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FISHERIES OCEANOGRAPHY—EASTERN BERING SEA SHELF

October 1979

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FISHERIES OCEANOGRAPHY - EASTERN BERING SEA SHELF[1/]

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OVERVIEW

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ABSTRACT

Although for decades general associations between fish and the eastern Bering Sea environment have been assumed or proposed, specific fisheries oceanography investigations designed to explore or explain such relations have not been carried out in spite of the fact that early investigators consistently pointed out the inadequacies of casual environmental observations obtained during fishing cruises and recognized the need for more complete studies. Although today the acquisition and processing of environmental (physical and chemical) data is rapid and straightforward using S-T-D and autoanalyser systems and shipboard computers, such integrated studies are still rare. This Overview is designed not only to put the subsequent Chapters in this Section in perspective in regard to fisheries oceanography, but also to suggest that although annual stock assessments may satisfy management criteria, conservation practices will require information on the year round distributions of juveniles as well as adults, multispecies interactions, and rather specific relations within the overall ecosystem. This is a large task but more emphasis on fisheries oceanography studies will accelerate acquisition of the required knowledge.

INTRODUCTION

The rapacious exploitation of whales in the Bering Sea to obtain whale oil in the mid-19th century was accomplished without any consideration of conservation principles or of impact on the ecosystem and it is gratifying to see the extensive efforts funded by the Outer Continental Shelf Environment Assessment Program (OCSEAP) to define conditions and processes in this area as in this century we seek to obtain petroleum from below the sea floor. Because of the nature of the OCSEAP program, to assess real and possible effects of oil exploration and exploitation, many of the individual grants are largely disciplinary (physical oceanography, fishery biology, ichthyoplankton, etc.), and area specific (i.e. Norton Sound, Navarin Basin, St. George Basin, Bristol Bay Basin, etc.). The purpose of this Section is to consider the continental shelf of the eastern Bering sea as an integral unit and briefly evaluate environmental and biological continuities and relationships throughout the area. The initial guidelines for this Section on Fisheries Oceanography were 100 (double-spaced) pages constituting about 5 Chapters and it is obvious that although we have far exceeded that amount the subject is still not adequately covered.

I believe that straight off a definition of fisheries oceanography (or fishery oceanography if one prefers) is in order. Of course the term stems from fisheries hydrography which originated at the turn of the century, and essentially embraced any and all factors influencing fisheries. Since the word "ecology" appar-

ently was avoided, one suspects that originally the term was meant to incorporate those immediate factors that would enhance catching fish, or perhaps explain why fish weren't caught, rather than the broad studies of the ocean or even very specific but basic research. The shift from fisheries hydrography to fisheries oceanography in mid-century dealt largely with semantics, rather than a shift in activities, during the period when those in the burgeoning field of ocean studies couldn't decide whether they would march under the banner of oceanography or oceanology. Although such a discussion may seem trivial, Chapman (1961) canvassed the world in an attempt to obtain an acceptable definition of fisheries oceanography without success.

The actual scope of studies embraced by fisheries oceanography is virtually unlimited -- from external forces, global or extraterrestrial, that alter the physics, chemistry, biology or geology of the sea, to internal forces that redistribute, modify, consume, or guide this energy, and including interactions of all life, life support systems and the effects of man. Currents, temperatures, density, etc. have long been considered a part of fisheries studies. Although one may consider dismissing studies of nutrient chemistry because the absence or abundance of nutrients is reflected in primary (plant) production, there will be no evidence of why phytoplankton are scarce or abundant. When considering pelagic fish one can argue that even primary production can be dismissed because it is reflected in secondary production (herbivores), but when considering demersal or bottomfish, that

part of the plant production reaching the bottom plays an important role in the development of benthos which are consumed by bottomfish. However, secondary production and the subsequent trophic level, tertiary production (carnivorous plankton), are used in various stages of fish development and must be considered.

Recently the role of starvation - the lack of abundance of the required kind and size of forage at the appropriate time for fish larvae, juveniles and adults - has become an important consideration in fisheries oceanography studies. In terms of larval fish, such studies in the Bering Sea raise numerous questions because (as will be pointed out) our knowledge of early life stages of fish is extremely fragmentary. Although some information is available on age 1 pollock and juvenile yellowfin sole distributions, certainly there are not only vast gaps in our knowledge of the distributions and movements of these juveniles and those of other commercial species for one or in some instances even several years before they are recruited to the fishery, but also almost ignorance of juveniles of non-commercial species. This has not been a primary concern in managing adult stocks, but if one considers the eastern Bering Sea as a potential area for shelf ranching, a concept approaching reality as a result of the Fisheries Conservation and Management Act (FCMA), an entire spectrum of fisheries and oceanographic information will be required to define this ecosystem.

Although fisheries oceanography studies are not considered to be limited to relations of adult, commercial fish and their envi-

ronment, discussions in this Section are restricted to this aspect because studies on physical and biological oceanography, benthos, ice and other aspects of the Bering Sea ecosystem are presented in other Sections of this Volume. However, it should be pointed out that even when considering adult fish the term fisheries oceanography carries the connotation of studies pertaining to relations among environmental conditions, processes, or events, and species behavior and multispecies interactions and does not mean merely matching climatic or casual marine observations obtained during fishing or other cruises with catch data in an attempt to obtain one to one relations. One would hope that it signifies carefully designed experiments to define relations or verify suspected associations. Such experiments, with the possible exception of parts of the Processes and Resources of the Bering Sea Shelf (PROBES) program, have not been conducted in the eastern Bering Sea even though a great deal of general information has been obtained from foreign fishing fleets, specifically Japanese and Soviet. Because of management demands much of the U. S. research effort in the eastern Bering Sea has been devoted to what is present, rather than why it is and what factors can and do cause fluctuations in distribution and abundance of stocks. However, this trend is changing slowly as attention is directed more toward ecosystem models.

BACKGROUND

During a discussion of fisheries oceanography in the eastern Bering Sea at Fairbanks, Alaska, in 1974, the dissimilar spawning

and migration patterns of halibut, yellowfin sole and Pacific salmon were noted and it was pointed out that PROBES offered an excellent opportunity to conduct multidisciplinary research in relation to or in concert with fisheries (Favorite 1974a). Although an excellent group of investigators joined PROBES, there was little effort focused on any fishery but pollock, and only the egg and larval stages have been studied. Now, 5 years later, this opportunity to investigate in greater detail these and other patterns of multispecies interactions and resource-environment relations was welcomed.

There is a saying that nature abhors an equilibrium, that natural forces do not necessarily operate to maintain the status quo and often man's intervention is all that is required to tilt the system, sometimes drastically. In our haste to evaluate present conditions we should not ignore the past or assume that steady state balances between primary production and biomass exists. Except for folklore our early knowledge of fish components stems largely from Cook's voyage in 1778 during which halibut, cod, salmon, and other fishes and mammals were encountered (Munford 1963) but of course relative abundances were unknown. For roughly a quarter of the 19th century the shelf area south of St. Matthew Island with the exception of inner Bristol Bay was considered a major whaling ground and the area between Nunivak and Unimak Islands was still in use in 1875. The exploitation of whales and fur seals in this area and the subsequent exploitation of cod in the same general area in the late 19th and early 20th

centuries must have altered several niches and extant transfers of energy between trophic levels, but there are no data to show cause and effect. For example, did the reduction in whale populations auger well for fish populations, either due to an increase in availability of planktonic forage or decrease in consumption of fish; did the extensive removal of cod by the fishery permit establishment of the current massive crab biomass; and, will the extensive present fishery on pollock result in a change in the feeding habits of fur seals that could trigger subsequent changes in the ecosystem?

The information on recent events is better but still fragmentary. The recent demise of halibut although not necessarily due to overfishing is certainly related to the extensive bottom trawling effort during the last one or two decades. Although the pollock resource is apparently large, it is not certain whether this is due to reductions of older age groups by the fishery thereby reducing the effects of cannibalism or the fact that there appears to be a substantial stock seaward of the shelf serving as a reservoir and source of replenishment. Yellowfin sole abundance was severely reduced after the initial fishing on this stock in the 1960's. Herring abundance has always been variable and attempts today to estimate stock size are subject to close scrutiny. And of course for years catches by Japanese salmon motherships have affected forecast estimates of salmon returns to various river systems based largely on counts of downstream migrants supplemented with data from oceanic monitoring.

There is little need to be defensive about the incompleteness of knowledge concerning environmental processes affecting fisheries and stock assessment in the eastern Bering Sea when one recognizes that such studies and evaluations are still being conducted in the North Sea where fisheries investigations have been carried out independently and cooperatively by numerous nations for centuries. It was not until the late 18th century that Vancouver showed the eastern side of Bering Strait was part of North America and provided a map of coastal features. And it was not until the early part of the 19th century that maps and charts indicated that the name Kamchatka Sea was changed to Bering Sea. Wilimovsky (1966) has summarized early voyages in this area.

Typically exploitation has come before scientific exploration. By the mid-19th century whaling grounds over the southeastern Bering Sea had largely been abandoned and whalers were entering the Arctic Ocean. At the turn of the century the cod on Slime and Baird Banks north of the Alaska Peninsula were heavily fished and numerous salmon canneries were in operation in Bristol Bay and surrounding areas. Yet it is only today that an understanding of oceanographic conditions and processes is being derived largely through studies by OCSEAP, PROBES, NWAFC and other agencies.

Knowledge of bathymetry has also been fragmentary. Although at the end of the 19th Century U. S. Coast and Geodetic Survey and U. S. Bureau of Fisheries charts revealed the existence of the broad shelf and its abrupt termination at the edge of the Bering

Sea basin, it has been only within the last decade that a large 300 m depression shown on Japanese and Soviet charts to occur between the Pribilof Islands and St. Matthew Island was found to be nonexistent (Favorite 1974b). And only within the last few years has some of the complexity of the bathymetry at the shelf edge been forthcoming as a result of fishing operations.

FISHERIES OCEANOGRAPHY

There are several periods during which fisheries and oceanographic data have been collected with wide-ranging degrees of synopticity and thoroughness. Certainly the whalers in the mid-19th century recorded casual environmental data that when combined with data from geographical explorations provided insight into resources and conditions (Dall 1882 - see Shelf Environment). At the end of the century the U. S. Bureau of Fisheries conducted studies from aboard the Steamer Albatross, but it was not until the 1930's that fisheries or oceanographic studies resumed and except for the World War II period the field efforts have markedly accelerated up to the present time.

Steamer Albatross

Rathbun (1894) reported that the Albatross explorations were noteworthy in that they constituted an innovation in support of the fishing industry beyond that ever attempted by any foreign nation. In a summary of cruises from 1888-1892 in the eastern Bering Sea he noted that although 3 cod banks had been recognized north of the Alaska Peninsula - Slime, Baird, and Kulukak - these banks were not necessarly separate and distinct, except that the

westernmost, Slime Bank, was characterized by immense numbers of a large jelly-fish, brownish or rusty in color, measuring from 15-45 cm inches across with long tenacles having great stinging powers. Although not observed upon the sea surface, and concentrations appeared abruptly around July 1, they interfered with the lowering of fishing hooks, the use of cod trawls, and even raising anchors. Today the general location may be construed as a frontal zone between oceanic and shelf water but other factors are certainly involved in the phenomenon. The largest and best cod during this summer period were taken 11-14 km north of the peninsula, those inshore were of smaller size and inferior quality. Even today there is little specific information concerning the nature or structure of a front along the coast. Rathbun noted also that problems concerning the habits of fur seals on the Pribilof Islands, near the outer edge of the bank, made it very important that the physical and biological features of the surrounding area should be thoroughly studied, and that the distribution of cod was greatly influenced by the movements of capelin, herring, and sand lance but scarcely anything was known regarding the habits of these species on the Alaska coast. However, shortly after the turn of the century the Albatross cruises in this area ceased. It is only in the last few years that such studies have commenced.

Salmon Studies, 1938-41

Except for some tagging studies in the 1920's (e.g. Gilbert 1924) near Port Moller of salmon returning to Bristol Bay streams there is little evidence of marine research in the area until the

1930's when the Japanese commenced a crab fishery and a small operation for bottomfish on the shelf. When it became apparent in 1937 that these operations were to extend to salmon fishing, funds were made available to the U. S. Fish and Wildlife Service (FWS) to conduct investigations on the migration routes and availability of salmon in western Alaska and particularly salmon of the Bristol Bay region. Oceanographic studies were conducted from aboard the U.S.C.G.T. Redwing in 1938 and salmon fishing aboard chartered fishing vessels in 1939; both operations continued until 1941 when they were interrupted by the outbreak of World War II and reports of results were delayed (Barnaby 1952, Favorite and Petersen 1959, and Favorite et al. 1961). Although salmon were caught in all areas fished over the southeastern part of the shelf, they were apparently more abundant in the area 54-108 km offshore along the north side of the Alaska Peninsula. The cause for this is still unexplained although it has been ascertained that seaward migrating smolts occur inshore of the shoreward migration of adults (Straty 1974). Further, there was a marked shift in dominance from sockeye to chum salmon northward of the Pribilof Islands believed to represent a migration path of the latter to more northern coastal streams. Prophetically Barnaby noted that there were large populations of bottomfish and shellfish in the area and it was only a matter of time before exploitation would occur.

Crab Studies, 1941

In 1940 Congress approved a special appropriation authorizing the FWS to conduct a king crab study off the coast of Alaska and

operations in the Bering Sea were conducted from April-September in 1941 (Fish. Tech. Lab. 1942). Bottom isotherms indicated a tongue of cold water between Cape Newenham and the Pribilof Islands in in the direction of Port Moller and sharp ingredients along the north side of the Alaska peninsula were believed to cause rapid changes in water temperature relatively close inshore particularly between Amak and Seal Islands where the greatest concentrations of crabs were found, but since similar conditions did not occur in other productive areas the significance of this possible relationship could not be evaluated. However, it was pointed out that the accidental catch of edible flatfish was phenomenal. Cod were found in offshore waters at depths deeper than usually fished commercially and were larger; pollock and yellowfin sole were found in great abundance and the possibility of a commercial fishery for halibut was indicated. These studies also ceased at the outbreak of the war.

Bottom Trawling and Oceanography, 1948-49

Crab studies resumed in 1947 aboard the charter vessel Alaska (King 1949) in a small area about 75 km northwest of Port Moller. When conditions permitted air, surface and bottom temperatures were obtained. Maximum crab catch occurred at a bottom temperature of 3 C and catches were made at temperatures from 1.65-7.25 C. Unusually large incidental catches of pollock and yellowfin sole obtained were roughly an order of magnitude larger than cod catches and undoubtedly this prompted the chartered mothership operation (Pacific Explorer with a fleet of 10 fishing vessels)

from April to July 1948 in the Amak Island and Black Hills area (Wigutoff and Carlson 1950); but no environmental data are reported.

Perhaps the first fishery cruise that seriously considered oceanographic conditions was conducted aboard the chartered Deep Sea from Unimak Pass to Norton Sound during the last week in June and the first week in July 1949. The report of the cruise (Ellson et al. 1950) indicates awareness of previous oceanographic studies (Ratmanoff 1937; Barnes and Thompson 1938; Goodman et al. 1942; and others) and results indicated: a correlation between depth and bottom temperatures except for the corridor of subzero bottom water extending past St. Matthew Island to the southwestern portion of St. Lawrence Island; bottom water temperatures were positively correlated more than any other factor with the abundance of fish taken over the entire area; temperatures at the surface and bottom were several degrees lower than those observed in the previous September from aboard the U.S.F.W.S. Washington; summer warming influenced the northward migration of many fish; the cold corridor effectively acted as a faunistic barrier to the movement of many species through the strait between Siberia and St. Lawrence Island; the fauna in this area consisted mainly of eelpouts, liparids, sculpins and Tanner crabs; the continuity of the corridor was believed to extend past St. Matthew Island and the Pribilof Islands into the southeastern Bering Sea and was believed to cause a shunting of species entering Bering Sea through the Aleutian passes to the eastward before continuing northward; cod

and flatfish in particular were assumed to "lead" along the edges of the cold water barrier thereby explaining the concentrations found in the approaches to Bristol Bay and northward along the warm water channel adjacent to the coast.

These cruises indicate there was ample evidence a number of years ago of numerous potential relations between these resources and the environment to justify conducting specific fisheries oceanography studies that would enhance conservation and management practices.

Recent Studies

Commercial exploitation of resources, largely by the Japanese, intensified in the 1950's. Scientific studies and conservation measures were enhanced by the formation in 1953 of the International North Pacific Fisheries Commission (INPFC) whose reports, documents and bulletins are readily accessible and contain reports of Japanese and U. S. investigations on crab and fish resources that are in progress even today. And the NWAFC has conducted an extensive annual survey of resources in the southern part of the area since the early 1970's. However, environmental observations are limited and only incidental to fishing effort.

The extensive Soviet Bering Sea Comprehensive Scientific-Commercial Expedition commenced in 1958 and resulted in numerous compilations of environmental conditions summarized by Favorite et al. (1976) and fishing reports (Moiseev 1963-72) that are cited throughout the following Chapters. Even though this Soviet activity prompted extensive analyses of existing oceanographic and

fisheries data, and environmental observations obtained from aboard fishing vessels contributed to general resource-environment relations, such observations were incidental to the fishing effort, fragmentary and not available through normal channels. Further, no major Soviet oceanographic vessel participated in the investigations.

Recently there has been a trend toward cooperative international fisheries research that becomes more coordinated and successful each year. Emphasis is still, however, largely on fishing at predetermined station locations that provide assessments of resource abundance and little emphasis in terms of funds, personnel and vessel time is allocated to specific fishery oceanography studies that may provide the key to more efficient and effective resource assessment and improved management and conservation.

SECTION SUMMARY

The eastern Bering Sea has numerous physical and biological characteristics that should be documented here. First it has an unusually broad, relatively flat continental shelf the slope of which abruptly increases largely near the 150 m isobath. Relatively isolated from currents of the North Pacific basin by the Alaska Peninsula, the Bering Sea basin by the abrupt shelf edge, and the Arctic basin by the narrow and shallow Bering Strait, it has three major embayments: Bristol Bay, Norton Sound and the Gulf of Anadyr. It is basically a subarctic environment with ice cover present and expanding seaward from October to a maximum in April, and largely absent by June. Although surface and coastal

water temperatures in summer are not unlike those as far south as the Washington coast, the -1.8 C water temperatures under the ice in winter and near the bottom at mid-shelf during summer identify the Bering Sea shelf regime. High river runoff in late spring markedly alters coastal water properties and flow, and oceanic perturbations greatly affect flow at the outer portion of the shelf; whereas, conditions at mid-shelf are largely influenced by tidal currents, formation of a surface layer in summer as ice melt and warming result in positive stability, and water overturn during winter as slight negative stability occurs during the freezing out of salt as ice is formed.

The sluggish circulation and nutrient replenishment as a result of winter overturn is conducive to high production and standing stocks in spring and summer and the ice in winter causes extensive fish migrations to the deeper, warmer water at the shelf edge and upper slope. Pollock are the dominant semidemersal species, yellowfin sole the dominant demersal species, and herring a dominant pelagic species although the anadromous salmon are abundant from June to September.

Although the largely discipline oriented approaches by individual OCSEAP research units and the generally independent field surveys make it difficult to make multispecies or interdisciplinary assessments, the opportunity to bring the fragmentary information on the various life stages of major biological components up to date, to assess dynamic aspects of the ecosysyem, and to extend the available knowledge through the use of simulation tech-

niques presented a great challenge, and is what we as a group have attempted to accomplish --in spite of frustrations associated with the lack of continuity of data in space and time, the multiplicity of sampling techniques, and large gaps in basic knowledge. It has been necessary to be selective in our approach and limit discussions of resource-environment relations to several commercial fish, which obviously prey on zooplankton, other fish and benthos, and are preyed upon by fish, birds and mammals. Even though such interactions are poorly documented numerical assessments have been made using simulation techniques.

First, background information on environmental conditions (Ingraham) and distributions of ichthyoplankton (Waldron) are presented. Next, distributions, abundance, migrations, spawning activities and environmental relations of 5 selected species are summarized: Pacific halibut (*Hippoglossus stenolepis*) - that spawn seaward of the shelf in winter and migrate shoreward in spring (Best); Pacific herring (*Clupea harengus pallasi*) - some of which migrate inshore across the shelf in spring and spawn along the coast from April to July, and others that overwinter inshore (Wespestad and Barton); walleye pollock (*Theragra chalcogramma*) - that spawn perhaps ubiquitously in subarctic waters but certainly in large numbers inshore in spring along the shelf edge (Smith); yellowfin sole (*Limanda aspera*) - that migrate inshore across the shelf in late spring and early summer and spawn in the southeastern part of the shelf (Bakkala); and, salmon (*Oncorhynchus* spp.) - that as adults migrate shoreward across the shelf to various

coastal areas in late spring and early summer to spawn and as juveniles migrate seaward across the shelf to oceanic areas in spring and summer (Straty). Then, having provided a general, descriptive assessment of temporal and spatial variations in fish distributions, migrations and spawning locations in relation to environmental conditions or events (Favorite and Laevastu), an overall evaluation of the total biomass of ecosystem components and their interactions is made using simulation techniques (Laevastu and Favorite).

After having perused the following Chapters, one cannot help but feel that OCSEAP studies, rather than having completed baseline data acquisitions for the eastern Bering Sea shelf and achieved basic or preliminary understandings of processes, have actually only permitted us to define the nature of the tasks that have to be accomplished if we are to obtain a sufficient understanding of the eastern Bering Sea ecosystem to assess the impact of oil exploration and exploitation and protect the extant living marine resources.

Up to this point little new information has been obtained and previous knowledge has been only marginally extended. One talks about warm and cold years, but nothing is known about what occurs under the ice. One attempts to measure primary and secondary production without concern about patchiness, predation and reproduction, or evidence of biomass balances. One conducts casual studies of ichthyoplankton without regard to the limitations in our knowledge of their identification or location and never pur-

sues organisms much beyond the egg stages. One knows little or nothing about the migrations or distributions of juveniles for the one or several years before they enter the fishery as adults. One notes that cold conditions appear to delay shoreward migrations of adults but in some instances also notes that migrations of more northerly stocks do not appear to be influenced at all by equivalent temperatures. And, in most cases, knowledge of year round distributions and migrations of adult fishes and specific causes for aggregations or movements is still severely limited.

It is easy to say the ocean is a turbulent regime, that each year is different, and that only gross assessment can be made and only general relations be ascertained. However, there is an apparent order to the Bering Sea ecosystem that implies in many instances some very specific fish responses that we do not understand and only dedicated, multidisciplinary research (fisheries oceanography) will provide the answers.

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SHELF ENVIRONMENT

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ABSTRACT

Monthly mean environmental conditions of ice, temperature, runoff and salinity for winter (January-March), May, July and September are presented for the eastern Bering Sea shelf area. Mean geostrophic flow (0/50 db) in summer (July) reflect the northwesterly flow at the shelf edge and a westward flow from the Yukon River area seaward south of St. Lawrence Island. Tidal currents as derived from a hydrodynamical-numerical model reflect a NW/SE flow over the outer shelf and NE/SW flow north of the Alaska Peninsula, between Nunivak and St. Matthew Island and in the southern Gulf of Anadyr. Although data are fragmentary, environmental conditions over the shelf are highly variable and examples of N-S surface wind components (1946-1975), ice cover (1976-1978), and bottom temperatures (1969, 1973, 1976 and 1977) reflect departures from mean conditions.

INTRODUCTION

The eastern Bering Sea shelf is characterized by several features that have pronounced effects on its hydroclimate. Sloping gently westward over 500 km, the shelf terminates abruptly as the

continental slope drops somewhat precipitously into the Aleutian basin and this results in a coastal-oceanic water interface that largely divides the surface area of the Bering Sea in half. The shelf is isolated from the direct effects of circulation in the Pacific Ocean by the Alaska Peninsula and sheltered from the Arctic Ocean by the narrow, shallow Bering Strait.

Seasonal advance and retreat of ice cover in winter and spring, and the extensive discharge of runoff in spring and summer dominate conditions and processes in the hydroclimate. Since physical processes have been discussed in another Section of this Volume, we are concerned here primarily with conditions over the entire shelf area, in so far as data are available. Brief reference is made to historical studies, mean conditions for January-March, May, July and September are presented, and variations in ice, winds and bottom temperatures are discussed.

Although even today the Bering Sea is considered a remote and hostile area, it must have been considerably more treacherous and foreboding to early explorers and particularly whalers with limited resources and technology. The loss of 33 whaling vessels north of Bering Strait in 1871, only 4 years after U.S. acquisition of Russian America, resulted in environmental studies in the northern shelf area (e.g. survey of Bering Strait from U. S. Schooner Yukon in 1880) and an assessment of logs and reports from whaling and other vessels transiting this area (Dall 1882), and considerable information was derived.

First, in respect to ice and surface temperatures: (1) the

southern limit of ice was shown first to extend to 56°N in the central Bering Sea and well below the Pribilof Islands in the shelf area; (2) in cold years ice remains around St. Paul Island until late May; (3) ice opened to the westward of St. Lawrence Island first, it frequently being navigable there and north of the island into Norton Sound, at a time in the season when the passage between Nunivak Island and St. Lawrence Islands is still blocked with decaying ice; (4) water opens first where the southerly cold set away from the ice is strongest; (5) the extent of ice in different years varies and depends on winds, with prolonged winds from the north bringing loose flow ice southward which is prevented from returning northward when the winds change by the formation of new ice; (6) the water retains nearly its normal temperature up to within a very short distance from a large field of ice; (7) the Yukon discharge during summer months gives rise to definite local currents; (8) in summer at depths of 10 ftm (18 m) a higher degree of temperature is found than that which obtains in adjacent deeper water; (9) surface temperatures in Norton Sound obtained at anchor on 7 July over a 24 hr period varied from 6.7-12.2 C, a range of 5.5 C. Recent cruises and satellite imagery have largely borne out these early observations.

Second, in respect to surface currents it was recognized that: (1) discharges from numerous large rivers and the westerly and northerly marching tide create a distinct set in the vicinity of their mouths more or less directed by local winds; (2) the Kuskokwim and Bristol Bay rivers have a southwesterly or southeasterly

set depending on prevailing wind and tide; (3) discharge from the Yukon River in calm weather would proceed in a northwesterly direction, but under northerly winds or ebb tide, or both, part or all of it would pass to the southward of St. Lawrence Island; (4) away from the influence of the rivers the current is influenced a great deal by the direction and force of the wind; (5) north of Nunivak Island (60°41'N, 166°04'W) the U.S.S. Corwin reported NW/SE tidal currents of 0.5-2 kts (~25-100 cm/sec) while in the ice; (6) at St.George Island a steady current of one to two kts (~50-100 cm/sec) from the west is sometimes observed for several days; (7) currents across Bering Strait (0705-1415 hrs, Sept. 5, 1880 from aboard U.S.S. Yukon under fresh NWly wind, transit west to east) varied as follows: E21.8°S, 3.4 kts; N24.3°W, 1.5 kts; W28.3°E, 3.8 kts; S1.3°E, 2.5 kts; W31.0°N, 2.2 kts. Numerous reports of drifts of whalers under various conditions of ice, winds, and sea were presented for analysis and provide considerable insight not only into tidal flow but also general drift. All this information reflected the complexity in flow and the difficulty even today in evaluating flow from a limited number of current meters.

Third, in respect to subsurface data, which of course were sparse because of limited instrumentation, there were reports of conditions across Bering Strait and of environmental divisions over the shelf of considerable value. The U.S.S. Yukon hydrothermal cross-section of Bering Strait in September 1880 clearly indicated: the 6 C temperature difference across the strait--vertically isothermal conditions of 2.6 - 8.6 C (36.7 - 48 F) in the western

third; the temperature gradient (3.3 - 7.2 C) regime in the central third; and the slight stratification of water of 7.8 - 9 C (46 - 48 F) in the eastern third with maximum values near the surface, offshore of the eastern side of the strait. However, in spite of the temperature differences and the implication of opposing currents existing in the strait, the fact that strong northerly and southerly currents had been experienced on both sides of the strait by various navigators suggested that there was not sufficient evidence to report that a southerly cold current occurs on the west side of the strait, and a warm northern current on the east; but it was recognized that the northerly flow on the east side of the strait was composed largely of river runoff. In addition, based upon temperature data only, the Bering Sea was separated into 3 divisions: (A) the shallows (e.g. Bristol Bay, Norton Sound, etc.) and the area seaward to the 25 ftm (~46 m) contour; (B) the moderate depths, between the 25 ftm (~46 m) and the 75 ftm (~137 m) contours, from Bering Strait to the Alaska peninsula; and (C) the deep waters to the south and west. Attempts to improve on this scheme have continued up to today and do not deviate significantly from this early assessment. Favorite (1974), prior to OCSEAP and PROBES studies denoted 4 sub-domains distinguished by temperature-salinity relations: Gulf of Anadyr, West Alaska Coast, Mid-Shelf and Shelf Edge (Fig. 1). PROBES studies have focused on the frontal zones between these sub-domains only in the southern part of the shelf (e.g. Coachman and Charnell 1979).

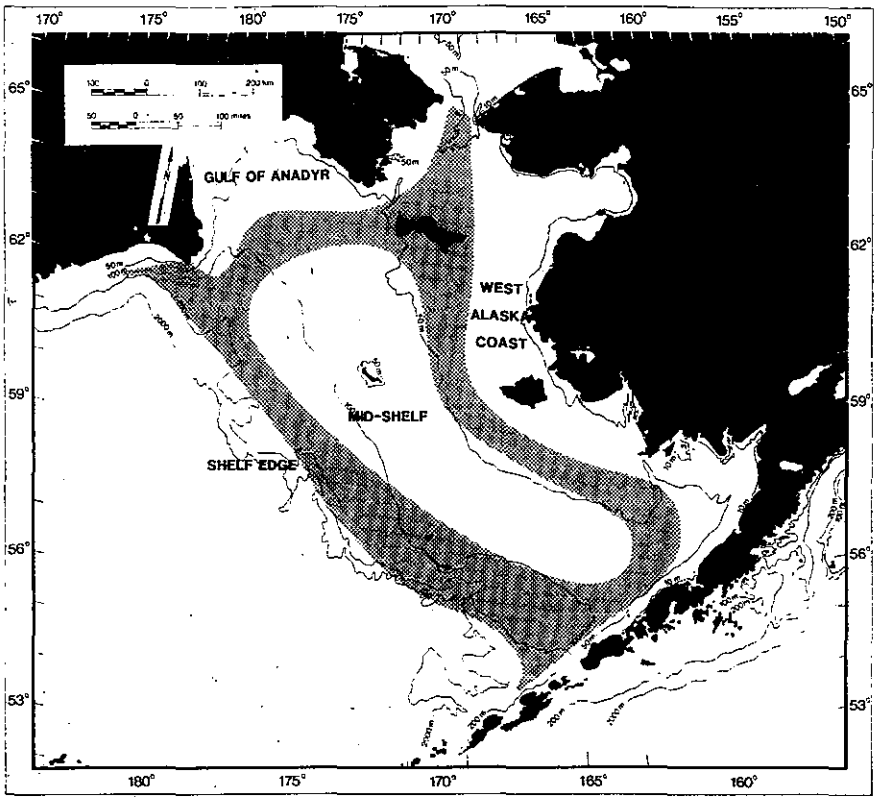

FIG. 1 Shelf sub-domains ascertained by T-S relations in 1x1° quadrangles.

Although most investigators are familiar with the University of Washington oceanographic studies in the 1930's (e.g. Barnes and Thompson 1938) and those by the U. S. Bureau of Fisheries in 1938-41 (e.g. Favorite and Pedersen 1959; Favorite et al. 1961), few are aware of the studies by the U.S. Naval Electronics Laboratory in 1949 because some aspects were classified. Some results are available (Saur et al. 1952) that describe general summer conditions, and temperature and salinity relations were used to identify 7 water masses in the eastern Bering and Chukchi Seas.

Oceanographic studies conducted from 1953 to the present time during fisheries investigations under the aegis of the International North Pacific Fisheries Commission (INPFC) and other studies during this period have been summarized by Dodimead et al. (1963) and Favorite et al. (1976) and recent OCSEAP and PROBES studies are summarized in the Physical Oceanography Section of this Volume.

MONTHLY MEAN CONDITIONS

Ice information presented is based on data from Potocsky (1975) and recent satellite imagery; temperature and salinity data are based on the current NODC geofile (including OCSEAP data) and Japanese and NWAFC fisheries cruises. The latter data have been computer processed into monthly means by ½° (lat.) and 1° (long.) quadrangles and anomalies are derived from these means, however, only summaries of conditions for winter (January-March), May, July and September are presented and discussed. There are several limitations to the presentations of mean conditions in this area:

First, there are not sufficient data for summaries by ½ x 1° quadrangles (nor even 2 x 2°) thus there are numerous gaps in each month and only limited data from October to March; second, there was no equivalent acquisition of data in warm and cold years, thus in some instances the values represent mean conditions or conditions in warm or cold years, possibly extremely anomalous conditions (there is not space to document the numbers of observations and years obtained, but this information is available at NWAFC); and, third, the paucity of data can also result in isolated anomalous values and tongue-like protrusions that may merely reflect a preponderance of data from a single year rather than a significant environmental feature. Nevertheless, the data reflect a high degree of continuity of conditions throughout the area that cannot be obtained in any other manner.

Ice

In the northern Bering Sea, monthly mean air temperatures vary from 10 C in summer to -20 C in winter and extreme conditions extend this range over 10 C higher in summer and lower in winter. Temperatures are below 0 C largely from October to May and thus sea ice plays a dominant role in the ocean environment. Freezing occurs at about -1.8 C in this area and the formation of ice limits winter cooling of sea water to this temperature.

Much of the increasing solar radiation in spring is consumed in the melting of ice and the seasonal increase of sea surface temperatures is delayed. However, when ice is no longer present, dilution and abrupt warming at the sea surface result in a shallow,

stable surface layer which retains most of the incoming radiation and permits nearly subtropical conditions to occur particularly in the inshore areas.

The area is free of ice only a short period usually from June or July to August or September. Usually by September ice begins to form near Cape Dezhnev and along the western shore of Bering Strait and by October it extends into the Gulf of Anadyr and across Bering Strait, even in the eastern part of Norton Sound. Mean conditions (Fig. 2) indicate a progressive southwesterly advance through March or April to the edge of the continental shelf, but a rapid retreat from May to June, from north of the Pribilof Islands to Bering Strait. Potocsky (1975) presents an excellent summary of mean ice conditions and indicates wide deviations from the monthly means and there is an entire Section on ice in this Volume.

Surface and Bottom Temperature

Mean surface temperatures primarily reflect the annual cycle of insolation; secondary effects are observed in nearshore areas affected by river runnoff and reduced cloud cover, and in areas of ice cover where spring warming is delayed until the ice is melted. Winter (January-March) surface temperatures of less than -1.5 C (Fig. 3) reflect the approximate extent of ice cover from Bristol Bay to Cape Navarin. The warmest water, 2 C, is located offshore in the ice free area and intermediate temperatures of 1-2 C are found just south of the ice on the southern portion of the shelf. By May temperatures over the southern shelf have increased to 3-5 C but over most of the shelf relatively low temperatures,

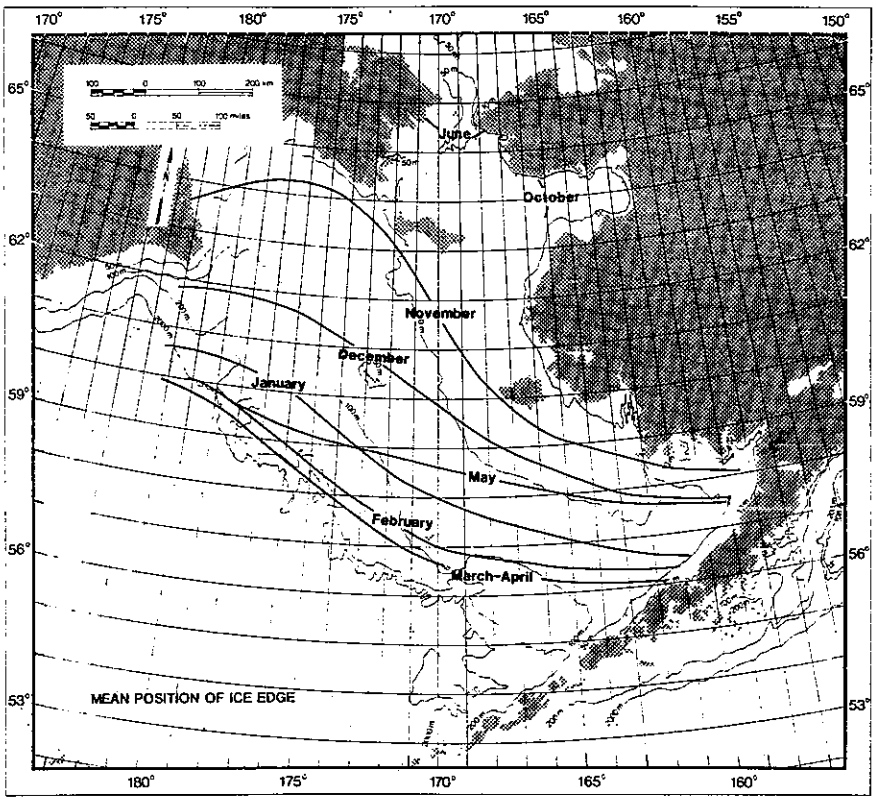

FIG. 2 Monthly mean location of ice edge.

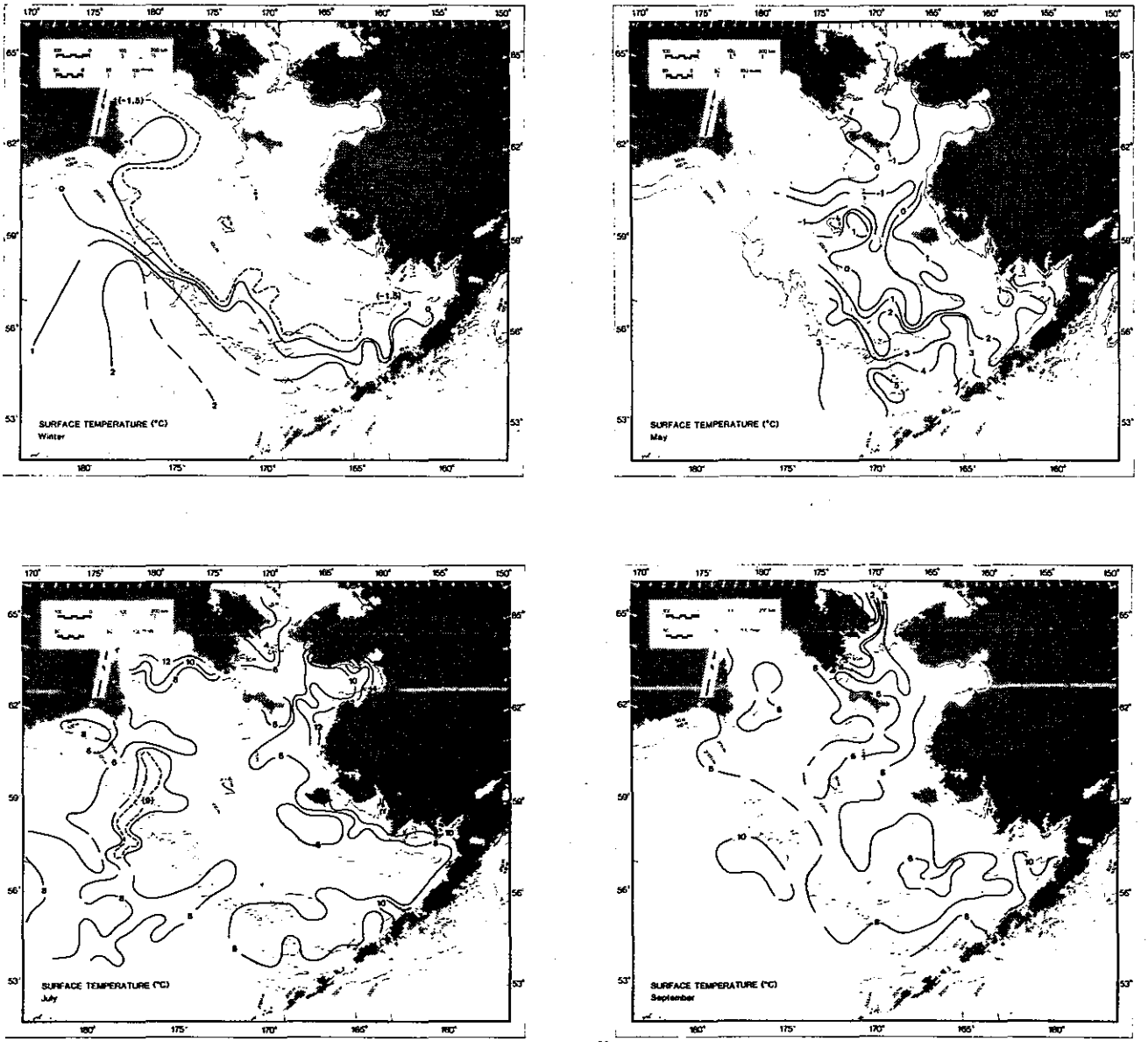

FIG. 3 Long-term mean sea surface temperature (C) for January to March, May, July and September.

between -1 and 1 C, prevail marking the initial stage of the heating cycle following the ice melt. Surface temperatures for July show most of the area has warmed rather quickly to 6 to 8 C and inshore temperatures have reached a maximum except in the extreme north with Bering Strait temperatures near 5-6 C and negative temperatures still present on the east coast of Siberia north of the strait. Local warm spots are seen with temperatures in excess of 16 C in Norton Sound and 12 C temperatures in Anadyr and Bristol Bays. August is the warmest month for surface water temperatures when the majority of the area reaches 8 to 10 C thus reducing the contrast between the offshore areas and the coastal areas where temperatures are nearly the same as in July. A dramatic change does occur, however, in Bering Strait with the apparent southward movement of cold, east Siberian coastal water and the apparent northward movement of the warm, Alaskan coastal water, thus producing a pronounced gradient of nearly 10 C between the cold western and warm eastern side of the strait. By September the effects of the beginning of the cooling cycle are seen as most of the area temperatures are between 7-9 C and coastal temperatures have decreased to about 10 C or less. The gradient across Bering Strait has decreased to about 6 C.

Bottom temperatures result primarily from the processes of vertical mixing and diffusion and to a lesser extent from the processes of horizontal mixing and advection. Mean temperatures less than -1.5 C in winter (January-March) were distributed over the majority of the shelf extending seaward as far southward as mid-

Bristol Bay and as far offshore as St. Matthew Island, but close to shore in Anadyr Bay (Fig. 4). Surface cooling, the formation of ice and overturn have produced a vertically isothermal water column which extends to a depth of at least 50 m and sometimes as much as 75 m. Warmer water of 2-4 C is found at depth near the shelf break associated with the general cyclonic (counterclockwise) circulation over the Bering Sea basin and the northward extension of Alaskan Stream water from the North Pacific Ocean. Thus, isotherms tend to be roughly parallel to the bathymetric contours. The presence of 0-1 C water just north of the Alaska Peninsula is probably correct in the mean sense, but the serpentine nature of the contours may be misleading due to the presence or absence of data during extreme winters when this area may be less than -1 C, or mild winters when temperatures are probably near 1 to 2 C; for this reason, the presence or absence of a northeastward flow which is implied if one interprets the contours as warm advection from the southwest, cannot be substantiated. Another area that appears to be influenced by some cross-shelf, warm advection, however, is Anadyr Bay.

By May there has been little change in the bottom temperature distribution in the outer shelf area between the 100-200 m isobaths, but the shallow area from inside the 50 m isobath to the Alaskan coastline, from Bristol Bay to the mouth of the Yukon River, has warmed from the winter condition of less than -1.5 C to between 0 and 2 C, with highest values occurring closest to shore. Therefore, the dominant feature is the area of the remnant negative temperatures which appears as a large southeastward tongue located

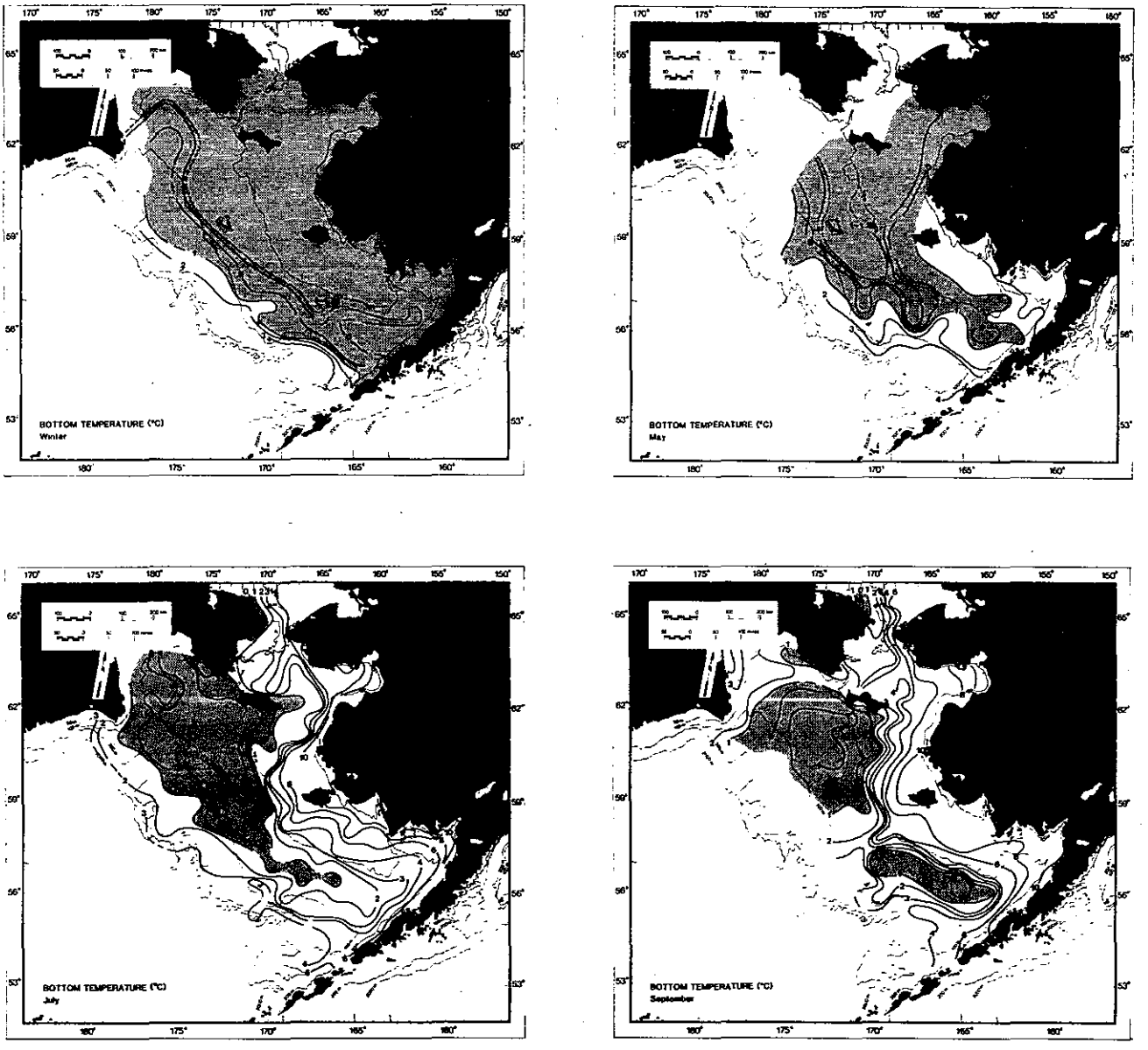

FIG. 4 Long-term mean bottom temperature (C) for January to March, May, July and September.

about mid-shelf. Apparently the dominant process in the warming of coastal bottom water at this time is downward mixing of surface-warmed water rather than horizontal warm advection from the south. The negative isotherms associated with the tongue appear discontinuous and in isolated areas, again, probably due to inadequate temporal distribution of data.

Because the best data coverage is during mid-summer, mean bottom temperatures for July show the most complete picture of shelf temperatures. The coastal area has warmed to in excess of 10 C from Bristol Bay to Norton Sound thus highly accentuating the inshore edge of the cold tongue where a large temperature gradient (10-12 C) occurs. Temperatures at the seaward side of the tongue remain about the same north of the Pribilof Islands. The cold core of the tongue appears to warm slightly as the portion south of 58°N is now more clearly defined by the 1 C isotherm; whereas to the north small remnant patches of less than -1.5 C water still occur. An increase of about 1 C is seen in a separate tongue advecting warm (greater than 4 C) water northwestward from Unimak Island. Similar to surface temperatures, bottom temperatures across Bering Strait reflect about a 4 C west to east gradient.

By September the warm coastal water (8-10 C) reaches its greatest seaward extent, thus sharpening the already high gradient on the eastern side of the cold tongue and shifting it slightly seaward to about 100 km offshore. A division appears to develop in the cold core near 58°N as 2-3 C water influenced by the westward movement of the warmer coastal water appears to separate the tongue

into two areas, which are each less than 1 C, to the north and south. The reappearance of some negative temperatures in the southern core reflects additional data in cold years in that July temperatures reflect higher values (0-1 C) and it is unlikely that the colder water was advected from the north across the intermediate warm area. In Norton Sound bottom temperatures increase to 6-8 C. And, on the northern edge of the cold core a tongue of 2 C water intruding from the west replaces the negative temperatures of July in Anadyr Bay.

River Runoff

Although data on river runoff are sparse, general characteristics for the area may be deduced from data for the Yukon River, the largest individual fresh water source. In terms of total land area which drains into the Bering Sea, the Yukon River comprises 45%, the Anadyr River 20%, the Kuskokwim 12%, the Nushagak 3%, and the remaining rivers 16%. Because of regional differences in precipitation, however, it may be misleading by as much as a factor of two to estimate the magnitude of discharge from the major rivers by comparing their drainage areas alone. The only data for an extended period of time are for the Yukon River at Ruby where 22 years of monthly mean discharge data are available. Long-term monthly averages (Fig. 5) indicate a pronounced seasonal pattern of runoff; low during the freezing period, decreasing from $2x10^3$ m^3/sec in November to $1x10^3$ m^3/sec in April, it increases rapidly to a peak of $13.5x10^3$ m^3/sec in June and then steadily decreases to low levels by November as the freezing period commences.

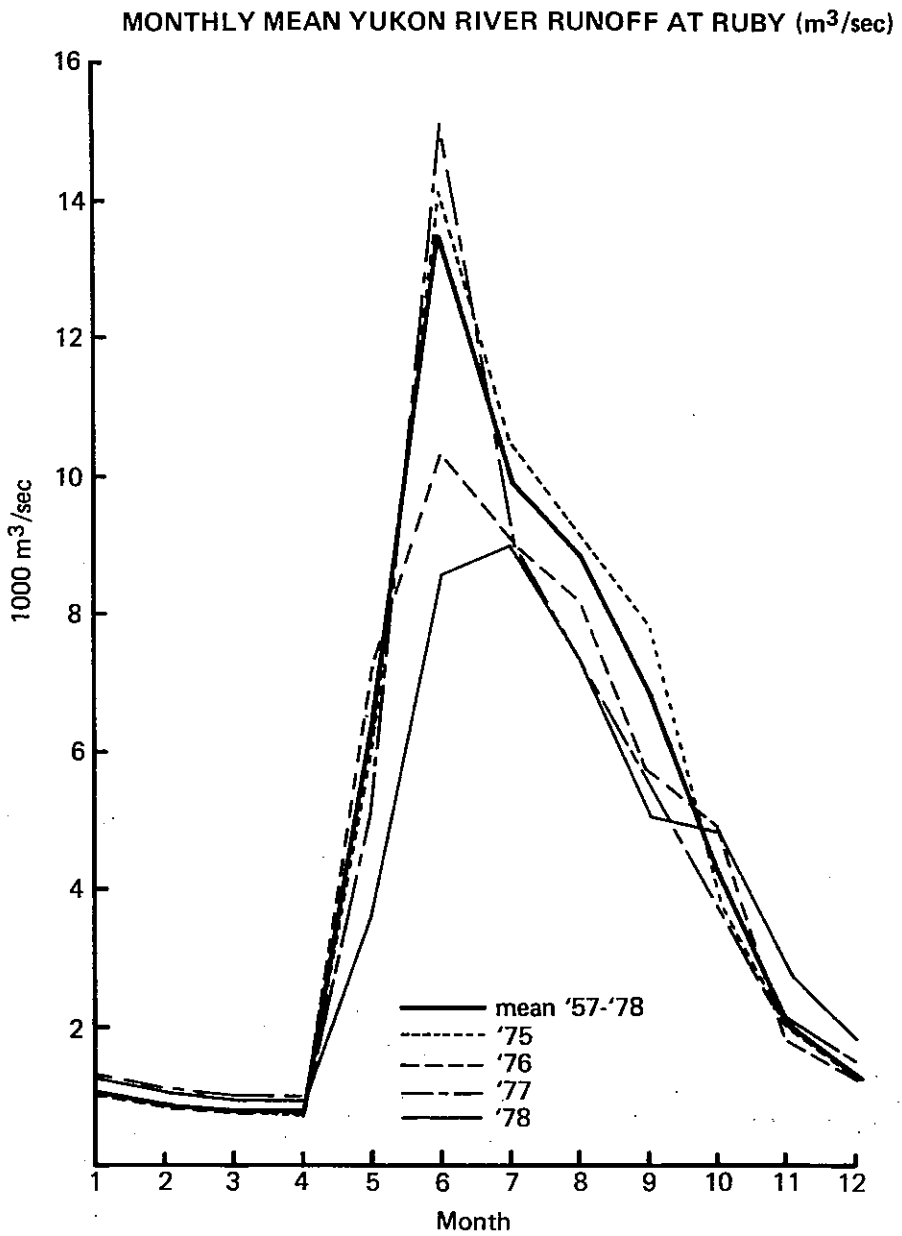

FIG. 5 Monthly mean Yukon River runoff (m^3/sec) at Ruby 1975-78 and long-term (22-year) mean.

Some examples of variability are evident in the last 4 years which are characterized by alternating high and low values. Commencing in 1975, above normal spring and summer runoff was followed by low values in spring and summer of 1976. This pattern was repeated with above normal runoff in spring 1977 and below normal values during spring and summer 1978. The lowest values in the last 4 years occurred in 1978 and a shift in the peak discharge from June to July. This shift also occurred in two other low discharge years, 1960 and 1963. For three consecutive summers (1976, 1977, and 1978) during the period following the annual peak discharge, runoff has been below normal.

Surface and Bottom Salinity

Mean surface salinities increase from November to April by the process of salt exclusion during freezing and decrease by precipitation and river runoff which delivers a large pulse of fresh water to the surface layer from May to October. Maximum values (greater than 33.3°/oo) occur in northern Anadyr Bay and north of St. Lawrence Island (Fig. 6) and are believed to be local results of the freezing process inasmuch as they are separated by large areas of lower salinity. Values less than 32.0°/oo occupy the majority of the shelf area south of St. Lawrence Island and out to about the 100 m isobath. By May several changes are evident. A decrease of 1-2°/oo is evident in inner Bristol Bay, Norton Sound and north of St. Lawrence Island, and a long tongue of less than 31.0°/oo extends eastward from the Yukon River mouth to just south of St. Lawrence Island. By July ice is no longer present and the river

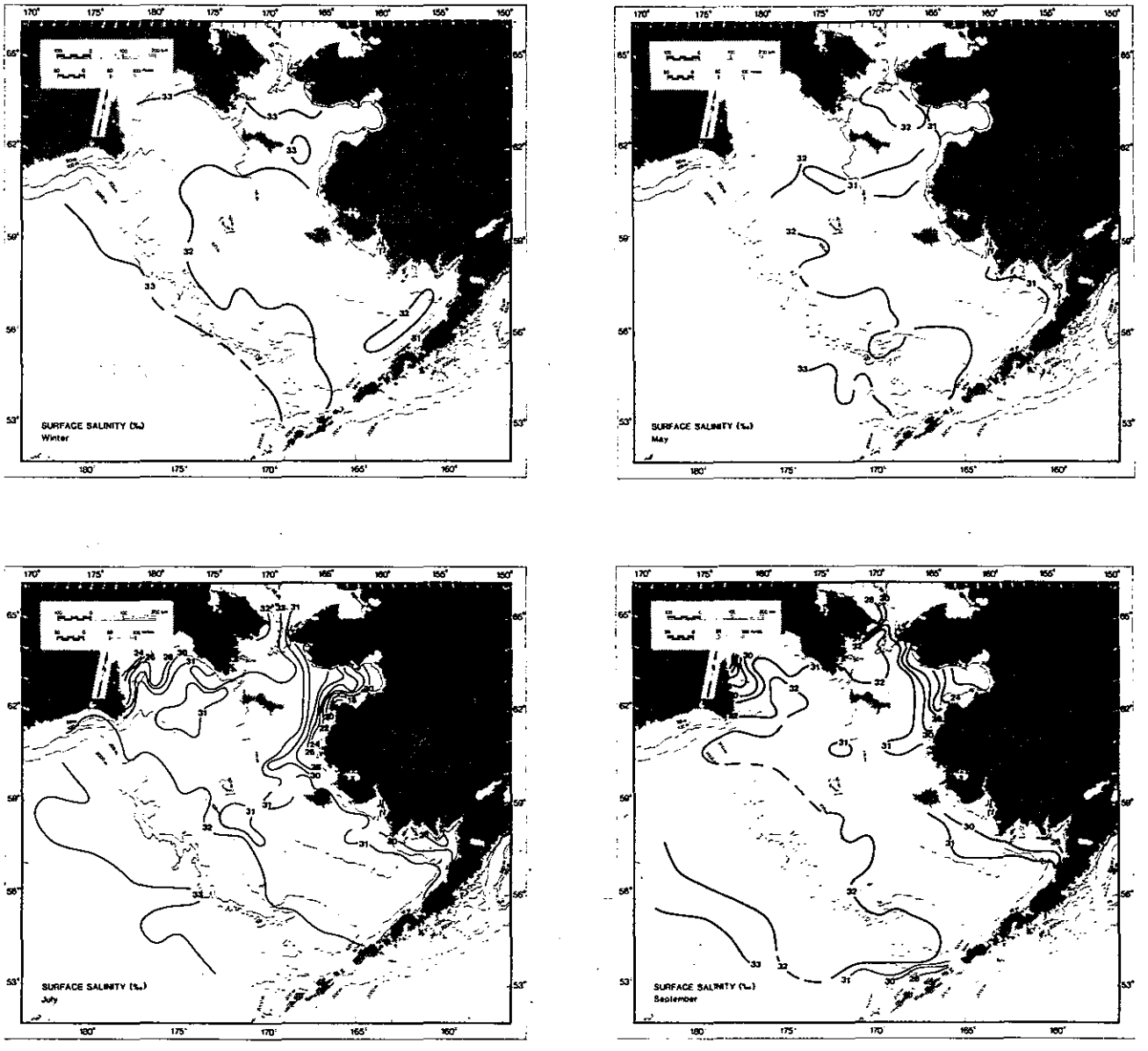

FIG. 6 Long-term mean sea surface salinity (°/oo) for January to March, May, July and September.

runoff has resulted in a pronounced dilution of surface water along the west coast of Alaska and in Anadyr Bay; and a minimum value of less than 16.0°/oo occurs in Norton Sound. Despite this marked dilution inshore and lesser changes offshore (evident in the westerly displacement of the 33.0°/oo - nearly 200 km), the 32.0°/oo isohaline appears to be in a consistent position roughly paralleling the 100 m isobath along an approxmate line from Unimak Island to Cape Navarin. By September the effect of further dilution seaward of the shelf is evident as very little water of greater than 33.0°/oo remains over the basin, but conditions in the shelf area are similar to those of July except for slightly higher salinities near the Yukon River mouth and in Norton Sound, probably the result of mixing and decreased runoff.

Mean bottom salinities below 50 m generally increase with depth. In January-March values of bottom and surface salinity are largely the same in water less than 50 m depth, essentially isohaline conditions (Fig. 7). In water deeper than 50 m, however, stratification appears to develop as shown by the displacement of both the 32.0 and 33.0 bottom isohalines about 100 km farther shoreward (northeastward) than the corresponding surface isohalines. This salinity increase with depth allows the higher temperatures at these depths to exist in a vertically stable density field. There is little change in bottom salinities in May except for the presence of some slight dilution of less than 31.0°/oo in inshore Bristol Bay and south of St. Lawrence Island. By July, however, strong dilution has occurred in Norton Sound with values

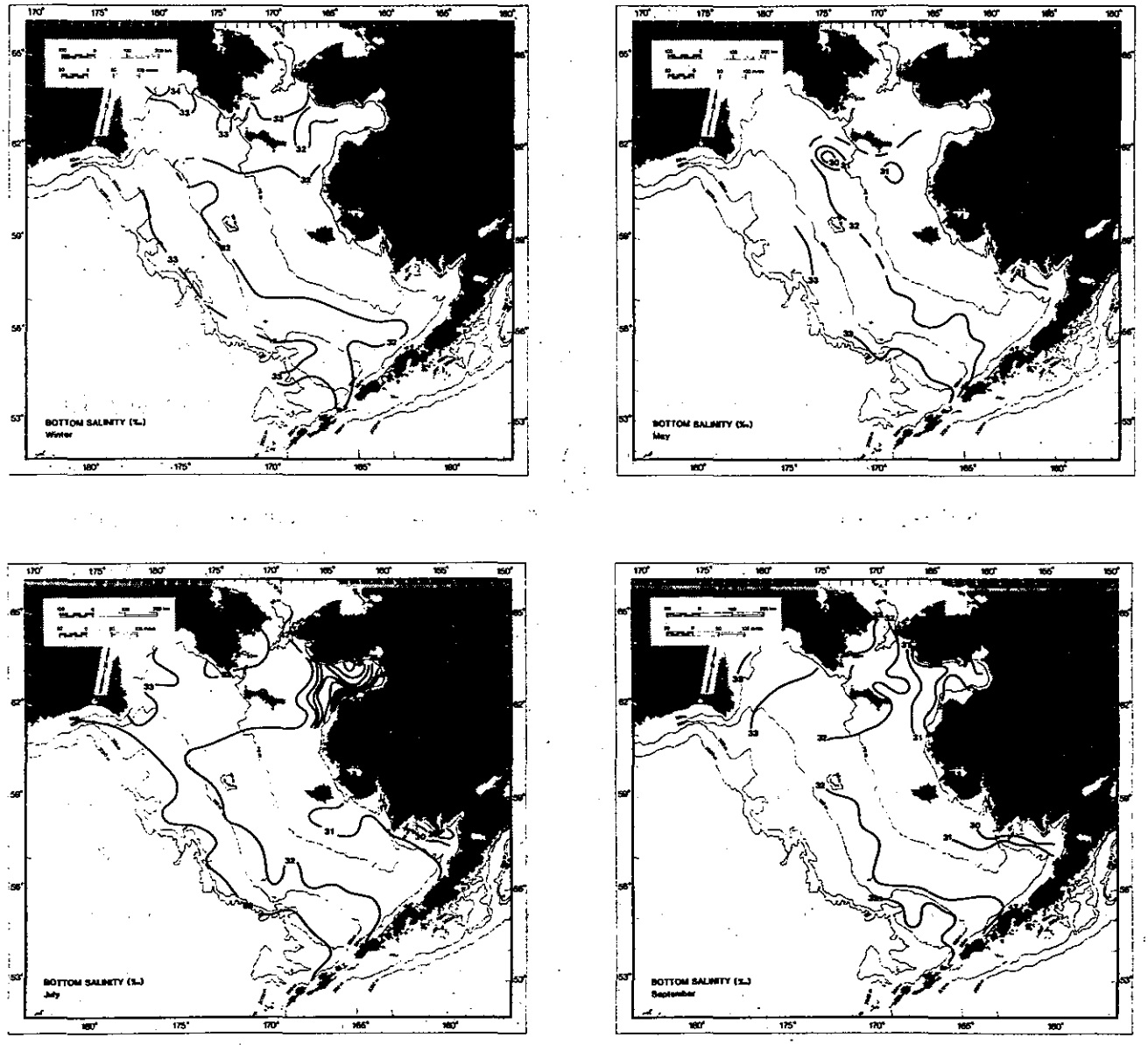

FIG. 7 Long-term mean bottom salinity (°/oo) for January-March, May, July and September.

less than 24.0°/oo and to a lesser extent in Bristol Bay (less than 28.0°/oo). A notable feature is the absence of dilution in Anadyr Bay at the bottom despite marked dilution at the surface and this condition persists through September as the area having salinities greater than 33.0°/oo continues to enlarge. Also evident in September is the extension of dilute water farther offshore in Norton Sound and the slight increase in bottom salinities in inshore Norton Sound and Bristol Bay, probably due to horizontal mixing.

Water Masses as Reflected by Surface and Bottom Temperatures

There have been numerous attempts to describe water masses in the Bering Sea using the classical method of T-S (temperature vs salinity) diagrams to recognize groups of data with similar water characteristics which are put into envelopes based upon dominant processes and/or the resulting water structure. Recent studies (e.g. Takenouti and Ohtani 1974) have considerably more detail than the early ones and OCSEAP studies have refined considerably our knowledge of water masses and their interactions over the southern shelf offshore from Bristol Bay (Kinder 1977; Kinder et al. 1978); however, 4 major distinct environments stand out -- Gulf of Anadyr, West Alaska Coast, Mid-Shelf, and Shelf Edge (Favorite 1974).

Although salinity characteristics influence the water mass definitions in the Gulf of Anadyr (where high salinities are associated with low temperatures due to the salt exclusion process) and also near the Shelf Edge area (from the influence of Bering Sea basin water) the most striking feature of the shelf environment is

the temperature regime, particularly in the mid-shelf and coastal waters. The coastal water mass is clearly distinct from the others because of its relatively constant vertically homogeneous nature; whereas, marked stratification occurs in summer at mid-shelf. Thus, to illustrate the extent and seasonal changes in mean water mass conditions, it is expedient to look at temperature changes between surface and bottom.

During January-March, mean temperature differences (surface minus bottom) are near zero over most of the shallow shelf as ice cover and deep vertical mixing result in isothermal conditions (Fig. 8). The most significant feature is the oblong area of -2 to -4 C differences which occurs all along the outer shelf where seasonally cold surface temperatures override a deep, warm, slightly more saline water mass. By May there is little change except west of St. Lawrence Island where two extreme values of -2 C and 2 C indicate local conditions at the beginning of spring warming following completion of ice melting. Dramatic changes are seen by July and continue through September as the dominant summer feature, a difference of 6-8 C, develops over the remnant tongue of cold mid-shelf bottom water. The eastern side of this area is clearly defined by a sharp decrease in temperature difference which approaches zero in coastal water; the western side, near the outer shelf, is less well defined as the decrease is due to the slightly warmer bottom temperatures.

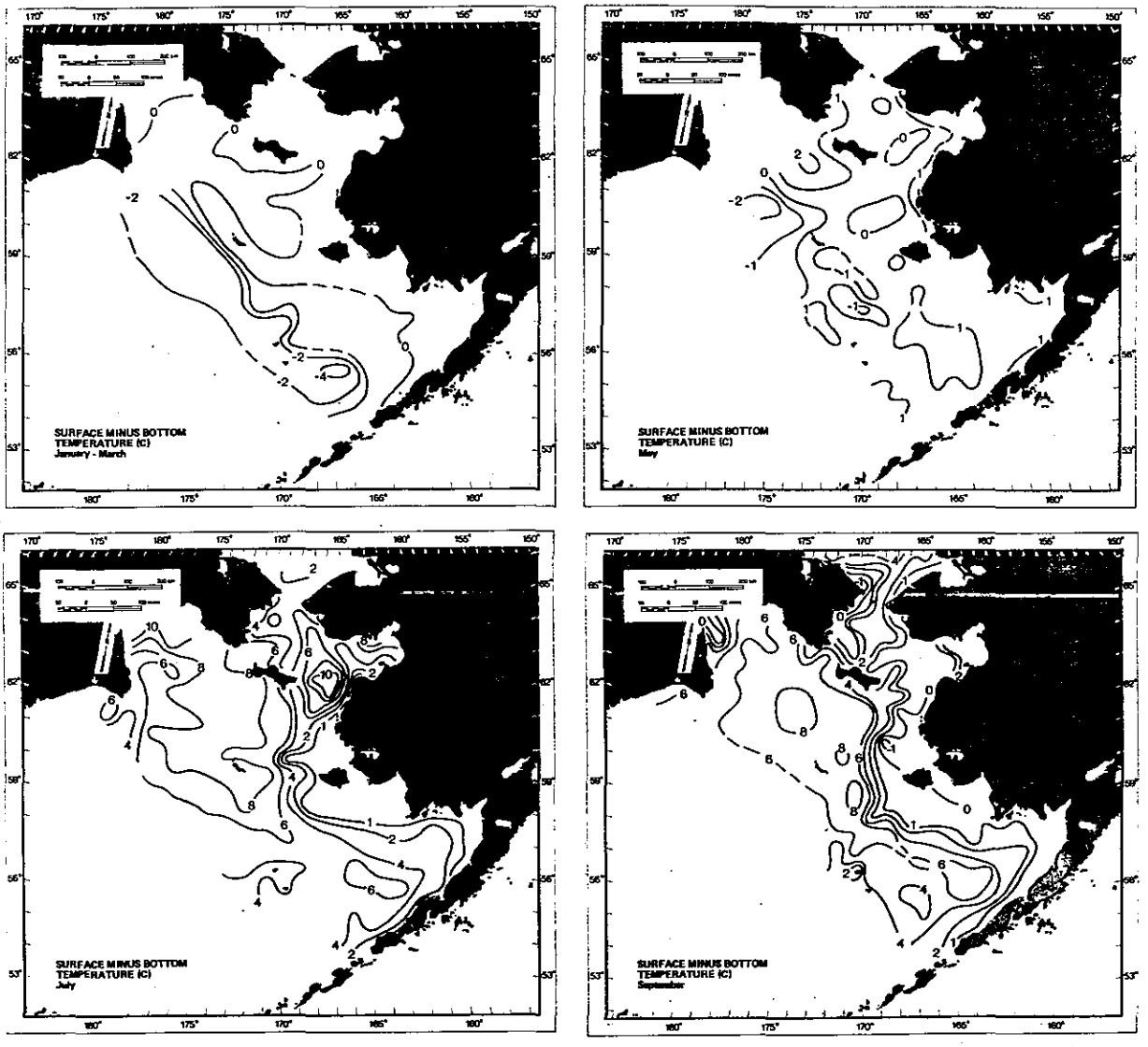

FIG. 8 Long-term mean surface minus bottom temperatures (C) for January to March, May, July and September.

Flow

Although the most reliable data on flow comes from direct current measurements, so few data have been taken and then only in local areas of individual interest such as Bering Strait and Bristol Bay (Coachman and Charnell 1979) that indirect methods are still required to imply net flow or mean circulation and these have proved effective in gaining knowledge of the general flow in the climatological sense which concerns us here. One must keep in mind that tidal components on the order of 50 cm/sec occur daily which reverse either diurnally or semi-diurnally, thus any estimate of mean flow will probably be at best about one order of magnitude of the instantaneous flow. An NWAFC tidal model study (Hastings 1975) indicated the reversals of flow largely NE/SW in inner Bristol Bay, between Nunivak and St. Matthew Islands and between St. Matthew Island and the Gulf of Anadyr; and NW/SE over much of the remainder of the shelf (Fig. 9). Although except in inner Bristol Bay (Dodimead et al. 1963) these flows have not been verified, the offshore/onshore flow south of St. Matthew was apparently noted by Dall (1882).

In the absence of direct measurements, the geostrophic approximation is widely used to calculate mean currents from the vertical distributions of temperature and salinity relative to an assumed level of no motion, usually below 1,000 m depth. This method has been used to establish the existence of northwestward mean flow Transverse Current (Favorite et al. 1976) seaward of the shelf edge, but is invalid in shallow water over the shelf except for

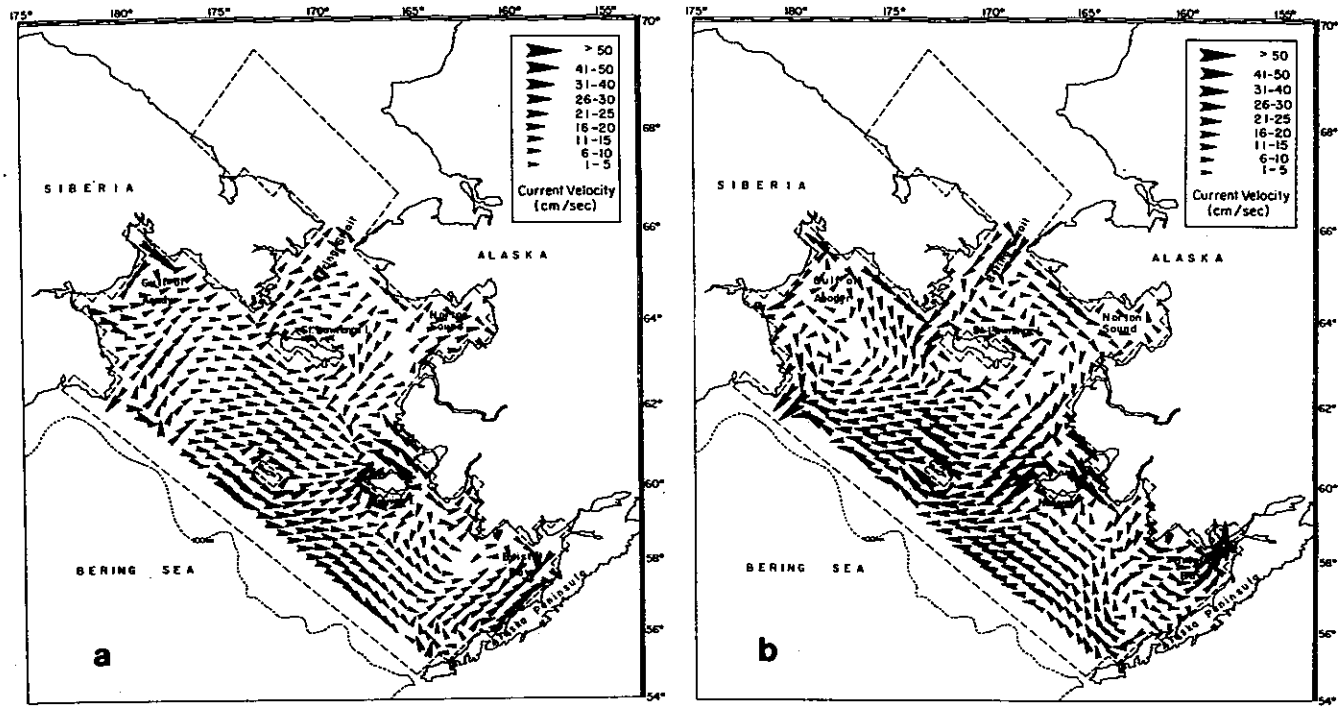

FIG. 9 Tidal currents (cm/sec) calculated from numerical tidal model for the times: (a) 4 hours before high tide, and (b) 4 hours before low tide at the eastern boundary (from Hastings 1975).

showing anomalies of specific volume from a geometric level. The mean data for July did have sufficient areal coverage to warrant examination and contours of anomaly of dynamic height computed from the surface relative to 50 db (0/50 db) that suggest several major features of flow are present (Fig. 10). Northwestward flow is indicated over the basin between Unimak Island and Cape Navarin and a component veers to the right around Anadyr Bay, eastward Figure 10 to St. Lawrence Island, and finally northward through Bering Strait. There is suggestion of a weak westward cross-shelf flow just north of St. Matthew Island and also a northeastward flow into Bristol Bay along the north coast of the Alaska Peninsula with a westward meandering return flow out of northern Bristol Bay. Although the action of surface winds could result in markedly different flows in the upper and lower portions of this 0-50 m layer, which are well isolated in summer by thermal and haline stratification, these results are interesting and should form the basis for further investigations.

VARIABILITY

McLain and Favorite (1976) have presented monthly anomalies of air and sea surface temperature in the vicinity of the Pribilof Islands (57°N, 170°W) from 1967-75 that reflect not only a long-term downward trend (which has reversed itself in 1977) but also considerable monthly and annual variability. Mean monthly north and south wind components for 1946-75 for the grid point 57°N, 170°W (Fig. 11) indicating potential periods of cooling (and ice

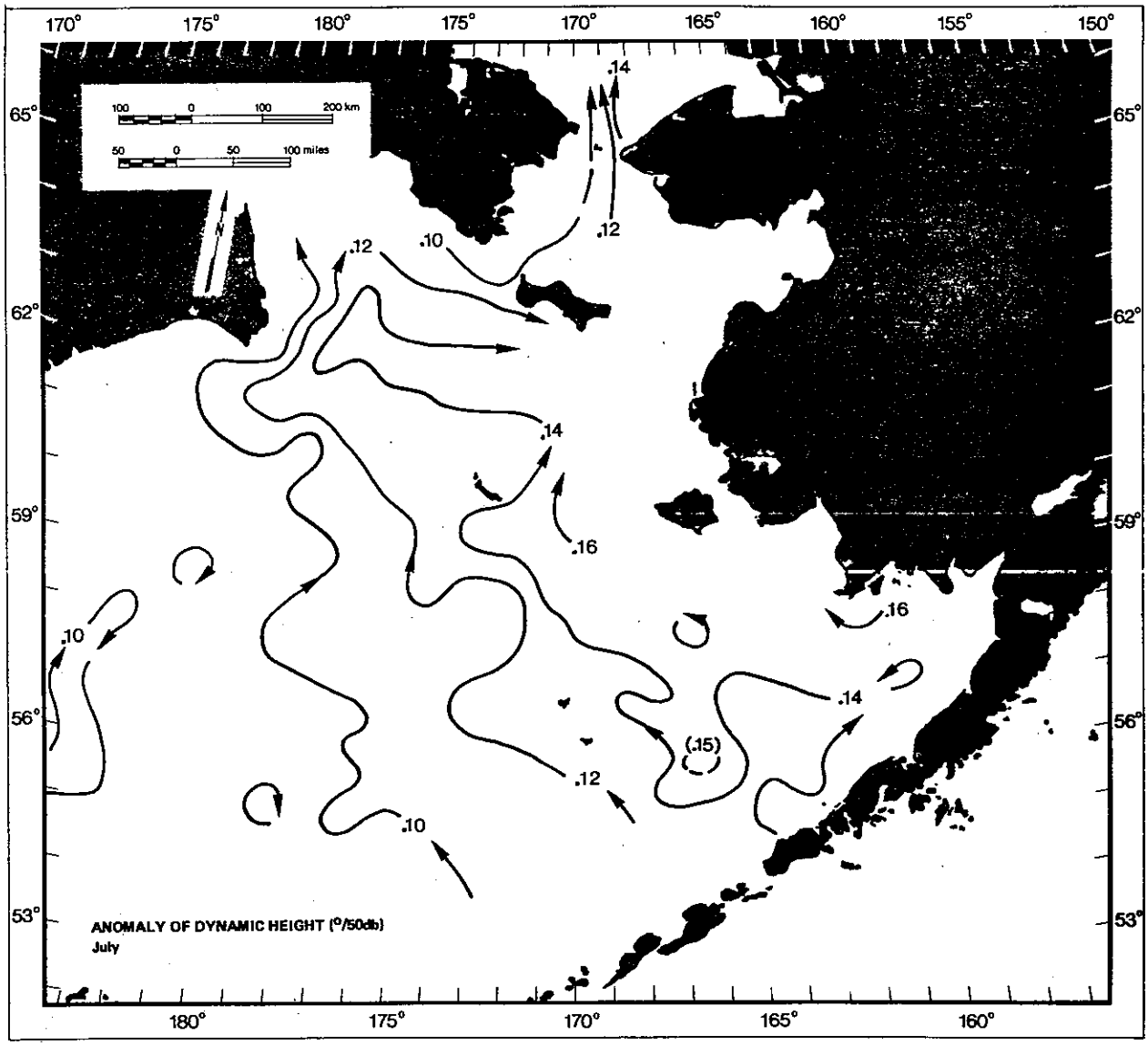

FIG. 10 Long-term monthly mean anomaly of dynamic height (0/50 db) for July.

