USNM, off Apalachicola Bay, 6 fm., October 31, 1953, *Oregon* Sta. 863. 3 ♂ 8 ♀, YPM, Pensacola Bay, September 9–15, 1932, M. D. Burkenroad. 16 ♂ 20 ♀, YPM, Pensacola Bay, 5 fm., March 3, 1935, *Atlantis* in port.

Alabama: 10 ♂ 5 ♀, USNM, off Mobile Bay, 7 fm., January 28, 1962, *Oregon* Sta. 3475. 2 ♂ 5 ♀, USNM, off Mobile Bay, 29 fm., February 1, 1962, *Oregon* Sta. 3486.

Mississippi: 3 ♂, USNM, off Pascagoula, 22 fm., August 21, 1962, *Oregon* Sta. 3713. 5 ♂ 11 ♀, GCRL, Mississippi Sound, June 4, 1964, J. Y. Christmas. 4 ♂ 2 ♀, GCRL, Mississippi Sound, September 30, 1964, J. Y. Christmas. 7 ♂ 10 ♀, USNM, off Mississippi, 29 fm., February 4, 1962, *Oregon* Sta. 3489. 10 ♂ 17 ♀, GCRL, Biloxi Bay, June 18, 1965, BCFFS-Pascagoula.

Louisiana: 2 ♂ 3 ♀, YPM, off Louisiana, 17 fm., March 21, 1937, *Atlantis* Sta. 2814. 1 ♂ 10 ♀, YPM, off Louisiana, 51 to 63 fm., April 10, 1931, *Atlantis* Sta. 2853–I. 5 ♂ 6 ♀, USNM, Lake Pontchartrain, 1954, R. M. Darnell. 1 ♂, YPM, off Pass a Loutre, 12 fm., January 31, 1931, M. D. Burkenroad. 4 ♂ 1 ♀, USNM, off Mississippi Delta, 33 fm., October 23, 1953, *Oregon* Sta. 845. 7 ♀, USNM, off Mississippi Delta, 40 fm., February 3, 1938, *Pelican*. 4 ♂ 1 ♀, USNM, off Mississippi Delta, 33 fm., October 23, 1953, *Oregon* Sta. 845. 2 ♂ 1 ♀, YPM, 48 km. S. of Barataria Pass, 16 fm., August 6, 1930, M. D. Burkenroad. 7 ♀, AMNH, S. of Barataria Pass, August 6, 1930, M. D. Burkenroad. 29 ♂ 33 ♀, USNM, lower Barataria Bay, May 21, 1959, E. Schrader and P. Landry.

Texas: 23 ♂ 23 ♀, USNM, Fort Livingston, May 14, 1934, M. J. Lindner and W. W. Anderson. 7 ♂ 7 ♀, off mouth of Sabine River, 10 fm., May 19, 1965, BCFBLG. 3 ♂ 9 ♀, USNM, Galveston Bay, March-May 1965, BCFBLG. 8 ♂ 2 ♀, USNM, Galveston Bay, April 1965, BCFBLG. 2 ♂ 9 ♀, USNM, off Galveston, 4½ fm., September 8, 1965, BCFBLG. 3 ♀, USNM, northwestern Gulf of Mexico, May 2, 1963, BCFBLG. 7 ♂ 8 ♀, USNM, northwestern Gulf of Mexico, May 6, 1963, BCFBLG. 3 ♂ 3 ♀, USNM, off Matagorda Bay, 25 fm., May 31, 1965, BCFBLG. 1 ♀, USNM, Port Aransas, April 28, 1948, J. W. Hedgpeth. 4 ♂ 1 ♀, USNM, Corpus Christi, November 27–30, 1891, B. W. Evermann. 2 ♂ 3 ♀, USNM, off Padre Island, 19 fm., January 27, 1964, *Oregon* Sta. 4643. 3 ♀, USNM, off Puerto Isabel, 18 fm., June 3, 1954, *Oregon* Sta. 1086.

MEXICO

Tamaulipas: 2 ♀, INIBP, N. of Tampico, November 7, 1962, U. Barron and A. Macías. 2 ♂ 4 ♀, INIBP–USNM, off Tampico, June 10, 1959, E. Ramírez and F. Aguilar. 4 ♂ 1 ♀, USNM, off Tampico, September 12, 1963, U. Barron. 12 ♂ 3 ♀, INIBP–USNM, Villa Cuauhtémoc, Tampico, August 4, 1962, J. García.

Veracruz: 3 ♂ 1 ♀, INIBP-USNM, Canal del Chijol, Laguna de Tamiahua, July 21, 1963. 2 ♂ 4 ♀, INIBP-USNM, Bocaina, Laguna de Tamiahua, June 9, 1964, R. Márquez and C. Tovar. 4 ♂ 2 ♀, INIBP-USNM, Tuxpan, August 29, 1963, S. Basulto. 1 ♂, INIBP, Tuxpan, August 29, 1963, S. Basulto. 3 ♂ 2 ♀, INIBP-USNM, La Bocana, Tuxpan, March 7, 1964, A. Mendoza and R. Márquez. 5 ♂ 3 ♀, INIBP-USNM, Estero Tabasco, Río Tuxpan, March 24, 1964, A. Mendoza. 9 ♂ 9 ♀, INIBP-USNM, Laguna de Pueblo Viejo, March 1, 1959, E. Ramírez and F. Aguilar. 8 ♂ 2 ♀, INIBP, Laguna de la Mancha, June 21, 1964, F. Lachica and A. Morales. 1 ♂ 1 ♀, INIBP, Laguna de Buen País, 12 km. W. of Alvarado, April 1965, F. Lachica and F. Carmona.

Campeche: 1 ♂ 5 ♀, INIBP-USNM, Laguna de Términos, February 1, 1964, F. Lachica and

F. Carmona. 3 ♀, INIBP-USNM, off Ciudad del Carmen, April 29, 1959, R. Ramírez and M. Flores. 2 ♂ 4 ♀, INIBP-USNM, NW. of Ciudad del Carmen, 16 to 20 fm., April 29, 1959, R. Ramírez and M. Flores. 1 ♂, MCZ, NW. of Arrecife Alacrán, 6.5 km. of Whale Rock, 35 fm., *Blake* Sta. 37.

Diagnosis

Adrostral sulcus broad posteriorly, and long, reaching near posterior margin of carapace. Median sulcus long, ending immediately anterior to posterior end of adrostral sulcus, and deep along its entire length. Dorsolateral sulcus broad. Petasma with distal portion of ventral costa increasing gradually in width and turning proximally in arc, unarmed along free border and with elongated group of closely set, small teeth on attached border; apex of costa adnate to membranous portion of ventrolateral lobule, latter bearing extensive armature of closely set spines; distal fold small, usually with numerous spinules but sometimes unarmed. Thelycum with anterior process relatively broad and with anteriorly bifurcate median carina on posterior process; carina exposed owing to wide divergence of anteromedian angles of lateral plates.

Description

ROSTRUM (fig. 39 a, b)

Teeth $\frac{5\text{–}10}{0\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—47, 9/2—44, 10/2—5, 9/3—1, 7/2—1.50, 6/2—0.50, 6/0—0.50, 5/2—0.50; N=200) + epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to last dorsal tooth; rostrum long, in juveniles and subadults reaching as far as base of distal ⅓ of thickened portion of lateral antennular flagellum, attaining maximum length in relation to carapace length at 13 to 20 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.80); decreasing progressively with increasing length of shrimp, rostrum reaching at least three-quarters of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.50); rostrum slender, sinuous, with apical portion usually upturned, posteroventral margin concave; highest portion of blade at level of second or third dorsal tooth; latter level with anterior margin of carapace; tip of rostrum narrow, long, ¼ to ⅓ r.l. Postrostral carina strong, prominent, uniform in width or slightly wider in anterior half, and long, extending to posterior margin of carapace. Median sulcus deep throughout, often slightly wider in anterior half, and long, ending near posterior margin of carapace. Adrostral sulcus broad posteriorly, four-fifths to twice width of postrostral carina, usually long, ending 1/11 to 1/20 c.l. from posterior margin of carapace. Adrostral carina prominent, sharp on carapace, long, same length as adrostral sulcus, and parallel to postrostral carina or inclined obliquely mesially at posterior end.

CARAPACE (fig. 40)

Length in proportion to total length apparently changing little, if at all, after juvenile stage is reached (fig. 40). Gastrofrontal sulcus broad, extending to about one-sixth c.l. Gastrofrontal carina sharp, turning slightly toward dorsal margin posteriorly, ending anteriorly in acute orbital angle. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below hepatic spine, there widening again into base of spine. Gastro-orbital carina sharp, occupying approximately posterior four-fifths of distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus ⅕ to ¼ c.l., ending slightly anterior to middle of carapace. Hepatic carina ⅕ to ¼ c.l., sharp, sloping slightly anteroventrally to end 1/18 to 1/23 c.l. from anterior margin of carapace. Antennal spine very prominent and acute; hepatic spine strong.

ANTENNULES

Lateral flagellum about two-thirds length of antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum. Anterolateral spine small, sharp. Stylocerite acuminate, extending to or slightly beyond midlength of first antennular segment. Prosartema reaching to distal end of proximal one-fifth of second antennular segment.

ANTENNAE

Scaphocerite length 2½ times maximum width, its length relative to carapace length decreasing slightly with growth; spine reaching base of antennular flagellum. Carpocerite length 1⅓ times width, extending slightly beyond base of eye. Antennal flagellum relatively short, 1⅖ c.l. (fig. 41).

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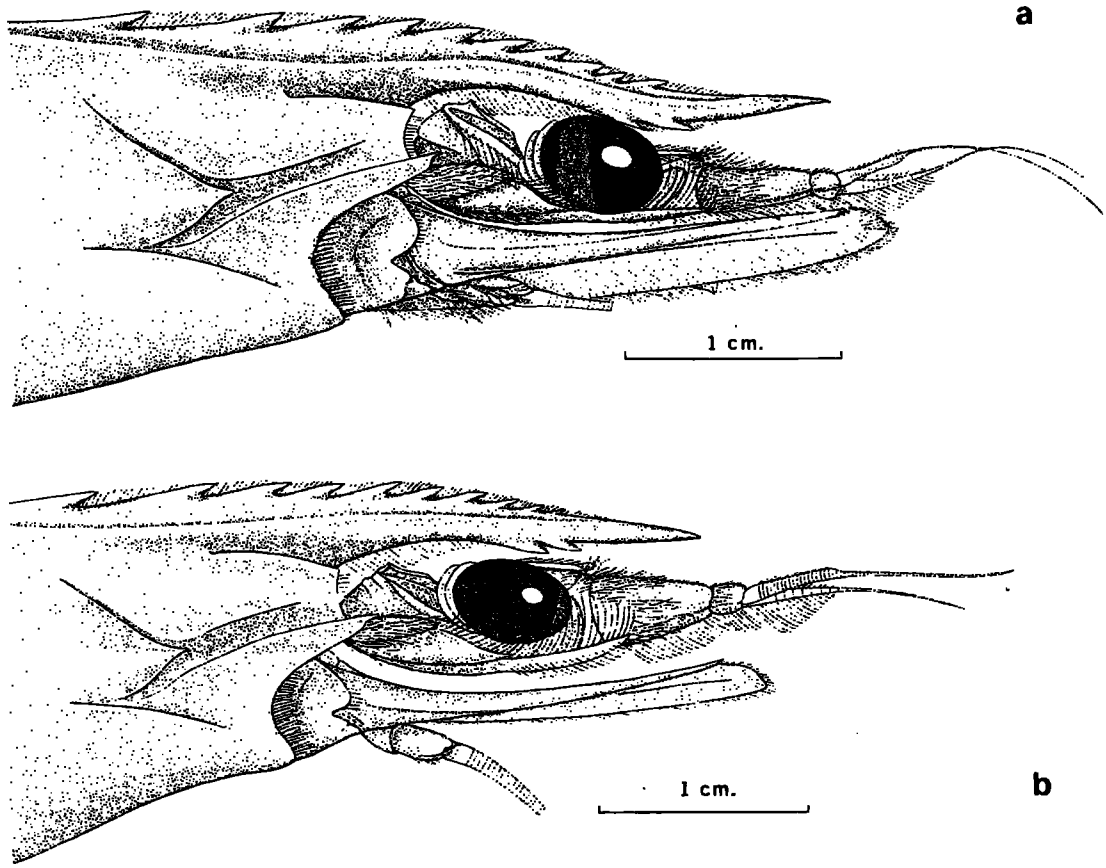

FIGURE 39.—*Penaeus* (*M.*) *aztecus aztecus* Ives. a. Rostrum, ♀ 35 mm. c.l. off Tampico, Mexico, b. Rostrum, ♂ 31 mm. c.l., off Tampico, Mexico.

THORACIC APPENDAGES

Third maxilliped reaching at least to base and, at most, to distal end of second antennular segment; length of dactyl about two-thirds that of propodus. First pereopod surpassing carpocerite by one-third length of dactyl to seven-eighths of propodus. Second pereopod exceeding carpocerite by one-half length of dactyl to entire length of propodus. Third pereopod reaching at least distal end of antennular peduncle, and, at most, exceeding it by as much as one-tenth length of carpus, proportionately longer in larger individuals. Fourth pereopod reaching at least distal end of carpocerite and, at most, exceeding it by length of dactyl. Length of fifth pereopod subequal to that of fourth pereopod. Exopods on all pereopods; long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

ABDOMEN

Carinate dorsally from posterior half of fourth somite posteriorly, carina increasing in height posteriorly to form median keel on sixth somite, there ending in sharp spine on posterior margin. Dorsolateral sulcus (figs. 42, 43) broad, ratio K/S ranging from 0.50 to 3.50, modally 1.25 (fig. 44), varying within same limits in males and females; in small size classes to 29 mm. c.l. (fig. 45), modal value of K/S higher than in larger individuals; dorsal lip of sulcus rounded, ventral lip sharp. Sixth abdominal somite with three conspicuous cicatrices on each side, first longest; fifth abdominal somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite, on rib in larger specimens. Fourth abdominal somite with series of minute pits dorsal to sinus on posterior margin of somite, also on rib in larger specimens. Telson unarmed, with deep median sulcus and sharp pointed tip.

PETASMA (fig. 46 a–d)

Width of ventral costa increasing uniformly proximally, mesiodistal portion forming gentle arc; distal portion unarmed along free border but

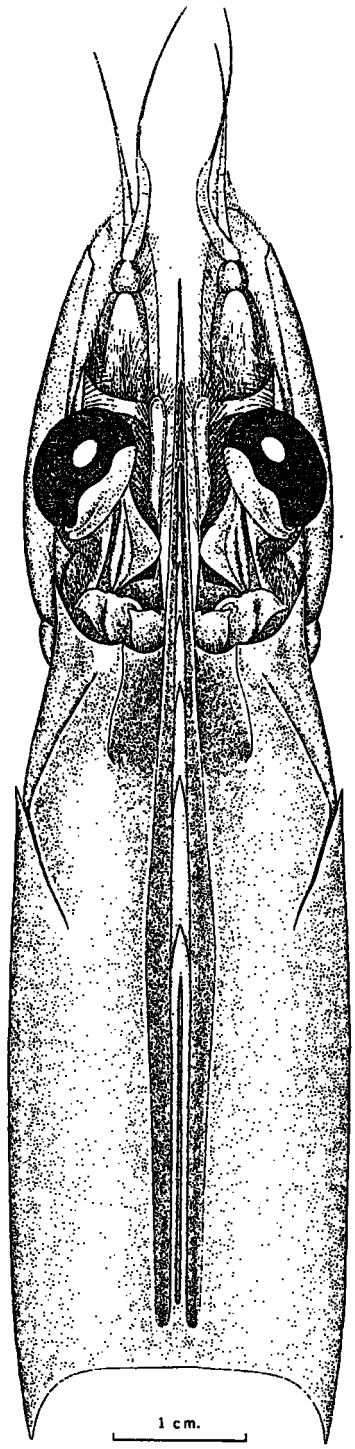

FIGURE 40.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Cephalothorax, ♀ 47.5 mm. c.l., off Tampico, Tamaulipas, Mexico.

attached border with elongated, narrow patch of 14 to 25 small, closely set teeth arranged in two or three series; apex of costa not projecting free but tightly joined to adjacent membranous portion. Ventrolateral lobule with extensive armature of rather closely set spines. Distal fold relatively small, armed with 2 to 33, perhaps more, spinules, occasionally unarmed. Distomedian projections rather thick and short, slightly overhanging distal portion of ventral costae.

APPENDIX MASCULINA (fig. 46 e)

Rather elongated, its length 1⅔ to 1⅘ width at base, armed with single row of short, strong spines along distal four-fifths of lateral margin, and with longer spines along median margin. Anterior surface slightly convex, posterior surface with rather deep excavation flanked by sharp longitudinal ridge projecting from median margin.

THELYCUM (figs. 47, 48)

Anterior process terminating ventrally in sharp semicircular to nearly triangular ridge, surrounding concave surface usually plain, although sometimes with knob or short rib at center; posterior process with median carina typically bifurcate anteriorly, forming two ribs; ribs turning mesially and almost coming together at anterior process, giving rise to diamondlike or ovate-acuminate structure; depression thus formed deep when ribs are high or very shallow, when ribs are low, usually plain but sometimes bearing median rib along anterior or posterior half, rarely along entire length. Lateral plates with anteromedian angles widely divergent leaving posterior process, including median carina, exposed.

COLOR

Although of variable color, *P. a. aztecus* is most frequently brown. Thus, the commercial name of brown shrimp or brownies in the United States and camarón café or camarón moreno in Mexico. Large offshore individuals often have an orange or lemon coloration, deeper on pereopods and around tailfan; the latter often has a darker edge which may be purple or reddish purple. Juveniles and subadults are frequently light grayish brown or brown with darker speckles on the sides; red and green specimens also occur and are commonly called red shrimp and green shrimp. *P. a. aztecus* occasionally has a lateral spot at the junction of third and fourth abdominal somites, in this character it resembles both subspecies of *P. duorarum* and also *P. brasiliensis*. Fishermen believe that brown

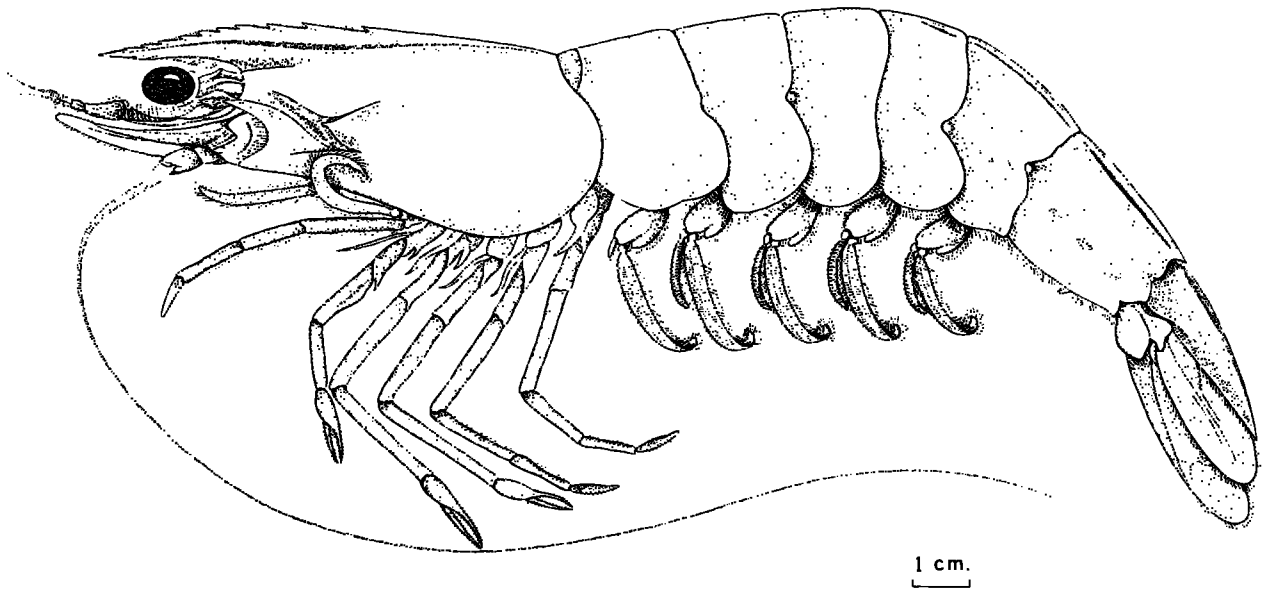

FIGURE 41.—*Penaeus (M.) aztecus aztecus* Ives. Lateral view, ♀ 54.5 mm. c.l., off Corpus Christi, Tex.

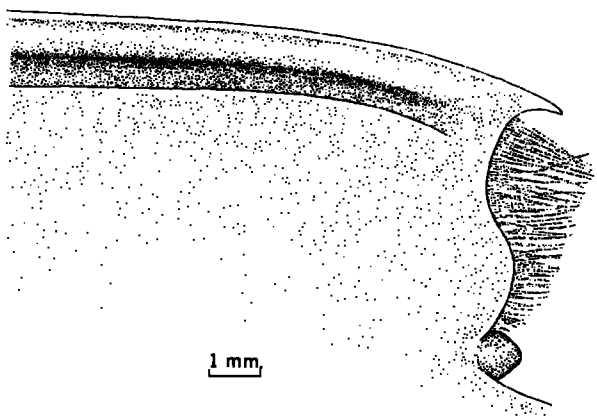

FIGURE 42.—*Penaeus (M.) aztecus aztecus* Ives. Sixth abdominal somite, posterodorsal portion, ♀ 33.5 mm. c.l., Ciudad del Carmen, Campeche, Mexico.

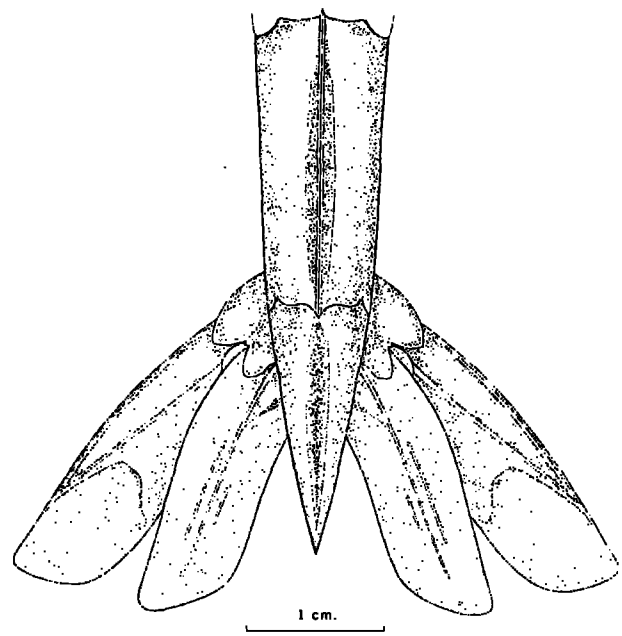

FIGURE 43.—*Penaeus (M.) aztecus aztecus* Ives. Dorsal view of sixth abdominal somite, telson, and uropods, ♂ 37.5 mm. c.l., off Matagorda Bay, Tex.

shrimp change color while moving, becoming reddish, especially on the pleopods.

Variations in the color of shrimps have been attributed to several factors, such as temperature, nature of bottom, and food.

Distribution and Morphological Variations

P. a. aztecus ranges from Martha's Vineyard south to the Florida Keys and north on the west coast of Florida to the northwest Sanibel grounds. Apparently, it is absent north of these grounds to the vicinity of Apalachicola Bay, where it appears again, ranging along the northern and western coasts of the Gulf of Mexico and the northwestern coast of Yucatán (fig. 49). The brown shrimp is found farther north than other species of the genus *Penaeus* occurring in the western Atlantic, but it rarely reaches the northernmost waters of its range. It seems to be a summer and early fall visitor from Chesapeake Bay northward to Martha's Vineyard; the northernmost breeding population lives along the coast of North Carolina.

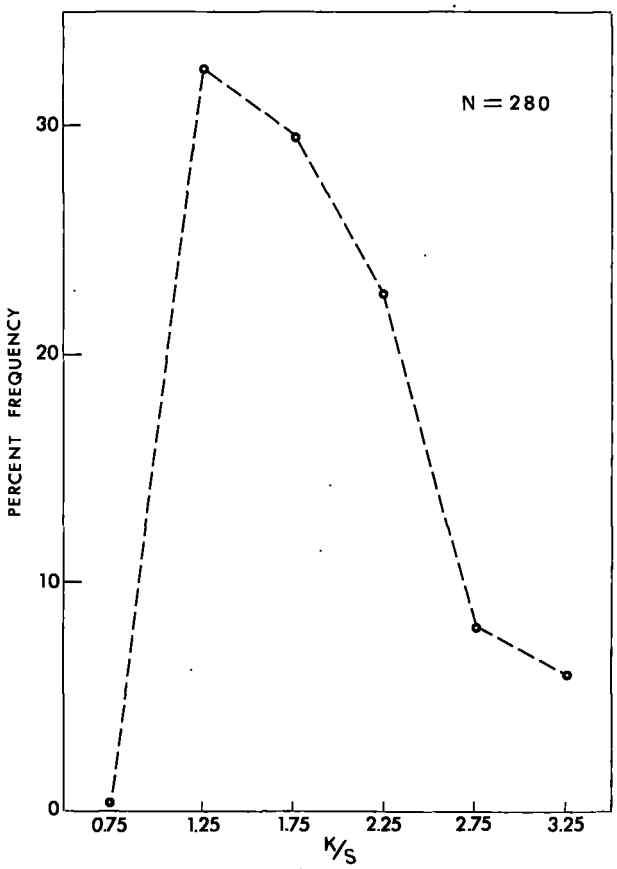

FIGURE 44.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *aztecus aztecus* Ives.

The range of *P. a. aztecus* is somewhat similar to that of *P. setiferus*. *P. a. aztecus*, however, wanders farther north and also farther south along eastern United States, reaching the Florida Keys. Both are absent along most of the Gulf Coast of peninsular Florida, and neither of the two shrimps reaches Cuba. The female *P. aztecus* from Cuba waters identified by Burkenroad as *P. aztecus* "Form A" is most likely one of the specimens of *P. a. subtilis* that show relatively long and broad adrostral sulci.

Brown shrimp are only moderately abundant from North Carolina to northeast Florida and are scarce in southern Florida. In spite of the extensive sampling in the area, only a small population has been found south of the Florida Keys, and very few specimens have been reported from Florida Bay (Tabb and Manning, 1961). Recently the brown shrimp was recorded for the first time (Costello and Allen, 1964) from the northwest Sanibel grounds, offshore from Fort Myers, in

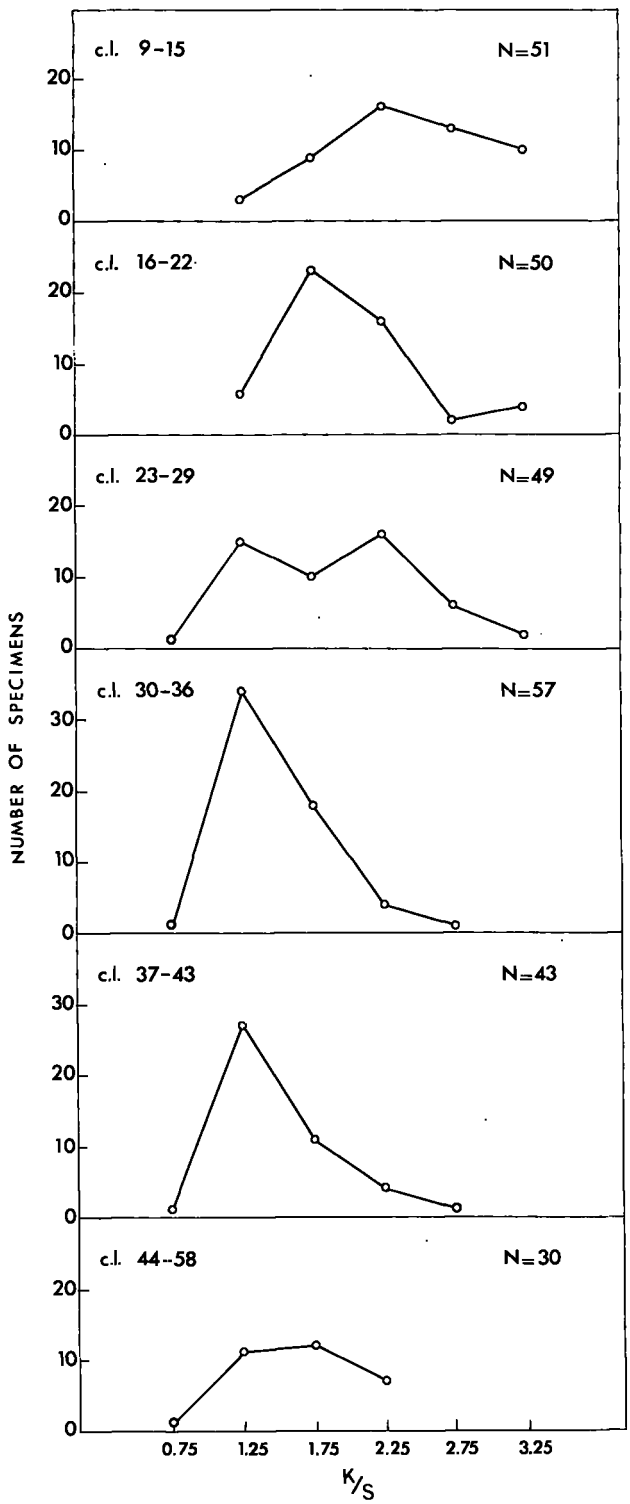

FIGURE 45.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *aztecus aztecus* Ives of different size classes.

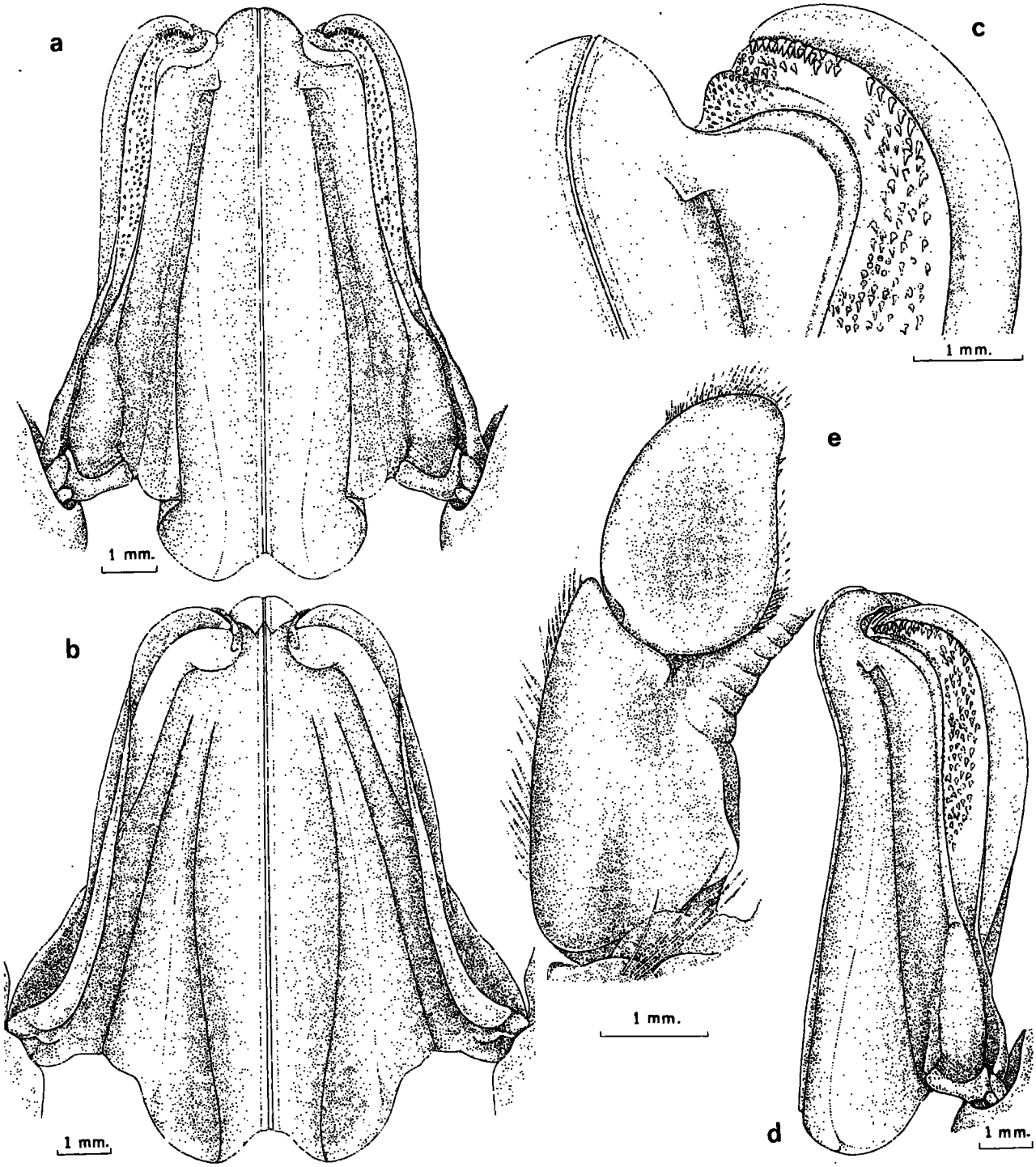

FIGURE 46.—*Penaeus (M.) aztecus aztecus* Ives. a. Petasma, exterior surface, ♂ 36 mm. c.l., off Matagorda Bay, Tex. b. Petasma, interior surface, ♂ 36 mm. c.l., off Matagorda Bay, Tex. c. Petasma, distal portion, ♂ 37 mm. c.l., off Matagorda Bay, Tex. d. Petasma, lateral view, ♂ 35 mm. c.l., off Sebastian, Fla. e. Appendix masculina, ♂ 37 mm. c.l., off Matagorda Bay, Tex.

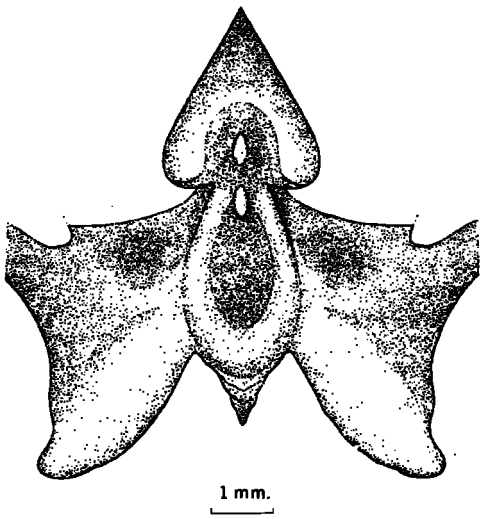

FIGURE 47.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Median protuberance with horns on posterior margin of sternite XIII, ♀ 55.5 mm. c.l., off Matagorda Bay, Tex.

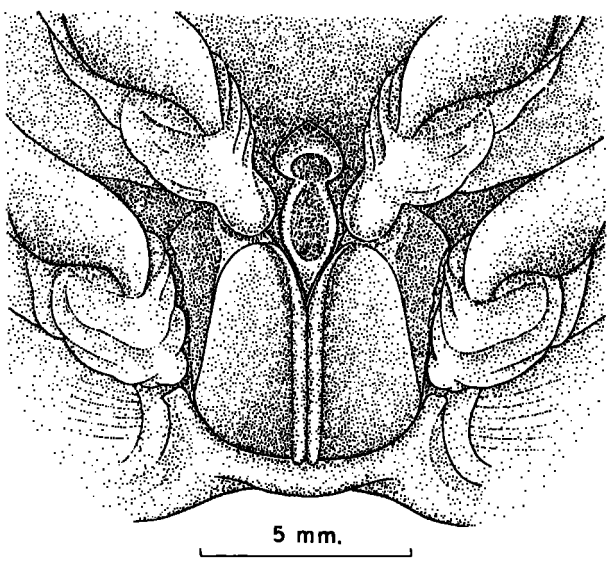

FIGURE 48.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Thelycum, ♀ 39 mm. c.l., northwestern Gulf of Mexico.

5 fm. The only reference to the presence of *P. a. aztecus* farther north on Florida's west coast is that by Eldred et al. (1965), who reported two postlarvae 145 km. off the mouth of Tampa Bay (also one postlarva about 96 km. off Fort Myers). This subspecies attains its maximum density along the coast of Texas but is also relatively abundant off the northeast coast of Mexico south to Veracruz, and a dense concentration exists in Campeche in the area west of Carmen.

Highest densities of brown shrimp are between 15 and 30 fm., but they are commercially abundant down to 60 fm. At depths less than 10 fm. they are immature and relatively small and move to deeper waters as they grow. Although most individuals stay in water shallower than 30 fm., some go three times as deep. At *Pelican* Sta. 114–4 (lat. 26°56.5′ N., long. 96°27′ W.) off Armstrong, Tex., two females were caught in 90 fm. These specimens were identified by Lipke B. Holthuis and are now at Tokyo University of Fisheries. *P. a. aztecus* was also found at *Pelican* Sta. 11 (lat. 29°11′ N., long. 88°30′ W.) off Mississippi in 88½ fm., and at Sta. 115–1 (lat. 26°55′ N., long. 96°27′ W.) off Armstrong, Tex., in 90 fm. The specimens taken at these latter stations were tentatively identified by Milton J. Lindner (personal communication).

P. a. aztecus shows no significant morphological variations within its range.

Relationships

P. a. aztecus differs rather strikingly from the southern subspecies *P. a. subtilis* in having a long and deep median sulcus and a long and broad adrostral sulcus. Figure 59 shows that, despite some overlapping in the length of the adrostral sulcus in the two subspecies, the adrostral sulcus reaches $\frac{1}{12}$ to $\frac{1}{20}$ c.l. from the posterior margin of carapace in the higher percentage of specimens of *P. a. aztecus*, whereas in the higher percentage of *P. a. subtilis* it reaches from $\frac{1}{5}$ to $\frac{1}{12}$ c.l. Furthermore, *P. a. aztecus* usually has a broader dorsolateral sulcus and its K/S has a modal value of only 1.25 (fig. 44), whereas in *P. a. subtilis* K/S has a modal value of 3.5.

Adult *P. a. aztecus* can be separated readily from the closely related *P. d. duorarum* and *P. brasiliensis*. Females may be distinguished by the anteriorly bifurcate median carina on the posterior process and the widely divergent anteromedian corners of the lateral plates. Males of *P. a aztecus* differ from those of *P. d. duorarum* by the shape and armature of the ventral costa of the petasma (turning proximally in an arc, lacking spines on free margin, and with a patch of small, closely set teeth on the distal portion of the attached margin) and the relatively elongated—rather than broad—appendix masculina. The compact patch of teeth on the attached margin of the ventral costa also distinguishes male brown shrimp from male *P. brasiliensis*, which

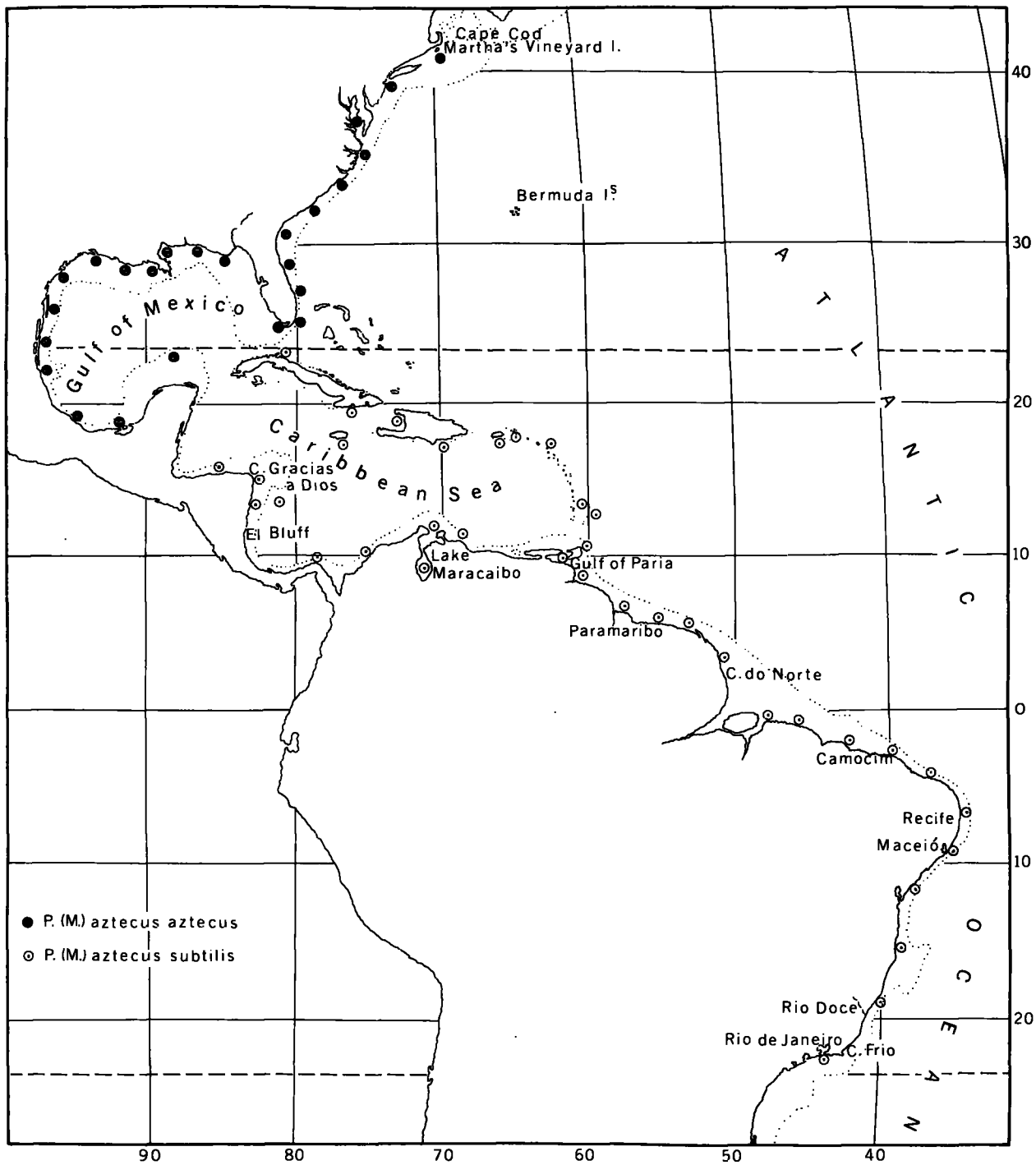

FIGURE 49.—Distribution of *Penaeus* (*M.*) *aztecus aztecus* Ives and *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante.

instead have slightly larger and fewer teeth. The shorter distomedian projection and the distal fold, however, are the most striking characters that set the males of *P. a. aztecus* apart from those of *P. brasiliensis*. In the former the distal fold is relatively small and unarmed, or, more frequently, armed with small spines on the outer surface, whereas in *P. brasiliensis* the fold protrudes inward to form a large auriclelike projection that bears strong spines on the inner surface.

P. a. aztecus also differs from *P. d. duorarum* and *P. brasiliensis* in northern waters by the broad dorsolateral sulcus and the often sinuous rostrum. Large brown shrimp also differ from the other two in having a proportionately longer abdomen. Furthermore, in *P. a. aztecus* the third pereopod is thinner and longer—reaching at least to distal end of the antennular peduncle and in large individuals exceeding it by as much as one-tenth length of carpus—than in *P. d. duorarum* and *P. brasiliensis*. The relatively longer length of the third pereopod in brown shrimp is illustrated in table 3, which includes the lengths of various podomeres (dactyl to ischium) for the three carapace-length intervals, and in figure 29, which shows the length of the carpus at various carapace lengths in *P. a. aztecus*, *P. d. duorarum*, and *P. brasiliensis*.

As stated earlier, it is difficult to distinguish small juvenile *P. a. aztecus* from *P. d. duorarum* and *P. brasiliensis*. Many juvenile brown shrimp, however, have a broad dorsolateral sulcus and, thus, may be readily identified. Also, small brown shrimp are usually more slender and their external genitalia are proportionately less well developed than those of the other two shrimps. Juvenile males of *P. a. aztecus* may also be recognized by having a low, rounded midrib on sternite XIV surrounded by a very shallow, horseshoe-shaped groove (fig. 50). Furthermore, in males of *P. a. aztecus* 11 mm. c.l., 51 mm. t.l. and larger, the ventral costa of the petasma lacks distomarginal spines, which are present in *P. d. duorarum*. Juvenile females of *P. a. aztecus* may be recognized by characters of the thelycum. Among females with a carapace length of 10 to 11 mm. c.l., 47 to 51 mm. t.l., those of *P. a. aztecus* may be distinguished by the presence of a knob on the midposterior margin of sternite XIII. In females 12 mm. c.l., 55 mm. t.l., a small triangular projection extends caudad from the midposterior margin of sternite XIII, and when

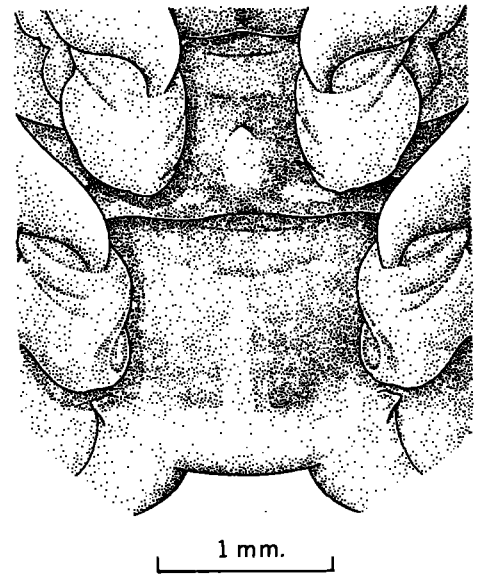

FIGURE 50.—*Penaeus (M.) aztecus aztecus* Ives. Sternites XIII and XIV, ♂ 10 mm. c.l., Laguna de la Mancha, Veracruz, Mexico.

attaining 14 mm. c.l., 64 mm. t.l., the anterior arms of the median carina are clearly distinct on the posterior process. At 16 mm. c.l., 73 mm. t.l., the posterior process has assumed its typical diamond-like shape. At 17 mm. c.l., 77 mm. t.l., the two ribs projecting from the median carina are strongly developed. The thelycum also attains the adult form at a greater size in females of *P. a. aztecus* than in *P. d. duorarum* and *P. brasiliensis*.

The length of the rostrum also aids in distinguishing juveniles of *P. a. aztecus* from those of *P. d. duorarum*. Brown shrimp, some as small as 8 mm. c.l., 36 mm, t.l., have rostrum proportionately longer than those in *P. d. duorarum;* the rostrum of the brown shrimp extends anteriorly as far as distal one-third of the thickened portion of the lateral antennular flagellum.

P. a. aztecus is separable from the closely allied *P. paulensis* by the broader dorsolateral sulcus, with its rounded rather than sharp dorsal lip. Females of brown shrimp have wider anterior and posterior processes, and in males the distal portion of the ventral costa is strongly arched and the attached margin is armed with numerous contiguous teeth.

Reproduction

SUBADULT STAGE-SEXUAL MATURITY

The smallest male I found with joined petasmal endopods was 19 mm. c.l., 85 mm. t.l., but indi-

viduals up to 22 mm. c.l., 97 mm. t.l., may have the petasma unjoined. Thus, males seem to attain the subadult stage at a carapace length of 19 to 23 mm., or 85 to 101 mm. t.l. It is possible, however, that some males attain this stage at a smaller size.

The smaller females I found to have reached the subadult stage were 18 mm. c.l., 82 mm., t.l. Individuals up to 22 mm. c.l., 97 mm. t.l., however, may have the thelycum with lateral plates noncontiguous; thus, the subadult stage is attained between 18 and 23 mm. c.l., 82 to 101 mm. t.l.

Burkenroad (1939) reported that female brown shrimp reach sexual maturity or gonadal ripeness at about 30 mm. c.l. or about 145 mm. t.l., and Renfro (1964) found that sexual maturity is usually first attained at a total length of about 140 mm.

COPULATION

Burkenroad (1939) was the first to suggest that copulation in *P. a. aztecus* takes place between a soft-shelled female and a hard-shelled male, as is now thought to be true for all *Penaeus* with a closed thelycum. Copulation occurs without respect to the developmental stage of the ovaries.

Impregnated females can usually be detected macroscopically, like those of the other *Penaeus* with a closed thelycum, by the bulging of the lateral plates and the tumid appearance—the "lip" of their borders. These criteria are not infallible however, because the lateral plates remain strongly convex in recently spent females.

OVARY DEVELOPMENT

Like many of its congeners, *P. a. aztecus* possesses ovaries consisting of one anterior lobe from which project six to eight lateral lobules and one posterior lobe that extends to the base of the telson. The size, color, and texture of the ovaries change with the degree of maturity.

Burkenroad (1939) distinguished three stages in the development of the ovary, which correspond approximately to the last three stages recognized by Cummings (1961) in *P. d. duorarum*. Five stages of ovarian development are now generally accepted.

1. Undeveloped. Ovaries slender, flaccid, and translucent. Ova small and translucent.

2. Developing. Ovaries opaque, yellowish with numerous heavily granular ova; diameter of ova 0.10 to 0.18 mm.

3. Nearly ripe. Ovaries large, yellowish brown, becoming darker brown. Diameter of ova 0.19 to 0.25 mm.

4. Ripe. Ovaries golden brown. Diameter of ova 0.26 to 0.28 mm.

5. Spent. Ovaries greatly reduced in diameter, flaccid, light brown to yellowish.

SPAWNING

The information on spawning—depths, seasons, and peaks—of brown shrimp has been largely deduced from records of the occurrence of females with ripe or spent ovaries and the distribution and abundance of larvae and postlarvae. *P. a. aztecus* spawns at sea, usually in water deeper than 10 fm. and down to at least 60 fm. (Renfro and Brusher, 1965). Laboratory experiments by Cook (1965) indicated that spawning takes place at night. Spawning activity varies through the range of the shrimp and with depth. According to studies on ovary development by Renfro and Brusher (1965) in the northwestern Gulf of Mexico, spawning is continuous in depth between 25 and 60 fm. and appears to be most intensive during the fall. At 15 fm., however, spawning is restricted, taking place from March–April through November–December, and maximum spawning activity apparently occurs in late summer. Recently, Temple and Fischer (1967) indicated from the seasonal abundance of larvae that the maximum peak of spawning was from September to November. Studies on abundance of juveniles (Gunter, 1950) and those on population dynamics, including general knowledge of maximum aggregations of postlarvae in the nursery grounds (Kutkuhn, 1962) indicated that two annual peaks of spawning occur in the northern Gulf of Mexico, one in early spring and the other in the fall.

Along the southeastern Atlantic Coast of the United States a single peak of spawning activity seems to occur in February or March (Williams, 1955a, 1959; Bearden, 1961; Joyce, 1965). In North Carolina, Williams' (1965) collection of postlarvae in the sounds from October to May indicates a protracted spawning season including fall and winter, but the postlarvae that reach inshore waters are apparently killed by low temperatures because no juveniles were found until mid-April.

In the northern Gulf of Mexico and the southeastern Atlantic Coast of the United States, the first peak of brown shrimp spawning occurs earlier in the year than do those of *P. setiferus* and *P. d. duorarum;* the postlarvae of the latter do not appear until May or June, after those of

P. a. aztecus have passed their peak of abundance. In the northern Gulf of Mexico the second peak of brown shrimp spawning occurs later in the fall than those of the white and pink shrimps.

Burkenroad (1939) indicated that because females first spawn at sizes only a little above 30 mm. c.l., the largest females may spawn more than once. He also observed that the ovaries of large females contained ripe ova together with young ova, which suggests preparation of the ovary for a second spawning. Studies by Renfro and Temple (personal communication) indicated that recovery and redevelopment are fairly rapid at least during the warmer months. They found in recently spent ovaries that the immature ova present at spawning were developing rapidly while remnants of ripe ova from a previous spawning were being reabsorbed. This finding is taken also as evidence of more than one spawning by one individual.

SEX RATIO

The sex ratio in inshore as well as offshore waters is about 1:1 (Renfro and Brusher, 1963; Joyce, 1965).

Postembryonic Development

LARVAE, POSTLARVAE, AND JUVENILES

Wheeler (1960) reared *P. a. aztecus* from eggs spawned in the laboratory through five nauplial stages to the first protozoea. Later Cook (1965) succeeded in rearing brown shrimp to postlarvae. The entire larval cycle was completed in a minimum of 12 days at about 29° C. Harry L. Cook (personal communication) found that the larval cycle of brown shrimp is similar to that of the white and pink shrimps, and includes, in addition to five nauplial stages, three protozoeal and three mysis stages. To date, no distinctive characters have been observed which will allow specific identification of the different larval stages of the various grooved *Penaeus* from the western Atlantic and the Gulf of Mexico.

Various investigations have been conducted on the morphology of the postlarvae of *P. a. aztecus*, *P. d. duorarum*, and *P. setiferus*.

Pearson (1939) described various postlarvae of *P. brasiliensis* (*P. a. aztecus* and *P. d. duorarum*) and distinguished them from those of *P. setiferus*. Williams (1959) separated the postlarvae under 12 mm. t.l. of *P. a. aztecus*, *P. d. duorarum*, and *P. setiferus* on the basis of two of the diagnostic characters pointed out by Pearson (length of rostrum and third pereopod) plus body size and shape of distal portion of antennal scale. Baxter and Renfro (1967) found that those morphological and morphometric characters, combined, allowed the identification of brown and white shrimp postlarvae below 10 mm. t.l. in the Galveston Bay area. Christmas et al. (1966), however, as a result of the examination of extensive collections from Mississippi, concluded that intraspecific variation among the postlarvae of the brown, white, and pink shrimps is wide. They found that during spring postlarvae of brown shrimp have a larger size than those of the pink and white shrimps, but that the differences disappear in summer when postlarval brown shrimp have more nearly the same size as the other two. Baxter and Renfro (1967) also reported an overlap in length distribution of the postlarvae of brown and white shrimps during the summer, but the mean length of the brown shrimp always exceeded that of the white shrimp.

Juvenile *P. a. aztecus* 18 mm. t.l. have very shallow but distinctly long adrostral sulci and at 20 mm. t.l., the sulci are well developed. Brown shrimp of this size and larger can, therefore, be readily separated from *P. setiferus*, as well as from *P. schmitti*, the only other nongrooved *Penaeus* in the western Atlantic.