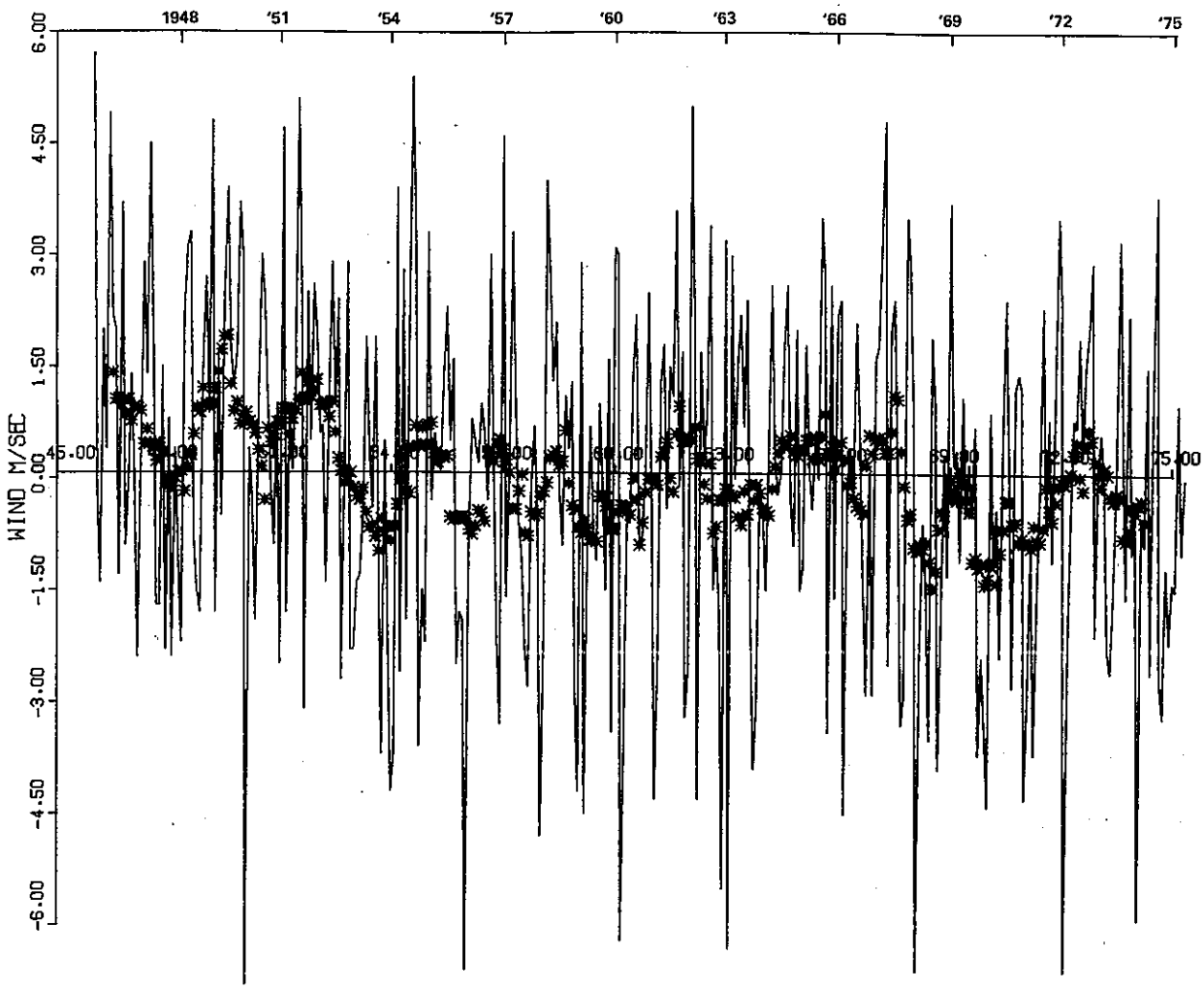

FIG. 11 Monthly mean wind (m/sec) components at 57°N, 170°W, 1946-75, (positive values indicate northward component, negative values indicate southward component) and 12-month running mean showing annual mean trends.

advance in winter and spring) and warming (and ice retreat in winter and spring) reflect the extreme variability of meteorological conditions and the 12 month running mean shows an indication of an approximate 3-year cycle, and a long-term trend of increasingly dominant northerly winds (cold conditions). Kihara (1971) has reported the extreme variability of extent of Alaskan Stream Extension water over the southern part of the outer shelf. Although polar waves considerably alter air temperature, wind, precipitation, etc. annual variability in shelf conditions are most easily shown by the extent of ice cover and by bottom temperatures.

Ice

In recent years, 1976-78, the extent of ice cover for November (when ice first extends seaward) indicates minimum ice cover in 1976 and a maximum in 1977; whereas, for April (usually the month of greatest ice cover) the maximum extent occurred in 1976 and the ice edge has been displaced farther northward each year with the greatest changes occurring on the eastern side of the shelf (Fig. 12). Thus, there is no correlation between spring conditions and subsequent fall conditions (i.e. summer conditions can obliterate cold trends established in spring).

Further, although the normal southerly winds in spring result in a compact ice edge and hasten its northerly retreat, northerly winds can cause anomalous conditions. In April 1976 an unusual and large southward displacement of part of the ice edge in the Bristol Bay area resulted in ice immediately northward of the Alaska Peninsula and forced vessels out of the area (Northwest Fisheries Center

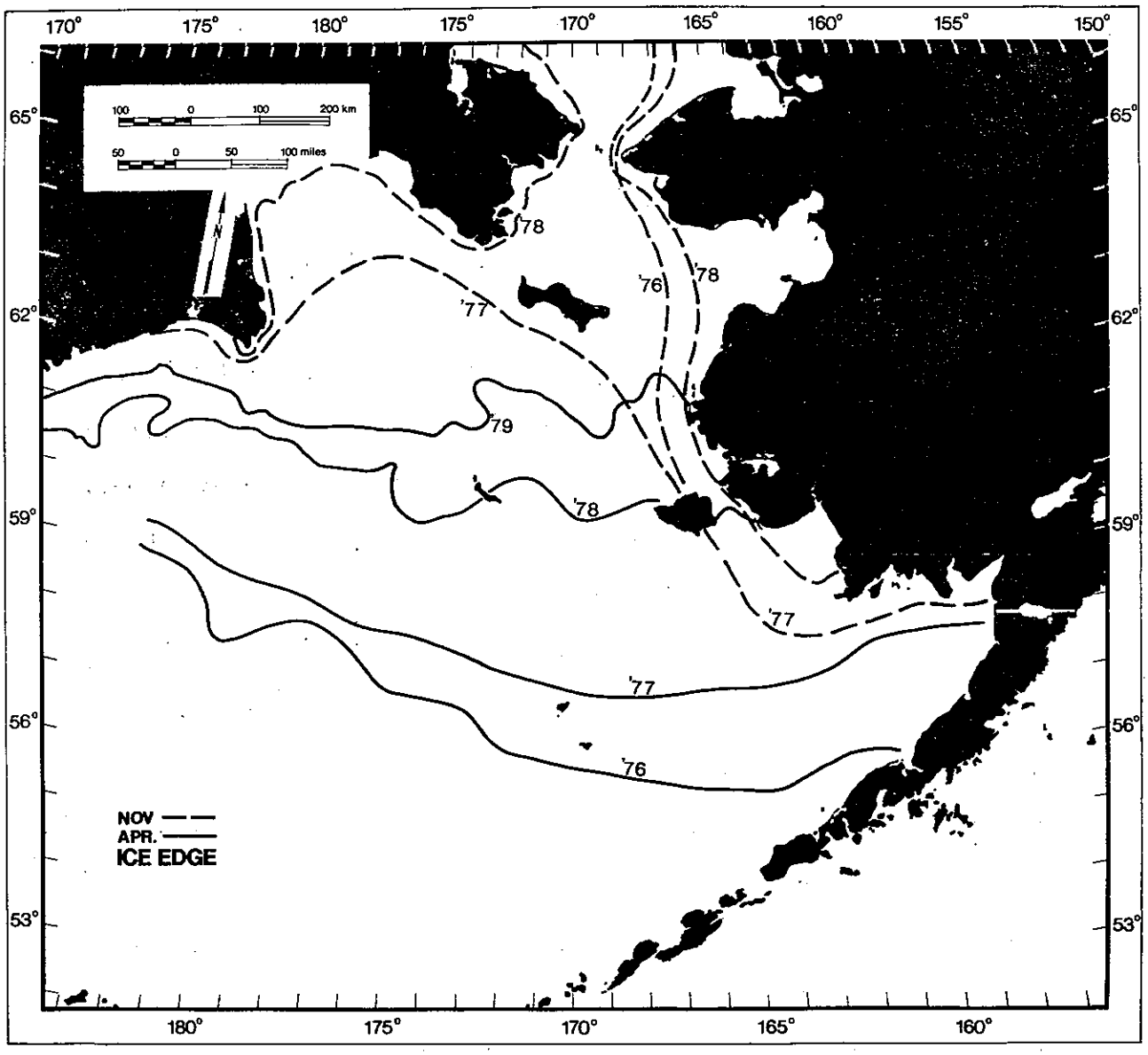

FIG. 12 Mid-month position of the ice edge, April 1976-79 and November 1976-78.

1976).[1/] This not only caused water in the open area in northern Bristol Bay to be subjected to early insolation (and thus warming), but considerably altered the temperature structure of the water in the area into which the ice was advected, because spring warming at the surface had already commenced; this resulted in extremely anomalous conditions in spring 1976.

Bottom Temperatures 1973 and 1977

The paucity and fragmentary nature of data on bottom conditions as well as the limit on the length of this report require selection of time periods to indicate variability. Bottom conditions largely reflect surface conditions (cold vs warm - not actual temperatures) but the reverse is not true, and the months of July 1973 and July 1977 were selected because data were available in Norton Sound and Bristol Bay even though it is known that extreme values occurred in other years (i.e. warm, 1968-69 and 1977-79; cold, 1971 and 1976). Temperature anomalies from long-term mean values discussed earlier indicate that when considering bottom conditions in summer a general overall shelf categorization of warm or cold years may be subject to error in that in July 1973 positive anomalies of 3 C occurred in Norton Sound and negative anomalies of 2 C in Bristol Bay; however, in July 1977 negative anomalies in excess of 4 C occurred in Norton Sound and positive anomalies of 2 C in Bristol Bay (Fig. 13). It is apparent that before one can

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1/Northwest Fisheries Center. 1976. Ice conditions in the eastern Bering Sea, April 1976. Northwest Fisheries Center Monthly Report, April 1976, pp. 7-9. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

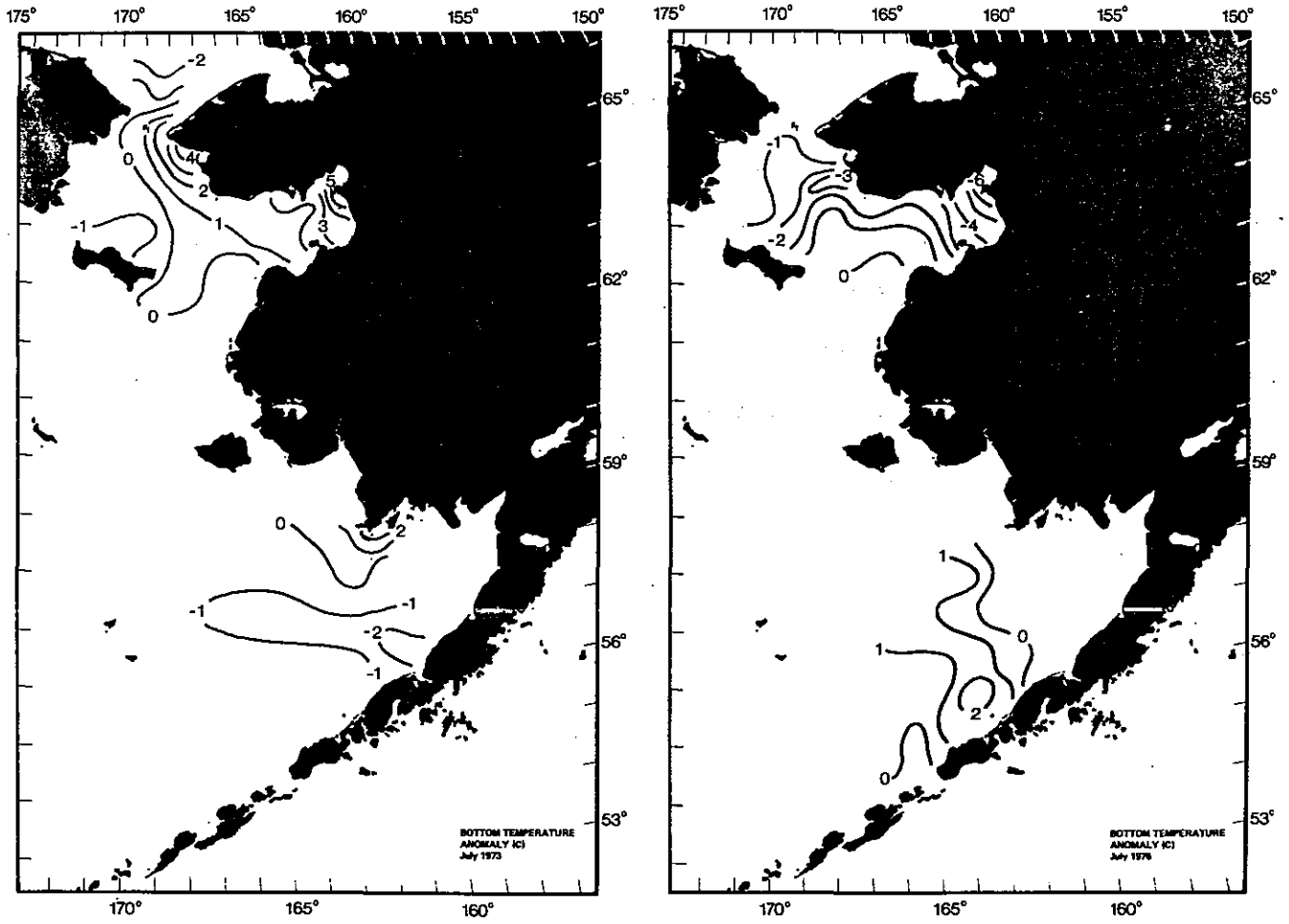

FIG. 13 Anomalies of bottom temperature (C) from the long-term mean, (a) July 1973, and (b) July 1977.

consider movements of fish throughout the shelf, knowledge of the environment over the entire shelf is required.

Bottom Temperatures, June and July 1969 and 1976

One further example of variability is given by comparing bottom temperatures in June and July 1969 with those of June and July 1976 (Fig. 14). These indicate that the temperature difference of warm conditions in 1969 (also in 1978) from cold conditions in 1976 was as high as 5 C. These conditions are shown in later Chapters to affect movements of fish but they also must have significant effects on the survival, reproduction and movements of benthos and other creatures of the shelf.

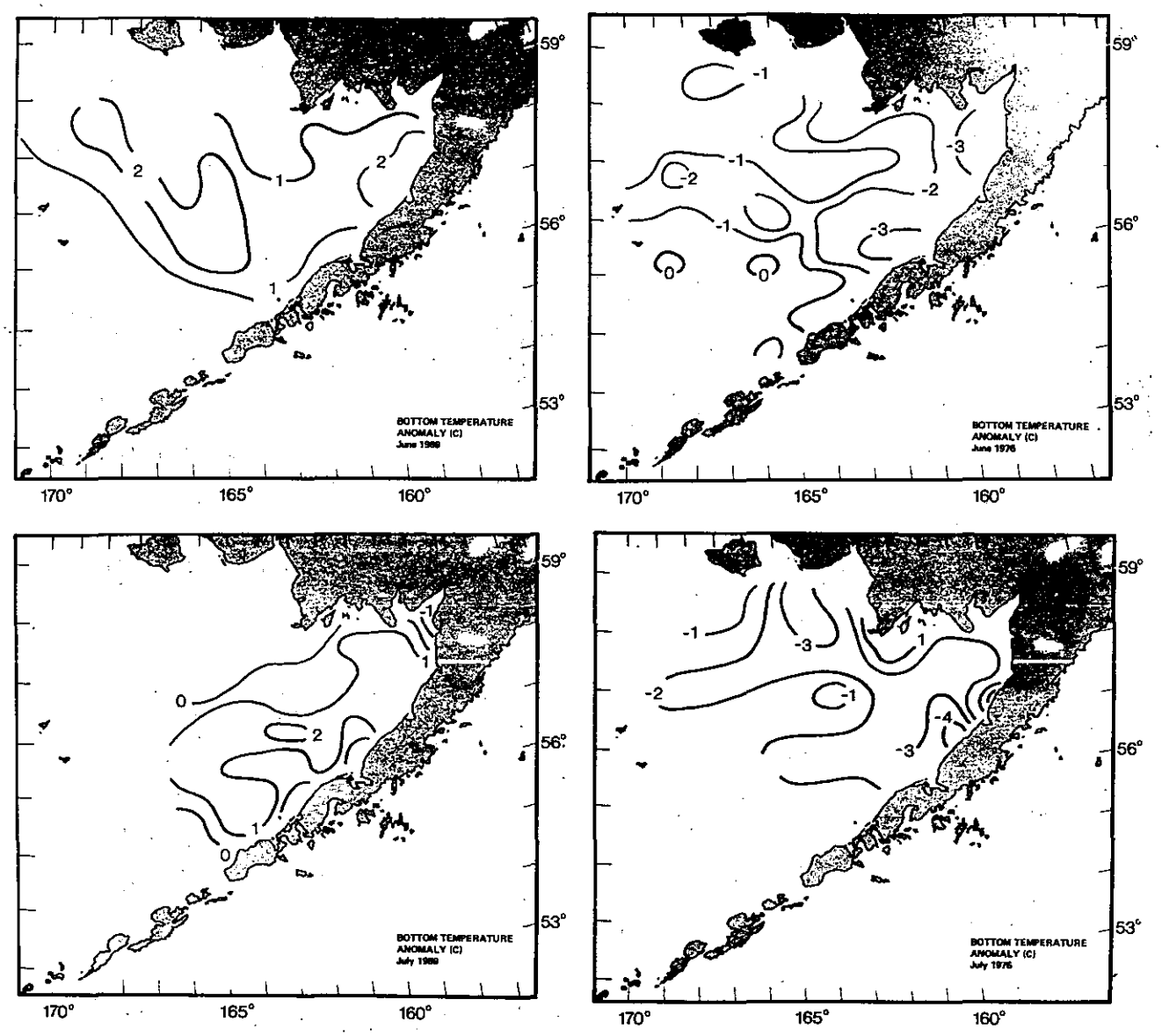

FIG. 14 Anomalies of bottom temperature (C) from the long-term mean, June and July 1969, and June and July 1976.

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ICHTHYOPLANKTON

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ABSTRACT

Ichthyoplankton studies in the Bering Sea have been conducted since 1955 by Japanese, Soviet and United States biologists. Comparison and integration of the results of the various surveys is difficult because surveys were conducted during different seasons, different nets and types of tows were used to collect the samples, and different areas were surveyed. Sampling effort was very unevenly distributed seasonally with only 1% expended during winter, about 9% during fall, 35% during spring, and 55% during summer.

Of the approximately 300 species of fish that occur as adults in the Bering Sea, eggs and/or larvae of about 270 species, divided among 137 genera in 34 families, might be expected to be present in plankton samples. Plankton collections made since 1955 contained 60 species divided among 52 genera in 24 families. Families that occurred most frequently in the 26 collections studied were Cottidae (26), Gadidae (23), Hexagrammidae (23), and Stichaeidae (23). Because of differences in seasonal and areal coverage, it is difficult to determine which larvae were most abundant. For collections made during spring between the Aleutian Islands and about 60°N and centered over the continental slope, larvae of pollock (*Theragra chalcogramma*) were much more abundant than any other species or genus.

An adequate knowledge of the ichthyoplankton of the Bering Sea can be gained only by a series of surveys covering the area from the Aleutian Islands to Bering Strait and from Bristol Bay and Norton Sound west to at least 175°E. Minimum sampling would be on a grid of stations spaced at about 50 km intervals with a neuston and an oblique net tow at each of about 600 stations.

INTRODUCTION

Ichthyoplankton data for the eastern Bering Sea are not as extensive as for some other areas, (e.g. off the California coast) and most of the work has been done since 1955. Between 1955 and 1975 most of the collections were made on cruises of the Japanese fisheries training ship Oshoro Maru and on a number of Soviet expeditions to the Bering Sea. Before 1975 there are only 3 reports compiled by U. S. biologists concerning ichthyoplankton in the Bering Sea. The purpose of this report is to summarize all available data east of 174°E and denote inadequacies of the information. It should be obvious that although damage from oil spills in local areas may cause infinitesimal losses to generally ubiquitous forage, it is not only the loss of forage in extensive spawning areas but the damage to ichthyoplankton itself that is a major problem. Assessment of damage will depend on knowledge of temporal and spatial distribution of fish eggs and larvae.

Beginning in 1975 the United States sponsored two programs, OCSEAP and PROBES, which included studies of ichthyoplankton of the Bering Sea, especially over the outer continental shelf. Since the inception of these two programs and up to summer of 1978, 10 cruises had studies of ichthyoplankton as a primary or secondary objective.

Cruises in the Bering Sea since 1955 for which there are reports dealing with general ichthyoplankton studies or of a single species of ichthyoplankton are listed in Table I. Information concerning some of the cruises made in 1978 is in the form of preliminary cruise reports, and reports of cruises of the Oshoro Maru made since 1969 denote only the number of stations and type of collections made. Some of the general reports include only taxa in the total collections, others taxa by station, while a few note only the distribution and abundance of a single species. There are other reports of collections of zooplankton in the Bering Sea and some include a general category of fish eggs or larvae, but such reports are not included in the table or elsewhere in this summary.

FACTORS AFFECTING INTER-CRUISE COMPARISONS

It has been necessary to use sources of information with different degrees of completeness and accuracy in the preparation of this summary. Information concerning Japanese cruises aboard the Oshoro Maru includes location of stations at which larvae were caught but do not denote stations at which eggs and larvae were not caught(i.e. non-productive effort is lacking). Reports of Soviet studies have usually been from sources which were originally published in Russian and subsequently translated to English and, for the most part, station positions had to be estimated from small charts contained in the original publications; further, in some instances it was impossible to determine catch by station.

TABLE I

Ichthyoplankton Cruises in the Bering Sea East of 174°E, 1955-1979

Cruise[1/]	Year	Vessel	Date	Lat. N. From To	Long. From To	Number stations[2/]	Type of tow[3/]	Net	Reference
1	1955	Oshoro Maru	8-20 July	52 -58	175 E-163 W	17	S	FLN	Faculty of Fisheries, Hokkaido Univ. 1957a
2	1956	Oshoro Maru	23 Jul-13 Aug	52 -63	174 E-168 W	34	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1957b
3	1957	Oshoro Maru	7-11 July	52 -54	174 E-172 W	9	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1958
4	1957	Brown Bear	3-29 Aug.	52 -56	177 E-166 W	20	O	IKMT	Aron, 1960
5	1958	Oshoro Maru	8-27 June	52 -62	175 E-175 W	21	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1959
6	1958	Zhemchug	29 Jun-5 Aug	53 -64	174 E-160 W	124	S,V	IKS-80	Musienko, 1963
7	1958	Zhemchug	19 Aug-18 Sep	55 -63	174 E-162 W	95	S,V	IKS-80	Musienko, 1963
8	1959	Alazeya	13-19 March	54 -59	174 E-165 W	60	S,V	IKS-80	Musienko, 1963
9	1959	Oshoro Maru	21 Jun-12 Jul	52 -58	174 W-167 W	17	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1960
10	1960	Oshoro Maru	19 Jun-13 Jul	52 -60	175 E-163 W	13	S	FLN,PC	Faculty of Fisheries, Hokkaido Univ., 1961
11	1961	Oshoro Maru	1-14 July	53 -60	174 E-172 W	11	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1962
12	1962	Ogon	21-31 July	58 -63	174 W-163 W	88	S,V	IKS-80 F/r-80/113	Kashkina, 1965, 1970
13	1963	(Halibut Comm. charter)	May	54 -55	166 W-165 W	10	-	-	Dunlop et al, 1964
14	1963	Oshoro Maru	14 Jun-14 Jul	54 -59	177 E-167 W	7	S	FLN,IKMT	Faculty of Fisheries, Hokkaido Univ., 1964
15	1965	Seskar	March-May	54 -61	179 W-160 W	95	S,V,T	IKS-80	Serobaba, 1968 (report only pollock)
16	1965	Seskar	June-July	54 -65	180 -163 W	86	S,V,T	IKS-80	Serobaba, 1968 (report only pollock)
17	1966	Oshoro Maru	13 Jun-31 Jul	53 -65	177 E-164 W	32	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1967
18	1967	Oshoro Maru	12 Jun-20 Aug	53 -65	175 E-161 W	22	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1968
19	1968	Oshoro Maru	12 Jun-8 Aug	52 -64	177 E-162 W	28	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1969
20	1969	Oshoro Maru[4/]	10 Jun-2 Aug	53 -58	180 -160 W	35	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1970
21	1970	Oshoro Maru[4/]	6 Jun-16 Aug	52 -58	172 W-161 W	50	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1972
22	1971	George B. Kelez	26 May-9 Jun	53 -56	173 W-168 W	6	O	B-60	Dunn and Naplin 1973
23	1971	Oshoro Maru[4/]	17 Jun-23 Jul	52 -58	174 E-161 W	31	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1973
24	1972	Oshoro Maru[4/]	11 Jun-12 Aug	52 -65	175 W-161 W	-	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1974
25	1972	Professor Deryugin	March-Jun	54 -62	174 E-164 W	-	O,H	IKMT(Cl.)	Serobaba 1974 (pollock-vertical sections)
26	1973	Oshoro Maru[4/]	11 Jun-23 Jul	52 -59	180 -160 W	36	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1975
27	1974	Oshoro Maru[4/]	7 Jun-22 Jul	52 -58	178 W-167 W	41	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1976a
28	1975	Shunyo Maru	4 Mar-3 Jul	54 -61	161 W-179 W	121	V	1.4mLN	Wakabayashi, Mito and Nagai, 1977
29	1975	Discoverer	20 May-15 Jun	53 -60	158 -175 W	108	V,O	1m,NIO	NODC Data[5/]
30	1975	Oshoro Maru[4/]	13 Jun-5 Jul	52 -59	180 -160 W	78	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1976b
31	1975	Discoverer	15-26 Aug	54 -60	159 -172 W	76	V,O	1m,NIO	NODC Data[5/]
32	1975	Miller Freeman	13-24 Nov.	54 -62	162 -170 W	38	V,O	1m,NIO	NODC Data[5/]
33	1976	Surveyor	17 Mar-26 Apr	54 -58	162 -174 W	57	V,O	1m,NIO	NODC Data[5/]
34	1976	Miller Freeman	26 Apr-31 May	54 -59	175 W-158 W	56	S,O	Sam.,B-60	Waldron and Favorite, 1977
35	1976	Oshoro Maru[4/]	14 Jun-25 Jul	52 -64	174 E-162 W	39	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1977
36	1976	Discoverer	5-17 Aug	55 -66	161 -168 W	80	V,O	1m,NIO	NODC Data[5/]
37	1977	Miller Freeman	16 Apr-13 May	53 -58	174 W-163 W	134	S,O	Sam.,B-60	Waldron and Vinter, 1978
38	1977	Oshoro Maru[4/]	12 Jun-24 Jul	52 -60	178 W-163 W	51	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1978
39	1978	Miller Freeman	11 Feb-18 Mar	54 -60	164 W-177 W	32	S,O	Sam.,B-60	Waldron, 1979
40	1978	T.G.Thompson	11-29 Apr	- -	- -	157	S,O	N,B,NIO	PROBES, 1979[6/]
41	1978	Ogon	10 Apr-20 May	54 -62	162 W-180	349	S,V	X-80	Moiseev and Bulatov, 1979[7/]
42	1978	Oshoro Maru	June-August	- -	- -	66	S	FLN	Faculty of Fisheries, Hokkaido Univ., 1979
43		Hakuho Maru	23-30 July	55 -65	168 W-173 W	5	S,O	ORI-100	Haryu, Endo and Nishiyama, 1979

FOOTNOTES FOR TABLE I

1/ Cruise No.--an arbitrary number assigned for the purposes of this summary.

2/ Type of tow: S = horizontal surface tow probably to a maximum depth of 1 m; O = oblique tow from the surface to a depth and back to the surface; V = vertical net tow; H = a horizontal net tow at some depth below 1 m; T = Total; definition of this not known, but the terminology appeared in Serobaba (1968).

3/ Net: FLN - fish larva net. See references for specifications which varied slightly between 1955 and 1977.
IKMT - Isaacs-Kidd Midwater Trawl (Isaacs and Kidd 1953).
IKMT(Cl.) - an IKMT with a closing type cod end.
IKS-80 - "...nets of 140 mesh with a mouth diameter of 80 cm." (Kashkina 1970)
B/r-80/113 - a reverse cone net with dimensions and mesh the same as the IKS-80.
B - bongo net, size not specified.
B-60 - bongo net with a mouth diameter of 60 cm and mesh of 0.505 mm.
1m - a simple one meter ring net.
N - a neuston net
Sam. - A Sameoto type sampler (Sameoto and Jaroszynski 1969).
NIO - a 2 meter National Institute of Oceanography trawl.
PC - underway plankton catcher.

4/ Reports of the Oshoro Maru cruises since 1969 do not list station positions or catch, but give only total stations sampled.

5/ Catch by station for these cruises was obtained from the OCSEAP data file at NODC.

6/ Cruise report PROBES 78, Leg I, 8 April to 1 May 1978

7/ Moiseev, E.I. and O.A. Bulatov. 1979. The state of pollock stocks in eastern Bering Sea. Pacific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok 1979, 8 p (processed).

Information collected during OCSEAP cruises is accurate with respect to position and catch, and was obtained from processed reports of the Northwest and Alaska Fisheries Center (NWAFC) or from the data file of the National Oceanographic Data Center (NODC). Because of the varying degrees of accuracy in position and for convenience in presentation, all data have been presented on the basis of geographic areas measuring ½° of latitude by 1° of longitude. These areas are designated by the coordinates of the lower right corner in west longitude (i.e. the area from 57½°N - 58°N and from 165°W - 166°W is designated 57½°N, 165°W), and by the lower left corner in east longitude.

Because it was not always possible to determine the number of net hauls made at one position, a station as used here is defined as one or more net tows made at a geographic location within a time span of a few hours. Samples separated in time by a few days or more were counted as separate stations. This treatment tends to minimize effort, and in terms of net hauls sampling effort is much greater than shown here.

Total sampling effort east of 174°E (Fig. 1) was estimated using cruise reports that listed station positions and includes only the cruises listed in Table II. Sampling covered the entire Bering Sea but with a concentration of effort along the continental slope south of the Pribilof Islands. Division of effort into quarter-years (Figs. 2-5) shows that 35% of the sampling was done in spring (March-May), 55% in summer (June-August), only 9% in fall (September-November) and less than 1% in winter (December-February).

TABLE II

Ichthyoplankton Collected During Various Cruises in the Bering Sea 1/ 2/

Taxa	Total	Cruises 3/ 1	2	3	4	5	6	7	8	9	10	11	12	14	17	18	19	20	22	29	31	32	33	34	36	37	39
Clupeidae	3																										
Clupea harengus pallasi	3																				+	+			+		
Osmeridae	12						+	+		+	+									+		+	+	+	+	+	
Mallotus villosus	11																					+					
Osmerus mordax	1																							+			
Unidentified osmerids	2		+																								
Bathylagidae	10																										
Bathylagus ailleri	1				+															+	+		+		+		
B. pacificus	6				+		+													+	+	+	+	+		+	+
B. schmidti 4/	10				+																						
Chauliodontidae	2																	+									
Chauliodus macouni	2				+																						
Myctophidae	10																										
Diaphus theta	1				+																						
Protomyctophum thompsoni 5/	3				+																			+			+
Stenobrachius leucopsarus 6/	9		+		+		–								+					+	+		+			+	+
Unidentified myctophids	2				+																+						
Gadidae	23																										
Eleginus gracilis	2																				+				+		
Gadus macrocephalus	3				+		+																	+			
Theragra chalcogramma	21		+		+		+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+		+	+
Unidentified gadids	8					+				+										+	+			+	+	+	+
Zoarcidae	3																										
Unidentified zoarcids	3	+																						+			+
Macrouridae	5																										
Unidentified macrourids	5						+													+	+	+				+	
Melamphaeidae	1																										
Melamphaes lugubris	1				+																						
Scorpaenidae	11																										
Sebastes sp. 7/	11				+		+	+					+		+	+				+	+	+		+		+	
Unidentified scorpaenids	1																					+					
Hexagrammidae	23																										
Hexagrammos sp.	19			+		+	+	+	+	+	+	+	+		+	+	+	+			+	+	+	+		+	+
H. decagrammus	6	+	+					+	+				+										+				
H. lagocephalus	4							+	+				+										+				
H. octogrammus	3							+	+				+														
H. stelleri	6	+	+				+	+	+													+					
H. superciliosus	3							+	+				+														
Pleurogrammus monopterygius	11	+				+			+						+	+	+	+					+	+		+	+
Unidentified hexagrammids	2				+															+							
Anoplopomatidae	11																										
Anoplopoma fimbria	11	+	+	+		+				+	+		+			+	+	+								+	
Erilepis zonifer ?	1										+																
Cottidae	24																										
Artedidiellus pacificus	1																				+						
Cymnocanthus sp.	2						+																		+		
Hemilepidotus sp.	17	+	+	+		+			+	+		+	+		+	+	+	+		+			+	+			+
H. hemilepidotus	2				+																					+	
H. jordani	3																	+				+				+	
H. papilio 8/	3						+						+													+	
Icelinus borealis	1						-																			+	
Malacocottus sp.	1																								+		
Myoxocephalus sp.	11		+			+	+			+	+		+		+	+	+	+							+		
Triglops sp.	2																								+		
Triglops pingeli	1																						+				
Unidentified cottids	11	+		+	+								+						+	+	+		+	+	+	+	
Agonidae	14																										
Agonus acipenserinus 9/	7		+							+					+	+		+	+		+						
Aspidophoroides sp.	2									+						+											
A. bartoni	1																				+						
A. olriki	1																								+		
Asterotheca infraspinata	1																				+						
Hypsagonus quadricornis	2						+																			+	
Ocella dodecaedron 10/	1						+																				
Odontopyxis trispinosa	1																								+		
Unidentified agonids	6				+					+							+			+				+		+	
Cyclopteridae	20																										
Aptocyclus ventricosus 11/	4				+					+							+									+	
Liparis sp.	12	+	+								+	+	+	+	+	+	+	+		+					+		
L. pulchellus	1																				+						
Rectoliparis pelagicus	4				+																+	+				+	
Unidentified cyclopterids 12/	10				+	+	+			+						+					+	+		+	+	+	
Bathymasteridae	18																										
Bathymaster sp.	14					+			+	+	+	+	+	+	+	+	+	+			+	+		+			
B. signatus	2																					+	+				
Unidentified bathymasterids	3				+																					+	+
Anarhichadidae	1																										
Anarhichas orientalis	1																									+	
Stichaeidae 13/	23																										
Alectridium aurantiacum	1		+																								
Chirolophis polyactocephalus	2																									+	+
Lumpenus sp.	10	+	+	+		+					+	+			+		+	+							+		
L. fabricii	3														+						+				+		
L. maculatus	3																				+			+		+	
L. medius	1																				+						
Stichaeus sp.	4		+										+		+									+			
S. punctatus	1	+																									
Unidentified stichaeids	11							+	+	+	+	+			+		+			+	+	+				+	
Cryptacanthodidae	1																										
Lycenectes aleutensis	1																										+
Ptilichthyidae	5																										
Ptilichthys goodei	5															+	+	+	+							+	
Pholidae	6																										
Unidentified pholids	6	+	+		+										+										+		+
Zaprioridae	3																										
Zaprora silenus	3				+																	+					+
Ammodytidae	20																										
Ammodytes hexapterus 14/	20	+	+	+	+		+	+		+	+	+	+	+	+	+	+	+			+			+	+	+	+
Pleuronectidae	20																										
Atheresthes sp.	4														+			+						+		+	
A. stomias	4						+												+		+	+					
Glyptocephalus zachirus (eggs only)	2						+	+																			
Hippoglossoides elassodon	11						+	+						+	+	+	+				+	+	+		+		+
Hippoglossus stenolepis	5								+											+	+				+		+
Lepidopsetta bilineata	4								+												+					+	+
Limanda aspera	6							+	+					+								+	+		+		
L. proboscidea 15/	1							+																			
Platichthys stellatus	2																				+				+		
Pleuronectes quadrituberculatus 16/	4							+						+											+		+
Reinhardtius hippoglossoides	11														+	+	+	+	+		+	+		+	+	+	+
Unidentified pleuronectids	12				+		+						+			+	+	+		+	+	-			+	+	+
Number of taxa per cruise		13	14	7	22	10	22	15	13	15	13		7	18	10	20	17	15	16	11	25	28	14	14	28	19	38	13
Number of families per cruise		8	11	6	14	8	13	7	6	10	10		7	10	8	12	12	11	11	8	12	14	9	8	15	9	19	11

FOOTNOTES FOR TABLE II

1/ Ichthyoplankton as used in this summary includes larvae, post-larvae, juveniles, and eggs caught with various plankton nets.
2/ The portion of the Bering Sea included here is from the Aleutian Islands to 66°N and east of longitude 174°E.
3/ These numbers refer to the cruises listed in Table I.
4/ Bathylagus schmidti includes Leuroglossus stilbius, L. schmidti, and B. stilbius.
5/ Protomyctophum thompsoni includes Electrona arctica.
6/ Stenobrachius leucopsarus includes Lampanyctus sp., and L. leucopsarus.
7/ Sebastes sp. includes Sebastodes sp.
8/ Hemilepidotus papilio includes Melletes papilio.
9/ Agonus acipenserinus includes Podothecus acipenserinus.
10/ Ocella dodecaedron includes Orcs dodecaedrum.
11/ Aptocyclus ventricosus includes Cyclopterichthys glaber
12/ Unidentified cyclopterids include Liparides
13/ Stichaeidae includes Lumpenidae.
14/ Ammodytes hexapterus includes A. tobianus peramatus.
15/ Limanda proboscidea includes L. punctatissima proboscidea.
16/ Pleuronectes quadrituberculatus includes Platessa quadrituberculata.

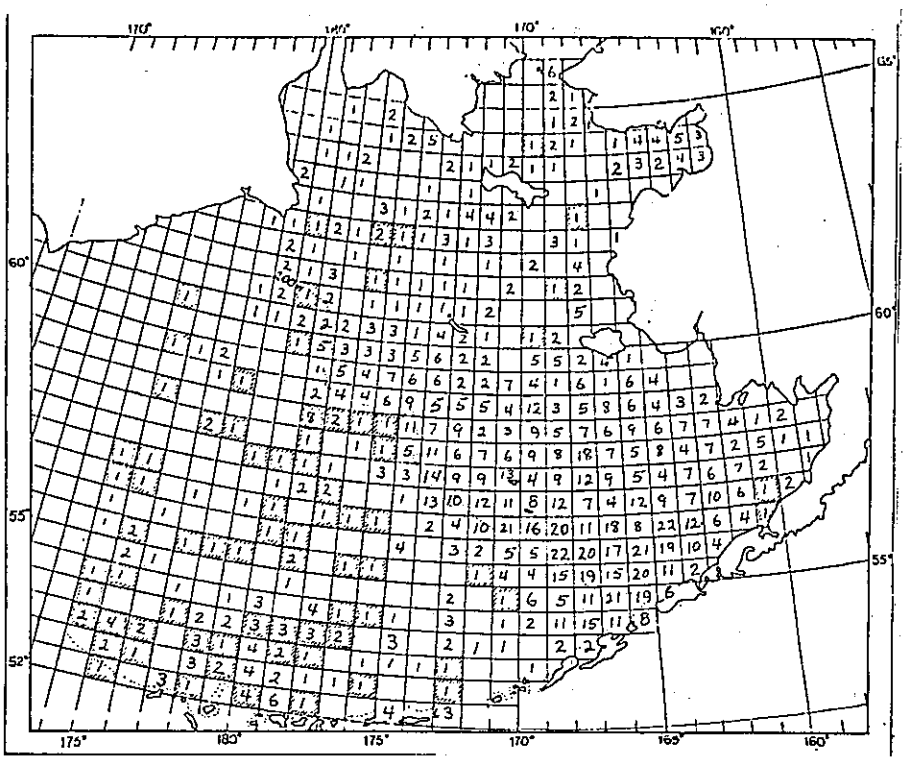

FIG. 1 Number of stations at which ichthyoplankton samples have been collected, 1955-1978. [No.] Stations with surface and oblique or vertical tows. [No.] Stations with only surface tows.

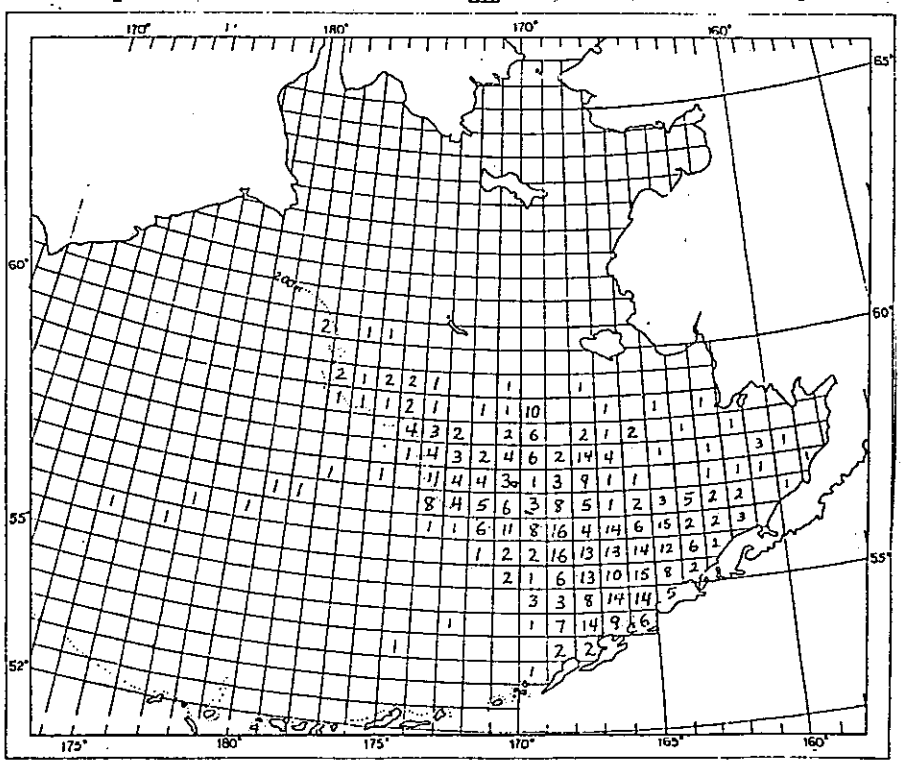

FIG. 2 Number of stations at which ichthyoplankton samples have been collected in spring, March-May.

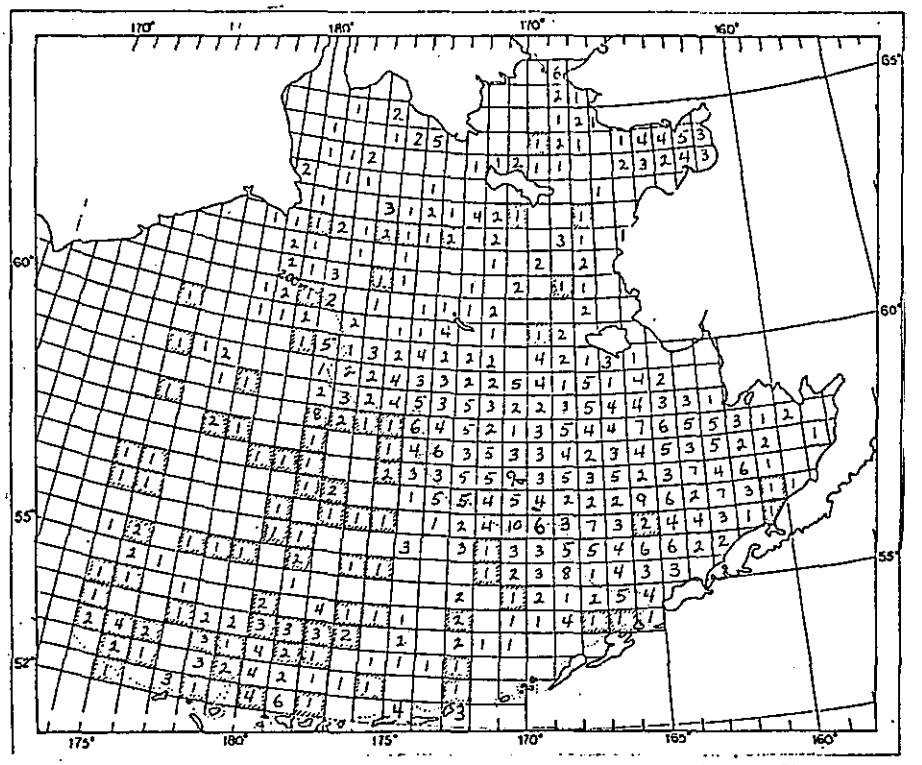

FIG. 3 Number of stations at which ichthyoplankton samples have been collected in summer, June-August.

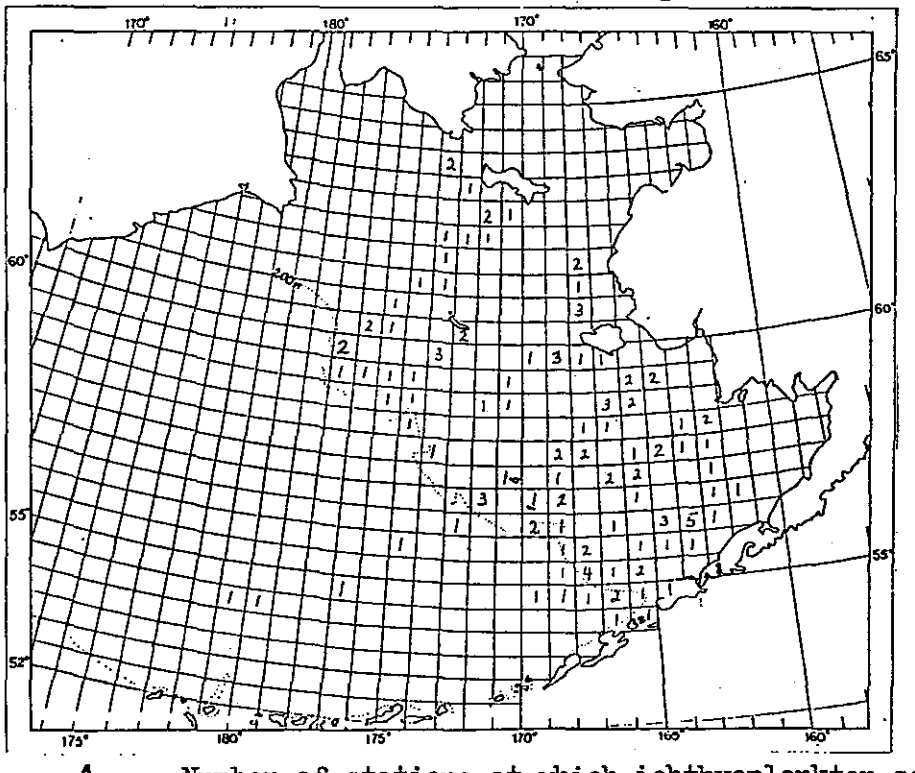

FIG. 4 Number of stations at which ichthyoplankton samples have been collected in fall, September-November.

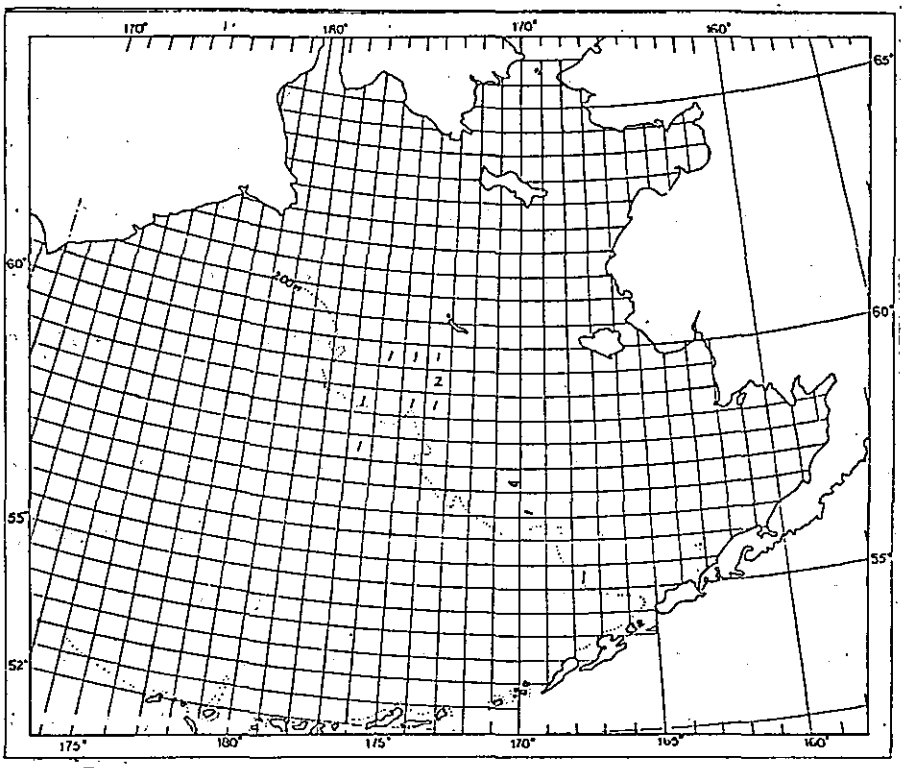

FIG. 5 Number of stations at which ichthyoplankton samples have been collected in winter, December-February.

Thus, fish whose eggs or larvae are planktonic during the six months from September through February were undersampled in comparison to those that are planktonic during spring and summer. Pleuronectidae, for example, show considerable diversity in time of spawning. Yellowfin sole spawn in mid-summer and thus are not available for capture with plankton nets in spring or early summer. Halibut and turbot, on the other hand, spawn in winter and by the following spring and summer their larvae are difficult to capture with plankton nets. Pollock, one of the most abundant fish in the Bering Sea, spawn mainly during spring and their larvae are relatively scarce in samples collected during late summer and fall.

A further obstacle to inter-cruise comparisons is the type of tow used in making the collections. Vertical net tows usually strain a relatively small volume of water resulting in the capture of only small numbers of fish larvae, and the more uncommon taxa are seldom found in collections made by this method. A horizontal tow at the surface, e.g. a neuston tow, may produce large numbers of eggs and larvae but these may belong to only a few taxa whose larvae characteristically inhabit this zone. Greenlings and Atka mackerel, family Hexagrammidae, and sculpins of the genus Hemilepidotus are often abundant in neuston collections, whereas flatfish larvae are almost completely absent from such tows. In general, an oblique tow from near bottom to the surface appears to capture a large number of species as well as large numbers of specimens. Examination of Table I shows that many of the collec-

tions were made with surface tows. This includes most of those made aboard the Oshoro Maru, and because those cruises represent a majority of sampling effort west of the continental slope the species composition in that area is biased towards those taxa with surface dwelling planktonic larvae.

A third point to consider in comparing samples collected during different cruises is the area coverage and station spacing. Considerations of economics, logistics, and program objectives usually dictate that a particular sampling effort be confined to a single vessel often operating within a small area and/or sampling at relatively few stations. The Oshoro Maru cruises often covered a large total area but with widely spaced stations. Most of the effort by the Miller Freeman consisted of sampling at closely spaced stations but within a relatively small area. Cruises by the Zhemchug and Seskar covered large areas within which stations were spaced at moderate intervals, but most sampling was restricted to the continental shelf and slope.

As a result of restricted areal coverage combined with uneven seasonal distribution of effort and type of tow that predominated in certain areas, the distribution of many species is not well defined. Yellowfin sole larvae are not reported in very many collections and this may relate to their spawning area which appears to be well up on the continental shelf in moderately shallow water while much of the sampling effort was devoted to the outer continental shelf and continental slope. Pacific herring spawn in intertidal areas and their larvae must remain close to shore while

they are planktonic for they are reported in very few collections. Pollock spawn along the continental slope and outer shelf and their eggs and larvae are seldom captured in water less than 75 m depth. Myctophids and bathylagids are two groups that are probably undersampled because of the predominance of surface tows in the central basin where they inhabit the deeper waters.

In summary, much of the sampling effort has been focused on the distribution and abundance of a few species, in particular pollock and yellowfin sole, and collections of other species have been incidental to this main objective. It is likely that definitive information about the total ichthyoplankton community in the Bering Sea can be gained only through a concerted cooperative effort by Japanese, Soviet, and U.S. biologists to promote at least one, year-round sampling effort covering the entire Bering Sea with sampling at moderately spaced stations and obtaining at least an oblique and a neuston tow at each station.

AVAILABLE FAUNA AND CATCH

There are generally considered to be about 300 species of fish in the Bering Sea divided among 150 genera and 40-45 families (Quast and Hall 1972; Wilimovsky 1974). Of these, 4 families -- Petromyzontidae, Squalidae, Rajidae, and Acipenseridae, with 6 genera and 12 species, are extremely unlikely to appear in plankton samples. In addition, larvae of Salmonidae and Gasterosteidae with 7 genera and 16 species are seldom found in marine plankton although they do occur in samples from estuaries and brackish water areas. There remain 34 families with 137 genera and 270

species that can reasonably be expected to occur in plankton samples either as eggs or larvae, or both.

Collections resulting from the cruises discussed here (see Table I) contain 87 separate taxa of which 60 are species, 13 are genera (9 of these are also included in the specific listing), and 14 are families. All told they include representatives of 52 genera in 24 families, and the various taxa and the collections from which they were obtained are presented in Table II. Thus, larvae of over one-third of the genera, over half of the families, but of only about one-fifth of the species of fish present in the Bering sea as adults have been collected and identified. Most of the species not included in the list are in the large families Cottidae, Zoarcidae, Cyclopteridae, and Stichaeidae which account for some 170 species. The 14 families not included in the collections contain only 23 species.

Because of the variations in spawning time and the logistical aspects of vessel cruises, it is seldom possible to sample the entire spectrum of ichthyoplankton during any single cruise. Examination of Table II shows that of a total of 87 taxonomic categories of larvae, no report lists more than 38 taxa and four reports list 10 or fewer taxa. Certain of the reports in Table I (e.g. Serobaba 1968, reporting on the 1965 cruise of the Seskar), deal with single species and do not include listings of other larvae and eggs that were almost certainly present in the collections.

DISTRIBUTION AND ABUNDANCE OF ICHTHYOPLANKTON

The following section contains charts showing location and frequency of capture of the different taxa and a brief discussion of each taxon--giving where possible distribution notes, season of capture, and a general estimate of the actual abundance in the samples. In addition, it is noted if eggs are pelagic or demersal, and if they are pelagic, whether or not they occurred in the samples. For a few species, a short discussion of egg distribution and abundance is included. The arrangement of families follows that proposed by Greenwood et al. (1966).

Clupeidae

The Pacific herring, *Clupea harengus pallasi*, is the only member of this family in the Bering Sea and as an adult it is abundant and commercially valuable, but larvae were caught at only 10 stations on 3 cruises in the summer and fall of 1975 and the summer of 1976. Only 24 herring larvae were caught, all at shallow water stations in Bristol Bay and Norton Sound (Fig. 6), and the largest catch was 9 larvae. A partial explanation of the scarcity of herring larvae is that spawning takes place in intertidal areas and larvae apparently remain close to shore during the period they would be susceptible to capture with plankton nets. Most of the sampling effort shown in Figure 1 was in areas outside of those occupied by herring larvae.

Herring eggs are demersal and none were reported.

Osmeridae

There are four species of smelt which occur in the Bering Sea

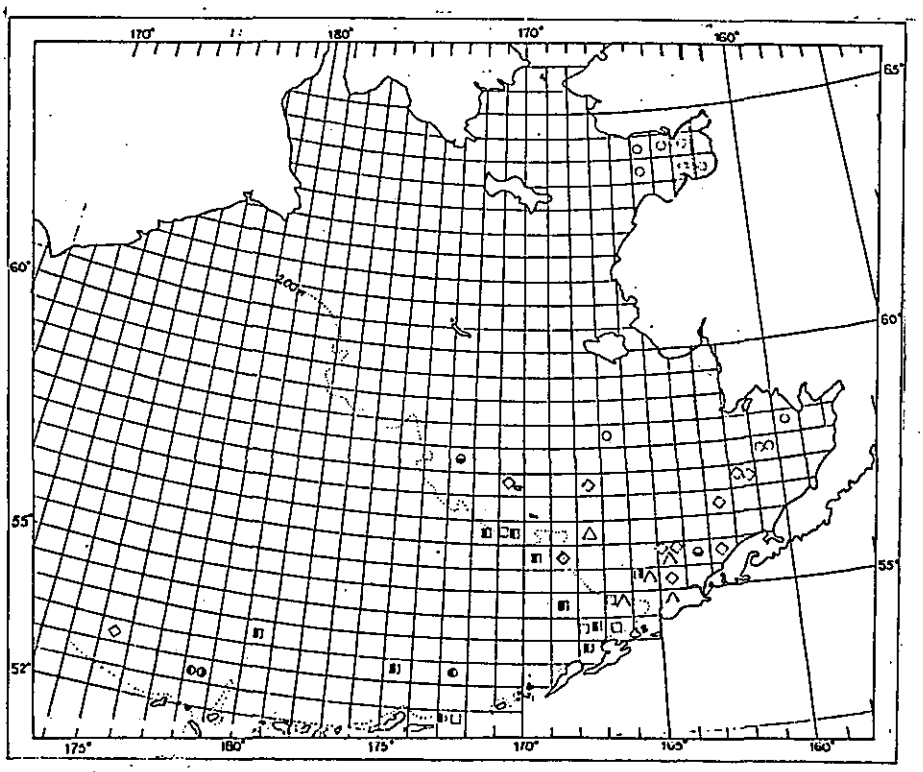

FIG. 6 Number of stations at which larvae of various taxa have been caught. Each symbol represents one station.
○ Clupea harengus pallasi, ◐ Chauliodus macouni, ◒ Zoarcidae, ◑ Melamphaes lugubris, ◧ Macrouridae, ◨ Lyconectes aleutensis, △ Anarhichas orientalis, ◇ Ptilichthys goodei, □ Zaprora silenus.

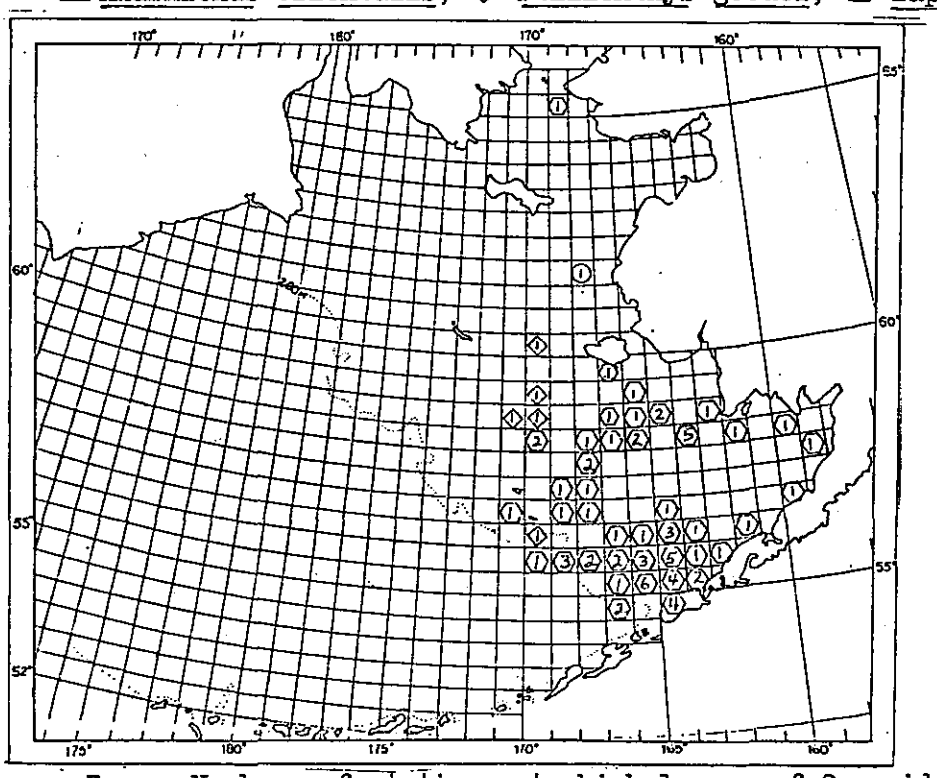

FIG. 7 Number of stations at which larvae of Osmeridae have been caught.
⬡ Mallotus villosus, ○ Osmerus mordax, ◇ Unidentified osmerids.

as adults and two of these were present in plankton samples. Capelin, Mallotus villosus, were caught at 76 stations on 10 cruises in spring, summer and fall (Fig. 7). With one exception, all occurred south of 60°N almost exclusively over the continental shelf and extending into the easternmost part of Bristol Bay. The single exception was a capelin larva collected just south of Bering Strait in August 1976. Based on collections made aboard the Miller Freeman in the spring of 1977 (Waldron and Vinter 1978) capelin are more easily caught with neuston nets than with deeper fishing bongo nets, and more specimens were collected at night than during the day.

Rainbow smelt, Osmerus mordax, were represented by a single juvenile caught in quadrangle 61½°N, 167°W in November 1975.

Unidentified osmerid smelt were reported at 5 stations on 2 cruises in spring and summer.

Osmerid smelt are demersal spawners and no eggs were reported.

Bathylagidae

The deepsea smelts are represented in the Bering Sea by 5 species (one name is of questionable validity), and larvae of 3 of the species were found in plankton samples. The most frequently collected species was the northern smoothtongue, Bathylagus schmidti, which was caught at 69 stations on 10 cruises in spring, summer, fall, and winter. Catches of B. schmidti were generally less than 5 larvae per tow with a maximum of 22 at one station.

The Pacific blacksmelt, Bathylagus pacificus, was collected at 51 stations on 6 cruises in spring and summer. Catches of B. pacificus were usually less than 5 larva per tow with a maximum of 8 at one station. The stout blacksmelt, Bathylagus milleri, was collected at only 2 stations on 1 cruise in summer, and the 2 specimens should be described as large juveniles or small adults even though they were collected with a plankton trawl. In contrast to Osmeridae, deepsea smelts were collected over the outer continental shelf, the continental slope, and the deep central basin south of 60°N and from 165°W to 178°E (Fig. 8). There did not appear to be any marked difference in distribution between the northern smoothtongue and the Pacific blacksmelt and so their distribution was plotted as one figure. The two stout blacksmelt were collected at 2 stations in quadrangle 52½°N, 178°E. As far as can be determined none of the bathylagid larvae were captured with surface nets. Because most of the sampling effort over the deep central basin was with surface tows, the lack of specimens from that portion of the Bering Sea may be a sampling artifact.

Eggs of deepsea smelt are pelagic and identifiable but none were reported.

Chauliodontidae

This family of bathypelagic fish has a single species in the Bering Sea, the Pacific viperfish, Chauliodus macouni. Larvae and juveniles of this species were collected at only 3 stations on 2 cruises in summer, all of which were close to the Aleutian Islands between 172°W and 178°E (see Fig. 6).

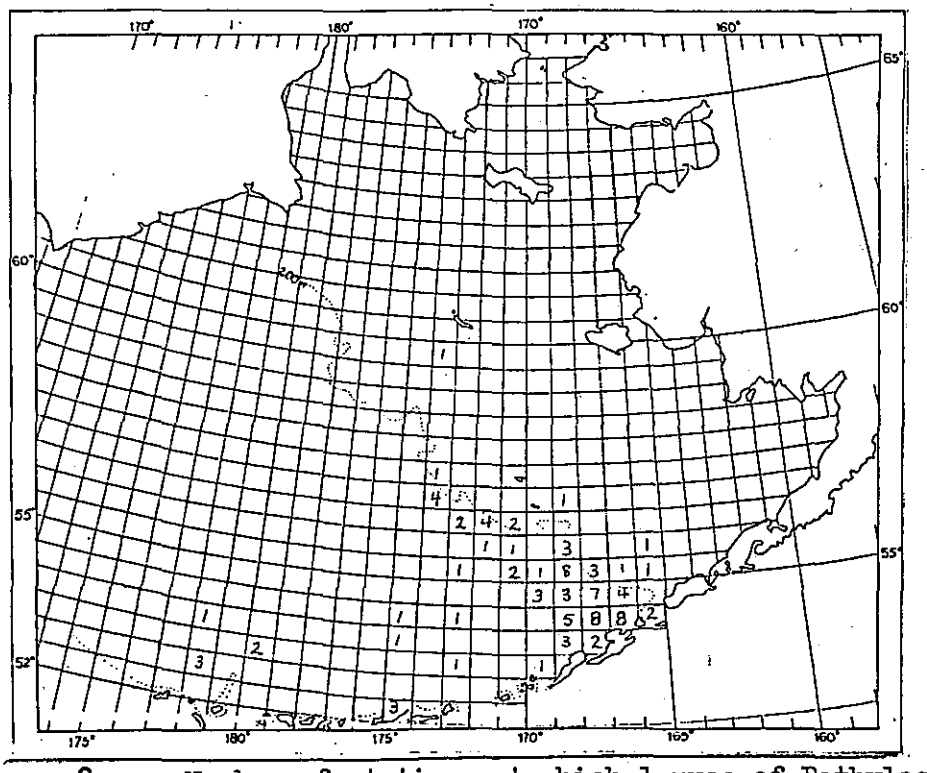

FIG. 8 Number of stations at which larvae of Bathylagidae have been caught.

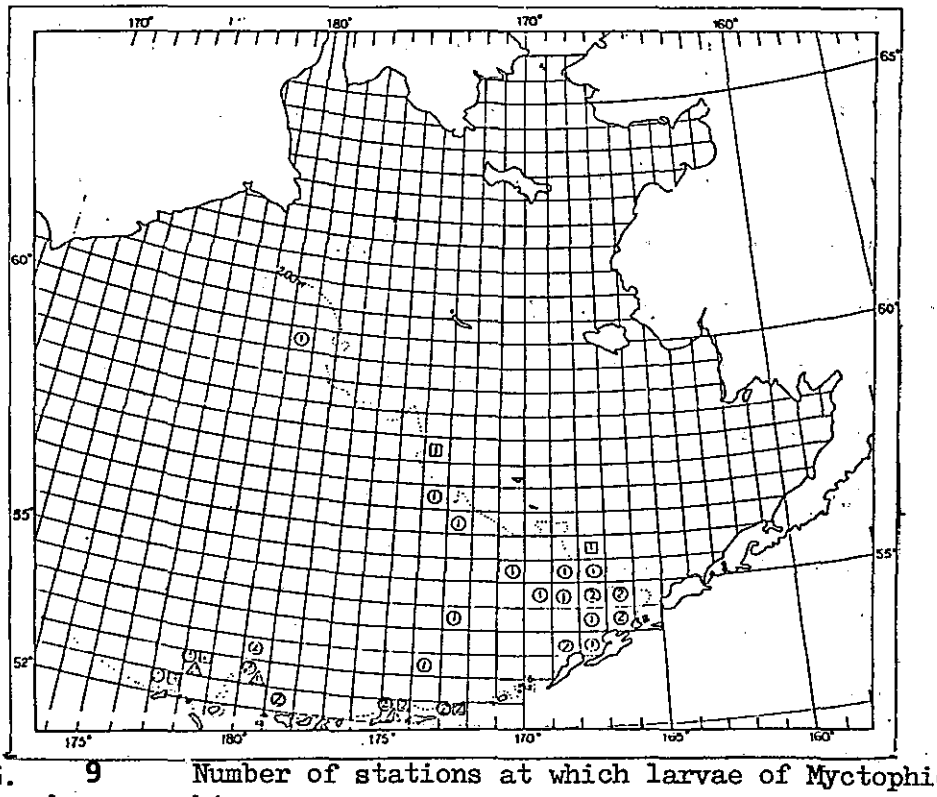

FIG. 9 Number of stations at which larvae of Myctophidae have been caught.

△ Diaphus theta, □ Protomyctophum thompsoni, ○ Stenobrachius leucopsarus.

Eggs of this species are pelagic but none were reported.

Myctophidae

The family of lanternfishes includes 7 species in the Bering Sea and larvae of 3 of these were reported from plankton collections. Larvae of the northern lampfish, Stenobrachius leucopsarus, were collected most frequently of the 3 species and were caught at 35 stations on 9 cruises in spring, summer, and fall. Northern lampfish larvae were distributed from the edge of the continental shelf across the slope and along the Aleutian Islands westward to 177°E (Fig. 9). Only one larva of this species was caught north of 57°N, and there were no large catches made at any station.

Larvae of the bigeye lanternfish, Protomyctophum thompsoni, were collected at 10 stations on 3 cruises in spring and summer. They were caught at 2 stations along the continental shelf and at 8 stations close to the Aleutian Islands westward to 177°E. Catches were small, consisting of only 1 or 2 larvae at any one station.

California headlightfish, Diaphus theta, were caught at only 4 stations on 1 cruise in summer. These specimens were juveniles or young adults close to the Aleutian Islands from 174°W to 178°E.

Almost all myctophid larvae were caught with obliquely or vertically towed nets that fished well below the surface. As with bathylagids, the absence of myctophid larvae from the central deep-water region of the Bering Sea may be a sampling artifact rather than an actual distribution pattern due to the predominance

of surface sampling in that area.

Little is known about eggs of myctophids and though they are assumed to be pelagic none were reported.

Gadidae

The codfishes have 4 or possibly 5 species in the Bering Sea, and larvae of 3 of these were found in 21 plankton collections made during all seasons.

Larvae and juveniles of saffron cod, Eleginus gracilis, were caught at 13 stations on 2 cruises in August 1975 and 1976. All of those classified as larvae were caught in Norton Sound and Bering Strait, but the juveniles were caught in outer Bristol Bay (Fig. 10). Most samples contained only 1 or 2 specimens but one sample from quadrangle 63½°N, 164°W yielded 54 saffron cod larvae.

Eggs of saffron cod are demersal and none were reported.

Larvae of Pacific cod, Gadus macrocephalus, were caught at 5 stations on 3 cruises in spring and summer. The total catch was only 10 larvae, 5 from a station in quadrangle 52°N, 174°W in the Aleutian Islands and 5 from 4 stations on the continental shelf south of Nunivak Island. They were caught in surface, oblique, and vertical net tows.

Eggs of Pacific cod are demersal or benthonic and none were reported.

Larvae identified only to the family level Gadidae were caught at 41 stations on 8 cruises in spring and summer. Catches at individual stations were usually less than 5 larvae, but at one

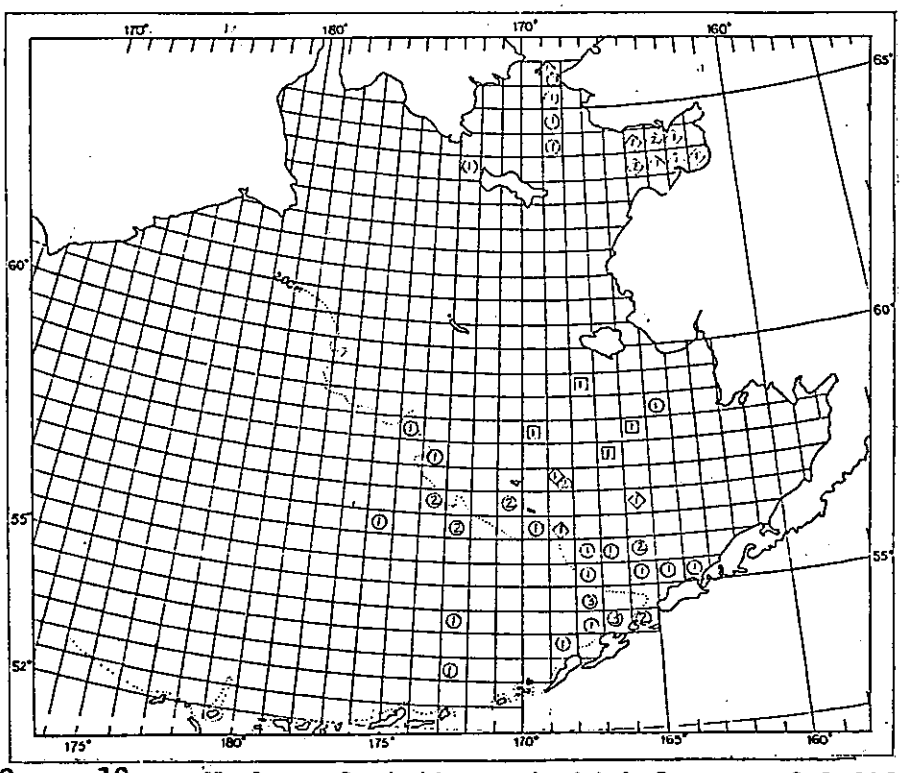

FIG. 10 Number of stations at which larvae of Gadidae have been caught.

◇ Eleginus gracilis, □ Gadus macrocephalus, ○ Unidentified gadids.

station just west of Unimak Pass 59 larvae of this taxon were caught during a spring cruise. Distribution of larvae identified only as Gadidae extended from the Aleutian Islands to Bering Strait and from 163°W to 176°W. Stations at which these larvae were caught were scattered from well up on the continental shelf across the slope and a few stations were over deep water. It seems likely that the unidentified gadids from north of St. Lawrence Island were a different taxon than those to the south.

Walleye pollock, Theragra chalcogramma, have probably been the primary objective of more ichthyoplankton surveys than any other fish in the Bering Sea. As a result the distribution and abundance of their eggs and larvae are quite well known and have been described in various reports (Musienko 1963; Serobaba 1968, 1974; Waldron and Favorite 1977; Waldron and Vinter 1978; Waldron 1978). These reports show larvae to be most abundant between Unimak Pass and the Pribilof Islands along the continental slope, with total distribution extending to 59°N in spring. During summer larvae show a more wide-spread distribution from the Aleutian Islands to 64½°N, and from well up on the continental shelf in Bristol Bay across the central basin to 177°E.

Because of the large number of samples containing larvae it was possible to show distribution for two periods, spring and summer, and for two types of net tows: surface tows and combined oblique and vertical tows. Larvae were caught in surface tows made at 40 stations on 2 cruises in March-May, plus an undetermined number of stations on one other spring cruise for which the

catch by station could not be determined. These surface samples showed them to be distributed along the continental slope in a somewhat discontinuous pattern (Fig. 11). During the same 2 cruises larvae were caught in oblique net tows made at 124 stations plus catches made at 15 stations on another spring cruise. Distribution shown by these oblique tows covered essentially the same areas as that shown by the surface tows but there was more continuity in the distribution (Fig. 12).

During June-August, larvae were caught in surface tows at 76 stations, mainly on 9 cruises of the Oshoro Maru, and were widely distributed over the entire Bering Sea (Fig. 13). Fewer vertical and oblique tows were made during summer and larvae were caught at only 31 stations yet these showed a wide distribution from the Aleutian Islands to 63½°N and from 164°W to 178°E (Fig. 14).

In spite of the intensive sampling for larvae along the continental slope and outer shelf, it is likely that there is a gap in our knowledge of their distribution and abundance over the deep central basin. Comparison of catches in surface and oblique net tows shows that relatively fewer larvae are caught in surface tows and at fewer stations. Most of the sampling over the central basin was with the surface tows (see Fig. 4) and most of those were during summer. It is reasonable to assume that sampling by means of oblique tows should reveal a larger population of pollock larvae over the deep central basin than is shown by surface tows.

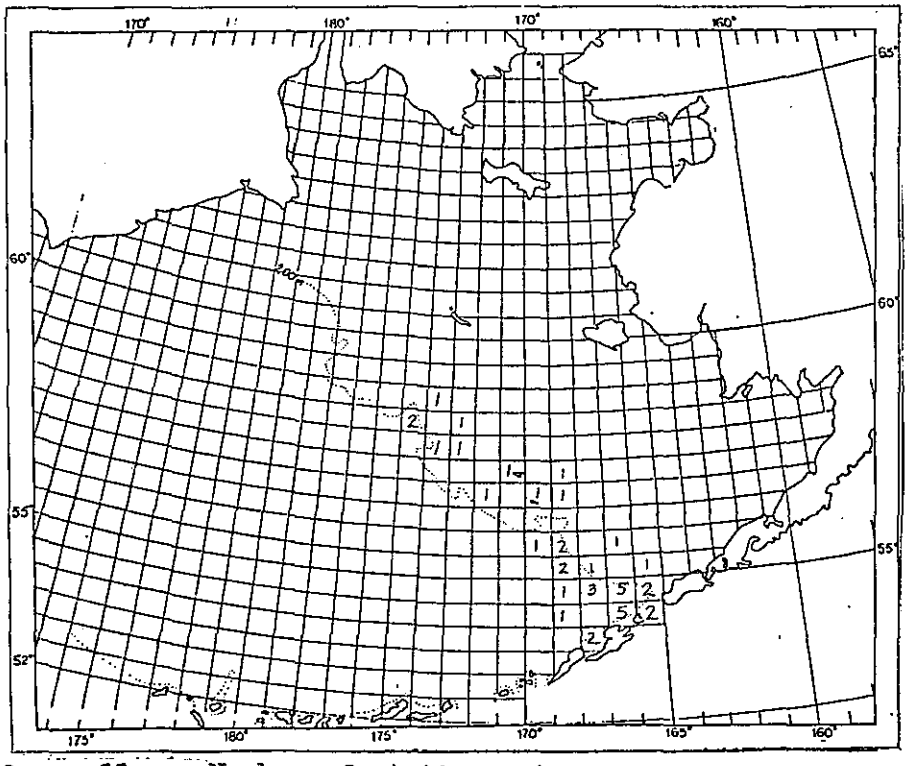

FIG. 11 Number of stations at which larvae of Theragra chalcogramma have been caught with surface tows in spring, March-May.

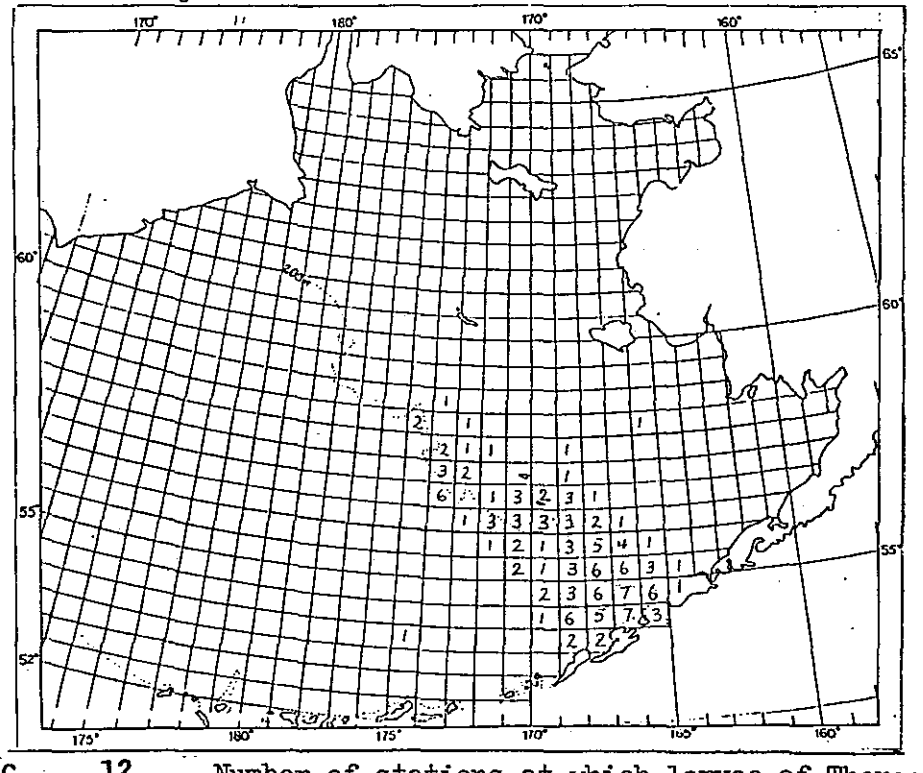

FIG. 12 Number of stations at which larvae of Theragra chalcogramma have been caught with oblique or vertical tows in spring, March-May.

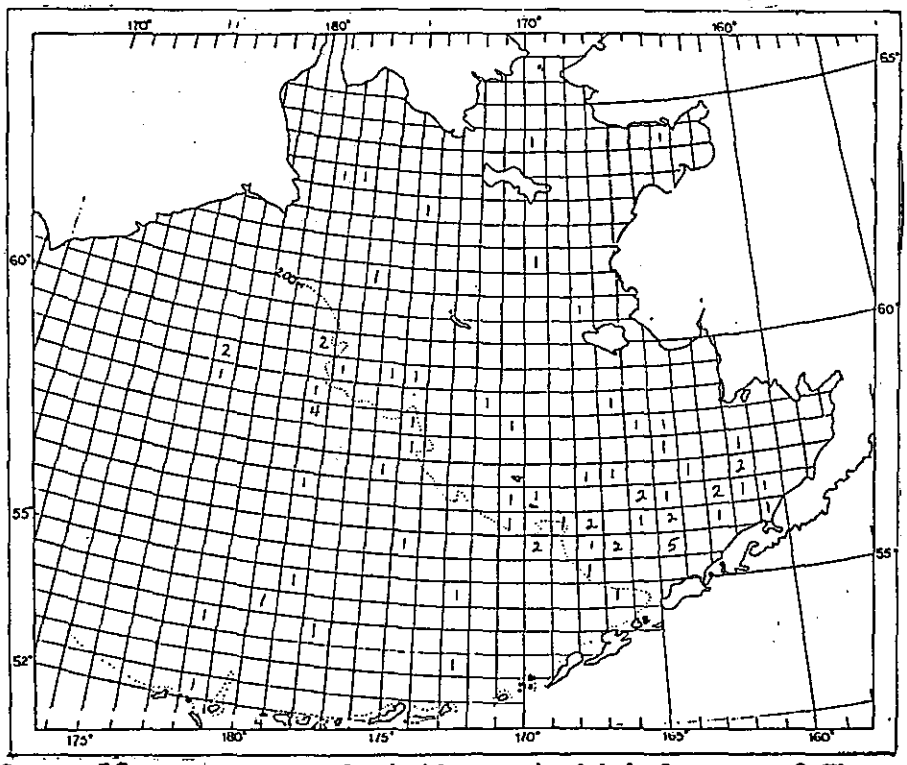

FIG. 13 Number of stations at which larvae of Theragra chalcogramma have been caught with surface tows in summer, June-August.

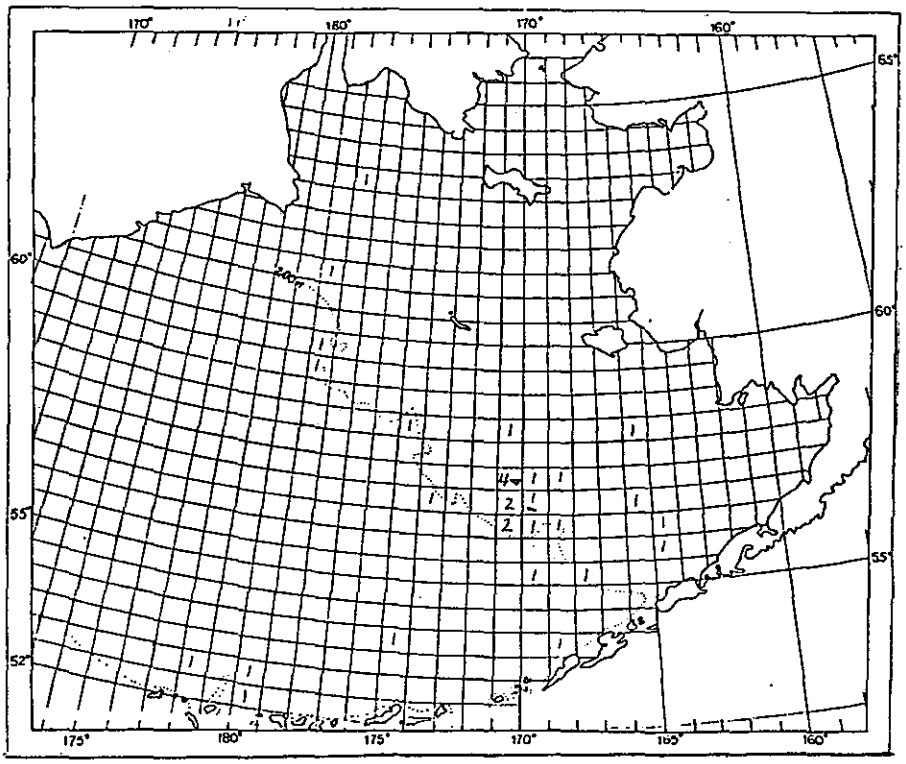

FIG. 14 Number of stations at which larvae of Theragra chalcogramma have been caught with oblique and vertical tows in summer, June-August.

Pollock eggs are one of the few egg species routinely identified in plankton samples and so their distribution can be shown in some detail. They are present generally along the outer continental shelf and continental slope from the Aleutian Islands to 60°N (Fig. 15). Within this area they occur from late February to late July but are most abundant from about mid-March to mid-May. Abundance of eggs has been treated in greater detail than that of larvae, probably because eggs are caught more readily than larvae in vertical net tows which were used on most of the Soviet cruises. Quantitative estimates of abundance are shown for cruises made in 1959 (Musienko 1963), for 1965 (Serobaba 1968), and 1972 (Serobaba 1974) although the latter shows only vertical distribution along section lines. Estimates of egg abundance based on oblique net tows are given for 1976 (Waldron and Favorite 1977), for 1977 (Waldron and Vinter 1978) and for 1978 (Waldron 1978). Maximum abundance of eggs beneath 1 m^2 of sea surface, as shown by vertical net tows, was 598 in March 1959 between Unimak Pass and the Pribilof Islands and over 2,000 eggs at some time from March to May 1965 immediately north of Unimak Pass. Maximum numbers of eggs beneath 1 m^2 shown by oblique net tows was 1,268 in May 1976 east of the Pribilof Islands, 1,041 in April 1977 north of Unimak Island, and 958 in March 1978 northwest of Unimak Pass.

Most of the samples of ichthyoplankton were collected with open nets that caught all plankton between the maximum tow depth and the surface, so there is little information on the vertical

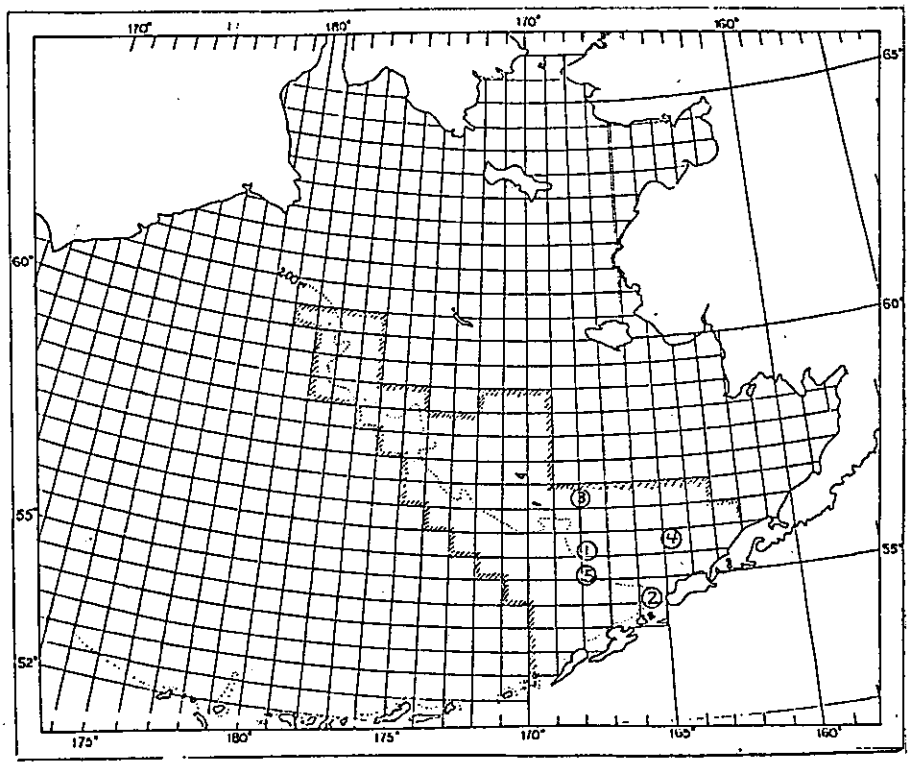

FIG. 15 Area within which eggs of Theragra chalcogramma have been caught, and centers of abundance in 5 years. ////// Limit of distribution, O Center of abundance in 1 - March 1959, 2 - March-May 1965, 3 - May 1976, 4 - April 1977, 5 - March 1978.

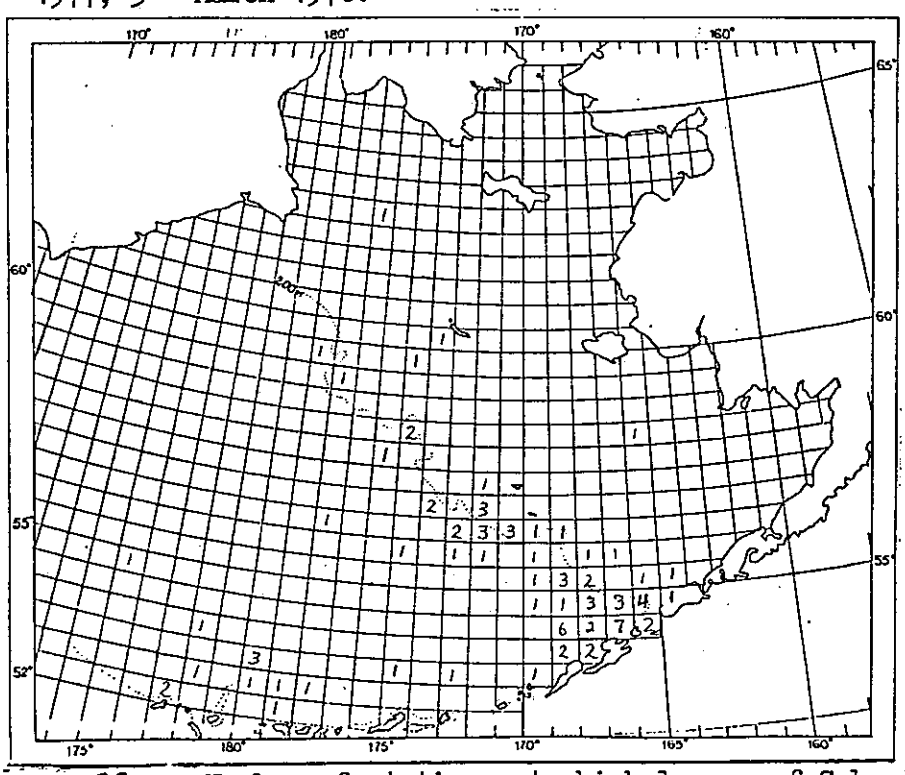

FIG. 16 Number of stations at which larvae of Sebastes sp. have been caught.

distribution of the different fish larvae and eggs. During a Soviet cruise in 1972 (Serobaba 1974) samples were collected with a closing type net fished at several different levels. Results of this survey show pollock eggs and larvae present to depths of 1000 m, but catches below 100 m depth were quite small and below 200 m they were less than 1 per 1000 m^3.

Zoarcidae

Eelpouts is one of the larger families with 29 species present as adults in the Bering Sea, yet larvae have been recorded for only 3 stations (see Fig. 6). All eelpouts were caught at stations over the continental shelf and were caught during spring, summer, and winter.

The lack of eelpouts in plankton collections probably reflects spawning characteristics, behavior of young, and configuration of the net tow used to collect most plankton samples. Reproduction among eelpouts may be oviparous or ovoviviparous according to Hart (1973), and Clemens and Wilby (1961) state that eelpouts may be viviparous. Eggs of some eelpouts are as large as 7 mm (*Lycodes palearis*, in Hart 1973) and hence the newly hatched young might be quite large, say on the order of 20 mm, and active. If large size and active behavior were coupled with dwelling on or close to the bottom, then it would be difficult to capture larva of eelpouts with standard plankton nets. In order to delineate the distribution of larval eelpouts it is likely that a special sampler must be used to fish the layer immediately above bottom.

Macrouridae

Rattails or grenadiers are represented in the Bering Sea by 9 species, and Coryphaenoides pectoralis is thought to be abundant enough to support a commercial fishery (Novikov 1970). Larvae of grenadiers were caught at 8 stations on 5 cruises in spring and summer All were caught close to or over the continental slope between the Aleutian Islands and 56½°N, and between 167°W and 180° (see Fig. 6), and only 1 or 2 larvae were caught at any one station.

Macrourid eggs are pelagic, identifiable to family, and were caught in a vertical tow near 55°N, 177°E (Musienko 1963).

Melamphaeidae

This family of bathypelagic fish is represented in the Bering Sea only by the highsnout melamphid, Melamphaes lugrubris, and 2 small adults were caught at 1 station in quadrangle 52½°N, 178°E in the western Aleutian Islands (see Fig. 6).

No melamphid eggs were reported.

Scorpaenidae

Rockfish are a commercially important group of fish with 12 species of Sebastes and 3 of Sebastolobus in the Bering Sea. At present it is difficult, if not impossible, to identify larval rockfish from the Bering Sea to species although it is possible to separate genera. Larval Sebastolobus were not reported from any of the plankton collections, but Sebastes sp. larvae were caught at 89 stations on 10 cruises made in spring and summer. Individual catches were not large, generally less than 20 larvae per

station, but a few samples contained 30-40 larvae each. Rockfish larvae were distributed mainly over the continental slope, the adjacent shelf and deep water, although a few were caught well up on the continental shelf. They were caught from the Aleutian Islands north to about 63°N, although only 2 stations were north of 60°N, and from 164°W westwards to 175°E (Fig. 16). Rockfish larvae were collected with surface, oblique, and vertical net tows though most appear to have been caught in oblique tows.

Rockfish of the genus Sebastes are ovoviviparous and no eggs were reported.

Hexagrammidae

The greenlings and Atka mackerel were one of the most commonly occurring groups of larvae in all plankton samples. In the Bering Sea the family contains 2 genera, Pleurogrammus, with 1 species, the Atka mackerel, P. monopterygius, and Hexagrammos or greenlings with 5 species. Identification to species of the greenlings is not always possible so these larvae have been treated here only as a genus. Greenling larvae were collected at 251 stations on 21 of the 26 cruises; only one other genus occurred as frequently and that was the sculpin genus Hemilepidotus. Greenling larvae appeared in catches made during all seasons of the year from late February to November. Catches at individual stations were moderate, usually less than 10 larvae, and the maximum catch was 253 larvae at a station in quadrangle 53°N, 178°E in June 1960. Larval Hexagrammos sp. were distributed widely across the Bering Sea from the Aleutian Islands to 62°N and

from 161°W in Bristol Bay to 174°W, but appeared to be caught more frequently south of the Pribilof Islands along the edge of the continental shelf and to the west in the vicinity of Bowers Ridge (Fig. 17).

Larvae of Atka mackerel were caught at 118 stations on 11 cruises in winter, spring, and summer from late February to August. Catches at individual stations were generally smaller than for greenling larvae and maximum catch was 37 larvae at a station in quadrangle 55°N, 170°W. Atka mackerel larvae were distributed over much the same area as were greenlings occurring from the Aleutian Islands to 62°N and from 160°W in Bristol Bay to 175°E, but they were present at less than half the number of stations as compared to greenlings (Fig. 18). Both greenlings and Atka mackerel larvae are caught more frequently with surface than with oblique and vertical net tows.

Eggs of Hexagrammidae are demersal and none were reported.

Anoplopomatidae

The family of sablefishes is composed of 2 species, both of which are present in the Bering Sea as adults.

One larva tentatively identified as skillfish, *Erilepis zonifer*, was caught at 57°41'N, 174°25'W in July 1960.

Larvae of sablefish, *Anoplopoma fimbria*, were caught at 28 stations on 11 cruises in spring and summer. Usually only a few were caught at any one station, but an unusually large catch of 45 larvae was made in quadrangle 55°N, 164°W near Unimak Island in 1968. Larvae of sablefish were distributed generally from the

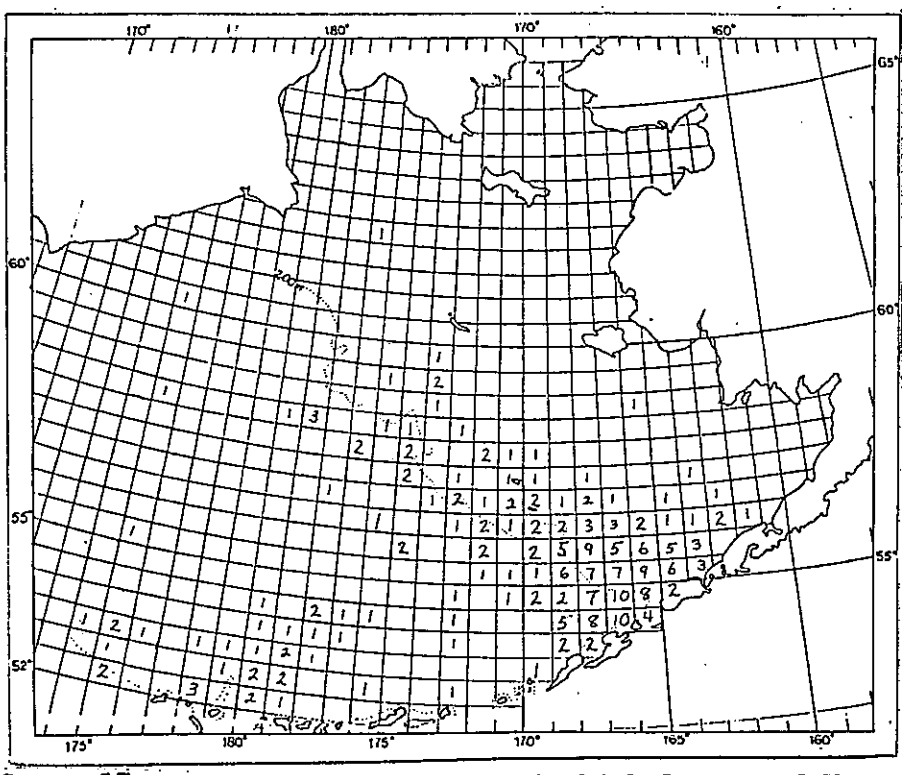

FIG. 17 Number of stations at which larvae of Hexagrammos sp. have been caught.

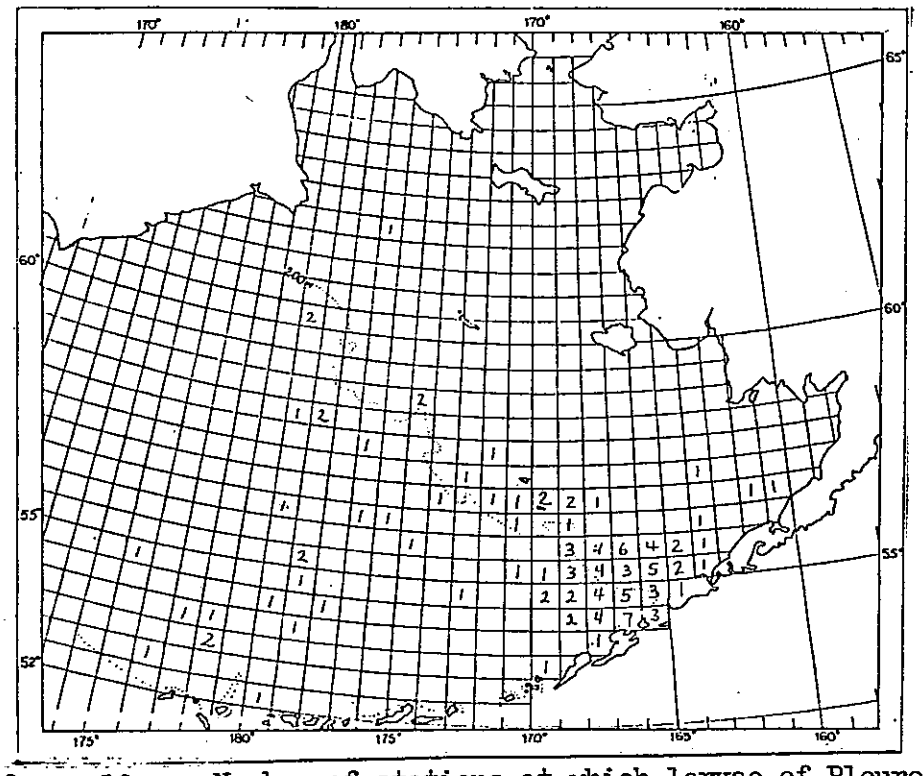

FIG. 18 Number of stations at which larvae of Pleurogrammus monopterygius have been caught.

Aleutian Islands to about 59°N and from 162°W to 175°W, but were found most frequently along the edge of the continental shelf and in the vicinity of Bowers Ridge in the central Aleutian Islands (Fig. 19). More appear to have been caught with surface rather than oblique or vertical net tows.

Eggs of sablefishes are reportedly pelagic, but none were reported.

Cottidae

With some 75 species in 36 genera, sculpins are by far the largest family of fish in the Bering Sea and were present in all 26 collections. Larvae of this group can often be identified as cottids but relatively few are identifiable to species. In these collections only 7 genera with 6 species were listed, the remainder coming under the heading of unidentified cottids (see Table II). Of these, 3 species and 1 genus each were captured on only 1 cruise.

The most commonly occurring and widespread sculpin larvae were the Irish lords, *Hemilepidotus* sp., which were caught at 208 stations on 21 cruises during all seasons of the year from late February to November. Irish lords include 5 species in the Bering Sea, 1 of which is found only on the western side. Identification to species is possible for larvae with countable finrays but the smaller larvae are usually identified only to genus, thus distribution is shown only for the genus. Irish lords have one of the widest distributions of any larvae in the Bering Sea, extending from the Aleutian Islands to 63°N and from 160°W in Bristol Bay to

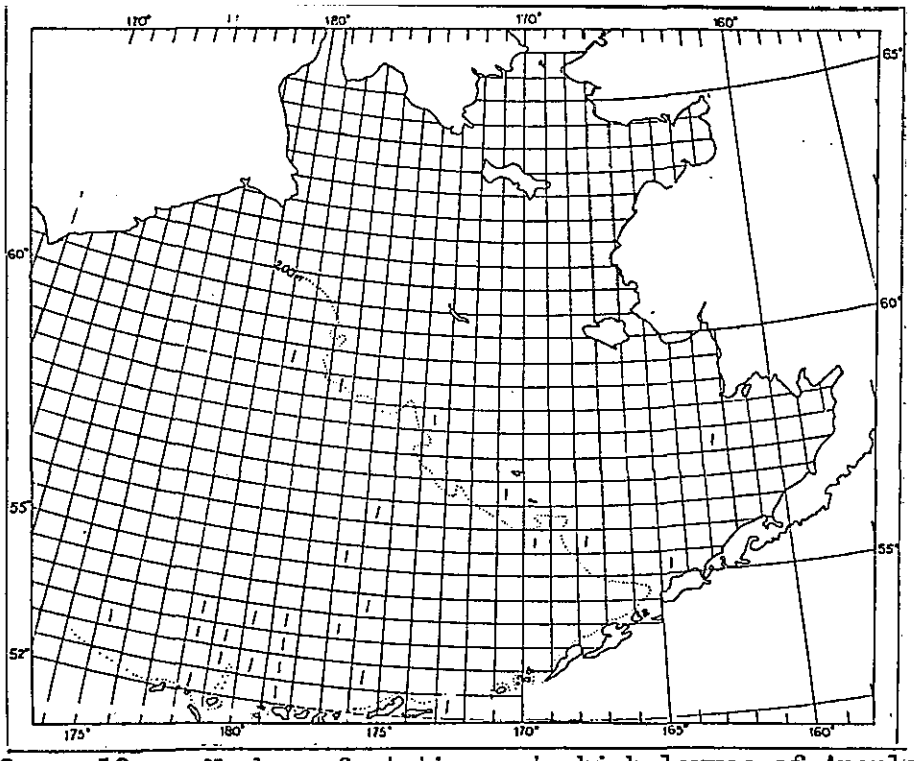

FIG. 19 Number of stations at which larvae of Anoplopoma fimbria have been caught.

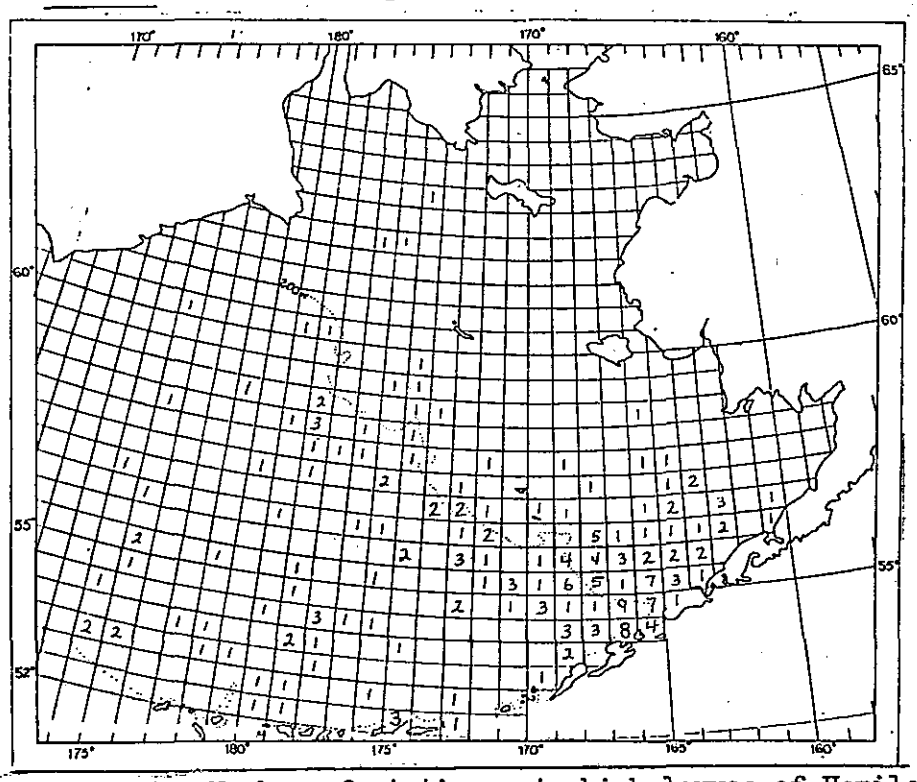

FIG. 20 Number of stations at which larvae of Hemilepidotus sp. have been caught.

174°E (Fig. 20). While there are insufficient quantitative data for the entire region, collections made aboard the Oshoro Maru during summer were all made by approximately the same type of surface tow, and these show no areas of consistently high abundance. Actual catches of Irish lord larvae for a 10-minute surface tow range from 1 to 3,709 with only 5 of 114 collections containing more than 100 larvae. The catch of 3,709 larvae was made in quadrangle 58½°N, 165°W. Only the northeastern area of the Bering Sea, roughly the Nunivak Island-St. Matthew Island-St. Lawrence Island area appears to be devoid of Irish lord larvae. This genus of sculpins appears to share the surface layer with the hexagrammid larvae as more of them are caught with neuston and other surface-towed nets than with nets sampling deeper waters. Irish lords differ from the hexagrammids in that there is a greater difference in day and night catches of these sculpins than there is for hexagrammids, with larger catches made at night.

A second genus of sculpins common in these collections was Myoxocephalus, great sculpins, with 10 species present in the Bering Sea. The taxonomy of the adults is unclear and no attempt was made in any of the collections to identify larvae to species. Larvae of great sculpins did not occur as frequently as those of Irish lords but were caught at 53 stations on 9 cruises in the summer. They have one of the widest north-south distributions, extending from the Aleutian Islands to 65½°N, but appear to be limited to the continental shelf with their east-west distribution extending from 161°W to 174°E (Fig. 21). Although the catches

were small, 1 or 2 larvae per station, the great sculpins are present in the northeastern area in which Irish lords were absent. The area of greatest abundance is in Bristol Bay where catches of up to 408 larvae per station were reported in quadrangle 57°N, 161°W, and several stations reported catches of more than 50 larvae. Most of the great sculpin larvae were caught with surface tows.

In addition to Hemilepidotus sp. and Myoxocephalus sp., 6 other taxa of sculpins plus a category called unidentified cottids were present in the samples. Distribution of these miscellaneous species is shown (Fig. 22).

Artediellus pacificus, the hookhorned sculpin, was collected at one station east of the Pribilof Islands on the continental shelf during late spring.

Icelinus borealis, the northern sculpin, was caught at 2 stations between Unimak Island and the Pribilof Islands on 1 cruise in spring.

Gymnocanthus sp. was caught at one station northeast of St. Lawrence Island during summer.

Malacocottus sp., probably M. kincaidi, the blackfin sculpin, was caught at 4 stations between Unimak Pass and the Pribilof Islands during a spring cruise.

Triglops pingeli, the ribbed sculpin, was caught at 1 station southeast of Nunivak Island during a fall cruise, and Triglops sp. was caught at 3 additional stations, 1 northeast of St. Lawrence Island on a summer cruise, 1 between Unimak Pass and the Pribilof Islands, and 1 near the Alaska Peninsula during a spring cruise.

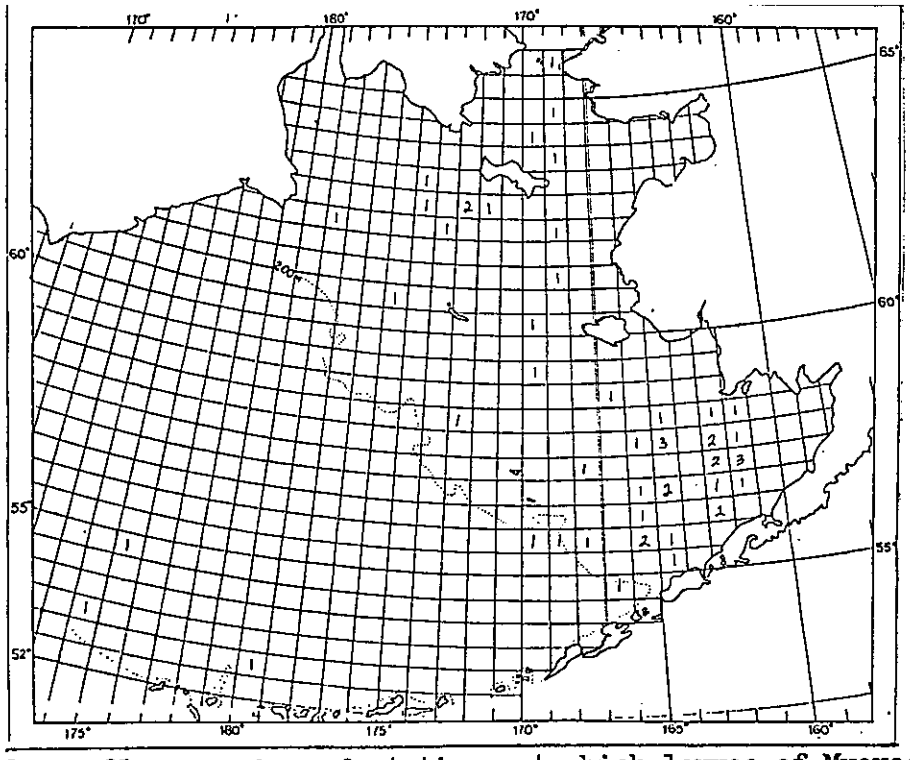

FIG. 21 Number of stations at which larvae of Myoxocephalus sp. have been caught.

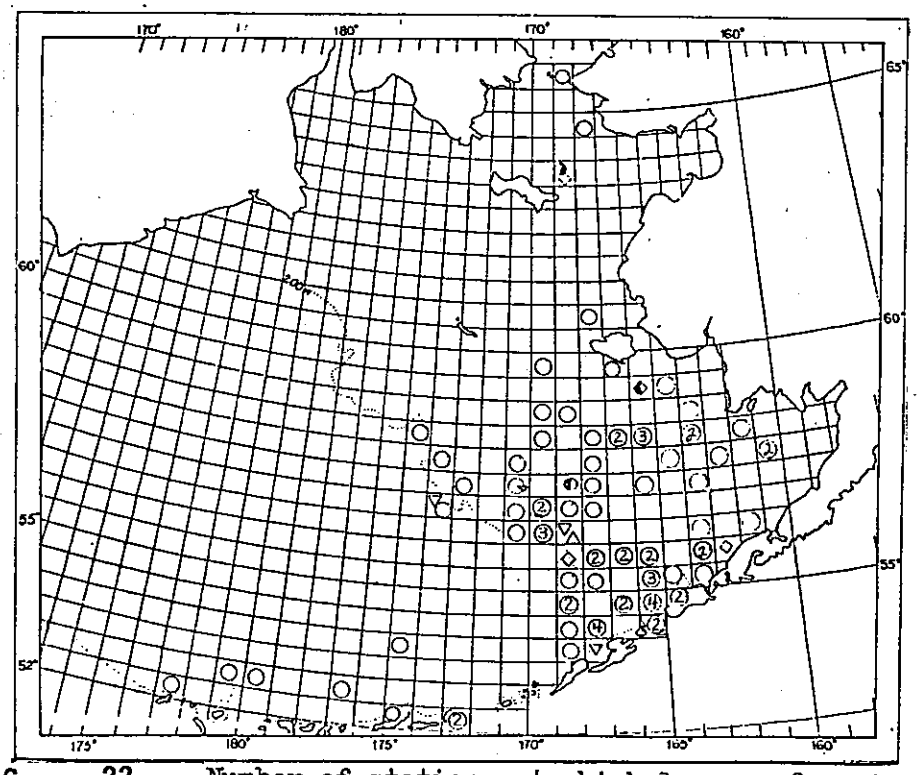

FIG. 22 Number of stations at which larvae of various cottids have been caught. Each unnumbered symbol represents one station. ◐ Artediellus pacificus, ◑ Gymnocanthus sp., △ Icelinus borealis, ▽ Malacocottus sp., ◇ Triglops sp., ◆ Triglops pingeli, ○ Unidentified cottids.

In addition to these taxa which could be identified, there were numerous cottids which could only be identified to family. These were distributed mostly over the continental shelf and slope south of 60°N, but a few were collected as far north as Bering Strait and west along the Aleutian Islands to 177°E. Unidentified cottids were collected at 83 stations on 11 cruises in spring and summer.

Eggs of cottids are demersal and none were found in any of the plankton collections.

Agonidae

The poachers are represented in the Bering Sea by 16 species and larvae of 7 of these were present in the plankton samples. Larval poachers were caught at 45 stations on 14 cruises in spring and summer.

Agonus acipenserinus, the sturgeon poacher, was caught at 18 stations on 7 cruises, all of which were in summer. They were distributed mainly in Bristol Bay and the adjacent continental shelf except for one larva caught at a station north of Nunivak Island (Fig. 23).

Odontopyxis trispinosa, the pygmy poacher, was caught at 4 stations on one cruise in summer, and all were caught north of St. Lawrence Island and in Bering Strait.

Asterotheca infraspinata, the spinycheek starsnout, was caught at 2 stations just north of Unimak Island in summer.

Aspidophoroides sp. larvae were caught on 2 cruises, A. bartoni on 1 cruise, and A. olriki on one other cruise, all in

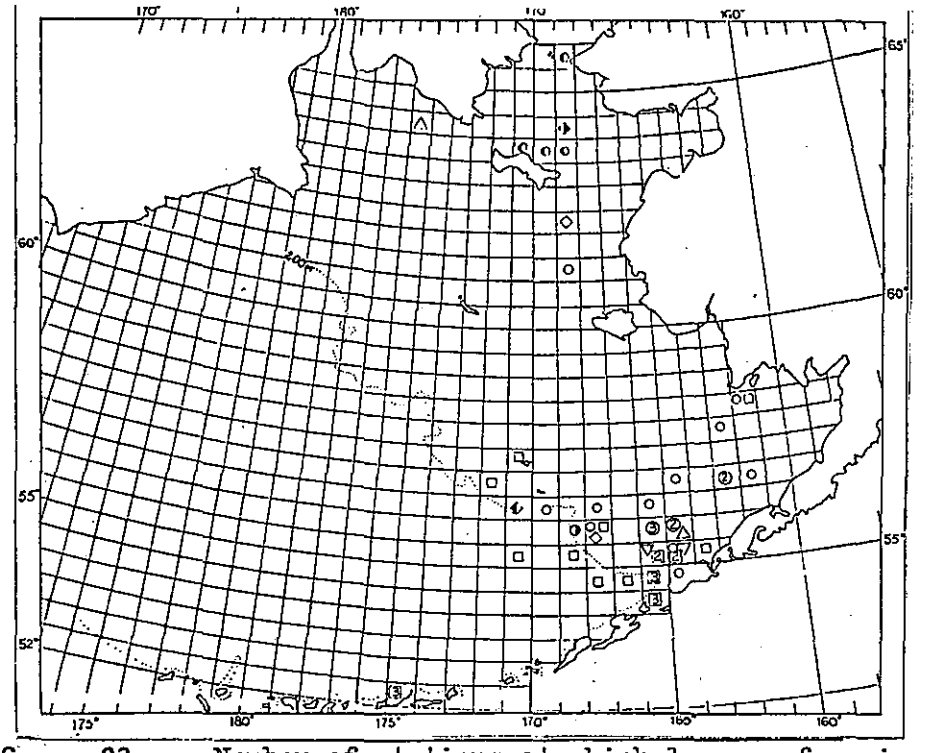

FIG. 23 - Number of stations at which larvae of various agonids have been caught. Each unnumbered symbol represents one station. ○ Agonus acipenserinus, ▽ Asterotheca infraspinata, ◇ Aspidophoroides sp., ◖◗ A. bartoni, ◖◗ A. olriki, △ Hypsagonus quadricornis, ◑ Ocella dodecaedron, ◐ Odontopyxis trispinosa, □ Unidentified agonids.

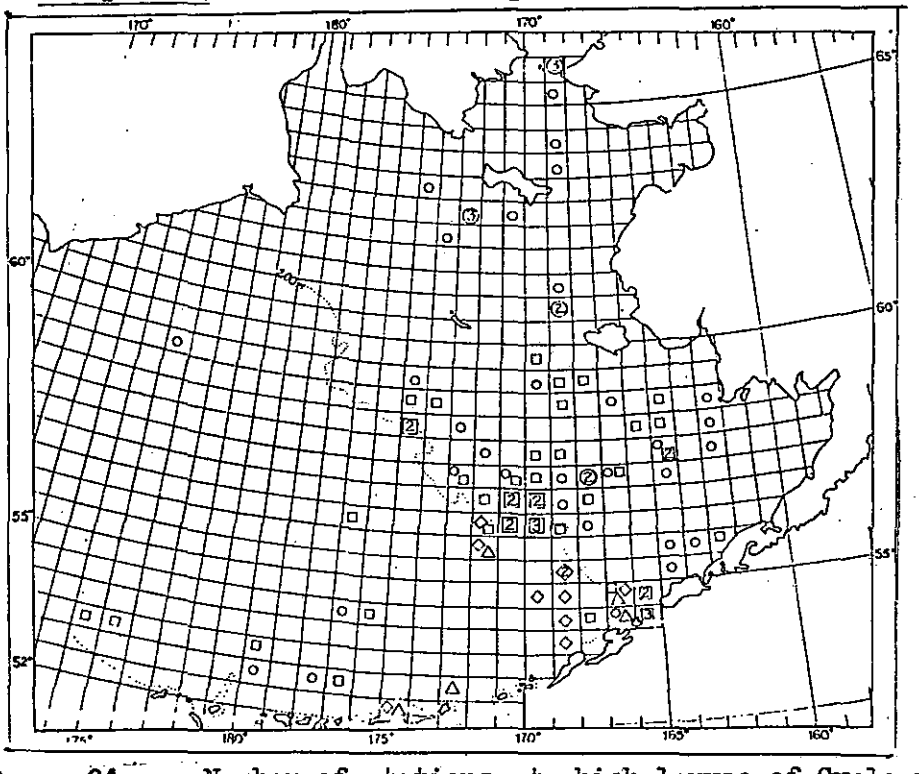

FIG. 24 Number of stations at which larvae of Cyclopteridae have been caught. Each unnumbered symbol represents one station. △ Aptocyclus ventricosus, ○ Liparis sp., ◇ Nectoliparis pelagicus, ⊡ Unidentified cyclopterids

summer. Larvae of this genus were distributed from north of St. Lawrence Island (A. olriki) and along the continental shelf edge south of the Pribilof Islands.

Hypsagonus quadricornis, the fourhorn poacher, was caught on 2 cruises in spring and summer, with 1 specimen from the Gulf of Anadyr and the other specimen north of Unimak Island.

Occella dodecaedron, the Bering poacher, was caught at 1 station in summer on the edge of the continental shelf between Unimak Pass and the Pribilof Islands.

Larval agonids identified only to family were caught at 22 stations on 6 cruises in spring and summer. They were distributed from the Aleutian Islands north to 58°N, and from 161°W in Bristol Bay to 174°W along the Aleutian Islands and along the continental slope.

Eggs of agonids are demersal and none were reported.

Cyclopteridae

The snailfish and lumpsuckers, with 49 species, are the second largest family (after Cottidae) in the Bering Sea and one of the least known with respect to both adult and larval identification. Cyclopterids were present in samples from 20 cruises, but only 4 taxa were identified, plus larvae identified to family level.

Aptocyclus ventricosus, the smooth lumpsucker, was caught at 5 stations on 4 cruises with a total catch of 6 specimens. All were caught with surface nets during spring and summer, 4 of them near the Aleutian Islands between 166°W and 175°W, and 2 specimens at a station in quadrangle 55½°N, 171°W (Fig. 24).

Nectoliparis pelagicus, the tadpole snailfish, was caught at 10 stations on 4 cruises during spring and summer, with a total catch of 20 specimens. Most were caught in nets fished below the immediate surface, but a few were taken with surface nets. The tadpole snailfish was found in a relatively small area between the Aleutian Islands and 56°N, and between 168°W and 175°W.

Larvae of snailfish of the genus Liparis, which has 13 species in the Bering Sea, were caught at 41 stations on 12 summer cruises. Most samples contained relatively few larvae but at one station in quadrangle 57½°N, 162°W, 671 larval Liparis sp. were caught (see Cruise 20, Table I). Larvae of this genus were distributed widely from the Aleutian Islands to Bering Strait and between 162°W to 175°E. They were caught most frequently over the continental shelf but were also found over the continental slope and adjacent deep water. Most of them were caught with surface nets.

Unidentified snailfish were caught at 46 stations on 10 cruises during spring and summer. These unidentified snailfish were found between the Aleutian Islands and 60°N, and from 162°W to 174°E, and within these limits were found over the same areas as were Liparis sp.

Cyclopterid eggs are demersal and none were reported.

Bathymasteridae

The searchers and ronquils are represented in the Bering Sea by 3 species in 2 genera, with 1 genus and 1 species present in the samples. Bathymasterids were caught at 76 stations on 18

cruises in spring, summer, and fall, but only 3 specimens were caught in fall. The family is quite widespread in the Bering Sea and occurred at stations from the Aleutian Islands to 63°N and from 163°W to 174°E (Fig. 25). They were found over the continental shelf, slope, and deep water of the central basin and more were collected with surface nets than with nets that fished deeper. Catches at individual stations were generally small, less than 5 specimens, but at 2 stations (in quadrangles 53°N, 174°E and 55½°N, 167°W) 262 and 245 were caught (Cruise 18, Table I). Only 6 specimens of Bathymaster signatus, the searcher, were caught, 3 each at 2 stations in quadrangles 54½°N, 169°W and 55°N, 167°W.

Eggs of bathymasterids are demersal and none were reported.

Anarhichadidae

The wolffishes have 1 or possibly 2 species in the Bering Sea, and were represented in the collections by 5 larval Anarhichas orientalis, the Bering wolffish, caught at 5 stations on 1 cruise in spring (see Cruise 37, Table I). All were caught with neuston nets at stations near the outer edge of the continental shelf between Unimak Pass and the Pribilof Islands (see Fig. 6).

Eggs of wolffish are demersal and none were reported.

Stichaeidae

The pricklebacks are a fairly large family with 21 species present in the Bering Sea and were represented in these collections by 6 species in 4 genera plus stichaeid larvae identified

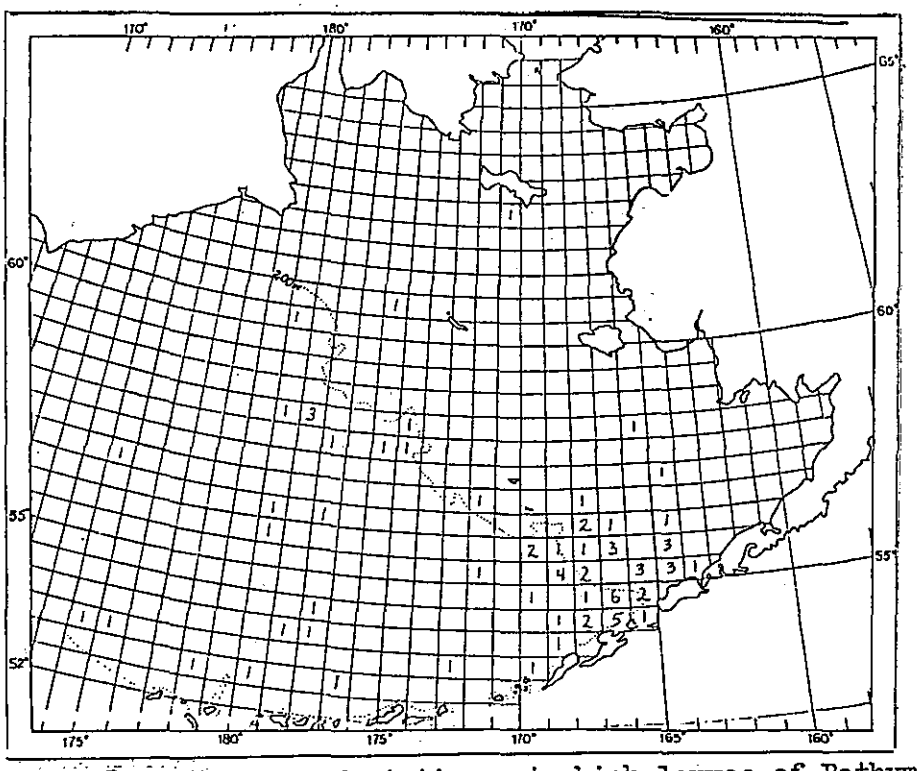

FIG. 25 Number of stations at which larvae of Bathymasteridae have been caught.

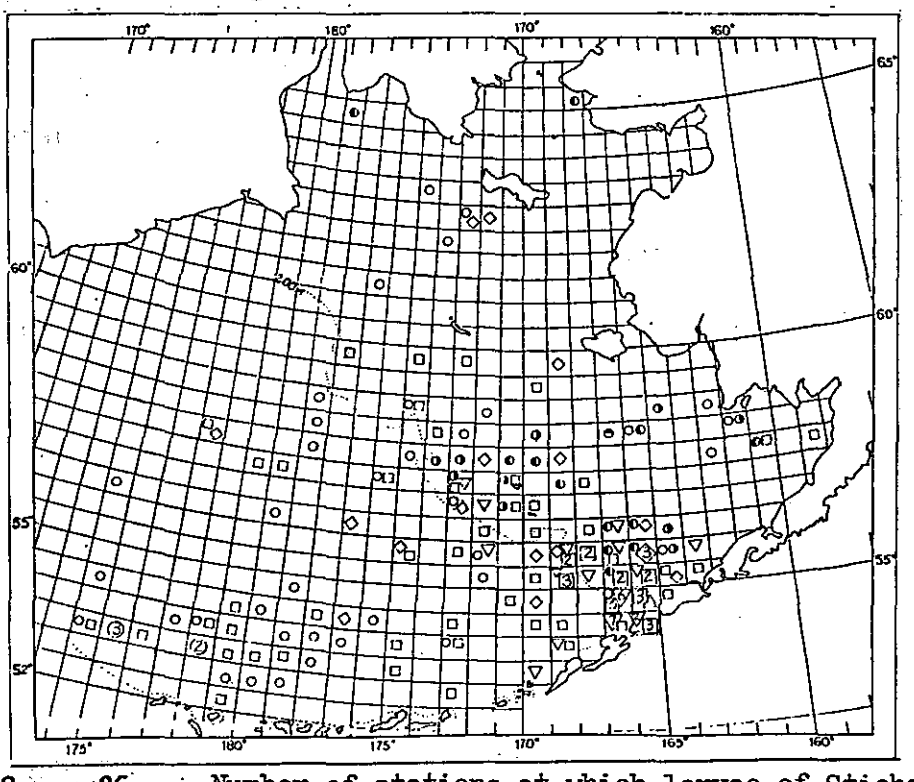

FIG. 26 Number of stations at which larvae of Stichaeidae have been caught. Each unnumbered symbol represents one station. △ Alectridium aurantiacum, ▽ Chirolophis polyactocephalus, ○ Lumpenus sp., ◐ L. fabricii, ◑ L. maculatus, ◓ L. medius, ◇ Stichaeus punctatus, □ Unidentified stichaeids.

only to family. Pricklebacks were present in 23 of the collections and had one of the widest distributions of any fish larvae being found from the Aleutian Islands to 65°N, and from 158°W in Bristol Bay to 174°E (Fig. 26). Most stichaeid larvae were caught with surface tows although some were taken with oblique and vertical tows. One species, Lumpenus maculatus, was caught more frequently in the oblique tows.

Alectridium aurantiacum, the lesser prickleback, was collected at only a single station (see Cruise 1, Table I) in quadrangle 54½°N, 165°W.

Chirolophis polyactocephalus, the decorated warbonnet, was caught at 27 stations on 2 cruises in spring in the general area between the Aleutian and Pribilof Islands from deep water to the outer continental shelf. Catches were moderate, usually less than 20 larvae per station with a maximum catch of 78 at a station in quadrangle 53½°N, 168°W.

The genus Lumpenus included those pricklebacks identified only to genus, plus 3 species, L. fabricii the slender eelblenny, L. maculatus the daubed shanny, and L. medius the stout eelblenny. Lumpenus sp. was caught at 43 stations on 10 cruises in spring and summer over an area almost as wide as for the family, from the Aleutian Islands to 63°N and from 161°W to 174°E at stations far up on the continental shelf, over the continental slope, and over the deep central basin. Catches at individual stations were generally small and the maximum catch was only 22 larvae.

Larvae of Lumpenus fabricii were caught at 12 stations on 3 cruises in summer over a wide area from the vicinity of Unimak Island to 65°N and from 160°W in Bristol Bay to 178°W in the Gulf of Anadyr. All catches of this species were made over the continental shelf and individual catches were only 1-2 larvae per station.

Lumpenus maculatus larvae were caught at 10 stations on 3 cruises made in spring and summer. They were more restricted in distribution, being found from the Alaska Peninsula to only 58½°N and from 161°W to 173°W. All larvae of this species were caught over the continental shelf and, in contrast to most of the other stichaeids, more larvae of L. maculatus were caught in oblique and vertical tows than in surface tows. Individual catches usually consisted of only 1-2 larvae with a maximum catch of 19 larvae at a station in quadrangle 58½°N, 170°W.

A single larva of Lumpenus medius was caught in summer at a station in quadrangle 58°N, 166°W.

Larvae of Stichaeus punctatus, the arctic shanny, were caught at 18 stations on 4 cruises in spring and summer. They had a fairly wide distribution over the continental shelf, continental slope, and deep water from 54°N to 62½°N and between 164°W and 177°E. Individual catches were small and variable, ranging from a few to moderate numbers with a maximum of 131 larvae at a station in quadrangle 62½°N, 172°W.

Stichaeid larvae identified only to family were caught at 69 stations on 11 cruises in spring and summer. They were found over

a range extending from the Aleutian Islands to 60°N and from eastern Bristol Bay at 158°W to 174°E, and were caught over the continental shelf, continental slope, and deep water of the central basin. Individual catches ranged from 1 or 2 up to a maximum of 556 per station, with the maximum caught at a station in quadrangle 54½°N, 170°W.

Stichaeids are demersal spawners and no eggs were reported.

Cryptacanthidae

The wrymouths have 2 species in the Bering Sea and one species *Lyconectes aleutensis*, the dwarf wrymouth, was represented in these collections by a larva caught during an early spring cruise at a station in quadrangle 55°N, 165°W (see Fig. 6).

The wrymouths are demersal spawners and no eggs were reported.

Ptilichthyidae

This family contains a single species *Ptilichthys goodei*, the quillfish and, although it is not a common species, quillfish larvae were caught at 11 stations on 5 cruises in spring and summer. Most of the larvae were captured in Bristol Bay and out to the shelf edge, but a single specimen was caught in quadrangle 53°N, 175°E (see Fig. 6). All of the quillfish larvae were caught in surface tows.

Nothing is known concerning the eggs or spawning habits of quillfish.

Pholidae

The gunnels, with 5 species in the Bering Sea, are one of the

lesser known families in the area and all larvae of this taxon have been identified only to family. Gunnel larvae were caught at 40 stations on 6 cruises in spring and summer; most were caught during summer. They have a wide east-west distribution extending from 161°W in Bristol Bay to 174°E, but are limited in their north-south distribution from the Aleutian Islands to 58°N (Fig. 27). They were taken at a few stations over the continental shelf but the majority were caught over the deep, central basin. Almost all larvae were caught with nets towed at the surface; catches were often of moderate size, exceeding 50 larvae at several stations in the vicinity of Bowers Ridge and a maximum catch of 131 gunnel larvae at a station in quadrangle 53½°N, 179°E.

Eggs of this family are demersal and none were reported.

Zaproridae

The prowfish have only one species, Zaprora silenus, that is present in the Bering Sea. Larvae were caught at 5 stations on 3 cruises in spring and summer with a total catch of 8 larvae. Most were caught near the Aleutian Islands but in the area over the continental slope, however, one was caught near the Pribilof Islands (see Fig. 6).

It is not known if the eggs of this species are pelagic or demersal.

Ammodytidae

The family of sand lances is represented in the Bering Sea by 1 species, Ammodytes hexapterus, the Pacific sand lance. Larvae were caught at 170 stations on 19 cruises in spring and summer,

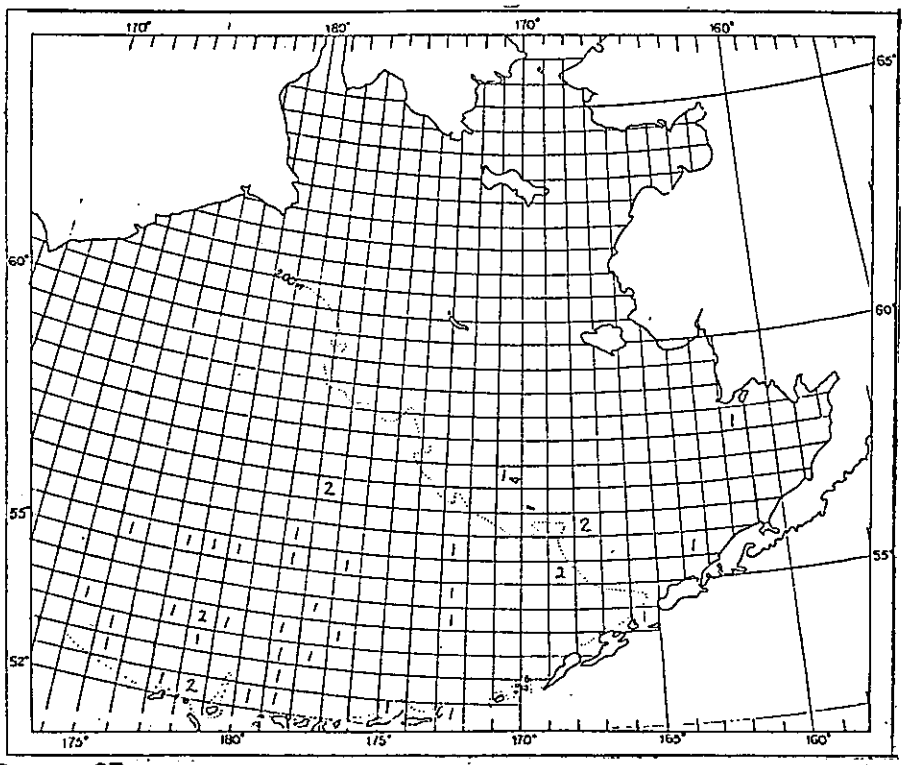

FIG. 27 Number of stations at which larvae of Pholidae have been caught.

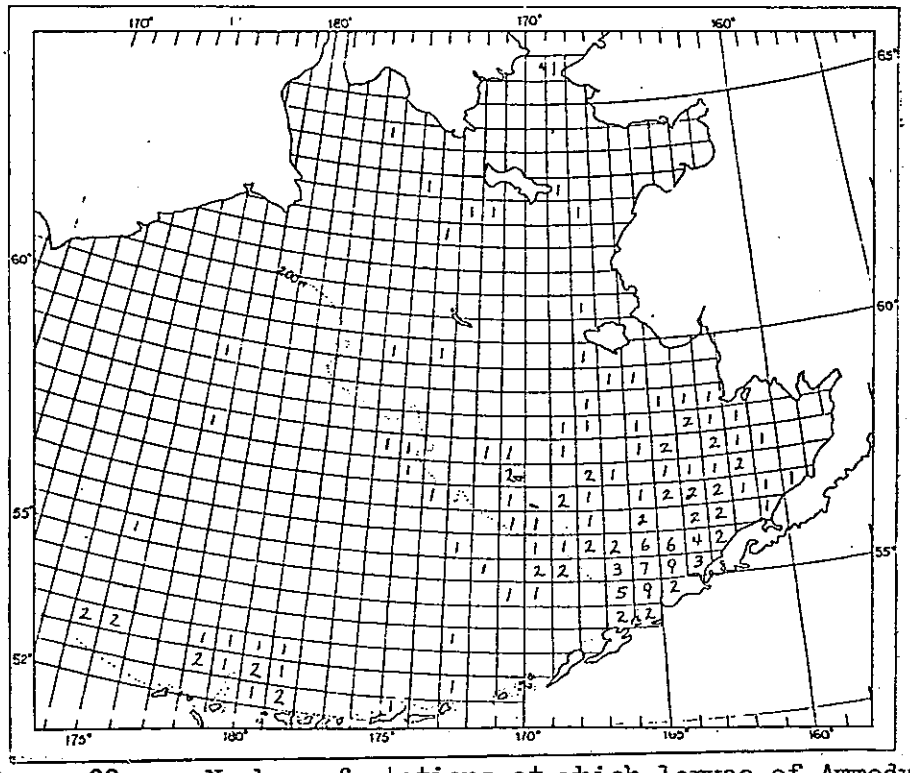

FIG. 28 Number of stations at which larvae of Ammodytes hexapterus have been caught.

few larvae were caught in early fall. They had a wide distribution from the Aleutian Islands to 65½°N and from 159°W in eastern Bristol Bay to 174°E with a majority of collections being made over the continental shelf (Fig. 28). Sand lances were one of the most numerous larvae in the collections with many samples containing more than 100 larvae and a maximum catch of 1,337 larvae at a station in quadrangle 56½°N, 164°W. During summer larvae appear to be concentrated in an area just north of the tip of the Alaska Peninsula and Unimak Island with several catches of over 400 sand lance larvae per tow. Most of the larvae were caught in surface tows, but during spring oblique tows seemed to catch more larvae although the catches were not large.

Sand lance are demersal spawners and no eggs were reported.

Pleuronectidae

The right-eyed flounders, one of the commercially important groups, have 17 species in 14 genera in the Bering Sea. Larvae of this group were collected during 20 of the 26 cruises and were caught during spring, summer, and fall, being more abundant in spring. In general, fewer flounder larvae were caught in surface tows than in oblique or vertical tows.

The genus *Atheresthes* contains 2 species, *A. stomias*, the arrowtooth flounder, generally considered an eastern Bering Sea species, and *A. evermanni*, the Kamchatka flounder, considered as a western Bering Sea species but possibly extending to the Pribilof Islands. Larvae of these two species have not been described adequately enough to permit specific identification so the records of

capture are combined and presented here as distribution of the genus. Larval Atheresthes sp. were collected at 74 stations on 8 cruises in spring and summer. Most of these larvae were caught over the outer continental shelf and the continental slope but a few were taken over deep water west of the slope and a few from shallower water in Bristol Bay (Fig. 29). The distribution extended from the Aleutian Islands to 58½°N and from 162°W to 177°W. Individual catches of this species were small and usually consisted of only a few larvae per tow.

Eggs of Atheresthes sp. are pelagic but none were reported.

The genus Hippoglossoides includes H. elassodon, the flathead sole, and H. robustus, the Bering flounder, two very similar species which occur in the Bering Sea and have overlapping ranges. Differentiation of the adults to species is difficult and larval descriptions are not adequate to permit identification to species and data are presented here for the genus. Larval Hippoglossoides sp. were caught at 22 stations on 7 cruises in summer and on 1 cruise in fall. As with all flounders, most larvae of this genus were caught in oblique or vertical tows, and catch per tow was small. Hippoglossoides sp. larvae were distributed from the vicinity of Unimak Pass north to 60°N and from 162°W to 173°W (Fig. 30). Most were caught over the continental shelf where but a few were caught over the deeper water of the continental slope.

As with most other flounders, the eggs of Hippolglossoides sp. are pelagic and are readily identifiable to genus and possibly to species on the basis of egg diameter. Hippoglossoides sp. eggs

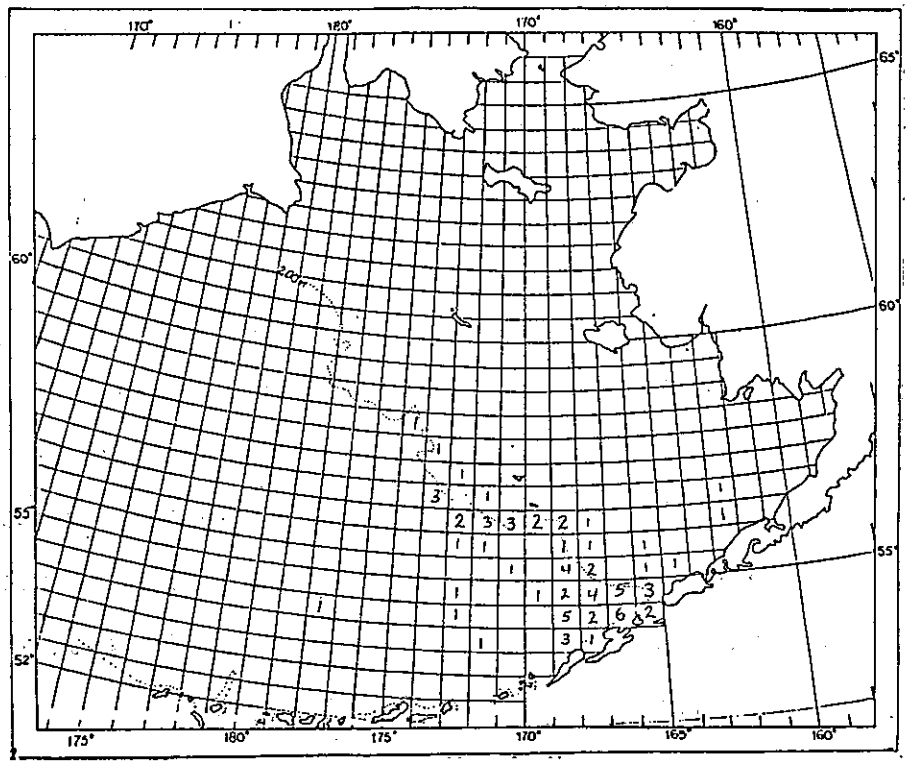

FIG. 29 Number of stations at which larvae of Atheresthes sp. have been caught.

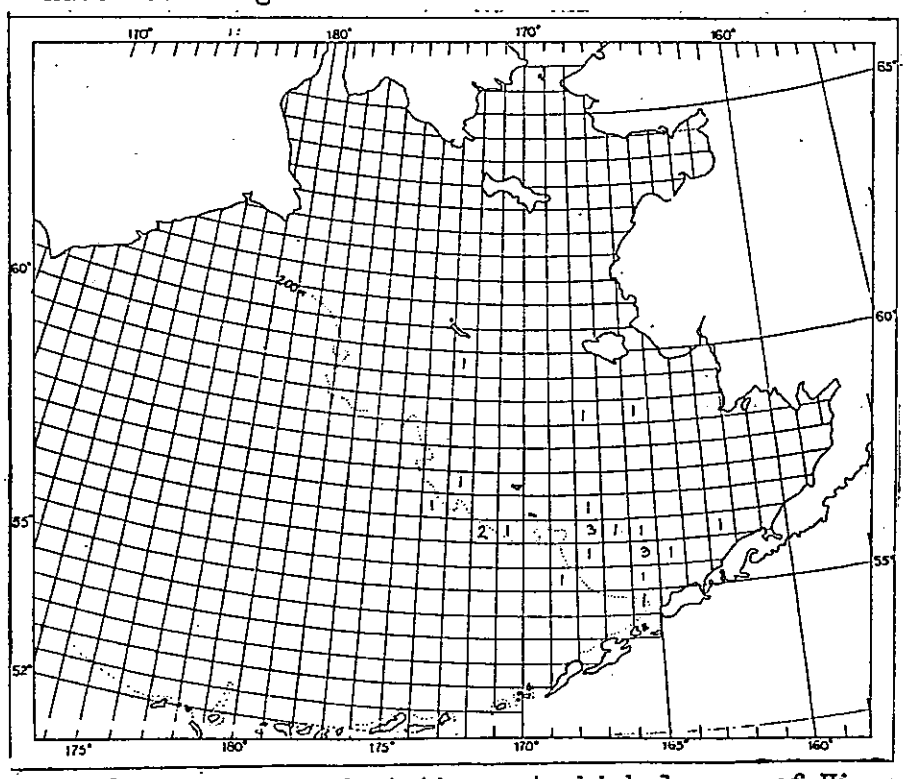

FIG. 30 Number of stations at which larvae of Hippoglossoides sp. have been caught.

were generally distributed along the outer continental shelf between about Unimak Island northwesterly to west of St. Matthew Island and were found in samples collected during April to August (see cruises 6, 7, 34 and 37, Table I).

Larvae of Pacific halibut, Hippoglossus stenolepis, were caught at 22 stations on 6 cruises in spring and early summer. They were usually found at stations over the continental slope or deeper water, but a few were caught on the edge of the continental shelf, and were distributed in a narrow band extending from the vicinity of Unimak Pass to quadrangle 58°N, 174°W, northwest of the Pribilof Islands (Fig. 31). Individual catches usually consisted of only one larvae but 5 were caught in a 1-hour tow in quadrangle 54°N, 165°W (Dunlop et al. 1964).

Eggs of Pacific halibut are pelagic but are generally found at depths greater than 200 m, and no halibut eggs were reported.

Larvae of Lepidopsetta bilineata, the rock sole, were caught at 41 stations on 4 cruises in spring and summer, but the catches on 3 of these cruises consisted of a single larva. The remaining larvae were caught in the area between Unimak Pass and the Pribilof Islands (see cruise 37, Table I). Except for one rock sole larva reported from Norton Sound, the distribution of this species was restricted to the continental shelf from the Aleutian Islands to 56½°N and between 163°W and 172°W (Fig. 32). Catches at individual stations were small with the largest catch being 12 larvae, and all were caught in vertical or oblique tows.

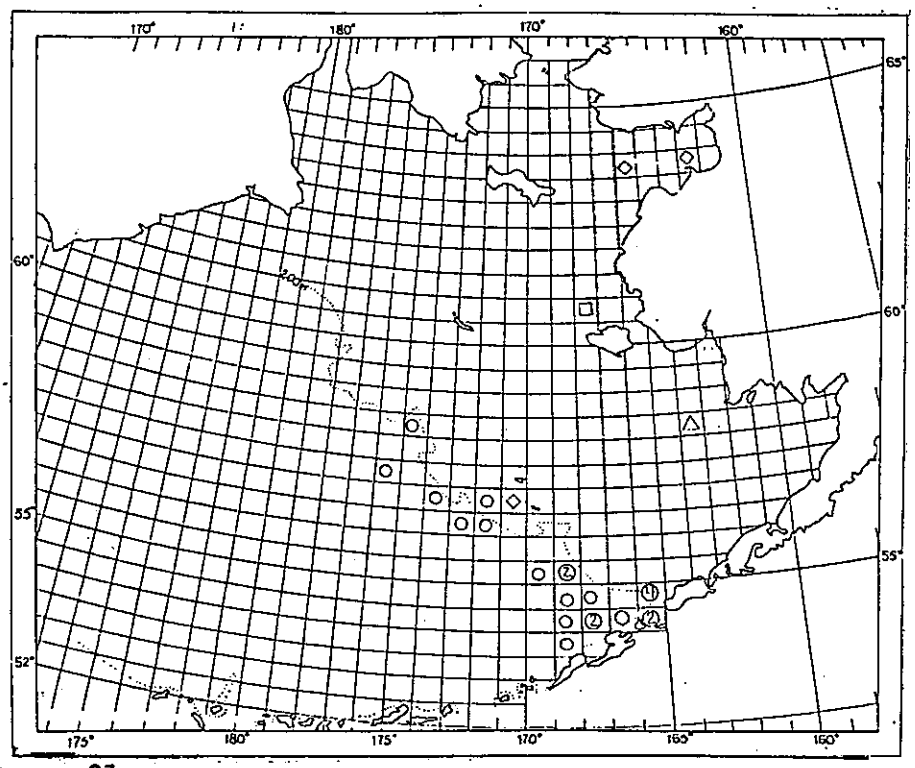

FIG. 31 Number of stations at which larvae of various Pleuronectidae have been caught. Each unnumbered symbol represents one station.

○ Hippoglossus stenolepis, △ Limanda proboscidea, ◇ Platichthys stellatus, □ Pleuronectes quadrituberculatus

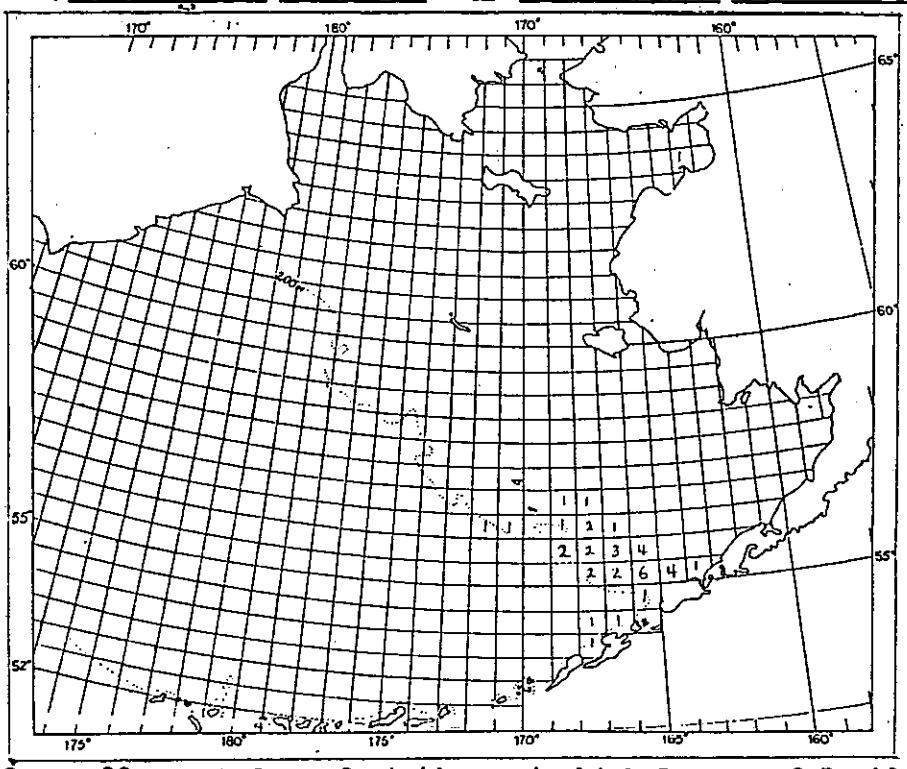

FIG. 32 Number of stations at which larvae of Lepidopsetta bilineata have been caught.

In contrast to most other flounders, the eggs of rock sole are non-planktonic and none were reported.

Larvae of Limanda aspera, the yellowfin sole, were caught at 29 stations on 4 summer and 1 fall cruise. Catches were generally small, usually less than 20 larvae per station. In contrast to most other flounders, larvae of yellowfin sole were found only on the inshore shallow portion of the continental shelf where they were distributed from 57½°N to 64°N and between 162°W and 170°W (Fig. 33).

Eggs of yellowfin sole are pelagic and large quantities were collected during several cruises (see cruises 6, 7, and 12, Table I). During 1958, eggs and larvae were caught but in 1962 only eggs were obtained. Musienko (1963) reported maximum densities of 500-1000 eggs/m^2 south of Nunivak Island in July 1958, and Kashkina (1965) reported maximum densities of 1684 eggs/m^2 northwest of Nunivak Island and 336 eggs/m^2 south of Nunivak Island in July 1962. These are the only reports of quantitative distribution of yellowfin sole eggs.

A single post larva of Limanda proboscidea, the longhead dab, was collected in early September in Bristol Bay (see Fig. 31). No eggs of this species were listed in any report.

Only 3 larvae of Platichthys stellatus, the starry flounder, were caught, 1 in the vicinity of the Pribilof Islands and 2 in Norton Sound (see Fig. 31); all were caught during summer. No eggs of this species were listed in any of the reports.

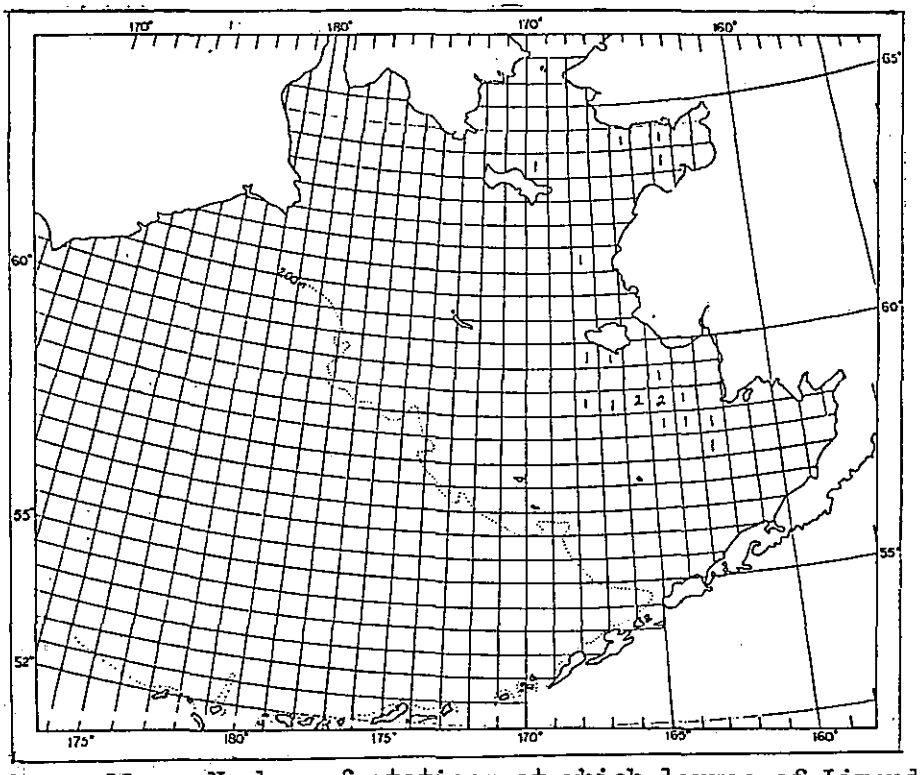

FIG. 33 Number of stations at which larvae of Limanda aspera have been caught.

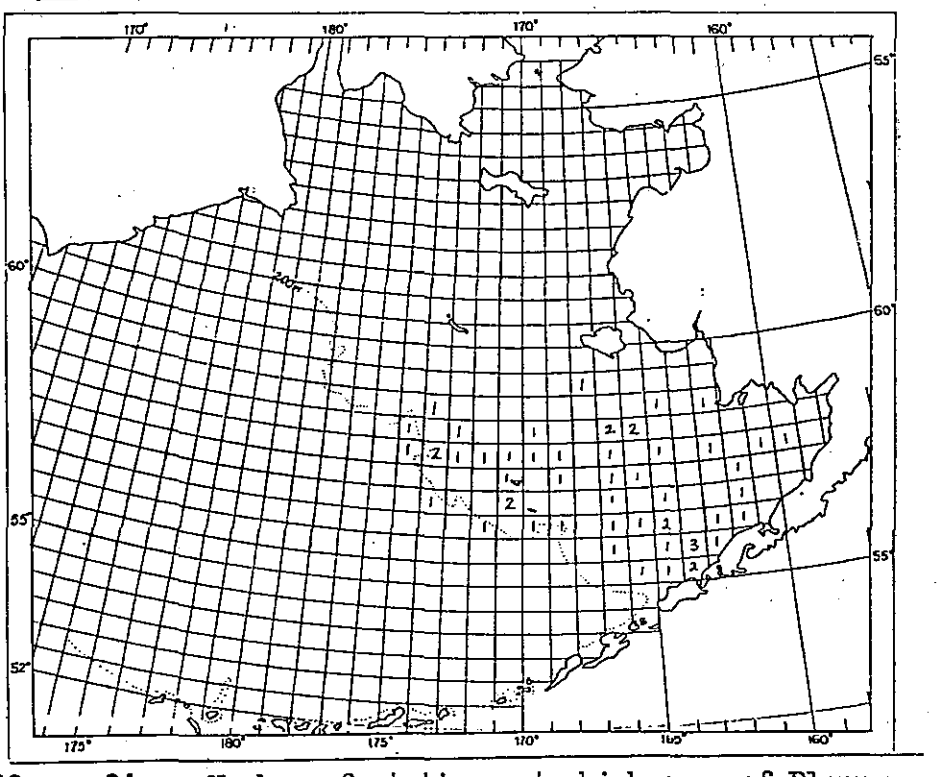

FIG. 34 Number of stations at which eggs of Pleuronectes quadrituberculatus have been caught.

Larvae of Pleuronectes quadrituberculatus, the Alaska plaice, were caught at single station north of Nunivak Island during July 1962 (see Fig. 31).

Eggs of Alaska plaice were caught at 57 stations on 4 cruises in spring and summer although during 2 cruises eggs were caught at only 3 stations. Eggs of this species were distributed from 55°N off Unimak Island to 59½°N and from 159°W in Bristol Bay to 175°W, and all were found over or very close to the continental shelf (Fig. 34). On one cruise (see cruise 34, Table I) eggs of Alaska plaice were widely distributed with centers of abundance near the Alaska Peninsula in quadrangle 55½°N, 162°W, just south of Nunivak Island in quadrangle 59°N, 167°W and northwest of the Pribilof Islands in quadrangle 57½°N, 171°W. All the large samples were caught with surface tows, but some eggs were caught with oblique tows.

Larvae of Reinhardtius hippoglossoides, the Greenland halibut or Greenland turbot, were collected at 109 stations on 10 cruises in spring and summer, occurring more frequently than any other flounder. They were caught with nets towed at the surface but most were caught with oblique and vertical tows. Catch per station was usually small, less than 10 larvae per tow, but at 4 stations (see cruise 29, Table I) between 57 and 102 larvae per tow were caught at stations over the shelf edge and slope. They were distributed more widely than those of any other flounder and were found from the Aleutian Islands to the Bering Strait and from 161°W to 177°W (Fig. 35), from well up on the continental shelf in outer Bristol Bay to deep water beyond the continental slope.