In juveniles sex can be determined when they reach about 20 mm. t.l. Males can be distinguished by the shape and position of the endopods of the first pair of pleopods, which are lower on the bases and longer than in females. Small males can also be recognized by having a low rib on the midline of sternite XIV, whereas in females the sternite XIV is produced ventrally, often bearing a minute knob at its extremity. (See also under Relationships.)

GROWTH

There are various estimates of the rate of growth of *P. a. aztecus* at different sizes and under different environmental conditions. Pearson (1939) reported that postlarvae of "*P. brasiliensis*," which most probably were *P. a. aztecus*, held in the laboratory grew at a maximum rate of 0.56 mm. per day. Zein-Eldin and Aldrich (1965) studied in the laboratory the growth of postlarvae 12.1 mm. t.l. at temperatures ranging from 7° C. to 35° C. through a 28-day period. They concluded that growth increased with temperature, with significant growth beginning at some temperature above 11° C. but below 18° C. The most marked increase in growth rate occurred in the temperature region

between 11° C. and 25° C., and the maximum increase was 1.4 mm. per day at 32° C. and 1.1 mm. per day at 25° C. Almost no growth occurred at 11° C.

Ringo (1965), using the difference in size between the largest shrimp in successive collections, calculated that in Galveston Bay, Tex., young brown shrimp grew an average of 0.1 mm. t.l. per day from March to early April; as temperature rose the rate of growth increased to an average of 1.7 mm. per day and reached a maximum of 3.3 mm. per day during late May. This growth rate is the highest reported for any *Penaeus* from the Gulf of Mexico and the western Atlantic.

Loesch (1965) estimated that in Mobile Bay, Ala., very young shrimp (20 mm. mean t.l. at the beginning of the investigation) grew at an average rate of as much as 50 mm. t.l. per month in spring, and juveniles and subadults increased 24 to 43 mm. t.l. per month during summer and 12 to 35 mm. t.l. in winter. St. Amant et al. (1966) studied the growth of *P. a. aztecus* in the Barataria Bay, La., area during March, April, and May from 1962 to 1965. Growth varied, the range of variation was from no growth to 2.5 mm. per day. They stated that "There appeared to be a trend, though not completely evident in these data, for the growth of brown shrimp to be less than 1.0 mm per day when the water temperature was below 20C and less than 1.5 mm per day when the water temperature was below 25C. Little or no measurable growth was noted at cumulative average water temperatures below 16C."

Klima and Benigno (1965), through a mark-recapture experiment in Mississippi, estimated that during a 4-week period in summer, nearshore, male brown shrimp grew from 104 mm. in total length to 132 mm., and females from 104 mm. to 135 mm.—monthly increases of about 28 mm. and 31 mm., respectively. Chin (1960), on the basis of length-weight relation, assumed that in Galveston Bay, Tex., the growth rate for the sexes is almost identical.

Williams (1955a), taking the upper extremes of size distribution, estimated that in North Carolina the mean length of juveniles increases at a rate of 45.7 mm. per month from April to June. This growth is slightly less than that of *P. d. duorarum*, but still extremely rapid. Joyce (1965) estimated a similar growth rate of 45 mm. per month for brown shrimp in northeast Florida.

SEX DIFFERENCES IN SIZE

The largest female on record, 236 mm. t.l., was reported by Renfro (unpublished data) from south of Morgan City, La., in 60 fm. The largest males, also reported by Renfro, were 195 mm. t.l.—one from off Galveston, Tex., in 60 fm. and one from southeast of Morgan City, La., in 45 fm. The survey of the northern Gulf of Mexico population by Renfro and Brusher (1964) indicated that size of shrimp varies with depth and, to some extent, distance from shore. Regardless of time of the year, the mean length of brown shrimp increased with increasing depth.

Brown shrimp exhibit a sex-size difference (females are larger than males) which becomes evident upon attainment of a length of about 100 mm. (Williams, 1955a). Burkenroad (1939) attributed the difference in size in offshore individuals to a longer life among females.

Ecology

FOOD

Brown shrimp are omnivorous, feeding upon different plants and animals as well as organic debris. (See also under Food in the discussion of *Penaeus setiferus*.)

SUBSTRATE

Juveniles of *P. a. aztecus* prefer muddy or peaty bottoms, but they also live on sand, silt, or clay frequently mixed with fragments of shells and rocks. They usually abound in areas covered with vegetation and plant debris (Williams, 1959). The adults prefer a substrate softer than the sympatric *P. d. duorarum* (Hildebrand, 1954; Kutkuhn, 1962). They are abundant on mud or silt bottoms and, occasionally, where the bottom consists of mud, sand, and shell.

DIEL CYCLE

Adult brown shrimp are mostly nocturnal and are usually taken at night, but, according to Springer and Bullis (1952), "The difference in the catch rate between day and night fishing is not so well marked in deeper parts of the range." Juveniles are more active diurnally than adults and can be highly active during the daytime—a fact clearly established by the sampling carried on by Joyce (1965), who took about 71 percent of his *P. a. aztecus* juveniles by day.

Information on the diel activity of postlarvae in approaching inshore waters appears to be somewhat conflicting. St. Amant et al. (1966) found no discernible difference between nocturnal and diur-

nal catches of postlarvae moving into the greater Barataria Bay, La., area, whereas Copeland and Truitt (1966) captured most of the postlarvae at night at Aransas Pass, Tex., inlet, and Baxter and Furr (1964) estimated that 70 percent of the postlarvae in their samples at the entrance of Galveston Bay, Tex., were caught between 9 p.m. and 6 a.m. Copeland and Truitt (1966) also reported that during the day no significant difference could be detected between surface and bottom samples and suggested that "Perhaps, penaeid postlarvae actively pursue the upper layers (even during the day) to take advantage of faster currents on the surface." Rearing experiments by Cook (1965) indicated that larvae are positively phototropic, for when reared under an overhead light they swim to the surface.

The effects of phases of the moon on the behavior of brown shrimp have not been well established. Hildebrand (1954) stated that some shrimpers maintain that fishing for brown shrimp is most successful during the full moon, but that others believe that catches do not change substantially at any moon phase. Copeland (1965) found that peak seaward migrations of brown shrimp through Aransas Pass, Tex., inlet occurred at times of full moon.

MOVEMENTS

The larvae of *P. a. aztecus* move from the high-salinity waters of the spawning grounds toward brackish waters where they arrive as postlarvae.

It was generally believed that larvae and postlarvae moved toward estuaries and that the latter entered them directly. Temple and Fischer (1967), however, have gathered evidence that in the northwestern Gulf of Mexico "brown shrimp larvae and postlarvae, or both, overwinter in waters of the Continental Shelf."

Postlarvae enter the nursery grounds at 8 to 14 mm. t.l. (Baxter and Renfro, 1967). They move into the estuaries on flood tides (St. Amant et al., 1966; Copeland and Truitt, 1966). Major postlarval brown shrimp influx into the nursery areas occurs earlier—in late winter or early spring—than do those of the sympatric *Penaeus*. Studies by Baxter and Renfro (1967) showed that postlarvae were scarce in the entrance of Galveston Bay and in Galveston Island Beach, Tex., throughout most of the winter. Their number increased rapidly and reached a peak between mid-March and mid-April. After the spring peak few postlarvae were caught until mid-June when their number increased again and reached a second peak in August and September. Copeland and Truitt (1966) in Aransas Pass, Tex., inlet observed two similar peaks of postlarval abundance. St. Amant et al. (1966) reported that in Barataria Bay, La., peak catches of postlarvae occurred in April in 1962 and 1963, in February in 1964, and in March in 1965. Christmas et al. (1966) first took postlarvae of brown shrimp in Louisiana in February. They observed that the period of inshore movement lasted through September and that few individuals were present during October and November.

Studies by Villalobos et al. (1967) in Laguna de Alvarado, Veracruz, Mexico, showed that postlarval stages of *P. a. aztecus* were abundant in March (dry season); in contrast, none were found during August (rainy season). In South Carolina, Bearden (1961) found the greatest abundance of postlarvae in February and March. Williams (1955a, 1965) collected postlarvae in the sounds of North Carolina from October to May and reported the peak of abundance from late March to early April.

The postlarvae molt to the juvenile stage 4 to 6 weeks after they arrive in estuaries (Parker, 1966). A number of investigators have studied the occurrence of juveniles and subadults in the nursery grounds of the United States adjacent to the Gulf of Mexico (Gunter, 1950; Ingle, 1957; Chin, 1960; St. Amant et al., 1966; Trent, 1967). Brown shrimp juveniles begin to appear in small numbers in the estuarine waters of Texas and Louisiana late in March or early in April. Their numbers increase to a maximum in May and June. They are abundant in July and August, become increasingly scarce from September to the end of October, and are almost absent during late fall and winter. Seaward migration begins and rapidly intensifies in May or June through August. Tabb, Dubrow, and Jones (1962) found that *P. a. aztecus* is extremely rare in the estuaries adjacent to Florida Bay, because only a few young specimens were taken during their extensive sampling from April through August.

Several investigations have also been conducted on the seasonal abundance of juveniles in the nursery grounds of the eastern United States. In St. Lucie estuary, eastern Florida, Gunter and Hall (1963) found the smallest specimens of brown shrimp in January, February, May, and October and suggested that summer and fall were the

periods of least abundance. Joyce (1965) concluded that in northeast Florida juveniles first appear in the nursery grounds in early May, or probably earlier; their number increases considerably in June to reach a maximum in July. In August, as subadults, they migrate toward the sea, few remain in September and October, and almost none from November to March. In North Carolina, Williams (1955a, 1959) found juveniles from mid-April throughout the summer [to November, according to a graph in his 1955a publication]; peak abundance was in the first half of May. The information above strongly suggests that in the brackish waters of North Carolina to northeast Florida juveniles appear in large numbers in April, reach a peak of abundance during the period May through July, and their numbers decline from August through October.

Brown shrimp leave inshore waters at different sizes. Copeland (1965) reported that brown shrimp move out to sea at 70 to 80 mm. t.l. Sampling by Joyce (1965), in turn, indicated that brown shrimp emigrate offshore at an average size 100 to 105 mm. t.l. Recently, Trent (1967) reported that the length of shrimp leaving the estuaries ranges from 60 to 130 mm. t.l., and that the size of those moving out of Galveston Bay, Tex., in 1966 increased as the season of emigration progressed.

Evidence is strong that shrimp migrate from inshore waters to sea during ebb tides. Copeland (1965) reported peak abundance of shrimp leaving through Aransas Pass, Tex., inlet on the ebb tide and usually during the full moon.

Information on migrations of brown shrimp after they leave estuaries is rather meager. Mark-recapture experiments by Klima (1964) indicated that in Texas most individuals moved parallel to the coast and remained within 48 km. of the release site in waters 16 to 30 fm. deep. In Texas and Louisiana, a large proportion of the marked small shrimp were recovered also within 48 km. of the release area. One individual, however, was caught about 314 km. away, the longest distance known to have been traveled by a brown shrimp. Studies by Klima and Benigno (1965) suggested that along the Mississippi Coast shrimp did not move great distances from the release site, at least during the summer; the most rapid migration observed was at a rate of 4.32 km. per day. These experiments, as well as a previous one by Inglis (1960), also indicate that at least part of the annually recruited population in the northern Gulf moves from east to west. There are also indications that brown, like white shrimp, migrate southward along the northeast coast of Mexico, from late summer through winter. This movement was first suggested by Gunter (1962c), who pointed out that the average monthly production from Texas waters suggested a southward drift, and later Klima and Benigno (1965) found that some of the shrimp marked off Port Aransas, Tex., in August moved south; one individual traveled 104 km. in a southerly direction.

Along the Atlantic Coast of the United States some brown shrimp move northward during the summer, apparently from the northernmost spawning grounds off North Carolina. In the lower portion of Chesapeake Bay juveniles and subadults are caught during summer and fall; information gathered from different laboratories suggests that only occasionally do brown shrimp move farther north along the coast. Such a movement seems to have taken place during the sampling reported by Burkenroad (1939) in Delaware Bay and southern New Jersey. Brown shrimp were first taken at the end of August (minimum of 13 mm. c.l. in males and 17 mm. c.l. in females), and they were no longer there at the end of October. Because no small juveniles were collected through the sampling period and because 2 months before shrimp arrived the water had reached higher temperatures than were registered when they were presumably leaving the area, Burkenroad concluded that juveniles had migrated from southern waters where spawning and larval development occurred. Small individuals have been caught as far north as southern Martha's Vineyard, Mass., but the small number of records strongly suggests that only rarely do stragglers reach that latitude. As a result of their mark-recapture experiment in North Carolina, McCoy and Brown (1967) stated that brown shrimp leaving Beaufort Inlet moved southward from June through October. The record migration was about 241 km. in 5 weeks.

EFFECTS OF TEMPERATURE

Temperature greatly influences survival and growth of brown shrimp. Laboratory experiments by Zein-Eldin and Aldrich (1965) indicated that postlarvae can tolerate wide fluctuations in temperature and salinities, but are adversely affected by extreme temperatures. Postlarvae survived temperatures from 11° C. to 30° C., at salinities of 21

to 40 p.p.t.; at temperatures below 15° C., however, their tolerance to low salinities (below 10 p.p.t.) decreased, and near 35° C. survival was reduced regardless of salinity. The authors suggested that the combined effect of low temperature and low salinity could be partly responsible for the time of postlarval influx into estuarine waters because they do not seem to enter estuaries until the temperature has increased to a degree that low salinities are not harmful. They further suggested that temperature may have a decisive effect on survival of postlarvae in estuaries because if the temperature becomes lower in an environment of intermediate temperature (18° C.) and low salinity, the survival rate will be adversely affected.

Experiments by Aldrich et al. (1967) showed that postlarval *P. a. aztecus* regularly burrowed into a silty clay substrate as temperature fell to 12° to 17° C., and emerged as temperature rose to 18° to 22° C. The postlarvae of brown shrimp, thus, may "hibernate" in burrows for a portion of the winter.

Williams (1960) investigated the influence of temperature on osmotic regulation in young brown and pink shrimps. He found that the brown shrimp have a less efficient osmoregulatory mechanism in low temperatures than do pink shrimp; at temperatures of 8.7° to 8.8° C. the brown shrimp's ability to regulate is impaired and its blood tends toward isotonicity. This difference may explain, in part, why brown shrimp do not winter in the estuaries of North Carolina whereas pink shrimp do. On the other hand, the brown shrimp seems to have a greater tolerance to lower temperatures than does the white shrimp. *P. a. aztecus* ranges farther north; intensive spawning seems to begin in late winter or early spring in the cold waters of North Carolina, at least 2 months earlier than that of *P. setiferus;* and postlarval movement into inshore waters begins earlier and ends later than that of *P. setiferus.*

Temperature also has a pronounced effect on growth. The studies by Zein-Eldin and Aldrich (1965) indicated that postlarvae were able to grow in a wide range of salinity, but that growth was arrested at low temperatures. Postlarvae survived but did not grow at 11° C. and 15 p.p.t. salinity, whereas growth rate increased with rises in temperature, the maximum occurred between 18° and 25° C. Experiments by Zein-Eldin and Griffith (1965) indicated that temperature affects growth of postlarvae of brown shrimp, as it does those of white shrimp, by hastening molts rather than by increasing the increment per molt. Cook (1965) determined that temperature also greatly affects the growth of larvae; the optimum range was 28° to 30° C. (see also under Growth).

Although the precise effects of extreme temperatures are largely unknown, shrimp exposed to 30° C. and above become flaccid and perish rapidly when handled. Zein-Eldin and Aldrich (1965) estimated that the maximum tolerable temperature for postlarvae is probably only slightly above 35° C. The lowest temperature that they can tolerate is not known, but Gunter and Hildebrand (1951) reported a mass narcosis of the young at 4.4° C. and below.

EFFECTS OF SALINITY

Field observations indicate that juvenile and subadult brown shrimp, like pink shrimp and white shrimp, are able to withstand a wide range of salinity. Gunter and Hall (1963) reported that small juveniles (28–38 mm. t.l.) were taken in St. Lucie estuary, Fla., at salinities of 0.22 p.p.t. and 0.36 p.p.t.; Loesch (*In* Gunter et al., 1964), found *P. a. aztecus* in Mobile Bay, Ala., at 0.0 to 1.00 p.p.t., the lowest range of salinity at which this subspecies has been reported. At the other extreme, Simmons (1957) in Laguna Madre, Tex., collected specimens in salinity of 69 p.p.t. Experiments by Zein-Eldin (1963a) showed that at constant temperatures of 24.5° to 26° C., postlarval *P. a. aztecus* survived and grew over a range of salinities of 27 to 40 p.p.t. Later, Zein-Eldin and Aldrich (1965) demonstrated that postlarval brown shrimp withstand a wide range of salinity-temperature combinations except at extreme temperatures (see above).

Although juveniles of *P. a. aztecus* tolerate a wide range of salinity, their optimum seems to be higher than that of *P. setiferus.* In North Carolina, Williams (1955b) found only small populations of brown shrimp juveniles on low-salinity nursery grounds, where *P. setiferus* was most abundant. Gunter et al. (1964) stated that in the bays of Texas, young brown shrimp "are found in the greatest abundance within the salinity range 10 to 30, and with considerably higher concentrations at salinities above 20 than at salinities below 10. This is in considerable contrast to the white shrimp in the same bodies of water, which are found at the greatest abundance below 10." Joyce (1965) concluded that although in northeast Florida the nurs-

ery grounds of *P. a. aztecus* overlap those of *P. setiferus*, the former are generally more saline than those of the white shrimp.

ENEMIES AND DISEASES

Like *Penaeus* in general, brown shrimp are prey to many carnivorous teleost fishes (Gunter, 1945; Knapp, 1950; Darnell, 1958). They are also infested by a number of parasites (Sprague, 1950, 1954; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959; Kruse, 1959; Hutton et al., 1962). Aldrich (1965) reported that brown shrimp, like white shrimp, serve as intermediate hosts for *Prochristianella penaei*, a trypanorhynchan cestode, which as an adult lives in the Atlantic stingray, *Dasyatis sabina*.

Commercial Importance

P. a. aztecus is fished along the Atlantic Coast of the United States from North Carolina to about Cape Kennedy, Fla. In North Carolina it ranks first among the three important commercial *Penaeus* found in the region, but farther south *P. setiferus* is taken in larger quantities than is *P. a. aztecus* (Anderson and Lunz, 1965; Lyles, 1967). Along the northern Gulf of Mexico, brown shrimp are taken commercially from Apalachicola, Fla., to northeast Tamaulipas, Mexico. The largest catches made in the region are along the Texas Coast. Farther south in Mexican waters, brown shrimp are caught from the southeasternmost end of Tamaulipas, along the coast of Veracruz, Tabasco, and the southwestern part of the coast of Campeche. The grounds off the latter two States are by far the most important.

According to Lyles (1967), the brown shrimp was the most valuable shrimp in the United States in 1965, as it was from 1956 to 1963 (in 1964 white shrimp landings exceeded those of brown shrimp). In 1965, of a total landing of 99,890,237 kg. (whole weight) of *Penaeus* shrimps, *P. a. aztecus* made up 49,264,265 kg. or about 49 percent of the landings.

Penaeus (Melicertus) aztecus subtilis PÉREZ FARFANTE

Figures 51 to 59

Nicaragua: camarón café. Venezuela: camarón marrón, langostino amarillo. Guyana: short feelered prawn. Brazil: camarão lixo, camarão vermelho, camarão branco. United States: brown shrimp, dark shrimp.

Penaeus brasiliensis: Rathbun, 1897: 46 [part]; Rathbun, 1901: 100, 101 [part]; Pesta, 1915: 113 [part]; Burkenroad, 1934: 92 [part]; Schmitt, 1935: 128, 129 [part?]; ?Magalhães Filho, 1943: 12–26, figs. 1–6. Not *P. brasiliensis* Lat., 1817.

Penaeus braziliensis: Moreira, 1901: 6, 7, 72 [part].

Penaeus aztecus: Burkenroad, 1939 [part "Form B"]: 20, 27, 34–45, figs. 28, 29, 34; Anderson and Lindner, 1945: 305 [part]; Whiteleather and Brown, 1945: 25; Holthuis, 1948: 1104, 1105; Holthuis, 1950: 27; Sánchez Roig and Gómez de la Maza, 1951: 113; Pérez Farfante, 1953: 233, 234, 237 (238, 241 [part]); Pérez Farfante, 1954a: 97; Pérez Farfante, 1954b: 29; Lindner, 1957: 11–15, 21, 22, 65, 153, 154, 162, 165; Lindner, 1958: 33; U.S. Fish and Wildlife Service, 1958a: 11, 13; Bullis and Thompson, 1959a: 33–35, 41; Bullis and Thompson, 1959b: 1, 6, 9; Holthuis, 1959: 42–44, 47, 63–67, fig. 6b; Eldred and Hutton, 1960: 91, 106, 108; Pérez Farfante et al., 1961: 40, 48, 56, 57, 61, 64; Anonymous, 1962: 56; Miles, 1962: 189, 193; Boschi, 1963: 26–29 [part], figs. 8 (3, left), 11; Davant, 1963: 9, 12, 18–20, 32, 34, 35, 68, 74–76, 85–89, 91, figs. 6, 15, 16a, b, 17a, b, 18, and bis; Simpson, 1963: 22, 23, fig. 15; Boschi, 1964: 39 (40, 41 [part]); Ewald, 1964: 10, 20–23 (24, 28, and tables [part]); Cervigón, 1965: 21; Ewald, 1965a: 29; Ewald, 1965c: 52, 59, 65, 67, 70, 72, 74, 80, 82, 84–87, 91, 93–96, 114 (72, 80, 88–90, 92, 97–99, 113, fig. 13 [part]); Holthuis and Rosa, 1965: 4 [part]; Pericchi López, 1965: 23; Simpson et al., 1965: 77; Williams, 1965: 25, 26; Croker, 1967: 63, 68, 73, 74, 79–81, 84, 87, 95, 98, 105, 106; Instituto de Fomento Nacional, 1967: 5, 8.

Penaeus astecus: Whiteleather and Brown, 1945: 27.

Penaeus aztecus subtilis Pérez Farfante, 1967: 87–94, fig. 2a, b (holotype, ♂, USNM 119130, off Gallinas Point, Departamento de la Guajira, Colombia, 95 fm., October 9, 1965, *Oregon* Sta. 5685, lat. 12°29′ N.; long. 71°54′ W.)

Brown shrimp: Higman, 1959: 8, 10, 12–14.

Study Material

For list of records see Pérez Farfante, 1967.

Diagnosis

Adrostral sulcus relatively short, narrow posteriorly, either tapering to a point or turning laterally and broadening slightly at the end. Median sulcus short, ending well anterior to posterior

end of adrostral sulcus, shallow, and often interrupted. Dorsolateral sulcus usually narrow. Petasma with distal portion of ventral costa increasing gradually in width proximally and turning in arc; unarmed along free border and with elongated group of closely set small teeth on attached border; apex of costa adnate to membranous portion of ventrolateral lobule; latter rather extensively covered with spines; distal fold small, usually with numerous spinules, but sometimes unarmed. Thelycum with anterior process relatively broad, and with anteriorly bifurcate median carina on posterior process; lateral plates with anteromedian angles widely divergent, leaving median carina exposed.

Description

ROSTRUM

Teeth $\frac{6\text{–}10}{1\text{–}2}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—57, 9/2—27, 7/2—7, 10/2—5, 8/1—1, 9/1—1, 7/1—1, 6/1—1, N=200)+ epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to last dorsal tooth; rostrum long, in larger juveniles and subadults reaching to base of distal one-third of thickened portion of lateral antennular flagellum, attaining maximum length in relation to carapace length at 18 to 23 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.85); decreasing progressively with increasing length of shrimp, rostrum reaching midlength of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.50); rostrum usually strongly sinuous, proximal half convex, distal half with dorsal margin strongly concave; highest portion of blade at level of second or third dorsal tooth; latter level with anterior margin of carapace; rostrum tip ¼ to almost ⅓ r.l. Postrostral carina strong, usually expanded in anterior half, and usually short, ending well anterior to posterior margin of carapace. Median sulcus shallow, usually interrupted, short, ending well anterior to posterior margin of carapace. Adrostral sulcus typically narrow posteriorly, ⅕ to ¾ width of postrostral carina, tapering to point posteriorly or turning laterally and broadening slightly at end; sulcus usually short, ending ⅙ to 1/14 e.l. from posterior margin of carapace, occasionally ending 1/15 to 1/19 c.l. from carapace margin. Adrostral carina prominent anteriorly, sharp on carapace, same length as adrostral sulcus.

CARAPACE (fig. 51 a, b)

Length in proportion to total length smaller in juveniles, increasing slightly at about subadult stage. Gastrofrontal sulcus broad, extending to about one-fifth c.l. Gastrofrontal carina sharp, turning slightly posterodorsally, ending in acute orbital angle anteriorly. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening again into base of spine. Gastro-orbital carina very pronounced, occupying approximately posterior four-fifths of distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus deep along entire length, ⅕ to ¼ c.l., ending slightly anterior to midlength of carapace. Hepatic carina ⅕ to ¼ c.l., sharp, sloping anteroventrally to end 1/22 to 1/18 c.l. from anterior margin of carapace. Antennal spine very prominent; hepatic spine pronounced and acute.

ANTENNULES

Lateral flagellum relatively long, two-thirds length of antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum. Anterolateral spine small, sharp; stylocerite acuminate, reaching slightly beyond midlength of first antennular segment. Prosartema reaching distal end of proximal one-fifth of second antennular segment.

ANTENNAE

Length of scaphocerite 2½ times maximum width; its length relative to carapace length decreasing slightly with growth; spine reaching basal thickened portion of antennular flagellum. Carpocerite about 1⅓ times longer than wide. Antennal flagellum relatively short, 1½ times total length.