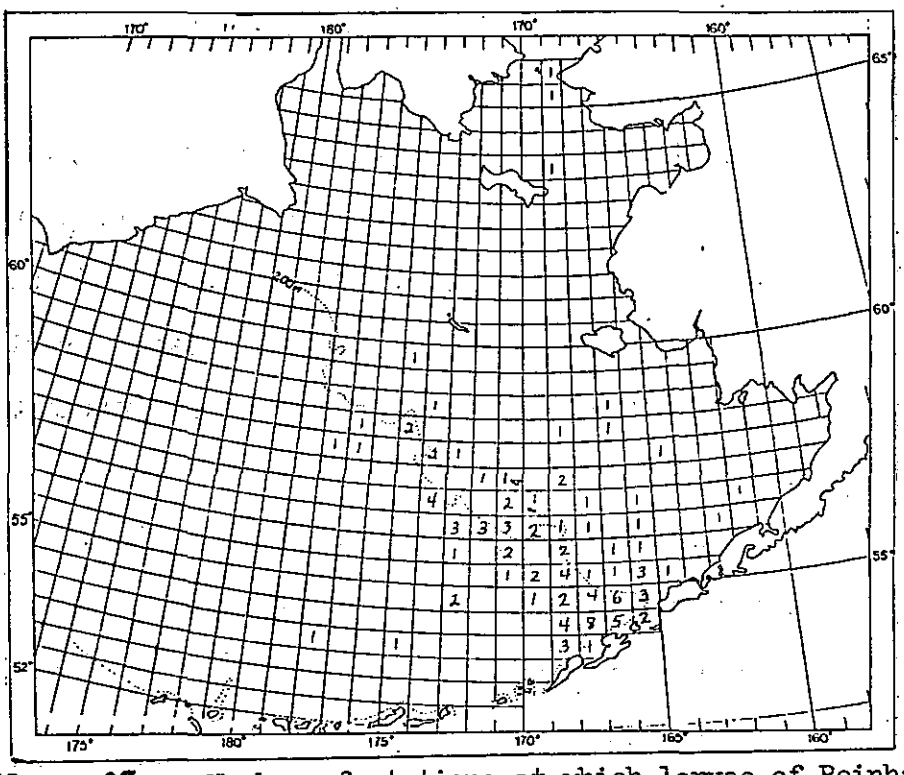

FIG. 35 Number of stations at which larvae of Reinhardtius hippoglossoides have been caught.

Eggs of Greenland turbot are pelagic and can be identified but none were reported.

DISCUSSION

Families Not Present in the Collections

Several families of fish are represented in the Bering Sea as adults but their eggs and/or larvae were not found in plankton samples. The following list of 14 families, which include 23 species, are listed by Quast and Hall (1972) as present in the Bering Sea. Some of these may spawn in waters south of the Aleutian Islands, some may be present in deep waters of the central basin, some may be present at very shallow inshore locations, and others may be part of the unidentified larvae component present in almost all plankton collections.

Synaphobranchidae (1)	Oneirodidae (2)
Notacanthidae (4)	Zeidae (1)
Gonostomatidae (4)	Gasterosteidae (2)
Alepocephalidae (1)	Pentacerotidae (1)
Alepisauridae (1)	Trichodontidae (2)
Anotopteridae (1)	Scytalinidae (1)
Moridae (1)	Bothidae (1)

Groupings of Taxa by Habitat

Vertical distribution of larvae could not be determined for any taxon except pollock, but certain larvae were present either exclusively or mainly in one type of tow or another. Table III shows taxa present in two types of collections, surface tows and combined oblique and vertical tows. Those caught exclusively with

one type of tow are marked with an asterisk (*), while those not marked were caught in both types of tows but predominantly in one or the other.

TABLE III

Taxa of Larvae Caught Either Exclusively or Predominantly in Surface Net Tows in Combined Oblique and Vertical Net Tows.

Surface Net Tows	Oblique or Vertical Net Tows
Osmeridae	*Bathylagidae
Hexagrammos sp.	Myctophidae
Pleurogrammos monopterygius	*Eleginus gracilis*
Anoplopoma fimbria	*Gadus macrocephalus*
Hemilepidotus sp.	*Theragra chalcogramma*
Myoxocephalus sp.	*Zoarcidae
**Aptocyclus ventricosus*	*Nectoliparis pelagicus*
Liparis sp.	*Lumpenus maculatus*
Bathymasteridae	**Lyconectes aleutenis*
**Anarhichas orientalis*	*Pleuronectidae*
Stichaeidae (except *L. maculatus*)	
**Ptilichthy goodei*	
Pholidae	
Ammodytes hexapterus	

It was more difficult to group larvae by water depth at stations where they were caught. In Table IV, 6 different areas are identified in which various taxa were found either exclusively or predominantly. Taxa found exclusively in a particular habitat are marked with an asterisk.

RESEARCH RECOMMENDATIONS

Serious shortcomings of previous cruises are that each cruise or series of cruises either focused on a particular species or area, or the ichthyoplankton study was of secondary importance to a primary objective. Before continuing with additional surveys of

TABLE IV

Taxa of Larvae Caught Either Exclusively or Predominantly in Various Habitats

Habitat	Taxa	
Inshore	*Clupea harengus pallasi	
Inner Continental Shelf	Limanda aspera	
Total Continental Shelf	Osmeridae	Lyconectes aleutensis
	Eleginus gracilis	Lepidopsetta bilineata
	Myoxocephalus sp.	Pleuronectes quadrituberculatus
	Cottidae, unidentified	
	Agonidae	Platichthys stellatus
	Lumpenus fabricii	
	L. maculatus	
	L. medius	
	Zoarcidae	
	Ptilichthys goodei	
Continental Shelf and Slope	Theragra chalcogramma (in spring)	
	Hippoglossoides elassodon	
	Hippoglossus stenolepis	
Continental Slope and Deepwater	Bathylagidae	
	Myctophidae	
	Anoplopoma fimbria	
	Aptocyclus ventricosus	
	Pholidae	
	Atheresthes sp.	
Continental Shelf, Slope and Deepwater	Gadidae, unidentified	
	Theragra chalcogramma (summer)	
	Sebastes sp.	
	Hexagrammos sp.	
	Pleurogrammus monopterygius	
	Hemilepidotus sp.	
	Bathymasteridae	
	Cyclopteridae	
	Stichaeidae (except those above)	
	Ammodytes hexapterus	
	Reinhardtius hippoglossoides	

* These were confined exclusively to a particular habitat.

this type, it is important to obtain a comprehensive view of the total ichthyoplankton community of the Bering Sea. Lack of such information in the past has resulted in surveys with limited objectives being carried out at the wrong time of the year or in the wrong areas. The knowledge gained from a comprehensive survey would not only clarify interpretations of past fragmentary data but would allow more economical and efficient planning of future surveys. Such a survey would almost certainly have to be a cooperative effort involving Japanese, Soviet, and United States vessels and biologists and be conducted over a period of at least one year. The following are some of the points to be considered in this research:

- The area encompassed by the survey should include the entire Bering Sea from the intertidal areas and bays to the deep-water central basin. During winter and early spring this would be reduced because of ice in the northern areas.

- The number of stations needed to cover such an area is large, on the order of 600 stations over the continental shelf and central basin, including close inshore areas. The stations should be arranged in a regular grid with one station in every area of ½° of latitude and 1° of longitude, or approximately a spacing of 50 km between stations.

- In order to sample ichthyoplankton of species that spawn at different times of year it is essential that the survey include a minimum of 4 occupancies at each station, i.e. once during each season. Samples collected in January, April, July, and October

would probably be adequate. Duration of any one cruise should not be longer than 1 month, and all areas should be sampled during the same months.

- At each station plankton should be sampled routinely with a quantitative neuston net and with an oblique net tow to the bottom or a depth of 200-300 m. At selected stations additional samples should be collected with nets fished to deeper depths, and if possible these should be opening-closing type nets. Sampling at inshore stations might require special net tows, e.g. use of fine-meshed seines.

- Vessel requirements for this survey would be a minimum of 16 vessel-months, not including transit time to and from the Bering Sea. There would be some 2,400 stations occupied with something on the order of 8,000-10,000 individual samples.

- Such an effort would require international cooperation and could be conducted under the aegis of the IOC as a component of WESTPAC.

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HALIBUT ECOLOGY [1/]

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ABSTRACT

A small but important halibut fishery exists in the Bering Sea. The distribution of halibut within the area is seasonal and dependent upon climatic conditions. The fish migrate to deep water for spawning during the winter and return to shallow areas for summer feeding. The timing and extent of the summer movement is controlled by oceanographic conditions. Spawning is known to occur between Unimak Island and the Pribilof Islands at depths of 250 to 550 m and probably occurs at other locations within the Bering Sea. All stages of life history forms from larvae to spawning adults have been taken.

Tagging studies have also shown a movement of halibut from the Bering Sea into the Gulf of Alaska. There is also a suggestion of a mixing of stocks of halibut within the Bering Sea.

Halibut in the commercial landings range from 7 years old and 4.5 kg to over 30 years old weighing over 100 kg. Commercial landings from the southeastern Bering Sea reached a peak of over 7,000 mt in 1963. Current landings are about 250 mt. Historically management of the halibut resource has been the responsibility of

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the International Pacific Halibut Commission. During 1963 to 1976 management was assumed by the International North Pacific Fisheries Commission, with recommendation from the International Pacific Halibut Commission to the Canadian and United States Governments. With the advent of the Fisheries Conservation and Management Act of 1976, management responsibility was returned to the International Pacific Halibut Commission subject to approval by Canada and the United States.

INTRODUCTION

The Pacific halibut, Hippoglossus stenolepis Schmidt, the largest member of the family of flounders called Pleuronectidae, occurs in waters of the North Pacific Ocean and Bering Sea. This large, commercially valuable flounder has been the object of an intense commercial fishery in the northeastern Pacific Ocean since 1888 and was used for subsistence purposes prior to that. A journal of Captain Cook's voyage of exploration reports the use of "holybret" by the crews of his vessels, natives, and Russian fur traders at Unalaska in 1777 (Munford 1963).

An intensive commercial fishery in the early 1900's off the continental United states, British Columbia, and in the Gulf of Alaska depleted the resource and created the political climate which brought into existence the Convention between the United States and Great Britain "For the Preservation of the Halibut Fishery of the Northern Pacific Ocean Including Bering Sea," which was ratified on October 21, 1924. This original Convention provided for the establishment of the International Fisheries Commission (IFC), which was renamed International Pacific Halibut Commission (IPHC) in 1953, to provide for the management of the halibut resource. This Convention, which was amended in 1930, 1937, 1953,

and 1979[2/], still provides the means of managing the halibut fishery on behalf of Canadian and United States citizens. During this 55-year-period there have been some trying times, particularly for the management regime established for the Bering Sea.

The "International Convention for the High Seas Fisheries of the North Pacific Ocean" between Canada, Japan, and the United States came into force in 1953. This Convention created the International North Pacific Fisheries Commission (INPFC) to manage the stocks of fish within the Convention area, including the Bering Sea. A notable feature of this treaty was the principle of abstention from fishing certain fully exploited stocks of fish. Under this provision Japan was required to abstain from fishing halibut in waters of the North Pacific Ocean and Bering Sea east of 175°W providing that stocks of that species continued to meet the qualifications for abstention. Also, no determination regarding abstention could be made until the Convention had been in effect for 5 years (Bell 1969).

From 1958 through 1961 INPFC annually reviewed the qualifications of the halibut stocks for continued abstention. In 1962, it was agreed by the three contracting parties that halibut in the Bering Sea east of 175°W no longer qualified and the halibut in that area was removed from the abstention list. Japanese nationals were permitted to fish halibut beginning in 1963. Other countries

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[2/] The 1979 amendment had not been ratified by either Canada or the United States at the time of writing.

not signatory to these Conventions were free to fish halibut in the Bering Sea without limitation outside of the fishing zone established by the United States.

With the enactment of the "Fisheries and Conservation Management Act of 1976" (FCMA), the control of fishing within 200 miles of the coast of the United States became the exclusive concern of the United States Government. Recommendations to the government for the management of the halibut fishery in the Bering sea are still the responsibility of IPHC.

The development of a halibut fishery in the Bering Sea was inhibited by the distance from established processing plants and transportation facilities and the presence of fishing grounds closer to the home ports of the fishing fleet. The relatively large landings from the Gulf of Alaska have dictated that much of IPHC's research activity be directed to that area to fulfill their management directives.

LIFE HISTORY

All stages in the life history of halibut from larvae to mature adults have been taken from the waters of eastern Bering Sea. The complex process of evaluating the contribution of each stage to the ecosystem has not yet been worked out.

Description

Early ichthyologists describing fish of the eastern Pacific Ocean felt that the halibut there was identical with the Atlantic halibut, *Hippoglossus hippoglossus*. Schmidt (1904, 1930) noted some differences in the shape of the scales, length of the pectoral

fin, and shape of the body and described it as a separate species, H. stenolepis. Vernidub (1936) in further investigations did not consider these differences to warrant specific status and considered the Pacific form to be a sub-species, H. h. stenolepis and Schmidt (1950) later agreed with Vernidub that the Pacific halibut was a sub-species. Since that time North American ichthyologists have detected other differences great enough to separate species and at the present time the American Fisheries Society (1970) accepts H. stenolepis.

Halibut are compressed laterally and, except in the larval stages, have both eyes on one side of the head. Adults can be distinguished from other North Pacific flounders by their large size; large, almost symmetrical mouth with conical teeth; a pronounced arch of the lateral line above the pectoral fin; and the crescent-shaped or lunate tail. Halibut usually are dextral, that is, both eyes are on the right side, which is heavily pigmented and is oriented toward the surface. On rare specimens the eyes and pigment occur on the left side of the fish. Pigmentation varies from olive to dark brown or black with lighter, irregular blotches that are often similar to the pattern and color pattern of the ocean floor. This protective coloration makes the fish less conspicuous to predators and prey. The left or blind side faces the ocean bottom and is white. Halibut are more elongate than most other flatfishes. The average width of the body is about one-third its length. The small scales are well buried in the skin.

Distribution

In the eastern Pacific Ocean halibut are found from northern California into the Bering Sea. The distribution continues across the Bering Sea and off the Asiatic Coast between Hokkaido Island and the Gulf of Anadyr, as well as in the Sea of Okhotsk. Presently the largest concentrations are in the Gulf of Alaska with a smaller population in the Bering Sea.

Halibut are demersal, living on or near the bottom, and usually in water of 2-8 C, although they will tolerate colder temperatures. Younger ages are found in relatively shallow inshore areas while adults have been reported as deep as 1000 m and adult halibut are regularly taken at depths of 300 to 500 m in the Bering Sea during the spring fishing season.

In trawl hauls made in the eastern Bering Sea, the youngest halibut have been found in the southern part but larger, older juveniles and adults are known to range into the more northerly part. The younger fish possibly do not have the strength and endurance to make the longer migration and compete with the larger individuals even though the environment is suitable during the summer.

The farthest north that halibut have been taken during IPHC surveys was 62°30'N. Two juveniles were caught in three hauls at this latitude during July. September surveys made by National Marine Fisheries Service (NMFS), when the waters are near their warmest temperatures, have reported a "small" halibut at 65°15'N, and a single adult halibut 66°02'N, 168°02'W (Best 1977).

Seasonal Movements

During the winter months ice covers much of the area and water temperatures near bottom drop to 0 C or less; this condition forces the halibut to concentrate in the deeper, warmer water along the continental edge. With the advent of spring the ice retreats and the water gradually warms to temperatures that permit the halibut to disperse over the expanse of shallow flats which provide a suitable environment for a nursery for young halibut as well as feeding grounds for the larger juveniles and adults.

Juvenile halibut were abundant at depths of 330-370 m between Unimak Pass and the Pribilof Islands during an IPHC survey in March with few halibut taken at shallower depths. Novikov (1964) reported concentrations of halibut in the same area in March. In April a concentration of halibut was reported near the northern entrance of Unimak Pass (ca. 54°40'N, 165° 09'W) at depths of 80 and 104 m where bottom temperatures were 3.1 and 3.8 C. On the same cruise east of 164°W , when bottom temperatures were -1.0 to 1.4 C, no halibut were taken (Best 1977).

As the warming progresses, young halibut move eastward along the north side of the Alaska Peninsula and usually are found throughout Bristol Bay in June. By late June, they spread northward toward Nunivak Island. An IPHC survey in the vicinity of St. Matthew Island (60°30'N) during the latter part of June found bottom temperatures to be 0 C or less and only 10 halibut were caught in 14 hauls. Temperatures of 4 C or greater were encountered south of 59°30'N and catches increased to 86 fish in 5 hauls. An IPHC

charter found a concentration of adults in the vicinity of St. Matthew Island in August and September but they left the area by mid-October. The occurrence of small halibut near shore in Norton Sound during July, August, and September was reported by Turner (1886).

Many of the tags released in the Bering Sea have been recovered within the area and have confirmed the annual migration from deep areas in winter to shallow areas in summer and return to deep water in the winter. Novikov (1970) reported that a halibut tagged in deep water north of Unalaska Island in April was recovered 32 days later on the flats. The fish had travelled 184 km for an average of 5.7 km per day.

IPHC tagged nearly 3,600 halibut near St. Matthew Island during August and September and 221 were subsequently returned. Although most (114) were recovered near the release site, 56 were recaptured from deep water along the continental slope between Unimak Pass, Pribilof Islands, and west to 180°. Most of the recoveries from the deeper areas were made by the North American setline fleet during the April fishing season, although some were from the Japanese trawl fleet during the winter. An additional 51 recoveries were made in the Gulf of Alaska. Several dense concentrations of adult halibut, such as the above, have been found. These concentrations have provided some excellent, short-term fishing but after the initial exploitation the concentrations do not exist.

A schematic diagram of the winter and summer distribution of halibut in the Bering Sea is given in Fig. 1.

Environmental Factors

Water temperature recorded near bottom during the IPHC summer surveys in the Bering Sea ranged from a low of -1.7 C at a station near mid-shelf in 1975 and to a high of 10.5 C at a shallow station in Bristol Bay in 1965. During the 1960's IPHC surveys caught few halibut at stations with temperatures of less than 2 C and catches were largest when the temperature was 4 or 5 C. Soviet research trawlers in the southeastern part reported the highest catch per hour at water temperatures of 3.5-5.5 C (Novikov 1964). The Fisheries Agency of Japan (1972) reported increased catches of juvenile halibut taken when bottom tempertaures were about 5 C. Commercial halibut fishing in the Gulf of Alaska is generally conducted in water of 3-8 C (Thompson and Van Cleve 1936).

A period of cooler water temperatures occurred during the period of 1970-76. Some of the IPHC stations, at which halibut had been taken in previous years, could not be sampled during June of 1972 and 1975 because of drifting ice. No halibut were taken at several ice-free stations in the survey area where water temperatures were 0 C or lower. A comparison of bottom water temperature during June of 1967 and 1972 (Figs. 2A,B) indicates that under the cooler conditions halibut were found to be concentrated in a smaller portion of the southeastern Bering Sea than in warmer years. The limiting effect of the 2 C isotherm was less noticeable in the colder years. Warm water conditions returned to the Bering

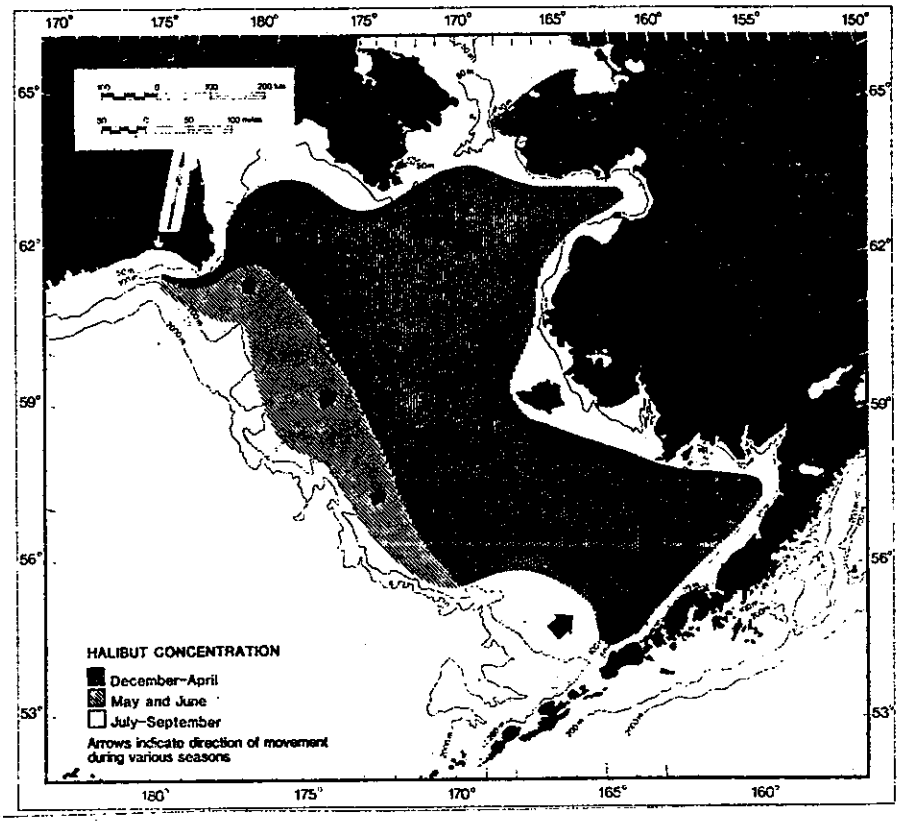

FIG. 1 Generalized pattern of halibut distribution in the eastern Bering Sea.

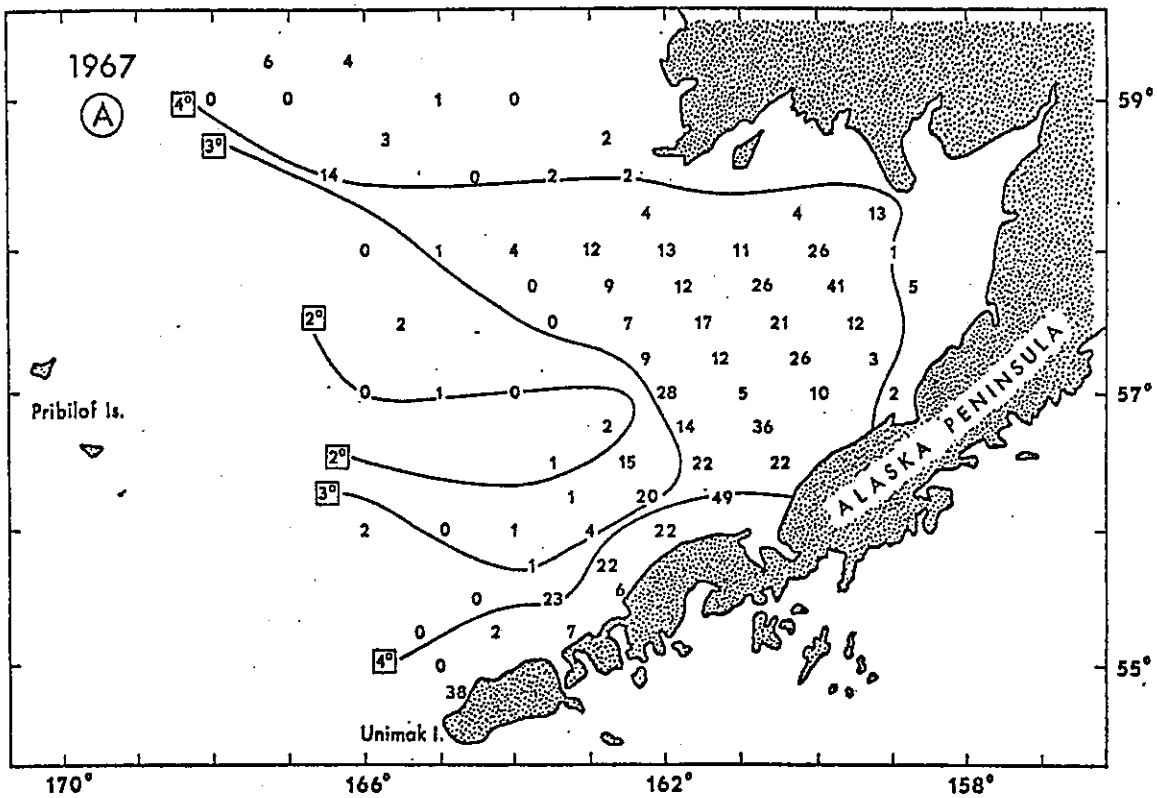

FIG. 2A Distribution of halibut in number per 60-minute haul and approximate location of bottom isotherms (C) in June 1967.

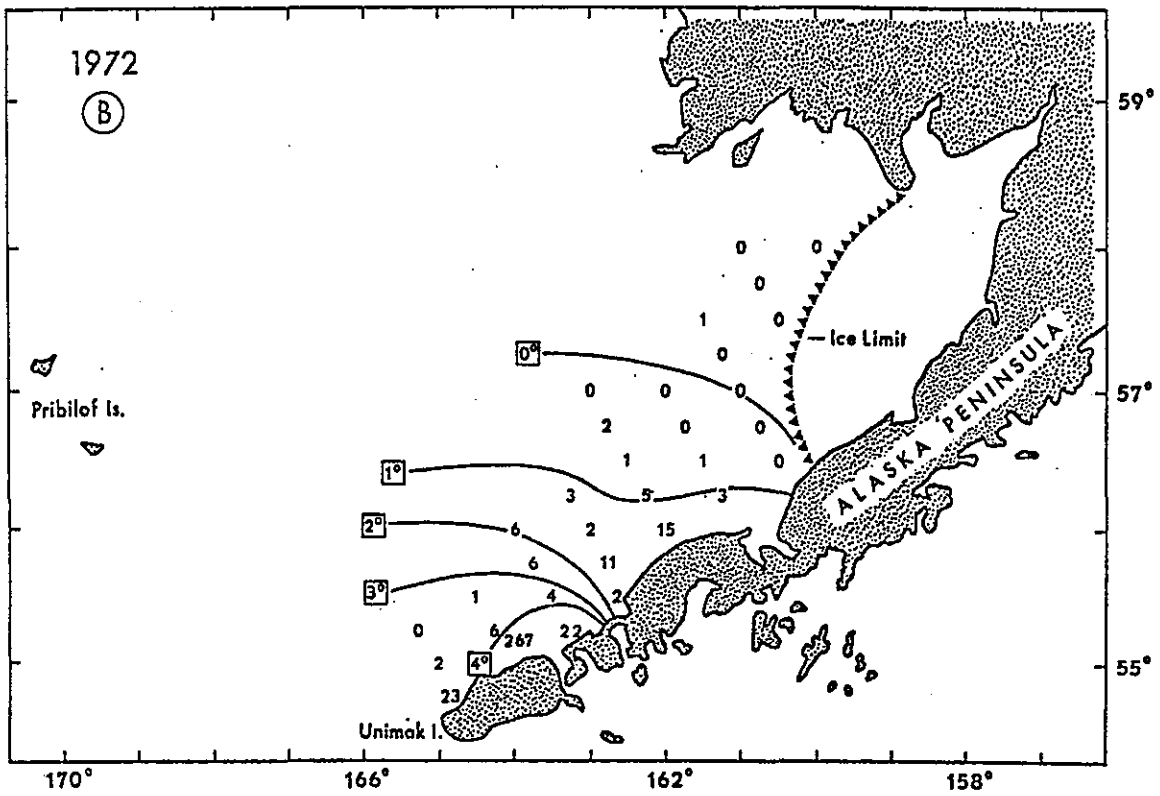

FIG. 2B Distribution of halibut in number per 60-minute haul and approximate location of bottom isotherms (C) in June 1972.

Sea again in 1977 and 1978 and juvenile halibut were distributed throughout the survey area similar to 1967.

The timing and extent of the annual movement from deep to shallow areas seems to be dependent upon the severity of the preceding winter. If the winter is mild and warming occurs early the suitable temperature range will extend father north. These conditions permit the halibut to migrate from the edge grounds onto the flats earlier in the year and opens a large portion of the Bering Sea for feeding during the summer. If conditions are favorable, halibut may disperse as far north as Bering Strait. Following a cold winter, warming is delayed and the area suitable for halibut is restricted to the more southerly portion of the Bering Sea. When conditions inhibit the northward dispersion, halibut tend to form more concentrated schools in the southern portion of the Bering Sea.

Subpopulation Structure

The tagging studies conducted by IPHC, Japan, and U.S.S.R. have shown some indication of the movement of stocks between the eastern and western Bering Sea as well as into the Gulf of Alaska. The most notable movement was made by a fish released July 5, 1975, at 61°18'N, 175°12'E during a joint IPHC-U.S.S.R. research cruise off Kamchatka and recovered May 19, 1977 near the Shumagin Islands in the Gulf of Alaska. The rate of the interchange has not been calculated due to the small number of tags recovered and the lack of effective fishing effort on adults in the western areas.

Migration from the Bering Sea into the Gulf of Alaska, documented during the first tagging experiment by IPHC in 1930 has been confirmed by all tagging studies since. Many of the recoveries of tagged halibut released in the Bering Sea were made off southeastern Alaska, British Columbia and as far south as northern California (Fig. 3). One of the longer movements was from St. Matthew Island to Hecate Strait, British Columbia, a distance of over 3,200 km and the fish was captured within one year after tagging. This is an average movement of about 8.8 km per day.

Dunlop et al. (1964), after making corrections for fishing effort, calculated that 24% of the halibut tagged in 1959 emigrated to the Gulf of Alaska. Best (1977) reported 3 tagged juveniles released in the southeastern Bering Sea were recovered by the setline fishery in the Gulf of Alaska.

The foreign trawl fleet made substantial recoveries from a group of tagged juveniles (mean length about 30 cm) released by IPHC near Unimak Island. These fish were tagged and released in July at 54°45'N, 164°45'W in depths of less than 50 m and were recovered from an area centered about 54°50'N, 165°30'W at depths in excess of 200 m, a distance of about 50 km from the release site, the following winter. Two longer-term recoveries from this release have been recorded, one from west of the Pribilof Islands (58°35'N, 177°18'W) and the other from the Aleutian Chain near Amukta Island (52°50'N, 171°25'W).

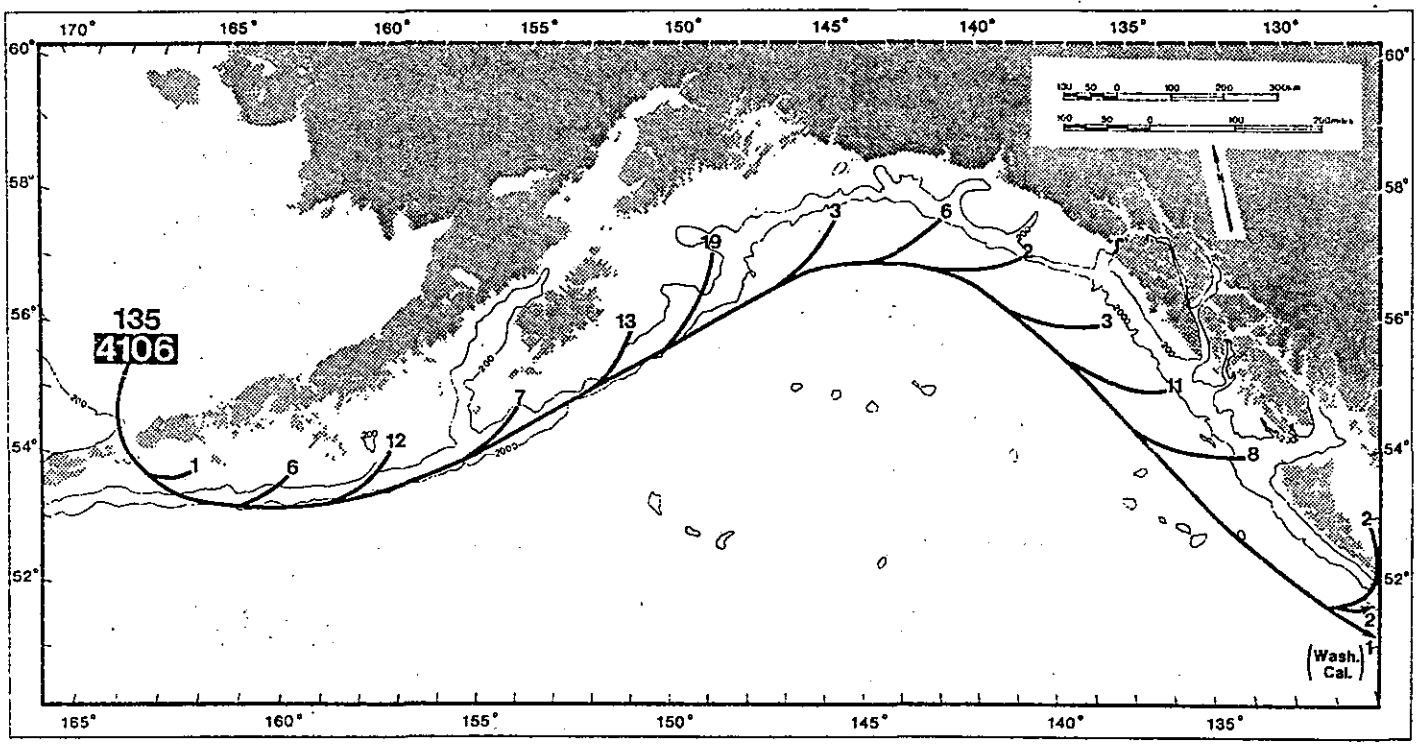

FIG. 3 Recoveries of halibut tagged in the Bering Sea during 1959. The number of fish tagged is shown in the black box.

If the theory of compensatory emigration by which young halibut migrate to "counteract the drift of the natant eggs and larvae and to maintain the species in its habitat" (Dunlop et al. 1964) is valid, the two longer-term tag recoveries would suggest that some of the juveniles in southeastern Bering Sea originate from spawning grounds to the west, while the three recoveries from the Gulf of Alaska suggest spawning to the east. Certainly these few tag recoveries are insufficient to reach any conclusion on migratory patterns but do make for some interesting speculation. A logical explanation is that the shallow areas of the southeastern Bering Sea may be a nursery area for more than one stock of halibut.

Two tagged juveniles released on the Pacific Ocean side of Unimak Island at approximately the same time as the above Bering Sea releases, were recovered in the Bering Sea the following winter by the same trawl fleet. While this movement of two small fish was only about 125 km it is the only record of any movement of halibut from the Pacific Ocean to the Bering Sea. These scattered fragments of information only open the door to speculation and do not define the interchange of halibut throughout the Bering Sea and the adjacent areas.

Maturity

Using all information on maturity collected from research cruises in the Bering Sea east of 175°W, the age at 50% maturity for female halibut was calculated to be 13.8 years at a length of 122 cm. Males averaged 7.5 years and 72 cm. This is older than the age of approximately 11 years but about the same size reported

for female halibut from the Gulf of Alaska (Schmitt and Skud 1978). In the Bering Sea less than 1% of the 9-year-olds and about 1% of the 90 cm females were observed to be mature. These data fit well with the information reported by Novikov (1964) for the eastern Bering Sea.

Novikov (1964) also reported an average fecundity of 1,164,000 eggs for 12 females between 100-120 cm in length and 2,338,000 for females between 120-140 cm from the Bering Sea during the period of 1957-1960. IPHC has no information on fecundity of halibut from this area. However, a 1973 study in the Gulf of Alaska (Schmitt and Skud 1978) reported only about half as many eggs for fish of the same size. The increased fecundity may be the result of an evolutionary process to insure survival in the environment of the Bering Sea or a discrepancy in the methods used in calculation in the two studies.

Spawning

Studies conducted in the Gulf of Alaska have provided information on halibut spawning (Thompson and Van Cleve 1936). Information to date indicates that halibut spawning in the Bering Sea is similar in nature. An IPHC research cruise during the winter of 1963-64 found mature unspawned fish at depths of 250-550 m between Unimak Island and the Pribilof Islands in December. The same general area was fished again in January and most of the fish were spawned out. Spawning undoubtedly takes place at other locations along the continental edge west of the Pribilof Islands as well as along the Aleutian Islands.

The temperature of water at that depth remains a fairly constant 3-4 C the year around; consequently the developing halibut ova probably experience nearly the same conditions as in the Gulf of Alaska. Van Cleve and Seymour (1953) estimated time to hatching would require about 23 days at 4.7 C. Under controlled laboratory conditions Forrester and Alderdice (1973) observed hatching after 20 days at 5 C but ova did not survive to hatching at 4 C. Under conditions found in the Bering Sea hatching would probably require at least three or four weeks.

The accepted pattern of circulation in the Bering Sea indicates that any spawning occurring southeast of the Pribilof Islands should be carried in a northwesterly direction along the continental slope to the Asiatic Coast (Favorite 1974). Larvae have been captured west of the Pribilof Islands (see Ichthyoplankton) to provide a measure of circumstantial evidence to support this theory and fish-of-the-year have been taken from shallow areas of the western Bering Sea. Halibut larvae also have been collected from locations near Unimak Pass (see Ichthyoplankton). These collections suggest that spawning takes place along the Aleutian Islands or the larvae drift through the Aleutian Island passes from the Gulf of Alaska.

Thompson and Van Cleve (1936) reported newly hatched larvae were at greater depths than the eggs in the Gulf of Alaska. However, by the age of 3-5 months all larvae were in the upper 100 m. Young halibut completed metamorphosis and were on the bottom by May or June at a length of 22-29 mm. Musienko (1957) reported taking

young-of-the-year halibut 34-42 mm long in September and October off the Kamchatka Peninsula. This period of time for development through metamorphosis seems reasonable for the temperature regime found in the Bering Sea.

Although the early larval development takes place in rather deep water the growing larvae gradually rise towards the surface waters. If conditions of currents and food are satisfactory the young halibut should find itself in relatively shallow water close to shore when metamorphosis occurs and the larvae change from a pelagic existence to a bottom dwelling habitat. Although metamorphosed young-of-the-year have not been reported from the eastern Bering Sea, they probably exist as IPHC regularly captures one-year-old halibut during late June from water less than 15 m deep along the northern shore of the Alaska Peninsula and from the bays on the Bering Sea side of the Aleutian Islands using special small-mesh nets.

Size and Age Composition

The size and age of halibut captured depends to a large extent upon the type of fishing gear used. The juvenile halibut survey by IPHC and fishery resource surveys by the NMFS are conducted with a standardized trawl net which catches small halibut primarily 25-60 cm. The minimum size limit for commercially-caught halibut is 81 cm which is about equal to 4.5 kg. Setline gear will catch some small halibut but the undersized fish are discarded at sea. The commercial landings sampled by IPHC contain halibut from 80 to over 200 cm. Some fish as young as 7 years old will begin entering the

setline fishery (a year class is not fully recruited until age 10) and a few fish are caught each year that are over 30 years old and weigh over 100 kg. The size distribution and age composition from the juvenile survey and commercial landings taken east of 175°W in 1977 are shown (Fig. 4).

A curious phenomenon of alternating strong and weak year classes was reported from the juvenile surveys (Best 1977). The pattern of relative year class strength generally has continued into the older ages in the 1977 commercial landings where ages 10, 12 and 16 have maintained greater abundance than the intervening ages (see Fig. 4). The 1961 year-class which produced the largest number of 2-year-olds recorded in the juvenile surveys was still above average as 16-year-olds.

Growth

Female halibut are larger than males at any given age, however, the difference is very small until about 5-6 years of age. After that time the difference becomes significant and continues throughout the life of the fish. The rate of growth slows noticeably for males at about 9 years of age and a length of 90 cm. The decrease in growth rate does not occur in females until age 13 and a size of about 125 cm. The size and age at which the decrease in growth rate occurs in the two sexes suggests that it may be tied to the onset of maturity. A comparison of the length and weight of male and female halibut is given in Table I. These data are actual measurements of fish examined on IPHC research or observer cruises during the period 1961-78.

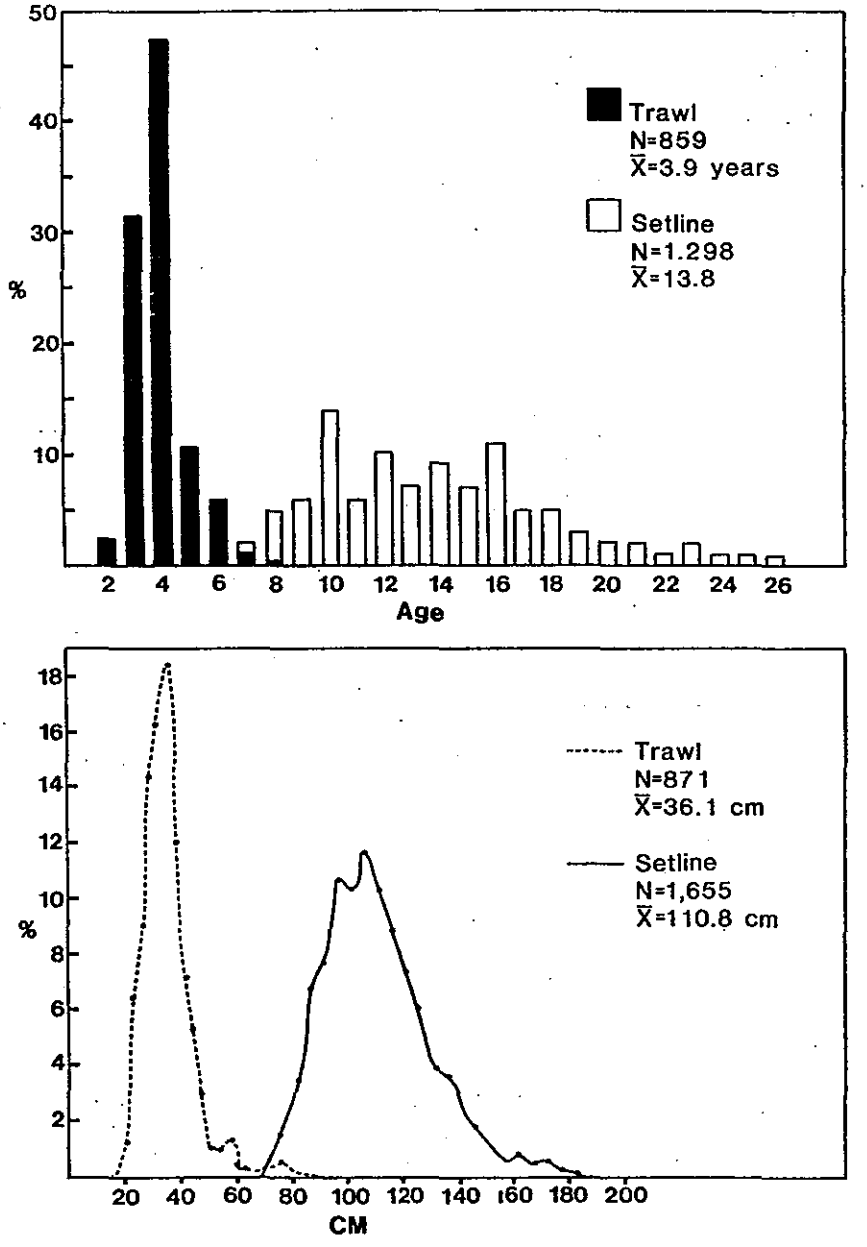

FIG. 4 Length and age distribution of halibut from survey trawl fishing and commercial setline landings.

A comparison of growth rates for halibut from different areas shows that fish in southeastern Bering Sea grow at a faster rate than halibut from western Bering Sea (IPHC 1976). However, according to Southward (1967), they do not grow as fast as fish in the Gulf of Alaska. He also reported an increase in growth of Bering Sea halibut beginning during the mid-1950's that apparently has continued until the present. Best (1977) reported that a series of cold years (1972-75) in the eastern Bering Sea had reduced the growth of juveniles. The year classes affected by the reduced growth are only now entering the commercial fishery and the short-term reduction in growth would likely be masked by the long-term average used in calculating the size at age.

TABLE I

Average Length in cm and Round Weight in kg at Age for Halibut Caught East of 175°W

	Males		Females			Males		Females	
Age	cm	kg	cm	kg	Age	cm	kg	cm	kg
1	11	.01	12	.01	16	92	9.62	133	31.76
2	20	.07	20	.07	17	94	10.32	137	34.97
3	29	.23	30	.25	18	105	14.77	142	39.27
4	37	.50	39	.60	19	100	12.61	147	43.93
5	45	.95	49	1.25	20	98	11.81	147	43.93
6	56	1.93	63	2.82	21	111	17.68	154	51.05
7	67	3.44	78	5.64	22	102	13.44	161	58.99
8	77	5.41	87	8.03	23	99	12.20	158	55.50
9	86	7.73	97	11.42	24	107	15.70	164	62.63
10	89	8.64	103	13.88	25	106	15.23	167	66.41
11	98	11.81	111	17.68	26	111	17.68	165	63.87
12	98	11.81	118	21.56	27	-	-	178	81.66
13	98	11.81	128	28.06	28	-	-	182	87.76
14	95	10.68	131	30.24	29	-	-	164	62.63
15	89	8.64	131	30.24	>29	-	-	197	113.43

Food Habits

Halibut are opportunistic feeders utilizing whatever is readily available, consequently a wide variety of food items has been found in halibut stomachs. Generally, the small halibut feed on small crustaceans; as they increase in size the food shifts to larger prey items and there is an increase in the amount of fish utilized. Little information is available on the food of adult halibut.

Examination of the stomachs of juvenile halibut from the Bering Sea indicated they were feeding heavily on shrimp, hermit crabs, small shore crabs, and sandlance (Table II). Novikov (1964) reported that halibut over 60 cm feed extensively on pollock and yellowfin sole.

Although not significant in the Bering Sea, in some areas of the Gulf of Alaska halibut were found to feed heavily on Tanner crab. Halibut also have been found to occasionally feed on large king crab, particularly during the soft-shell stage (Gray 1964). In earlier years when the population of halibut was larger it is possible that halibut played some part in keeping the king and Tanner crab populations at lower levels of abundance. Reduced predation may have been partially responsible for the increase in crab abundance.

Some predation upon halibut must take place, particularly at the smaller sizes although there is little documented evidence. IPHC has found rare cases of cannibalism upon young halibut in the course of the food habit studies. By the age of five or six years

halibut are one of the dominant predatory fishes and as such must be immune from predation except for the larger marine mammals. Halibut hooked on setline gear are easy prey for sea lions which can render a portion of a catch unmarketable.

TABLE II

Food Items Observed in Halibut Stomachs, Southeastern Bering Sea, 1976-1977. the Numbers Indicate Stomachs in which Each Item was Observed.

	Fish Length in cm								
Food Item	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	Total
Shrimp	9	47	36	7		2	1		102
Sand lance	1	11	12	7	4			1	36
Hermit crab		6	12	6					24
Shore crab			6	4	2	1			13
Isopod		7							7
Tanner crab		1			2			1	4
Pollock			2	1	1				4
Cottids		2					1		3
Smelt			2						2
Cod			1	1					2
Annelid worm		1							1
Euphausid		1							1
Blenny		1							1
Sandfish							1		1
Sea Poacher							1		1

STOCK BIOMASS

The limited and sporadic nature of the commercial fishery has precluded reaching any reasonable estimate of the biomass of adult halibut. However, IPHC was able to calculate a maximum sustained yield from the southeastern sector (between Unimak and Pribilof Islands) of 2,268 mt from data available between 1958-63 (Dunlop et al. 1964). This yield was exceeded in 1962 and 1963 and abundance as indicated by catch per unit of effort dropped sharply.

With the added mortality of juveniles by the trawl fleets in southeastern Bering Sea the fishery has never again reached that level.

Trawl surveys conducted by NMFS in 1975 and 1976 each produced estimates of nearly 31,000 mt of juvenile halibut (Bakkala and Smith 1978). The addition of adults, not available to the trawls used in this survey, would substantially increase this figure.

The removals of small halibut as incidental catch of the foreign trawl fleets during the 1960's and early 1970's have reduced the potential for recruitment and rebuilding of the adult halibut stocks. Time and area closures on the foreign trawl fleets have reduced the incidental catch of halibut in recent years. The FCMA will provide for even greater control of fishing in the southeastern Bering Sea, but the halibut stock probably will never return to a size that will permit catches as large as those of 1962 and 1963 which were made from a virtually unfished stock.

The strength of year-classes observed as juveniles has fluctuated on an alternating year basis through the 1960's. Recent surveys indicate that the 1973 year-class is large, however, this group of fish will not become available to the setline fishery until 1981. A single large year-class cannot significantly improve the size of a population which is ordinarily made up of over 20 year-classes. Several above average years, preferably occurring in successive years will be needed to noticeably improve the supply of halibut.

HISTORY OF COMMERCIAL UTILIZATION AND REGULATION

The development of a fishery for halibut in the eastern Bering Sea was slow. The lack of processing facilities, distance from home ports, often adverse weather conditions, small stock size, and profitable fishing in the Gulf of Alaska all combined to keep fishing effort in the Bering Sea at low levels.

Fishery

A small fishery took place in the southeastern Bering Sea between 1930-34 by a few U. S. vessels. At that time the Bering Sea was open to fishing at the same time as the Gulf of Alaska. No further fishing occurred in the area until 1952, when U. S. vessels began taking about 100 mt annually from fishing grounds east of 175°W (Fig. 5). To encourage fishing in the Bering Sea the fishing season was opened one month earlier than the Gulf of Alaska beginning in 1958. The catch began to increase, reaching nearly 4,400 mt in 1962 (Myhre et al. 1977) and was about equally divided between United States and Canadian vessels. INPFC determined that halibut in the Bering Sea no longer qualified for abstention and Japan was allowed to enter the fishery in 1963 (Forrester et al. 1978). Up to this time, removals were limited only by the length of fishing season. In 1963 a three-nation catch limit of 5,000 mt was established by INPFC for that portion of the Bering Sea along the edge of the shelf between Unimak Island and the Pribilof Islands (roughly between 165-170°W) despite the fact that IPHC had calculated the maximum sustained yield from this 5° of latitude to be 2,268 mt for the period of 1958-63 (Dunlop et al. 1964). The

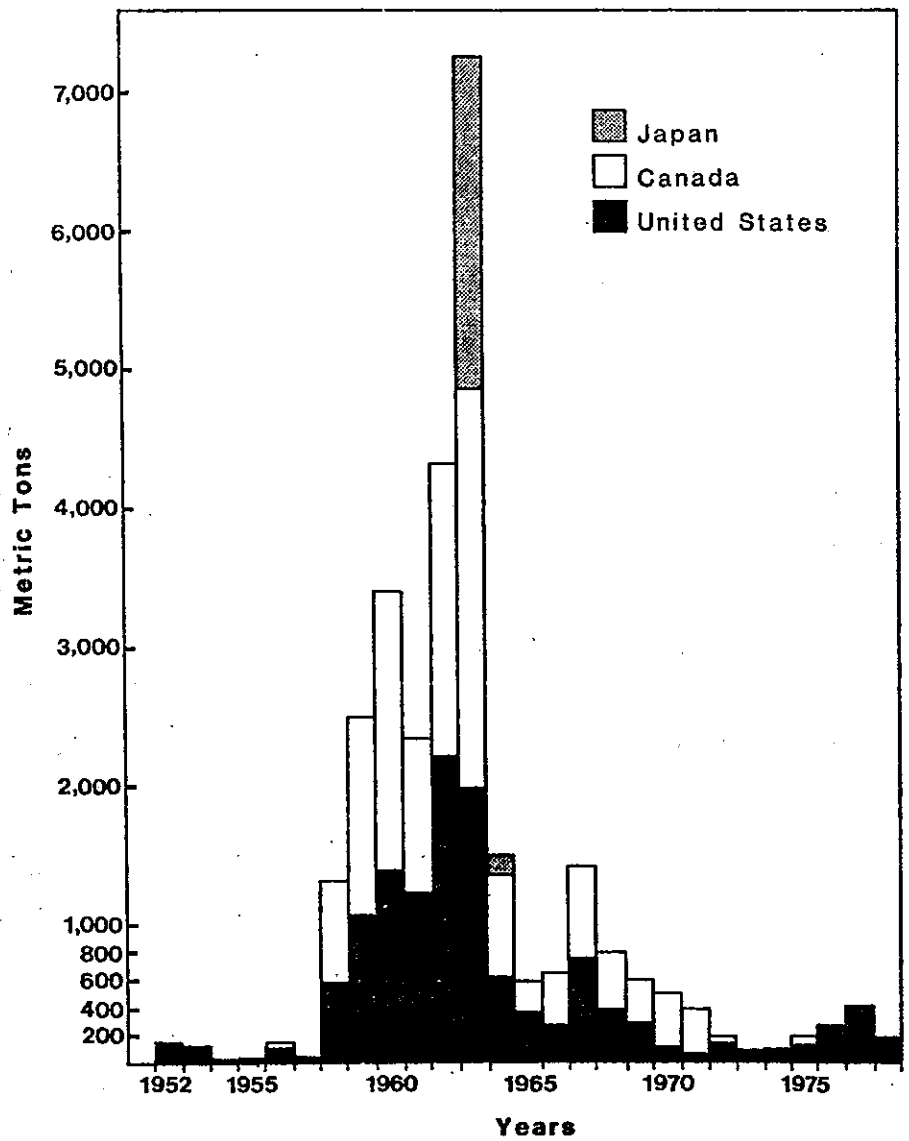

FIG. 5 Landings of halibut reported by Canadian, Japanese, and United States fishermen from the Bering Sea east of 175°W.

1963 catch from the quota area reached 4,974 mt and the total catch for the area east of 175°W was 7,254 mt. In 1964, a catch limit of 2,900 mt was set for the area between Unimak Island and the Pribilof Islands but only 972 mt could be taken from the depleted stocks. Japan discontinued longlining for halibut after the 1964 season. Catches declined after that time, and since 1970 have averaged about 250 mt, largely caught by U. S. vessels.

Regulations

After the poor catches of the 1964 fishing season the open period was limited to only 7 days in 1965 on the advice of IPHC. Since then the open period for the area east of 175°W has been gradually increased to its present 20 days in April and September, respectively. West of this line continuous fishing is permitted from April 10 to November 15. Poor catches in the eastern sector stimulated interest in fishing farther west, particularly along the Aleutian Islands.

Canadian interest in the Bering Sea fishery has declined with the growth of their domestic herring fishery, which occurs at approximately the same time as the spring season. The new "Protocol for Regulation of the North Pacific Halibut Fishery" eliminated Canadian participation in the Bering Sea commencing in 1979.

IPHC adopted a minimum size for commercially caught halibut of 5 pounds dressed weight with head off in 1940. This minimum size was further described to be a fish of 26 inches (66 cm) in 1944. The minimum size was increased to 32 inches (81 cm) in 1974. This size is about equal to a 10-pound (4.5 kg) fish, dressed with the head off.

In addition to the directed setline fishery for adult halibut very large numbers of young halibut have been taken incidentally in the fisheries for other species. Hoag and French (1976) estimated the incidental catch of halibut by foreign fleets from the entire Bering Sea was 11,519 mt in 1971. No estimate of the additional catch by the traps of the domestic crab fishery has been made. Incidental catches of mostly young individuals reduced the recruitment into the adult stocks. International negotiations initiated time-area closures beginning in 1974 for locations and times of greatest incidental catches of halibut. These restrictions have significantly reduced the incidental catches of small fish which should improve recruitment to the adult stock in the future. The first indication of improvement has been noted in the increased numbers of juveniles in the annual surveys conducted by IPHC (Fig. 6).

HISTORY OF RESEARCH

The U. S. Bureau of Fisheries' Steamer Albatross reported a few small halibut taken in the course of a survey of the codfish resource of the Bering Sea in 1890 (Rathbun 1894). The Albatross returned in 1911 while making a survey of the halibut grounds of the Pacific Coast (Alexander 1912). However, only a few small halibut were caught off Akun and Akutan Islands and 2 sets with longline gear made near Unimak Pass caught no halibut and the vessel proceeded to the Pacific Ocean. The next research in this area was the tagging of setline-caught halibut in Makushin Bay off Unalaska Island by IFC in 1930. A small United States fishery

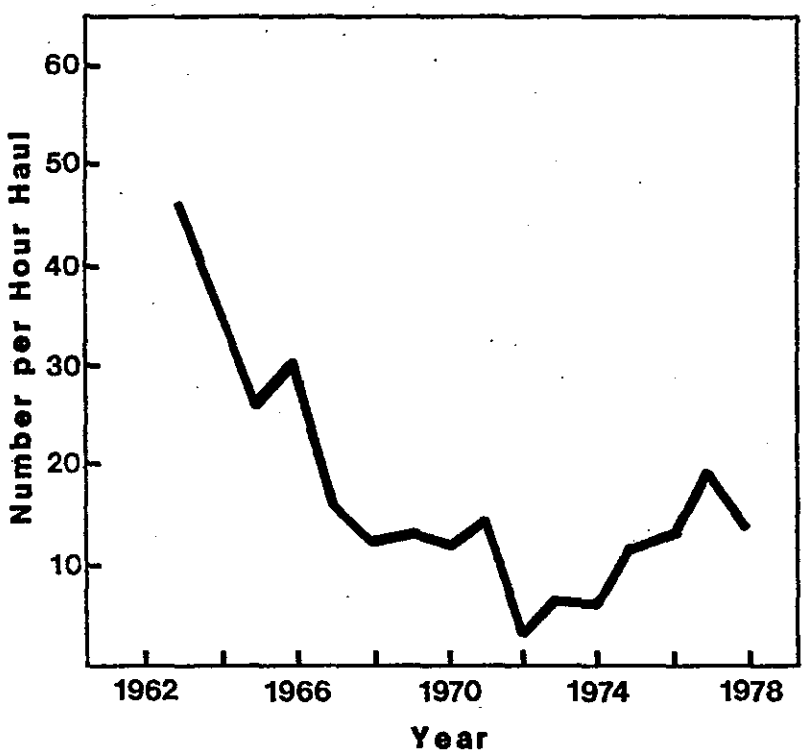

FIG. 6 Abundance of juvenile halibut (<65 cm) in the southeastern Bering Sea.

began about this time and lasted for about 3-4 years. With the rebuilding of the stocks in the Gulf of Alaska the fleet was able to secure profitable catches from grounds closer to port than the Bering Sea. The increased fishing in the Gulf of Alaska required that IPHC direct its research and management efforts to that area.

Research in the Bering Sea had a very low priority until funds were appropriated that permitted the initiation of a large tagging program by IPHC in the 1950's. In 1956 an IPHC chartered setline vessel found substantial numbers of commercial-sized fish along the edge between Unimak and the Pribilof Islands. The chartered trips were primarily to tag halibut but much life history information was collected from fish unsuitable for tagging. The accumulated information was summarized by Dunlop et al. (1964).

In addition to the investigations of the halibut stocks available to setline gear, IPHC began a trawl survey of the flats (continental shelf) in 1963 which has continued to date. This was primarily a study of the juvenile halibut in the area and has been summarized through 1977 by Best (1977). The NMFS has also collected information on halibut numbers and distribution in conjunction with king crab and groundfish surveys (Pereyra et al. 1976; Bakkala and Smith 1978). Japan also contributed to halibut research as part of its commitment to INPFC. Most of the data collected by Japan and IPHC contributed to the management decisions of the INPFC and are included in Pereyra et al. (1976). The U.S.S.R. made a comprehensive trawl survey between 1957 and 1961 and the information on halibut collected during this period was summarized by Novikov (1964).

A joint IPHC-U.S.S.R. research program to tag halibut began in 1975 with a cooperative cruise in the western Bering Sea by a U.S.S.R. vessel with IPHC and U.S.S.R. scientists on board (IPHC 1976). IPHC has continued releasing tags with legends in English, Japanese, and Russian since 1975. The agreement called for the U.S.S.R. to conduct a similar program in the western regions. Information gained from this cooperative research will provide a better assessment of the halibut resource.

The role that the Bering Sea plays in the life history and distribution of Pacific halibut, although of great importance, is not well understood. Looking at a map of Alaska, the first impression one gets of the Bering Sea is a large water mass isolated from the Pacific Ocean by the chain of the Aleutian Islands. In reality, the impression of isolation is false as the many passes between the Islands provide passage for Pacific Ocean water, immigration routes for the pelagic eggs and larvae of halibut, as well as pathways for later emigration of adults.

RESEARCH RECOMMENDATIONS

The research carried out in the Bering Sea to date has been concentrated in the eastern part. Even the research efforts of Japan and the U.S.S.R. have been conducted in a disproportionate amount in the eastern part with little if any research reported for the western part.

A basic need is the development of standardized catch and effort statistics on all fishing by all nations for the entire

Bering Sea. Forrester et al. (1978) did an excellent job of compiling the available information through 1970 but were hampered by the lack of adequate original information.

A coordinated tagging program should be developed stressing areas of the western Bering Sea and Aleutian Islands. Emphasis should be placed on tagging of the juvenile halibut which apparently make extensive movements from the nursery areas to the grounds where they become available to the commercial fisheries. Tagging of adults is also needed to provide information on the seasonal exchanges of the commercial sized halibut between winter spawning grounds to summer feeding grounds. Emphasis must be placed on the return of recaptured tags to provide the greatest information from these efforts.

In conjunction with the tagging program much basic biological information on halibut can be collected from the fish unfit for tagging. A simple but neglected project is the comparison of specimens from eastern and western Bering Sea and the eastern and western Pacific Ocean areas by serological or electrophoretic techniques to determine population similarities or differences.

Any future research should be coordinated between scientists of all nations fishing in the Bering Sea. Communication between researchers is necessary for the best utilization of collected information. In a tag recovery program, communication with the actual fishing fleet is essential or much of the information may be lost or distorted before reaching the issuing agency.

SUMMARY

The Pacific halibut are found from northern California into the Bering Sea and across the Asian Coast. Their center of abundance is in the Gulf of Alaska with a smaller but important population in the Bering Sea.

An inshore feeding migration in summer and an offshore spawning migration in winter have been observed. The timing and extent of the inshore migration is influenced by environmental conditions with cooler water tending to restrict the movement. A period of relatively cool water temperatures altered the summer feeding migration between 1970 and 1976. A directed movement of young fish, probably to counteract the drift during the prolonged egg and larval stages has also been noted. Movement by tagged young halibut in both an easterly and westerly direction away from the tagging location suggests that there is a mixing of stocks in the Bering Sea. Based on returns of tagged fish a 24% immigration into the Gulf of Alaska was calculated.

Female halibut in the Bering Sea mature at about 13 years of age and a size of 122 cm. A female will produce from 1-2 million eggs or more depending upon its size. Males mature at a smaller size of about 72 cm and at an age of about 7 years.

Based on scientific observation spawning occurs at depths of 250-550 m in the area between Unimak Island and the Pribilof Islands between December and February. Capture of a few larval halibut suggest that spawning also occurs at locations west of the Pribilof Islands and along the Aleutian Islands. Halibut larvae

have a pelagic life for at least 5 or 6 months and then settle in shallow water near shore.

Halibut in the commercial landings are from 7 to occasionally over 30 years old and range in size from 80 to over 200 cm. Female halibut are larger than males at each age with the difference becoming quite large at the older ages.

Examination of the stomachs of young halibut indicates a preference for shrimp, small crabs, and small fish, with larger fish utilizing larger prey items. The diet is varied and locally abundant prey of the proper size is heavily utilized.

Development of a commercial fishery for halibut in the Bering Sea was hampered by lack of facilities, distance from the home port, and adequate fishing in the Gulf of Alaska. Special seasons stimulated interest in the halibut of the area and landings slowly increased during the early 1950's, accelerated as the fleet developed a knowledge of the area, and reached a peak of over 7,000 mt in 1963. Catches have averaged about 250 mt during the 1970's. Rebuilding of the adult stocks has been hampered by the massive incidental catch of small halibut by the trawl fisheries for other species. Restrictions on the trawling activities give promise of improved stock condition in the future.

Regulation of halibut fishing by U. S. and Canadian fishermen has been the responsibility of the IPHC since 1932. The INPFC managed the halibut resource from 1963-76, while IPHC made recommendations to the Canadian and United States Governments for presentation to INPFC. After 1976 management of the fish resources of

the area became the responsibility of the United States under the FCMA. However, the responsibility for halibut remains with IPHC, a joint Canadian-United States agency.

Research on halibut has been strongly influenced by the need for stock assessment and management of the resource. Between 1950 and the present a considerable amount of research has been conducted in the southeastern Bering Sea by IPHC and fishery agencies of the United States, Japan, and the U.S.S.R. This research was largely uncoordinated and of an exploratory nature to develop and monitor the commercial fisheries in the area. Future research should be coordinated to provide a broad spectrum of information and to reduce costs of research by preventing duplication of effort.

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DISTRIBUTION AND MIGRATION AND STATUS OF PACIFIC HERRING

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ABSTRACT

Pacific herring are an important part of the Bering Sea foodweb and form the basis of a major commercial fishery. Until recently Japan and the U.S.S.R. have been major exploiters of herring. Catch peaked in the early 1970's at 145,579 mt, and then declined in response to overfishing and poor recruitment. Recently herring abundance has increased, and the United States has become the dominant exploiter of herring.

Most herring are harvested in coastal waters during the spawning period which commences in late April/mid-May along the Alaska Peninsula and Bristol Bay and progressively later to the north. Spawning occurs at temperatures of 5-12 C and the time of spawning is related to winter water temperatures with early spawning in warm years and late spawning in cold years. During spawning eggs are

deposited on vegetation in the intertidal zone of shallow bays and rocky headlands. Eggs hatch in 2-3 weeks as planktonic larvae and metamorphose to juveniles after 6-10 weeks. Little is known of larval and juvenile stages in the eastern Bering Sea.

Sexual maturity begins at age 2, but most herring mature at ages 3 and 4, the ages of recruitment to the fishery. Herring as old as age 15 occur; very few beyond age 10 are present in commercial catches. Age specific mortalities are unknown but the average instantaneous natural mortality rate is estimated to be 0.46-0.47. The rate of growth is generally greater in the Bering Sea than in the Gulf of Alaska, but within the Bering Sea growth decreases to the north. Herring feed on the predominant larger zooplankton--euphausiids, and copepods.

Three major stocks occur in the Bering Sea: northwest of the Pribilof Islands, Gulf of Olyutorski, and Cape Navarin. These have been identified as individual stocks based on differences in growth and maturation rates, and dissimilar age structures. Herring wintering northwest of the Pribilof Islands migrate to the Alaska coast in spring and spawn in Bristol Bay and between the Yukon and Kuskokwim Rivers. Although some may also spawn in the eastern Aleutian Islands, Alaska Peninsula, and Norton Sound, herring in these areas may also winter inshore near spawning grounds. Northward of Norton Sound some herring winter in brackish lagoons and estuaries.

Herring wintering northwest of the Pribilof Islands arrive on the winter grounds in October and concentrate in waters of 2-4 C at depths of 105-137 m through the winter. In March schools migrate to the coast for spawning. After spawning they appear to remain in coastal waters because few are found on the shelf or slope. In late August, they reappear in offshore waters in the areas of Unimak and Nunivak Islands, and the seaward migration to the winter grounds continues through September and October.

Although assessments of eastern Bering Sea herring have ranged from 374 thousand mt to 2.75 million mt, the current estimate of spawning biomass is 432-864 thousand mt. Fisheries data indicate that herring declined rapidly following peak harvests in the early 1970's and that peak catches were supported by a few strong year-classes. Weak year-classes occurred through the early 1970's, and recruitment appears to be normalized in recent years.

Research is required to refine estimates of abundance and biological characteristics of stocks, to improve the capability for predicting changes in resource abundance, composition and availability, and to identify the origin and distribution of herring in offshore areas.

INTRODUCTION

The Pacific herring (*Clupea harengus pallasi*) is a member of the family Clupeidae which has a global distribution and includes about 50 genera and 190 species found mostly in tropical and temperate waters (Svetovidov 1952). They occur in the North Atlantic and North Pacific areas, are similar in appearance and differ primarily in the number of vertebra (55-57 vs. 52-55). Pacific and Atlantic species also differ biochemically, with significant differences observed in the frequencies of eight genes (S. Grant, Northwest and Alaska Fisheries Center, Seattle, Washington, Personal Communication). Svetovidov (1952) believes that Pacific herring arrived from the Atlantic some time between the Pliocene and the "post-glacial 'transgression'" via the Asian Arctic. Pacific herring also differ from Atlantic herring in spawning and migrational behavior; the former are spring spawners, whereas the latter are divided into spring, winter, summer, and autumn spawners. Pacific herring spawn between the intertidal zone and about 20 m and deposit eggs on vegetation, whereas, Atlantic herring spawn in deep water on a gravel bottom. Pacific herring generally remain near the spawning ground year round and do not make extensive seasonal migrations as many Atlantic stocks do.

In the North Pacific Ocean, herring are distributed along the Asiatic and North American continental shelves (Fig. 1): in Asia they range from Taksi Bay, near the mouth of the Lena River, to the Yellow Sea (Andriyashev 1954); and in North America, from Cape Bathurst in the Beaufort Sea, to San Diego Bay, California (Hart 1973).

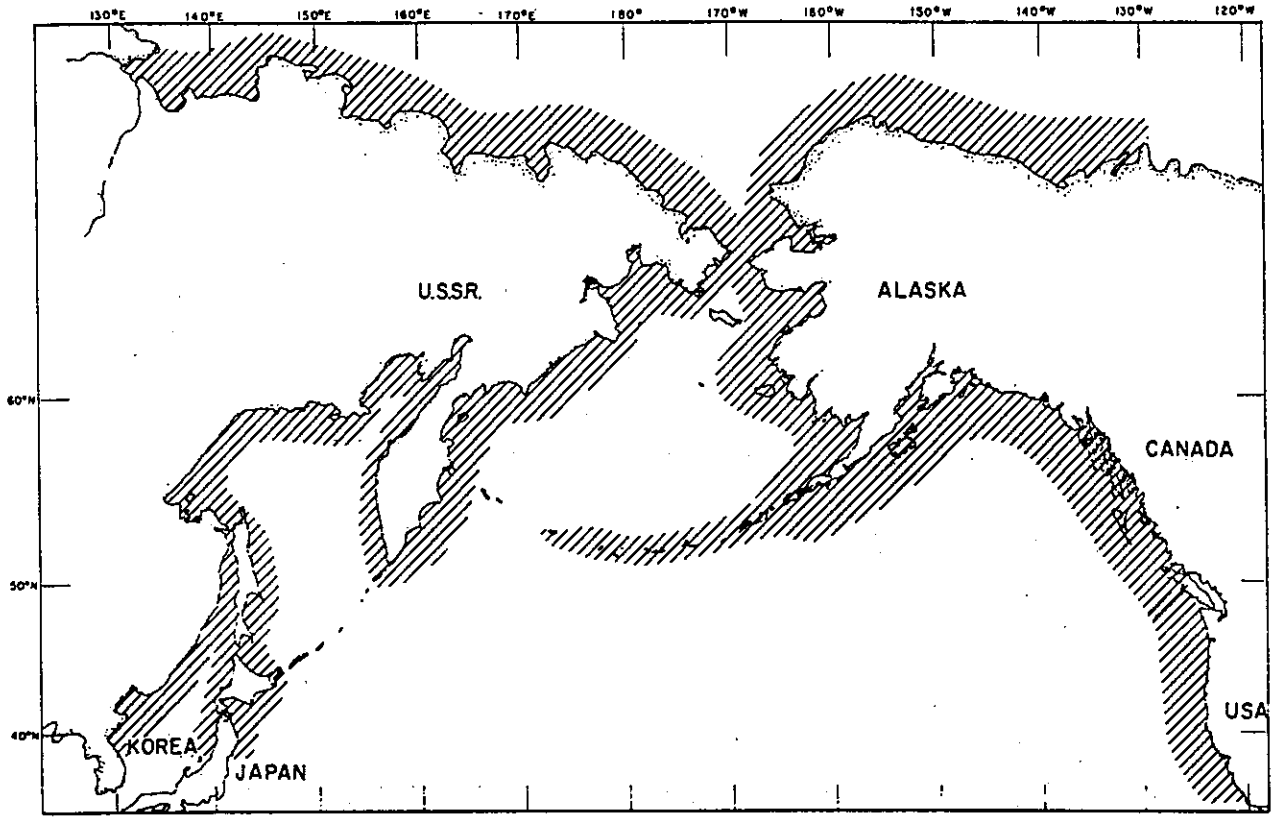

FIG. 1 Geographic range of Pacific herring (Clupea harengus pallasi) in the North Pacific Ocean.

Herring are an important part of the eastern Bering Sea foodweb. They are pelagic planktivores which are highly adapted with large mouths and numerous fine gill rakes for efficient utilization of euphausiids, copepods and other zooplankton. In turn, herring are important prey for marine mammals, birds and roundfish. Mathematical simulations of the ecosystem in this area by Laevastu and Favorite (1978) indicate that annual total mortality equals one half of herring biomass production and that 95% of total mortality is by predation. Given this level of mortality, it is understandable that herring stocks exhibit strong fluctuations in abundance with seemingly small changes in fishing or environmental factors.

The abundance of herring declined sharply in the early 1970's and only recently has an increase become apparent. Although several hypotheses could be advanced to explain the cause of the strong population fluctuations observed, data are insufficient to establish conclusively a causal factor. Since rapid, marked changes in abundance are expected to occur in the future, it will be necessary to be able to identify the causes and predict their occurrence and magnitude.

Present knowledge is rudimentary and inferences on many aspects of life history must be drawn from other more thoroughly studied populations. Research is needed on all aspects of herring biology, especially of interspecies interactions and environmental effects on herring.

FISHERIES

Archeological excavations in the area indicate that net fisheries had been developed as early as 500 BC (Hemming et al. 1978), and subsistence fishing for herring continues in many native villages, especially in villages between the Yukon and Kuskokwim Rivers where alternative food resources (salmon, moose, etc.) are absent or in low abundance (Barton 1978). Commercial herring fisheries developed in the northern Bering Sea around the turn of the century. Marsh and Cobb (1910) reported that a small fishery developed in Grantley Harbor on the Seward Peninsula about 1906 to supply salt herring to Nome. Prior to 1909, another small herring fishery developed in Golovin Bay, Norton Sound (Rounsefell 1930). Although the Grantley Harbor fishery apparently was short-lived, the last reported catch was in 1917 when 300 barrels were packed, the Golovin Bay fishery operated until 1941.

The first large scale herring fishery began in 1928 when a purse-seine fleet fished at Unalaska. Salteries were established at Dutch Harbor in following years, and the catch increased to a peak of 2,277 mt in 1932 (Barton 1978). Catches ranged between 1-2 thousand mt until 1937, and thereafter declined until 1946 when the fishery ended. Lack of demand and accompanying low prices for cured herring was the principal reason for the demise of this fishery (Wespestad 1978a). A herring fishery resumed in 1959 when Soviet exploratory trawlers located wintering concentrations along the continental slope northwest of the Pribilof Islands (Dudnik and Usol'tsev 1964). During the first season, 10,000 mt were harvested

(Fig. 2). Catches increased in following years as effort increased but declined sharply in 1965 and 1966 when herring could not be located and effort was greatly reduced.

Japanese vessels began targeting on herring in the late 1960's. A trawl fishery was established on the winter grounds from November to April and a gillnet fishery, which operated off the western Alaska spawning grounds, from April through June (Wespestad 1978b). In 1977, the area east of 168°W and north of 58°N was closed to foreign herring fishing to protect native subsistence fisheries, and in 1978 the 168°W closure line was extended to the Alaska Peninsula. This greatly limited the gillnet fishery; no foreign gillnetting occurred in 1978 and only a very limited amount in 1979.

Catch and effort peaked in the late 1960's/early 1970's and then declined (Fig. 3). The peak catch occurred in 1970 when 145,579 mt was harvested (see Fig. 2). Catch dropped abruptly the following year, increased slightly in 1972, and then declined until 1976 when an increase occurred. In 1977, an allowable catch of about 21,000 mt was established by the U.S. when the 200-mile Fishery Conservation Zone was established. Herring harvests have been maintained at this level to the present time.

U. S. herring fisheries resumed on a small scale in Norton Sound and northern Bristol Bay in the late 1960's for herring roe and herring roe-on-kelp for the Japanese market. Harvests were small, generally under 100 mt, until 1977, when the catch increased to 2,550 mt. The fishery expanded further in 1978, and the catch

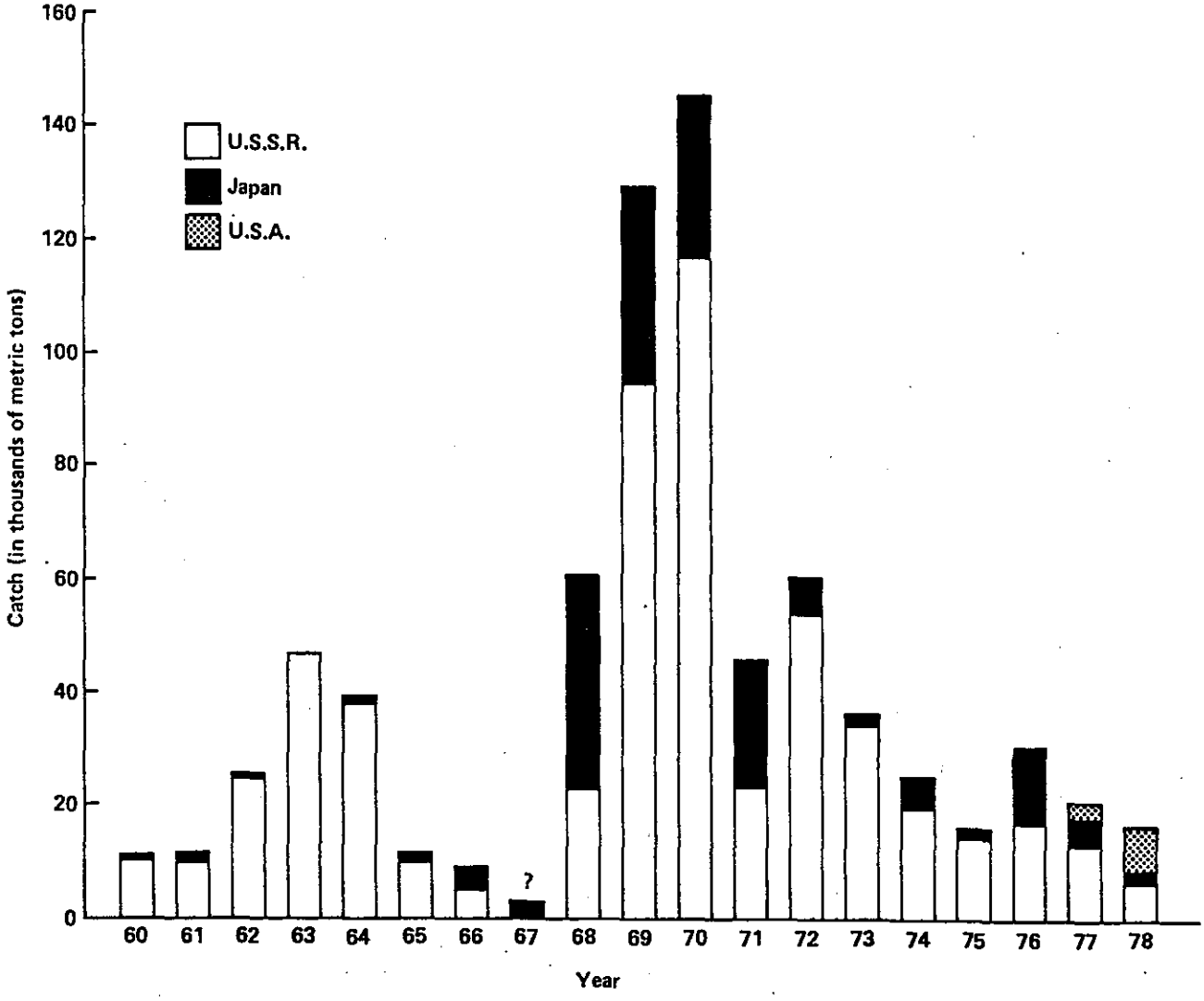

FIG. 2 Eastern Bering Sea herring catch 1960-78.