THORACIC APPENDAGES

Third maxilliped reaching at least end of first antennular segment and at most two-thirds length of second antennular segment; length of dactyl three-fifths that of propodus. First pereopod reaching only to midlength of carpocerite and at most exceeding it by entire length of dactyl. Second pereopod exceeding carpocerite by at least length of dactyl and at most by one-quarter length

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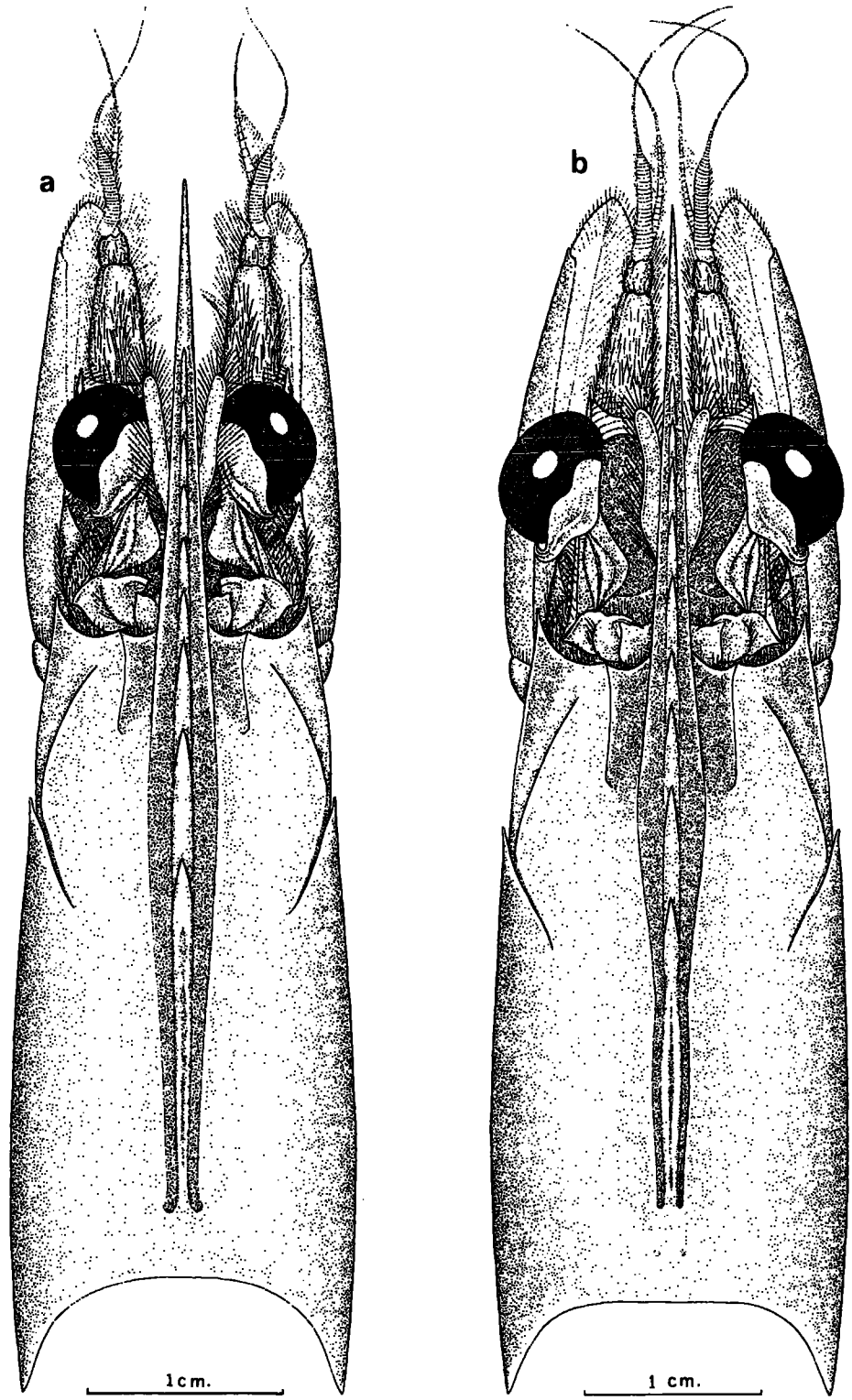

FIGURE 51.—*Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante. a. Cephalothorax, ♀ 36 mm. c.l., Gulf of Venezuela, Venezuela. b. Cephalothorax, ♀ 35 mm. c.l., off mouth of Surinam River, Surinam.

of carpus. Third pereopod reaching at least to distal half of second antennular segment and at most exceeding peduncle by entire length of dactyl. Fourth pereopod reaching at least midlength of carpocerite and at most exceeding it by entire length of dactyl. Fifth pereopod equal in length to fourth or surpassing it by ⅕ to ½ length of dactyl. Exopods on all pereopods. Long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

ABDOMEN

Carinate dorsally from posterior half of fourth somite posteriorly, carina gradually increasing in height posteriorly to form median keel on sixth somite, ending in sharp spine on posterior margin. Dorsolateral sulcus (fig. 52) usually narrow, ratio of height of keel to width of sulcus from 2 to 8.5, modally 3 in the Caribbean region and eastern Brazil (fig. 53), and 3.5 from the Gulf of Paria to Camocim, Brazil (fig. 55); in the Caribbean region and eastern Brazil modal value of K/S is 3 or less in all size classes (fig. 54) whereas in the Gulf of Paria to Camocim modal values of K/S range from 2 to 8 in the various size classes, although figure 56 shows a strong tendency toward a grouping of these values around 4; range of K/S is same in males and females; dorsal lip of dorsolateral sulcus rounded, ventral lip sharp. Sixth abdominal somite with three prominent cicatrices on each side, anterior one the longest; fifth abdominal somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite; fourth abdominal somite with similar series of pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

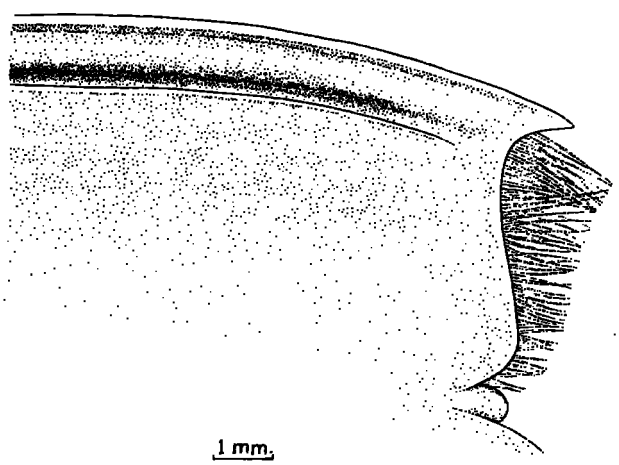

FIGURE 52.—*Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante, sixth abdominal somite, posterodorsal portion, ♀ 36 mm. c.l., Gulf of Venezuela.

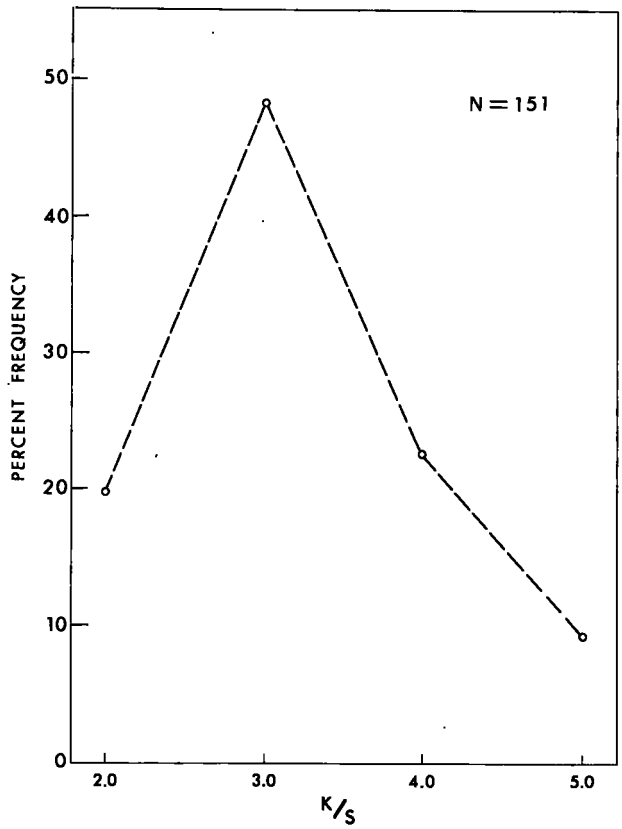

FIGURE 53.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante from the Caribbean region and eastern Brazil.

PETASMA (fig. 57)

Ventral costa increasing uniformly in width proximally, mesiodistal portion forming gentle arc, distal portion unarmed along free border—rarely with two or three widely spaced spinules—and with two to four series of small teeth arranged in elongate, narrow patch on attached border; apex of costa adnate to adjacent membranous portion of ventrolateral lobule, latter with extensive armature of thickly set spines. Distal fold rather small, usually armed with spinules, often in large numbers, but occasionally plain. Distomedian projections rather thick, and short, overhanging slightly distal portion of ventral costae.

APPENDIX MASCULINA

Relatively elongate, length 1⅖ to 1⅗ times maximum width, armed with strong, short spines along slightly concave outer margin and with longer

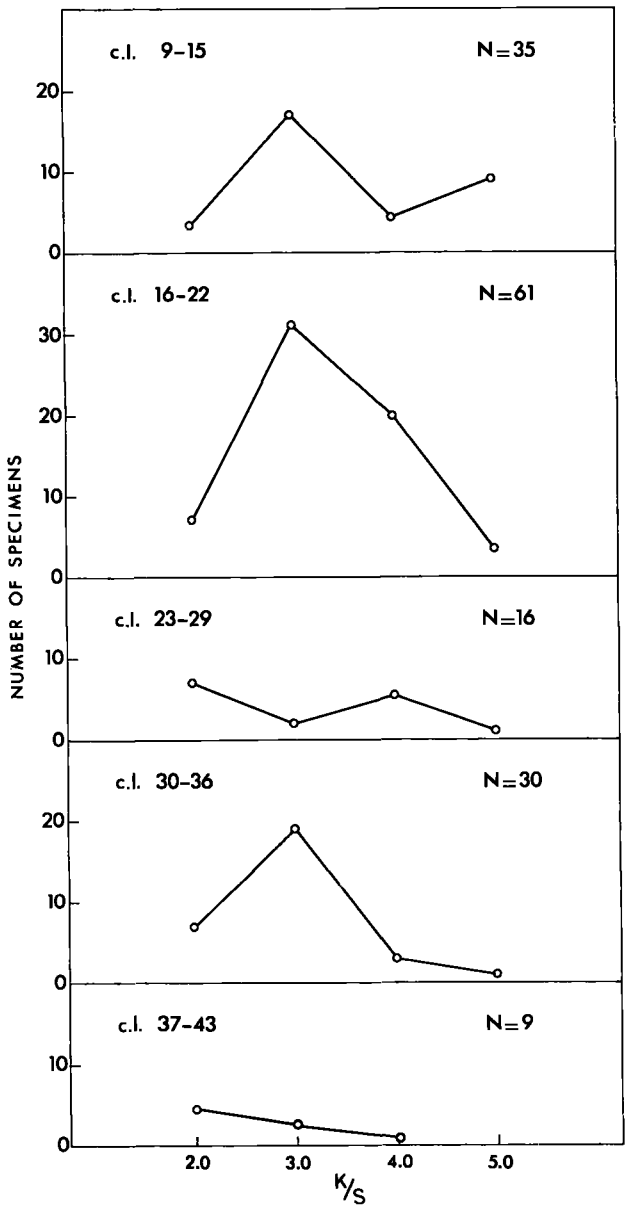

FIGURE 54.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante of different size classes from the Caribbean region and eastern Brazil.

spines along distomedian margin. Anterior surface subplane, posterior surface strongly concave, with sharp longitudinal ridge projecting from median margin.

THELYCUM (fig. 58)

Anterior process projecting ventrally in sharp, relatively low, marginal arc-shaped ridge, often expanding on both sides, and surrounding shallow depression with knob usually present at center.

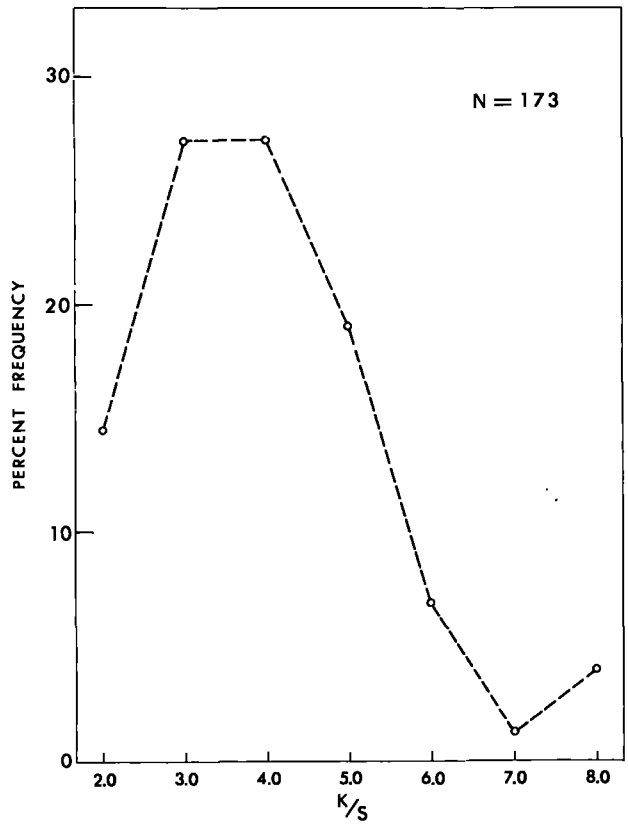

FIGURE 55.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante from the Gulf of Paria to Camocim, Brazil.

Posterior process broad, with anteriorly bifurcate median carina, resulting ribs turning medially and converging at base of anterior process, giving rise to diamondlike structure; enclosed area deeply concave or almost flat, plain, or, more often, bearing median rib anteriorly, posteriorly, or along entire length.

COLOR

P. a. subtilis, although variable in color, is most often brown—thus, the name camarón marrón (brown shrimp) in Venezuela, and camarão lixo (dirty shrimp) in Brazil. Grayish brown or yellowish specimens are rather common, and in some localities individuals are translucent pale yellow and are called camarão branco (white shrimp) in Brazil.

According to Holthuis (1959) and Davant (1963), no large dark spots have been observed on the sides, at the junction of the third and fourth abdominal somites, in this shrimp, at least in those along the northern and northeastern coasts of South America.

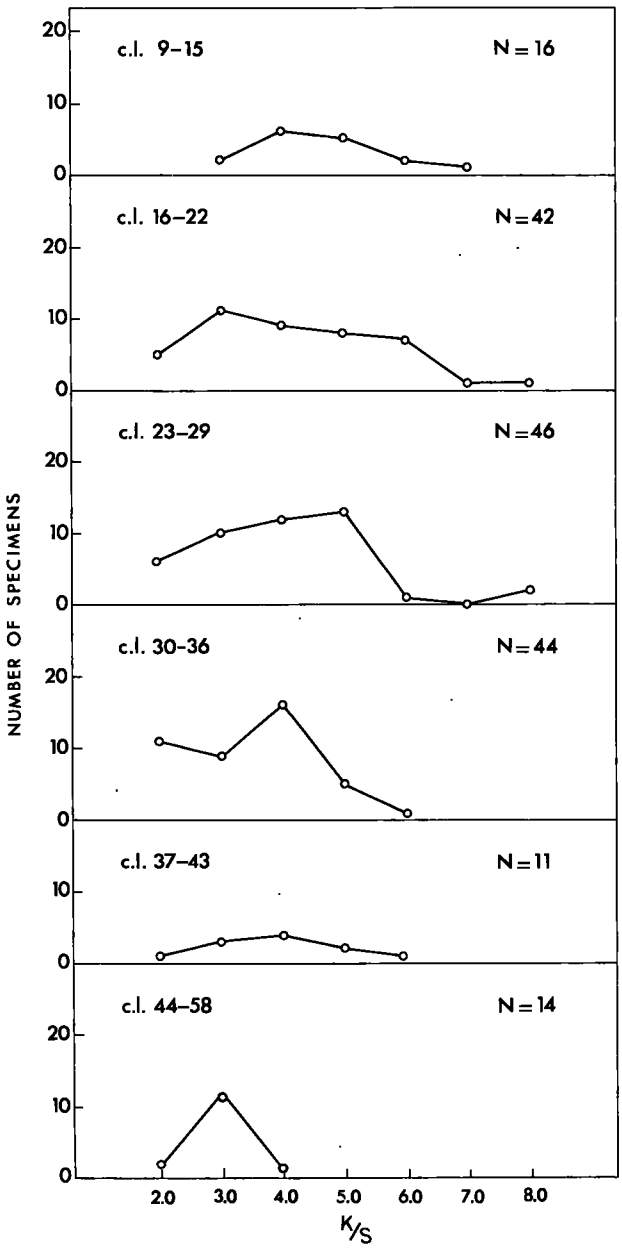

FIGURE 56.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante of different size classes from the Gulf of Paria to Camocim, Brazil.

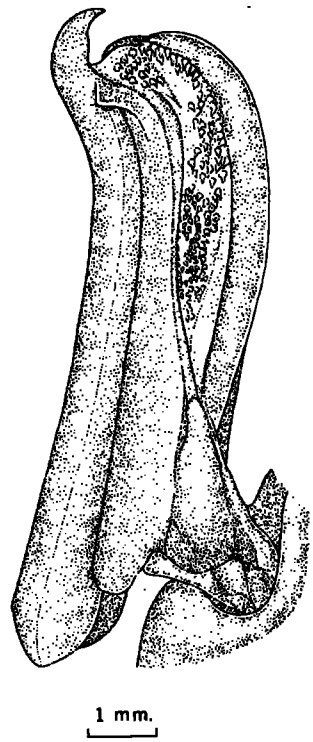

FIGURE 57.—*Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante. Petasma, lateral view, ♂ 34 mm. c.l., off Punta Gallinas, Departamento de la Guajira, Colombia.

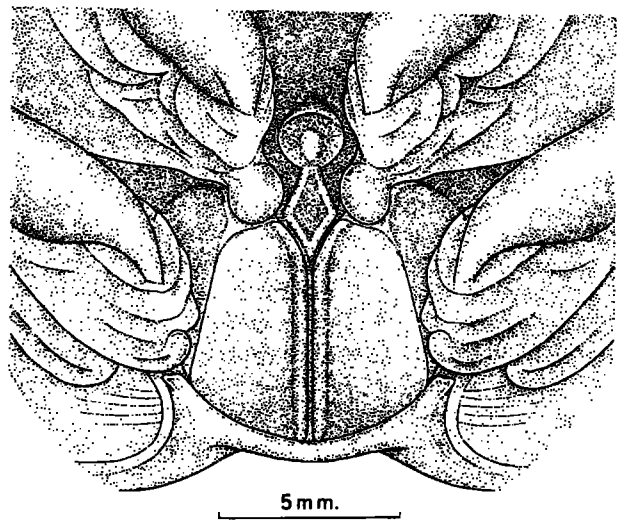

FIGURE 58.—*Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante. Thelycum, ♀ 45.5 mm. c.l., off Isere Point, French Guiana.

Distribution and Morphological Variations

P. a. subtilis ranges from Cuba through the Antilles and from Honduras throughout the Caribbean Coast of Central and South America and the Atlantic Coast of South America to at least Cabo Frio, Brazil. Burkenroad (1939) reported and illustrated specimens of this subspecies from "Rio de Janeiro" (fig. 49). The distribution of the dark shrimp is far from uniform, because population

densities differ greatly over its range. It is scarce on the northern coast of Cuba and rare on the southern coast, except in Oriente province, where I collected many specimens in the bays of Guantánamo and Santiago de Cuba. It is not common in the rest of the Greater Antilles, the Virgin Islands, and the Lesser Antilles. *P. a. subtilis* is moderately abundant in some areas along the coast of Central America.

Croker (1967) did not cite this subspecies as constituting part of the commercial catches in the northeast coast of South America, but collections from that region identified by Holthuis (1959), Bullis and Thompson (1959a, b), and me show that *P. a. subtilis* is not only present, but is apparently rather abundant in the area. Curiously enough, whereas Croker reported *P. d. notialis* as present in the commercial catches, Holthuis recorded but a single female of *P. d. notialis* from Surinam, and Bullis and Thompson did not find it along the northeast coast of South America. *P. a. subtilis* abounds along the southernmost part of its range.

P. a. subtilis has a rather wide bathymetric range; it has been caught in waters as deep as 105 fm., NE. of Punta de Gallinas, Departamento de la Guajira, Colombia (*Oregon* Sta. 5684, lat. 12°30′ N., long. 71°48′ W.), at 100 fm., west of Cabo de la Vela, Colombia (*Oregon* Sta. 4913, lat. 12°09′ N., long. 72°47′ W.), and at 95 fm. off Punta de Gallinas, Departamento de la Guajira, Colombia (*Oregon* Sta. 5685, lat. 12°29′ N., long. 71°54′ W.), the type locality.

The population of *P. a. subtilis* from the Gulf of Paria to the neighborhood of Camocim, Brazil, as discussed by Pérez Farfante (1967), is distinguishable from the populations at both ends of the range of the subspecies. In the Paria-Camocim population, the adrostral sulci are shorter (fig. 59) (ending 1/5 to 1/11 of the length of the carapace from its posterior margin), shallower and acuminate posteriorly, and the rostrum is longer and more sinuous. Many individuals, however, show feeble indications of the posterior portion of longer adrostral sulci as well as isolated pits where these sulci would seem to have terminated. In addition, at both ends of the range of this intermediate population, in the Gulf of Paria, and near Camocim, individuals with the above characters were found intermingled with individuals possessing the characters typical of the shrimp found to the north and south. Also, in Colombia and Venezuela, the ranges of variations of the length and width of the adrostral sulci and the length of the rostrum overlap those of specimens from the Gulf of Paria to northeastern Brazil; figure 59 shows the overlapping in length of adrostral sulci. Furthermore, the ratio K/S is not significantly different throughout the range: in the samples from the Caribbean region and eastern Brazil the ratio K/S is modally 3 and in those from the Gulf of Paria-Camocim, 3.5. In the Caribbean and eastern Brazil areas, K/S ranges from 2 to 5 and at Gulf of Paria-Camocim K/S ranges from 2 to 8, but in only a small percentage of the samples does the K/S reach values above 5. It appears as if the observed differences could be due to environmental conditions, because the intermediate population occupies the area receiving the discharge of the Orinoco and Amazon Rivers.

Relationships

P. a. subtilis differs from all the other grooved *Penaeus* in the western Atlantic by the narrower, shorter, and peculiarly shaped posterior portion of the adrostral sulci and (except from *P. paulensis*) by the shallower, usually interrupted, and shorter median sulcus. It may also be distinguished from typical *P. a. aztecus* by the K/S ratio, which is modally 3.5 (dorsolateral sulcus narrow), whereas in *P. a. aztecus* it is 1.25. Also, females of *P. a. subtilis* tend to have the anterior and posterior processes wider and often the anterior process flat instead of deeply concave. In both subspecies the third pereopod has about the same lengths for each carapace length to 40 mm. c.l.; in larger individuals of *P. a. aztecus* it is longer (compare figures 29 and 38, which show the lengths of the carpus—indicative of the lengths of the third pereopod—for various carapace lengths in *P. a. aztecus* and *P. a. subtilis*, respectively). The third pereopod of *P. a. subtilis* less than 40 mm. c.l. appears shorter than that of *P. a. aztecus* for, at most, it exceeds the antennular peduncle by only the length of the dactyl, whereas in *P. a. aztecus* it exceeds the peduncle by the entire length of the propodus. This apparent difference in length is due to the shorter antennular peduncle in *P. a. aztecus*.

P. a. subtilis may be distinguished from its close relative *P. paulensis* (which has a similar ill-defined median sulcus) by the broader dorsolateral sulcus with a rounded dorsal lip and by the sinuous rather than straight rostrum. Moreover, in *P. a. subtilis* males the ventral costa of the petasma has a different shape, and its attached border is

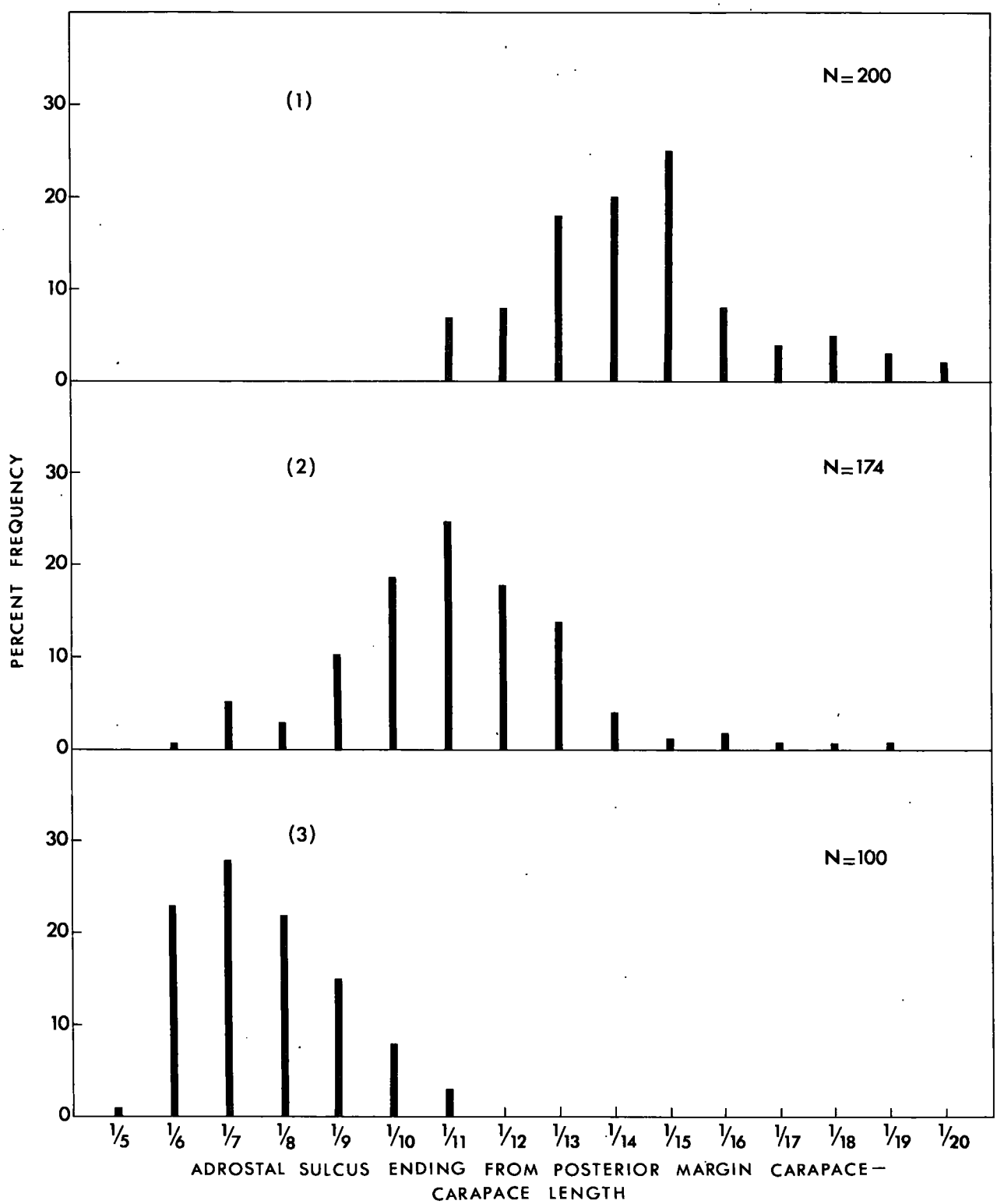

FIGURE 59.—Percent frequency of ratio of postsulcal carapace length to carapace length in 1. *Penaeus* (*M.*) *aztecus aztecus* Ives; 2. *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante, from the Caribbean region and eastern Brazil; 3. *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante, from the Gulf of Paria to Camocim, Brazil.

differently armed (with a narrow patch of closely set teeth). In females the anterior and posterior processes are much broader than those of *P. paulensis*.

Reproduction

SUBADULT STAGE-SEXUAL MATURITY

The smallest size at which males were found with the petasma joined was 16 mm. c.l., 72 mm. t.l. and the smallest size at which females were found with a functional thelycum was 18 mm. c.l., 83 mm. t.l. The size at which *P. a. subtilis* reaches sexual maturity is not known.