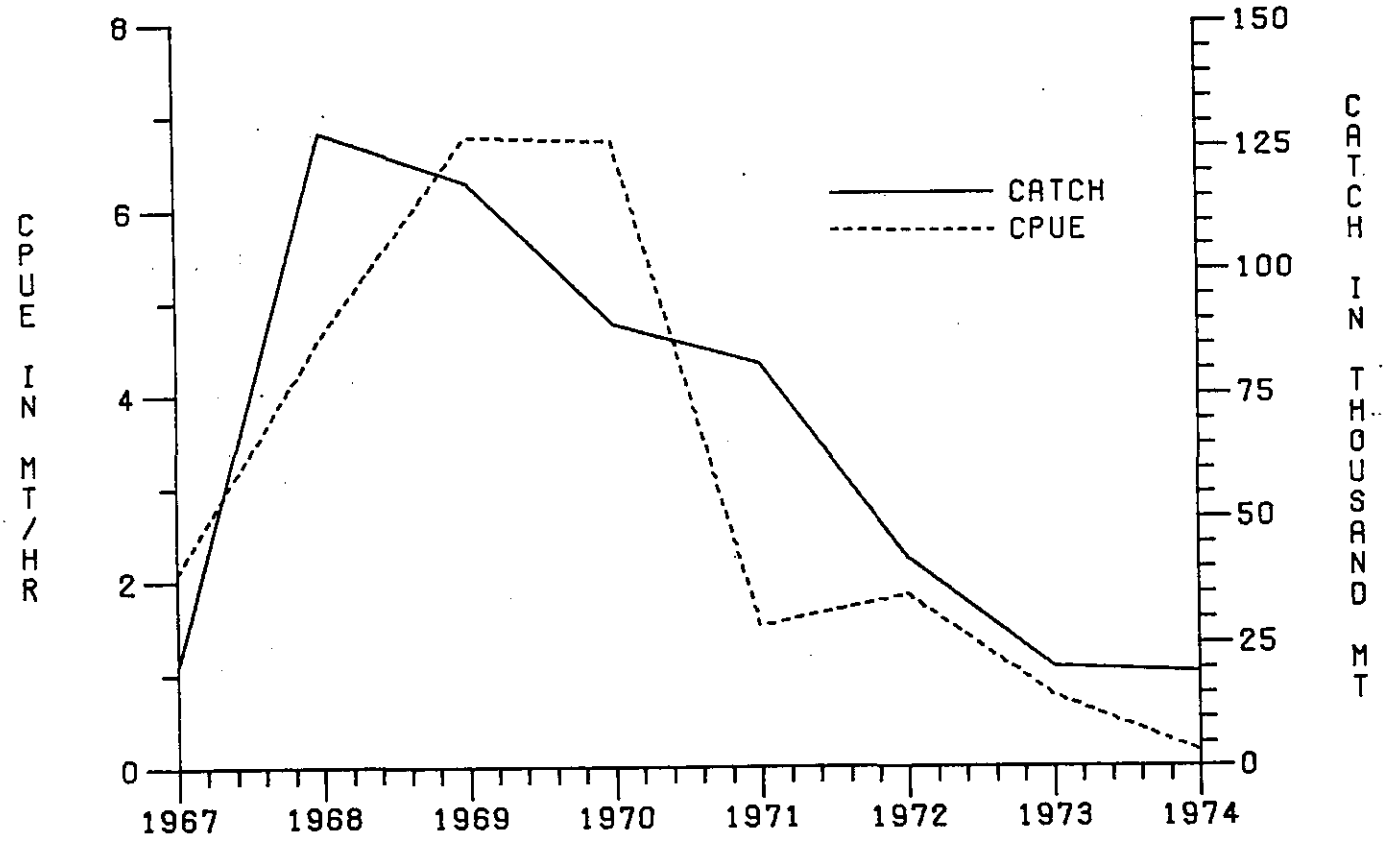

FIG. 3 Catch and catch per unit effort (CPUE) relationship for large Japanese stern trawlers in the eastern Bering Sea, 1967-1974.

rose to 7,025 mt. In 1979, catch increased again to approximately 12,000 mt. Most of the U. S. harvest is taken with purse seines and gillnets in northern Bristol Bay between Cape Constantine and Cape Newenham. Additionally, smaller fisheries occur in Goodnews Bay, Security Cove, Cape Romanzof and Norton Sound (Fig. 4).

GENERAL BIOLOGY

Spawning

Herring spawn along the western Alaska coast in late spring to midsummer (see Fig. 4). In most years, spawning occurs first along the Alaska Peninsula and in Bristol Bay in late April to mid-May and progressively later to the north. In Kotzebue Sound, it may extend from July through mid-August (Barton 1978). It usually commences soon after the spawning grounds become ice-free and has been noted to commence when water temperatures are approximately 3-5.5 C (Scattergood et al. 1959), although it has been recorded over a range of 6-10 C in northern Bristol Bay (Warner and Shafford 1977) and in a range of 5.6-11.7 C on spawning grounds between Norton Sound and Bristol Bay (Barton 1979).

Prokhorov (1968) found that the approximate time of spawning in the western Bering Sea is related to winter and spring water temperatures with early maturation in warm years and delayed development in cold years. The past two years (1978-1979) have been mild winters, 1979 especially so, and herring have arrived on the spawning ground several days to two weeks earlier then average; while in 1976, a cold year, spawning herring were not evident until mid-June. Svetovidov (1952) believes that the shore spawning be-

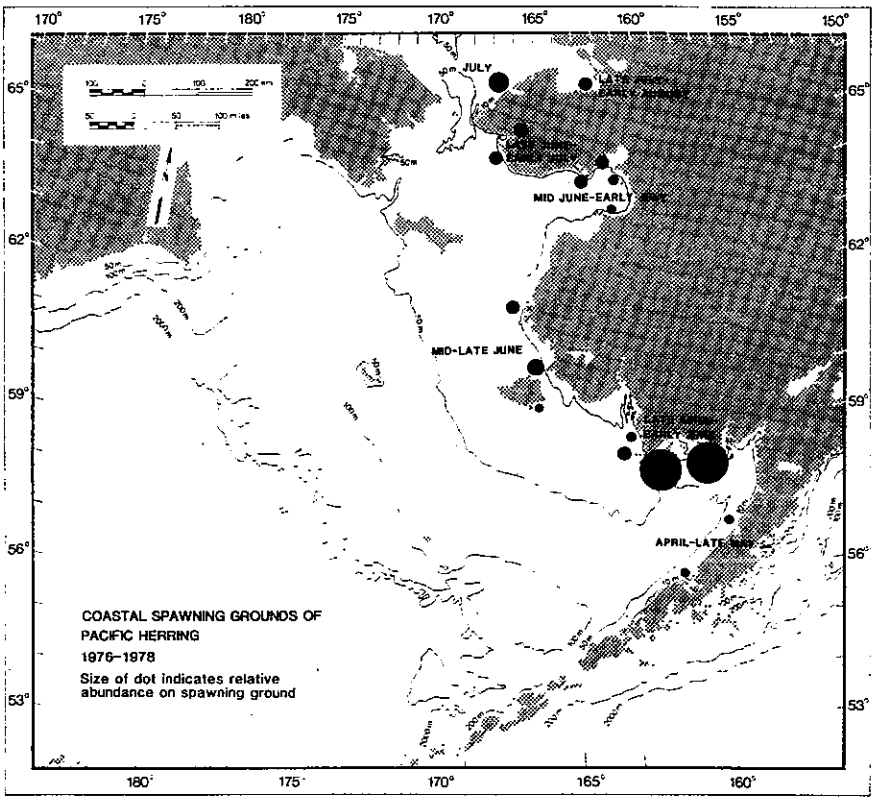

FIG. 4 Distribution, time of spawning and relative abundance of Pacific herring on coastal spawning grounds observed during aerial surveys, 1976-1978.

havior of Pacific herring is due to a lack of high water temperature in deeper water.

The duration of spawning may range from a few days to several weeks. Generally, the older herring are the first to spawn, followed by successively younger fish. Eggs are deposited on vegetation in intertidal and shallow subtidal waters, predominantly on rockweed (*Fucus* spp.) and eelgrass (*Zostera* spp.) (Barton 1979). There are two types of spawning habitats: rocky headlands, and shallow lagoons and bays (Barton 1978). Southward of Norton Sound most spawn is found in the intertidal zone on rockweed, while from Norton Sound northward most spawn is found in the shallow subtidal zone on eelgrass. Barton believes area differences are partially due to smaller tide changes in the northern areas.

Eggs take 10-21 days to hatch depending on water temperature. In northern Bristol Bay, this takes 13-14 days at 8-11 C (Barton 1979). However, Alderdice and Velson (1971) have suggested that optimum temperatures for Pacific herring egg development are 5-9 C and that below 5 C egg mortality occurs.

Little is known of the magnitude or causes of egg mortality on eastern Bering Sea spawning grounds, but studies in British Columbia revealed wave action, exposure to air and bird predation as major factors (Taylor 1964). Wave action may be a major cause in the Bering Sea because it has been observed that a severe storm subsequent to spawning activity destroyed both deposited eggs and rockweed in the upper intertidal zone along the south shore of

Cape Romanzof (Gilmer 1978). Predation of fish may also be an important egg mortality source. Concentrations of flatfishes, particularly yellowfin sole, have been observed on the spawning grounds in northern Bristol Bay (John Clark, ADF&G, personal communication). Stomach examinations of flatfish in spawning areas by both authors have revealed a high rate of egg consumption.

Larval and Juvenile Development

General Background Information from Barkley Sound, B.C. Studies

Herring hatch as larvae averaging 8 mm in size, and this planktonic larval stage lasts for approximately 6-10 weeks, at which time the larvae have grown to approximately 30 mm and begin to metamorphose into juveniles (Taylor 1964). During the larval stage, they are subject to high and variable mortality rates. An important source of mortality may be failure to obtain proper food after yolk sac absorption and from passive transport away from the coast by prevailing currents (Outram and Humphreys 1974). Stevenson (1962) found that when larvae in Barkley Sound were transported to the open sea, few of the transported larvae survived. He did not find temperatures and salinity to be important factors in inshore areas but believed the high mortality of larvae offshore was possibly connected to the increased salinity of the open sea. There are indications that the direction and magnitude of surface stress may affect larval survival, a northward wind stress (along a N/S coast) will result in net onshore flow and a piling up of water against the coast, causing onshore retention of larvae and good year-classes, offshore movement is associated with poor year-classes

(Outram and Humphreys 1974).

Upon completion of metamorphosis, juveniles are free-swimming and begin to form schools that enlarge and move out of the bays as summer progresses (Taylor 1964). Hourston (1959) found that juveniles moved from the spawning grounds on the northwest side of Barkley Sound to rearing grounds on the southeast side. No specific reason could be found for migration to the southeast other than a preference for calmer, sheltered water found there. Juveniles in Barkley Sound actively feed at depths of 0.6-5 m at dawn and dusk. No sampling was done at night, but some inactive schools were observed near surface. Juvenile schools were found in a range of salinities, but most were found at 25 ^{o}/oo salinity, which corresponds to Fujita and Kokudo's (1927) point of best fry survival.

Bering Sea

Little is known about the juvenile stage in the Bering-Chukchi Sea region from the time herring leave the coast in their first summer until they are recruited to the adult population. Rumyantsev and Darda (1970) indicate that juveniles feed in coastal waters in summer and move to deeper water in winter (juvenile herring in British Columbian and southern Alaska waters winter offshore and reappear in bays the following summer -- Taylor 1964; Rounsefell 1930). In the western Bering Sea, ages 0 and 1 herring inhabit areas nearer shore and at lower temperatures than adults (Prokhorov 1968).

Juveniles were found in the Port Clarence area in 1977, and more than 50% of the juveniles were captured in Imuruk Basin, the

brackish forebay of the Port Clarence/Grantley Harbor complex. Apparently herring in the northern Bering Sea and Chukchi Sea may have a much lower salinity tolerance as eggs and fry were found in Imuruk Basin near Port Clarence in water of $4^{o}/oo$ salinity (Barton 1978). Although juveniles were present in the spring spawning period (late June-early July), significant numbers were not captured until mid-August. Their presence in Hotham Inlet in November was indicated by stomach analyses of sheefish (Stenodus leucichthus). Further substantive numbers of age 1 herring were captured in June in Hagemeister Strait of northern Bristol Bay (Barton 1979).

Wolotira et al. (1977) found both mature pre-spawning and immature herring in autumn (September-October) trawl catches made in the offshore waters of the northern Bering Sea and southern Chukchi Sea; however, age 0 herring were only found in the pelagic area of Norton Sound between Cape Douglas and Golovin Bay.

Maturation and Fecundity

Herring spawn for the first time at ages 2-6 but the majority do not spawn until ages 3 (50% mature) and 4 (78% mature). By age 5, 95% of the population has matured (Rumyantsef and Darda 1970). Sexual maturity of eastern Bering Sea herring coincides with recruitment into the fishery, primarily at ages 3 and 4. The onset of sexual maturity occurs earlier in the herring's southern range (stocks mature between ages 3 and 4 in British Columbia and ages 2 and 3 in California -- Hart 1973, Rabin 1977).

In mature herring fecundity varies as a function of body length and latitude, increasing in size and latitude (Nagasaki

1958); it also appears to be higher in the eastern Bering Sea area than in the Gulf of Alaska or western Bering Sea (Table I).

Age and Growth

Herring have been found to attain an age of up to 15 years (Barton 1978), and generally occur in substantial numbers from ages 3-6, but when strong year-classes occur, ages 7-10 may comprise a substantial portion of the catch.

TABLE I

Fecundity (thousand of eggs) of Pacific Herring in Different Areas of the Northern Pacific Ocean

Area	Age	4	5	6	7	8	Source
E. Bering Sea	1963	26.6	34.4	46.1	59.5	70.8	Shaboneev (1965)
	1964	26.6	32.1	52.4	53.5	77.8	(Rumyantsev & Darda (1970)
Alaska Peninsula	1976	Mean: 26.4	Range:	12.6-84.8	Ages IV-VI		Warner (1976)
Karaginskii Bay	1963		26.8	30.1	37.4		Kachina[1]
W. Bering Sea	1964			39.2	43.3	50.6	Kachina
Vancouver	1955	19.9	23.8	29.6	38.2	30.4	Nagaski (1958)

[1]Cited in Rumyantsev & Darda (1970).

Stocks grow at about the same rate as those in the Gulf of Alaska and British Columbia until ages 3-4, but growth is greater

in the Bering Sea for older fish, and they achieve a greater maximum length and weight than the more southern stocks (Fig. 5). Rounsefell (1930) reported many herring of 380 mm in the catch at Unalaska (compared to a maximum of 330 mm reported for British Columbia -- Hart 1973). In more recent investigations, Rumyantsev and Darda (1970) and Warner (1976) have found Bering Sea herring of 340-345 mm. Barton (1978) found that size-at-age in spawning concentrations along the western Alaska coast from Norton Sound northward are significantly smaller than stocks to the south (Fig. 5).

A general growth curve was derived for eastern Bering Sea herring by applying von Bertalanffy's equation to data reported by Shaboneev (1965) from the winter trawl fishery:

$$L_t = L_\infty \quad 1-e^{k(t-t_o)}$$

The parameters of von Bertalanffy's equation are: L_∞ (maximum length in mm) = 324.5, k (growth rate) = 0.35 and t_o (age in years, fish was 0 length) = 0.0261.

Warner (1976) computed a von Bertalanffy curve for fish captured in trawl samples in Bristol Bay. His coefficients were L_∞ = 299, k = 0.18 and t_o = 2.10. These estimates, although lower, do not differ significantly from Shaboneev's data, given the variances reported by Warner.

Mortality

Beyond the larval stage the rate of natural mortality decreases sharply and continues to decrease slightly until about age 5 when it begins to increase from senility, disease and spawning

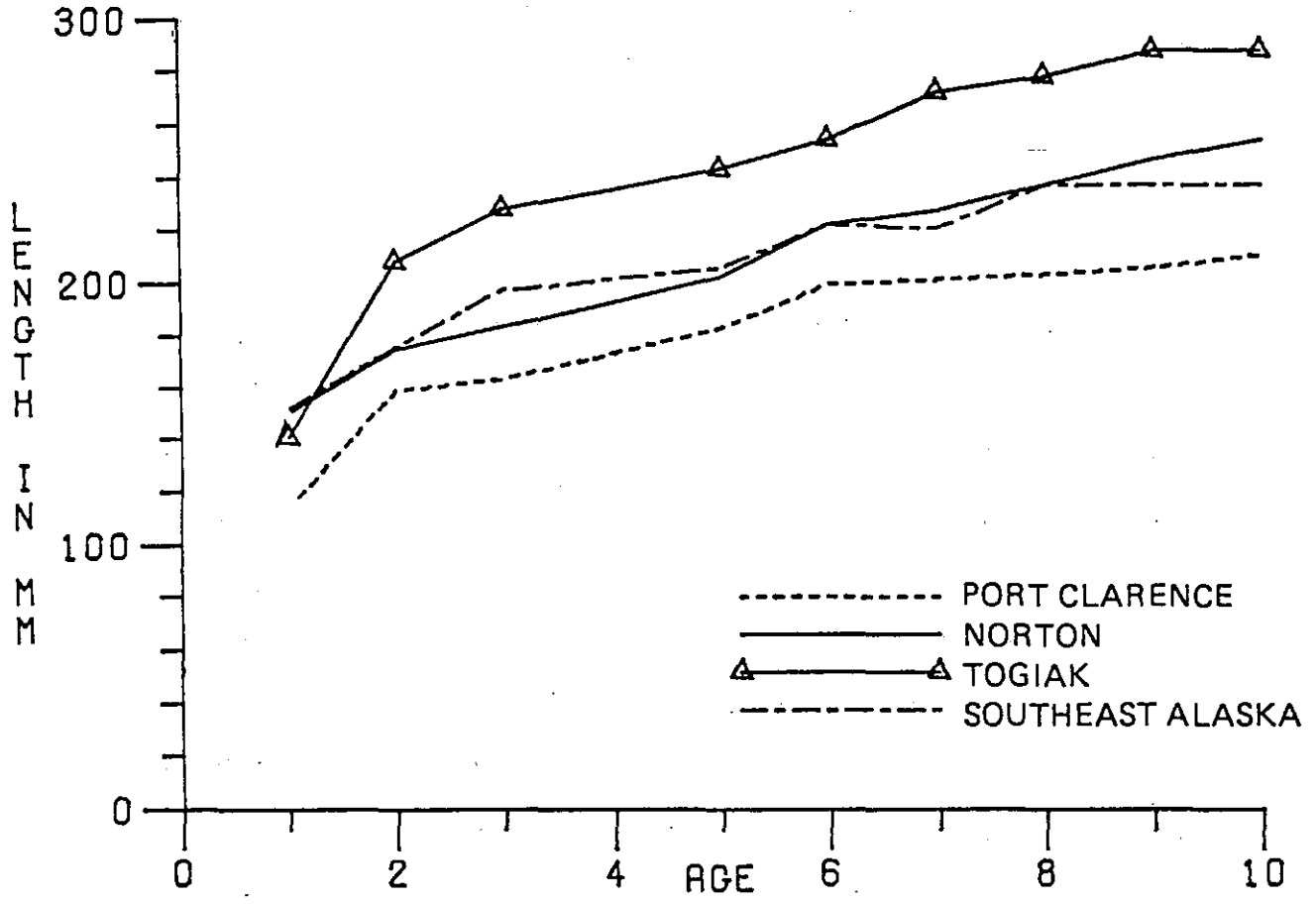

FIG. 5 Size-at-age comparisons of Pacific herring from selected areas in the eastern Bering Sea and the northeastern Pacific Ocean.

mortality (Fig. 6). In the juvenile stage the magnitude of mortality is actually unknown but inferences from other fish populations suggest that it is maximum in years of high egg and larval survival through intense intraspecies food competition (Ricker 1975).

A general estimate of the natural mortality rate for eastern Bering Sea herring was derived by Wespestad (1978a), using the procedure of Alverson and Carney (1975). This method estimates the natural mortality rate for eastern Bering Sea herring to be 0.47. Natural mortality can also be determined by an analysis of catch curves using regression techniques (Ricker 1975). Applying this method to data presented by Laevastu and Favorite (1977), the instantaneous mortality rate for fully recruited ages of eastern Bering Sea herring is determined to be 0.46. Age-specific natural mortality estimates are unavailable for the eastern Bering Sea stocks; however, they are probably similar to natural mortality rates estimated for herring stocks in southeastern Alaska and British Columbia (Table II).

TABLE II

Instanteous Rate of Natural Mortality (M) for Herring in the Northeastern Pacific

Area/Age	3	4	5	6	7	8	Source
S.E. Alaska	.20	.33	.46	.59	.72	.85	Skud (1963)
E. Vancouver Is.		.40	.64	.77	.85		Tester(1955)
W. Vancouver Is.		.46	.61	.72	.79		Tester(1955)

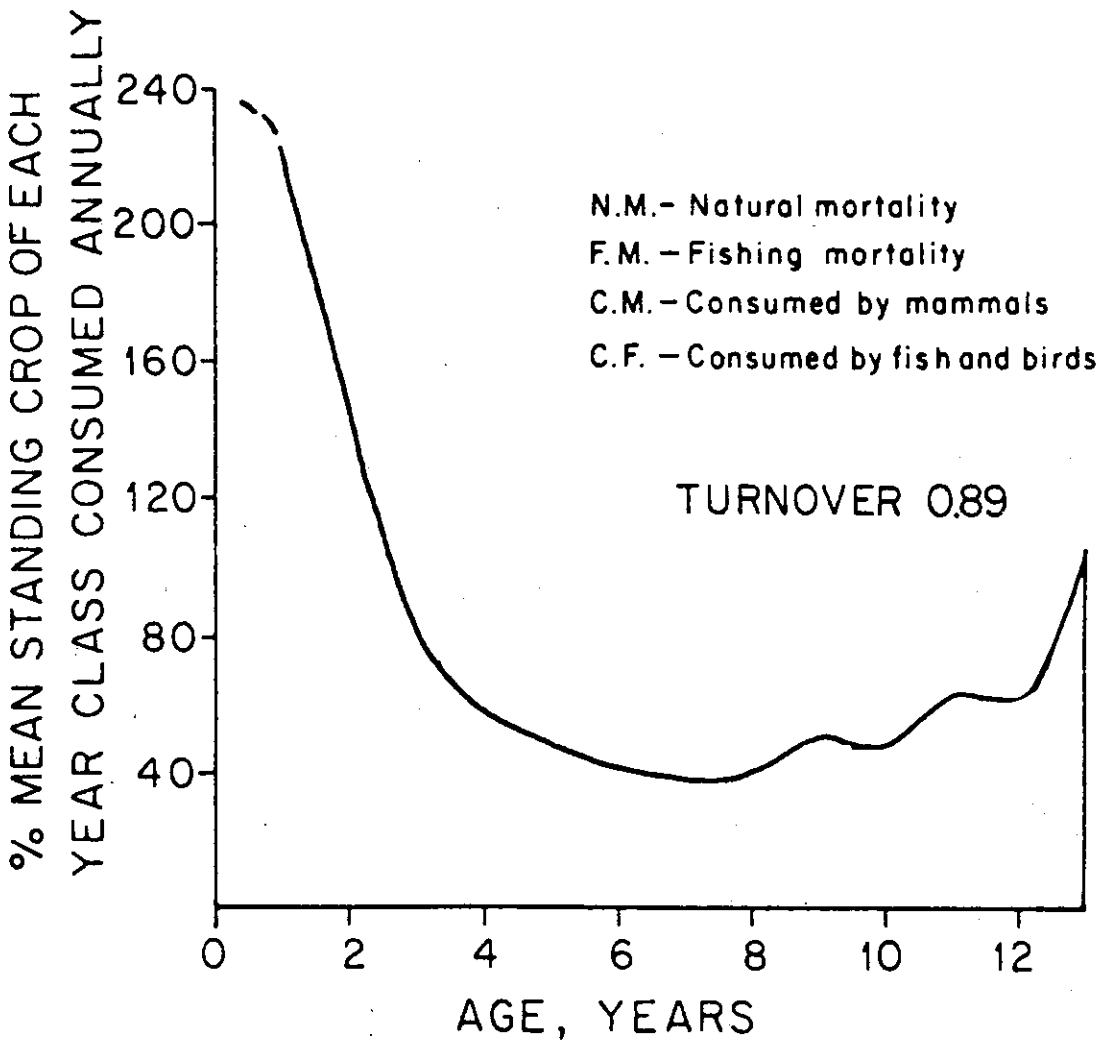

FIG. 6 Total mortality of Pacific herring expressed as percent annual cohort biomass loss.

Food and Feeding

The first food of larvae is usually limited to small and relatively immobile plankton organisms that the larvae must literally nearly run into to notice and capture. Earliest food is sometimes more than 50% microscopic eggs, other items include diatoms and nauplii of small copepods.

Herring do not have a strong preference for certain food species but feed on the comparatively large organisms that predominate in the plankton of a given area (Kaganovskii 1955). Feeding generally occurs prior to spawning and intensifies following spawning (Svetovidov 1952). During the winter, feeding declines and ceases in late winter (Dudnik and Usol'tsev 1964). During November-December, in Kamchatka waters of the western Bering Sea, Kachina and Akimova (1972) found that juvenile herring consumed small and medium forms of zooplankton (chaetognaths, copepods, tunicates) and benthoplankton (mysids). Euphausiids, amphipods, mollusks and other organisms were found rarely and usually in small quantities. In the demersal zone, herring stomachs contained quantities of tubes of polychaete worms, bivalve mollusks, amphipods, copepods, juvenile fish and detritus.

In the eastern Bering Sea, stomachs in August were 84% filled with euphausiids, 8% with fish fry, 6% with calanoids, and 2% with gammarids (Rumyantsev and Darda 1970). Fish fry, in order of importance, were walleye pollock, smelt, capelin and sandlance. In spring, food was mainly Themisto (Amphipoda) and Sagitta (Chaetognatha). After spawning, the main diet was euphausiids, Calanus spp. and Sagitta spp. (Dudnik and Usol'tsev 1964).

Nearly 75% of herring stomachs examined in the spring from Bristol Bay to Norton Sound were either empty or contained only traces of food (Barton 1978). Only 25% of the stomachs examined were at least 25% or more full, and only 3.4% were 100% full. Major food items were cladocerans, flatworms (Platyhelminthes), copepods and cirripeds.

DISTRIBUTION

Stock Distribution

Three major herring wintering rounds have been identified within the Bering Sea: northwest of the Pribilof Islands and in the Gulf of Olyutorski (Prokhorov 1968); and near Cape Navarin (N. Fadeev, TINRO, Vladavostok, U.S.S.R., Personal Communication) (Fig. 7). Differences in the pattern of migration between the coast and the outer continental shelf has effectively isolated Asian and North American herring in the Bering Sea. Different growth and maturation rates, and dissimilar age structures reported by Prokhorov (1968) occur between those wintering near Cape Navarin and northwest of the Pribilof Islands, suggesting that although these groups winter in close proximity there is little or no mixing between them. Most herring which winter near the Pribilof Islands are believed to spawn in Bristol Bay and in areas between the Yukon and Kuskokwim Rivers. This conclusion is based on Soviet research, similarities in age composition, and the distribution of Japanese trawl catches during the spawning migration (Wespestad 1978b, Barton 1979). ADF&G aerial surveys indicate that the greatest abundance of spawning herring occurs in the Bristol Bay area and

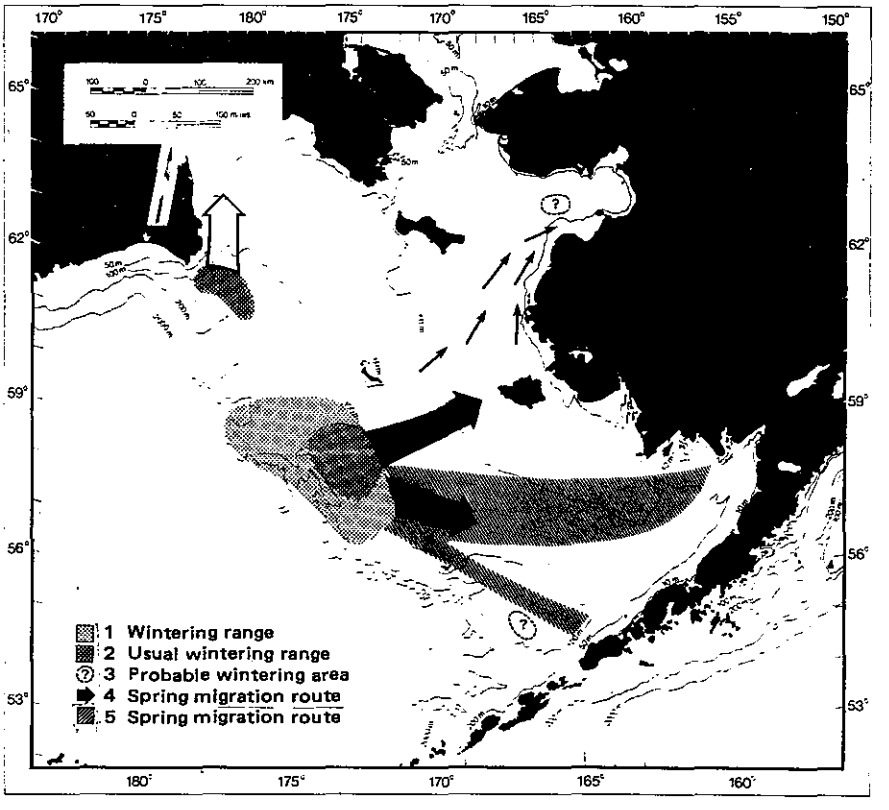

FIG. 7 Range of Pacific herring wintering area northwest of Pribilof Islands and average winter location of Pribilof and Gulf of Anadyr wintering area (1 and 2); possible wintering areas in Norton Sound and north of Unalaska Island (3); migration routes from Pribilof grounds to spawning areas: routes reported by Soviet researchers (4); routes shown by Japanese trawl catches during April and May (5); small arrows--possible routes to Norton Sound and Cape Romanzof.

smaller spawning concentrations occur to the north and south (see Fig. 4).

The relation of herring spawning in Norton Sound to spawning stocks to the south is unclear. Those in Norton Sound are genetically similar to spawning stocks to the south (Grant 1979) and appear in inshore waters in late May-early June (Barton 1978) which suggests they may winter offshore. However, it is possible that some or all herring remain in Norton Sound year-round. Barton (1978) reported that an autumn, non-spawning run occurs in Golovin Bay in northern Norton Sound, and herring have been caught through the ice by local residents jigging for cod in this area and near Nome. Further, herring have been found in ringed seal (P. hispida) stomachs collected near Nome in November. To the north of Norton Sound herring occur in Port Clarence, in inlets from the Bering strait to areas within Kotzebue Sound. Many, if not all, stocks found northward of Nome remain in the immediate area year-round and winter in coastal lagoons and brackish bays, even though in several locations (e.g., Port Clarence, Shismaref Inlet, and inner Kotzebue Sound) ice cover may occur (Barton 1978).

Herring may also occur along the Alaska Peninsula and throughout the Aleutian Islands. Marsh and Cobb (1911) reported that a large spawning occurred at Atka Island in 1910, and that spring and autumn runs (the latter presumably non-spawning) occurred at Unalaska and Port Heiden. The fishery which operated at Unalaska in the 1930's and 1940's harvested herring in summer and early autumn, averaging 1,337 mt between 1929-37. The current status of

these stocks or their relationship to other eastern Bering Sea stocks is unknown. Recent aerial surveys by ADF&G have found small spawning concentrations on the north shore of Unimak Island, in Heredeen Bay, and in Port Heiden (Warner and Shafford 1977). Catches by Japanese trawlers just north of Unimak Pass in winter indicate that this may be the wintering area of herring spawning on the Alaska Peninsula (Wespestad 1978b).

Seasonal Distribution- Pribilof Stock

Temperature may be the major factor influencing seasonal distributions. Soviet scientists found the herring moving through subzero water temperatures in the spring on the way to spawning grounds, but during summer months they were found on the shelf in the warmer, upper layers of the water column (see Fig. 7). As stated previously, Svetovidov (1952) believes that migrations to the coast for spawning developed because of the lack of sufficiently warm water in spring and summer in the North Pacific Ocean. Also, earlier warming of coastal waters provides an earlier development of phytoplankton and zooplankton and better feeding conditions.

Winter

The major wintering grounds of eastern Bering Sea herring is located northwest of the Pribilof Islands, approximately between 57-59° N lat. representing an area of 1600-3000 km^2 (Shaboneev 1965) that shifts in relation to the severity of winter. In mild winters herring concentrate farther north and west, and in severe winters they move south and east (Fig. 8).

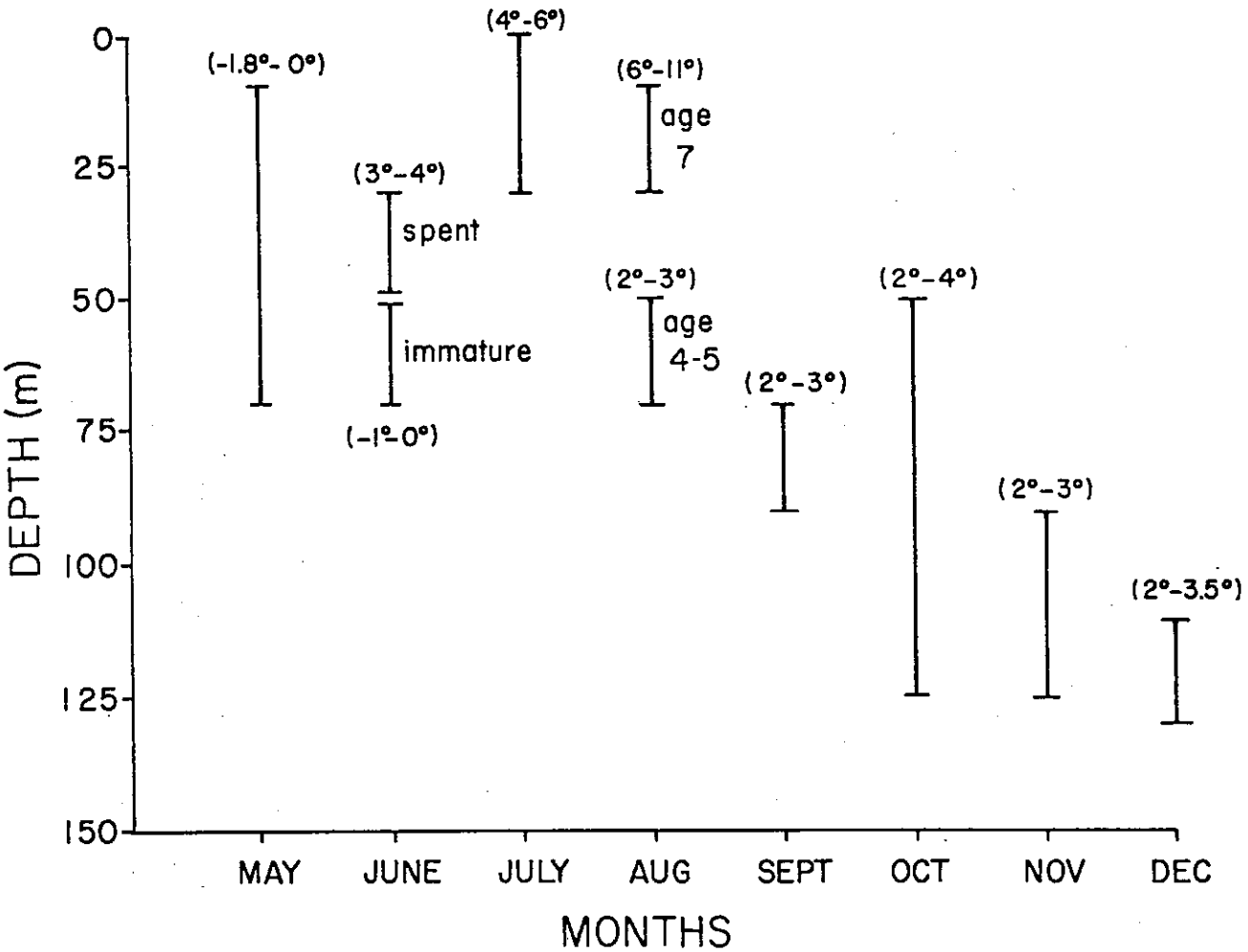

FIG. 8 Monthly distribution of Pacific herring by temperature and depth in the eastern Bering Sea. May-November data from Rumyant'sev and Darda (1970), December data from Shaboneev (1965).

Dense schools are found during the day a few meters off the bottom at depths of 105-137 m and at water temperatures of 2-3.5 C (Dudnik and Usol'tsev 1964). Very few were found shallower on the continental shelf where cooler temperatures prevailed. Distinct diurnal vertical migrations occur in early winters; however, as the season progresses diurnal movements diminish and herring remain on bottom during the day and slightly off bottom at night (Shaboneev 1965).

Spring

Soviet scientists investigating herring distribution in the mid-1960's found that herring left the wintering grounds in late March and believed that herring followed two routes to the coast, and Japanese trawl catches in April and May indicate one major and one minor path (see Fig. 8). The past two years (1978-79) have been mild winters and 1979 especially so. In these years, herring arrived on spawning grounds along the coast several days to two weeks earlier than average; while in 1976, a cold year, herring were not found until mid-June.

Summer

The failure of Soviet surveys in the mid-1960's using gillnets and trawls to locate herring concentrations on the Bering Sea slope or shelf in the summer suggested that most herring apparently remain temporarily in coastal waters after spawning. Annual NWAFC summer trawl surveys covering much of the continental shelf of the eastern Bering Sea support this conclusion, as very few herring have been taken in summer surveys (Pereyra et al. 1976; Bakkala and

Smith 1978). A hydroacoustic survey conducted along the outer shelf between Unimak Pass and the U.S.-U.S.S.R. convention line in June-July 1979 found only one herring in 2,558 nm and 35 midwater trawl hauls. These results indicate that only a small amount of herring may remain or return offshore in summer and the bulk remains in coastal waters. Summer distribution may be influenced by the availability of food and heavy phytoplankton blooms (1-3 g/m^3) (Rumyantsev and Darda 1979). They concluded that herring remained in coastal waters during the summer because heavy phytoplankton blooms occur there, and poor feeding conditions exist on the outer shelf. Those captured on the outer shelf during the summer were in poor condition and had been feeding on items of low nutritional value --items other than their preferred zooplankton diet. Herring are believed to avoid the areas of heavy bloom because of low nutritional value of phytoplankton and the gill clogging properties of certain phytoplankton species which interfere with respiration (Henderson et al. 1936).

Concentrations began reappearing in offshore waters in the areas of Nunivak and Unimak Islands in August (Rumyantsev and Darda 1970). The movement to offshore in the area of Unimak Island in August appears to be an annual occurrence, as U.S. fishery observers on foreign vessels first encounter herring in trawl catches in greater than trace amounts at that time and area.

The distribution of herring between the time they leave the spawning grounds and the time they reappear in offshore waters is unknown. Salmon fishermen report catching large herring frequently

in salmon gillnets in coastal areas of Bristol Bay in late June and July. Also, Dudnik and Usol'tsev (1964), using drift nets, found commercial quantities of herring only in littoral areas along the northern portion of the Alaska Peninsula. The reappearance of seaward migrants in late summer in two locations suggests a summer migration along the coast (Fig. 9). Migration to winter grounds continues through September with the herring progressively moving to deeper water and concentrating in the 2-4 C temperature stratum.

Fall

Concentration on the winter grounds begins in October and continues into winter. Mature fish were found to arrive on the wintering grounds prior to the arrival of immature fish (Ramyantsev and Darda 1970). It was also found that immature fish had a preference or tolerance for lower temperature and saline waters of the shelf than did adult fish (Fig. 10).

Seasonal Distribution - North of Norton Sound

The annual cycle of herring occurring to the north of Norton Sound appears to be markedly different from that of herring in the central and southern Bering Sea. In these areas herring appear to move into brackish bays and estuaries for spawning and wintering, presumably finding suitable temperatures from fresh water rivers and streams. Barton (1978) found herring spawning in Imuruk Basin, a brackish forebay of Port Clarence, in 4 ^{o}/oo salinity. The herring dispersed following spawning and then reappeared in Imuruk Basin in mid-autumn.

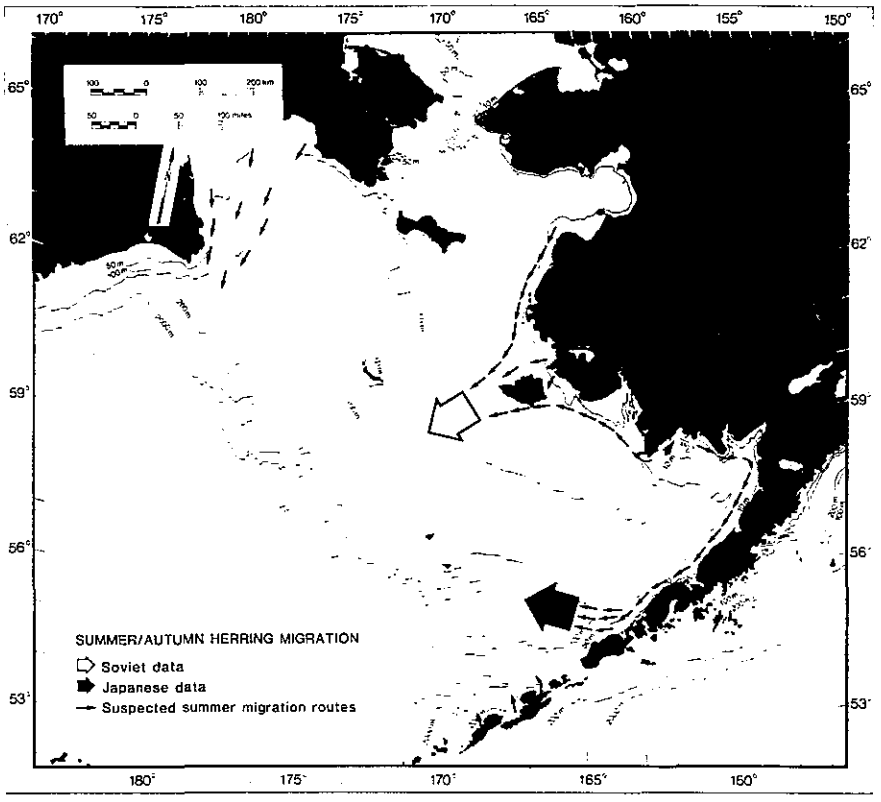

FIG. 9 Summer and autumn migration routes to winter grounds. Large solid arrow: area of reappearance in offshore waters as determined by Soviet research and Japanese catches, large dashed arrow: area of autumn reappearance in offshore waters reported from Soviet research, small arrows: possible summer feeding routes and autumn migration routes.

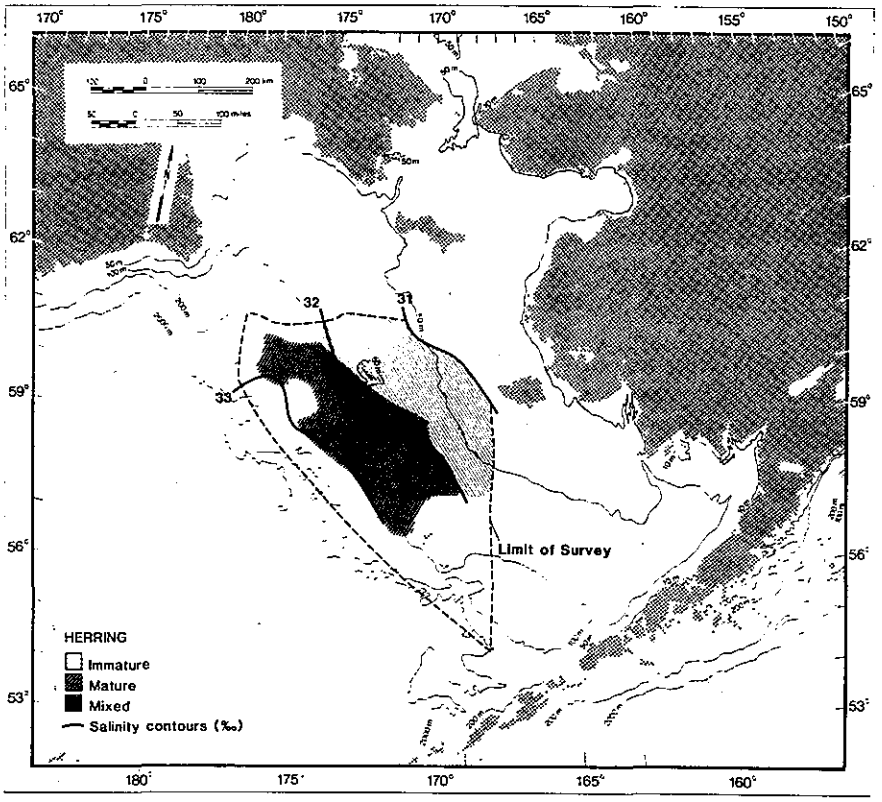

FIG. 10 Distribution of Pacific herring in October and the relationship of adults (mature) and juveniles (immature) to salinity gradients. (Modified from Rumyant'sev and Darda 1970.)

Large numbers of herring were found concentrated just outside Kotzebue Sound in 6-8 C water in September and October (Wolotira et al. 1977). It is possible that these herring move south with the advancing edge of the ice field, however some evidence suggests that they remain in the area through the winter. The phenomenon of herring moving into coastal waters in winter and offshore in summer has also been reported from Asia; Andriyashev (1954) reported that populations occur in Kamchatka, Sakhalin and Honshu which winter and spawn in brackish lakes and lagoons. Barton (1978) cites ADF&G records of herring being found in sheefish (Stenodus leucichthus) stomachs which were collected in Hotham Inlet, Kotzebue Sound in late November.

To the south of Kotzebue, on the northwest side of the Seward Peninsula, herring occurred in 11 of 14 stomachs of spotted seals (P. largha) collected at Shishmaref in October, and in 13 of 30 ringed seals collected in January and February. Marine mammal biologists who analyzed the stomachs indicated that there was little doubt herring were ingested in the area where seals were captured.

ABUNDANCE TRENDS AND STOCK STATUS

Estimates of absolute abundance are scant, and even relative abundance data are rather limited. Attempts have been made to estimate herring biomass by: 1) a Soviet hydroacoustic trawl survey; 2) ecosystem modeling; and 3) aerial surveys of spawning biomass.

In 1963, three years after the fishery began, the eastern Bering Sea herring biomass was estimated to be 2.16 million mt

based on a Soviet hydroacoustic survey of the wintering grounds (Shaboneev 1965). A recent paper by Kachina (1978), using the same data, reduced this earlier estimate to 0.374 million mt by using a lower mean school density of 0.5 fish/m^3 compared to 3.38 fish/m^3 used for the original estimate. According to Shaboneev, schools were surveyed at night and the area and height of schools were mapped acoustically; school composition and age distribution were determined by trawling. The original density (3.38 fish/m^3) was determined by comparing acoustic echograms from the eastern Bering Sea to echograms of schools sampled by purse seines in western Bering Sea coastal water. The revised estimate of 0.5 fish/m^3 is based on densities observed in subsequent surveys of herring concentrations on the winter grounds northwest of the Pribilofs during 1969-71 (N. Fadeev, TINRO, Vladivostok, U.S.S.R., personal communication). The densities derived are questionable but cannot be fully evaluated because few specific details are available regarding Soviet survey methods and accuracy. However, data reported in the literature and from individuals involved with herring hydroacoustic surveys indicate that the range of densities used by the Soviets may be extreme and an intermediate value may be more realistic.

Recently, a numerical ecosystem model was applied to estimate biomass of eastern Bering Sea herring (Laevastu and Favorite 1978). This model simulated herring abundance based on the amount of herring needed to sustain the diet of herring predators at reported rates of consumption. Although the accuracy of input parameters,

such as predator population size and consumption rates, has not been sufficiently evaluated, model results show that a minimum stock size of 2.75 million mt of herring is required to maintain components of the ecosystem, including predators, at a level observed in the mid-1960's prior to the start of intensive fishing.

Aerial surveys have been flown in the past several years along the western Alaska coast during the spawning period and the number of schools recorded by surface area (Barton 1979). Estimates of biomass were obtained by converting estimated school surface area, using densities of 0.1 and 0.2 mt/m^2 surface area.

The estimated spawning biomass along the coast from Bristol Bay to Norton Sound in 1978 was 432-864 thousand mt. These estimates include errors in determining surface areas and volumes of schools, recording schools of other fish such as capelin, smelt or sandlance as herring, and recording the same school more than once during the season; and, therefore, may be an overestimate of actual spawning biomass (Barton 1979).

Although biomass estimates are rather rudimentary, CPUE of the Japanese trawl fishery and ADF&G aerial surveys indicate that herring abundance declined sharply in the early 1970's and increased in the late 1970's. The CPUE (mt/hr) for Japanese large stern trawlers decreased from a high of 6.80 in 1969-70 to 0.77 in 1973-74 (Table III). The CPUE of small stern trawlers also declined. The CPUE of the Japanese gillnet fishery exhibited no trend, presumably because vessels were targeting on spawning concentrations which may not reflect population abundance (Wespestad 1978b).

TABLE III

Herring Catch Per Unit Effort Data for the Japanese Trawl and Gillnet Fisheries in the Eastern Bering Sea.

Year	Stern trawl		Gillnet
	Small Trawlers (mt/hour)	Large Trawlers (mt/hour)	(mt/10 tons)
1967	1.25	2.09	-
1968	1.75	4.63	.28
1969	0.81	6.80	.39
1970	1.06	6.74	.24
1971	0.56	1.52	.34
1972	-	1.84	.04
1973	-	0.77	.14
1974	0.29	0.17	.35
1975	-	-	.16
1976	-	-	-

ADF&G aerial surveys have indicated an increase in herring abundance in all major spawning areas during the 1976-78 period (Table IV). Preliminary assessment of observations in 1979 indicate a similar or slightly greater abundance relative to 1978. The longest series of aerial counts is from southern Norton Sound, extending back to 1968 and, similar to the trawl CPUE data, indicate a decrease in abundance during the early 1970's.

The current level of herring abundance cannot be related to former levels due to changes in the fishery. The catch and CPUE of foreign trawlers are no longer useful as indicators of abundance because herring are now largely incidental catches to other fisheries due to increased targeting on pollock, and the allowable catches of herring have been low in recent years (Wespestad 1978b).

Also, the absence of aerial surveys in major spawning areas prior to 1976 precludes the use of this method for determining the relationship of past to present biomass levels.

TABLE IV

Relative Abundance Indices of Spawning Herring Standardized to 1976 In Major Spawning Areas of the Eastern Bering Sea.[1/]

	1968	1972	1974	1975	1976	1977	1978
Bristol Bay	--	--	--	--	1.0	2.1	20.0
Goodnews Bay/ Security Cove	--	--	--	9.5	1.0	20.9	61.6
Nelson Island	--	--	--	0.5	1.0	1.0	3.2
Norton Sound: St. Michaels to Unalakleet	20.8	8.4	2.9	0.0[2/]	1.0	--	4.2

1/ Relative abundance indices are corrected school counts weighted by surface area obtained from aerial surveys.
2/ Minimal survey effort.

Length and age frequency data indicated that catches in the late 1960's and early 1970's were composed of larger and older herring than in the past few years (Table V). These data suggested that recruitment was poor until recently and may have been a major contributing factor to a lower herring abundance. Recruitment appears to have increased beginning with the 1972 year-class (Fig. 11).

TABLE V

Mean Length of Herring Taken in the Fisheries by all Gear in all Months in the Eastern Bering Sea and Alaska Coastal Water.[1/]

	Foreign Trawl Fishery			Coastal Fishery		
Year	Mean Length (cm)	Sample Size	Probable Average Ages	Mean Length (cm)	Sample Size	Location of Sample
1964	26.60	3,101	7	23.30	339	Norton Sound
1965	29.83	155	8-9			
1966	27.16	48	6-7			
1967	26.20	99	5-6			
1968	29.04	4,771	8-9	28.60	350	Bristol Bay
1969	30.66	3,951	9-10			
1970	30.81	3,813	9-10			
1971	29.21	4,299	8-9			
1974						
1975						
1976			3-4	20.11	791	Bristol Bay
1977	23.40[2/]	1,981	4-5	23.00	2,847	Bristol Bay
1978	23.28[3/]	3,607	4-5-6	23.27	1,031	Bristol Bay

1/ Standard length for all coastal samples; fork length for foreign samples prior to 1978.
2/ Fork length (Nov. 1976-Feb. 1977) estimated standard length is 22.40 m.
3/ Standard length (Dec. 1977-Jan. 1978).

Sources: Foreign Fishery: Fisheries Agency of Japan, Rumyantsev and Darda (1970). U.S. observers on Japanese and Soviet vessels.

Coastal Fishery: Alaska Dept. Fish & Game, 1964 Annual Report; Bristol Bay Data Report No. 17; Barton et al. (1977). Warner & Shafford (1977).

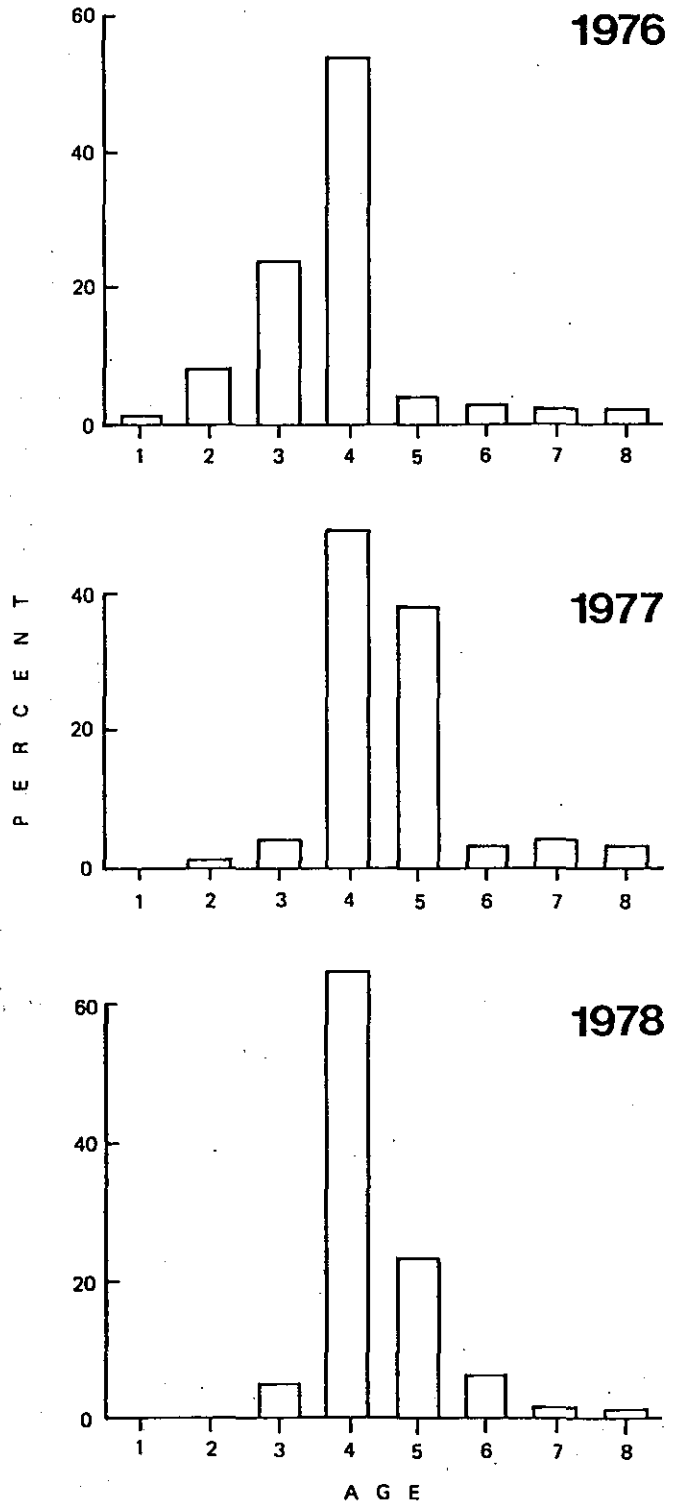

FIG. 11 Age frequency of Pacific herring in the Bristol Bay herring roe fishery, 1976-1978.

Age 4 herring comprised 54% of the catch in 1976, 50% in 1977; and in 1978 comprised 65% of the purse seine catch. In 1979, preliminary results suggest that the recuitment of age 4 herring is decreased from that observed in 1976-78; however, it appears that age 3 fish are present in higher amounts than in the recent past.

Year-class strength data presented recently by Naumenko (1979) show several years of relatively weak year-class strength in the 1960's and early 1970's (Fig. 12). These data suggest that the peak catches of the fishery were sustained by a few strong year-classes and that future yields of this magnitude are likely only in the event of a series of much above average year-classes or change in the ecosystem.

RESEARCH REQUIREMENTS

Research is required to refine estimates of abundance and biological characteristics of stocks; to improve the capability for predicting changes in resource abundance, composition and availability; and to identify the origin and distribution of herring in offshore areas.

Estimates of biomass of specific groundfish resources have been obtained through resource surveys using bottom trawls; however, herring are not generally available to bottom trawls, and other gear and methods must be used for assessing biomass. Hydroacoustic surveys, spawn deposition surveys and aerial surveys of schooled fish are some of the methods under consideration for biomass estimation.

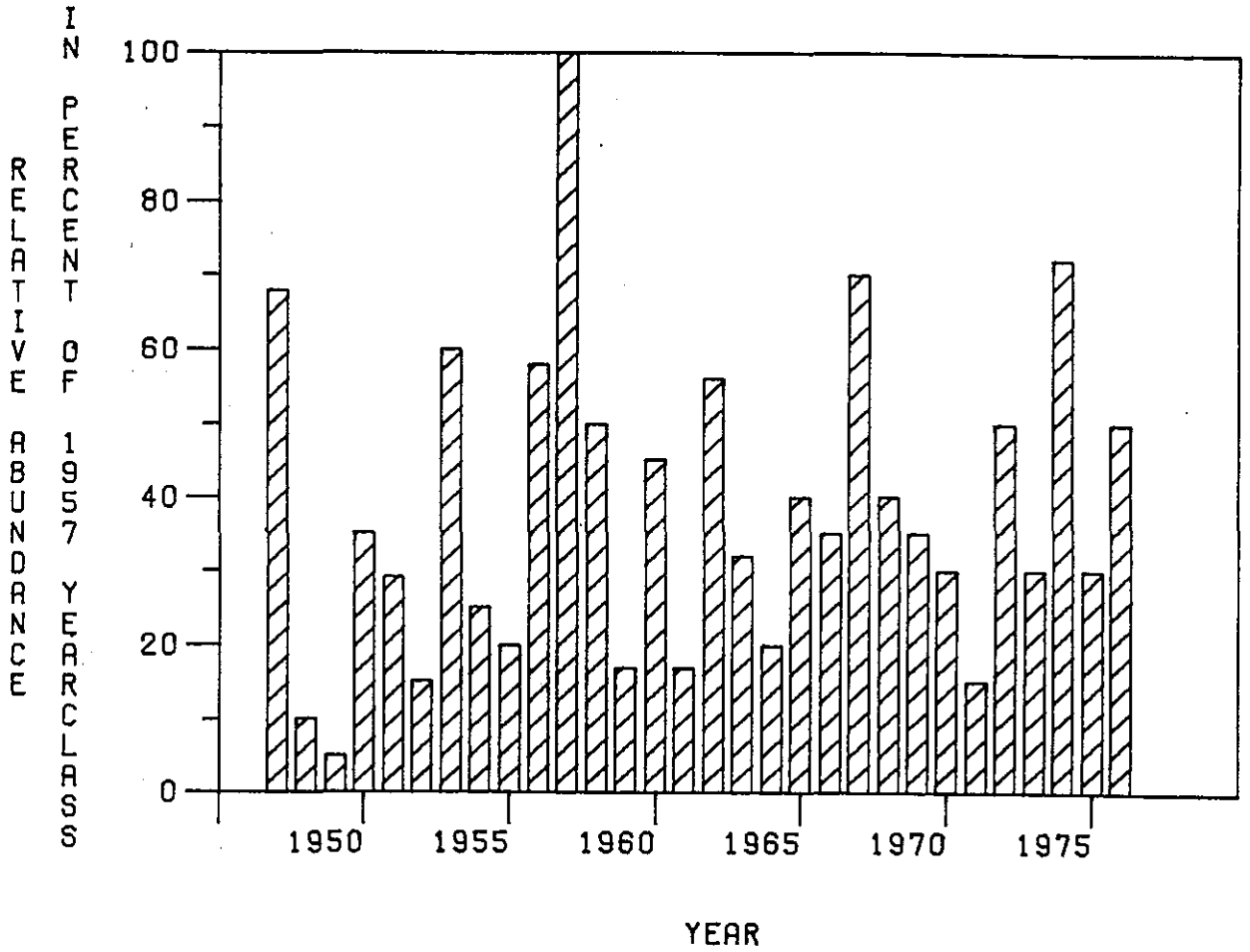

FIG. 12 Abundance of Pacific herring year-classes in the eastern Bering Sea relative to the 1957 year-class. (From Naumenko 1979.)

Hydroacoustic surveys in the nearshore areas just prior to or during spawning are probably not practical due to the many widely scattered schools that are constantly moving through the shallow waters. Optimum results can be expected on the winter grounds when herring are relatively stationary and concentrated. Results of surveys conducted during late winter-early spring could be applied in time for management of the roe fisheries.

Spawn surveys convert the amount of spawn deposited to the size of the adult population, using age-sex-size composition and fecundity data. Such surveys would have to be conducted immediately after spawning so as to not be affected by losses from predation and storms. The vast size of the area, including distances between spawning areas, lack of sub-tidal spawning information and various logistical problems, currently render this method impractical for the eastern Bering Sea.

In spite of limitations due to weather and narrow time-area coverage, aerial surveys may be one of the more cost-effective ways of measuring the abundance of spawning herring. Intensive testing should be made of school distribution within a limited area to determine if surveys are more effective at particular times and to investigate the variability of schools along sighting tracks. Also, aerial biomass estimation procedures and species identification procedures need to be developed. If a model of spawning school distribution could be developed, then statistical procedures could be used to overcome some of the weather and time limitations. Satellite technology may be a means of augmenting aerial surveys in

that large schools may be observable at distances from the coast or spawn deposition (milt) may be observable from satellites. A combination of low level aircraft and satellite observations may provide answers to the effective coverage of tracklines and time-space distribution of schools.

Long-term fisheries management requires reliable forecasting of stock conditions. Until now, forecasts have been based mainly on past events, such as trends in abundance indices (CPUE's) and size and age composition of specific resources without any consideration of the interactions of these resources with each other and the environment. Studies need to be continued to determine for predictive purposes those factors that have major influences on the abundance, composition and distribution of resources. Monitoring certain oceanographic and climatological conditions (temperature, currents, etc.) in both the nearshore spawning-rearing grounds and the offshore wintering grounds may be very important in understanding fluctuations in herring abundance.

There is a critical need for annual pre-recruit surveys (i.e., of young fish before they enter the fisheries) so that a measure of their abundance can be used to forecast later contribution to the exploitable stock. Assessment of pre-recruit abundance could be made of juveniles in nearshore nursery areas or at a later age in more offshore waters. The major limitation for use of this method is the virtual absence of information relating to distribution of eastern Bering Sea herring during the first 2-3 years of their life cycle.

Basic biological research is needed to systematically investigate population parameters, such as age specific mortality rates, growth rates and recruitment rates. Investigations are also needed to establish the degree of utilization of herring in the diet of marine mammals, salmon and other predators so ecological effects of harvesting can be better evaluated.

Lastly, stock distribution needs to be investigated so that individual stocks within the eastern Bering Sea can be monitored with regard to relationship to other stocks and occurrence in fisheries.

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THE BIOLOGY OF WALLEYE POLLOCK

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ABSTRACT

Walleye pollock, Theragra chalcogramma, occur broadly distributed over the eastern Bering Sea outer continental shelf, and at their presently estimated population size of 5 million mt, are a large source of organic production. Within the food web pollock are an important food resource for a wide variety of other fish species, marine mammals, and avifauna. Pollock also represent a major source of predation directed toward zooplankton and cannibalistic behavior. In addition, trawl fisheries harvest approximately 950,000 mt of pollock annually.

Although the genetic identity of eastern Bering Sea pollock is apparently distinct from populations in the western Pacific, genetic differentiation observed within the eastern Bering Sea is low, and the entire eastern Bering Sea population may be regarded as effectively a unit stock. The population is composed of approximately fifteen year-classes that show differences in geographical distribution and behavior based upon age. The overall rate of population mortality is high, approximately 51% dying annually, and age class abundance is variable between years.

Spawning occurs predominantly along the southeastern Bering Sea outer shelf, just west and northwest of Unimak Island. Migratory movements that accompany ontogeny include northwest drift and broad dispersal by age 1-yr. In general, the adult fraction of the population undergoes seasonal movements to deep water during

winter, to spawning sites in spring, then to the outer and central shelf during summer. Two apparent influences of ocean climate, warm or cold years, are to affect the timing and extent of these seasonal changes in geographical range.

There are fundamental needs for better understanding of important factors affecting the population dynamics of eastern Bering Sea pollock, to ensure collection of adequate time series data, and further studies of interspecific relationships and population exchange.

INTRODUCTION

The gadoid fish species walleye pollock, Theragra chalcogramma (Pallas 1811), is now recognized as perhaps one of the most important components of the Bering Sea biological system. Pollock have been found to represent a large fraction (ca. 20-50%; Pereyra et al. 1976) of the total standing stock of eastern Bering Sea demersal fishes, and the annual production of this organic pool is large. In 1978, commercial trawl fisheries operating in the eastern Bering Sea harvested 977,700 mt of pollock (Pileggi and Thompson 1979). This amount represented 56% of all foreign fish catches in the fishery conservation zone (i.e., inside the 200-mile limit) of the entire United States, and a total dockside (ex-vessel) value of approximately $92.4 million.

Because of their large standing stock, wide geographical distribution, and large rates of total food intake and production (growth), pollock represent an important part of the Bering Sea food web. During different life history stages pollock can be a major source of predation, feeding upon a broad spectrum of primarily zooplankton and fish prey. In turn, pollock themselves serve

as an important food source for a variety of other demersal and pelagic fish species, pinnipeds, cetaceans, and avifauna.

POPULATION CHARACTERISTICS

Nomenclature

The walleye pollock, *T. chalcogramma*, is the only recognized member of the genus *Theragra* and is endemic to the North Pacific (Fig. 1). The overall species range extends continuously around the continental shelf areas of the northern Pacific Ocean and Bering Sea. In the northwest Pacific the species extends from the Sea of Japan, through the Okhotsk Sea and Kurile Islands, and along the Kamchatka Peninsula and Anadyr Gulf. In the northeast Pacific the range extends from St. Lawrence Island through the eastern Bering Sea, through the Gulf of Alaska, and along the northeastern Pacific coast to central California (Hart 1973). Pelagic populations have also been recently found over deep water in the central Bering Sea (Okada 1977, 1978).

In the eastern Bering Sea, *T. chalcogramma* is by far the most abundant of the four common gadid species. These other species include *Gadus macrocephalus* (Pacific cod), *Boreogadus saida* (Arctic cod), and *Eleginus gracilis* (saffron cod).

Genetic Structure

Although pollock are distributed (and perhaps spawn essentially continuously) along the northern rim of the Pacific Ocean and Bering Sea, genetic differentiation might reasonably be expected due to the isolating effects of both geographical distance and barriers (Kimura and Ohta 1971). This is because individual

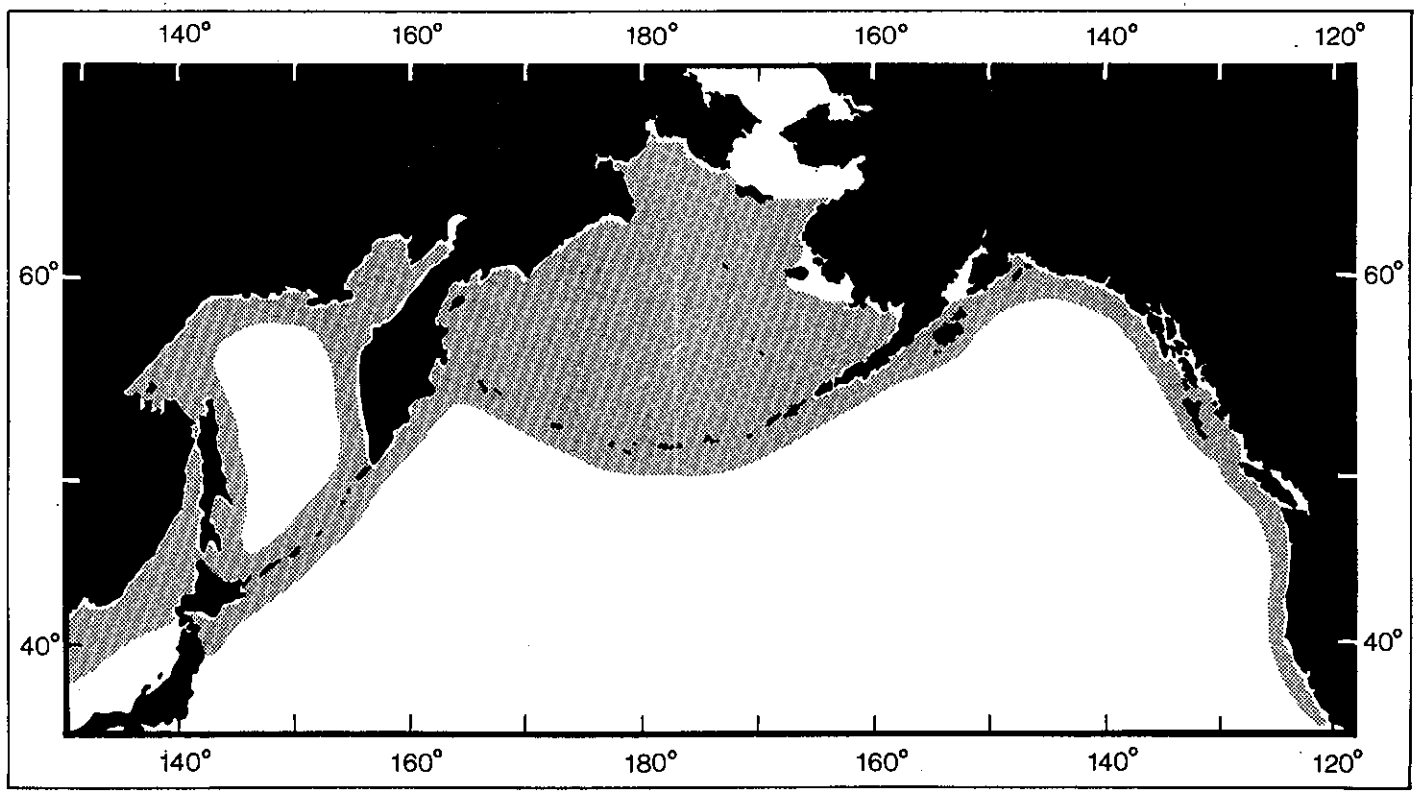

FIG. 1 The worldwide distribution of walleye pollock, *Theragra chalcogramma* (shaded area).

migrations will nearly always be considerably less than the total distributional range of the species, and instead, effectively form regional breeding populations. Similarly, diffusive exchange of eggs and larvae due to advective transport may be expected to be higher within regional current systems than between, although progressive transport of successive generations may be significant.

Consistent with these hypotheses, recent studies of biochemical genetic variation have found relatively large genetic differences between pollock sampled from extremes of the species range, but relatively small genetic differentiation within regions (Iwata 1973, 1975, 1977; Johnson 1977). Based upon differences in allelic frequencies for the protein locus tetrazolium oxidase, Grant et al. (1978) concluded that the widely separated populations of the western and eastern Pacific are relatively genetically isolated and distinct. Only weak regional differentiation was observed, however, among pollock collected from north and south areas of the eastern Bering Sea and from the Gulf of Alaska.

Other investigators have proposed a more complex population structure in the Bering Sea. From analyses of morphometric characters, Serobaba (1977) recognized four principal Bering Sea pollock populations: southeastern, northern, western, and Aleutian Island. Maeda (1972) proposed two distinct eastern populations based upon apparent migrations to separate spawning areas northwest and southeast of the Pribilof Islands. After comparisons of the age structure of commercial catches in northwest and southeast regions from 1963 to 1970, however, Chang (1974) concluded that the

pollock population exploited by fisheries in the eastern Bering Sea is a unit stock.

Description of Habitat

In the eastern Bering Sea, pollock occur widely distributed over the continental shelf, but show highest densities along the shelf edge (Figs. 2 and 3). The overall distribution pattern varies seasonally and between years, dominated by movements between deep and shallow water. Over the continental shelf pollock show a "semidemersal" behavior, tending to form schools near the bottom during daytime, then dispersing up into the water column at night. Along the outer continental shelf and slope, dense shoals are formed that may exceed 20-50 km in length and have mean densities of up to 9 mt per hectare.

Figures 4 and 5 show two examples of the apparent depth distribution of pollock on the eastern Bering Sea continental shelf, determined from research vessel surveys. During August-October 1975, pollock were relatively symmetrically distributed around a median depth of approximately 200 m. During April-June 1976, the vertical pattern was less symmetrical but similar, although apparent densities were lower among all depth intervals except 400-450 m.

The domain within which pollock occur demersally in the eastern Bering Sea, then, is a broad section of the outer continental shelf and slope primarily within the 100-300 m depth range. The bottom morphology of the continental shelf in most of this region is featureless and level, with sand and silt surface sediments

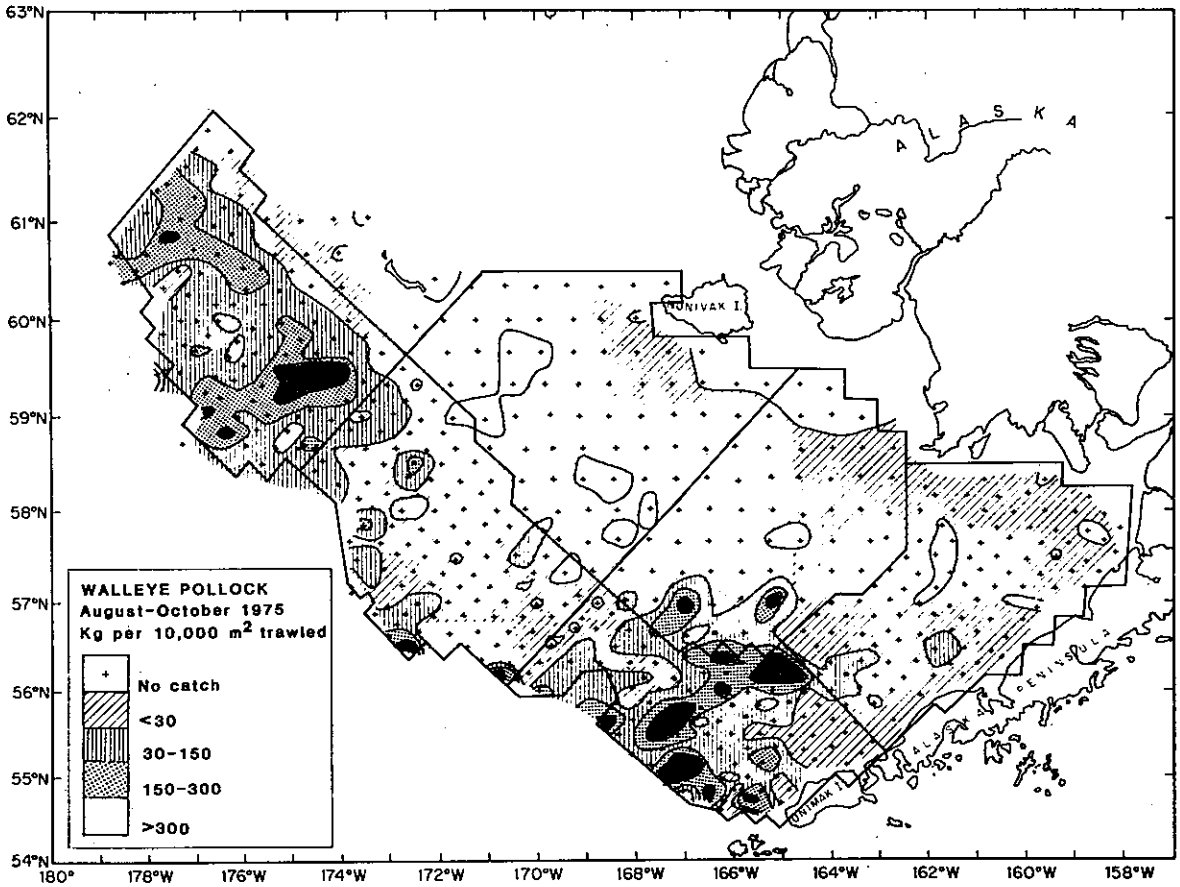

FIG. 2 The apparent density distribution of walleye pollock during August-October 1975, determined by a research vessel survey (Pereyra et al. 1976).

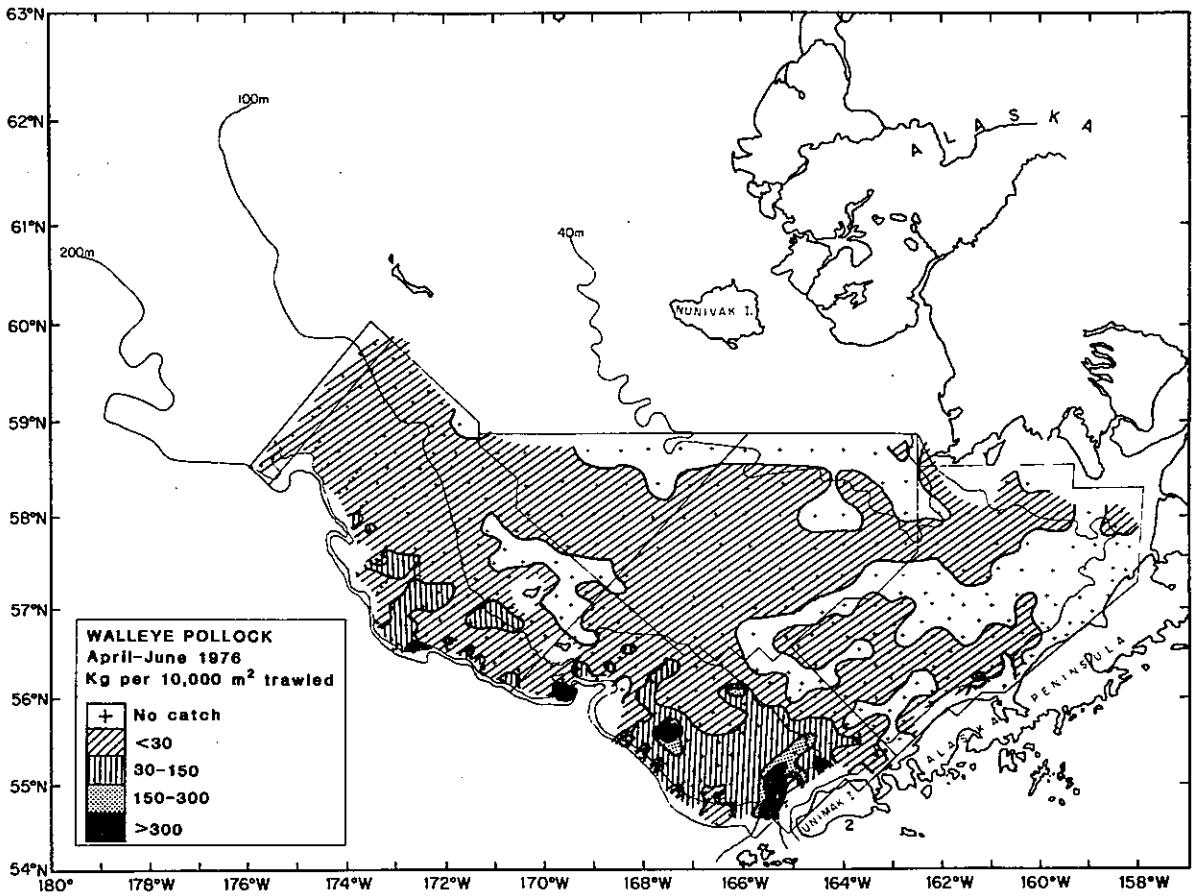

FIG. 3 The apparent density distribution of walleye pollock during April-June 1976, determined by a research vessel survey (Bakkala and Smith 1978).

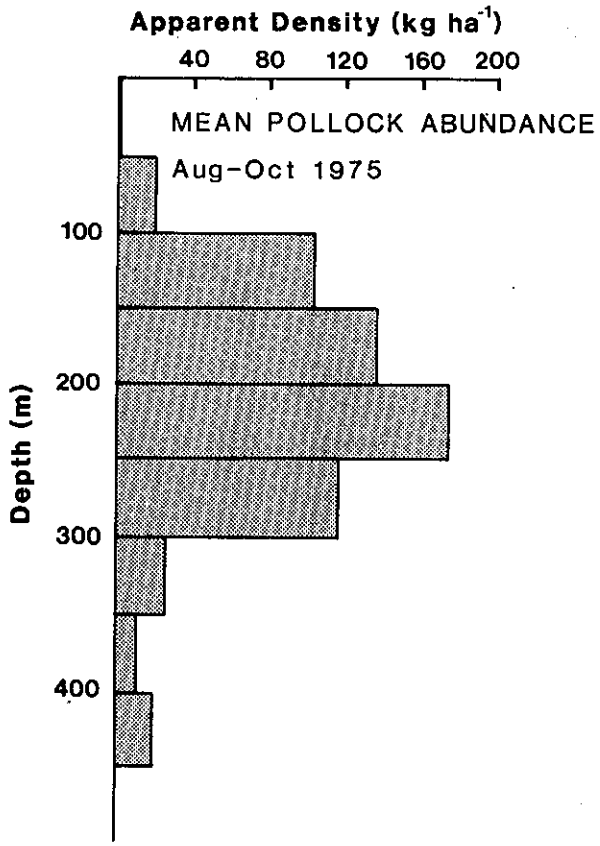

FIG. 4 Apparent vertical distribution of pollock densities on the continental shelf during August-October 1975 (based upon the data shown in Fig. 2).