OVARY DEVELOPMENT

The studies by Magalhães Filho (1943) of the external genitalia and gametogenesis of "*P. brasiliensis*," as he identified his material, seem to me to have been taken on *P. aztecus subtilis*. His illustrations of the thelycum with widely gaping lateral plates leaving exposed a broad posterior process and of a petasma with apparently short distomedian projections indicate that the specimens were probably dark shrimp.

Postembryonic Development

LARVAE, POSTLARVAE, AND JUVENILES

No studies have been made on the larval and postlarval stages of this shrimp.

My studies of small individuals showed that the adrostral sulci are distinctly developed in *P. a. subtilis* juveniles 18 mm. t.l. Because the sulci are shorter than in other grooved *Penaeus* from the western Atlantic, the juveniles can be readily distinguished from those of the nongrooved shrimps. Small males may be distinguished from females by the larger size of the petasmal endopod and its more proximal position on the basis. Males also have a low rib on the midline of sternite XIV, whereas females have sternite XIV ventrally produced to a midpoint.

Females with a 10.5 mm. c.l., 47 mm. t.l., bear a small spine projecting caudad from the posterior margin of sternite XIII. This conspicuous character also makes it possible to distinguish them at that small size from the grooved sympatric *Penaeus*.

GROWTH

It has been reported (Anonymous, 1962) that in Guyana *P. a. subtilis* kept in ponds grew from 25 mm. t.l. to 200 to 225 mm. t.l. in 7 or 8 months.

SEX DIFFERENCES IN SIZE

The largest female examined, caught off Surinam in 50 fm., *Oregon* Sta. 2016, had 55 mm. c.l., 205 mm. t.l.; the largest male, caught off Isère Point, French Guiana, in 34 fm., *Oregon* Sta. 2322, measured 36 mm. c.l., 152 mm. t.l. Boschi (1963) cited under *P. aztecus* an unusually large male, 200 mm. long, but no locality was given; neither was reference given as to which "Form" it belonged. It is not possible to ascertain if the specimen was typical *P. a. aztecus*, *P. a. subtilis*, or *P. paulensis*.

Offshore dark shrimp show a sex-size disparity: females are larger than males; the difference in size between sexes increases with depth.

Ecology

FOOD

No studies have been made on the food of this shrimp. I found a tentacle of the squid *Doryteuthis plei* Blainville hanging from the mouth of a specimen from off Departamento de la Guajira, Colombia.

SUBSTRATE

Juvenile as well as adult *P. a. subtilis* prefer muddy substrates. Holthuis (1959) reported that in Surinam it was taken on bottoms of soft and hard mud, and mud with shells. Bullis and Thompson (1959a) stated that on the Continental Shelf of South America, from off Trinidad to the Amazon River, camarón marrón was found predominantly on muddy bottoms. It also lives on bottoms consisting of a mixture of mud and sand and on those which consist predominantly of coral sand, where I collected specimens in northern Cuba.

DIEL CYCLE

No information is available on the diel activity of camarón marrón inshore. Bullis and Thompson (1959a) noted that in the Atlantic Coast of northeastern South America sizes of the catches were approximately the same day and night, whereas Croker (1967) stated that off Nicaragua this subspecies is fished at night.

MOVEMENTS

Postlarvae of *P. a. subtilis* move into inshore waters where the young are known to live. Most of the specimens I examined from the Antilles came from bays. Ewald (1965c) reported that in Venezuela juveniles are found in abundance in lagoons and mouths of rivers and are taken commercially in Lake Maracaibo. Davant (1963) had previously reported specimens up to 100 mm. long from various estuarine waters of Venezuela. Farther along the

Atlantic Coast, juveniles and subadults are fished in brackish water in Surinam and Brazil.

Little is known of the seasonal abundance of the young. According to Lijding (1956, fide Holthuis 1959), inshore catches in Surinam are higher during July and August; Lindner (1957) reported that in northern Brazil they are caught the year round, but reach a peak of abundance from May to October.

EFFECTS OF TEMPERATURE

No information is available on the effects of temperature on *P. a. subtilis*. Its distribution, however, seems to indicate that it requires relatively high temperatures because it is restricted to the Caribbean Sea and the warmest waters of the western Atlantic.

EFFECTS OF SALINITY

The young, from late postlarvae to subadults, can live within a considerable range of salinities—from estuarine waters to small lagoons of high salinity, for example in Laguna Doctor, Playa de Baracoa, Cuba, and in pools in Surinam which have a salinity higher than sea water because of strong evaporation (Holthuis, 1959).

ENEMIES AND DISEASES

No investigations on camarón marrón predators and enemies have been undertaken. Like its congeners, it most probably constitutes an important component of the diet of various carnivorous animals, particularly fishes. Holthuis (1959) reported one specimen from the stomach of the kingfisher *Chloroceryle americana* (Gmelin).

Commercial Importance

P. a. subtilis is fished commercially in some areas throughout its range. It is taken in small numbers in many Antillean islands, usually along with the other abundant *Penaeus*. The fact that often no common name identifies this subspecies, whereas the other *Penaeus* are known by a variety of descriptive names, indicates that it is not frequent in the catches here. Camarón marrón contributes to the commercial catches in Honduras (Loesch, 1962; Croker, 1967), Nicaragua (Croker, 1967; Instituto de Fomento Nacional, 1967), Colombia and Venezuela. Ewald (1965c) reported that young are caught in the northern portion of Lake Maracaibo and adults in the Gulf of Venezuela; Lindner (1957) mentioned a fishery for adults at Puerto Cabello. Sampling by the *Oregon* along the coast of both Venezuela and Colombia has suggested that large adults of this subspecies are found throughout the region at depths beyond the present range of fishing. Lindner (1957) and Lijding (1956, fide Holthuis, 1959), reported that the young are fished in the estuarine waters of Surinam, and, in recent years, adults have been caught off the Guianas.

Camarón marrón is also commercially exploited in Brazil. In inland waters and off beaches along the northern coast, from the eastern shore of Baía de Marajó through São Luis to Parnaiba, fishing is very active; the young are also caught in Salvador. Finally, for many years, a fishery for adults has existed along the eastern coast, from Rio Doce to Cabo Frio.

Penaeus (Melicertus) paulensis
PÉREZ FARFANTE

Figures 60 to 67

Brazil: camarão rosa. Uruguay: langostino.

Penaeus setiferus: Heller, 1865: 121 [part]. Not *P. setiferus* (L.), 1767.

Penaeus braziliensis: Kingsley, 1882: 106 [part?]; Moreira, 1901: 6, 7, 72 [part]; Moreira, 1905: 130 [part?].

Penaeus brasiliensis: Ortmann, 1890: 446, 447, 449 [part], pl. 36, fig. 1 a–c; Sharp, 1893: 109 [part]; Pesta, 1915: 113 [part]; Lindner, 1957: 15; Devold, 1958: 20 [part]; ?Lindner, 1958: 32; Barattini and Ureta, 1960: 49. Not *P. brasiliensis* Lat., 1817.

Penaeus aztecus: Burkenroad, 1939 [part, "Form C"]: 20, 27, 35, 36, 38, 39, 41, figs. 32–34; Lindner, 1957: 11, 12, 14; Lindner, 1958: 33; Eldred and Hutton, 1960: 91, 106, 108; Miles, 1962: 193 [part]; Boschi, 1963: 26–29, fig. 11 [part]; Boschi, 1964: 40, 41 [part]; Mistakidis and Neiva, 1964: 472; Neiva and Wise, 1964: 132, (133 [part]); Tremel et al., 1964: 6, 7, 12, 14, 15, 19, 24, 30, 32, 34, 36, 38, 40, 42 [part]); Holthuis and Rosa, 1965: 4 [part]; Mistakidis, 1965: 9, 11–13, 38 (4, 8, 35 [part]); da Silva, 1965: 3, 4 (7 [part]); Tremel and Mistakidis, 1965: 2, summary (4, table 3 [part]); Williams, 1965: 25, 26; Mistakidis and Neiva, 1966: 434; Neiva and Mistakidis, 1966: 2, 5, 6, fig. 10 a–d; [fide] Pérez Farfante, 1967: 84, 87. Boschi, 1968: 222–223. Not *P. aztecus* Ives, 1891.

Penaeus paulensis Pérez Farfante, 1967: 84, 86, 87, 93, fig. 1 a–d (holotype, ♂, USNM 119128, Santos, São Paulo, Brazil, April 1964, M. Vannucci); Boschi, 1968: 223.

Camarão rosa: Richardson and Moraes, 1960: 8, 10–12, 16–18, 32–34, 42, 48, 53, 70, 71, 80, 81 [part]; Braga, 1962: 48, 49, 51, tables 1, 2 [part].

Taxonomic Remarks

The specimens at the Academy of Natural Sciences of Philadelphia (No. 69) collected at Rio de Janeiro by W. S. Ruschenberger and recorded by Sharp (1893) as *P. brasiliensis* are actually two female *P. paulensis*.

Study Material

For list of records see Pérez Farfante, 1967.

Diagnosis

Adrostral sulcus broad posteriorly and long, almost reaching posterior margin of carapace. Median sulcus short, ending well anterior to posterior end of adrostral sulcus, shallow, continuous or interrupted, often limited to anterior concavity. Dorsolateral sulcus very narrow. Petasma with ventral costa extending proximally in slight curve, or almost straight line, broad and blunt at distal end, with free distal border even or with faintly undulating flange and bearing group of medium-size, irregularly set teeth close to apex; distal fold relatively small, usually armed with spinules. Thelycum with anterior process small, posterior process very narrow and bearing anteriorly bifurcate median carina; lateral plates with anteromedian angle markedly divergent, leaving median carina exposed.

Description

ROSTRUM (fig. 60)

Teeth $\frac{6-8}{1-2}$, mode $\frac{7}{2}$ (percentage distribution: 7/2—50, 8/2—47, 7/1—1, 8/1—1, 6/2—1; N=100) + epigastric; position of ventral teeth variable, first tooth situated well anterior to slightly posterior to last dorsal tooth; rostrum relatively short, longer in larger juveniles and subadults, reaching at most to distal end of antennular peduncle: maximum length in relation to carapace length apparently obtained at about 20 to 25 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.75); decreasing progressively with increasing length of shrimp, rostrum reaching distal half of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.50); rostrum straight apically, often along entire length, occasionally with tip upturned; highest portion of blade at level of third dorsal tooth; latter level with anterior margin of carapace; rostrum tip about ¼ r.l. Postrostral carina strong, prominent and long, extending almost to posterior margin of carapace. Median sulcus shallow, continuous or interrupted, often limited to anterior concavity and minute posterior pit, and short, end-

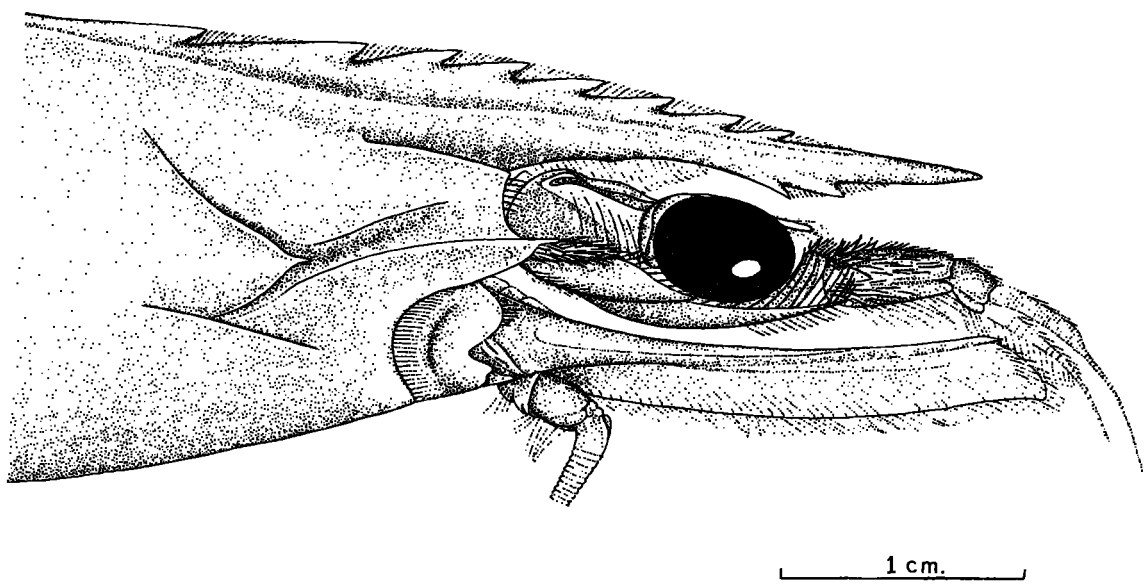

FIGURE 60.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. Rostrum, ♀ 37.5 mm. c.l., off southernmost end Rio Grande do Sul, Brazil.

ing well anterior to posterior margin of carapace. Adrostral sulcus broad posteriorly from same to twice width of postrostral carina, and long, ending 1/12 to 1/20 c.l. from posterior margin of carapace. Adrostral carina prominent and long, same length as adrostral sulcus.

CARAPACE (fig. 61)

Gastrofrontal sulcus broad, rather deep, extending to about one-fifth c.l.; gastrofrontal carina pronounced. Orbito-antennal sulcus slightly less than one-third c.l., wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening again into base of spine. Gastro-orbital carina pronounced, sharp and long, occupying 4/5 to 6/7 distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus 1/5 to 1/4 c.l., ending slightly anterior to midlength of carapace. Hepatic carina sharp, sloping anteroventrally to end 1/16 to 1/20 c.l. from anterior margin of carapace. Antennal spine prominent and acute; hepatic spine very pronounced.

ANTENNULES

Lateral flagellum relatively long, two-thirds length of antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum; anterolateral spine sharp; stylocerite very acute, reaching midlength of first antennular segment. Prosartema reaching proximal one-sixth of second antennular segment.

ANTENNAE

Scaphocerite length 2 1/2 times width at base; spine reaching distal end of antennular peduncle. Carpocerite length 1 1/3 width, its distal end reaching base of eye. Antennal flagellum short, 1 2/5 body length.

THORACIC APPENDAGES

Third maxilliped reaching approximately distal end of first antennular segment; length of dactyl 3/5 to 2/3 that of propodus. First pereopod reaching at least to distal end of carpocerite, but not exceeding it by more than three-quarters length of dactyl. Second pereopod surpassing carpocerite by entire length of dactyl or four-fifths that of propodus. Third pereopod reaching at least to distal third of second but not beyond distal end of third antennular segment. Fourth pereopod reaching distal end of carpocerite or surpassing it by one-half length of dactyl. Fifth pereopod extending anteriorly one-quarter dactyl length beyond

FIGURE 61.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. Cephalothorax, holotype, ♂ 35 mm. c.l., Santos, São Paulo, Brazil.

fourth pereopod. Exopods on all pereopods. Long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

ABDOMEN

Carinate dorsally from posterior half of fourth somite posteriorly, carina gradually increasing in height to form keel on sixth somite, ending in sharp spine on posterior margin. Dorsolateral sulcus (fig. 62) extremely narrow, ratio between height of keel and width of sulcus from about 3 to 16, modally 6 (fig. 63); K/S ratio showing same modal value of 6 for all sizes of both sexes (fig. 64); dorsal and ventral lips both sharp. Sixth abdominal somite with three cicatrices on each side, anterior the longest, posterior very small. Fifth abdominal somite with one cicatrix and row of minute pits anterior to sinus on posterior margin of somite. Fourth abdominal somite with similar row of minute pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

PETASMA (fig. 65 a, b)

Ventral costa slightly curved with distal portion blunt, bearing group of 6 to 12 (modal 6) irregularly set teeth close to apex, its free distal margin even or with faintly undulating flange, apex adnate to ventrolateral lobule. Ventrolateral lobule with band of spines consisting of single row or pair of rows distally, with three to six series of spines extending proximally to about midlength of lobule. Dorsolateral lobule often with single row of widely spaced minute spines along midline. Distomedian projections relatively short, slightly overhanging distal portion of ventral costae.

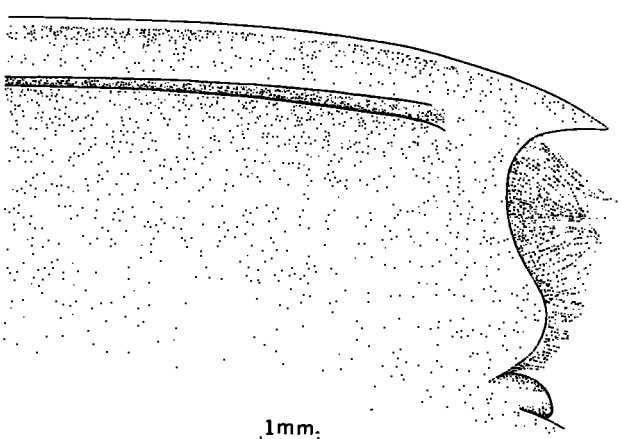

FIGURE 62.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. Sixth abdominal somite, posterodorsal portion, holotype, ♂ 35 mm. c.l., Santos, São Paulo, Brazil.

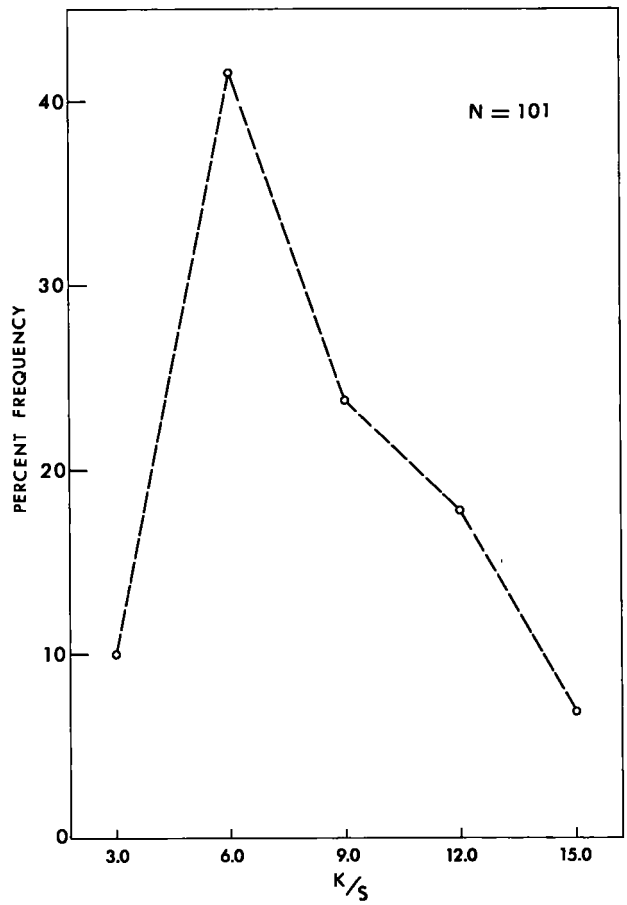

FIGURE 63.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *paulensis* Pérez Farfante.

APPENDIX MASCULINA (fig. 65c)

Slightly elongated, length 1¼ to 1⅓ maximum width, with long spines projecting from distomedian margin and with slightly concave lateral margin armed with short, strong spines. Anterior surface subplane or slightly convex, posterior surface strongly concave, with sharp longitudinal ridge along median margin.

THELYCUM (fig. 66)

Anterior process narrow, projecting ventrally in subtriangular or highly arched ridge, surrounding shallow depression with minute knob usually present at center. Posterior process with median carina bifurcate anteriorly, resulting ribs turning medially and converging at base of anterior process, giving rise to very narrow diamondlike structure. Lateral plates with anteromedian corners divergent, leaving posterior process exposed.

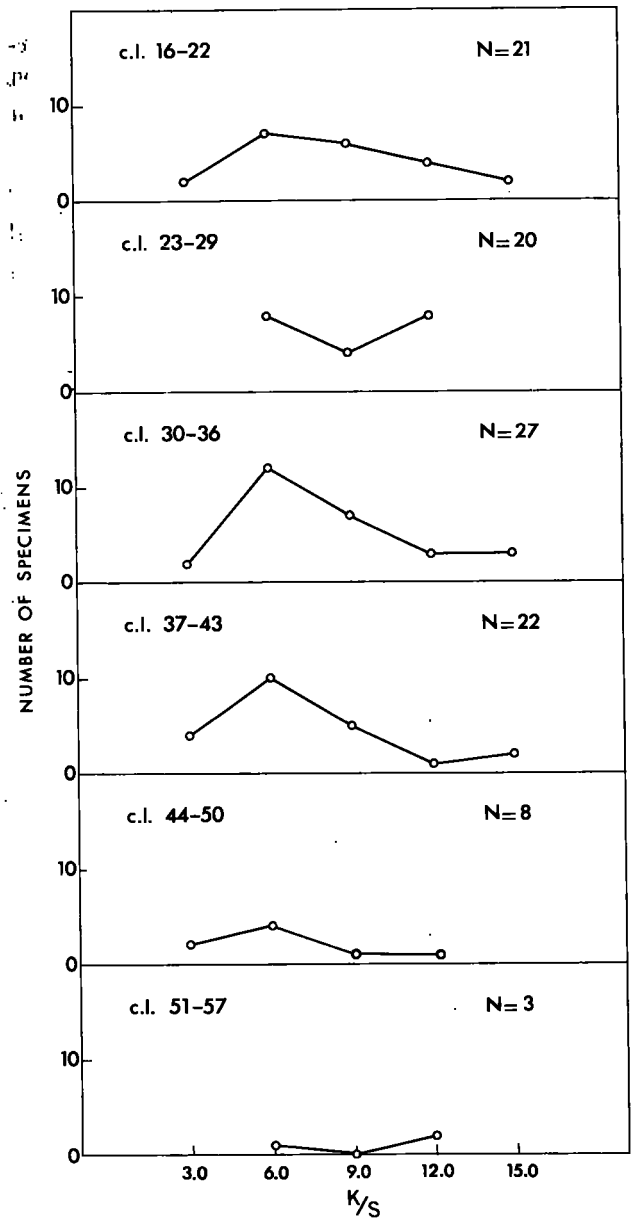

FIGURE 64.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *paulensis* Pérez Farfante of different size classes.

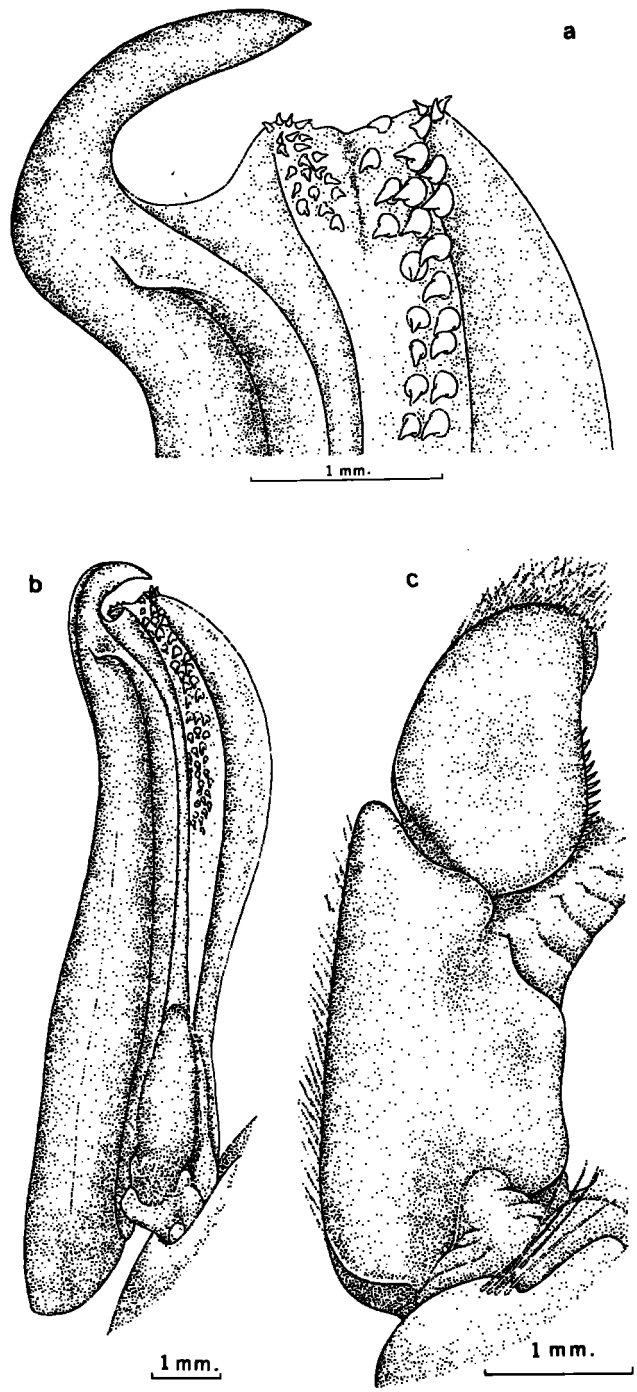

FIGURE 65.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. a. Petasma, distal portion, ♂ 39 mm. c.l., Ponta do Boi, São Paulo, Brazil. b. Petasma, ♂ 39 mm. c.l., Ponta do Boi, São Paulo, Brazil. c. Appendix masculina, ♂ 39 mm. c.l., Santos, São Paulo, Brazil.

COLOR

Like other *Penaeus*, *P. paulensis* is variable in color, but most often is pinkish; thus, the name camarão rosa (pink shrimp) applied to it in Brazil.

Distribution and Morphological Variations

The range of *P. paulensis* extends from south of Cabo Frio along the coast of southern Brazil and Uruguay as far as northeast Argentina (fig. 67). Boschi (1968) has found *P. paulensis* along the eastern coast of Buenos Aires Province (lat. 38°30′ S; long. 57°20′ W.) and has, thus, confirmed the belief (Pérez Farfante, 1967) that the species ex-

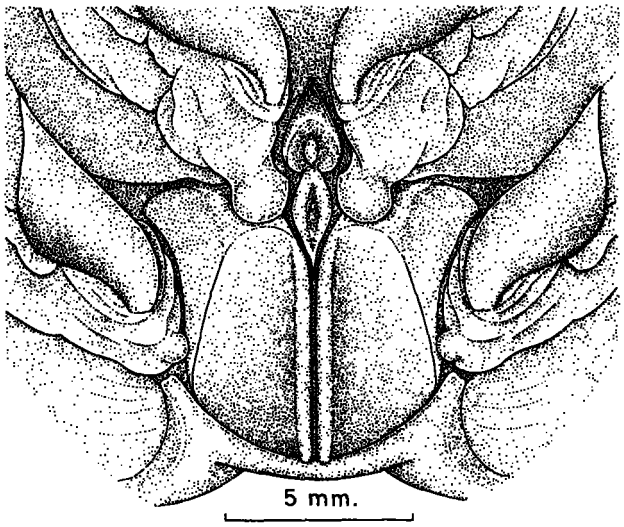

FIGURE 66.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. Thelycum, ♀ 49.5 mm. c.l., Santos, São Paulo, Brazil.

tends farther south than the previously generally accepted southernmost limit of its range, Montevideo. It is abundant along the northern portion of its range and the coastal waters of Santa Catarina. Farther south, the young are very numerous in Lagoa dos Patos and the coastal lakes of Uruguay, but adults are rare along the southernmost portion of the range. Mistakidis (1965) reported having caught but one adult during exploratory fishing between Rio Grande and Cabo Polonio. Possibly the breeding populations extend only to the neighborhood of Rio Grande. The young seem to be able to invade waters that the larger adults cannot tolerate.

These shrimp live as deep as 65 fm.; large concentrations are found between 20 and 30 fm.