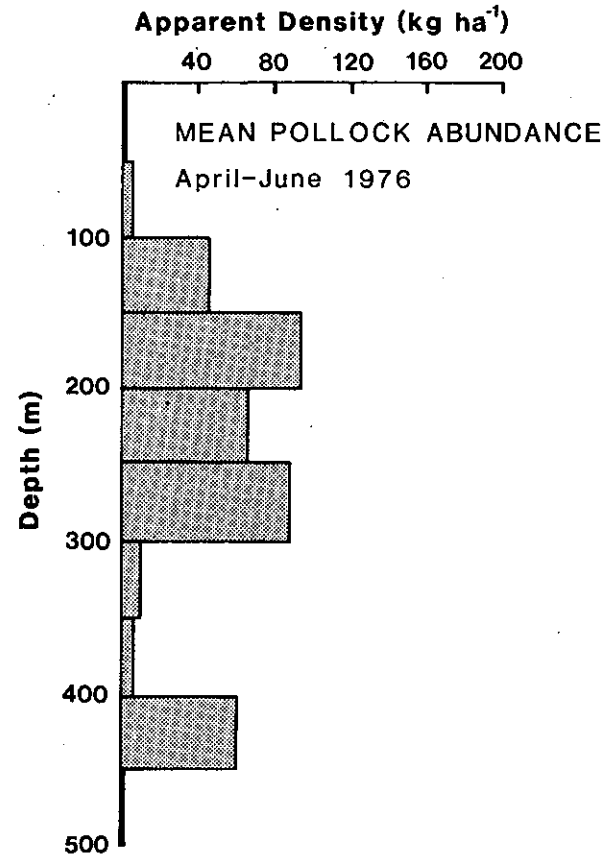

FIG. 5 Apparent vertical distribution of pollock densities on the continental shelf during April-June 1976 (based upon the data shown in Fig. 3).

(Sharma 1974). In deeper water, the continental margin is steep and cut by large submarine canyons that substantially affect the flow and mixing of water currents along the shelf edge (Kinder et al. 1975).

In comparison to temperature and salinity characteristics of water masses in other regions of the North Pacific Ocean, pollock occur within a relatively extreme seawater environment in the eastern Bering Sea (Fig. 6). These distinctive conditions--cold and low salinity--result from mixing of shelf and oceanic waters within apparently broad zones of interaction along, and over, the eastern continental shelf (Takenouti and Ohtani 1974; Coachman and Charnell 1979). Source waters, mixing characteristics, and associated hydrographic features must all be important in determining the composition of both pollock prey and predators.

Stock Size

Seven well-documented estimates of the absolute bulk biomass of eastern Bering Sea pollock are summarized in Table I. A confusing feature of these results is the use of different, and sometimes unspecified, geographical boundaries among the different analyses. In addition, because all of the estimates are based upon selective sampling (namely, demersal trawl nets, and in the case of estimates based upon commercial data, targeted fisheries), the relationships between statistical populations included in the analyses and true field populations are unclear. Management policies for eastern Bering Sea trawl fisheries assume a present pollock stock size of approximately 5 million mt (NPFMC 1978).

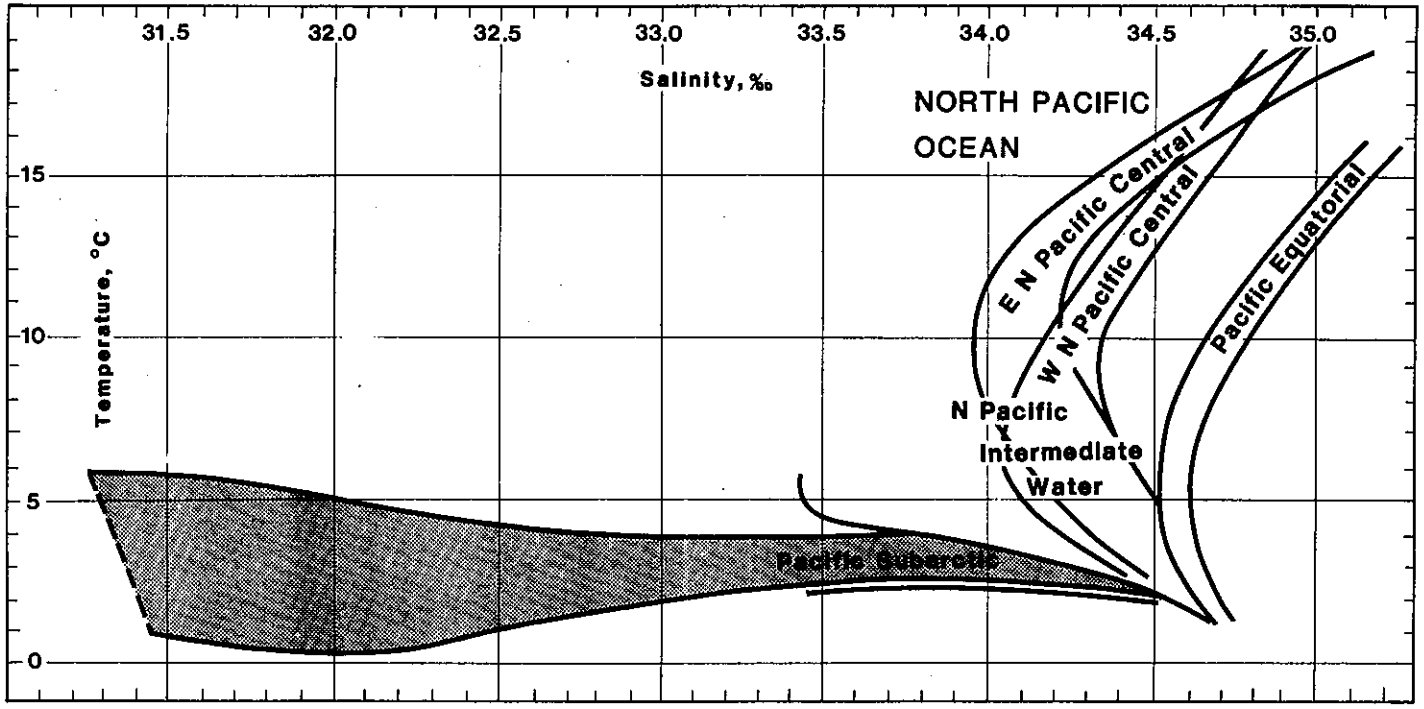

FIG. 6 Temperature and salinity characteristics of the environment of walleye pollock in the eastern Bering Sea (shaded area). Pollock T-S data re-plotted from Kihara and Uda (1969); North Pacific Ocean water mass data are from Sverdrup et al. (1946).

TABLE I

Summary of Estimates of Absolute Population Size for Eastern Bering Sea Walleye Pollock.

Source	Region and time period 1/	Method 2/	Estimated population (x 10^6 mt)
A. Based upon research survey data			
Pereyra et al. 1976	Eastern Bering Sea shelf, Unimak Pass to 61° N (August-October 1975)	1	2.426
Bakkala and Smith 1978	Eastern Bering Sea shelf, Unimak Pass to 59° N (April-June 1976)	1	0.679
Okada 1978; Nunnallee 1978	Aleutian Basin (June-July 1978)	1	0.840
B. Based upon commercial fisheries data			
Chang 1974	Eastern Bering Sea shelf, INPFC areas 1 and 2 (1969-1970)	1	2.3 - 2.6
Chang 1974	Eastern Bering Sea shelf, INPFC areas 1 and 2 (1970)	2	2.3 - 2.4
Low 1974	Eastern Bering Sea, primarily INPFC areas 1 and 2 (1964-1971)	1	3.45 - 5.83
C. Based upon model estimates			
Laevastu and Favorite 1977	Eastern Bering Sea shelf	3	8.235

1/ A description of INPFC (International North Pacific Fisheries Commission) statistical areas is given in Forrester et al. (1978).

2/ Estimation methods: 1 = "area swept" (Baranov 1918; Alverson and Pereyra 1969); 2 = "cohort analysis" (Pope 1972); 3 = "model fitting," based upon commercial fisheries data.

Table II and Figure 7 show the observed variability and trends for five indices of the relative annual abundance (biomass) of pollock in the eastern Bering Sea. During the sixteen years of observations 1963 to 1978, apparent pollock densities have varied approximately ±50% of the long-term mean values. Rather than showing large random year-to-year differences, most variations in index values seem to have represented longer-term trends. Judging by the longest time series (Bakkala et al 1979b), pollock are relatively less abundant now in the eastern Bering Sea region than during the period 1965 to 1970.

The research survey data shown (see Table II) as, "NMFS Crab-Groundfish," are results determined from demersal trawl surveys conducted by the U.S. National Marine Fisheries Service (NMFS). A central 159,100 km^2 "core" area (Fig. 8) has been surveyed using uniform methods during approximately June 1 to August 15 of each year (Pereyra et al. 1976: Section VIII).

Size and Age Composition

Rather than being a homogeneous pool, the eastern Bering Sea pollock population exhibits a size and age structure that reflects pulsed annual birth inputs, birth and survival rates, and a differentiation of distributional patterns based upon age. Pollock are generally considered to spawn during only one period each year. In the eastern Bering Sea, the spawning period has been reported to extend from the end of February through June, with peak activity in May (Serobaba 1968). This concentration of spawning within a four month period, loosely synchronized with the timing of spring plank-

TABLE II

Summary of Indices of the Relative Abundance of Walleye Pollock in the Eastern Bering Sea, 1963 to 1978.[1/]

Source	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	Mean	s.d.	c.v.
A. Research survey data																			
NMFS Crab-Groundfish surveys (Pereyra et al. 1976: section VIII updated to 1978), units = mean kg ha^{-1} trawled (nominal).	--	--	--	--	--	--	--	--	--	--	29.2	27.5	21.1	46.7	37.7	47.1	34.9	10.7	0.31
B. Commercial fisheries data																			
Japanese fisheries statistics (Chang 1974), units = mt hr^{-1} combined gear.	3.09	2.72	4.80	4.40	7.09	7.67	7.79	13.1	--	--	--	--	--	--	--	--	6.33	3.38	0.53
Japanese fisheries statistics (Bakkala et al. 1979b), units = mt hr^{-1} pair trawl.	--	9.5	18.3	23.6	21.3	23.8	31.5	18.7	14.2	14.2	8.6	10.4	9.3	9.4	8.6	9.4	15.4	7.15	0.46
Japanese fisheries statistics (Low 1974), units = 10^6 mt.	--	3.77	4.02	3.46	5.83	3.81	4.92	5.41	4.92	--	--	--	--	--	--	--	4.52	0.87	0.19
Japanese fisheries statistics (Ikeda et al. 1977; Okada et al. 1979), units = % of 1976 pair trawl catch per unit of effort.	--	--	--	--	--	--	--	--	--	--	121	102	91	100	86	93	98.8	12.4	0.12

1/ "Mean" = arithmetic mean; "s.d." = standard deviation of mean; "c.v." = coefficient of variation (= ratio of standard deviation to mean).

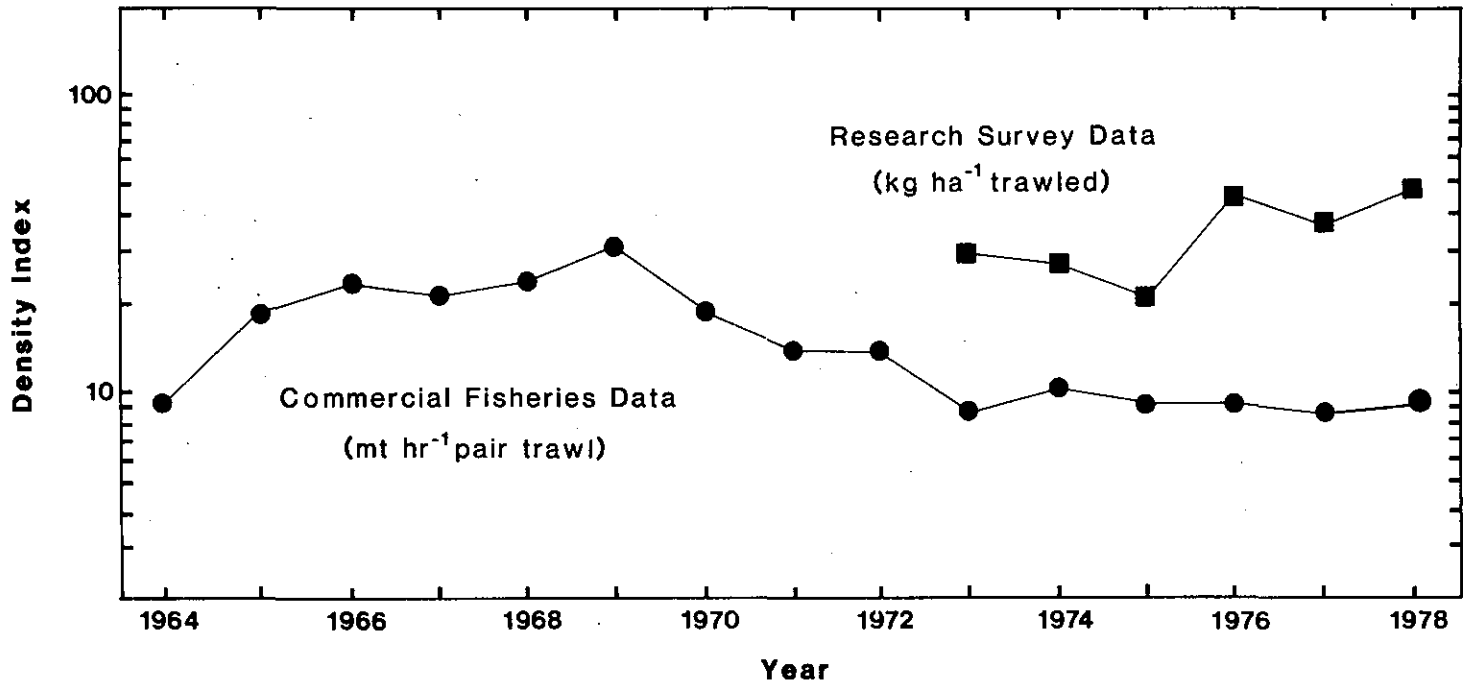

FIG. 7 Annual variations in apparent relative abundance, based upon the indices of Pereyra et al. (1976), updated to 1978, and Bakkala et al. (1979b) summarized in Table II.

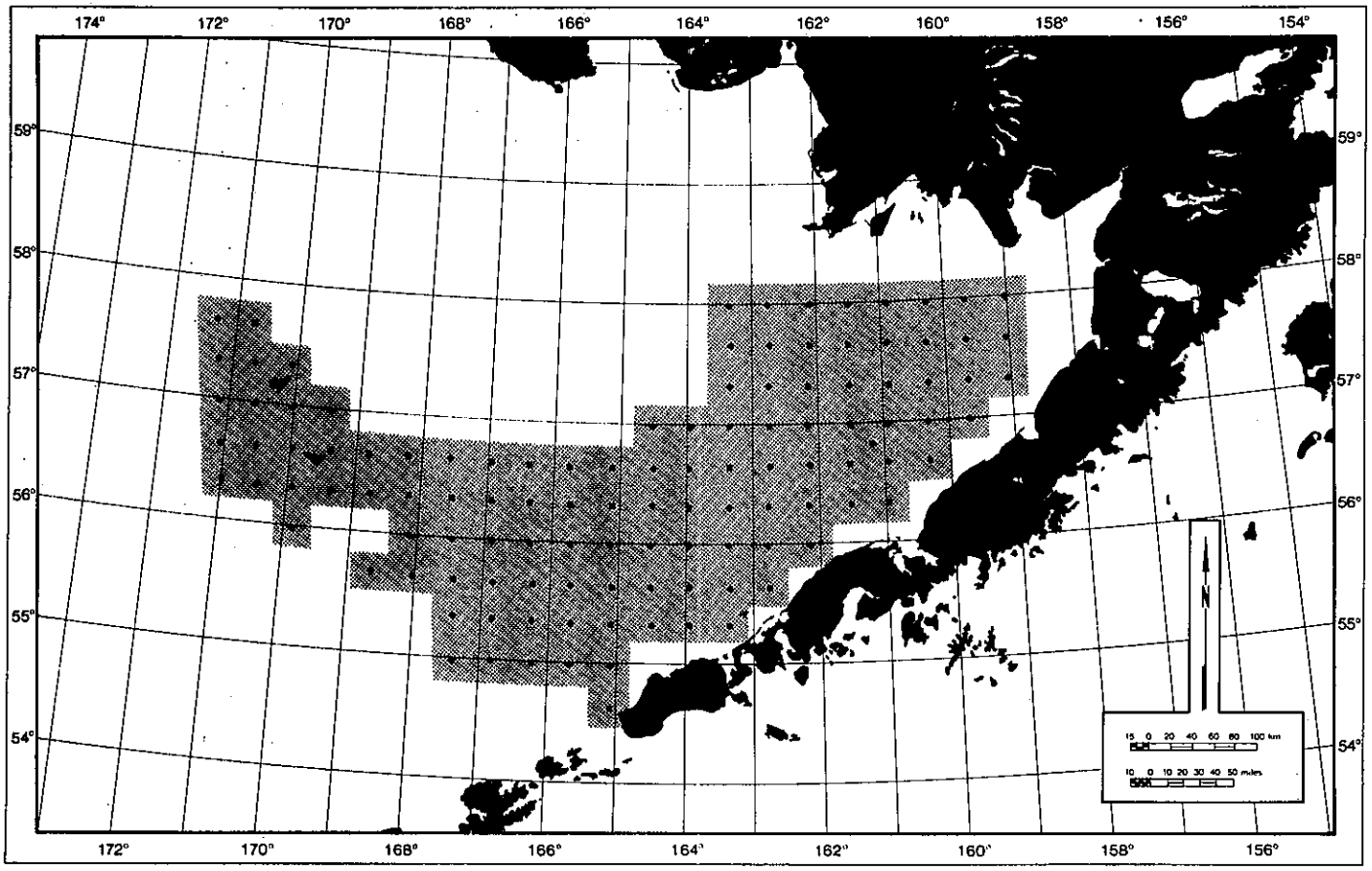

FIG. 8 NMFS index area (shaded) for annual eastern Bering Sea crab and demersal fish population assessment surveys. Dots indicate routine sampling locations.

ton production, provides for a large annual pulse of eggs and larvae.

Table III and Figure 9 summarize the apparent age frequency distributions observed for pollock within the central region of the eastern Bering Sea (shown in Fig. 8), determined from NMFS demersal trawl surveys during the period 1973 to 1978. The data represent an overall range in body size (fork length) of approximately 6 to 90 cm. Ages were determined from readings of saccular otoliths.

Features of the observed age structure include: (1) a maximum age of 15 years; (2) a relatively high overall average mortality rate; (3) variable age class abundance between years; and (4) large, dominant year classes were apparently not maintained over successive years. Figure 10 shows the overall pattern of survivorship, based upon the mean apparent abundance of each age group (i.e., column means) during the six years of observations. Assuming that rates of in-migration to, and out-migration from, the index area were equal, and that:

$$N_2 = N_1 e^{-Zt} \qquad (1)$$

where

N_1 = the number of individuals at any moment,

N_2 = the number of individuals at some later time,

Z = an instantaneous rate of total mortality,

t = the intervening time interval, and

e = the natural constant 2.71828...,

then the overall observed instantaneous mortality rate ($\underline{Z}$) was 0.72

TABLE III

Indices of Relative Age Class Abundance Measured by NMFS Crab-Groundfish Research Vessel Surveys within a Central Area of the Eastern Bering Sea during June to Mid-August, 1973-1978 (units = 10^6 individuals per 159,100 sq km). 1/

Survey year	Number of trawls	Number of otoliths	Age classes (yr) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1973	111	490	756.9	518.2	146.0	193.4	99.4	34.4	91.5	117.8	18.9	17.9	4.51	--	0.401	0.072	--
1974	111	954	2840.6	850.3	287.9	56.1	67.7	38.0	39.1	29.0	29.5	5.12	3.00	0.176	0.190	--	--
1975	111	766	758.4	402.4	614.2	108.0	24.6	27.5	14.7	14.2	7.98	5.99	0.52	0.594	0.009	--	--
1976	107	1990	729.0	500.4	479.7	1014.1	132.5	35.0	38.8	46.2	41.0	22.3	8.28	1.850	0.607	0.032	0.171
1977	112	944	2241.9	630.2	145.8	245.3	231.9	72.0	29.8	23.7	23.6	13.1	11.9	3.200	0.491	0.180	--
1978	116	1256	1170.9	400.4	806.9	507.0	139.5	92.3	29.1	24.2	29.1	19.0	6.26	5.100	--	--	--
Overall mean (1973-78)			1416.3	550.3	413.4	354.0	115.9	49.9	40.5	42.5	25.0	13.9	5.75	1.82	0.280	0.050	0.030
Standard deviation (1973-78)			906.7	169.9	267.7	359.4	71.0	26.0	26.5	38.4	11.2	7.11	4.02	2.01	0.260	0.070	0.070
Coefficient of variation (1973-78)			0.64	0.31	0.65	1.02	0.61	0.52	0.65	0.90	0.45	0.51	0.70	1.10	0.93	1.40	2.33

1/ Based upon estimates of nominal sampling effort, uncorrected for differences in effective fishing power. Underlined values were apparently affected by in- or out-migrations.

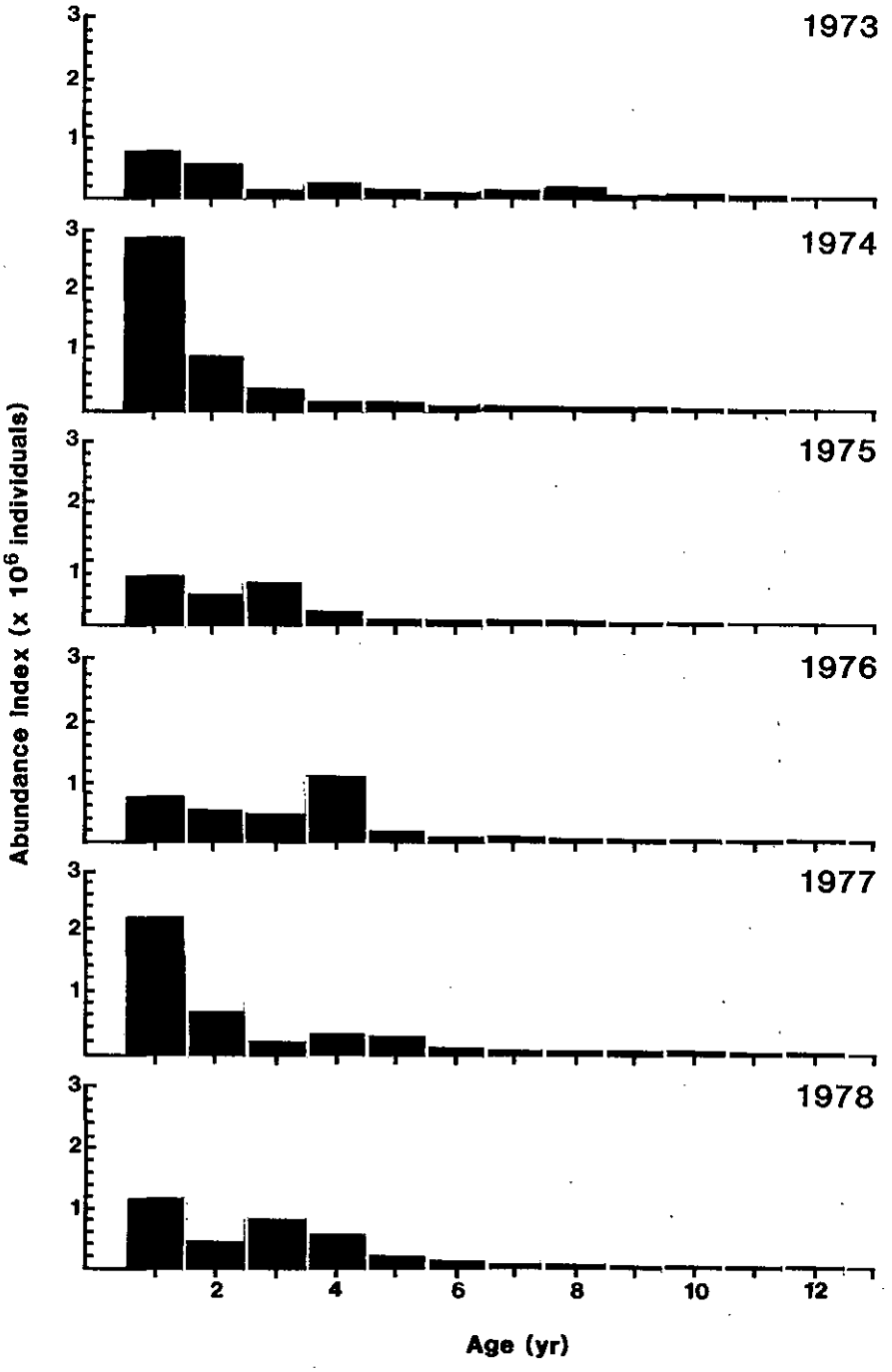

FIG. 9 Annual variations in apparent age frequency distributions, based upon the data in Table III.

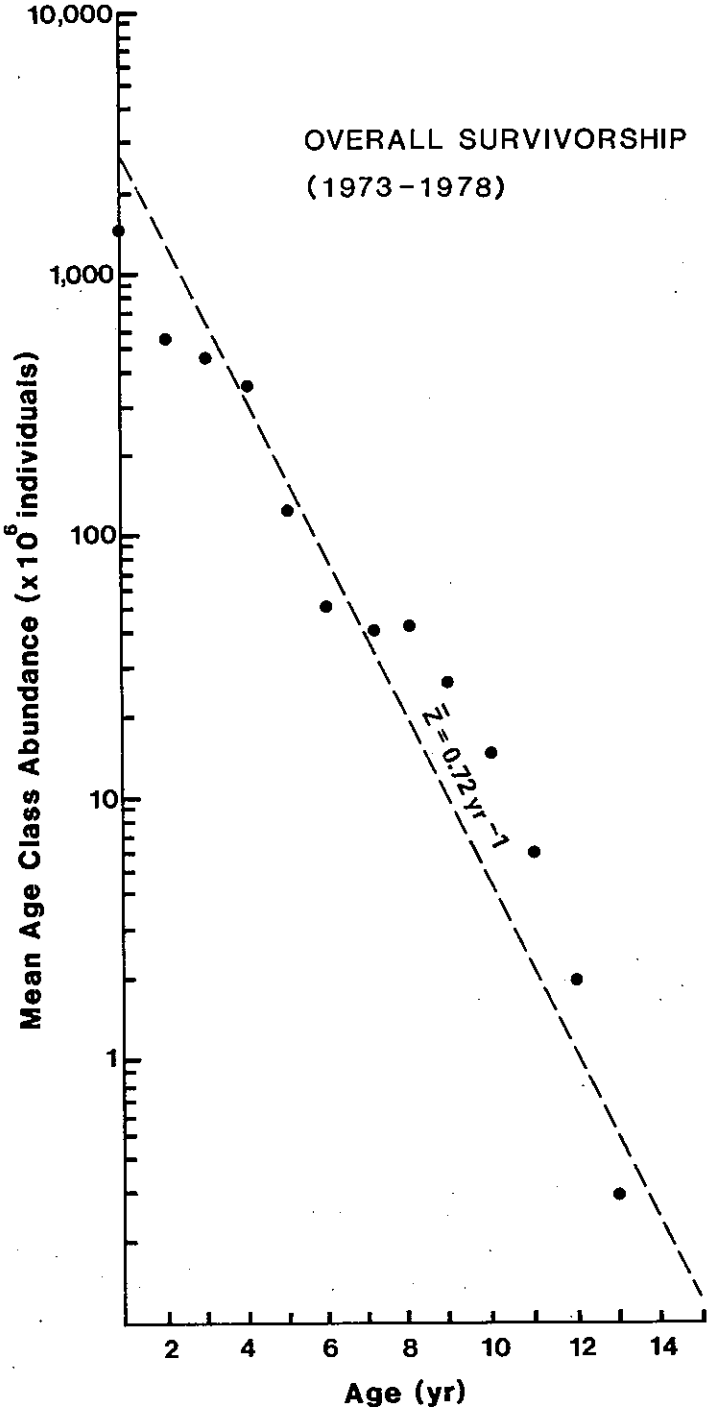

FIG. 10 Overall survivorship curve, based upon the data in Table III.

yr^{-1}. This rate corresponds to 51% of the pollock population dying each year. Rather than being constant, mortality was relatively higher for ages 1, 4, 5 and 10 or more years (Fig. 11). Factors that may have contributed to apparently higher mortality at ages 4 and 5 yr include the possibilities of increased selective removal by fisheries, increased migratory activities associated with ontogeny, and effects of reproductive stress. Senescence was presumably a major cause of higher mortality at ages 10 and older. Life table characteristics are summarized in Table IV.

Contrary to the assumption of a closed population, or that in- and out-migrations were in equilibrium, the indices of abundance observed in 1975 for all age classes except the age-1 population were inconsistently low (relative to cohort abundances observed in 1976), apparently indicating a distributional shift out of the index area during that survey period.

Another interesting result was the indication of density-dependent mechanisms possibly regulating age class size (Fig. 12). Although the relative year-to-year variation in abundance of one-year old populations was slightly less than the overall average of age classes 1 to 12 yr, the apparent sizes of 2-year old populations were relatively constant. The lack of evidence for persistence of strong year classes--such as the 1973 and 1976 year classes that were unusually abundant at age 1--was also unexpected, particularly since cohort dominance seems to be a feature of the dynamics of at least some simple animal populations with a large cannibalistic adult fraction (Fox 1975).

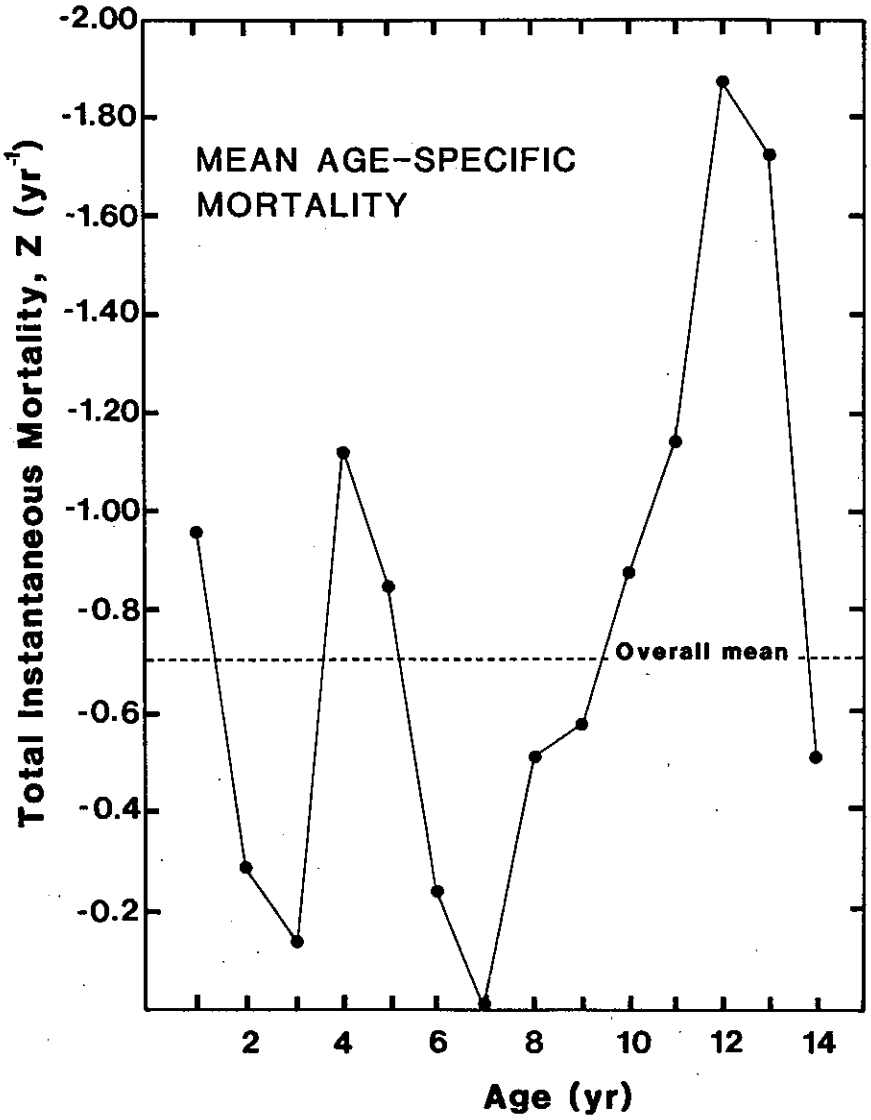

FIG. 11 Age-specific instantaneous mortality rates, based upon the data in Table III.

TABLE IV

Life Table Characteristics for Walleye Pollock, Based upon NMFS Crab-Groundfish Research Vessel Surveys, 1973-1978.

Age 1/ (yrs) x	Mean apparent 2/ abundance (x 10^6) n_x	Survival 3/ l_x	Mortality 4/ (yr^{-1}) m_x
0.2 - 1.2	(5100.)	1.0000	--
1.2 - 2.2	1416.3	0.2777	-0.95
2.2 - 3.2	550.3	0.1079	-0.29
3.2 - 4.2	413.4	0.0811	-0.15
4.2 - 5.2	354.0	0.0694	-1.12
5.2 - 6.2	115.9	0.0227	-0.84
6.2 - 7.2	49.9	0.0098	-0.21
7.2 - 8.2	40.5	0.0079	(+0.05)
8.2 - 9.2	42.5	0.0083	-0.53
9.2 - 10.2	25.0	0.0049	-0.59
10.2 - 11.2	13.9	0.0027	-0.88
11.2 - 12.2	5.75	0.0011	-1.15
12.2 - 13.2	1.82	0.0004	-1.87
13.2 - 14.2	0.28	0.00005	-1.73
14.2 - 15.2	0.05	0.00001	-0.51
15.2 - 16.2	0.03	0.000006	--

1/ Assuming a median birthday of April 1.

2/ Number of individuals reaching age x at time t. The value for age 0.2 yr was extrapolated from the n_x values of ages 1.2 to 15.2 yr, assuming constant mortality.

3/ Probability that an individual survives to age x.

4/ Age-specific instantaneous mortality rate, computed as $m_x = \ln(n_{x+1}) - \ln(n_x)$. The value in parentheses at age 7.2 yr may indicate sampling error or effects of migration.

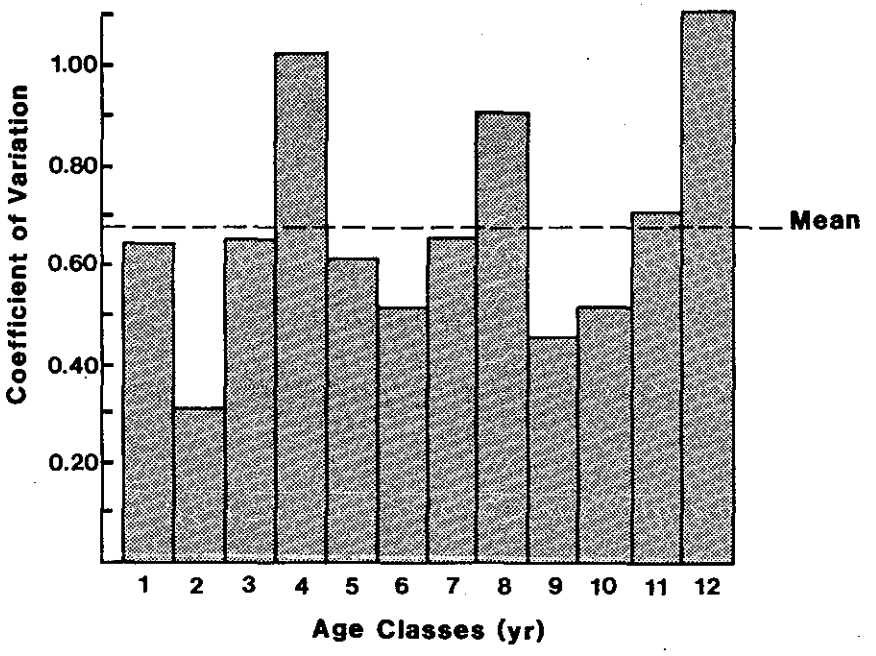

FIG. 12 Comparisons of relative year-to-year variability in age class size, based upon the data in Table III. The coefficient of variation is used as the ratio of standard deviation to mean.

The NMFS Crab-Groundfish and other research vessel surveys of the eastern Bering Sea continental shelf have also found a geographical differentiation of age structure (Pereyra et al. 1976: Figure IX-34; Bakkala and Smith 1978: Fig. 38). During summer, low-density populations in central and inner areas of the continental shelf--particularly northeast of the Pribilof Islands--have tended to be almost exclusively composed of one-year old individuals. Along the outer continental shelf and slope, populations have been composed of a complex mix of age classes 2 to 10 or more years.

Growth

Although gross characteristics of the growth of eastern Bering Sea pollock have been described (Yamaguchi and Takahashi 1972; Chang 1974; Pereyra et al. 1976; Bakkala and Smith 1978), no studies have yet attempted to analyze or mathematically model details of the growth curve(s) or the energetics of growth processes. The approach taken here will be to analyze original data to examine fundamental characteristics of growth in length, growth in weight, and growth and decay of cohort weight.

Table V summarizes the mean lengths of individuals in each age class represented in Table III, determined from annual NMFS demersal trawl surveys of the index area (shown in Fig. 8). To examine growth in length, a generalized form of the von Bertalanffy (1938) growth model was fitted to the overall mean lengths (see Table V - column means) of ages 1 to 13 years. The form of the generalized growth model used was:

TABLE V

Summary of Mean Lengths-at-Age Determined from NMFS Crab-Groundfish Research Vessel Surveys Conducted during June to Mid-August, 1973-1978 (units = cm fork length)

Survey year	Age classes (yr) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1973	15.7	25.7	32.9	39.2	42.0	43.4	46.0	47.3	49.5	52.4	56.1	--	63.5	66.0	--
1974	15.5	25.2	34.9	38.5	44.3	44.3	47.7	49.6	51.0	53.4	51.7	57.6	57.8	--	--
1975	14.3	24.3	32.5	39.6	44.3	47.1	50.5	53.4	55.3	56.2	55.6	63.4	64.0	--	--
1976	11.6	23.9	30.6	37.1	41.5	44.2	46.4	48.2	48.6	51.0	55.1	57.8	58.5	66.1	72.0
1977	15.9	23.9	33.7	41.7	44.8	47.5	50.0	51.7	52.0	53.3	54.4	54.5	52.0	60.0	--
1978	13.7	25.2	33.7	37.7	44.0	46.7	51.6	53.3	53.1	53.0	55.6	53.0	--	--	--

$$Y_x = y_{\infty}[1 - e^{-K(x - x_o)}]^d \qquad (2)$$

where

Y_x = the length or weight at age $\underline{x}$,

y_{∞} = an asymptotic value of length or weight,

K = a relative growth completion rate,

x_o = a hypothetical age of zero size, and

d = a dimensionless exponent reflecting absolute growth rate.

The model was fitted to the data by a computer program using a Taylor-series method for least squares approximation (Draper and Smith 1966). The results are shown in Figure 13, and the parameter values of best fit describing growth in length (sexes combined) were:

y_{∞} = 64.81 cm

K = 0.132 yr^{-1}

x_o = 0.78 yr

d = 0.520 .

In summary, the pattern of growth in length observed was fast growth between ages 1 to 15 yr, relatively rapid decrease in annual length increments with increasing age, and an asymptotic body length of approximatey 65 cm.

To examine characteristics of growth in weight, the mean weights-at-age were approximated by applying a power relationship to the length data in Table V. The relationship used was (Pereyra et al. 1976):

$$W = 0.0075\ L^{2.977} \qquad (3)$$

where

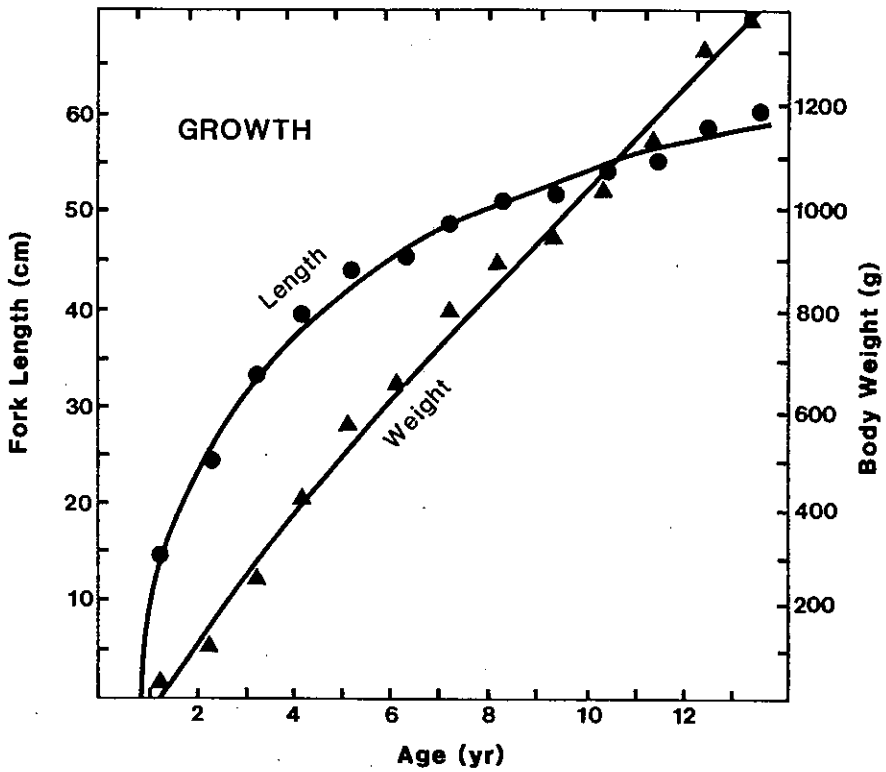

FIG. 13 Growth in length and weight, based upon the data in Table V. Symbols indicate the overall mean at each age.

W = estimated body weight in grams, and

L = body (fork) length in cm.

After converting the mean length of each age class to a computed "mean weight," for all years, the overall mean weights (i.e., column means) were determined, and the generalized growth model (Equation 2) was fitted to the results (see Fig. 13). The parameter values of best fit describing growth in estimated weight were:

$y_\infty = 7057$ g

$K = 0.016\ yr^{-1}$

$x_0 = 1.18$ yr

$d = 0.944$.

In contrast to growth in length, growth in body weight was nearly linear within the age range 1 to 13 yrs, with almost constant increments in weight of 114 g yr^{-1}.

Table VI summarizes the overall mean body sizes at each age and, combining the observed survivorship from Table IV with mean weights-at-age, illustrates the apparent growth and decay of cohort weights. According to this model, a pollock cohort attains maximum biomass at approximately 4 yr of age.

Reproduction

Because seasonal spawning aggregations and roe production have been of particular interest to commercial fisheries, major features of the reproductive biology of pollock have been fairly well described (Gorbunova 1954; Zver'kova 1969; Serobaba 1968, 1971, 1974; Maeda and Hirakawa 1977). The attainment of sexual maturity is

TABLE VI

Characteristics of the Growth of Walleye Pollock, Based upon NMFS Crab-Groundfish Research Vessel Surveys, 1973-1978.

Age 1/ (yrs) x	Mean body 2/ length (cm) y_x	Mean body 3/ weight (g) w_x	Relative age class 4/ weight (g) $l_x w_x$
0.2 - 1.2	--	--	--
1.2 - 2.2	14.4	21.9	6.08
2.2 - 3.2	24.7	105.2	11.35
3.2 - 4.2	33.0	251.0	20.36
4.2 - 5.2	39.0	409.6	28.43
5.2 - 6.2	43.5	565.0	12.83
6.2 - 7.2	45.5	650.9	6.38
7.2 - 8.2	48.7	796.6	6.29
8.2 - 9.2	50.6	892.6	7.41
9.2 - 10.2	51.6	945.4	4.63
10.2 - 11.2	53.2	1034.	2.79
11.2 - 12.2	54.8	1125.	1.24
12.2 - 13.2	57.3	1298.	0.52
13.2 - 14.2	59.2	1436.	0.07
14.2 - 15.2	(64.0)	(1800.)	(0.02)
15.2 - 16.2	(72.0)	(2537.)	(0.02)

1/ Assuming a median birthday of April 1.

2/ Overall observed mean fork lengths. The lengths in parentheses were based upon limited observations.

3/ Overall mean predicted body weights (wet tissue).

4/ Computed as the product of "survival" times "mean body weight."

related to body size. On the basis of a classification of macroscopic gonad conditions observed during a large demersal trawl survey of the eastern Bering Sea during April to June 1976, Bakkala and Smith (1978) found that the relationship between "fork length" and "proportion of individuals sexually mature" was best described by a sigmoidal curve of the model:

$$P = e^{-be^{-cL}} \qquad (4)$$

where P is the proportion of the apparent population mature at size L cm, e is the natural constant 2.71828..., and b and c are constants. The fitted model for male pollock was found to be (Fig. 14):

$$P = e^{-725.947e^{-.224L}} , \qquad (5)$$

and the length at which 50% of the individuals were mature was 31.0 cm. Female pollock matured at longer lengths than males, and the fitted model was:

$$P = e^{-867.088e^{-.209L}} \qquad (6)$$

with the length at 50% maturity equal to 34.2 cm.

In the eastern Bering Sea, the sexually mature fraction of the pollock population undergoes a seasonal cycle of gonad development and reproductive activity (Yamaguchi and Takahashi 1972). Despite a relatively extended spawning period of February through June, the majority of the breeding population appears to ripen and spawn during April to mid-May. Within this spawning period, it is not yet clear whether a mature female releases eggs in one short pulse, or as multiple releases over a period of days or weeks.

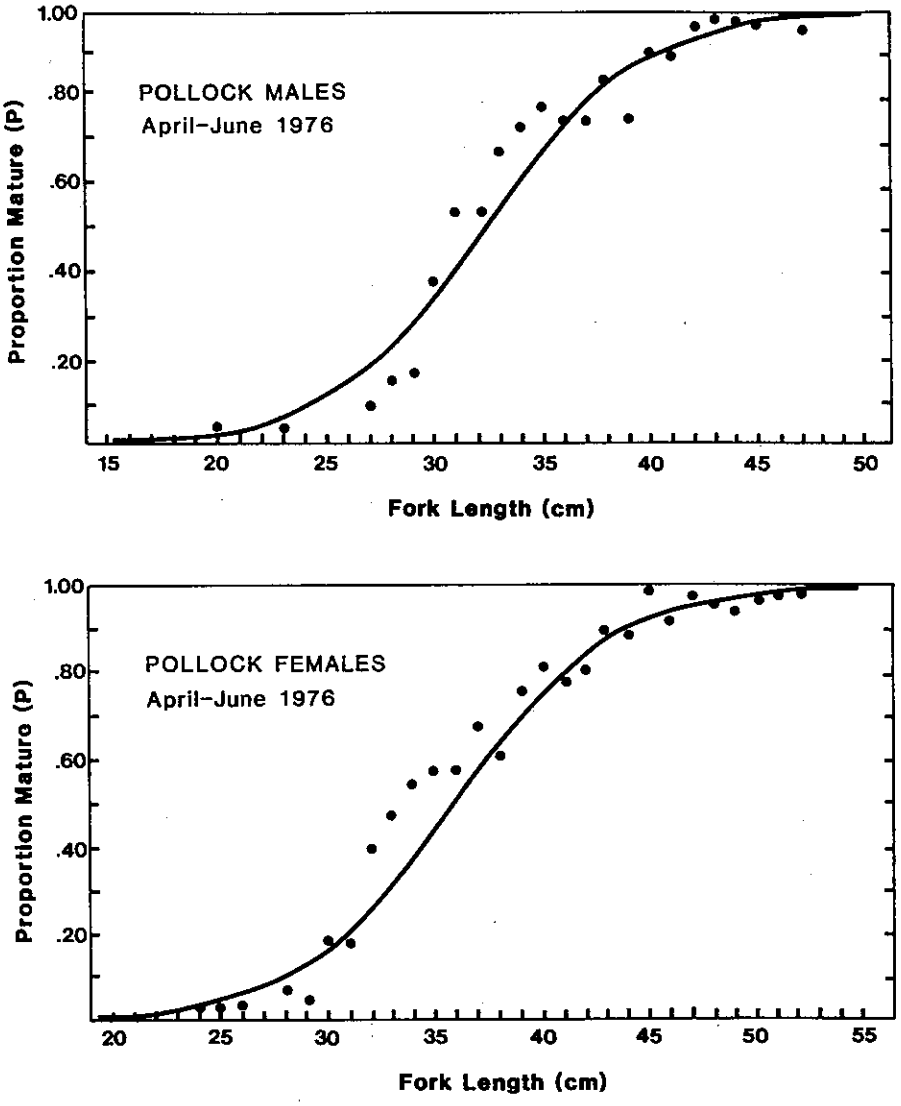

FIG. 14 Length-maturity relationships observed from pollock taken during the April-June 1976 demersal trawl survey (Bakkala and Smith 1978).

As for many other fish species, attempts to measure individual female fecundity (i.e., number of viable eggs released per year) have largely been premature to an adequate understanding of the biological processes of oocyte development, oocyte release, and the extent of resorption (Foucher and Beamish 1977). This has resulted in uncertainty over which sizes of oocytes to include in estimates of annual zygote production, uncertainty of spawning model (namely, single- or multiple-spawning), and failure to assess the number of oocytes remaining in the ovary after spawning (Shew 1978).

The ovaries of female pollock contain oocyte populations often composed of two or three distinct size classes (Gorbunova 1954; Serobaba 1974; Shew 1978). Although details of the production and fates of these different size groups remain to be studied, it seems likely that the small classes (oocyte diameters ca. 60-550 m) may represent a "reserve fund" (Foucher and Beamish 1977) from which only a fraction develop each season to be spawned. Assuming that only oocytes in the largest size class (ca. 600-1500 m diameter) are actually released during spawning and viable, the relationship Shew (1978) found between body size and potential fecundity was:

$$F = 0.29\ L^{3.462} \qquad (7)$$

where

F = estimated number of oocytes in the 600-1500 m diameter size class, and

L = body (fork) length in cm.

By applying Equations 6 and 7 to the surviorship and growth data in Tables IV and VI, estimates could be made of individual and age class fecundity (Table VII). Interesting features of

TABLE VII

Reproductive Characteristics of Walleye Pollock, Based upon NMFS Crab-Groundfish Research Vessel Surveys, 1973-1978.

Age 1/ (yrs) x	Pivotal 2/ length (cm) y_s	Proportion of 3/ females mature P_s	Individual 4/ fecundity (x 10^3) b_s	Potential age 5/ class fecundity $l_s P_s b_s$
0.2 - 1.2	--	--	--	--
1.2 - 2.2	13.7	0.	0.	0.
2.2 - 3.2	23.5	0.008	16.2	0.02
3.2 - 4.2	31.4	0.289	44.1	1.09
4.2 - 5.2	37.0	0.641	77.9	3.59
5.2 - 6.2	41.3	0.842	114.	2.72
6.2 - 7.2	43.2	0.901	133.	1.39
7.2 - 8.2	46.3	0.947	169.	1.33
8.2 - 9.2	48.1	0.963	193.	1.54
9.2 - 10.2	49.0	0.970	206.	1.10
10.2 - 11.2	50.5	0.978	229.	0.69
11.2 - 12.2	52.1	0.984	255.	0.35
12.2 - 13.2	54.4	0.990	296.	1.17
13.2 - 14.2	56.2	0.993	331.	0.03
14.2 - 15.2	60.8	0.997	435.	0.004
15.2 - 16.2	68.4	0.999	654.	0.004

1/ Assuming a median birthday of April 1.

2/ The size at time of spawning ("April 1") was computed as 95% the y_x value.

3/ Values for ages 1 to 4 from Bakkala and Smith (1978), Table 26.

4/ Number of oocytes ($\geq$ 600 µm diameter) produced per year, using the relationship from Shew (1978).

5/ Potential age class fecundity = product of survival (at time of spawning), proportion mature, and individual fecundity; l_s values were computed using the age-specific mortality rates, assuming equal survival of males and females. Units = 10^3 oocytes.

the results are that age classes 4 and 5 years apparently contribute most to the potential reproduction of the population, 2 and 3 year olds contribute little because of their small sizes, and the cumulative contribution of rare old (≥6 yr) individuals is large.

The behavior of pollock during the spawning period (February to June) apparently includes migrations to, and aggregations along, the outer continental shelf and slope (Fig. 15). Although spawning probably occurs along the entire eastern Bering Sea shelf edge, the outer shelf region just west and northwest of Unimak Island has been repeatedly identified as a major reproductive site (Maeda 1972; Maeda and Hirakawa 1977; Serobaba 1968, 1974). Trawl fisheries target upon pre-spawning and spawning populations, obtaining high catch rates. Some fishing vessels harvest pollock only for roe, discarding their catches after stripping the ovaries from ripe females.

Schools of pre-spawning and spawning pollock apparently move high into the water column, forming dense midwater layers (Takakura 1954; Serobaba 1974). Mating presumably involves pairing, and broadcasting of the pelagic non-adhesive eggs (ca. 1.5 mm diameter) with no parental care. Consistent with reported locations of principal spawning areas, pollock eggs and larvae have been observed in highest concentrations along the outer continental shelf between the Pribilof Islands and Alaska Peninsula (Serobaba 1968; Waldron and Vinter 1978).

Although some studies of the early life history of pollock in the eastern Bering Sea have presupposed a simple counterclockwise

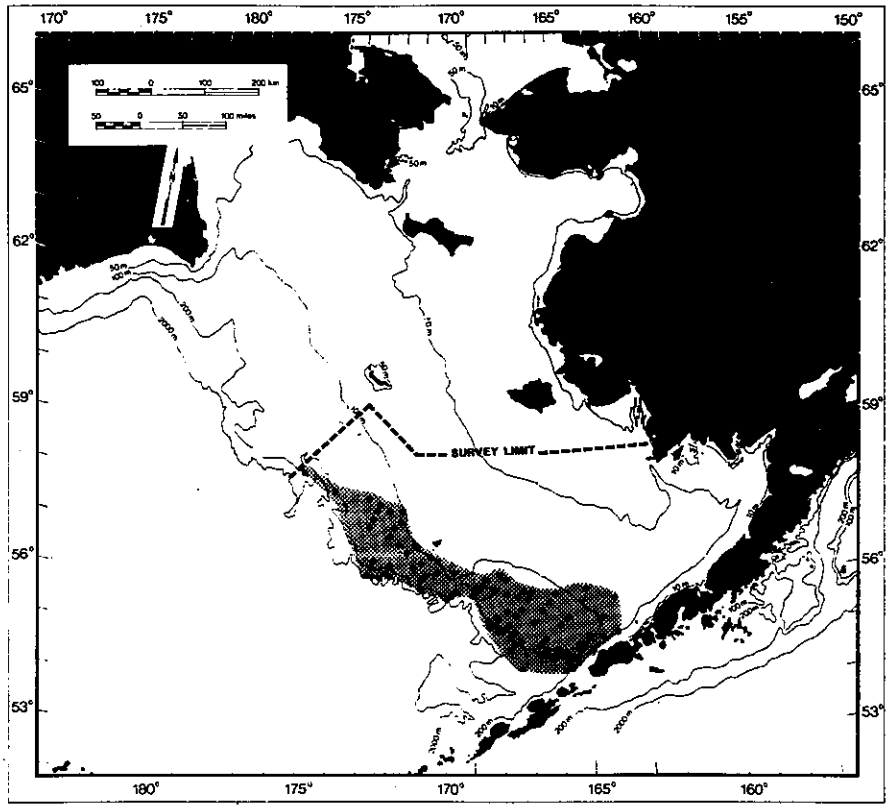

FIG. 15 Locations of individuals observed in spawning condition during April-June 1976. Dots show exact positions, shading indicates inferred range of spawning activities.

current transport through the central shelf region during the first one or two years of age, recent data suggest a different and more complex pattern of movement (Figs. 16 and 17). As opposed to the previous impression of predominantly counterclockwise water motion over the eastern Bering Sea shelf, the present concept of dominant long-term mean circulation is an extremely slow (1 cm sec^{-1}) drift to the northwest approximately parallel to the bathymetry (Coachman 1979).

If spawning occurs predominantly along the southeast outer shelf, then several months of northwest drift would carry larvae to the vicinity of the Pribilof Islands. In fact, during NMFS Crab-Groundfish trawl surveys conducted from June to mid-August, 0-group pollock (approximately 2-4 months old, and 35-80 mm fork length) have been observed over a large area of the northwestern outer shelf (see Fig.

16). Highest concentrations of 0-group juveniles, showing as dense midwater or near-bottom layers, have been noted directly west of the Pribilof Islands. Inspections of the stomach contents of demersal fish species throughout the eastern continental shelf region have found 0-group pollock (lengths 50-80 mm) to occur as an abundant food item only in this same area.

By one year of age, pollock are broadly distributed over the entire central and outer continental shelf, completely overlapping and extending inshore beyond the adult range (see Fig. 17). By two years of age, pollock remain more restricted to deep water--and with growth, begin to recruit to the trawl fisheries.

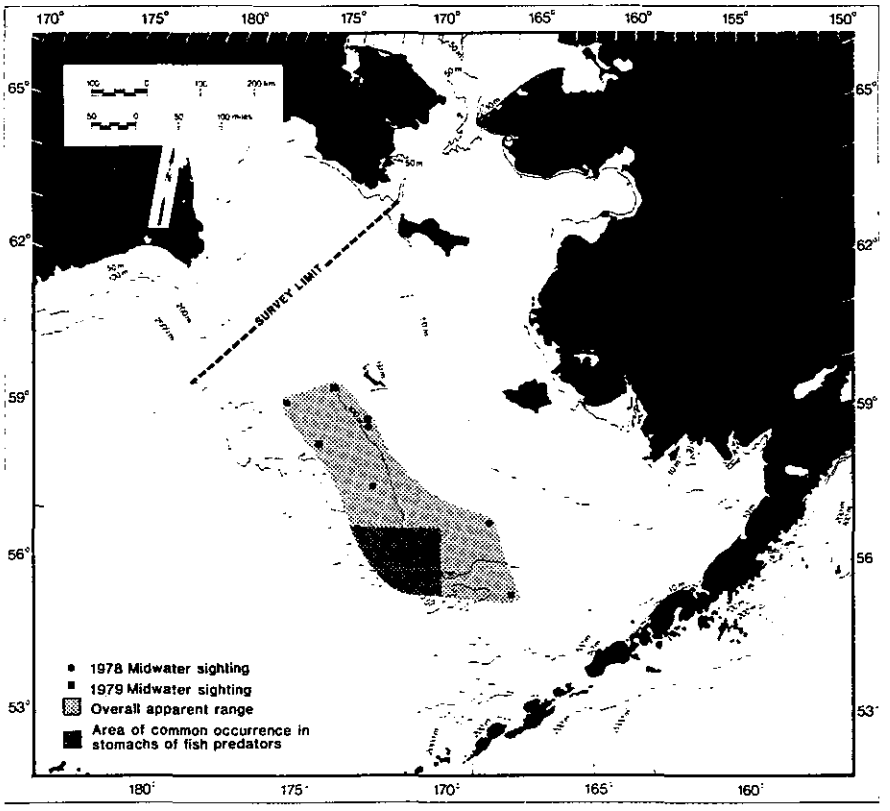

FIG. 16 Observations of 0-group (2-4 month old) pollock during June to mid-August, based upon NMFS research surveys during 1978 and 1979.

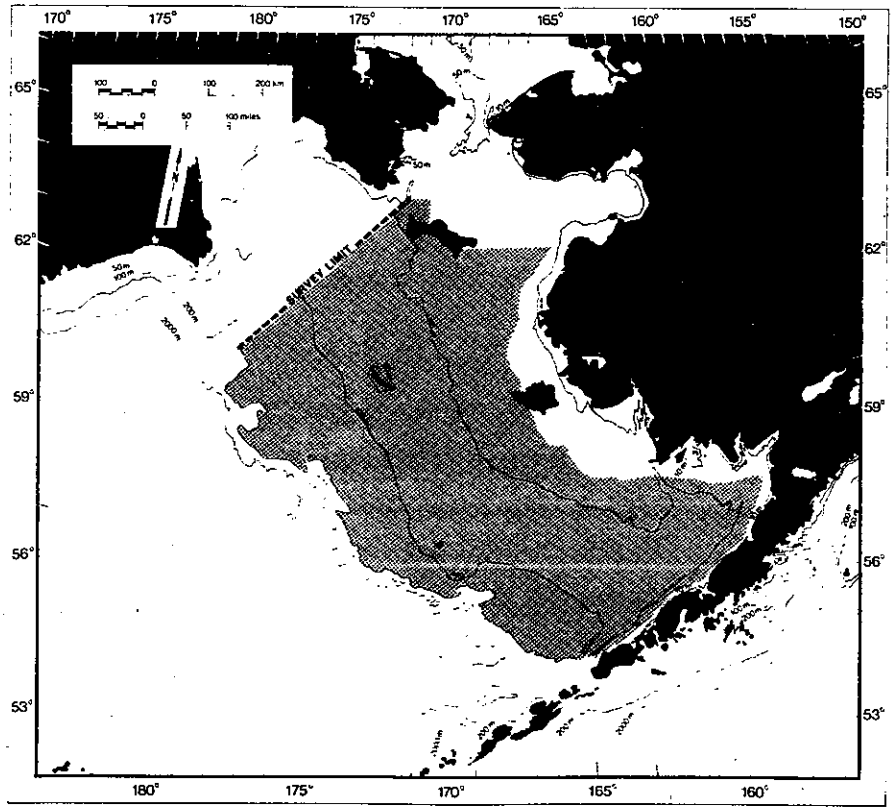

FIG. 17 Overall apparent range of one-year old pollock during June to mid-August, based upon NMFS research surveys, 1975-1979.

FOODWEB RELATIONSHIPS

One of the most striking features of the eastern Bering Sea food web is the extent to which pollock are represented in feeding relationships and overall energy exchange (Fig. 18). During different life history stages, pollock feed upon a broad spectrum of prey (Takahashi and Yamaguchi 1972; Mito 1974; Clarke 1978; Feder 1978; Smith et al. 1978; Bailey and Dunn 1979). In turn, pollock serve as a major food resource for a wide variety of primarily high trophic level predators (Mito 1974; Feder 1978; Hunt 1978; Lowry et al. 1978; Smith et al. 1978).

Food and Feeding

The feeding characteristics of pollock are apparently largely a function of body size, regional location, and time of year. Body size sets certain morphological and behavioral limits--such as size of the feeding apparatus, extent of dentition, and swimming speeds --that affect the types of prey that can be captured and ingested. Body size is also strongly related to vertical migratory behavior within the water column and geographical location -- factors that also determine available prey. Although regional, seasonal, and yearly variations in prey densities must be important in determining food composition and feeding rates, these have not yet been well described in the eastern Bering Sea.

Larval pollock (5-20 mm) have been reported by Clarke (1978) to undergo shifts in selection of prey sizes during ontogeny. The gut contents of small larvae (5-10 mm) consisted mainly of copepod

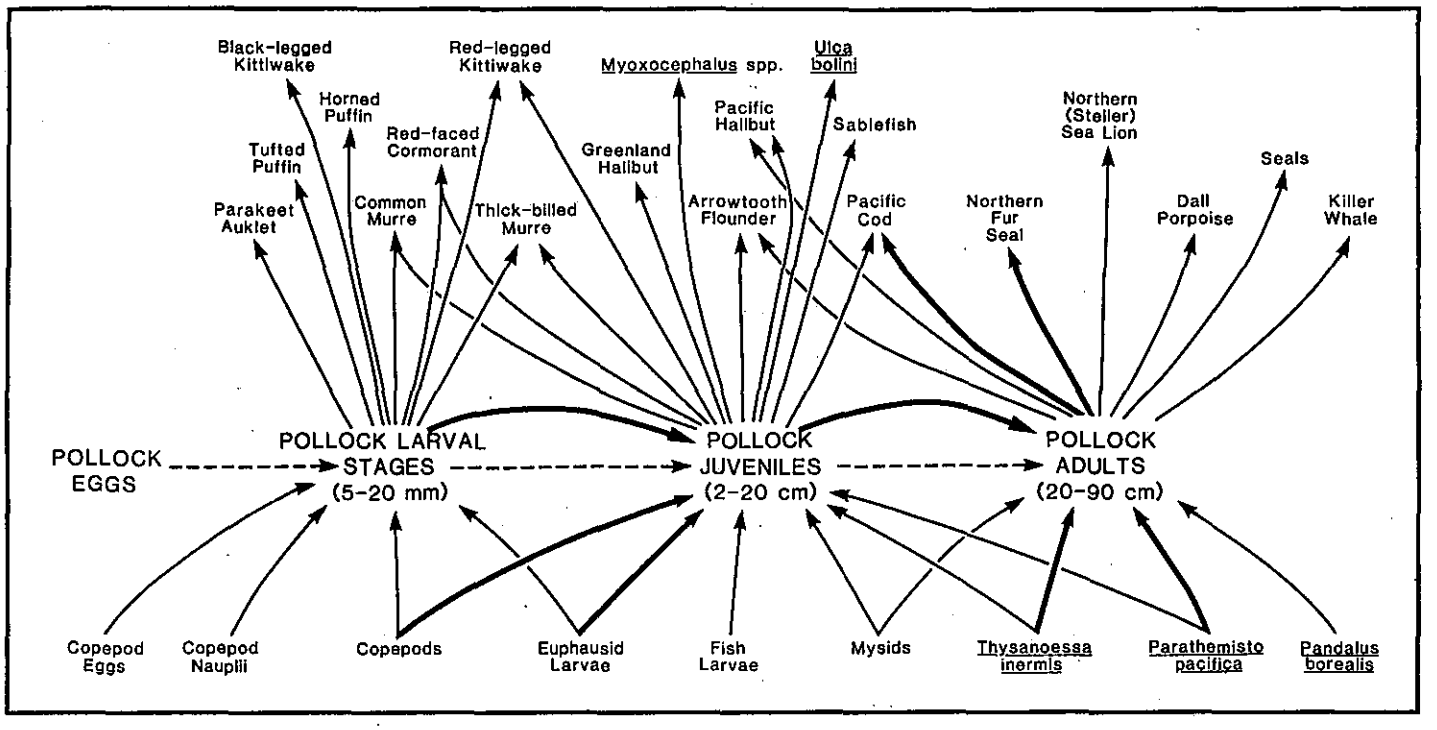

FIG. 18 Apparent food web based upon pollock in the eastern Bering Sea. Dotted lines indicate pollock ontogeny. Solid lines show important feeding relationships, with arrowheads and line weights indicating the direction and relative magnitude of carbon flows.

eggs and nauplii. Larger larvae showed progressively increasing fractions of cyclopoid copepods, calanoids, and larval euphausids.

Juvenile pollock (2-20 cm) presumably feed on a corresponding series of primarily zooplankton prey of increasing sizes, perhaps foraged from areas high in the water column. Although not well studied, important food items probably include copepods, amphipods, juvenile and adult euphausids, eggs, and larval fishes.

As adults (lengths 20-90 cm), pollock are generalized predators that appear to follow a "diurnally schooling-nocturnally active" behavior pattern, although freshly ingested food items can be found in the gut at any time of day. Large eyes are apparently adaptive for visual feeding, hunting at night, and foraging during low winter light intensities. The sleek, fusiform body indicates capabilities of fast swimming speeds. A large mouth and abundant, fine needle-like dentition provide good apparatus for seizing and ingesting large, active zooplankton (primarily Thysanoessa spp. and Parathemisto spp.) and fish (mainly juvenile pollock) prey (Fig. 19).

To place the role of pollock in the eastern Bering Sea food web in perspective, estimates were made of the food requirements for three overall average stock densities and related to primary production (Table VIII). At the average pollock densities that can be inferred from research vessel surveys (50-100 kg ha^{-1}), the estimated daily food requirements represented approximately 2 to 4% of average photosynthetic production.

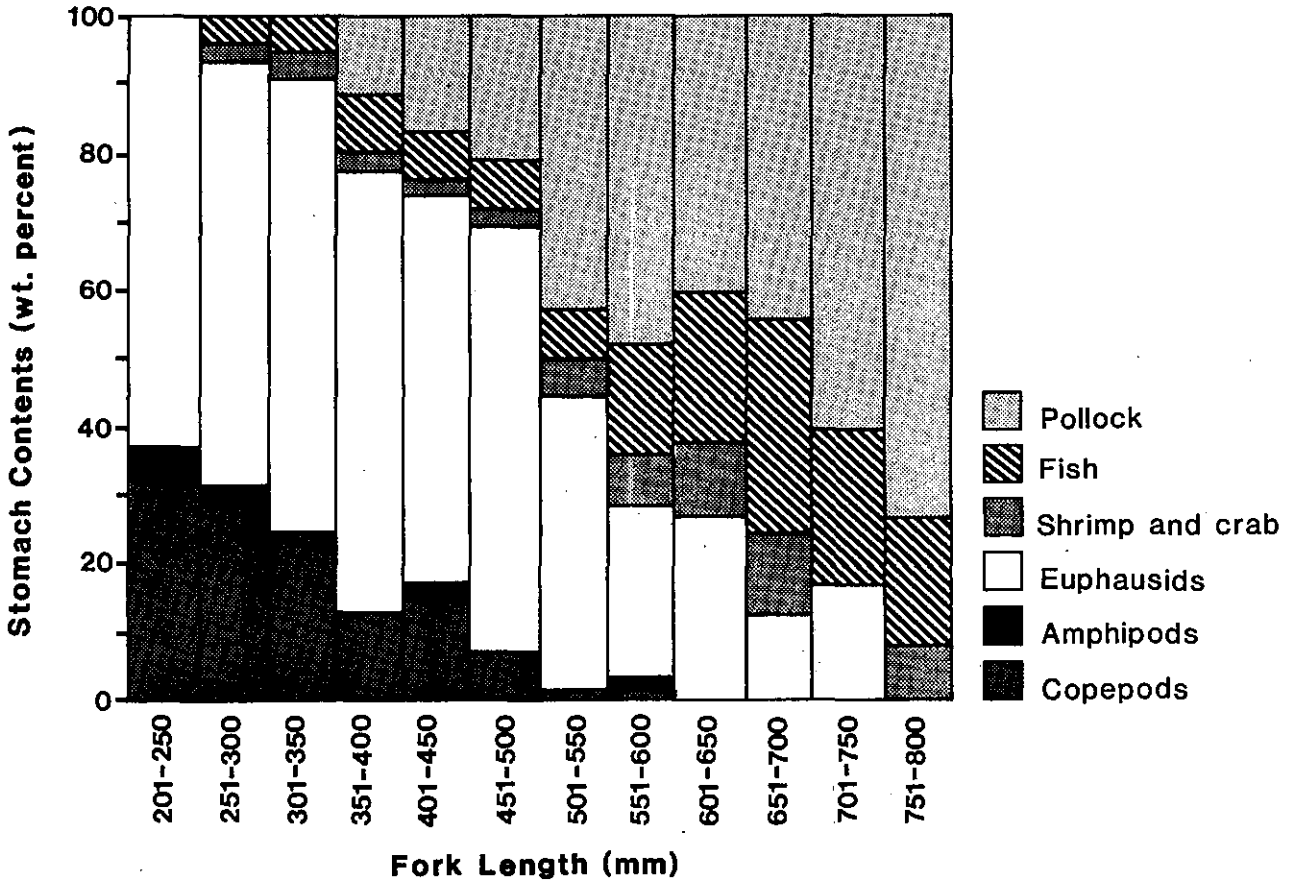

FIG. 19 Changes in prey selection with size (from Takahashi and Yamaguchi 1972).

TABLE VIII

Comparisons of Estimates of Food Intake Rates by Walleye Pollock in the Eastern Bering Sea to Primary Production.

Pollock 1/ density (mg wet wt m^{-2})	Pollock 2/ density (mg C m^{-2})	Food 3/ intake rate (mg C m^{-2} day^{-1})	Food intake rate as 4/ percentage of primary production rate
2500	133	2	1
5000	266	4	2
10000	532	8	4

1/ Overall absolute density; the underlined value was the overall mean density observed by Pereyra et al. (1976), assuming 100% trawl efficiency.

2/ Carbon equivalents were computed assuming a dry wt. of 14% wet tissue wt., and carbon fraction of 38% of dry wt. (Parsons et al. 1977: Table 12).

3/ Assuming an overall mean feeding rate of 1.5% of body weight per day (Daan 1973).

4/ Assuming an overall mean primary production rate (water column) of 200 mg C m^{-2} day^{-1} (McRoy et al. 1972).

Predation

Pollock are fed upon by a wide variety of other species, and cannibalism (or "intraspecific predation") is also high. To a certain extent, the pattern of predation upon pollock shows regional variations reflecting the range overlaps and activity areas of the different predator populations. In deep water along the outer continental shelf, juvenile and adult pollock are a major food item of Pacific cod , Pacific halibut (*Hippoglossus stenolepis*), Greenland halibut (*Reinhardtius hippoglossoides*), arrowtooth flounder (*Atheresthes* spp.), and sablefish (*Anoplopoma fimbria*). In the vicinity of the Pribilof Islands where large colonies of seabirds and pinnipeds occur, predation upon larval and juvenile pollock from the nearsurface layer by seabirds the cormorant (*Phalacrocorax urile*; kittiwakes, *Rissa tridactyla*, *R. brevirostris*; murres, *Uria aalge*, *U. lomvia*; puffins, *Fratercula corniculata*, *Lunda cirrhata*; and parakeet auklet *Cyclorrhynchus psittacula*) is significant, and larger pollock are actively dived and fed upon by the northern fur seal (*Callorhinus ursinus*).

Other widely ranging predators apparently feed upon pollock throughout their eastern Bering Sea distribution: cottids (particularly *Myoxocephalus* spp. and *Ulca bolini*), the Steller sea lion (*Eumetopias jubata*), other seals (*Phoca* spp.) and toothed whales (perhaps particularly *Phocoenoides dalli* and *Orcinus orca*).

Although cannibalism upon eggs and larvae during the post-reproductive period is a common behavior of many fish species, pollock are unusual due to the extent that intraspecific predation is a normal activity and represents a large fraction of total food

intake. It is not unusual to find 35 cm pollock feeding upon 5-10 cm juveniles, and 60-80 cm adults feeding upon pollock 10-30 cm. This peculiar feeding strategy--by which cannibalistic adults gain a meal and eliminate potential competitors at the expense of their juveniles--may result in sensitive density-dependent processes for regulating both the age structure and total size of the population (Fox 1975).

FISHERY CHARACTERISTICS

Present Status and History

Detailed reviews of the history and characteristics of the different eastern Bering Sea trawl fisheries are given in Pruter (1973, 1976), Forrester et al. (1978), Low and Akada (1978), NPFMC (1978), and Bakkala et al. (1979a). In summary, large trawl fisheries for walleye pollock have been a relatively recent development (Table IX), representing a shift from targeting upon other fish species--primarily Pacific ocean perch (*Sebastes alutus*) and yellowfin sole (*Limanda aspera*)--prior to 1964. This shift was a consequence of declining catch rates (i.e., apparent overfishing) of the other species, and the development of new processing techniques and end products designed to improve the world market demand for pollock.

During the period 1966-70, annual pollock catches increased steeply (see Table IX). Peak yields were taken during 1971-73, then catches declined to the present levels of 950,000-980,000 mt yr^{-1}. These recent catch levels represent management quotas established under the authority of the U.S. Fishery Conservation and

TABLE IX

Summary of Annual Removals of Pollock from the Eastern Bering Sea by Trawl Fisheries, 1964 to 1979 (metric tons). 1/

Year	Japan	USSR	Republic of Korea	China, Taiwan	Poland	Total
1964	174,792	0	0	0	0	174,792
1965	230,551	0	0	0	0	230,551
1966	261,678	0	0	0	0	261,678
1967	550,362	0	0	0	0	550,362
1968	700,981	0	1,200	0	0	702,181
1969	830,494	27,295	5,000	0	0	862,789
1970	1,231,145	20,420	5,000	0	0	1,256,555
1971	1,513,923	219,840	10,000	0	0	1,743,763
1972	1,651,438	213,896	9,200	0	0	1,874,534
1973	1,475,814	280,005	3,100	0	0	1,758,919
1974	1,252,777	309,613	26,000	0	0	1,588,390
1975	1,136,731	216,567	3,438	0	0	1,356,736
1976	913,279	179,212	85,331	0	0	1,177,822
1977	868,732	63,467	45,227	944	0	978,370
1978 2/	821,306	92,714	62,371	3,040	0	979,424
1979 3/	(774,630)	(60,000)	(85,000)	(5,000)	(25,000)	(950,000)

1/ Data from Bakkala et al. (1979b), unless otherwise cited. 2/ Preliminary estimates. 3/ Foreign fishing allocations (Pileggi and Thompson 1979).

Management Act of 1976, Public Law 94-265. During 1978, 84% of the total eastern Bering Sea pollock catch was taken by Japanese vessels, 9% by U.S.S.R., 6% by Republic of Korea, and 0.3% by Taiwanese. The present fishing fleets include factoryships, factory stern trawlers, independent stern trawlers, pair trawlers, and refrigerator transports.

Selective Characteristics

Contrary to general impressions, trawl fisheries in the eastern Bering Sea are composed of specialized units (i.e., national and company fleets, and individual fishing vessels) that selectively target upon specific fish populations (particular species and size mixes) so as to maximize the economic return from the particular catching, processing, and storage capabilities of each vessel. The market products that a fishing vessel is oriented towards--frozen products (fillets or blocks), minced fish ("surimi"), meal, or roe--largely determine fishing strategies. Depending upon seasonal variations in the availabilities of fish populations, different fishing units may: (1) exclusively target their trawling activities upon pollock; (2) "switch" the direction of trawling among several higher-valued species, taking pollock incidentally; or (3) at times, even discard mistakenly-caught pollock as a "trash" item.

Figure 20 shows the overall geographical distribution of pollock catches (total annual yield) by Japanese fishing vessels in the eastern Bering Sea during 1977. In general, vessels targeting specifically upon pollock would probably have mainly fished along

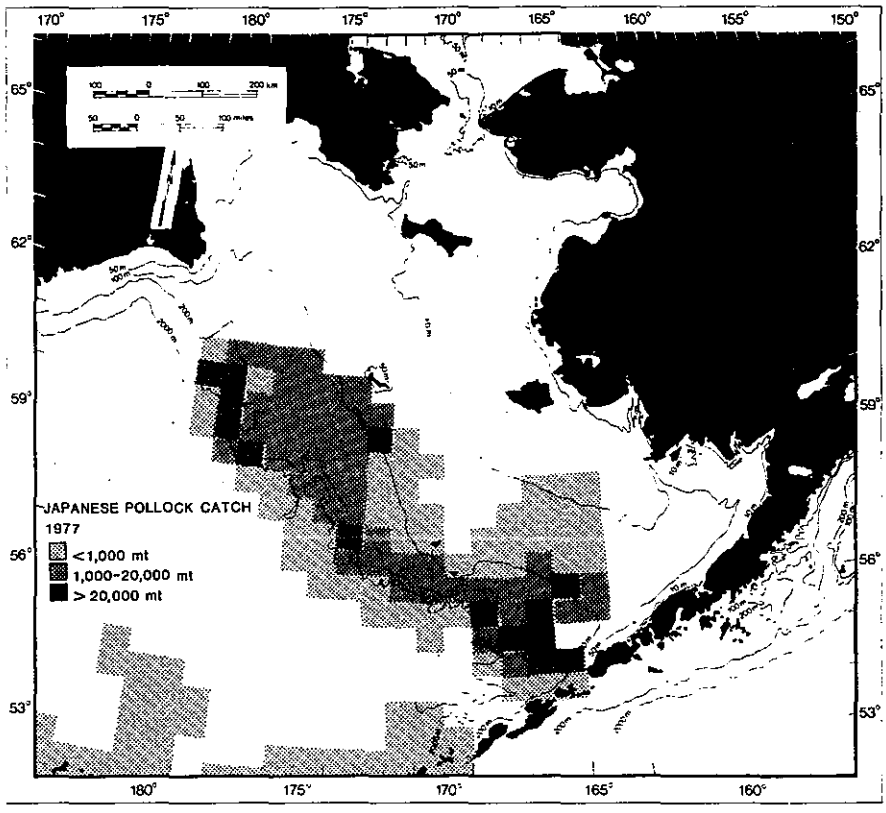

FIG. 20 Geographical distribution of the total annual Japanese pollock catch during 1977, summarized by 1/2° latitude and 1° longitude squares.

the outer shelf. Vessels taking pollock incidentally to other species--such as yellowfin sole, Alaska plaice (Pleuronectes quadrituberculatus) and deep pleuronectids (Reinhardtius hippoglossoides and Atheresthes spp.)--are represented by the extended distributions of low-level catches over deep water and in the central shelf.