My studies indicate little variation in the diagnostic characters of *P. paulensis*. The only rather striking variation is that shown by the median sulcus, which is usually interrupted but occasionally continuous. Both types of sulcus were observed in specimens from the same locality.

Relationships

P. paulensis is closely related to *P. a. aztecus* and *P. a. subtilis*. It differs from both by having the rostrum usually almost straight and shorter; by having a K/S ratio with a modal value of 6, which indicates a very narrow dorsolateral sulcus; and by having both lips of the sulcus sharp. The external genitalia are also distinct. In males, the ventral costa of the petasma is almost straight or only slightly curved instead of markedly convex distally and is armed with a group of medium-size, irregularly set teeth almost at the apex. In females, the anterior process is smaller and the posterior process narrower than in *P. a. aztecus* and *P. a. subtilis*. *P. paulensis* also differs from *P. a. aztecus* by the shorter, shallower, and often interrupted median sulcus and the shorter third pereopod and from *P. a. subtilis* by the broader adrostral sulci.

P. paulensis tends toward a smaller number of rostral teeth than any other species of *Penaeus* from the western Atlantic; the mode of the rostral teeth formula is $\frac{7}{2}$ instead of $\frac{8}{2}$. Also, specimens with a formula greater than $\frac{8}{2}$ must be uncommon because no specimen in the samples examined had more than 8 dorsal and 2 ventral teeth.

Reproduction

SUBADULT STAGE-SEXUAL MATURITY

The series of small specimens available was too small to permit a determination of the size range at which males and females become subadults.

No studies have been made on the size at which females attain sexual maturity.

OVARY DEVELOPMENT

No studies have been made.

SPAWNING

No studies are known on the spawning characteristics of *P. paulensis*. The information available on stages inshore, however, gives some indication of the spawning season through the range of this shrimp.

According to Tremel (1965), fishing for the young in Conceição and Imaruí Lagoons, Santa Catarina, Brazil, is carried out from August to April (peak from December to February). This timing appears to indicate that some spawning occurs from mid-fall through early winter, but that mass spawning probably takes place through late winter and early spring. Mistakidis (1965) reported that in Lagoa dos Patos, southeast Brazil, small shrimp are found from September to November, that postlarvae have been taken in the lakes of Uruguay in October and November, and that fishing for young in both areas is carried out from March to May, with a peak in March. The young, thus, arrive on these nursery grounds later than those that arrive in the lagoons of Santa Catarina. Because large adults are apparently rare off southern Brazil and Uruguay, the difference in time of arrival may be due to the longer dis-

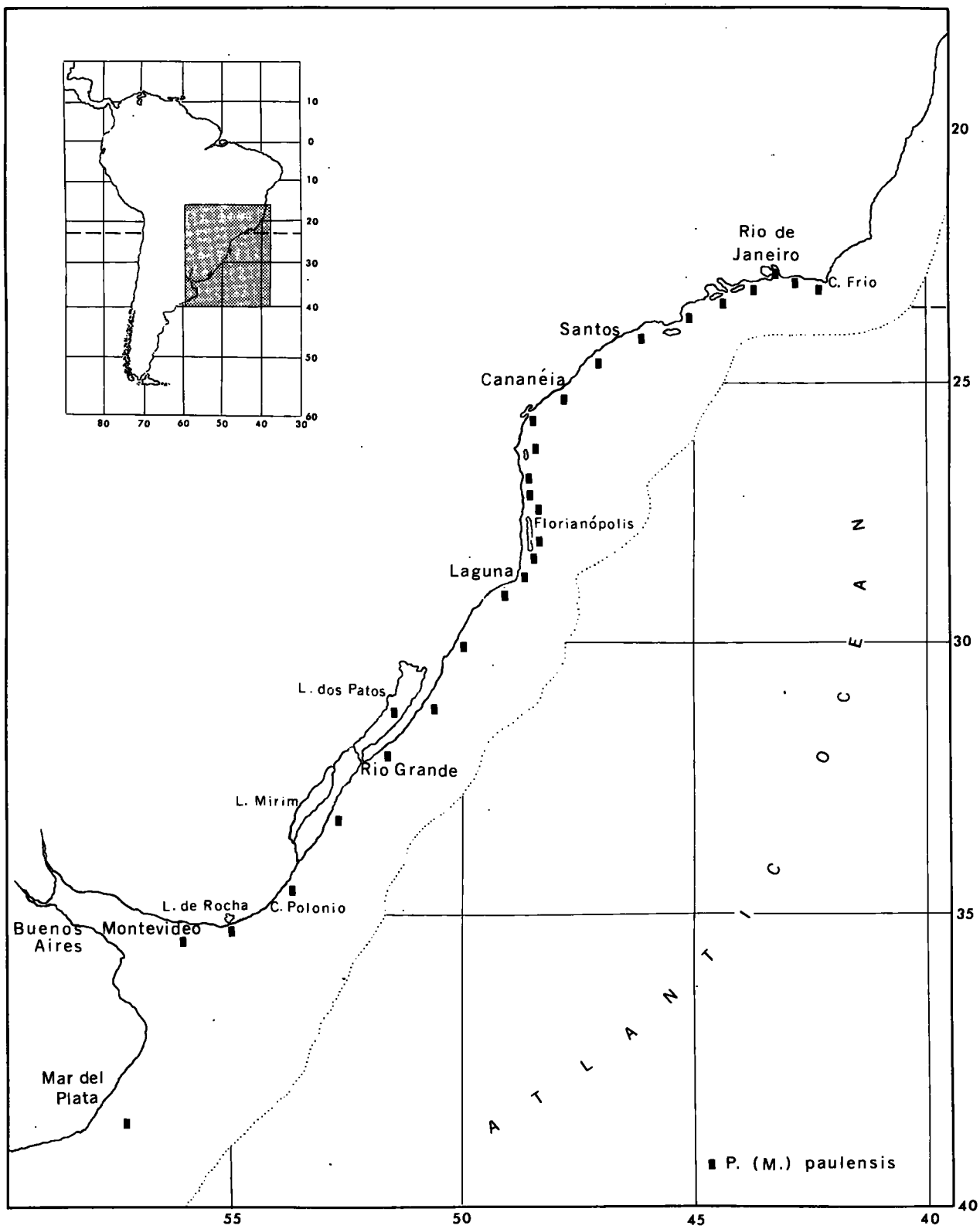

FIGURE 67.—Distribution of *Penaeus* (*M.*) *paulensis* Pérez Farfante.

tance larvae must travel from the spawning grounds to the southern areas.

Postembryonic Development

LARVAE, POSTLARVAE, AND JUVENILES

No studies have been conducted on either larval or postlarval stages of *P. paulensis*. The number of juvenile specimens available to me was too small to permit conclusions.

GROWTH

No studies have been made.

SEX DIFFERENCES IN SIZE

The largest female I examined was 54 mm. c.l., 215 mm. t.l., from off Rio de Janeiro; the largest male was 40 mm. c.l., 171 mm. t.l., from off Ponta do Boi, São Paulo, Brazil. Offshore the females are larger than males, and the size of both sexes increases with depth.

Ecology

SUBSTRATE

Little is known of the habits of this shrimp. Juveniles and subadults occupy soft muddy bottoms, but the largest concentrations of adults are on bottoms of firm mud.

DIEL CYCLE

P. paulensis is mostly nocturnal; fishing for young on the nursery grounds and for adults offshore is carried on at night.

EFFECTS OF TEMPERATURE

P. paulensis has a wide range of temperature tolerance since it occupies the waters of southeastern Brazil, where temperature is highly variable, and penetrates into the coast of northeast Argentina, where the water is relatively cold.

EFFECTS OF SALINITY

There is little information on the effect of salinity on *P. paulensis*.

According to Closs (*In* Mistakidis, 1965), salinities in the southern portion of Lagoa dos Patos, the single largest nursery area for the species, vary from 1 p.p.t. to 29 p.p.t., and Mistakidis (1965) reported that in the coastal lakes of Uruguay salinities range from 2 p.p.t. to 26 p.p.t. This shrimp, thus, seems to be able to withstand a rather wide range of salinity during the inshore phase of its life cycle. Production from the nursery areas, however, shows large fluctuations from year to year, and it has been suggested by Lindner (1957) and Mistakidis (1965) that in Lagoa dos Patos, at least, declines in production are probably caused by excessive rainfall. Lindner states that "excessive quantities of fresh water in Lagoa dos Patos might restrict the area of shrimp nursery grounds." The reduced production could be due also to swift currents following heavy rainfalls which might prevent the shrimp from gaining access to inshore water.

Commercial Importance

This species is not locally distinguished from *P. brasiliensis*. Both are known and classified in statistical studies as camarão rosa. Consequently, it is not possible to ascertain the quantities of *P. paulensis* that are caught.

The young of *P. paulensis* are commercially taken in Baía de Guanabara, Brazil, and from numerous lagoons and coastal lakes as far south as Laguna de Rocha, Uruguay. Offshore fishing is more restricted and is carried out only in the northern portion of the range, from off Baía de Guanabara to the neighborhood of Rio Grande.

It seems that the majority of the camarão rosa landed at Santos, São Paulo, is *P. paulensis* (Mistakidis, 1965). The Instituto de Pesca Marítima of São Paulo, Brazil, calculated that landings of camarão rosa in Santos—the most important port for landings from the ocean fishery—were 891,000 kg. in 1964, 1,868,000 kg. in 1965, and 2,157,300 kg. in 1966.

Landings of camarão rosa in the State of Rio Grande do Sul—almost entirely *P. paulensis* (Mistakidis, 1965)—present large annual fluctuations as shown by the landings from 1963 to 1966. The Centro de Pesquisas Oceanograficas do Rio Grande reported that the production reached 4,913,700 kg. in 1963, decreased to 1,568,600 kg. in 1964, rose to an all-time high of 5,844,400 kg. in 1965, and amounted to only 648,300 kg. in 1966.

Penaeus (Melicertus) brasiliensis LATREILLE

Figures 68 to 77

United States: pink spotted shrimp, spotted pink shrimp, brown shrimp, Caribbean brown shrimp. Nicaragua: camarón rojo. Venezuela: langostino rosado con manchas, camarón rosado con manchas, langostino amarillo. Brazil: camarão rosa, camarão lixo.

Penaeus brasiliensis Latreille, 1817: 156 (neotype, designated by Burkenroad, 1939, ♀, British Museum (Natural History), Brazil); H. Milne Edwards, 1837: 415; Stimpson, 1871: 132 [part]; Miers, 1878: 299, 306 [part]; Bate, 1881: 175; Smith, 1885: 170; Doflein, 1899:

185; ?Doflein, 1900: 127; Young, 1900: 452; Moreira, 1901: 6, 7, 72; Rathbun, 1901: 100, 101 [part]; Moreira, 1905: 130; de Man, 1911: 95 [part]; Pesta, 1915: 113 [part]; Bouvier, 1918: 6; Burkenroad, 1934: 61, 75, 77, 78 [part]; Schmitt, 1935: 128, 129 [part?]; Schmitt, 1936: 364; Johnson and Lindner, 1934: 68; Wheeler, 1937: 325, 326, 329–332, 343, 344; Burkenroad, 1939: 26–31, 34, 39, 42–45, 50, figs. 16, 17, 22, 34; von Ihering, 1940: 194, 871; de Oliveira, 1940: 141; Magalhães Filho, 1944: 100, 101, fig. 4A; de Oliveira, 1944: 133; Anderson and Lindner, 1945: 305; Holthuis, 1948: 1104, 1105; Anderson et al., 1949: 16; Gunter, 1950: 22; Holthuis, 1950: 27; de Oliveira, 1950: 371, 386; Sánchez Roig and Gómez de la Maza, 1951: 113–119; Gómez de la Maza, 1952: 167, 169; Sánchez Roig and Gómez de la Maza, 1952: 153, fig. 6; Pérez Farfante, 1953: 232, 233, 238; Pérez Farfante, 1954b: 30, 31; Voss, 1955: 5, 8, 10, figs. 12–13; Anderson, 1956: 4, 12, 13 [part?]; Dall, 1957: 142, 226, 227; Lindner, 1957: 11–15, 34–36, 159, 160, 165; ? Rossignol, 1957: 111; Woodburn et al., 1957: 24; Devold, 1958: 20; Lindner, 1958: 31, 33; Suárez Caabro, 1958: 7; Bullis and Thompson, 1959a: 33–35, 41; Bullis and Thompson, 1959b: 1, 4–6, 9; Higman, 1959: 8, 10, 14; Holthuis, 1959: 43, 66, 67, fig. 6c; Young, 1959: 15; Eldred, 1960: 164, 165; Eldred and Hutton, 1960: 91, 98, 99, 101, 106, fig. 7b; Anonymous, 1961: 34; Costello and Allen, 1961: 21; Eldred et al., 1961: 87, 89, 101, 107, 109; Pérez Farfante et al., 1961: 40, 52, 58, 59, 61, 65; Gunter, 1962a: 108; Hutton et al., 1962: 327; Kutkuhn, 1962: 343; Tabb, Dubrow, and Jones, 1962: 11, 28; Boschi, 1963: 5, 6, 13, 20, 23, 25, 26, 29, 35, 37, figs. 7 (1–5), 11; Davant, 1963: 9–15, 29–31, 33, 35, 65–71, 85–89, 91, figs. 6a, 7a, b, 8a, b, 9a, b, 10 and bis; Simpson, 1963: 22, 23; Costello and Allen, 1964: 31; Ewald, 1964: 20–23, (24, 28, tables, [part]); Hutton, 1964: 440, 445; Iversen and van Meter, 1964: 549–552; Jones et al., 1964: 1; Mistakidis and Neiva, 1964: 472; Neiva and Wise, 1964: 132, 133 [part]; Tremel et al., 1964: 7, 24, (6, 12, 14, 15, 19, 30, 32, 34, 36, 38, 40, 42, fig. 2 [part]); Broad, 1965: 89; Bullis and Thompson, 1965: 6; Cervigón, 1965: 21; Ewald, 1965a: 29; Ewald, 1965c: 52, 59, 63, 67, 70, 72, 74, 80, 82, 84–86, 91, 93–96, 114 (80, 88–90, 92, 97–99, 113 [part]); Holthuis and Rosa, 1965: 4; Joyce, 1965: 115, 116, 132, 134, 170, 220, 221; Mistakidis, 1965: 9, 11, 13, 38 (4, 8, 35 [part]); Pericchi López, 1965: 24; da Silva, 1965: 3, 4, (7 [part]); Simpson et al., 1965: 77; Tremel and Mistakidis, 1965: 2, summary (4, table 3 [part]); Williams, 1965: 26; Alves Coelho, 1966: 163, 168, 171; Costello and Allen, 1966: 450, 452; Joyce and Eldred, 1966: 11, 25, 33; Neiva and Mistakidis, 1966: 1, 2, 5, 6, fig. 9a–d; Croker, 1967: 63, 72, 73, 78, 80, 81, 87, 95, 98; Instituto de Fomento Nacional, 1967: 5, 8; Pérez Farfante, 1967: 84, 94.

Penecus brasiliensis: H. Milne Edwards, 1837: 414.

Penaeus setiferus: Heller, 1865: 121 [part]. (According to Pesta, 1915.) Not *P. setiferus* (L.), 1767.

Peneus brasiliensis: Smith, 1869a: 27; Smith, 1869b: 390; von Martens, 1872: 140, 141 [part?]; von Ihering, 1897: 156; ? Torralbas, 1917: fig. 69; Rathbun, 1919: 319; Schmitt, 1924: 61; Boone, 1930: 15, 101–105 [part?].

Penaeus braziliensis: Kingsley, 1882: 106 [part]; Verrill, 1900: 580; Moreira, 1901: 6, 7, 72 [part]; Moreira, 1905: 130 [part]; Verrill, 1922: 41–43 [part], pl. 13, fig. 3, pl. 14, fig. 2, 2a (?); Idyll, 1950: 10; Ingle et al., 1959: 6; Anonymous, 1962: 56; Lyles, 1967: 371.

Penaeus sp. (*brasiliensis*): Scholander, Flagg, Walters, and Irving, 1953: 72, 75, 79, 80.

Camarão rosa: Richardson and Moraes, 1960: 8, 10–12, 16–18, 32–34, 42, 48, 52, 53, 70, 71, 80, 81 [part]; Braga, 1962: 48, 49, 51, tables 1, 2 [part].

Taxonomic Remarks

The specimens cited by Pérez Farfante (1967) from Antigua, Lesser Antilles, as *P. a. subtilis* were actually two juvenile *P. brasiliensis* (see under Study Material).

Study Material

UNITED STATES

North Carolina: 1 ♂, YPM, off Cape Hatteras, October 19, 1884, *Albatross* Sta. 2285. 1 ♀, USNM, between Cape Hatteras and Cape Lookout, 32 fm., October 18, 1885, *Albatross* Sta. 2605.

Florida: 1 ♀, USNM, off St. Augustine, 12 fm., January 12, 1965, *Oregon* Sta. 5158. 1 ♂, USNM, N. of Oak Hill, July 4, 1963, E. A. Joyce. 1 ♀, USNM, S. of Cape Kennedy, 22 fm., March 23, 1956, *Pelican* Sta. 14. 1 ♀, USNM., off Melbourne, 38 fm., January 16, 1966, *Oregon* Sta. 5860. 4 ♂ 4 ♀, USNM, off Sebastian, 20 fm., November 11, 1961, *Silver Bay* Sta. 3529. 1 ♂

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1 ♀, USNM, off Sebastian, 31 to 28 fm., January 15, 1965, *Oregon* Sta. 5203. 2 ♂, USNM, Biscayne Bay, 1⅝ fm., February 6, 1962, J. Y. Christmas. 1 ♂ 1 ♀, USNM, Matheson Hammock, Biscayne Bay, July 10, 1960, R. Still. 1 ♀, USNM, S. of Key Largo, 36 to 25 fm., October 25, 1960, *Silver Bay* Sta. 2364. 4 ♂ 7 ♀, USNM, off Key Largo, 40 fm., November 10, 1961, *Silver Bay* Sta. 3523. 1 ♂, USNM, off Key Largo, 50 fm., November 10, 1961, *Silver Bay* Sta. 3524.

BERMUDA ISLANDS

1 ♂, YPM, Hayward's Bay, David's Island, September 6, 1905. 1 ♀, USNM, off Harrington Sound, February 12, 1888, C. M. Allen. 1 ♂ 1 ♀, YPM, Port Royal Bay, September 21, 1905. 1 ♀, YPM, St. Georges, January 27–29, 1935. 1 ♀, YPM, Bermuda, April 1898. J. M. Jones. 1 ♀, AMNH, Bermuda, W. Beebe. 1 ♀, YPM, Bermuda, 1936. 1 ♀, AMNH, Bermuda, August 31, 1935, W. Beebe. 1 ♀, USNM, Harrington Sound, February 17, 1881, C. M. Allen. 1 ♀, YPM, Mullet Bay, St. Georges Island, January 27–29, 1935.

BAHAMAS

18 ♂ 7 ♀, USNM, 79 km. W. of Andros Island, 150 fm., November 11, 1960, *Silver Bay* Sta. 2471. 1 ♂ 1 ♀, USNM, Little Bahama Bank, November 1953, *Antilles*.

CUBA

1 ♂, USNM, Dimas, Pinar del Río, May 17, 1915, *Tomas Barrera* Sta. 5. 1 ♂, USNM, off Puerto Esperanza, Pinar del Río, 1924, M. Sánchez Roig. 1 ♂, USNM, Laguna Doctor, Playa de Baracoa, La Habana, J. Mayor. 1 ♀, USNM, Laguna Doctor, Playa de Baracoa, La Habana, G. Mayor. 1 ♂, YPM, La Habana, February 1, 1932. 6 ♂ 8 ♀, CIP, S. of Cayo Cruz del Padre, Matanzas, March 1954, L. Howell Rivero. 15 ♂ 15 ♀, CIP, Bahía de Cárdenas, Matanzas, August 1955, G. Canet and I. Pérez Farfante. 15 ♂ 16 ♀, CIP, Bahía de Santa Clara, Las Villas, August 1955, G. Canet and I. Pérez Farfante. 8 ♂ 9 ♀, CIP, Bahía de Santa Clara, Las Villas, March 1954, L. Howell Rivero.

JAMAICA

1 ♂ 1 ♀, USNM, Salt Pond, Montego Bay, August 1, 1910, E. A. Andrews. 1 ♂ 1 ♀, USNM, off Portland Point, May 14, 1962, 14 fm., *Oregon* Sta. 3538.

PUERTO RICO

1 ♂, USNM, Bahía de Boquerón, January 26–27, 1899, *Fish Hawk*. 1 ♂ 1 ♀, USNM, off Bahía de Boquerón, January 27, 1899, *Fish Hawk*. 6 ♂ 3 ♀, USNM, Bahía de Boquerón, January 26–27, 1899, *Fish Hawk*. 1 ♀, USNM, off La Parguera, winter 1957–58, D. E. Erdman. 2 ♂ 4 ♀, USNM, off Hucares, February 13–14, 1899, *Fish Hawk*.

VIRGIN ISLANDS

St. Thomas: 3 ♂ 1 ♀, USNM, Submarine Dock, October 2–3, 1959, H. R. Bullis. 4 ♂ 5 ♀, USNM, N. of St. Thomas, 42 fm., April 19, 1960, *Oregon* Sta. 2607. 1 ♂ 3 ♀, USNM, S. of St. Thomas, 26 fm., September 27, 1959, *Oregon* Sta. 2618. 2 ♂ 8 ♀, USNM, off St. Thomas, 40 fm., September 29, 1959, *Oregon* Sta. 2625.

St. Croix: 16 ♂ 6 ♀, USNM, Kranse Lagoon, H. A. Beatty.

LESSER ANTILLES

Antigua: 1 ♂, USNM, English Harbor, April 4–9, 1956, Smithsonian-Bredin Exped., Sta. 83–56, F.A. Chace and D. V. Nicholson. 1 ♂, USNM Tank Bay, English Harbor, April 3, 1956, Smithsonian-Bredin Exped., Sta. 74–56, W. L. Schmitt, F. A. Chace, D. V. Nicholson, and Jackson.

Aruba–Curaçao: 1 ♂ 3 ♀, USNM, off Aruba, 40 fm., October 3, 1965, *Oregon* Sta. 5656. 4 ♂ 5 ♀, USNM, off Aruba, 38 fm., October 3, 1965, *Oregon* Sta. 5654. 1 ♂ 1 ♀, USNM, Riftwater, Curaçao, ½ fm., July 26, 1905.

MEXICO

Quintana Roo: 1 ♂ 1 ♀, INIBP, "90° NNE." of Isla Contoy, July 17, 1967, H. Chapa Saldaña, D. Fuentes, and J. M. de la Garza. 1 ♂ 1 ♀, INIBP, "90°NNW." of Isla Mujeres, 21 fm., July 17, 1967, H. Chapa Saldaña, D. Fuentes, and J. M. de la Garza. 1 ♀, USNM, Isla de Cozumel, June 29, 1885, *Albatross*. 1 ♀, USNM, halfway point between Punta Nicchehabin and Vigía Chico, N. end of Bahía de la Ascensión, Smithsonian-Bredin Exped., Sta. 93–60. 18 ♂ 13 ♀, USNM, Punta Nicchehabin, Bahía de la Ascensión, less than ⅓ fm., April 13, 1960, F. C. Daiber, Smithsonian-Bredin Exped., Sta. 65–60.

NICARAGUA

1 ♂ 2 ♀, USNM, N. of Bluefields, 1965, A. Flores.

PANAMA

3 ♂ 8 ♀, YPM, Limón Bay, N. of Sweetwater River, Colón, February 12, 1934. 7 ♂ 11 ♀, USNM, Fox Bay, Colón, March 22, 1912, S. E. Meek and S. F. Hildebrand. 2 ♀, USNM, Fox Bay, Colón, January 12, 1912, S. E. Meek and S. F. Hildebrand. 1 ♀, USNM, Fox Bay, Colón, January 27, 1912, S. E. Meek and S. F. Hildebrand. 4

♂ 3 ♀, USNM, off Toro Point, Canal Zone, May 11, 1911, S. E. Meek and S. F. Hildebrand.

COLOMBIA

2 ♂ 1 ♀, USNM, Isla de S. Andrés, June 6, 1964, H. R. Bullis. 1 ♀, Golfo de Urabá, 34 fm., October 17, 1965, *Oregon* Sta. 5728. 2 ♂ 3 ♀, USNM, Golfo de Morrosquillo, 23 fm., May 25, 1964, *Oregon* Sta. 4886. 3 ♂ 3 ♀, USNM, off Puerto Colombia, 15 fm., May 23, 1964, *Oregon* Sta. 4866. 1 ♂ 2 ♀, YPM, Sabanilla, March 16–22, 1884, *Albatross*. 4 ♀, USNM, off Punta Faro, 13–14 fm., May 18, 1964, *Oregon* Sta. 4849. 2 ♂, USNM, off Tucuracas, Departamento de la Guajira, 15 fm., October 12, 1965, *Oregon* Sta. 5704, 1 ♂ 7 ♀, USNM, off Carrizal, Departamento de la Guajira, 19 fm., October 12, 1965, *Oregon* Sta. 5703. 1 ♀, USNM, off Carrizal, Departamento de la Guajira, 28 fm., October 12, 1965, *Oregon* Sta. 5702. 2 ♀, USNM, off Carrizal, Departamento de la Guajira, 10 fm., June 1, 1964, *Oregon* Sta. 4919. 1 ♂ 1 ♀, USNM, off Cabo de la Vela, Departamento de la Guajira, 38 fm., October 12, 1965, *Oregon* Sta. 5700. 1 ♀, USNM, off Cabo de la Vela, Departamento de la Guajira, 26 fm., October 12, 1965, *Oregon* Sta. 5697. 1 ♀, USNM, off Cabo de la Vela, Departamento de la Guajira, 15 fm., October 12, 1965, *Oregon* Sta. 5695. 1 ♀, USNM, NE. of Departamento de la Guajira, 53 fm., September 6, 1963, *Oregon* Sta. 4400. 3 ♂ 13 ♀, USNM, NE. of Departamento de la Guajira, 40 fm., September 25, 1963, *Oregon* Sta. 4392.

VENEZUELA

2 ♂ 3 ♀, USNM, Gulf of Venezuela, February 28, 1964, J. J. Ewald. 1 ♂ 3 ♀, USNM, Gulf of Venezuela, 32 fm., October 5, 1965, *Oregon* Sta. 5665. 3 ♂ 3 ♀, USNM, off Las Piedras, Gulf of Venezuela, 26 fm., *Oregon* Sta. 5664. 3 ♂, USNM, off La Guaira, 40 fm., October 17, 1963, *Oregon* Sta. 4466. 1 ♂, USNM, off Isla de Margarita, 30 fm., September 22, 1963, *Oregon* Sta. 4481. 12 ♂ 9 ♀, USNM, off Península de Paria, 31 to 34 fm., September 23, 1964, *Oregon* Sta. 5034. 2 ♂ 2 ♀, USNM, off Güiria, Gulf of Paria, 10 fm., October 24, 1963, *Oregon* Sta. 4493.

TRINIDAD

1 ♀, USNM, Caroni Swamp, August 6, 1965, P. R. Bacon. 1 ♀, USNM Cocorite Swamp, August 31, 1966, P. R. Bacon.