Although pollock are taken during all months of the year, a majority of the annual catch is taken during the summer from June through September.

Fishing efforts directed toward pollock are highly size-selective (Chang 1974: Figure 12), a consequence of the fish densities (more specifically, catch rates) available at different body sizes, trawl mesh sizes, and processing requirements of the different vessels. Figure 21 shows the size frequency distributions observed from "survey" and "fishery" populations during 1978. Compared to the size distribution of the pollock population determined from the more evenly weighted and inshore survey coverage of the eastern shelf, trawl fisheries were selecting relatively larger individuals at the shelf edge.

A disturbing recent trend of eastern Bering Sea pollock fisheries, however, has been the selection of an increasingly larger proportion of small and young fish. The size distribution of the 1978 fishery catch shown in Figure 21 represents an age composition of approximately 2% 1-year olds, 20% 2-year olds, 40% 3-year olds, 18% 4-year olds, and 20% 5 or more years of age. In the perspective of the apparent growth and reproductive schedules for the

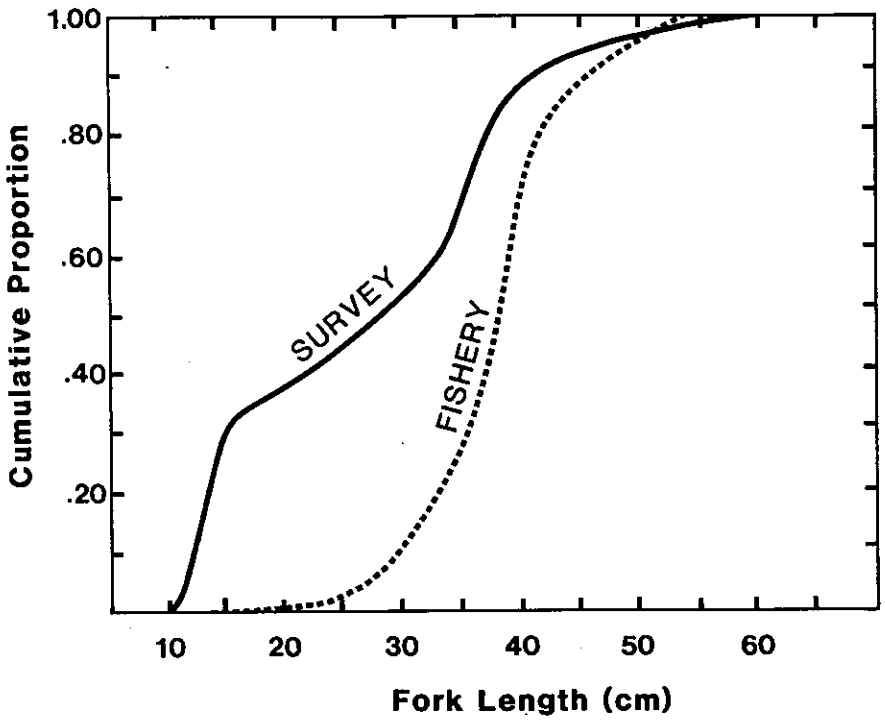

FIG. 21 Comparison of the size frequency distributions of "survey" and "fishery" pollock populations. Survey results are from the 1978 NMFS Crab-Groundfish sampling survey of the index area shown in Figure 8. Fishery results are from 1978 NMFS Foreign Fisheries Observer Program sampling of the commercial catches of Japanese motherships, Japanese large stern trawlers, and Korean large stern trawlers in INPFC area I.

population (see Tables VI and VII), it would appear prudent to reduce fishing pressures upon age classes 1-3 years.

SEASONAL AND INTER-ANNUAL VARIABILITY

Seasonal Variations

The eastern Bering Sea environment is characterized by strong seasonality. Temperatures are seasonally cyclic and extremely cold during winter. Mixing and overturn of the water column occurs as a result of heat loss from surface layers during winter, followed by increased water column stability during summer warming. Biological production processes follow a cycle of pulsed high activities during spring and summer, followed by a long winter period of low activity.

Apart from these generalizations, distinctive biological domains (i.e., geographical subregions and water mass layers) are apparently formed in the eastern Bering Sea characterized by differences in mean and extreme values of environmental conditions, relative variability, and timing of events. These different domains, or habitats, are presumably used by biological species according to their resource value (in terms of Darwinian fitness) at specific times.

If we broadly define migration as, "an act of moving from one spatial unit to another" (Baker 1978), then walleye pollock can be seen to exhibit a continuum of movement types. At short time scales (hours or days), the movements of individuals reflect the daily activity pattern--forming and dispersing from schools, searching for food, and avoiding predators. At longer time scales

(weeks and months), individuals and large subpopulations (such as certain age classes) show movements between different biological domains--from deep water up onto the continental shelf and back, along the shelf, and between major regions.

A dominant behavior of pollock appears to be seasonal movements on- and off-shelf (i.e., movements normal to bathymetry). During winter months, shelf populations appear to retreat to deep water along the outer shelf edge and may extend pelagically out over deep water. During summer, vertical and onshore movements occur that result in high concentrations of adults along the outer shelf and a dispersal of primarily juveniles (age classes 1 and 2 yr) into the central and inner shelf regions. These seasonally-related bathymetric shifts are reflected in the trawling depths of the commercial fishery (Fig. 22).

Since pollock are ectotherms, with body temperatures in equilibrium with their surroundings, on- and off-shelf migrations appear to be an adaptive response to the extremely cold temperatures (0.0 to -1.7 C) of the shelf domain during winter. Along the shelf edge at depths of 200-300 m, water temperatures are relatively constant -- 3-5 C throughout the year, providing a warm winter refuge (i.e., freezing avoidance) layer. Dispersal from this layer out onto the continental shelf during summer presumably maximizes the exploitation of different food resources by different size and age classes.

Along-shelf movements (i.e., parallel to bathymetry) have been found from tagging studies and inferred from month-to-month changes in the patterns of commercial fisheries catches (Serobaba 1970;

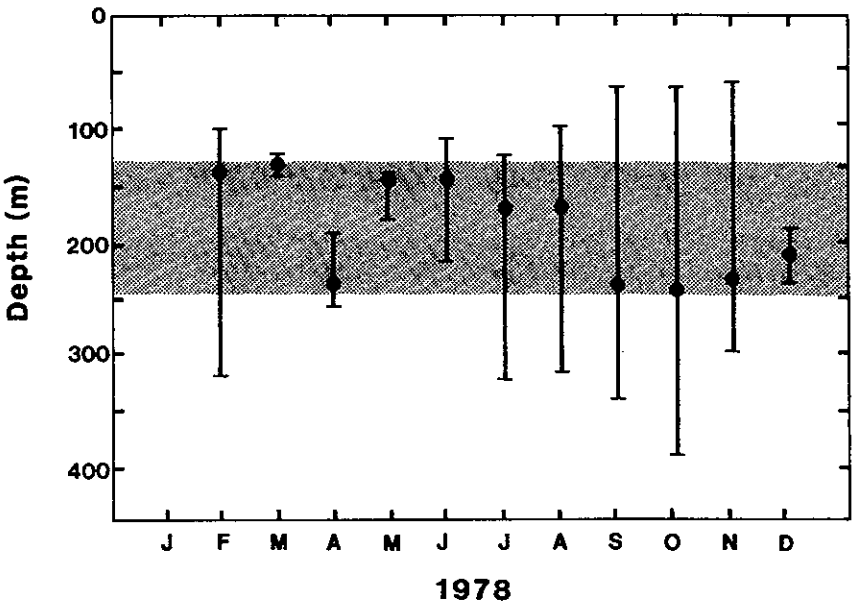

FIG. 22 Monthly variations in fishing depths for pollock, based upon 1978 NMFS Foreign Fisheries Observer Program data from Japanese and U.S.S.R. independent stern trawlers in INPFC area I. Dots indicate the median fishing depth during each month, vertical bars indicate the monthly range. The shaded area, depths 135-245 m, represents the principal range of values during the year. Only gear operations in which pollock represented 25% or more of the total catch (by weight) were included in the analysis.

Maeda 1972; Takahashi and Yamaguchi 1972). These have been suggested to represent the directed, seasonally-related movements of subpopulations between exclusive "wintering," "spawning," and "summer feeding" areas. Although the outer continental shelf area just west and northwest of Unimak Island does appear to be a major reproductive site, other resource areas (including winter refuge, other low-level spawning areas, and summer ranges) now appear to be broadly distributed, and there do not seem to be clear long-distance migration routes to particular seasonal activity centers.

Two large subsurface domains that appear fundamentally different are the outer continental shelf areas northwest and southeast of the Pribilof Islands. Temperature conditions are colder in the northern area, winter sea ice extends seaward of the continental shelf, and winter overturn penetrates the water column to depths below the shelf edge (Favorite et al. 1977). As a result, in this northern region the timing of spring and summer events--movements related to spawning, the spawning period, and dispersal onto the shelf--appear to follow the southeastern region by a lag of approximately 1-2 months. A characteristic progression of the commercial fisheries from south to north along the outer shelf during spring to mid-summer may represent targeting upon time-lagged spring aggregations along the shelf edge, following a northward migrating subpopulation, or perhaps partly result from restrictions due to ice and weather conditions.

Evidence has been presented for a progressive decrease in the size composition of pollock in the southeast area during the post-

spawning period, presumably due to movements of large adults from the reproductive site (Serobaba 1970; Yamaguchi 1979). Whether these same, migrating, spent individuals account for increases in population size composition that occur in the northwest area during the same time period, will need to be verified by mark and recapture studies.

The responses of pollock to winter ice cover may be expected to be largely determined on the basis of thermal characteristics of the subsurface (particularly bottom water) environment. Since an arctic distribution is not shown, and there is no evidence of the development of biochemical mechanisms for adapting to freezing conditions, then it must be assumed that pollock are excluded from shallow regions of the continental shelf during winter ice cover. Along the outer continental shelf, the penetration of relatively warm (1-5 C) subsurface circulation under ice cover may still provide an adequate thermal refuge.

As suggested by genetic similarities and some tagging studies, interregional exchange is apparently an important process that may also vary seasonally. A relevant research problem is the question of determining the origins and relationships (to shelf populations) of pelagic walleye pollock found over deep water in the central Bering Sea. During an acoustic survey of the Aleutian Basin during June and July 1978, Okada (1978) observed "spotted type" echo patterns from large pollock throughout essentially the entire region, mainly from midwater layers at approximately 30-80 m depths during daytime. Pollock in these layers were extremely uniform in size,

with 82% of all individuals sampled between 44-50 cm.

Variations Between Years

Even if the eastern Bering Sea were a more constant physical environment, important properties of the walleye pollock population (e.g., abundance, size and age structure, growth, food requirements) might still be expected to undergo long-term fluctuations resulting from (1) internal processes of population regulation, and (2) the external, and variable, influences of predators (including fisheries) and prey. Density-dependent processes of population control may be expressed as variations in life table characteristics. Because the population is composed of approximately 15 age classes, and because inter-age class predation (and perhaps competition) is significant, interactions between age classes may alone result in inherent variations in age class abundances (and hence, total population density) between years. Similar control mechanisms must also result from the size-selective activities of predator populations, producing varying patterns of age-specific mortalities.

Particular properties of the population are apparently sensitive to certain age classes. The weight density, or biomass, of the population will largely be dependent upon the abundances of age classes 2-5 yr (see Table VI). Potential fecundity will primarily be dependent upon the abundances of age classes 4-9 yr (see Table VII).

The actual high year-to-year variability of the eastern Bering Sea physical environment adds other components that contribute to,

and perhaps accentuate, fluctuations in population properties. Potentially important variations in physical environment include changes in general climate (McLain and Favorite 1976), anomalously extensive ice cover and formation of cold bottom water during winter, and changes in the flow and characteristics of eastern Bering Sea source waters.

"Climate" is apparently important in determining the timing and extent of seasonal migrations of pollock both on- and off-shelf. During warm years, spring movements into shallower water have appeared to occur earlier, and the density distribution of the population has appeared to shift farther inshore than during cold years (Pereyra et al. 1976: Figs. VIII-11 and VIII-12). The direct importance of thermal conditions in determining distributional characteristics of the population may be overemphasized, however, and other factors that covary with temperature (e.g., particular food items) may be more of a direct cause.

Hydrographic conditions and short-term climate (weeks) presumably have large influences upon annual reproductive success by contributing high variability to the survival of eggs, larvae, and early juveniles. The effects of variable early survival upon year class abundances at subsequent ages, however, may be dampened or obscured by later density-dependent mortality processes.

FUTURE RESEARCH

Because of the importance of pollock in the eastern Bering Sea and other regions of the North Pacific, there are needs for substantially increased research activities studying their basic bio-

logy, population dynamics and ecological relationships. In order of priority:

1. There is a need to develop mathematical simulation models to examine the behavior of the population dynamics of pollock under different assumptions of biological interactions and process rates. Single-species age-structured models are needed to examine detailed processes of internal regulation. Multispecies models are needed to study effects of interactions between species. Yield-oriented models are needed to enable more objective evaluation of potential effects of different harvesting levels by fisheries, and to test consequences of feedback and non-feedback management policies. Simulations of environmental randomness should be included in all three types of models.

2. We need to ensure the collection of more uniform population data, and in particular, to strive for developing longer observational time series based upon consistent procedures. This information is needed for use in mathematical models, and will provide the basis for scientific management of the fisheries. Fisheries surveys of pollock in the eastern Bering Sea would be more productive in the long run if the participating agencies better coordinated their research efforts, standardized sampling methods and gear, and agreed upon uniform statistical areas. There is also a need to improve the uniformity and quality of data reported from the commercial fisheries.

3. There is a need to study relationships between spawning population size, reproductive success, and subsequent age-class abun-

dances and survival rates. Size- and age-specific mortality rates need to be evaluated as potentially important density-dependent mechanisms regulating population age structure and size.

4. The interrelationships of pollock with other species need to be studied, particularly marine mammals.

5. We need a better understanding of seasonal movements and population exchange: (1) along the eastern Bering Sea continental shelf; (2) between populations associating with the eastern Bering Sea continental shelf and pelagic populations over deep water in the Aleutian Basin; and (3) between major geographical regions.

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POPULATION CHARACTERISTICS AND ECOLOGY OF YELLOWFIN SOLE

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ABSTRACT

Yellowfin sole is a major component of the demersal fish community of the eastern Bering Sea continental shelf and has been fished commercially on a regular annual basis since 1954; in 1975 it made up 64% of the total flounder biomass and 23% of the total sampled fish biomass. Intense exploitation in 1959-62 (when 1.6 million mt were harvested) was the apparent cause of a severe decline in abundance of the resource and an estimated virgin exploitable biomass of 1.6-2.0 million mt decreased to 0.8 million mt in 1963. The biomass remained at this lower level of abundance through the early 1970's, but since 1972 it has shown a marked increase and may have reached 1.4 million mt in 1978. This increase stems from the recruitment of a series of abundant year classes originating in the years 1966-70.

Seasonal migrations are conducted from outer continental shelf and slope waters (> 100 m) occupied in winter and early spring to inner shelf waters (15-75 m) where spawning occurs in summer. Offshore migrations by adults in fall and winter are an apparent response to ice cover and cold water temperatures that characterize inner and central shelf waters in winter.

Unlike the adults, the young remain in shallow nearshore nursery areas throughout their first few years of life. They begin to disperse to more offshore waters at 3-5 years of age, and by 5-8 years of age, they occupy much the same waters as older fish.

Yellowfin sole are slow growing and reach a length of 25 cm at 8-9 years of age, which is about the average size of fish taken in the commercial fishery. They first become recruited to the fishery at 4-5 years and become fully recruited at 7 years, which corresponds to the age when the exploitable stock reaches its maximum biomass. Growth declines between ages 7-8 when a high proportion of the population reaches sexual maturity. Mortality increases rapidly after the 9th year possibly due to spawning stress mortality.

Climatic variations in the eastern Bering Sea since the mid-1960's have produced some apparent changes in year-class abundance and in distributions and migrations of yellowfin sole. Abundant year-classes were produced in years of relatively warm climatic conditions whereas abundance of year-classes produced in cold years were relatively low. Evidence has also suggested that extensive ice cover may delay the start of spring inshore migrations, and residual cold water in central shelf areas may alter patterns of summer migrations and distributions.

INTRODUCTION

Yellowfin sole (*Limanda aspera*) is a right-eyed flounder of the family Pleuronectidae and is one of two species of *Limanda* found in the eastern Bering Sea, the other being the long-nosed dab (*L. proboscidea*). Yellowfin sole is a major component of the Bering Sea ichthyofauna while the longhead dab is a minor nearshore species. External characters that distinguish yellowfin sole from other flounders are the sharply arched lateral line over the pectoral fin and the absence of an accessory branch; light brown color on the eyed side with darker mottling; yellow cast to the unpaired fins; and narrow black lines at the base of the paired fins (Hart 1973; Fig. 1). It is a relatively small flounder, and commercial catches in recent years reflect an average size of 25 cm and 175 gms. Fish of 25 cm are 8-9 years old; however, maximum lengths

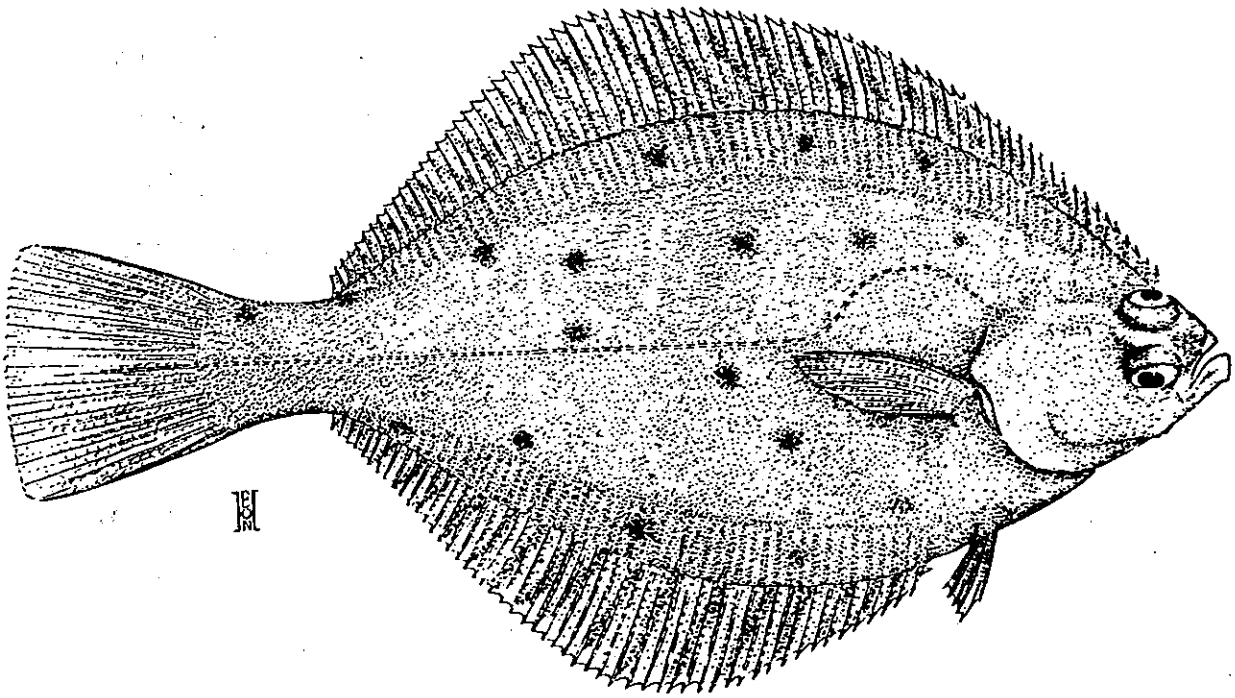


FIG. 1 Yellowfin sole (Illustration from J. L. Hart, 1973, Bull. 180, Fish. Res. Board Canada; courtesy Environment Canada, Ottawa).

of 53 cm (Ellson et al. 1950) and ages in excess of 20 years (Wakabayashi 1975) have been reported.

The distribution of yellowfin sole is limited to continental shelf and slope waters of the North Pacific Ocean, the Bering Sea and, to a limited extent, the Chukchi Sea (Fig. 2). It ranges along the Pacific coast of North America from Barclay Sound (about 49°N), Vancouver Island, British Columbia northward into the Chukchi Sea (Hart 1973) and along the Asian coast from the Gulf of Anadyr southward to the east and west coasts of Hokkaido Island, Japan, and along the Asian mainland in the Okhotsk Sea and the Sea of Japan to about 35°N off South Korea (Fadeev 1970a). Their bathymetric range is from about 5-360 m, although in some regions such as the Gulf of Alaska, it is limited to continental shelf waters of generally 100 m or less. The deepest recorded occurrence (360 m) is in the eastern Bering Sea.

They reach their maximum abundance in the eastern Bering Sea and are by far the most abundant flounder in this area. Based on an extensive trawl survey in 1975 (Pereyra et al. 1976) the biomass was approximately 1.0 million mt, representing 64% of the total flounder biomass on the eastern Bering Sea continental shelf and 23% of the total sampled fish biomass. It was the second most abundant demersal fish after walleye pollock (*Theragra chalcogramma*).

Although it is the predominant flounder in the eastern Bering Sea, yellowfin sole becomes a relatively minor species among the

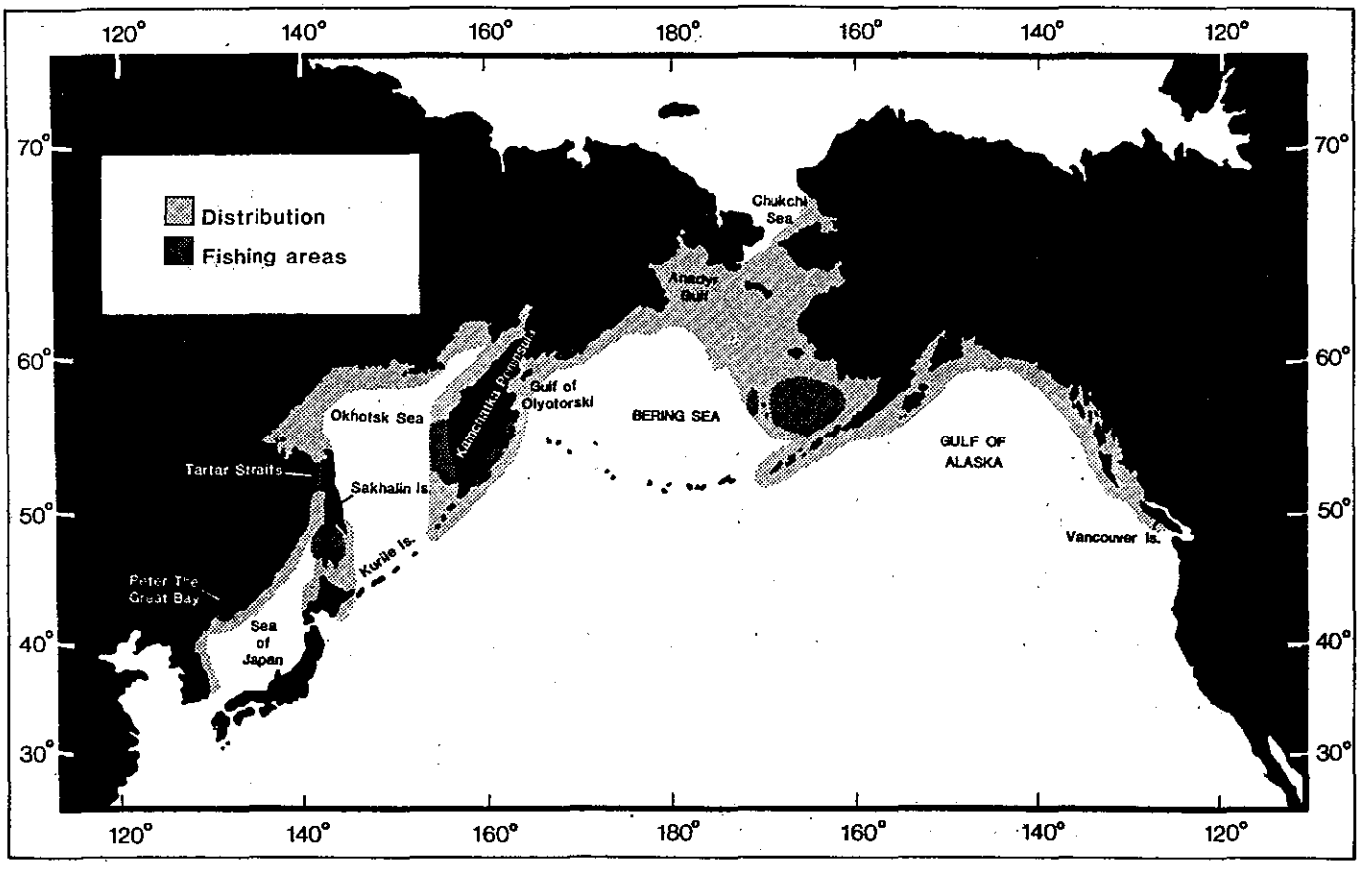


FIG. 2 Overall distribution and areas of commercial fishing for yellowfin sole.

flounder complex in the Gulf of Alaska. It ranked eighth in relative abundance in flounder catches in the northern Gulf of Alaska (Hughes 1974) and is only occasionally taken in southeastern Alaska waters (Schaefers 1951; Ellson and Livingston 1952).

The abundance of yellowfin sole is lower in U.S.S.R. waters than in the eastern Bering Sea, but concentrations are large enough in certain regions to attract commercial fisheries (see Fig. 2).

COMMERCIAL UTILIZATION

Yellowfin sole and other groundfish resources of the eastern Bering Sea were first exploited commercially by Japan, initially by exploratory vessels in 1930 and by a mothership-catcher boat operation in 1933 (Forrester et al. 1978). Fishing was conducted off Bristol Bay for pollock and flounders which were reduced for fish meal and continued until 1937 with catches ranging up to 43,000 mt annually. Another mothership fishery was conducted in 1940 and 1941 that targeted on yellowfin sole for human consumption (Forrester et al. 1978). Total catches were 9,600 and 12,000 mt respectively.

Following World War II, Japanese distant water fisheries resumed operations in the eastern Bering Sea in 1954 with mothership and independent trawler fleets targeting on yellowfin sole. In the initial period of this fishery (1954-57), catches ranged from about 12,500-24,700 mt (Table I).

TABLE I

Annual Catches (mt) of Yellowfin Sole in the Eastern Bering Sea (East of 180° and North of 54°N).

Year	Japan	USSR	ROK[1/]	Total
1954	12,562	0	0	12,562
1955	14,690	0	0	14,690
1956	24,697	0	0	24,697
1957	24,145	0	0	24,145
1958	39,153	5,000	0	44,153
1959	123,121	62,200	0	185,321
1960	360,103	96,000	0	456,103
1961	399,542	154,200	0	553,742
1962	281,103	139,600	0	420,703
1963	20,504	65,306	0	85,810
1964	48,880	62,297	0	111,177
1965	26,039	27,771	0	53,810
1966	45,423	56,930	0	102,353
1967	60,429	101,799	0	162,228
1968	40,834	43,355	-	84,189
1969	81,449	85,685	-	167,134
1970	59,851	73,228	-	133,079
1971	82,179	78,220	-	160,399
1972	34,846	13,010	-	47,856
1973	75,724	2,516	-	78,240
1974	37,947	4,288	-	42,235
1975	59,715	4,975	-	64,690
1976	52,668	2,908	625	56,201
1977	58,139	284	55	58,478
1978	62,102	50,053	69	112,224

1/ 0 indicates no fishing, - indicates fishing but no reported catch.

In 1958 the U.S.S.R. also entered the fishery and from 1959-62 the exploitation of yellowfin sole was very intense with annual catches ranging from 185,000-554,000 mt. There is evidence that catches of this magnitude severely reduced the abundance of the stock (Wakabayashi et al. 1977). In the subsequent period of 1963-71, catches were much lower, ranging from 53,800-167,100 mt. Catches declined further in the period of 1972-77 as the U.S.S.R. discontinued their target fishery for yellowfin sole, presumably because of low catch rates. Catches in this period, primarily by Japan, ranged from 42,200-78,200 mt. In 1978 the U.S.S.R. resumed their target fishery for yellowfin sole and preliminary data indicates that all-nation catches rose to about 112,000 mt.

STOCK BIOMASS

The virgin biomass of exploitable yellowfin sole (age 6 years and older) in the eastern Bering Sea has been estimated to range from 1.3-2.0 million mt (Alverson et al. 1964, Wakabayashi 1975). Based on a virtual population analysis (Wakabayashi 1975), the exploitable population was reduced to approximately 40% (801,500 mt) of the maximum estimate of virgin size by 1963. This decline occurred during the period of intense exploitation by Japan and the U.S.S.R. when 1.6 million mt were harvested in 1959-62. The analysis also showed some recovery of the resource in the mid-1960's when the exploitable population was estimated to reach about 950,000 mt (Table II). This was followed by another decline to about 790,000 mt in 1970.

TABLE II

Estimates of the Exploitable Biomass (age 6 and older) of Yellowfin Sole in the Eastern Bering Sea.

Year	Virtual Population Analysis[1/]	Cohort Analysis[2/]	Trawl Surveys[3/]
1959	2035.1		
1960	1924.0		
1961	1521.6		
1962	1054.6		
1963	801.5		
1964	856.2	912.5	
1965	872.8	960.7	
1966	948.1	969.0	
1967	946.5	879.0	
1968	862.7	635.4	
1969	880.8	604.0	
1970	786.7	720.8	
1971		648.2	
1972		660.0	
1973		849.1	
1974		761.4	
1975		910.2	991.9
1976			
1977			
1978			1414.6

1/ Wakabayashi (1975)
2/ Wakabayashi et al. (1977)
3/ Pereyra et al. (1976); Bakkala et al. (1979)

A cohort analysis covering the period 1964-75 (Wakabayashi et al. 1977) showed trends in abundance similar to those indicated by the virtual population analysis, but yearly biomass estimates varied to some degree between the two studies (see Table II). The cohort analysis showed the exploitable population reaching a

low level in 1969 of 604,000 mt and then increasing to 910,000 mt in 1975. This increase in abundance has also been evident from indices of relative abundance from research vessel surveys and from the commercial fisheries (Bakkala et al. 1979). The estimated biomass in 1975 based on the cohort analysis was similar to that obtained from an extensive trawl survey of the eastern Bering Sea in 1975.

Indices of relative abundance and biomass estimates from trawl surveys have shown that the abundance has continued to increase through 1978 (Bakkala et al. 1979). The exploitable biomass may have reached 1.4 million mt by 1978, perhaps reaching 70% of the virgin population size. The primary reason for the increase in abundance of the resource has been the recruitment of a series of relatively strong year-classes originating in the years 1966-70 (Fig. 3). The accumulative contribution of these year-classes may have resulted in a doubling of the overall exploitable biomass over the period of 1973-78.

STOCK STRUCTURE

Yellowfin sole form dense concentrations on the outer continental shelf of the eastern Bering Sea in winter. The largest of these concentrations is located in the vicinity of Unimak Island and the second largest is west of St. Paul Island (Fadeev 1970a; Wakabayashi 1974). Other lesser winter concentrations have also been recognized by these authors; one that may be located south or east of St. George Island and the other in Bristol Bay, the latter consisting of small fish. Japanese tagging studies have shown that

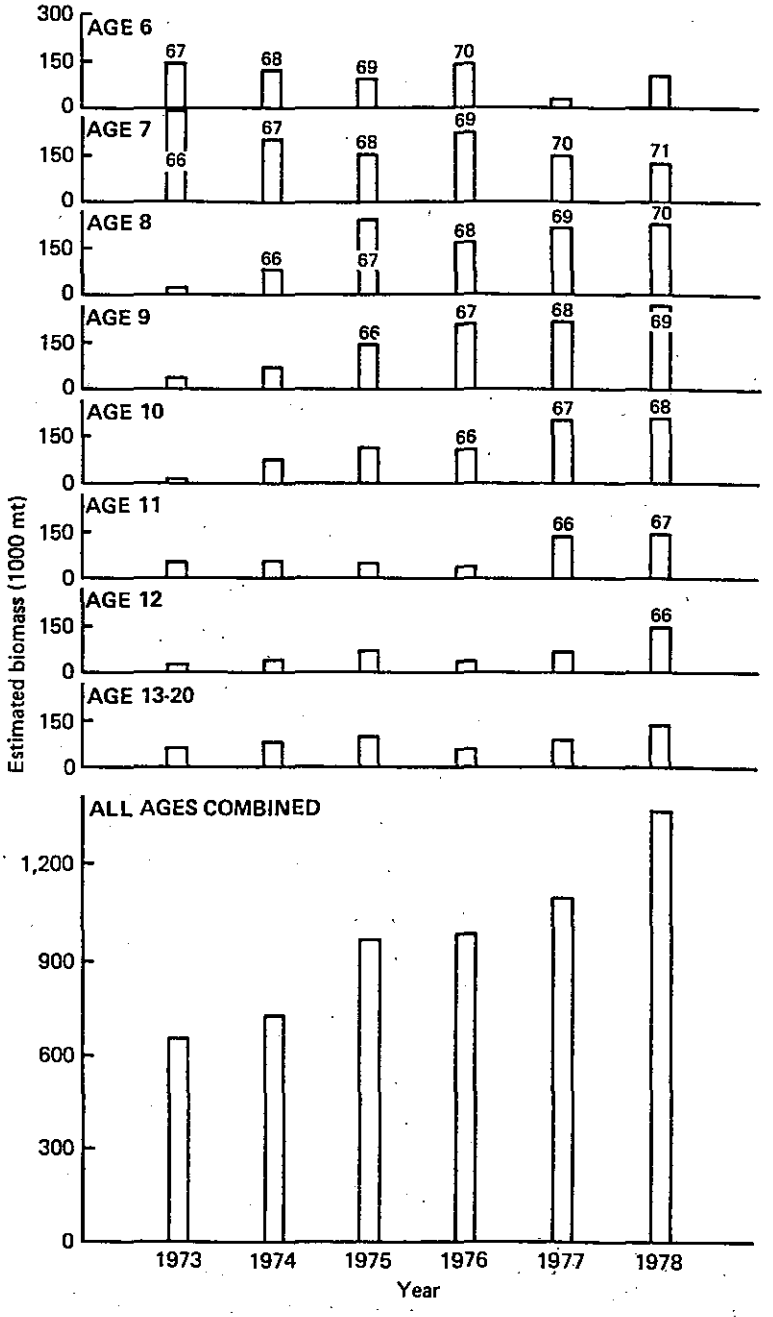


FIG. 3 Biomass estimates for the exploitable population of yellowfin sole in the southeast Bering Sea. Year-classes for certain ages are shown with appropriate bars.

the wintering concentrations near St. George Island and Unimak Island combine in spring prior to onshore migrations to areas off Bristol Bay (Wakabayashi et al. 1977). The wintering concentration of small fish in Bristol Bay is also thought to be a part of the Unimak Island-St. George Island group, perhaps representing a segment of the juvenile portion of the population.

The second largest wintering concentration, that located west of St. Paul Island, appears to remain relatively independent of the Unimak Island-St. George concentrations throughout the year. This group probably migrates inshore between St. Paul and St. Matthew islands and forms concentrations in the vicinity of Nunivak Island in summer.

The apparently independent movements and distributions of the St. Paul Island and Unimak Island-St. George Island populations have suggested the existence of independent spawning stocks of yellowfin sole in the eastern Bering Sea, a northern stock (St. Paul group) and a southern stock (Unimak Island-St. George Island-Bristol Bay group) (Wakabayashi 1974; Wakabayashi et al. 1977). Japanese tagging studies through 1973 indicated only limited mixing of the two groups (Wakabayashi 1974) and some studies suggested differences in biological characteristics (such as growth rates, length-weight relationships, and egg diameters) between populations in the proposed north and south stock areas (Kashkina 1965; Wakabayashi 1974).

Other studies of biological characters, however, have not supported the two stock concept (Fadeev 1970a; Wakabayashi 1974). In

addition, returns from Japanese tagging studies since 1973 have shown greater intermixing of fish between the proposed stock areas (see Fig. 4 for results of Japanese tagging results through 1977).

Results of biochemical genetic studies using electrophoretic techniques (Grant et al. 1978) have provided no evidence of major genetic differences between fish from the proposed north and south stock areas. The authors point out, however, that the samples on which the studies were based were not taken during the spawning season when the two stocks (if they exist) would be most clearly segregated. In addition, the findings of similar gene frequencies between fish from the two areas is not positive evidence that differentiation has not occurred. For example, if the populations had become isolated from one another in fairly recent times, genetic differences might not be easily detected with present electrophoretic methods.

Thus, although accumulating evidence from tagging and genetic studies tends to suggest the presence of a single spawning stock of yellowfin sole in the eastern Bering Sea, this question has not been entirely resolved.

BIOLOGICAL CHARACTERISTICS

Size Composition

The length range of yellowfin sole taken by U.S.S.R. research vessels in the eastern Bering Sea in the period of 1958-64 was 5-49

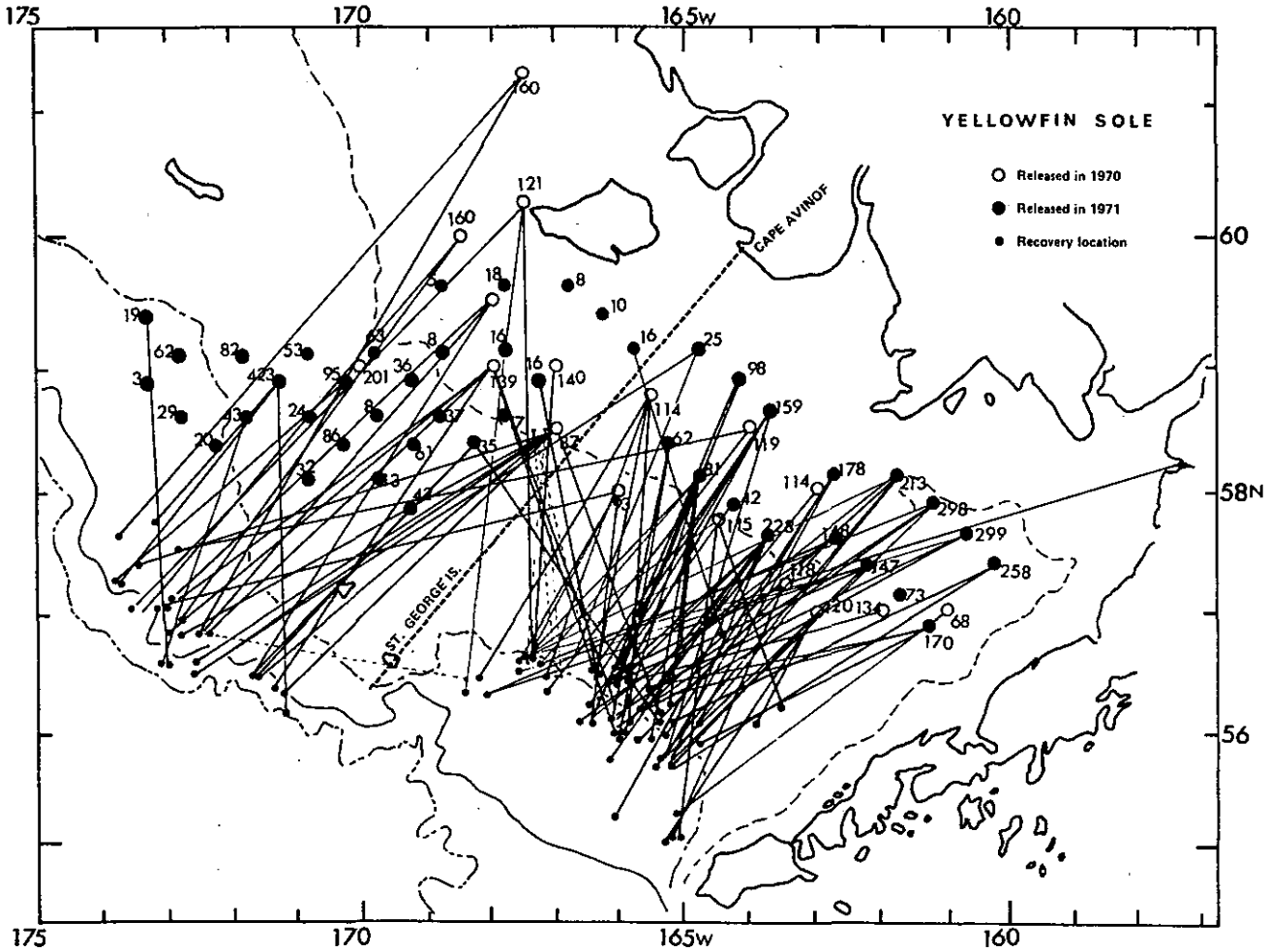


FIG. 4 Release and recovery locations of yellowfin sole tagged by Japanese research vessels in 1970 and 1971 and recovered by commercial fishing vessels (from Wakabayashi et al. 1977). Numbers of fish released are shown at each tagging location; a few fish (as indicated by light dashed lines) were released by commercial vessels. The heavy dashed line between St. George Island and Cape Avinof represents the line separating proposed north and south stock areas.

cm (Fadeev 1970a). The average size of fish taken by the commercial fishery was 26-27 cm in 1958 and 1959, years immediately preceding the period of intense exploitation of the population. The dominant sizes according to Fadeev (1970a) were 24-30 cm. In recent years, the average size has been about 25 cm in the commercial fishery.

Length data taken on large-scale Northwest and Alaska Fisheries Center (NWAFC) trawl surveys in 1975, 1976 and 1978 (Fig. 5) show fish ranging from 5-44 cm and averaging 22.2-22.6 cm for combined sexes. More than 96% of the surveyed population was less than 30 cm. The relatively high proportion of fish in the 12-16 cm range in 1978 represents the recruitment of the apparently strong year class of 1973.

Age Composition

The observed age range since the early 1970's has been 2-19 years for males and 2-21 years for females (Pereyra et al. 1976, Bakkala and Smith 1978); however, about 97% of the sampled population numbers were less than age 13.

Age data collected during NWAFC research vessel surveys and from the commercial fishery show the population undergoing marked changes in age structure during 1973-78 (Fig. 6). In 1973 a high proportion (86%) of the population sampled by research vessel surveys was made up of fish age 7 or younger, but by 1978 these age groups were only 36% of the sampled population, while fish age 8-11 were 54%. These changes are the result of the recruitment and advancement through the population of the series of relatively

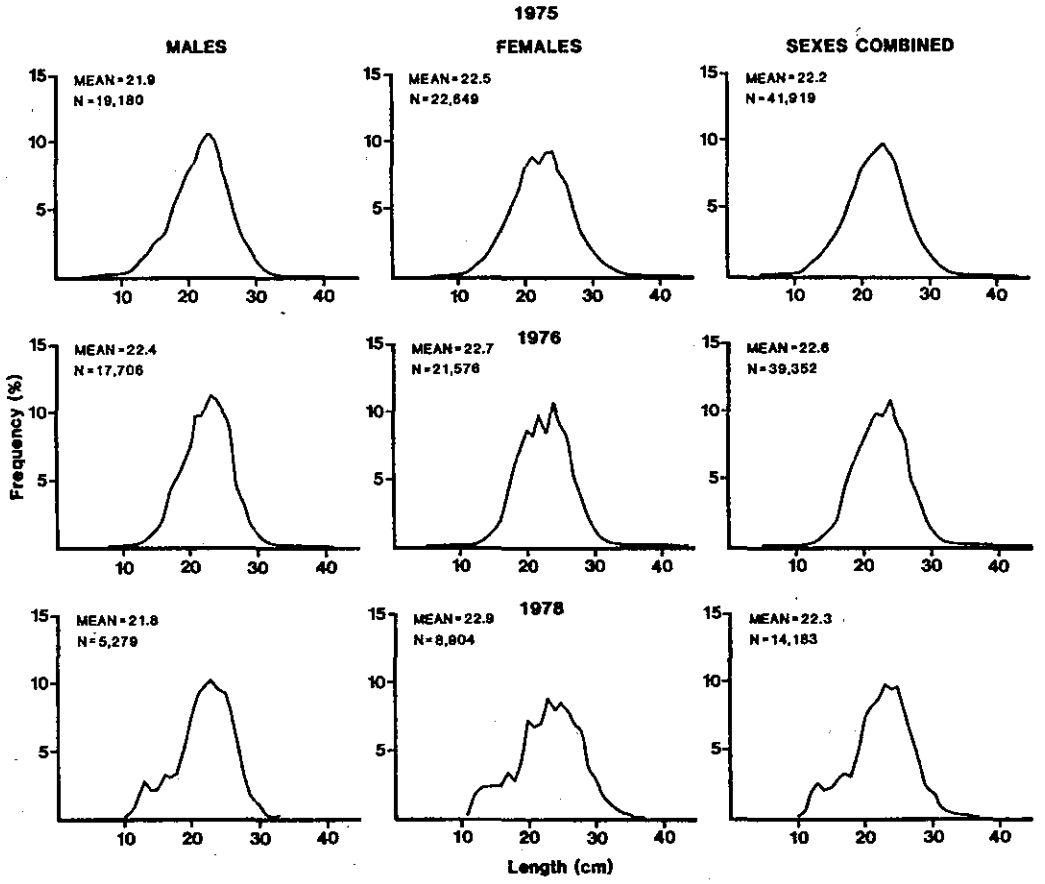


FIG. 5 Length composition of yellowfin sole of the eastern Bering Sea as determined by research vessel surveys in 1975, 1976 and 1978.

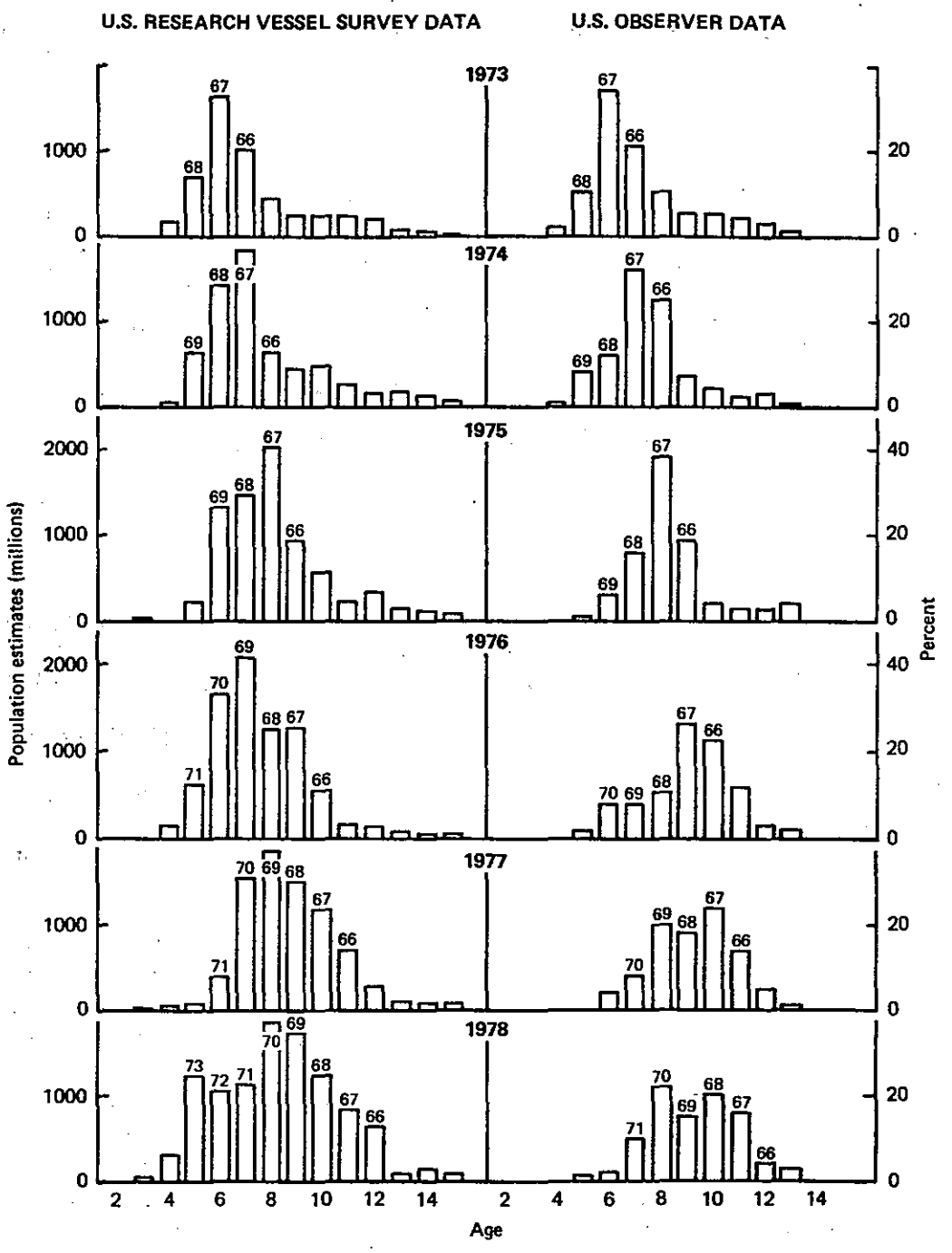


FIG. 6 Age composition of yellowfin sole as shown by data from NWAFC research vessel surveys in June-August and by U. S. observer samples from the Japanese flounder fishery in September-December. Year-classes for certain ages are shown above appropriate bars.

strong year-classes originating in the years 1966-70. Research vessel data indicate that the 1971 and 1972 year-classes may not be as abundant as those of 1966-70 but that the 1973 year-class may be of above average strength.

Size and Age at Maturity and Recruitment to the Fishery

Yellowfin sole begin to mature at a length of 10.5 cm for males and 18.5 cm for females (Wakabayashi 1974; see also Fig. 7). The length at which 50% of the population is mature is 12.8 cm for males and 25.2 cm for females. All males are mature at 25 cm and most females at 30 cm.

Based on samples collected in 1959-64, Fadeev (1970a) reported that males first begin to mature at 12 cm and females at 16-18 cm but that 50% of the population reached maturity at 16-18 cm for males and 30-32 cm for females. Wakabayashi (1974) suggested maturity may have been reached at a smaller size in 1973 because abundance of the population was lower than in 1959-64.

In relation to age, females begin to mature at age 6 and reach 50% maturity at about age 9; 100% of the females were mature at age 15 (Fig. 7).

Yellowfin sole first become recruited to the fishery at 13 or 14 cm which corresponds to ages 4-5. They become fully recruited to the fishery at age 7 (Laevastu and Favorite 1978) which is also about the age (7-8 years) when the exploitable stock reaches its maximum size in weight (Wakabayashi 1975).

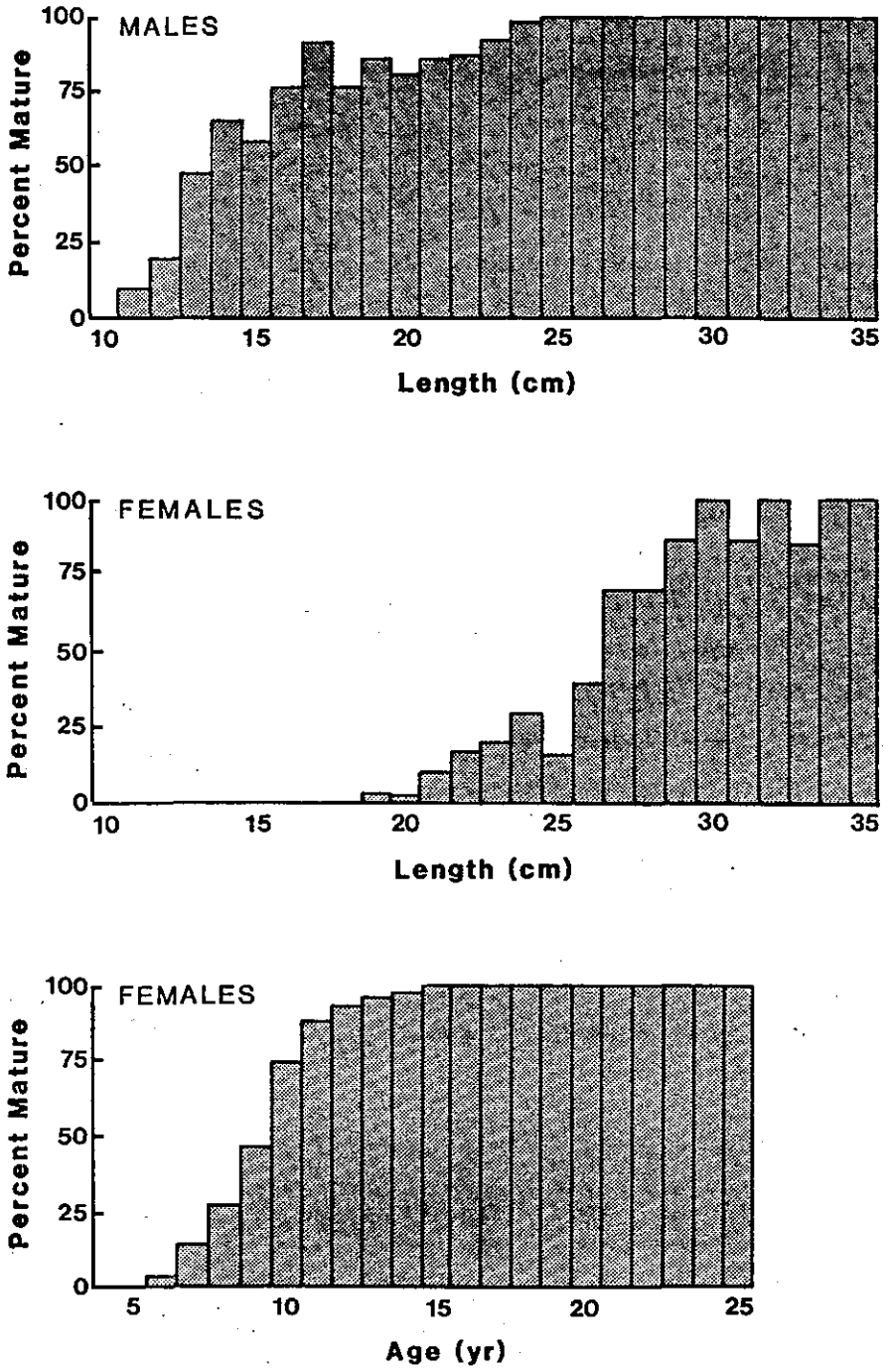


FIG. 7 Maturity composition of yellowfin sole from the eastern Bering Sea in May-June 1973, by length for males, by length and age for females (after Wakabayashi 1974).

Length-Weight Relationships, Growth, and Mortality

Length-weight relationships obtained in 1975 and 1976 show that females are only slightly heavier than males (approximately 1-10%) from lengths of 20-30 cm (Table III). Von Bertalanffy growth curves (Fig. 8) and their parameters (Table IV) illustrate the similarity in growth characteristics of males and females. Six-year means of observed lengths and calculated weights (Table V) indicate that annual increments of length increase from age 4 to age 6 and then decline at older ages. Annual increments of weight also increase from ages 4-6, but are relatively constant from ages 7-13. Laevastu and Livingston (1978) have also shown a decline in the growth rate between ages 7 and 8 that they attribute to a large portion of the population reaching sexual maturity at this age and the diversion of energy from growth to development of sex products.

TABLE V

Six Year Means of Observed Lengths and Calculated Weights at Age for Yellowfin Sole of the Eastern Bering Sea from NWAFC Survey Data of 1973-78.

Age	Mean Length (cm)	Annual Increment (cm)	Mean Weight (g)	Annual Increment (g)
3	12.0		19.5	
4	14.1	2.1	32.3	12.8
5	16.6	2.5	51.7	19.4
6	19.3	2.7	81.5	29.8
7	21.0	1.7	103.9	22.4
8	22.4	1.4	126.4	22.5
9	23.9	1.5	154.2	27.8
10	25.2	1.3	181.0	26.8
11	26.4	1.2	206.3	25.3
12	27.4	1.0	230.3	24.0
13	28.7	1.3	265.2	34.9
14	29.1	0.4	278.3	13.1
15	29.4	0.3	286.6	8.3

TABLE III

Length-Weight Relationships for Yellowfin Sole of the Eastern Bering Sea (data of Pereyra et al. 1976; Bakkala and Smith 1978).

Sex	Year	Time Period	Sample Size	Length Range of Sample	Length-Weight Coefficients		Predicted Weight (g) at length		
							10cm	20cm	30cm
Males	1975	Aug-Oct	701	7-40	0.0128	2.956	11.6	89.8	297.6
	1976	Apr-Jun	213	9-33	0.0208	2.779	12.4	85.6	264.2
Females	1975	Aug-Oct	844	8-40	0.0102	3.035	11.1	90.6	310.2
	1976	Apr-Jun	293	10-37	0.0168	2.870	12.4	91.1	291.9

TABLE IV

Growth Parameters for Yellowfin Sole of the Eastern Bering Sea (data of Pereyra et al. 1976; Bakkala and Smith 1978).

Sex	Year	Number of Age Readings	Age Range	Length Range	Standard Error of Curve Fit	Parameter		
						L_{oo}	K	t_o
Male	1975	609	0,8-15	0,17-30	1.50	40.79	0.11	0.22
	1976	507	0,4-12	0,13-33	0.31	31.88	0.17	-0.02
Female	1975	707	0,8-15	0,19-39	0.80	40.28	0.11	-0.09
	1976	600	0,4-14	0,13-36	0.66	32.23	0.18	0.10

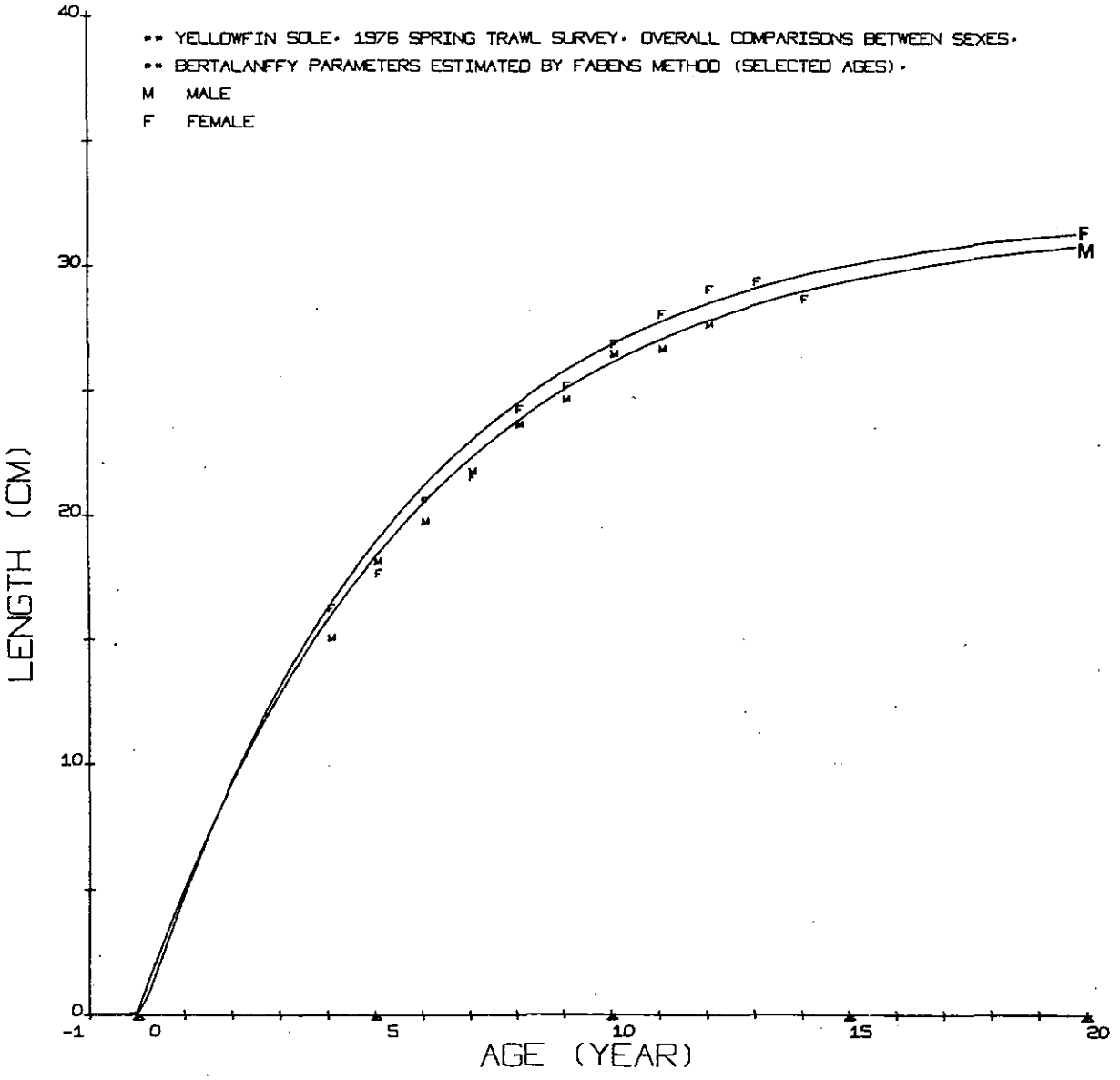


FIG. 8 Von Bertalanffy growth curves for yellowfin sole taken during spring 1976 (Bakkala and Smith 1978). Symbols indicate the mean length at each age.

Mortality decreases rapidly with age in juvenile year classes and reaches a minimum between ages 5-9, about the age of entry into the fishery. Mortality increases rapidly after the 9th year when a high proportion of the population reaches sexual maturity. The higher mortality of ages 10 and above may be due to spawning stress mortality.

Wakabayashi (1975) using the method of Alverson and Carney (1975) estimated instantaneous natural mortality (M) for age 4 and older fish as 0.25, corresponding to an annual mortality rate of 22%.

PREDATORS AND PREY

An important predator of yellowfin sole in the eastern Bering Sea according to Novikov (1964) is the halibut (*Hippoglossus stenolepis*). He found a close relationship between the distribution of halibut and that of yellowfin sole during the summer and autumn and suggested that the movements of halibut are governed to a large degree by the movements of its principal prey, yellowfin sole. The incidence of yellowfin sole in halibut stomachs in his studies ranged from 33-70% and, in terms of composition by weight, from 30-55% over various areas of the southeastern Bering Sea. Although there must be other predators of yellowfin sole, particularly during larval and juvenile stages, they have not been documented.

Yellowfin sole are capable of feeding on a variety of animals from strictly benthic forms such as clams and polychaete worms to zooplankton (mysids and euphausiids) to pelagic fish (capelin and

smelt) (Pereyra et al. 1976). About 50 different taxa have been found in stomachs of yellowfin sole in the eastern Bering Sea (Skalkin 1963). The kinds of organisms consumed vary by season, area, and size of fish. Feeding generally stops in winter although instances of fairly intense feeding have been recorded in this season (Fadeev 1970a). During the onshore migrations in May and June 1971, 73% of the fish that had wintered near Unimak Island were feeding, but feeding intensity was lower for fish that had wintered near St. George Island (0.05%), St. Paul Island (19%), and in Bristol Bay (0%) (Wakabayashi 1974). Feeding intensity increases as they move onto the central shelf and diet varies by area, apparently depending on the availability of food organisms. Fadeev (1970a) suggests that scarcity of benthic organisms results in a greater dependence on zooplankton for food.

Contents of 2,357 stomachs taken over a broad area of the eastern Bering Sea (Table VI) show that the primary food items, representing 65% of stomach content by weight, were bivalves, amphipods, polychaete worms and echiuroid worms. Polychaete worms and amphipods were the principal food items in smaller fish (10-20 cm), polychaete worms and bivalves followed by echiuroid worms and amphipods in larger fish (20-30 cm), and bivalves and echiuroid worms in fish greater than 30 cm.

SPECIES ASSOCIATIONS

Recurrent group analyses (Fager 1957, 1963; Fager and Longhurst 1968) have been used to demonstrate species associations within the demersal community of the eastern Bering Sea (Kihara 1976; Mito 1977;

Pereyra et al. 1976; Bakkala and Smith 1978). The procedure identifies species relationships on the basis of cooccurrence within samples. When joint occurrences are equal to or exceed 0.50, the species are considered to show affinity.

TABLE VI

Stomach Contents (in grams) by Size Group of Yellowfin Sole Collected in the Eastern Bering Sea in 1970 (Wakabayashi 1974).

Food Item	Size Group 101-200mm	201-300mm	300mm	Total
Gadidae	-	60.3	26.8	87.1
Osmeridae	-	12.7	-	12.7
Ammodytidae	-	12.5	56.4	68.9
Other Pisces	-	36.4	18.4	54.8
Amphipoda	22.6	180.2	45.3	248.1
Euphausiacea	1.6	61.7	38.1	101.4
Macrura	3.7	22.8	24.1	50.6
Mysidacea	0.4	-	0.2	0.6
Brachyura	-	39.4	7.8	47.2
Anomura	1.7	51.5	18.3	71.5
Crangonidae	0.3	10.0	0.8	11.1
Polychaeta	31.4	360.9	63.1	455.4
Cephalopoda	-	-	1.7	1.7
Bivalvia	6.5	403.6	553.1	963.2
Gastropoda	-	1.3	10.4	11.7
Ophiuroidea	2.3	36.1	1.4	39.8
Scutellidae	6.4	33.2	17.2	56.8
Echiurida	9.2	245.4	398.4	653.0
Ascidia	0.2	13.7	4.2	18.1
Holothuroidea	-	34.8	3.5	38.3
Sand[1/]	7.2	91.9	13.7	112.8
Others	12.8	108.2	163.6	284.6
Indistinct	12.9	64.2	27.7	104.8
Total	119.2	1,878.3	1,496.7	3,494.2
No. of Stomachs	275	1,708	374	2,357

1/ Possibly tubes of polychaeta.

The above four studies showed wide variation in the species that cooccurred with yellowfin sole. This might arise from differences in areas, time periods, and years of the surveys from which the data was analyzed. However, certain species cooccurred more consistently with yellowfin sole than others (Table VII): Alaska plaice were found to cooccur in all studies and rock sole and Pacific herring in more than one study. Pacific halibut was not one of the species showing close association with yellowfin sole based on recurrent group analysis as was suggested in the food habits study of halibut by Novikov (1964).

DISTRIBUTION AND SEASONAL MOVEMENTS OF ADULTS

Wakabayashi (1974) summarized Japanese commercial catch data from December 1967 to October 1968 to illustrate seasonal changes in fishing grounds. These data probably also generally illustrate seasonal changes in distribution of major concentrations (Fig. 9). In winter months (December-March), catches were concentrated near the 200 m isobath in the area west of the Pribilof Islands; but from the Pribilof Islands to Unimak Island, they occurred between 100-200 m. Beginning in April and clearly evident in May, major catches were made near the 100 m isobath or in even shallower areas. In June, largest catches occurred between 50-100 m and in July and August near the 50 m isobath. In September main catches again shifted to deeper water (50-100 m) and in October the greatest proportion of the catches near Unimak Island were taken at the 200 m isobath.

TABLE VII

Species Showing Close Association with Yellowfin Sole as Indicated by Recurrent Group Analysis.

Authority	Season	Years of Study	Species Showing Affinity with Yellowfin Sole
Kihara (1976)	Summer	1966-71, 1974	Alaska plaice (*Pleuronectes quadrituberculatus*)
			Rock sole (*Lepidopsetta bilineata*)
			Flathead sole (*Hippoglossoides elassodon*)
			Pacific cod (*Gadus macrocephalus*)
			Walleye pollock (*Theragra chalcogramma*)
			Cottidae
			Agonidae
Mito (1977)	Winter	1972, 1974-75	Alaska plaice (*P. quadrituberculatus*
			Rock sole (*L. bilineata*)
			Yellow Irish Lord (*Hemilepidotus jordani*)
			Plain sculpin (*Myoxocephalus jaok*)
Pereyra et al. (1976)	Summer	1975	Alaska plaice (*P. quadrituberculatus*)
			Pacific herring (*Clupea pallasi*)
Bakkala and Smith (1978)	Spring	1976	Alaska plaice (*P. quadrituberculatus*
			Pacific herring (*C. pallasi*)
			Sturgeon poacher (*Podothecus acipenserinus*)
			Capelin (*Mallotus villosus*)

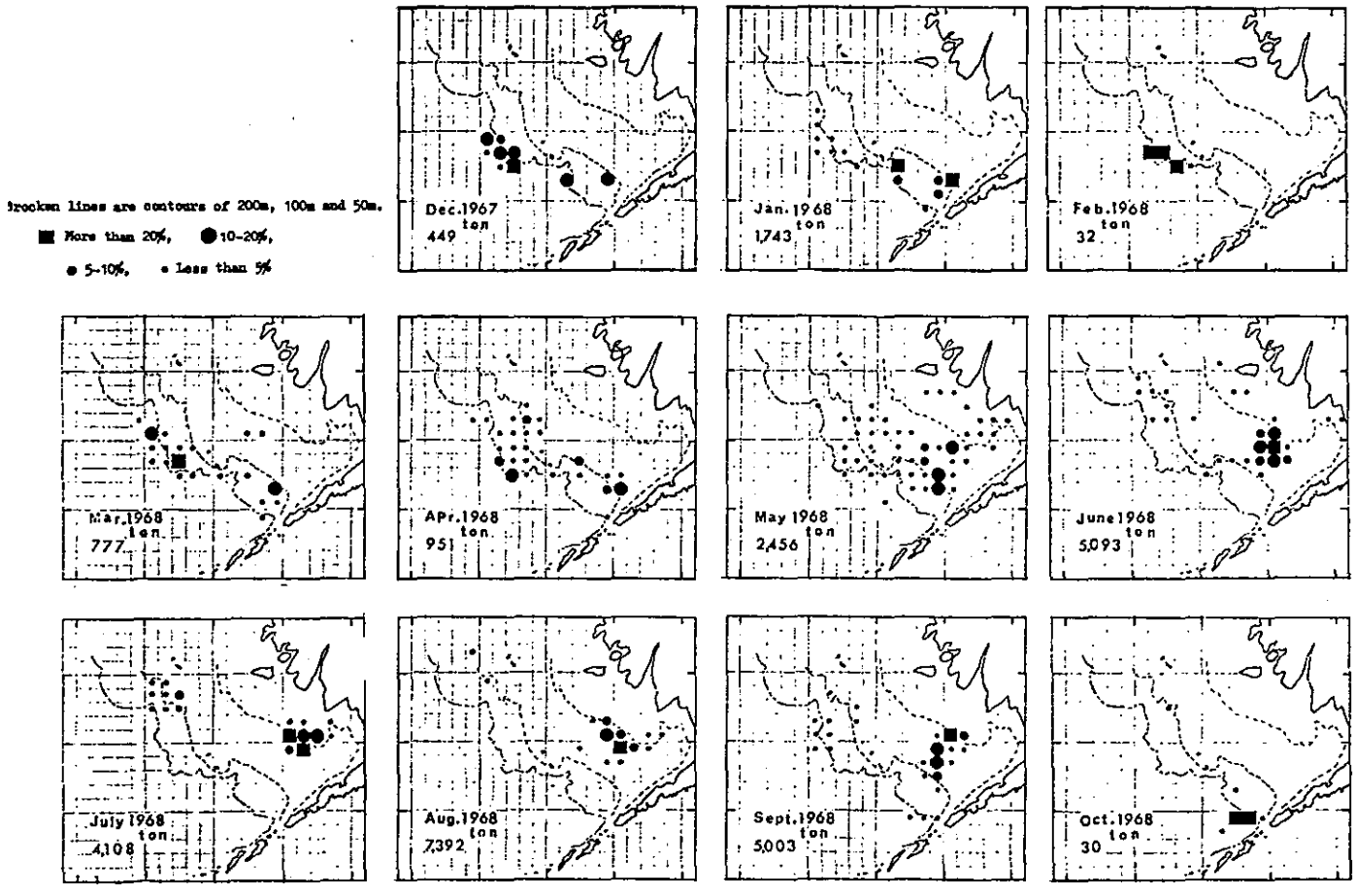


FIG. 9 Seasonal changes in Japanese fishing grounds for yellowfin sole, December 1967 to October 1968 (Wakabayashi 1974). Symbols represent the percentages of the total monthly catches taken in various 1/2° latitude and 1° longitude statistical blocks.

More recent data from a large-scale NWAFC trawl survey in April-June 1976 illustrate the apparent routes of movement during spring onshore migrations for the two major wintering concentrations located north of Unimak Island and west of St. Paul Island. The spring of 1976 was unusually cold and the location of the ice edge in April 1976 approximated an extreme southern location based on observations over the seventeen-year period of 1954-70 (Bakkala and Smith 1978). Because of the extensive ice cover, research vessel fishing operations in April were mainly limited to the outer shelf southeast of the Pribilof Islands. The Unimak Island wintering concentration was clearly evident north of Unimak Island immediately offshore of the ice edge (Fig. 10). Yellowfin sole were highly concentrated in this area with catch rates ranging up to 6,800 kg/km trawled. Bottom temperatures near the leading edge of this concentration were near 0 C and the densest portion of the concentration was located in bottom temperatures of 0.1-2.0 C.

In May, as the ice edge receded, the Unimak Island wintering concentration shifted eastward towards Bristol Bay, apparently moving with the receding ice edge and 0 C isotherm (Fig. 10). In June (Fig. 11), a number of independent concentrations were observed east of the location of the principal concentration observed in May. The nearshore concentration in Bristol Bay was made up of small fish not encountered in offshore waters. A concentration of juvenile fish was also observed in this area in spring by Fadeev (1970a) and, as noted in his findings, is believed to indicate overwintering in Bristol Bay.

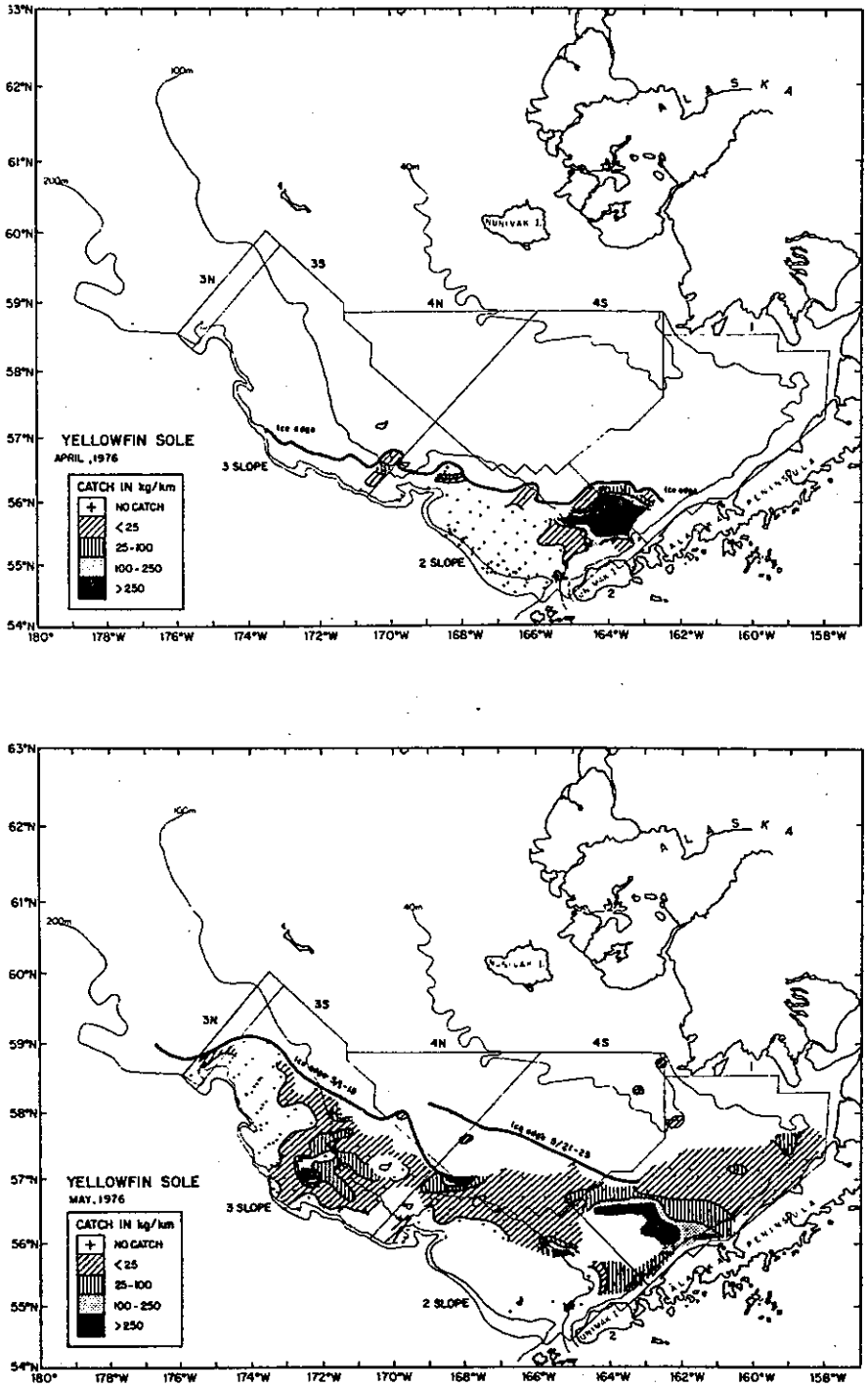


FIG. 10 Distribution and relative abundance of yellowfin sole in April and May as shown by a NWAFC trawl survey in 1976 (after Bakkala and Smith 1978). As indicated in the text, concentrations of yellowfin sole can be noted in the vicinity of Unimak Island, west of St. Paul Island and east of St. George Island.