TOBAGO

1 ♂, USNM, off Crown Point Hotel, July 8, 1959, Smithsonian-Bredin Exped. 3 ♂ 4 ♀, USNM, off Plymouth, 34 fm., March 14, 1966, *Oregon* Sta. 5964. 1 ♂, USNM, S. of Plymouth, 34 fm., March 14, 1966, *Oregon* Sta. 5970. 9 ♂ 10 ♀, USNM, N. of Tobago, 36 fm., March 14, 1966, *Oregon* Sta. 5971.

GUYANA

4 ♂ 3 ♀, USNM, off Guyana, 50 fm., August 28, 1958, *Oregon* Sta. 2221. 2 ♀, USNM, off Guyana, 28 to 46 fm., August 29, 1958, *Oregon* Sta. 2232. 1 ♂ 1 ♀, USNM, off Guyana, 23 fm., August 29, 1958, *Oregon* Sta. 2235. 1 ♂ 1 ♀, USNM, E. of Georgetown, 26 fm., February 19, 1963, *Oregon* Sta. 4168. 1 ♂ 1 ♀, USNM, off Guyana, 24 fm., June 28, 1957, *Coquette* Sta. 297. 2 ♂ 4 ♀, USNM, off Guyana, 75 fm., November 4, 1957, *Oregon* Sta. 1993. 1 ♂ 1 ♀, USNM, off Guyana, 45 fm., November 5, 1957, *Oregon* Sta. 2000.

SURINAM

1 ♀, USNM, off Surinam, 50 fm., November 8, 1957, *Oregon* Sta. 2016. 1 ♂ 1 ♀, USNM, NE. of mouth Surinam River, 25 fm., May 12, 1957, *Coquette* Sta. 28. 1 ♂ 1 ♀, USNM, NE. of mouth Surinam River, 27 fm., May 12, 1957, *Coquette* Sta. 31. 1 ♂, USNM, NE. of mouth Surinam River, 28 fm., May 12, 1957, *Coquette* Sta. 33. 3 ♂ 4 ♀, USNM, between mouths of Coppename and Surinam Rivers, 13 fm., June 19, 1957, *Coquette* Sta. 251. 1 ♂, USNM, between mouths of Coppename and Surinam Rivers, June 26, 1957, *Coquette* Sta. 279. 9 ♂ 5 ♀, USNM, off mouth of Surinam River, 24 fm., June 28, 1957, *Coquette* Sta. 297. 1 ♀, UMML, off Surinam, summer 1960, H. Lijding.

FRENCH GUIANA

2 ♂, USNM, off French Guiana, 34 fm., September 14, 1958, *Oregon* Sta. 2322. 2 ♂ 2 ♀, USNM, off French Guiana, 38 fm., November 12, 1965, *Oregon* Sta. 2045.

BRAZIL

Maranhão: 2 ♀, USNM, off Ilha do Caju, 20 fm., March 11, 1963, *Oregon* Sta. 4241.

Ceará: 2 ♂ 3 ♀, USNM, off Camocim, 15 fm., March 12, 1963, *Oregon* Sta. 4247. 1 ♂, USNM, off Camocim, 18 fm., March 12, 1963, *Oregon* Sta. 4250.

Bahia: 1 ♂ 1 ♀, MCZ–USNM, Salvador.

Espírito Santo: 2 ♂ 3 ♀, MNHNP–USNM, off Itaúnas, 21 fm., November 29, 1961, *Calypso* Sta. 89.

Rio de Janeiro: 5 ♂ 6 ♀, USNM, off Baía de Guanabara, 3½ fm., da Silva. 3 ♂ 4 ♀, MNHNP–USNM, off mouth Baía de Guanabara, 12 ⅗ fm.,

December 8, 1961, *Calypso* Sta. 115. 1 ♀, YPM, Rio de Janeiro. 1 ♂ 1 ♀, YPM, Rio de Janeiro Market, M. W. Feingold. 26 ♂ 29 ♀, YPM, Rio de Janeiro, M. W. Feingold and C. Moreira. 5 ♂ 3 ♀, MNHNP–USNM, Baía de Sitio Forte, Ilha Grande, December 9, 1961, *Calypso* Sta. 119.

São Paulo: 1 ♂, USNM, Santos, September 12, 1925, W. L. Schmitt. 11 ♂ 5 ♀, USNM, Cananéia, December 16, 1963, V. Sadowsky. 1 ♂ 6 ♀, USNM, Cananéia, April 1965, V. Sadowsky.

Santa Catarina: 1 ♀, USNM, Lagoa da Conceição, Ilha de Santa Catarina, November 11, 1965, E. Tremel. 2 ♂ 4 ♀, USNM, Lagoa da Conceição, Ilha de Santa Catarina, November 19, 1965, E. Tremel. 1 ♀, USNM, Armação da Piedade, Ilha de Santa Catarina, November 19, 1965, E. Tremel. 2 ♂ 2 ♀, USNM, Arvoredo, Ilha de Santa Catarina, October 9, 1964, C. de Jesús.

Diagnosis

Adrostral sulcus broad posteriorly and long, almost reaching posterior margin of carapace. Median sulcus long, ending immediately anterior to posterior end of adrostral sulcus, and deep along its entire length. Dorsolateral sulcus variable in width, broad to almost closed, narrower in northern portion of range of species. Petasma with distal portion of ventral costa increasing gradually in width proximally and turning proximally in arc, unarmed along free border and with elongate group of sharp teeth on attached border; apex of costa free; distal fold forming large auricle with prominent spines; distomedian projection long. Thelycum with anterior process small, posterior process with median carina, if present, located deep between horns of median protuberance; lateral plates with anteromedian corners produced to form projections covering posterior process.

Description

ROSTRUM (fig. 68)

Teeth $\frac{7-11}{0-3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—44, 9/2—43, 7/2—4, 10/2—3, 11/2—3.50, 9/1—1, 8/0—0.50, 7/0—0.50, 8/1—0.50; N=200) +epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to last dorsal tooth; rostrum in larger juveniles reaching base of distal one-third of thickened portion of lateral antennular flagellum; attaining maximum length in relation to carapace length at 11 to 15 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.78); decreasing progressively with increasing length of shrimp, rostrum reaching distal end of first antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.50); rostrum straight apically, often along entire length, occasionally with tip upturned; highest portion of blade at level of third dorsal tooth, latter level with anterior margin of carapace; rostrum tip about ¼ r.l. Postrostral carina strong, prominent, and long, extending almost to near posterior margin of carapace. Median sulcus deep, sometimes widening either in anterior or posterior half; long, ending near posterior margin of carapace. Adrostral sulcus deep, expanded at level of epigastric tooth, broad, ¾ to 1½ width of postrostral carina, and long, continuing posteriorly to end 1/13 to 1/15 c.l. from posterior margin of carapace. Adrostral carina prominent and long, same length as adrostral sulcus.

CARAPACE (fig. 69)

Length in proportion to total length smaller in juveniles, increasing slightly at about subadult stage. Gastrofrontal sulcus broad, extending to about one-sixth c.l.; gastrofrontal carina sharp. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening again to base of spine. Gastro-orbital carina pronounced, sharp, occupying approximately posterior four-fifths distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus about one-quarter c.l., ending slightly anterior to midlength of carapace. Hepatic carina sharp, ⅓ to ¼ c.l., sloping anteroventrally to end 1/15 to 1/18 c.l. from anterior margin of carapace. Antennal spine slender, acute, and long; hepatic spine prominent.

ANTENNULES

Lateral flagellum almost three-quarters length of antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum. Anterolateral spine very prominent, long, slender, and sharp. Stylocerite acute, reaching slightly beyond midlength of first antennular segment. Prosartema reaching distal end of proximal fifth of second antennular segment.

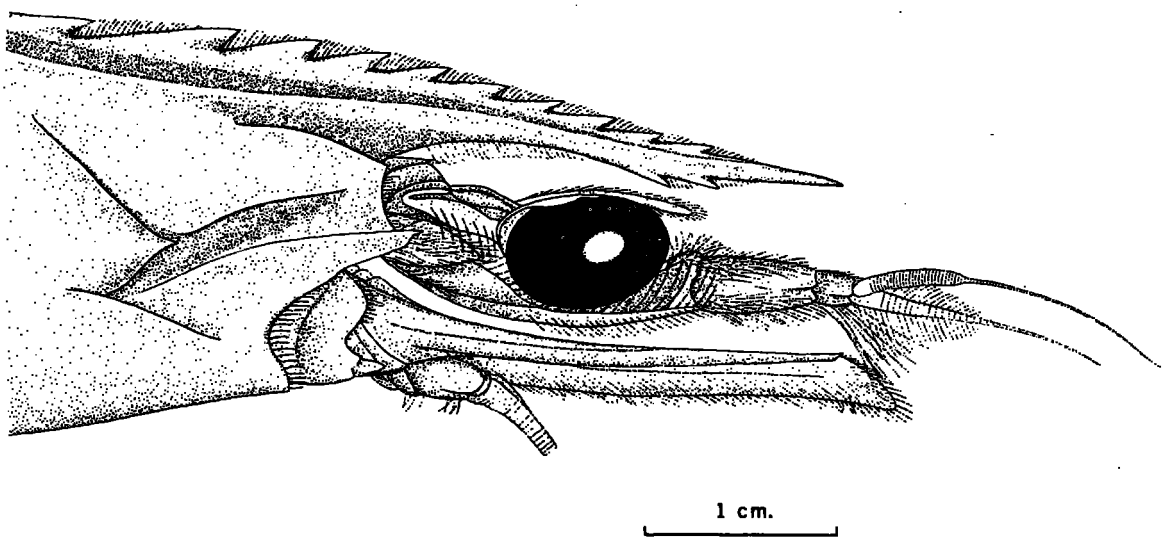

FIGURE 68.—*Penaeus* (*M.*) *brasiliensis* Lat. Rostrum, ♂ 38 mm. c.l., Arvoredo, Santa Catarina, Brazil.

ANTENNAE

Scaphocerite length 2½ to 2¾ times maximum width, its length, relative to carapace length, decreasing slightly with growth; spine reaching distal end of antennular peduncle. Carpocerite length 1⅓ width. Antennal flagellum about 1⅖ t.l. of shrimp.

THORACIC APPENDAGES

Third maxilliped reaching at least one-half of first, but not beyond distal half of second antennular segment; length of dactyl ⅗ to ⅔ that of propodus. First pereopod reaching at least three-fifths length of carpocerite or exceeding it by dactyl. Second pereopod surpassing carpocerite by half length of dactyl to one-tenth that of carpus. Third pereopod reaching at least base of second antennular segment and, at most, exceeding third antennular segment by entire length of dactyl; proportionately longer in juveniles. Fourth pereopod reaching at least base of carpocerite and at most surpassing it by length of dactyl. Fifth pereopod subequal to fourth.

ABDOMEN

Carinate dorsally from posterior half of fourth somite, posteriorly carina gradually increasing in height to form keel on sixth somite, ending in sharp spine on posterior margin. Dorsolateral sulcus (fig. 70 a, b) with both lips sharp, variable in width, broad in populations from South America, ratio between height of keel and width of sulcus (K/S) ranging 1 to 4.5, modally 2 (fig. 71), narrower in specimens from the West Indies northward, K/S ranging from 3 to 9, modally 5 (fig. 73). In South America, K/S is also modally 2 in all size classes except 16 to 22 mm. c.l. with K/S modally 2.75 (fig. 72). In West Indies-Central America region and northward, K/S mode varies in different size classes—5 in the smallest class and at 23 to 29 mm. c.l.; 3 in the class intermediate between these two, and 3 in the largest (fig. 74). It does not seem that any significance could be attached to such a variation that does not show a trend. Sixth abdominal somite with three cicatrices on each side, posterior the smallest; fifth abdominal somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite; fourth abdominal somite with similar series of pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

PETASMA (fig. 75 a–c)

Ventral costa broadening and curving gradually from apex to distal end of ventromedian flap, extending almost straight proximally; distal portion unarmed along free border and with 6 to 12 pointed teeth set in two irregular rows on attached border; apex free from distal margin of ventrolateral lobule. Distal fold intruding considerably inside petasma, forming large, rounded auricle with numerous prominent spines arranged distally in half moon on inner surface. Ventrolateral lobule with external armature consisting of single or pair of series abreast distally, increasing in number proximally. Distomedian projections long, fingerlike in appearance, extending well over distal portion of ventral costae.

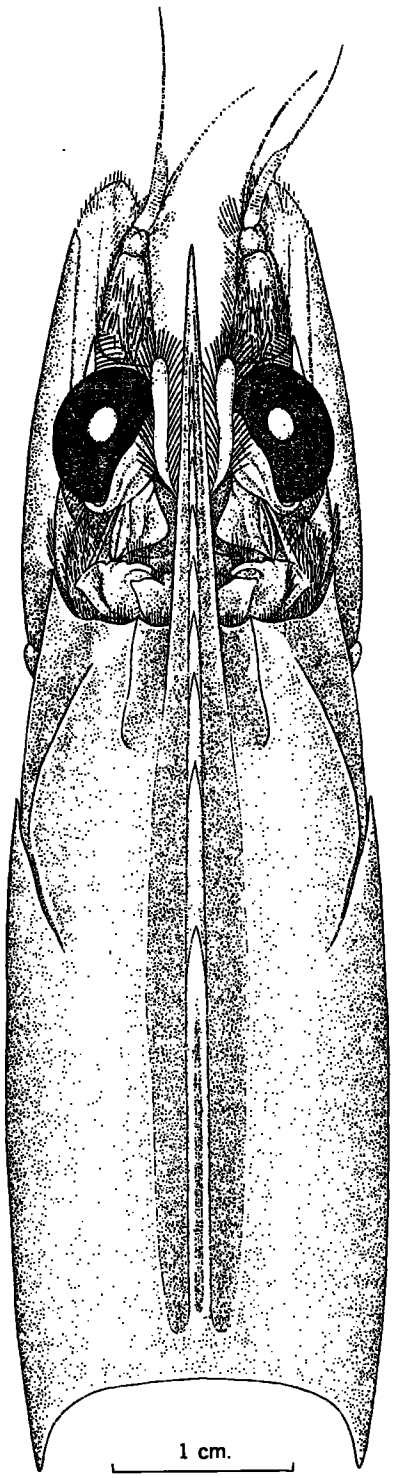

FIGURE 69.—*Penaeus* (*M.*) *brasiliensis* Lat. Cephalothorax, ♀ 43 mm. c.l., off Itaúnas, Espírito Santo, Brazil.

APPENDIX MASCULINA (fig. 75 d)

Relatively broad, its length 1⅕ to 1¼ maximum width, lateral margin with short spines reaching apex, median margin with long spines (almost half length of appendix) on distal half. Anterior surface slightly concave, posterior surface concave, with sharp longitudinal ridge projecting from median margin.

THELYCUM (fig. 76 a–c)

Anterior process typically small, projecting ventrally in subtriangular ridge, enclosed surface slightly to deeply concave. Posterior process rather weakly developed, often (not always) with short median carina situated deeply between horns of median protuberance, delimited by narrow sulcus on each side. Lateral plates with anteromedian corners extended anteriorly forming projections meeting along midline, and reaching base of anterior process, thus covering posterior process. Projections pointed or rounded anteriorly; if rounded, overlapping.

COLOR

The range of colors varies considerably. The usual pink or brownish-red specimens are designated camarão rosa in Brazil, and langostino or camarón rosado in Venezuela, both meaning pink shrimp. Yellow individuals, also common, are called camarón amarillo (yellow shrimp) and brown ones are not infrequent. The young are usually brownish and are called camarão lixo (dirty shrimp) in Brazil. *P. brasiliensis* usually possesses a roundish, dark reddish-brown spot on each side at the juncture of third and fourth abdominal somites, similar to that in *P. d. duorarum* and *P. d. notialis*. Davant (1963) and Holthuis (1959) pointed out that individuals of *P. brasiliensis* from Venezuela and Surinam-French Guiana, respectively, always seem to have the two spots, but that *P. a. subtilis* and *P. d. notialis* lack them. The two spots were also observed in individuals from Baía de Guanabara, Brazil, by da Silva (1965).

Distribution and Morphological Variations

P. brasiliensis ranges from off Cape Hatteras south to the Florida Keys and, although rarely, reaches the Tortugas grounds. It also ranges from the Bermudas through the Bahamas and Antilles and along the Atlantic Coast of South America, to Rio Grande-Lagoa dos Patos, Brazil. It also occurs

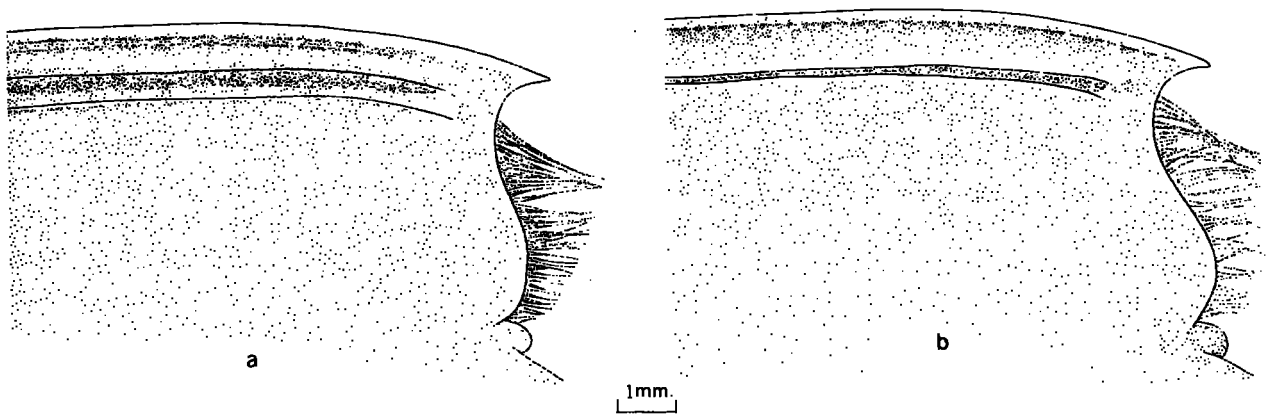

FIGURE 70.—*Penaeus (M.) brasiliensis* Lat. a. Sixth abdominal somite, posterodorsal portion, ♀ 37 mm. c.l., off Camocim, Brazil. b. Sixth abdominal somite, posterodorsal portion, ♀ 39.5 mm. c.l., Little Bahama Bank.

from the Isla Contoy along the Caribbean Coast of Mexico, Central America, and South America (fig. 77). It is absent from the Gulf of Mexico, north of Tortugas-Florida Bay to the vicinity of Cabo Catoche. Lindner (1957) indicated that it might be present in the coastal lakes of Uruguay. This probably erroneous assumption was based on the observation of specimens in the commercial catches at Rio Grande do Sul (Milton J. Lindner, personal communication); however, as implied above, no specimens have been collected so far south.

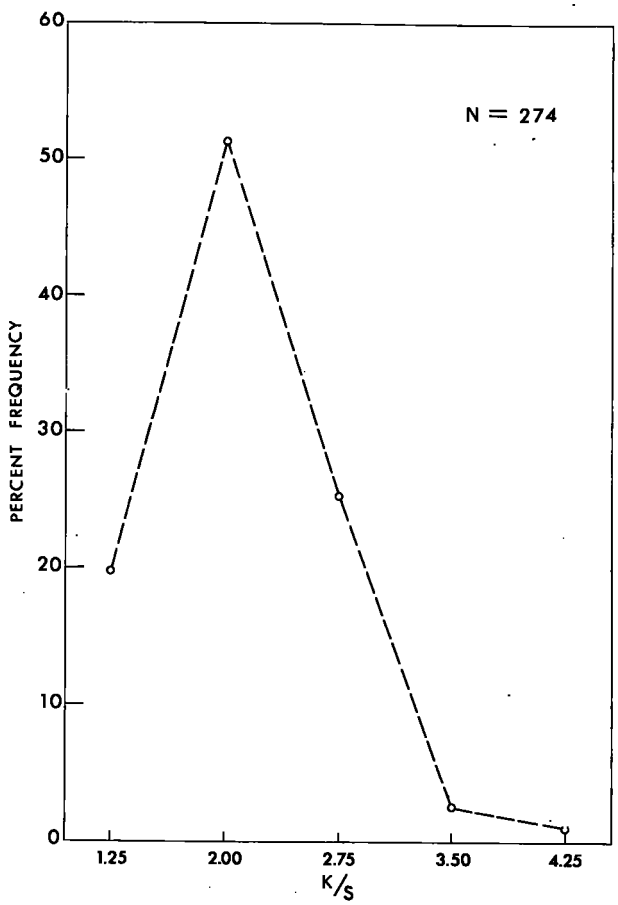

FIGURE 71.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus (M.) brasiliensis* Lat. from the coast of South America.

P. brasiliensis is generally very scarce in the northernmost portion of its range. The record from off Cape Hatteras given by Burkenroad (1939) was the first positive evidence of the presence of the species, as restricted by him, in the waters of the United States. Previous references of the occurrence of *P. brasiliensis* along the Atlantic Coast of the United States were based on collections of *P. a. aztecus* and *P. d. duorarum*, which were previously identified as *P. brasiliensis*. It may be that specimens of *P. brasiliensis* were represented in the collections. Eldred and Hutton (1960) stated that the range of the species included the Caribbean and Atlantic Coasts of South America and indicated the possibility (probably based on Burkenroad's only record) that it also occurs along the North American coast. Eldred (1960) found *P. brasiliensis* in Biscayne Bay, Fla., and, thus, corroborated its presence in the southeastern United States. Recently, Costello and Allen (1964) collected this species in eastern Florida Bay; and Joyce (1965) recorded it from northeast Florida. I have also examined specimens from other localities in Florida, north of Fort Pierce and off Key Largo (see Study Material). The presence of this species in the Tortugas is based on a single male specimen deposited in the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex. It was taken in a commercial catch made at approxi-

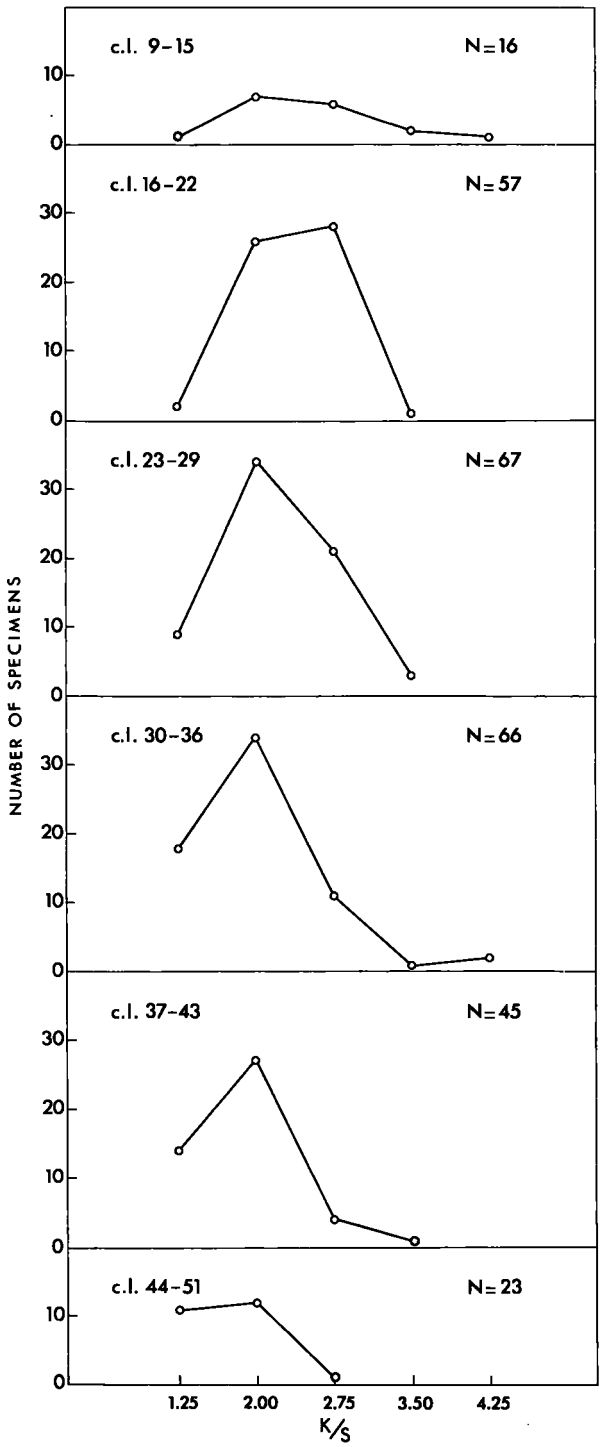

FIGURE 72.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *brasiliensis* Lat. of different size classes from the coast of South America.

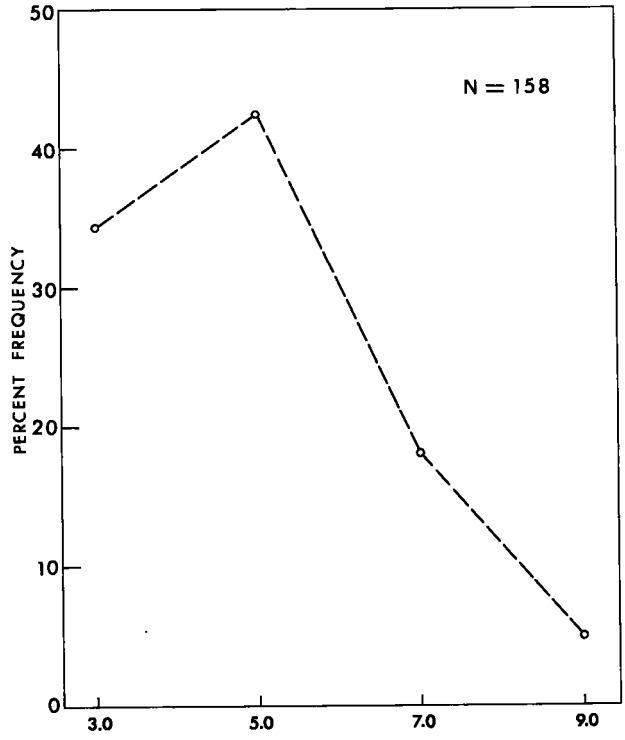

FIGURE 73.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *brasiliensis* Lat. from the West Indies, Central America, eastern United States, and the Bermudas.

mately lat. 24°54′ N., long. 82°15′ W., in water 13 fm. deep (Milton J. Lindner, personal communication).

P. brasiliensis apparently is not abundant in the Greater Antilles, although it is taken with *P. a. subtilis* through the Lesser Antilles, whereas *P. schmitti* seems to be extremely rare and *P.d. notialis* has not been recorded. The 1-year sampling carried out by Pérez Farfante et al. (1961) at Laguna Doctor, Playa de Baracoa, Cuba, showed that *P. brasiliensis* is the least common among the shrimp living in this body of water, making up only 10 percent of the total sample. This percentage seems to be representative of the relative abundance of the species, at least in northern Cuba. Although present along the southern coast of the island, P. *brasiliensis* is extremely scarce. I found only a very few individuals in the stomach of snappers (Lutjanidae). The three specimens listed by Boone (1930) as "*P. brasiliensis*" from Cuba, two from the "south coast" and a third from Guantánamo, I found to be *P. d. notialis*.

Holthuis (1959) reported that in Surinam *P. brasiliensis* is far less common in shallow water

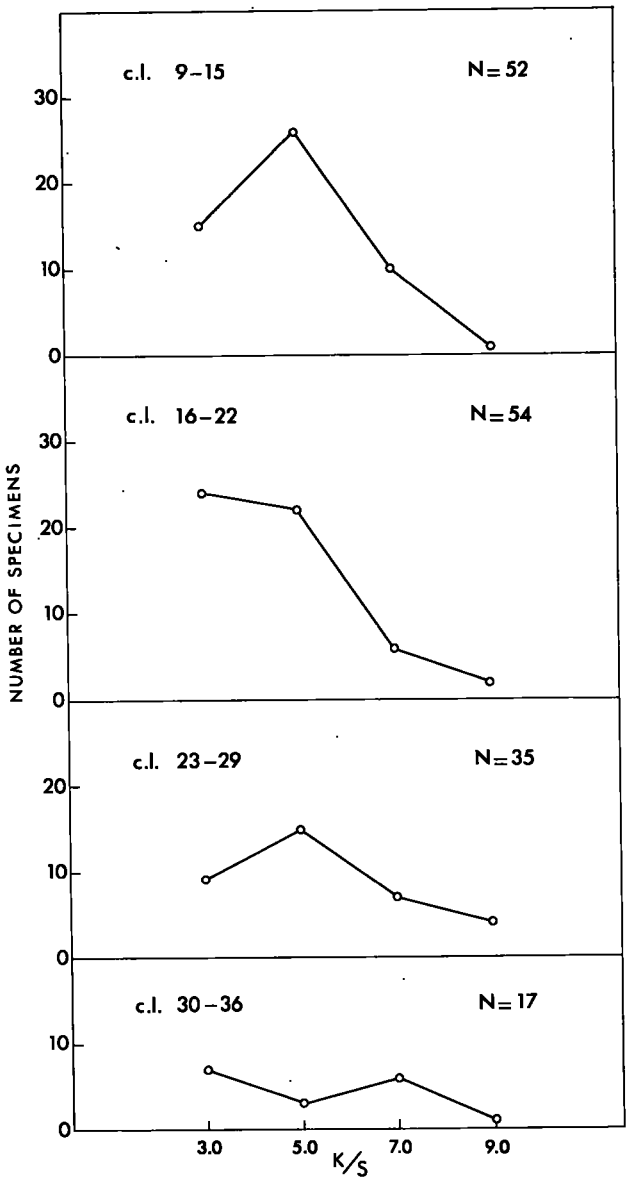

FIGURE 74.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *brasiliensis* Lat. of different size classes from the West Indies, Central America, eastern United States, and the Bermudas.

than *P. a. subtilis*, although it is more frequent in deeper water (20 to 30 fm.). He also indicated a similar finding in French Guiana, where most *P. brasiliensis* were caught between 22 and 38 fm. Bullis and Thompson (1959a) stated that commercial quantities of this species are present off the Guianas, and that maximum catches were taken near the 30-fm. curve. The same depth distribution seems to persist along the coast to Brazil, where it is also abundant.

The bathymetric range of *P. brasiliensis* while broad, is not so great as that of *P. d. notialis*. The greatest depth at which it has been collected is 150 fm. At this depth a collection was made west of Andros Island, Bahamas, at *Oregon* Sta. 2475. Other deep water records (see Study Material) include depths of 95, 100, and 105 fm.

Rossignol (1957) reported *P. brasiliensis* from West Africa. It seems probable that the specimens were actually *P. duorarum notialis*, and that the author identified them using the old name *P. brasiliensis*, a name employed before Burkenroad (1939) recognized that three species were included under the latter name.

In *P. brasiliensis* both the petasma and the thelycum vary, but none of the variations may be correlated with a restricted portion of the range. In the petasma the number of teeth on the attached edge of the ventral costa vary in number, and the band of spines along the membranous portion of the ventrolateral lobule may be narrow or relatively broad. The thelycum, in turn, may or may not have a median carina projecting caudad from the posterior process; the protracted anteromedian corners of the lateral plates may taper anteriorly or may be expanded into disklike projections that overlap. Neither of the characters mentioned, however, is typical of shrimp from a limited region.

As stated above, the keel-sulcus ratio increases progressively (the dorsolateral sulcus narrows) from northern South America northward; no distinct break occurs in the range of this ratio anywhere within the range of the species. The length of the rostrum also shows a south-north cline, a tendency to increase from south northward, reaching a maximum in the populations from the Bahamas, the United States, and the Bermudas.

Relationships

Adults of *P. brasiliensis* are readily separable from adults of the other species of *Penaeus* from the western Atlantic. Females can be identified by the small anterior process and the anteromedian corners of the lateral plates, which are produced anteriorly and completely cover the posterior process, and by the lack of a median carina on the latter or the possession of a short one which is situated at the posterior end, sunk between the horns of sternite XIII. Males may be recognized by the free apex of the ventral costa, the distal fold that forms a large auricle armed with strong

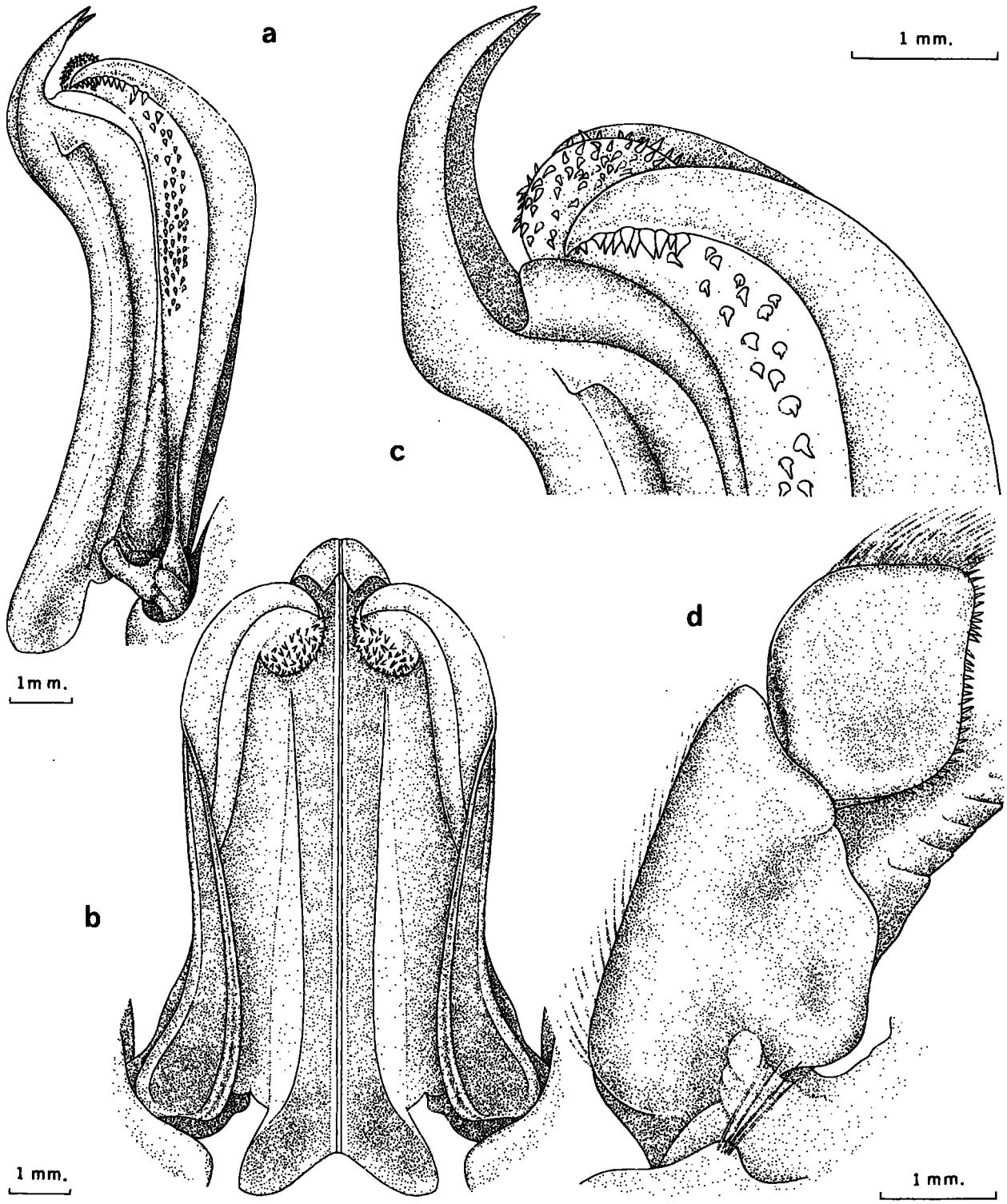

FIGURE 75.—*Penaeus* (*M.*) *brasiliensis* Lat. a. Petasma. ♂ 36 mm. c.l., N. of Península de Paria, Venezuela. b. Petasma, interior surface, ♂ 36 mm. c.l., N. of Península de Paria, Venezuela. c. Petasma, distal portion, ♂ 36 mm. c.l., N. of Península de Paria, Venezuela. d. Appendix masculina, ♂ 42 mm. c.l., off Guyana.

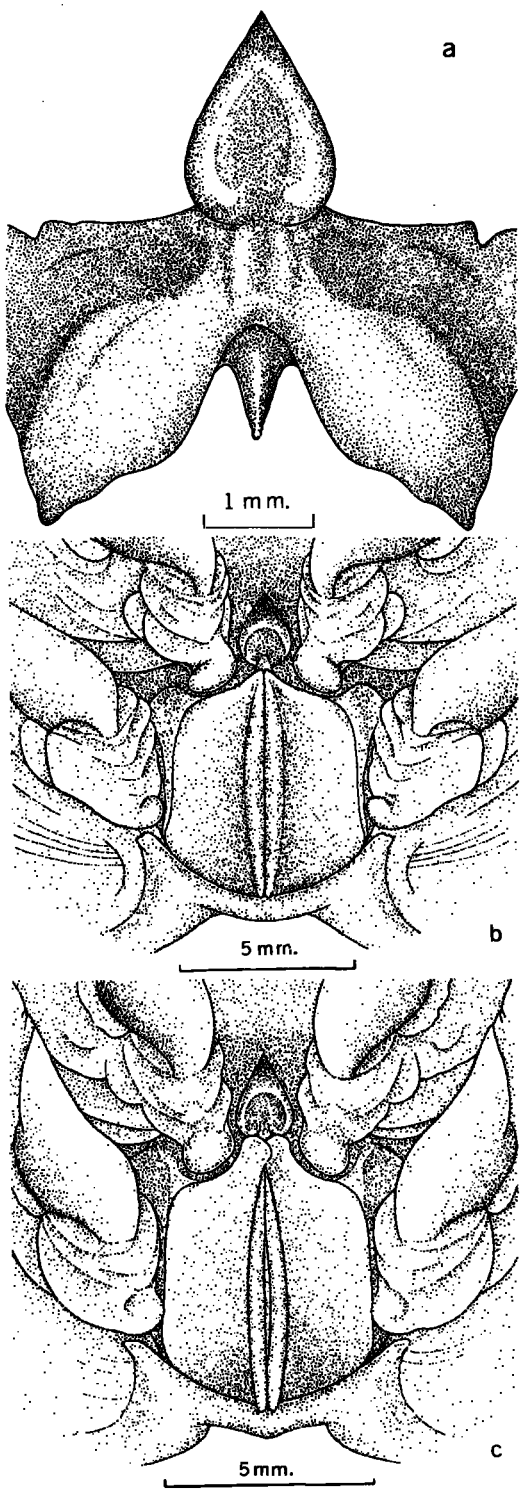

FIGURE 76.—*Penaeus* (*M.*) *brasiliensis* Lat. a. Median protuberance with horns on posterior margin of sternite XIII, ♀ 43.5 mm. c.l., E. of Georgetown, Guyana. b. Thelycum, ♀ 41 mm. c.l., off Surinam. c. Thelycum, ♀ 42 mm. c.l., off Surinam.

spines on its inner surface, and the long distomedian projections of the petasma.

P. brasiliensis also often has the cicatrices on the sixth abdominal somite conspicuously smaller, particularly the posterior one, than those of any other *Penaeus* from the entire region.

P. brasiliensis juveniles closely resemble those of *P. d. duorarum* and *P. d. notialis;* in *P. brasiliensis* males, however, the median ridge on sternite XIV is higher, particularly in the anterior portion which is produced in a triangle (as seen in lateral view), and the groove surrounding the ridge is deeper than that found in the two subspecies of *P. duorarum*. Furthermore, in males 10 to 11 mm. c.l., 47 to 51 mm. t.l., the ventral costa of the petasma lacks distomarginal spines. Males 12 mm. c.l., 55 mm. t.l., usually have the distomedian projections of the petasma longer and more slender than those of *P. d. duorarum* and *P. d. notialis* of corresponding size. In females, 12 mm. c.l., 55 mm. t.l., the anterior process is smaller; the lateral plates have the anteromedian corners angular or pointed anteriorly rather than rounded, and if the posterior process bears a median carina, it is located between the horns. In addition, in the Caribbean region, the dorsolateral sulcus in *P. brasiliensis* is usually narrower than in *P. d. notialis*.

Juveniles of *P. brasiliensis* are distinguished from those of *P. a. aztecus* and *P. a. subtilis* by the usually almost straight rostrum which is also shorter than in *P. a. subtilis* through their common range; males may also be distinguished by the sharp median ridge on the ventral surface of sternite XIV, and females by the posterior process, which is less prominent, is not produced caudally, and often lacks a median carina, which, if present, is situated more dorsally. The median sulcus is also deeper and longer, and the adrostral sulcus much wider and longer than in juveniles of *P. a. subtilis*. The typical characters of the external genitalia mentioned above also distinguish *P. brasiliensis* juveniles from those of *P. paulensis*. Furthermore, the dorsolateral sulcus is usually broader in *P. brasiliensis* throughout their common range.

Reproduction

SUBADULT STAGE-SEXUAL MATURITY

The smallest males observed with joined petasma were 15 mm. c.l., 69 mm. t.l.; many individuals to 22 mm. c.l., 97 mm. t.l., however, had unjoined petasmal endopods. It, therefore, appears that males reach the subadult stage within the

FIGURE 77.—Distribution of *Penaeus* (*M.*) *brasiliensis* Lat.

size range 15 to 23 mm. c.l., 69 to 101 mm. t.l. The smallest females with functional thelyca were 15 mm. c.l., 70 mm. t.l., but in many females 19 mm. c.l., 86 mm. t.l. the lateral plates were non-contiguous. Thus, they reach the subadult stage within the size range 15 to 20 mm. c.l., 70 to 90 mm. t.l. No studies have been made to allow conclusions as to the size at which females first reach maturity.

COPULATION

As it seems to be true in other *Penaeus* with a closed thelycum, copulation in *P. brasiliensis* is believed to take place between a hard-shelled male and a soft-shelled female.

OVARY DEVELOPMENT AND SPAWNING

No studies have been conducted.

SEX RATIO

No intensive sampling has been carried out to determine the male-female ratio.

Postembryonic Development

LARVAE, POSTLARVAE, AND JUVENILES

No studies have been made on either larval or postlarval stages of this shrimp.

My studies showed that juvenile *P. brasiliensis* of 18 mm. t.l. have distinctly long adrostral sulci. This character allows for the separation of early juveniles of this as well as those of the other grooved *Penaeus*, from those of the nongrooved *P. setiferus* and *P. schmitti*. At a minimum of about 20 mm. t.l. males and females are distinguished, as are those of the other grooved *Penaeus* in the western Atlantic, by the endopods of the first pair of pleopods, which in the males are longer and are located more proximally on the bases than in the females. In addition, males have a sharp, high ridge on the midline of sternite XIV, whereas in females the sternite XIV is produced on the midline where a knob is frequently present. (See also under Relationships.)

GROWTH

No studies have been made.

SEX DIFFERENCES IN SIZE

The largest females on record were 250 mm. t.l., reported from eastern Venezuela by Davant (1963), whereas the largest I measured was 58.5 mm. c.l., 214 mm. t.l., from off Guyana. The largest male recorded was 191 mm. t.l., reported by Holthuis (1959) from Surinam waters. Offshore samples indicate that, as in other *Penaeus* from the western Atlantic, *P. brasiliensis* females become larger than males.

Ecology

SUBSTRATE

P. brasiliensis juveniles are more abundant where the bottom consists of soft mud. Laguna Doctor, Playa de Baracoa, Cuba, where Pérez Farfante et al. (1961) carried on their sampling, has a bottom of very soft mud covered with vegetation, a habitat typical of most nursery grounds for *Penaeus* shrimp. Adults seem to prefer rather firm bottoms. According to Bullis and Thompson (1959a), along the Continental Shelf of South America, from Trinidad to the Amazon River, this species is most abundant on bottoms consisting chiefly of a mixture of mud and sand.

DIEL CYCLE

P. brasiliensis has mostly nocturnal habits; the young in inshore water are fished at night. Tremel and Mistakidis (1965) described in detail the night fishing for camarão rosa (*P. brasiliensis* and *P. paulensis*) in the coastal lagoons of the State of Santa Catarina, Brazil. Adults are also active at night; Bullis and Thompson (1959a) stated that during their exploratory fishing, "catches fell off at or before daylight, and daytime trawling was unproductive for this species."

The only information available concerning the influence of the lunar phases on the behavior of this species is that given by Wheeler (1937); his observations were made in the Bermudas. This author stated that *P. brasiliensis* showed a rhythmic pattern of activity and quiescence over the new and full moon, respectively, and concluded that the most probable cause of periodic swarming is the cyclic absence of light. He also indicated that the effect of light is occasionally subject to interference by such factors as the opacity of the water.

MOVEMENTS

No information is available regarding migrations of *P. brasiliensis* at any stage of its life cycle. The only data gathered are a few records of the time juveniles and subadults occupy inshore waters in different areas throughout the range. Eldred (1960) reported juveniles and subadults in Biscayne Bay, Fla., in July, December, and February. Later this species was found to form a large percentage of the shrimp that live in the Bay during the summer. I have identified specimens from in-

shore waters of Florida taken during both summer and winter.

It appears that in the Caribbean region *P. brasiliensis* occupy the nursery grounds at least from December to June. The sampling carried out by Pérez Farfante et al. (1961) in Laguna Doctor, Playa de Baracoa, Cuba, showed that small individuals to 95 mm. t.l. were present during two periods each year, March–June and September–December. Individuals up to 110 mm. t.l. were collected in January and February, and larger shrimp, 126 to 130 mm. t.l., from March through May. No specimens were taken in July or August. According to Lindner (1957), fishing for the young is usually carried out in the marshes of northern Colombia from January through May; farther east, in the Gulf of Venezuela, Ewald (1964, 1965c) found specimens 18 to 23 mm. c.l. from December to June.

Tremel and Mistakidis (1965) reported that in the State of Santa Catarina, Brazil, *P. brasiliensis* and *P. paulensis* are caught in the coastal lagoons from August to April.

EFFECTS OF TEMPERATURE

P. brasiliensis seems to prefer waters of relatively high temperatures. It is the only one of the four *Penaeus* in the southeastern Atlantic Coast of the United States that does not invade the colder waters north of Cape Hatteras, and in the Southern Hemisphere only stragglers seem to wander south of Laguna, Brazil. Furthermore, the densest concentrations of *P. brasiliensis* are found in the warmest portion of its range. Experiments by Scholander et al. (1953) showed that "*Penaeus* sp. (*brasiliensis*)" could not tolerate temperatures lower than 8° to 12° C., nor those above 35° C.

EFFECTS OF SALINITY

P. brasiliensis, like other species of *Penaeus*, appears to have a wide range of salinity tolerance during the inshore phase of its life. The meager information available, however, suggests that at least the young have a high optimum salinity. Lindner (1957) reported that although the young are fished intensively during the dry season— January through May—in Ciénaga Grande de Santa Marta, Colombia, the extensive marsh area in northern Colombia between Barranquilla and Santa Marta, they are caught during the entire year when rainfall is not heavy and the marsh waters are not greatly diluted. During floods fishermen are unable to locate shrimp in the area.

ENEMIES AND DISEASES

Iversen and van Meter (1964) published the first record of a parasite in *P. brasiliensis*. In Biscayne Bay they found this shrimp infested with *Thelohania duorara* Iversen and Manning, the microsporidian that causes the condition known as "cotton" or "milk" shrimp. Infestations of this parasite in *P. d. duorarum* are common.

Commercial Importance

P. brasiliensis is important to the fisheries of several Latin American countries, although it ranks lowest among the commercial *Penaeus* from West Indies northward. In Biscayne Bay, the only area in the United States where it is known to be significantly represented in the catches, this species may contribute to 41 percent of the shrimp caught during July (Costello, 1963; Joyce and Eldred, 1966). It abounds there in summer and fall.

This species forms only a very small percentage of the catches in the Greater Antilles. Milton J. Lindner has informed me that the U.S. boats have been taking spotted pink shrimp in numbers off Contoy, Mexico, for several years. *P. brasiliensis* contributes substantially to the catches made off Nicaragua (Croker, 1967; Instituto de Fomento Nacional, 1967). Lindner (1957) reported that the young are taken in Ciénaga Grande de Santa Marta, Colombia. Ewald (1964, 1965c) stated that it is the least important of the commercial species of *Penaeus* in western Venezuela, where it is caught only seasonally in the northeastern portion of the Gulf of Venezuela and outside the Gulf proper, north of Cabo San Ramón. *P. brasiliensis* supports the fishery of Isla Margarita, which, according to Croker (1967), probably accounts for most of the 236,757 kg. of shrimp taken along the coast of Venezuela, east of the Gulf.

P. brasiliensis makes up most of the gigantic catches made along the Atlantic Coast of South America, from Guyana to Baía de Marajó, Brazil. In 1965, exports to the United States from that area amounted to about 7 million kg.

This species apparently has limited commercial value throughout the coastal waters of northeastern Brazil, but it is important to the fisheries in the neighborhood of Cabo Frio and southward. Da Silva (1965) stated that the young of *P. brasiliensis* are the most abundant shrimp in Baía de Guanabara; offshore the adults make up a relative-

ly large percentage of the shrimp catches. Landings of camarão rosa (*P. brasiliensis*, *P. paulensis*, and perhaps *P. a. subtilis*) in Rio de Janeiro during 1965 amounted to 63,900 kg., but in 1966 to only 10,700 kg. (SUDEPE).

The estimates by Braga (1962) indicate that *P. brasiliensis* together with *P. paulensis* make up a large percentage of the landings at Santos, São Paulo. The majority of the shrimp landed there under the name camarão rosa, however, seems to be *P. paulensis*. According to Tremel and Mistakidis (1965), camarão rosa (*P. brasiliensis* and *P. paulensis*) is fished in the State of Santa Catarina in the lagoons and the ocean throughout the year. The production in that State during 1965 amounted to 248,600 kg., and during 1966 reached an all-time high of 688,500 kg. (Centro de Pesquisas de Pesca).

Mistakidis (1965) found, contrary to previous information, that *P. brasiliensis* is very scarce in Lagoa dos Patos, where *P. paulensis* is responsible for the large commercial catches in that vast body of water.

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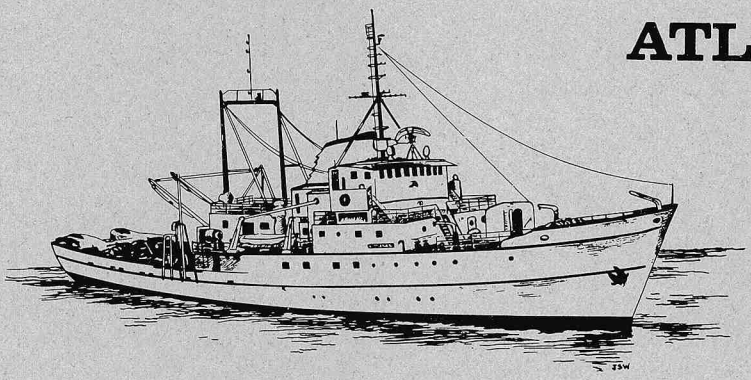

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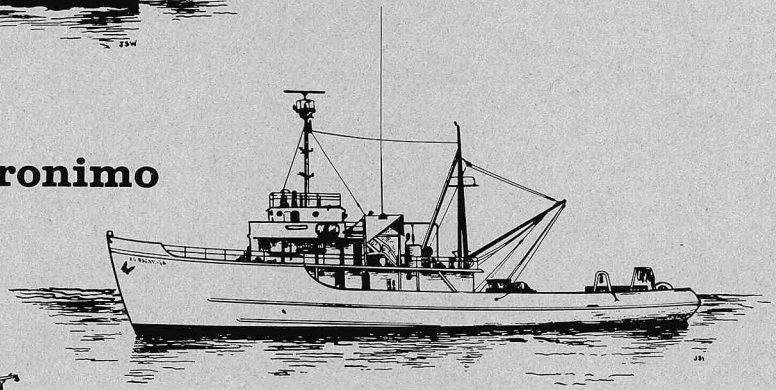

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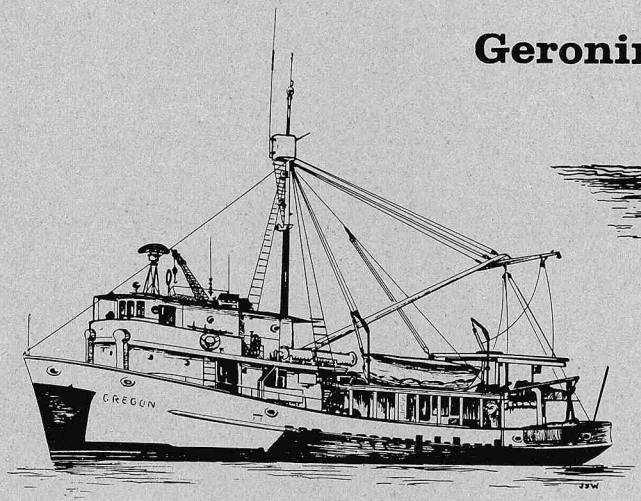

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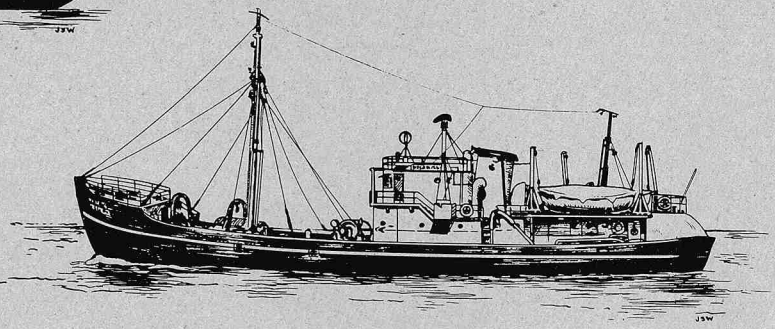
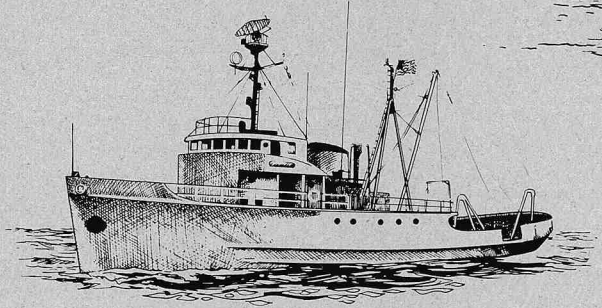


Delaware



Undaunted

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