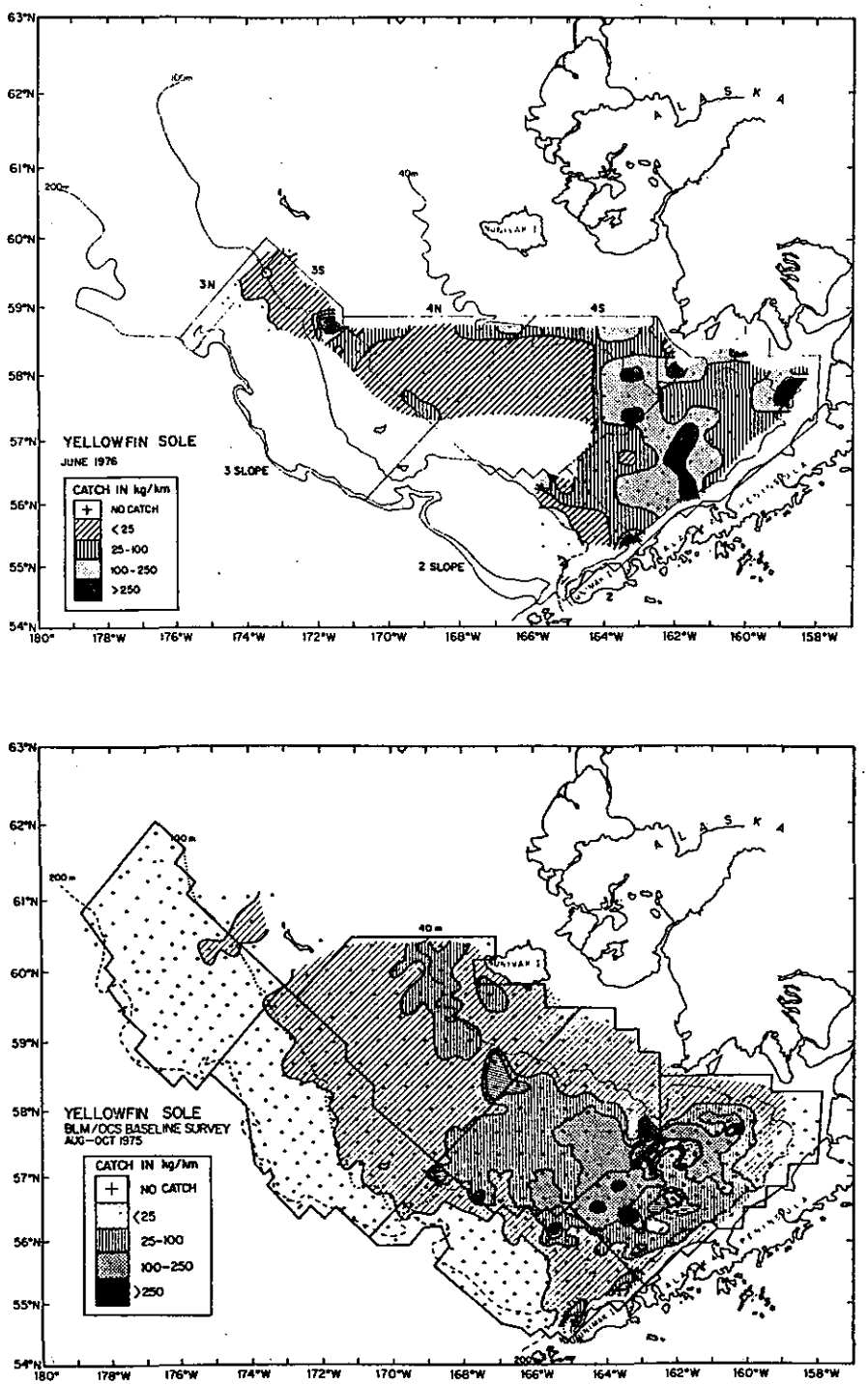


FIG. 11 Distribution and relative abundance of yellowfin sole in June 1976 and August-October 1975 as shown by NWAFC trawl surveys (after Bakkala and Smith 1978). As mentioned in the text, concentrations of yellowfin sole can be noted in Bristol Bay in June 1976 and on the inner shelf off Nunivak Island and in the southeastern Bering Sea in August-September 1975.

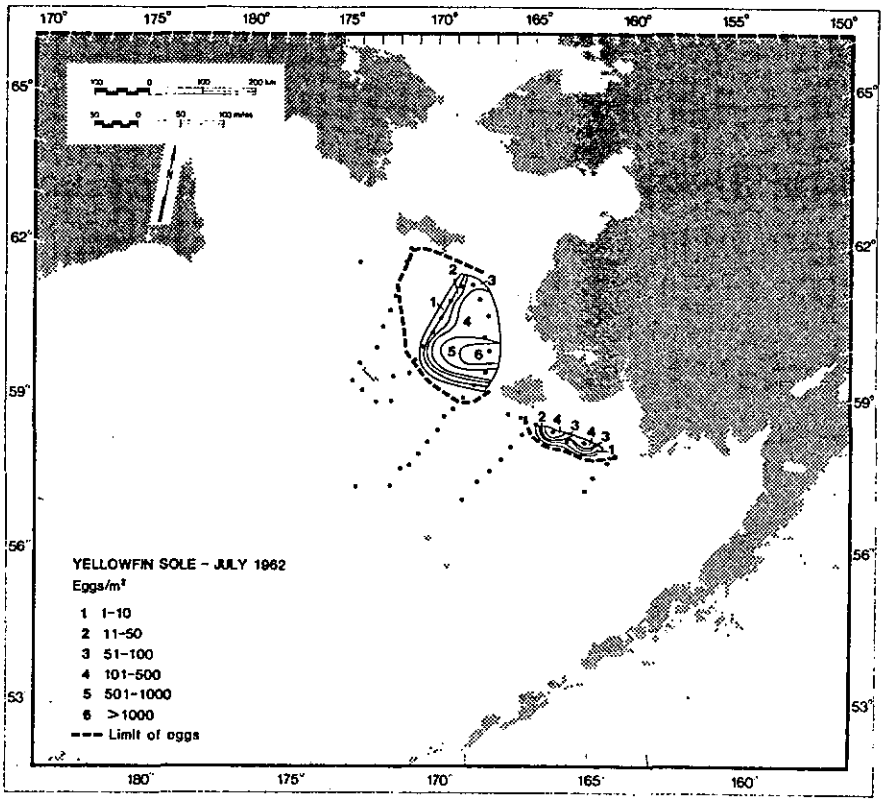
Based on survey data in August to October 1975 (see Fig. 11) and earlier survey data (see Figs. VIII-23 to 29 of Pereyra et al. 1976), yellowfin sole form a large summer concentration in outer Bristol Bay between the 40-100 m depth contours. Tagging data suggest that these fish winter off Unimak Island and St. George Island (see Fig. 4).

The second major wintering concentration that is located west of St. Paul Island may have been under the ice in April 1976 (see Fig. 10). This assumption is based on their location in May, an area covered by ice in April. In June, the concentration of fish located between St. Paul and St. Matthew Island may represent a migration of this wintering group towards Nunivak Island as Japanese tagging data show that most of these fish become distributed in the vicinity of Nunivak Island in summer (see Fig. 4).

DISTRIBUTION AND DISPERSION OF EGGS, LARVAE, AND JUVENILE FISH

The location and timing of spawning is based mainly on catches of eggs during plankton surveys; spawning adults have rarely been observed. Spawning begins in early July and probably terminates in September according to Musienko (1963). Eggs were observed over a broad area of the eastern Bering Sea shelf from off Bristol Bay to off Nunivak Island (Fig. 12), and densities indicated that spawning was most intense south and southeast of Nunivak Island. Depths of spawning ranged from 15-75 m.

Kashkina (1965) also observed spawning between Nunivak Island and St. Lawrence Island (see Fig. 12). Spawning also occurs in



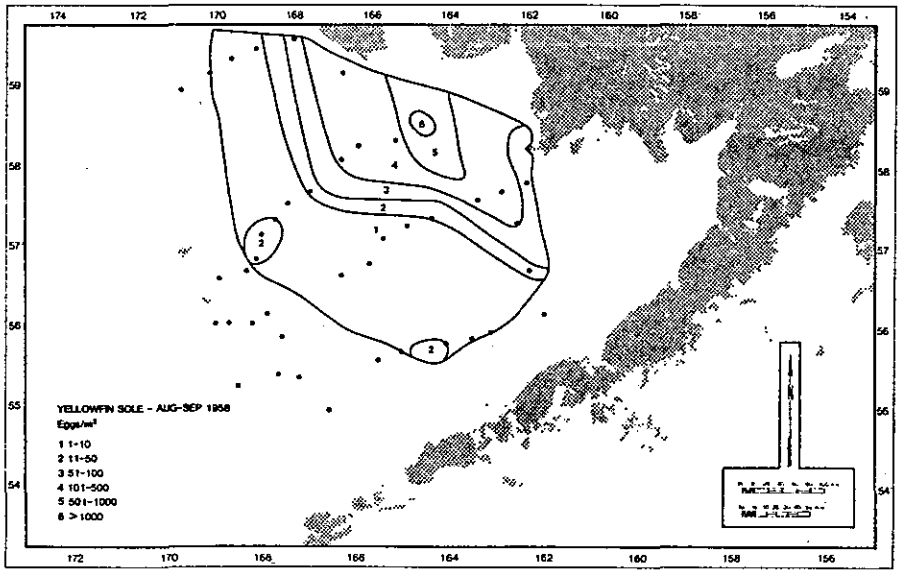


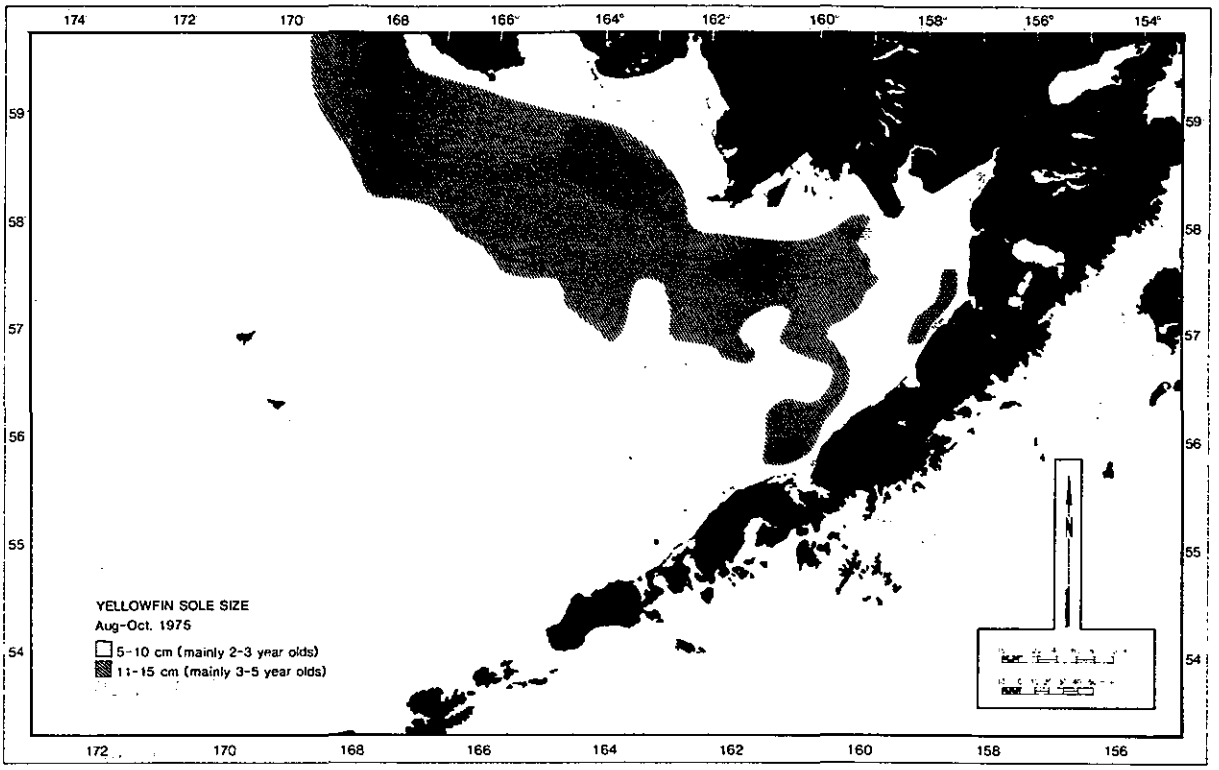
FIG. 12 Distribution of yellowfin sole eggs as shown by plankton surveys in July 1962 (upper panel; after Kashkina 1965) and in August-early September 1958 (lower panel; after Musienko 1963).

northern Bristol Bay based on my observations of females with "running" eggs in July 1979.

Eggs are pelagic, and laboratory studies of eggs from the Okhotsk Sea indicate that hatching occurs in about 4 days at 13 C. (Pertseva-Ostrovmova 1961). The lower threshhold temperature for successful egg development was 4 C. Eggs have been encountered in the eastern Bering Sea at temperatures of 6.4-11.4 C (Kashkina 1965; Musienko 1963). At hatching, the prolarvae are small (2.2-3.1 mm), transparent, have large yolk sacs, and are capable of swimming (Pertseva-Ostroumova 1961; Musienko 1963). About three days after hatching, the yolk sac is absorbed and the larvae begin to feed and at this stage range in length from 3.3-3.8 mm.

The time from hatching to metamorphosis to the juvenile stage is unknown. Partially metamorphosized young have been found in plankton hauls at 16.5-17.4 mm in length, but larger juveniles have not been collected in plankton tows and are assumed to have begun a bottom existence in shallow nearshore waters.

Juvenile yellowfin sole of 5-10 cm (2 and 3 year olds) are first observed in research vessel bottom trawls in inshore regions (Fig. 13). These age groups have been observed in low abundance off Kuskokwim Bay, in Bristol Bay, and along the Alaska Peninsula. They subsequently disperse to the more offshore waters occupied by adults, and at lengths of 16-20 cm (mainly 5-8 year olds) occupy much the same waters as the larger fish.



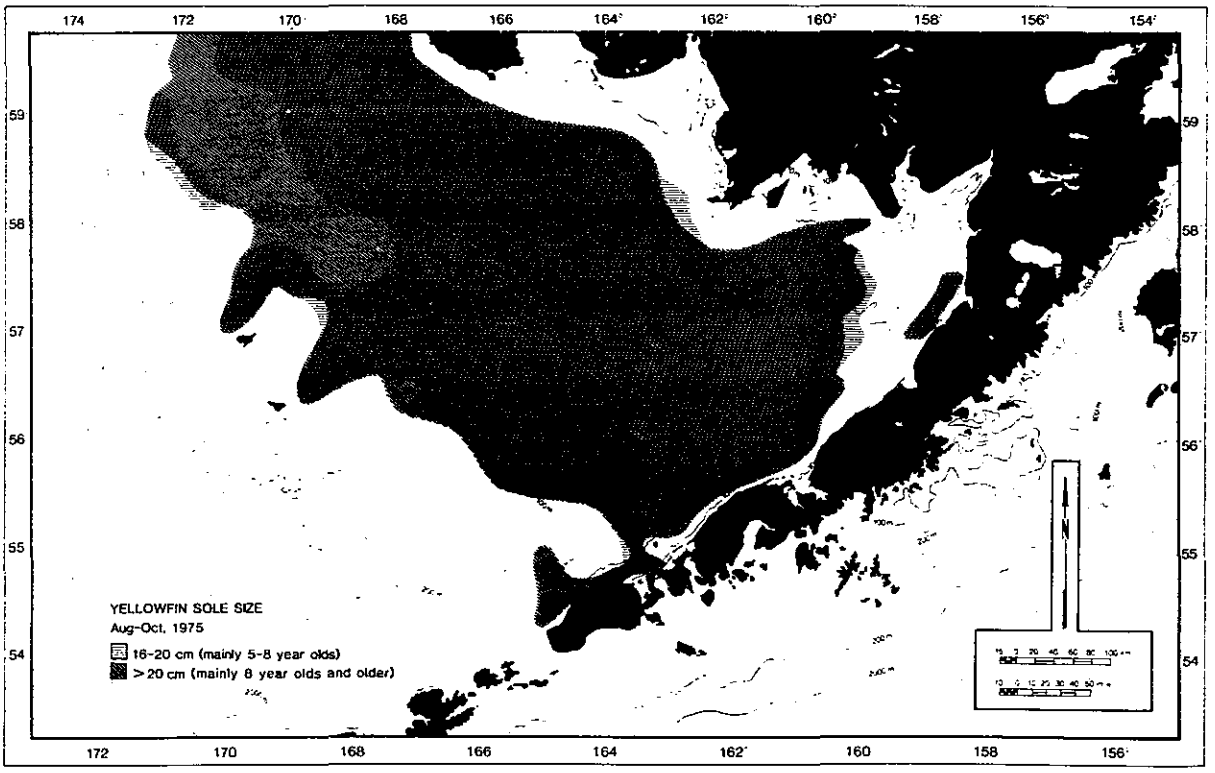


FIG. 13 Distribution of yellowfin sole by size group, August-October 1975.

ENVIRONMENTAL INFLUENCES ON THE RESOURCE

The eastern Bering Sea continental shelf is subject to wide fluctuations in environmental conditions both seasonally and annually. In winter and early spring much of the continental shelf may be covered by pack ice, but is ice-free by late sprng or early summer. Water temperatures under the pack ice are near the freezing point of seawater (-1.8 C) while bottom water temperatures on the shelf in summer may reach 10 C or more in shallow nearshore areas.

Annual variation in environmental conditions on the continental shelf have also been observed. Potocsky (1975) has documented the wide annual variation in distribution of pack ice in the eastern Bering Sea for the 17-year period of 1954-70. Annual variations in surface and bottom water temperatures have also been observed (McLain and Favorite 1976; Maeda 1977; Bakkala and Smith 1978).

As discussed in another Chapter (see, Shelf Environment), climatic conditions in the eastern Bering Sea appear to vary by multi-year cycles rather than randomly (Kihara 1977; McLain and Favorite 1976; Maeda 1977). These cycles are governed by the direction of prevailing winds. In years of prevailing northerly winds, the distribution of pack ice extends farther south and Alaskan Stream water entering the southeastern Bering Sea from the North Pacific Ocean is prevented from intruding onto the continental shelf. Prevailing southerly winds, on the other hand, limit the southward advance of pack ice in winter and allow Alaskan

Stream water to intrude onto the continental shelf in summer to replace residual cold water (0 C or less).

One multiyear temperature cycle in the eastern Bering Sea ended in 1976. Maeda (1977) has shown that temperatures increased from 1961-67 and then decreased from 1968-76. The 1971-76 period has been recognized as a particularly cold period in the eastern Bering Sea (McLain and Favorite 1976; Bakkala and Smith 1978). In 1977 and 1978, temperatures were again warmer than in the preceding six years.

Research vessel surveys to assess the condition of crab and groundfish resources in the eastern Bering Sea have been carried out by the NWAFC on an annual basis since 1971; a more comprehensive series of data is available from 1973. The 1973-78 time series provides information on the distribution and abundance of yellowfin sole during the last four years of the cold phase of the recent climatic cycle and the initial two years (1977-78) of a warmer phase. Examination of these data provides some evidence that the fluctuations in environmental conditions observed over the past several years may have influenced the distribution, migrations, and abundance of yellowfin sole.

Distribution and Migrations

Possible influences of pack ice on the distribution and migration of yellowfin sole are illustrated by data from an NWAFC survey in April-June 1976. Temperature conditions were unusually severe during the survey; bottom water temperatures in June of the survey period were the lowest recorded in the southeastern Bering Sea

since 1966 (Bakkala and Smith 1978), and during April, the ice edge approximated an extreme southern location based on 17-year observations of pack ice distribution in 1954-70 (Potocsky 1975). In April 1976, the leading edge of the large Unimak Island wintering concentration of yellowfin sole was near the ice edge with extremely dense concentrations of fish located immediately offshore from the ice edge (Fig. 14). The impression gained from these data is that the fish were highly concentrated, waiting for conditions favorable for initiating onshore movements. As shown by later survey data (see Fig. 10), this concentration moved inshore in May, apparently following the receding ice edge. The apparent sequence of behavior in relation to the ice edge suggests that the Unimak Island wintering group avoided migrating under the ice and that ice cover in spring 1976 may have delayed inshore migrations.

The seasonal timing of inshore migrations is not well defined although Fadeev (1970a) has observed inshore migrations starting from late April to mid-May over the three-year period of 1959-61. Ice-induced delays to spring migrations are probably infrequent and of relatively short duration. The ice must reach an extreme southern location in spring months, such as in 1976, to interfere with migrations beginning in late April and early May.

In contrast to this apparent avoidance of ice cover by the Unimak Island concentration, other concentrations of yellowfin sole may at times inhabit waters covered by pack ice. As shown earlier (see Fig. 10), the location of the St. Paul Island wintering

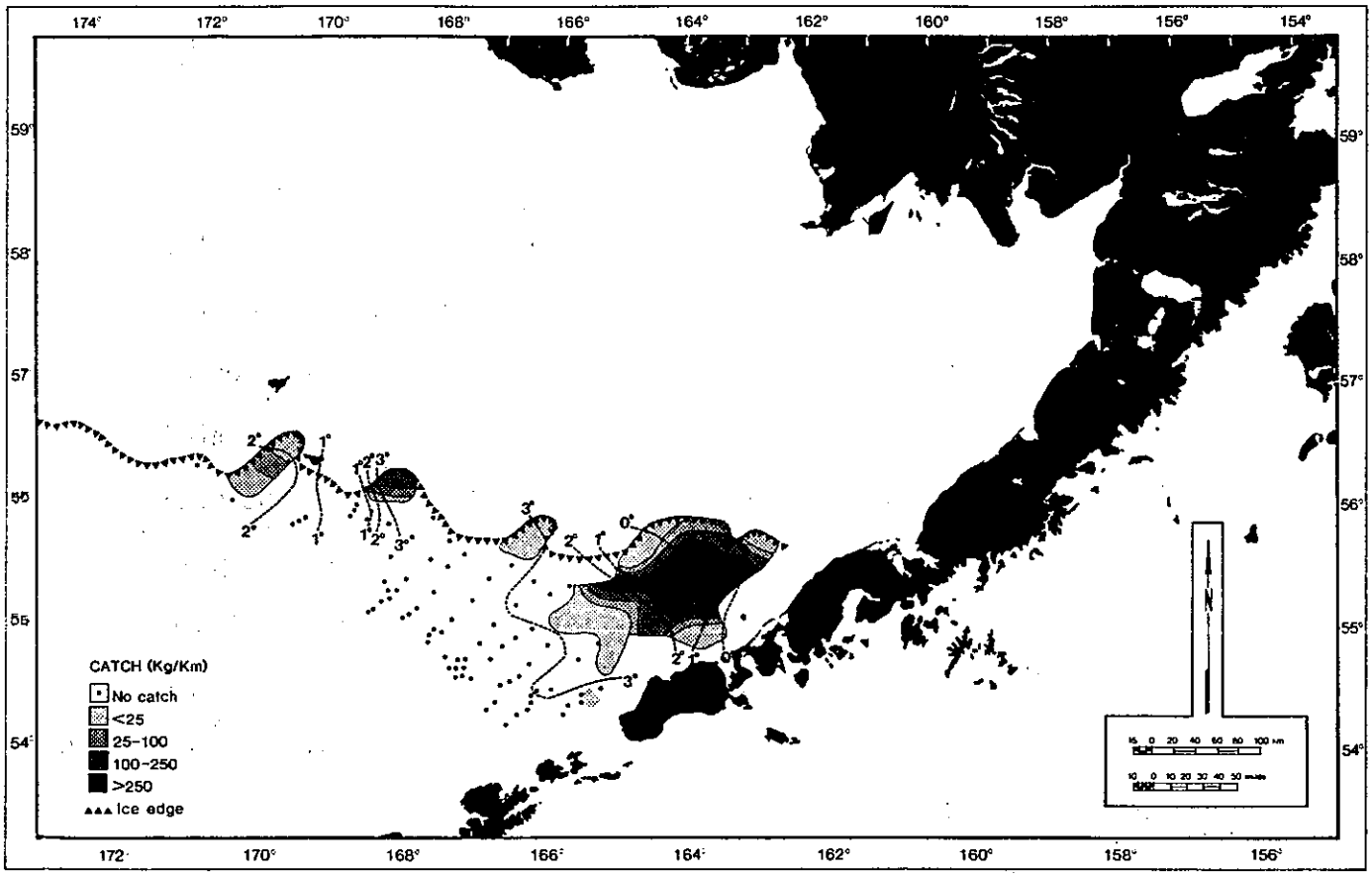


FIG. 14 Distribution of yellowfin sole in April 1976 relative to temperature contours and the edge of the pack ice.

concentration in May suggests that it was under the ice in April. That young yellowfin sole may overwinter under the pack ice in Bristol Bay has also been noted earlier.

Temperatures may also influence seasonal movements and distributions. Offshore movements in fall and winter may be an avoidance response to the cold bottom temperatures existing over the eastern Bering Sea shelf in winter. Most of the population winters on the outer continental shelf and slope in temperatures of 3.5-6.0 C (Fadeev 1970b). Spring onshore migrations, however, are not restricted by relatively cold water on the shelf; they commonly occur from relatively warm waters (up to 3-4 C) of the outer continental shelf to cold waters of the central shelf (Fadeev 1970b). The non-avoidance of cold water is illustrated by the survey data in April 1976 (see Fig. 14). Although warmer water in the range of 2-3 C was accessible to the Unimak Island wintering concentration farther offshore, they were mainly located in temperatures of 0-2 C, with largest catches in the vicinity of the 1-2 C isotherms.

Data from the series of NWAFC crab-groundfish surveys in June to mid-August 1973-78 illustrate the relationship of the distribution of yellowfin sole to temperature isotherms in early to mid-summer (Figs. 15 and 16). During this series of years, bottom water temperatures, encompassing the surveyed distribution of yellowfin sole, were variable ranging from relatively low in 1974, 1975 and 1976 to relatively high in 1973, 1977 and 1978. Highest catch rates (~200 kg/hectare) were located in a rather wide range of temperatures from -1 C to 7 C. Fadeev (1970b) has also commented

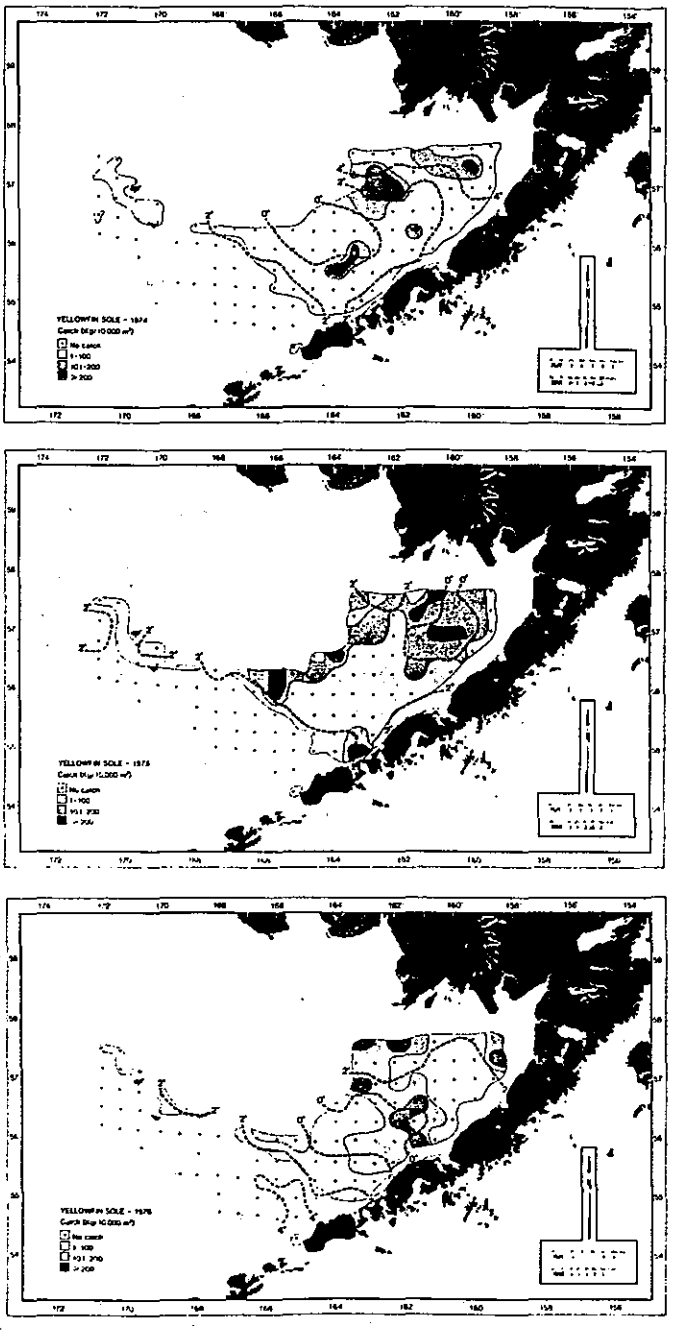


FIG. 15 Distribution of yellowfin sole in relation to isotherms in June-August during the relatively cold years of 1974, 1975 and 1976.

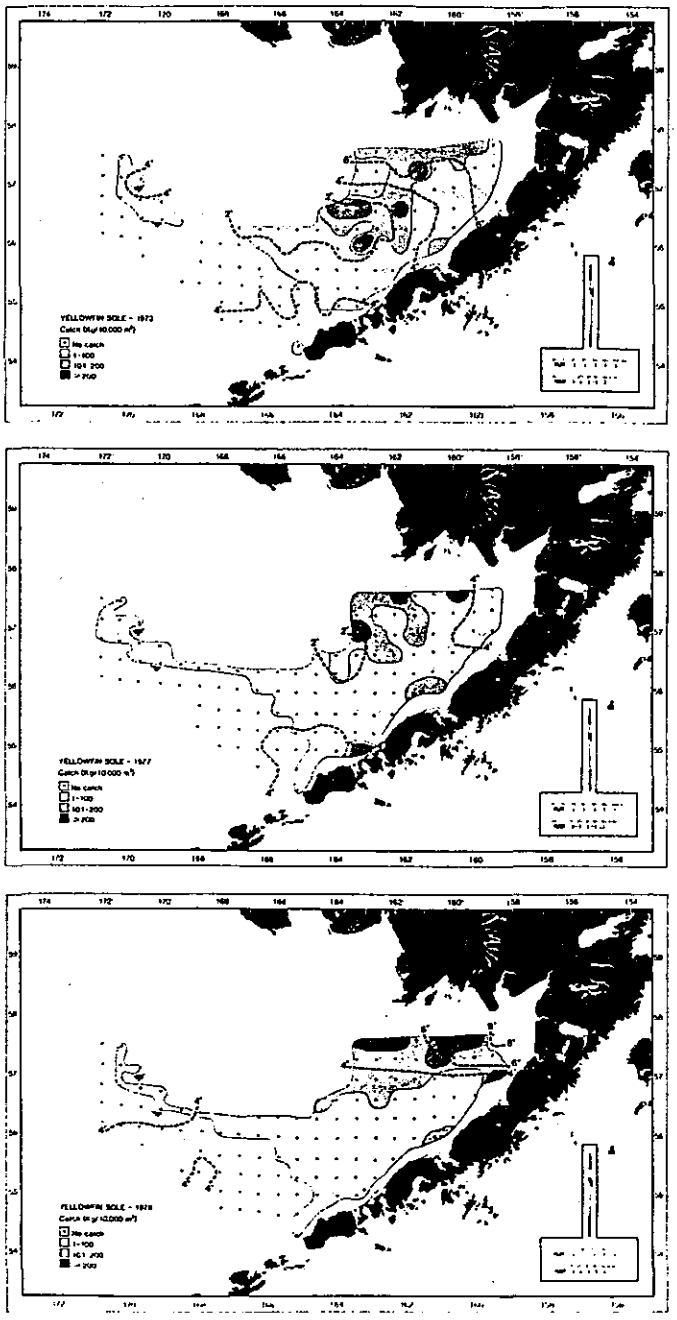


FIG. 16 Distribution of yellowfin sole in relation to isotherms in June-August during the relatively warm years of 1973, 1977 and 1978.

on the wide temperature range (0-10 or 11 C) inhabited by yellowfin sole in summer. His data showed highest catch rates in bottom water temperatures of 1-6 C.

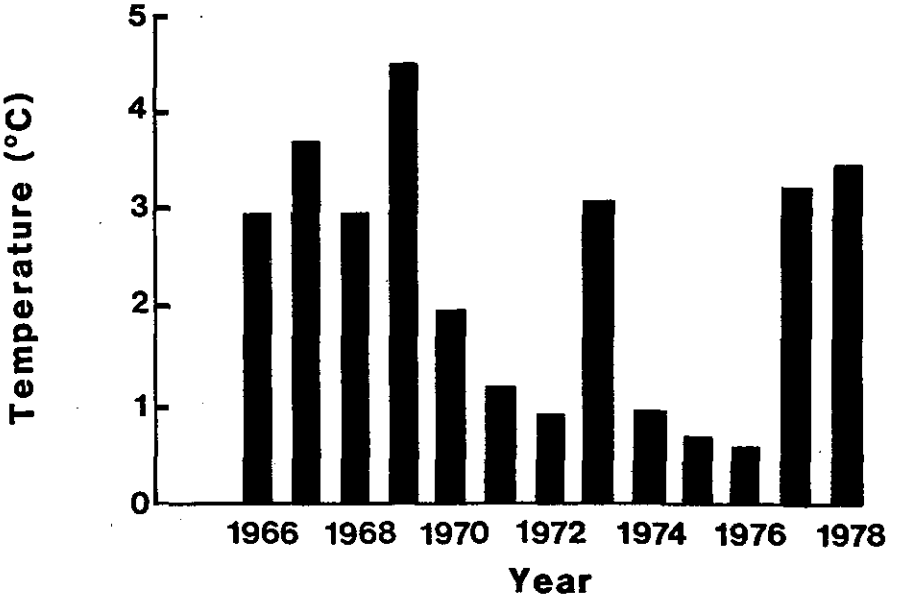
Although high concentrations were observed in a wide range of water temperatures during the 1973-78 crab-groundfish surveys, there was also some indication of differences in distribution relative to temperature conditions. In summer 1978, a relatively warm year, main concentrations were located in northern Bristol Bay. In the coldest years of the data series, 1975 and 1976, a number of widely separated concentrations were observed with some located far to the south and west of northern Bristol Bay. In 1973, 1974, and 1977, years of intermediate temperature conditions in the series, concentrations appeared to be located between the more northerly waters occupied in 1978 and the more southerly locations occupied by some of the concentrations in the colder years of 1975 and 1976. These data imply that the rate of migration to more northern waters of the inner shelf may be slower in cold years than in warm years or that summer distributions differ with temperature conditions.

Abundance

Accumulating evidence suggests that variations in water temperatures observed in the eastern Bering Sea may also affect the year-class strength of yellowfin sole. Maeda (1977) has shown predominant year-classes orginating in years of relatively high temperatures in the eastern Bering Sea and year-classes of below-average abundance originating in years of relatively low tempera-

tures. This relationship also appears to be evident with more recent data. Bottom water temperatures taken in the southeastern Bering Sea in June of 1966-78 are used as a measure of temperature variation and to relate to year-class abundance (Fig. 17). Year-classes originating in the warmer years of 1966- 70 when June bottom temperatures ranged from 2.0-4.5 C were relatively strong. In 1971 and 1972 when June bottom temperatures were colder (near 1.0 C), abundance of year-classes was much lower than in the previous five years. Based on this relationship, temperatures in succeeding years would indicate that the 1973 year-class will be relatively strong, but that the 1974, 1975, and 1976 year-classes may be relatively weak. Preliminary data suggest that the 1973 year-class is, in fact, relatively strong. Recruitment of the 1974-76 year-classes to research vessel gear is not yet adequate to measure their abundance.

Environmental conditions would be expected to have greatest influence on survival of yellowfin sole during early life history stages. Yellowfin sole spawn from July to September; and although June temperatures would therefore not be expected to directly influence the survival of eggs, larvae, or juvenile fish, they may provide an index to environmental conditions that will prevail during the subsequent spawning and early life history stages.



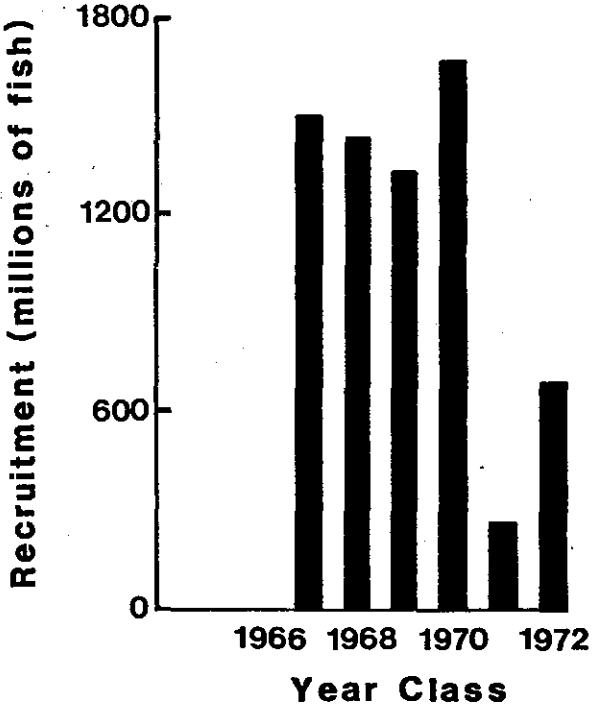


FIG. 17 Mean bottom water temperature in June at 34 standard survey stations in the southeastern Bering Sea (International Pacific Halibut Commission, 1976a,b; 1977; 1978) and year-class strengths of yellowfin sole. Year-class strength is based on estimated recruitment of age 6 fish measured by NWAFC research vessel surveys.

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TRANS-SHELF MOVEMENTS OF PACIFIC SALMON

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ABSTRACT

Five species of Pacific salmon are produced in the rivers and streams tributary to the Bering Sea shelf. All spend a portion of their juvenile and adult lives as residents of the shelf. Although this residency is transitory, salmon comprise a significant and highly variable portion of the total pelagic fish biomass of the shelf. Knowledge of the distribution and abundance of salmon while residents of the shelf is vital to our future attempts to assess the impact of their exploitation upon other living components of the shelf and man's modification of the shelf environment on the salmon resource.

Both maturing salmon and juvenile salmon are present on the shelf from May through September, but their migration routes do not overlap appreciably. Maturing salmon remain in the offshore waters of the shelf until within the vicinity of their home river systems. Juvenile salmon migrate seaward along the coast, eventually moving to offshore waters as their size increases. The shelf distribution of maturing salmon appears similar for all species migrating to rivers located in the same geographic areas. Chinook salmon are the first to enter the shelf during both spawning and seaward migration, followed in order by sockeye, chum, pink, and coho salmon.

Annual and seasonal variability in sea temperature, food type and abundance appear to influence the distribution, growth, and,

indirectly, the survival of salmon while residents of the shelf. Significant gaps exist in our knowledge of the shelf distribution and dynamics of Pacific salmon. The greatest contribution to this knowledge can accrue from studies conducted between 168°W and the shelf edge from 56°N-66°N.

INTRODUCTION

Five species of Pacific salmon, Oncorhynchus spp., are produced in the river systems tributary to the Bering Sea shelf. The sockeye salmon, O. nerka, is the most abundant species followed in order by chum salmon, O. keta; pink salmon, O. gorbuscha; chinook salmon, O tshawytscha; and coho salmon, O. kisutch; (Table I).

Salmon are anadromous, i.e., mature in the ocean and spawn in freshwater. All spend a portion of their juvenile and adult lives as residents of the Bering Sea shelf. Although this residency is transitory, salmon comprise a significant and highly variable portion of the total pelagic fish biomass of the Bering Sea shelf during spring and fall. Therefore, knowledge of the seasonal movements, migration routes, and magnitude of annual variations in the biomass of salmon while in this area is vital to future attempts to assess the impact of their exploitation upon other living components of the shelf ecosystem and man's physical modification of the shelf environment upon the salmon resource.

The greatest biomass of salmon (from commercial fishery catch statistics) originates from the rivers and streams flowing into Bristol Bay (Table I) at the southeastern terminus of the Bering Sea shelf (Fig. 1). Information from the early 1900's (Pravdin 1940) and recent data available at TINRO indicate that the rivers

TABLE I

Relative Abundance of Pacific Salmon (Oncorhynchus spp.) Produced in River Systems Tributary to the Bering Sea Shelf as Indicated by Average U. S. Commercial Catches (1961-77, inclusive[a])[b] and Available Soviet Catch Statistics[c] (in thousands of fish)

Area	Species					Total	Percentage of total of all areas
	Sockeye	Chum	Pink[d]	Chinook	Coho		
Bristol Bay	7,349.2	496.9	1,181.6	97.6	43.0	9,168.3	82.1
Gulf of Anadyr	150.0[e]	410.5[f]	9.9[g]	scarce	scarce	570.4	5.1
Yukon River	0.002	315.6	0.54	98.1	14.2	428.4	3.8
Alaska Peninsula (north side)	285.3	75.2	8.8	4.7	32.8	406.8	3.6
Kuskokwim Bay	9.0	90.6	26.3	38.7	78.4	243.0	2.2
Norton Sound	0.02	114.5	59.5	3.0	5.8	182.8	1.6
Kotzebue Sound[a]	0.006	168.1	0.004	0.003	--	168.1	1.5
Arctic coast[h]	i	j	j	i	--	--	--

[a]No reported catches for Kotzebue Sound in 1961.
[b]Source Alaska Department of Fish and Game, Juneau, Alaska.
[c]Pravdin (1940) and data available at TINRO.
[d]Even years only for U.S. waters.
[e]Even years only for U. S. waters.
[f]Average 1974-78 inclusive.
[g]Average 1975, 1977, and 1978.
[h]No estimates of number available.
[i]Unreliable reports of this species in American arctic rivers (Walters 1955).
[j]Documented reports of this species in Siberian and American rivers (Walters 1955).

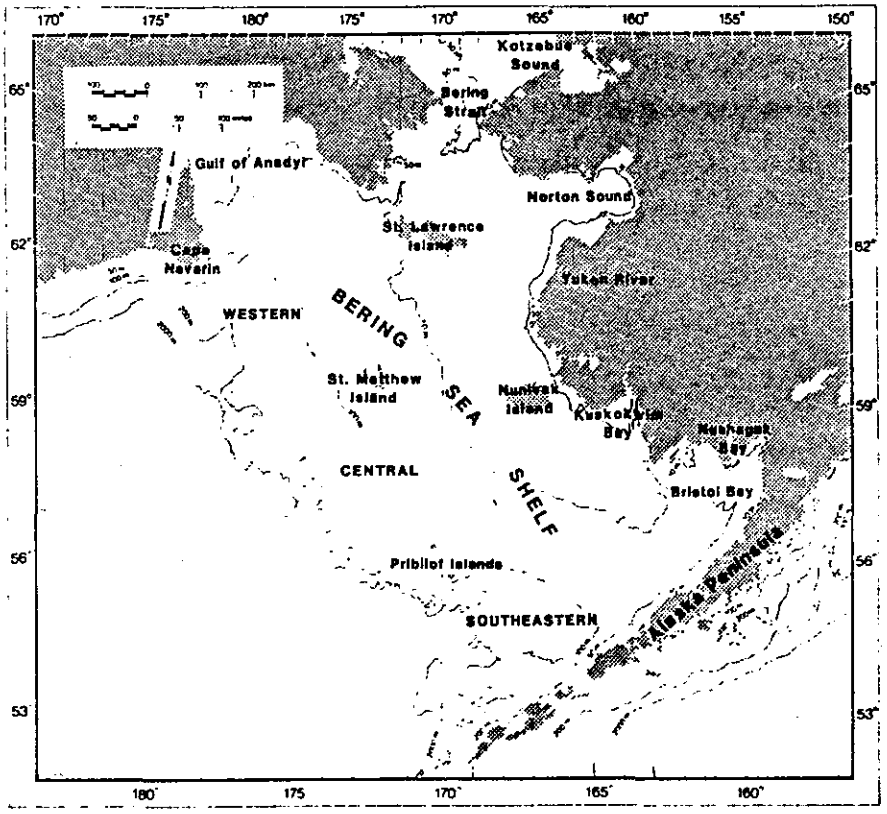

FIG. 1 Index map showing place names and locations of salmon-producing regions.

and streams flowing into the Gulf of Anadyr in the northwestern shelf area are a distant second to Bristol Bay in the biomass of salmon produced. Pacific salmon are produced in certain rivers of the Siberian and American arctic coasts (Walters 1955) but estimates of their relative abundance are not available. Apparently, chum salmon, Oncorhynchus keta, are sufficiently abundant in the lower Lena River, which enters the Siberian arctic, to support a commercial fishery. Salmon produced in arctic rivers must traverse the Bering Sea shelf and Bering Strait.

BIOLOGY OF PACIFIC SALMON

All species of Pacific salmon have similar life histories but differ in fecundity (Table II), food habits, growth rate, migration patterns, freshwater and ocean age, age and size at maturity, and time and location of spawning. In late summer and fall, salmon return from the sea to spawn in the rivers and streams from which they originated. Salmon cease feeding when they enter freshwater and derive their nourishment from body stores. All Pacific salmon die after spawning.

Salmon eggs are deposited in gravel beds of rivers, streams or lakes, and the eggs hatch during the winter. The young, known as alevins, remain in the gravel until their large yolk sacs have been absorbed and emerge from the gravel in the spring as fry. Greatest natural mortality occurs in this freshwater environment during the early life stages, and is greatly influenced by environment.

TABLE II

Life History of the Five Species of Pacific Salmon in Alaska
- exceptions are frequent - (from Bailey 1969; Merrell 1970; and Hartman 1971).

Species of Salmon	Freshwater habitat	Time spent in freshwater after emergence from gravel	Time spent at sea (yr)	Age at Spawning (yr)	Average adult weight[a] (kg)	Average number eggs per female (thousands)
Sockeye	short streams and lakes	12-36 months	1-4	3-6	2.27	3.5
Chum	short and long streams	1 month	2-4	3-5	2.96	3.0
Pink	short streams	1 day, usually	1	2	2.00[b]	2.0
Chinook	large rivers	3-12+ months	1-6	3-6	7.26	4.0
Coho	short streams and lakes	12-24 months	1-3	3-4	3.04	3.5

[a]Mean weight for Alaska Peninsula (north side), Bristol Bay, and Yukon River stocks combined. Source INPFC Statistical Year Book (1961).

[b]Mean for Alaska Peninsula (north side) and Bristol Bay only.

The fry of some species of salmon proceed immediately to sea; fry of other species reside in freshwater for a few weeks to one or more years. Depending upon the species, salmon usually spend from a few months to several years at sea (Table II).

Growth is slow during freshwater life, very rapid during the first summer or two at sea and slower thereafter. The growth rate of salmon in both freshwater and the ocean varies among species, years, and stocks of the same species. Regardless of the amount of time spent in freshwater, however, salmon attain most of their growth in the ocean.

Specific Life History Features

- Sockeye Salmon -- Because of the great abundance and high commercial value of sockeye salmon, it is probably the best researched species of all Pacific salmon and its life history is described in greater detail than the life history of other species of salmon of the Bering Sea shelf.

Sockeye salmon carry about 3,500 eggs and spawn in the inlet streams and lakes, lake outlets, and along the beaches of the lakes themselves. The eggs hatch during the winter, and inch-long fry emerge from the gravel in spring and enter the lakes.

After growing from one to four years in the nursery lakes, the fish, now known as smolts, migrate downstream after the spring ice-breakup in May or early June and enter the bays and esturies adjacent to the Bering Sea. At this time, depending on their freshwater age and the river system of origin, most smolts range between 70-115 mm in length and 7.8-9.6 g in weight (NMFS, ABL 1979 data).

Most sockeye salmon smolts enter the eastern Bering Sea at Age 1.0, or Age 2.0[1/], or in their second and third year of life. In Bristol Bay, the larger Age 2.0 sockeye salmon smolts precede Age 1.0 smolts in order of their entry into the Bering Sea.

The numbers of sockeye salmon smolts migrating seaward from Bristol Bay in a single year have been estimated at between 47-647 million (from returning adults and estimates of marine survival) (Rogers 1977) or 409-5,629 mt (from a mean weight of 8.7 g for Age 1.0 and Age 2.0 at the time they enter the Bristol Bay estuaries). Estimates of the numbers of sockeye salmon smolts entering the Bering Sea from areas other than Bristol Bay are unavailable at this writing.

After entering the estuaries of Bristol Bay, sockeye salmon smolts (hereafter referred to as juveniles[2/]) apparently do not immediately begin rapid growth (Straty 1974). True marine growth[3/] does not begin until the juveniles have been at sea for at least 4-6 weeks and have reached the more productive waters of outer Bristol Bay and the Bering Sea.

1/ Number of annuli in freshwater is indicated by figure preceding the decimal and the number of annuli in the ocean is indicated by the figure following the decimal. Thus, a 0.3 fish is one whose scales reflect 3 annuli at sea (freshwater age unspecified), a 2.0 fish is one whose scales show 2 annuli in freshwater (ocean age unspecified), and an Age 2.3 fish is one with 2 annuli in freshwater and 3 at sea. Total age (year of life) is obtained by adding one to the sum of the freshwater and ocean annuli. For example, an Age 2.3 fish is six years old.

2/ The term "juvenile" as used herein refers to seaward-migrating salmon of Age .0 which have already entered estuarine or marine waters.

3/ Marine growth is indicated by wide spacing of circuli as opposed to close spacing of circuli formed in freshwater.

After entering the eastern Bering Sea, the juvenile sockeye salmon migrate seaward and eventually enter the North Pacific ocean. Sockeye salmon spend from 1-4 years at sea, but most return to their rivers of origin after 2 or 3 years of ocean life at 4, 5 or 6 years of age.

Mature sockeye salmon weigh an average of 2.27 kg (see Table II) and range between 457-762 mm; some may exceed 4.54 kg (Hartman 1971). Runs of sockeye salmon returning to Bristol Bay tributaries from 1951 through 1976 have ranged between 2.4-53.1 million fish (mean, 15.68 million). Based on a mean weight of 2.27 kg per fish, this is equivalent to 5,443-120,429 mt.

- Chum Salmon -- The chum salmon is the second most abundant of the five species of Pacific salmon inhabiting the Bering Sea shelf (see Table I).

The fecundity of chum salmon averages 3,000 eggs per female and in late summer and fall eggs are deposited in gravel riffles of streams; some streams are close to tidewater, others, like tributaries of the Yukon River, are more than 1600 km from the sea. The next spring, chum salmon fry may immediately migrate downstream after emerging from the gravel and enter the sea, or they may remain in freshwater for several weeks.

Chum salmon fry range from 30-55 mm in length when they enter the estuaries and range from 100-150 mm when they enter the open sea (Fredin et al. 1977). Juvenile chum salmon have been captured with juvenile sockeye salmon in inner and outer Bristol Bay from

mid-July through August in 1967, 1969, and 1972 (NMFS, ABL data), indicating their seaward migration route is similar to that of the sockeye. In late July, the juvenile chum salmon in inner Bristol Bay are 79-128 mm; in late August after migrating to the outer bay they are 102-168 mm (the rivers of origin of these chum salmon were unknown); by September, juvenile chum salmon average between 170-220 mm (Hartt and Dell 1976).

Between 1950 and 1974, 23-134 million (median, 55 million) juvenile chum salmon entered Bristol Bay annually (Rogers 1977) -- 13.8-80.4 mt if the mean weight of Bristol Bay juvenile chum salmon (0.6 g) at entry into the estuary is used for calculatons. Estimates of the numbers of juvenile chum salmon entering the eastern Bering Sea from areas other than Bristol Bay are unavailable.

By late fall or early winter of their first year, juvenile chum salmon leave the Bering Sea (Fredin et al. 1977) and enter the North Pacific Ocean where they spend from one to six winters before reaching maturity; most return to spawn at 3, 4 or 5 years of age. Mature chum salmon in northwest Alaska are from 530-800 mm long and weigh 1.8-5.9 kg (Bakkala 1970).

Estimates of the annual adult chum salmon runs to Bristol Bay from 1951 through 1976 range between 0.5-2.7 million fish (Rogers 1977). Based on a mean weight of 2.96 kg per fish, the fish weigh a total of 1,481-7,997 mt.

- Pink Salmon -- Pink salmon rank third in abundance in the eastern Bering Sea and have the shortest and simplest life history of any Pacific salmon. Because of their rigid 2-year life cycle,

populations from any two consecutive years are genetically separated, and there is no consistent relationship between the even- and odd-year cycles.

Mature pink salmon average about 2,000 eggs per fish and eggs are deposited in late summer and in fall in stream riffles with gravel bottoms. Throughout much of their range, pink salmon usually spawn in the lower reaches of short streams, but in some tributaries of Bristol Bay, such as the Nushagak River, they may spawn more than 180 km from saltwater.

Pink salmon have a short freshwater life because the fry proceed seaward shortly after emergence from the gravel in spring. At this time, the fry are just over 25 mm long (Bailey 1969). In the estuaries of upper Bristol Bay (Nushagak Bay), juvenile pink salmon this size have been observed around cannery docks in early June (Mike Nelson, ADF&G, personal communication). In mid to late August 1969, juvenile pink salmon captured in inner Bristol Bay were from 68-98 mm.

Between 300,000 and 203 million juvenile pink salmon entered Bristol Bay in odd years between 1951 and 1975, inclusive (Rogers 1977). Based on a mean weight of 260 mg per fry for 32.5 mm fry (Bailey and Pella 1976), this is equivalent to between 78 kg and 53 mt.

Juvenile pink salmon produced in river and stream systems adjacent to the eastern Bering Sea migrate to the North Pacific Ocean where they grow to maturity (Thorsteinson 1959). All pink salmon mature after a year in the ocean and return to freshwater to spawn.

At maturity, they are the smallest of five North American Pacific salmon species and average about 2.0 kg.

Currently, the largest runs of pink salmon to Bristol Bay occur in the even years (Stern et al. 1976). Historically, small runs occurred in both even and odd years until the mid-1950's. From 1951 through 1976, pink salmon runs to Bristol Bay have ranged between 0.1-4.1 million fish; equivalent to 200-8,201 mt if 2.0 kg is used as the mean weight per fish.

- Chinook Salmon -- Based on catch data alone, chinook salmon rank fourth in abundance in the Bering Sea and they are the largest and most fecund of the Pacific salmon, averaging 4,000 eggs.

Chinook salmon generally spawn in larger rivers, like the Nushagak River in Bristol Bay, the Kuskokwim River, and the Yukon River. Eggs are deposited in areas of coarse to fine gravel and sand that are characterized by stream underflow rather than upwelling groundwater (Major et al. 1978). Eggs hatch in late winter or early spring, and the fry spend from a few months to more than a year in freshwater before migrating to sea. Most smolts entering the Bering Sea from the Yukon River (Trasky 1974), and probably from other major rivers systems as well, appear to be in their second year of freshwater life (the scales of these fish possess one freshwater annulus).

Adequate data are not available on the mean length and weight of smolts when they enter the Bering Sea estuaries. The mean length and mean weight of 488 Salcha River chinook salmon smolts in their second year of life were 73.0 mm and 4.3 g, respectively

(Trasky 1974), but the mean size was undoubtedly somewhat larger by the time they entered the Bering Sea, 1500 km downstream.

Estimates of mean and peak numbers of chinook salmon smolts entering the Bering Sea from Bristol Bay and the north side of the Alaska Peninsula river systems from 1955 through 1975 (Stern et al. 1976) are 4.3 and 10 million fish, respectively; or an average of 18.5 mt and a peak of 43 mt of smolts (calculated from the average size of Salcha River smolts entering the Bering Sea). Estimates of the numbers of chinook salmon smolts entering the Bering Sea from other river systems are not available.

In general, juvenile chinook salmon tend to be close to shore during their first summer in the ocean (Major et al. 1978). A few juveniles in their first year of ocean life were taken in the eastern Bering Sea during June through August 1956-70 (Hartt and Dell 1976). Except the few chinook salmon smolts captured in extreme inner Bristol Bay in early June 1966, none were taken in subsequent purse-seine hauls (NMFS, ABL 1966 data) between late June and August 1967 and 1969-72. Young chinook salmon (judged by their 26-35 mm fork lengths to have been in their first year of ocean life) have been taken in bottom trawls during mid-winter near the shelf edge in the central Bering Sea (Major et al. 1978).

The central Bering Sea (as far west as 172°12'E) may be a feeding ground or migration path for immature western Alaska chinook salmon stocks (Major et al. 1978). Scale pattern studies also indicate, tentatively, that they may extend from 160-170°E to at least 175°W in the North Pacific Ocean.

Chinook salmon, the largest of the five species of Pacific salmon, mature and return to spawn after 1-6 years at sea, but from Bristol Bay northward, most returning to spawn have spent 4-5 years at sea.

The size of the total run of mature chinook salmon returning to Bristol Bay from 1951-1976 has been estimated at approximately 60,000-240,000 fish (Rogers 1977); 436-1,743 mt (calculated with 7.26 kg, the average weight of a mature chinook salmon).

- Coho Salmon -- Coho salmon are the least abundant of the Pacific salmon native to the Bering Sea shelf (see Table I), have an average of 3,500 eggs per fish, and spawn in late summer and fall. The progeny emerge from the gravel the following spring and reside in rivers or lakes for 1 to 2 years (see Table II)

Coho salmon smolts from the Karluk River on Kodiak Island apparently migrate seaward somewhat later than sockeye salmon smolts (Drucker 1972) when the water is warmer; and the same pattern is believed to occur in the eastern Bering Sea.

Few measurements or weights are available for coho salmon when they enter the Bering Sea. Juvenile coho salmon captured in purse seiners by ABL in Bristol Bay in late June 1969 ranged between 122-145 mm; most were probably Age 2.0 juveniles. Drucker (1972) gives the size range of Karluk Lake coho salmon smolts as mean lengths of 136.3-141.7 mm, with mean weights of 26.4-30.7 g, respectively.

The estimated mean and peak number of coho salmon smolts entering the Bering Sea from Bristol Bay and the north side of the

Alaska Peninsula river systems are 3.3 and 7.2 million fish, respectively (Stern et al. 1976). If a mean weight of 29 g per fish for all freshwater age groups of coho salmon smolts entering the Bering Sea is assumed, this is equivalent to an average of 96 mt and a peak of 209 mt. No estimates of the numbers of coho salmon smolts entering the Bering Sea from other river systems adjacent to the Bering Sea shelf are available.

Bristol Bay juvenile coho salmon probably migrate seaward along a route similar to that followed by juvenile sockeye salmon. Juvenile coho salmon have been captured with juvenile sockeye salmon in the same area between late June and October (NMFS, ABL 1966, 1967 and 1970 data; Hartt and Dell 1976).

Juvenile coho salmon stocks of western Alaska origin apparently enter the North Pacific Ocean where most spend about 18 months at sea before returning to their river systems of origin to spawn (while at sea, they grow more rapidly than other species of salmon, including the pink salmon whose ocean life is also 18 months, Fredin et al. 1977).

Mature coho salmon average 3.04 kg. The estimated mean and peak numbers of mature coho salmon returning to Bristol Bay between 1955 and 1975 is 98,600 and 253,400 fish, respectively (Stern et al. 1976) -- a mean of 271 mt and a peak of 698 mt.

Seasonal Movements

The marine life of Pacific salmon (beginning 1 January) may be divided into three phases: ocean life, spawning migration and seaward migration. The seasonal timing and length of each phase is

species and stock specific, and fluctuates, within limits, because of environmental variation.

- Ocean Life -- When salmon are distributed throughout the vast area of the Bering Sea and North Pacific Ocean (French et al. 1975), they undergo rapid growth and attain sexual maturity. This period of ocean life may last from a few months to several years depending on the species of salmon (see Table II) and ocean growing conditions. More than one generation of sockeye, chum, chinook, and coho salmon are present together during ocean life. Immature and maturing salmon of different races, ocean ages, and continents or geographic areas of origin may, depending on the season, become segregated from or intermix with one another (Royce et al. 1968). Immature chinook salmon (Age 0.1) apparently are abundant in the central Bering Sea near the edge of the continental shelf in June and July (Major et al. 1978). Immature chum salmon, older than Age 0.1, have been captured in research gillnets in July in the western Bering sea shelf and slope area in the vicinity of Cape Navarin and the Gulf of Anadyr (Nishiyama et al. 1968). A few immature chum and sockeye salmon have also been taken during research fishing on the Bering Sea shelf as far north as 62°N in late July (Yonemori 1967).

Research fishing and salmon tagging have been conducted on the Bering Sea shelf only during the spring, summer, and early fall periods when juvenile salmon are migrating seaward and maturing salmon are migrating to spawning grounds. The species composition and proportion of immatures of Age 0.1 or older, of maturing salmon, and of seaward-migrating juvenile salmon residing in the shelf

area between November and April are unknown but are probably negligible. Young chinook salmon (judged by their 26-35 cm fork lengths to have been in their first year in the ocean) have been taken incidentally by a Japanese trawler fishing in mid-winter for walleye pollock, Theragra chalcogramma, in the eastern Bering Sea at the shelf edge near 56°N, 168°W and 56°N, 173°W (Major et al. 1978).

- General Spawning Migration -- The spawning migration, the time sexually-maturing fish leave the high seas of the North Pacific Ocean and western and central Bering Sea until the time they arrive at the mouths of their respective home streams or river systems, is species and stock specific. Maturing salmon are most abundant on the Bering Sea shelf from mid-May to early September (Table III). Maturing chinook salmon are the first to enter the Bering Sea shelf followed in order by sockeye, summer chum, pink, fall chum, and coho salmon. The length of time a given salmon stock is present and its distribution in the shelf area during spawning migration depends upon the geographic location of its home river system, the size and/or ocean age of individual fish comprising the population, and environmental factors which influence the rate of migration and directional movements.

Sockeye, chum and pink salmon have been captured in varying numbers during United States and Japanese research fishing and tagging studies at numerous locations throughout the shelf during spawning migration. The number of catches of chinook and coho salmon, however, have been lower because of the lower abundance of these species and because research fishing has not taken place when

TABLE III

Inclusive Dates of Peak Abundance of Maturing Pacific Salmon on the Bering Sea Shelf during Spawning Migration (from commerical fishery and test fishing catches and migration rates).

	Salmon species					
		Chum				
Location	Sockeye	(summer)	(fall)	Pink	Chinook	Coho
Estimated at Shelf edge[a]	15 June-25 Jun	22 June-13 Jul	-	5 Jul-15 Jul	30 May-19 Jun	20 Jul-2 Aug
Estuaries or river entrances:						
Alaska Peninsula[b]	20 June-25 Aug[c]	4 Jul-25 Jul	20 Jul-20 Aug	1 Aug-15 Aug	1 June-20 Jun	10 Aug-10 Sep
Bristol Bay[d]	30 Jun-10 Jul	25 June-15 Jul	g	20 Jul-30 Jul	10 Jun-3 Jun	1 Aug-20 Aug
Kuskokwim Bay[e]	17 Jun-5 Jul		g	g	10 Jun-30 Jun	25 Jul-15 Aug
Yukon River[f]	g	11 Jun-9 Jul	24 Jul-10 Aug	15 Jul-10 Aug	13 Jun-28 Jun	9 Aug-29 Aug
Norton Sound[f]	g	30 Jun-16 Jul	g	3 Jul-25 Jul	10 Jun-30 Jun	3 Aug-25 Aug
Kotzebue Sound[f]	g	g	1 Aug-20 Aug	g	g	g

[a]Estimated dates are for Bristol Bay salmon only. Dates are based on migration rates of 45 km/day for sockeye and pink salmon, 56 km/day for chum and coho salmon, and 60 km/day for chinook salmon during the last 30 days of spawning migration. A travel distance of 680 nautical miles from shelf edge to the head of Bristol Bay (the mouth of the Kvichak River) was used in these calculations. The 2000 m isobath in the vicinity of the heaviest concentration of a salmon species was delineated as the "shelf edge."
[b]A. R. Shaul, ADF&G, Cold Bay, Alaska, pers. comm. Dates are based on commercial fishery catches.
[c]There are two types of sockeye salmon spawning migrations to river systems of the northern Alaska Peninsula, i.e. those that reach peak abundance in the fishery in a short period of time between 25 June and 10 July, and those that occur over a long period of time between 20 June and 25 August with no definable peak period of abundance. A. R. Shaul, ADF&G, pers. comm.
[d]C. P. Meacham, ADF&G, Anchorage, Alaska, pers. comm. dates are based on commercial fishery catches.
[e]W. Arvey, ADF&G, Anchorage, Alaska, pers. comm.
[f]W. Arvey, ADF&G, Anchorage, Alaska, pers. comm. Dates are based on commercial fishery catches.
[g]Low abundance precludes estimates.

they are most abundant. Research fishing and tagging experiments have taken place largely between mid-June and late July when sockeye and chum salmon are most abundant on the shelf. Chinook salmon begin entering the shelf area in mid- to late May, and coho salmon begin entering the shelf area in mid- to late July. As a result, significantly less information is available to show the distribution and direction of movement of chinook and coho salmon than for sockeye, chum, and pink salmon.

The distribution and direction of migration, and relative abundance for all five species of Pacific salmon on the Bering Sea shelf are depicted in Figures 2-6. These figures were prepared by plotting the locations of capture of each species on a chart of the Bering Sea shelf for all years for which data are available. For sockeye, chum, and pink salmon, certain areas of the shelf consistently yielded larger catches or catch per unit of effort values than other immediately adjacent or more distant areas. For chinook and coho salmon, abundance data were available only for Bristol Bay where these species have been captured most frequently. Direction of migration of each species was derived from the published results of tagging experiments and direction of movement studies. The probable direction of migration was based on the geographic location or proximity of the home river system of the species and the verified direction of movement of other salmon species captured in the same area. For example, maturing sockeye and chum salmon

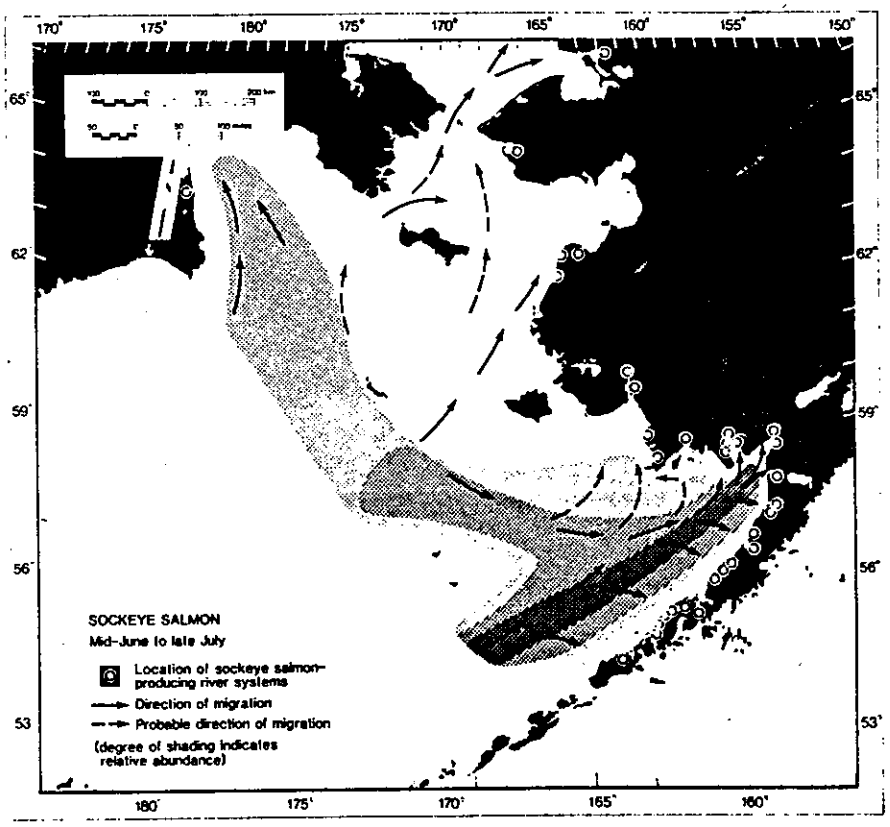

FIG. 2 Distribution of sockeye salmon during spawning migration, mid-June to late July.

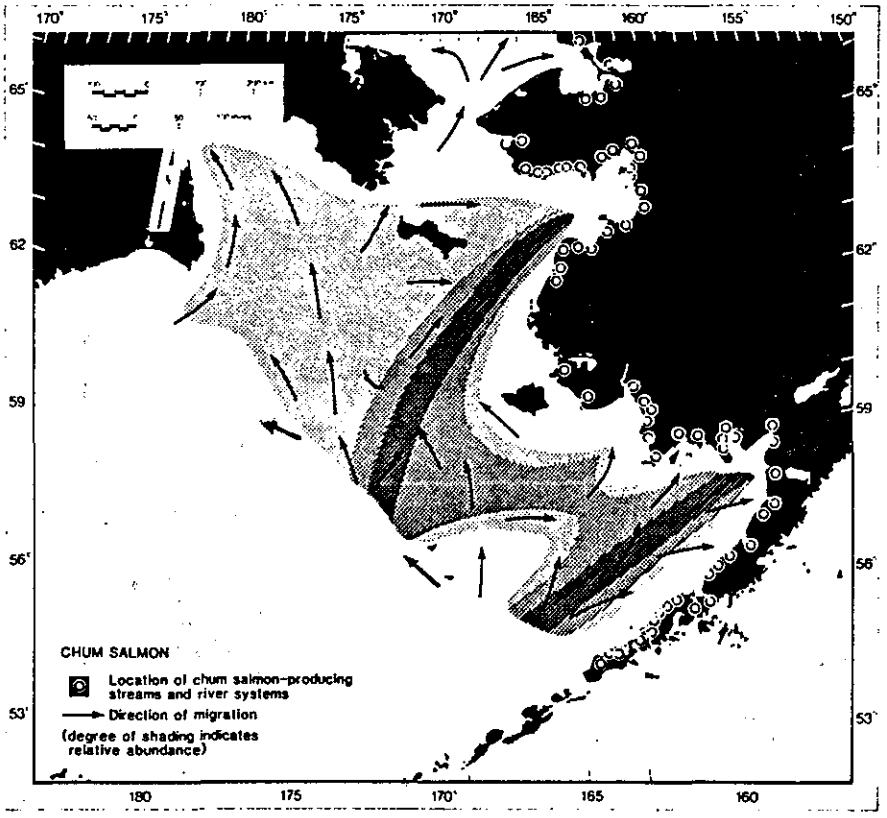

FIG. 3 Distribution of chum salmon during spawning migration, mid-June to early August.

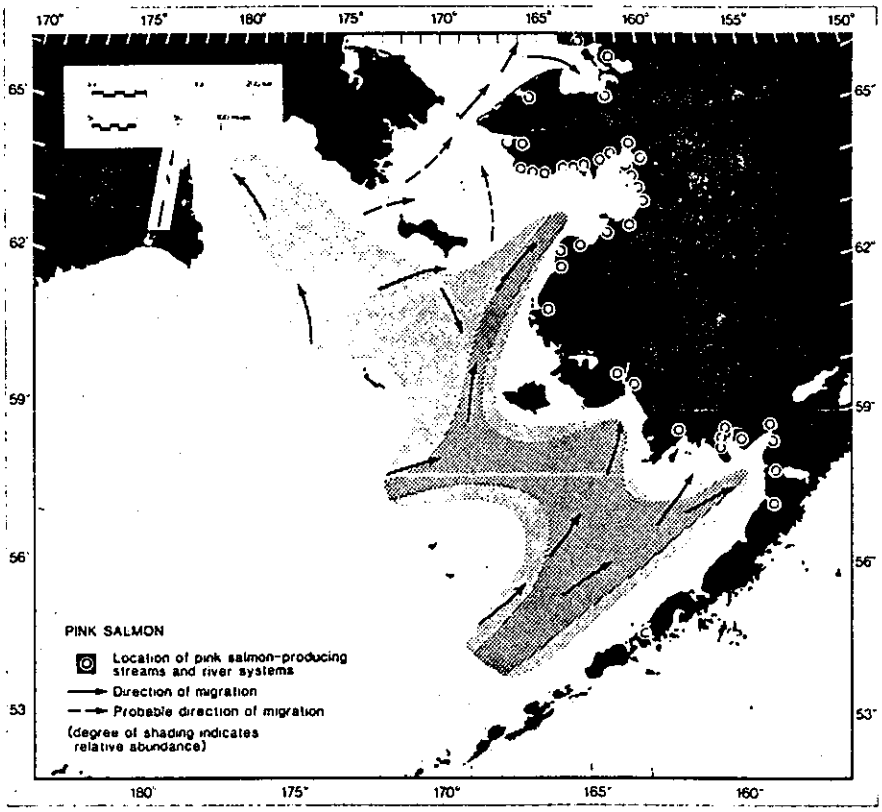

FIG. 4 Distribution of pink salmon during spawning migration, mid-June to mid-August.

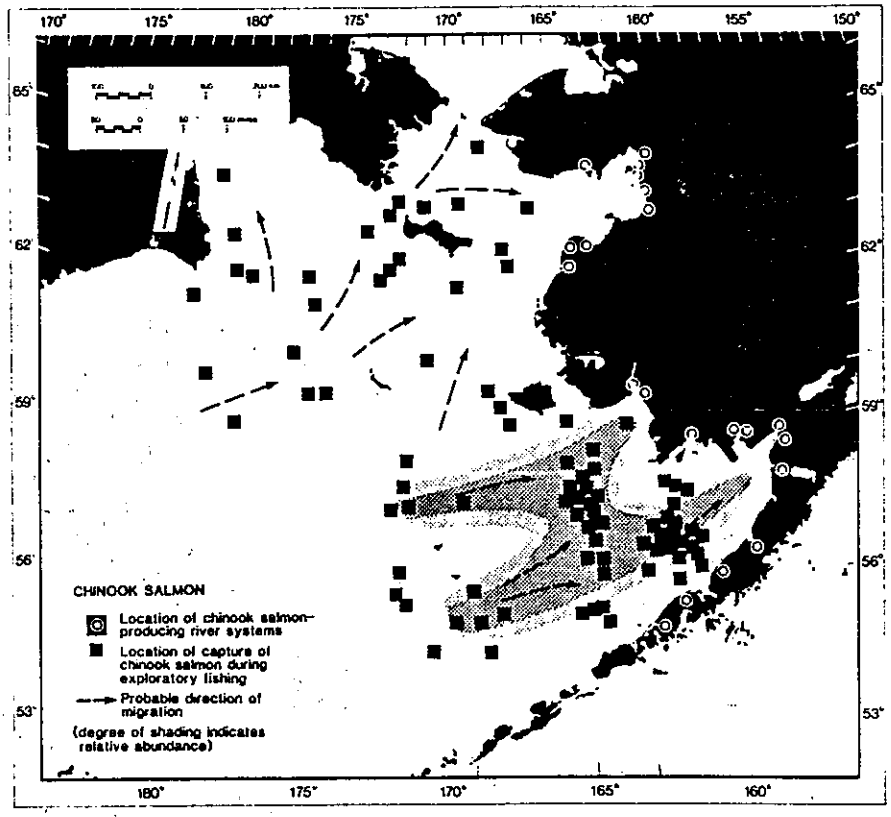

FIG. 5 Distribution of chinook salmon during spawning migration, early June to mid-July.

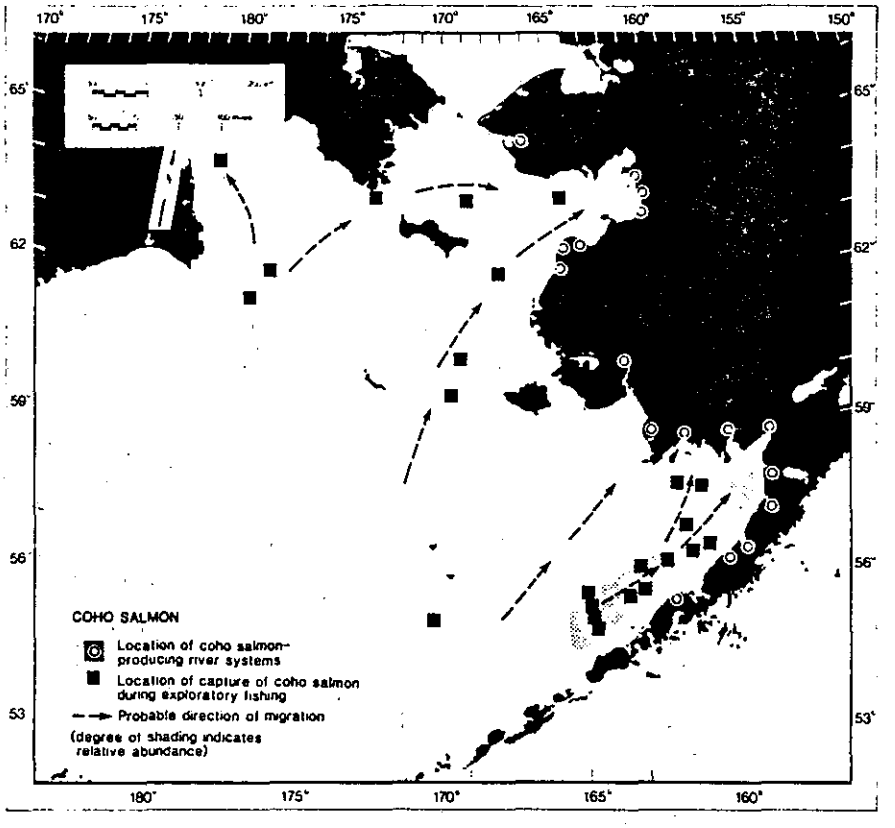

FIG. 6 Distribution of coho salmon during spawning migration, early July to early September.

appear to migrate eastward north of St. Lawrence Island, and maturing chum and pink salmon appear to migrate eastward south of St. Lawrence Island (Yonemori 1967) (Figs. 3 and 4). Major spawning streams of chum and pink salmon are to the northwest and east of St. Lawrence Island in Kotzebue and Norton Sounds, respectively. Spawning streams of chinook and coho salmon are also to the east and northwest of St. Lawrence Island.

- Spawning Migration, Sockeye Salmon -- The greatest abundance of sockeye salmon during spawning migration occurs in the southeastern shelf area (Fig. 2). Sockeye salmon are concentrated in two bands offshore, north and south of the Pribilof Islands, and are bound for rivers on the north side of the Alaska Peninsula and those rivers flowing into Bristol and Kuskokwim Bays. As they migrate across the shelf toward the head of Bristol Bay, they progressively segregate according to their rivers of origin (Straty 1975). This segregation begins when the fish are still as far as 200 km from the mouths of their home river systems. Bristol Bay sockeye salmon remain in offshore waters, rather than coastal waters, until they are within 32-80 km of the mouths of their home river systems. Sockeye salmon bound for rivers on the north side of Bristol Bay (i.e., those rivers entering Nushagak and Togiak Bays) are apparently more abundant in the northern portion than in the southern portion of the eastern shelf distribution of sockeye salmon.

An eastward migration is indicated for sockeye salmon captured north of St. Lawrence Island (Yonemori 1967). These fish are most

probably bound for the few sockeye salmon-producing river systems north of St. Lawrence Island in Norton and Kotzebue Sounds (see Fig. 2). Northward migration of sockeye salmon east of St. Lawrence Island is uncertain because only one has been caught in this area (Faculty of Fisheries, Hokkaido University 1968). Research fishing north of 62°N has been in late July and early August, probably after most sockeye salmon have entered their home river systems.

Mature sockeye salmon captured in offshore waters near Cape Navarin and the Gulf of Anadyr in the western Bering shelf area are most probably bound for the Tumana and Anadyr Rivers.

- Spawning Migration, Chum Salmon -- Chum salmon are more widely distributed throughout the shelf during spawning migration than sockeye salmon, probably because chum salmon spawn in many more streams in Norton and Kotzebue Sounds than sockeye salmon (see Figs. 2 and 3).

In the southeastern shelf area along the approaches leading to Bristol Bay, chum salmon appear to be more abundant farther offshore than sockeye salmon--undoubtedly related to the size of the chum salmon populations returnng to the river systems tributary to Bristol Bay. On the average, the Nushagak River and Togiak River systems, which enter on the north side of upper Bristol Bay, produce over 70% of the commercial chum salmon catch of the Bristol Bay area (ADF&G 1974). Chum salmon are probably segregated according to the geographic location of the major chum salmon-producing river systems on the north side of Bristol Bay when they

are more than 200 km seaward of the river mouths.

Chum salmon, apparently bound for the Yukon River, arctic coast, Gulf of Anadyr, and Norton and Kotzebue Sounds are more abundant in the western than in the eastern shelf areas. Some have been found to be moving eastward both north and south of St. Lawrence Island (Yonemori 1967). These were most probably bound for the Yukon River, Norton Sound and Kotzebue Sound rivers, and rivers entering the Bering Sea along the eastern and western arctic coast. A few tagged very near the shelf edge in the southeastern Bering Sea (between 54-56°N and 170°W) were recovered on Hokkaido and Sakhalin Islands and in the eastern Kamchatka area, which indicated westerly movement for these fish. Chum salmon captured in research gillnets in the western shelf area were moving northward in Anadyr Bay (Yonemori 1967) and were most likely bound for the rivers entering this bay.

- Spawning Migration, Pink Salmon -- Pink salmon have been captured throughout the offshore areas of the shelf during spawning migration (Fig. 4) As with sockeye and chum salmon, the heaviest concentrations of pink salmon on the shelf appear to be related to the size of the population migrating to specific stream or river systems and the geographic location of these systems.

The Nushagak River system, the single most important pink salmon-producing river system in Bristol Bay, drains into the north side of the bay. Between 80% and 90% of the total Bristol Bay catch of pink salmon is taken in the Nushagak fishing district (ADF&G 1974). The other major pink salmon-producing river systems

in Bristol Bay include the Togiak River system, which also enters the bay on the north side, and the Naknek and Kvichak River systems, which enter at the head of the bay. Reatively few pink salmon are produced in the streams along the north side of the Alaska Peninsula as indicated by the commercial catch in the north side peninsula commercial fishing districts (see Table I). Like chum salmon, which are also produced in greater abundance in river systems entering on the north side than in river systems entering the south side of Bristol Bay, pink salmon are more abundant farther offshore in the northward approaches to the bay than sockeye salmon (see Figs. 2 and 4).

Some pink salmon of Bristol Bay origin apparently migrate a considerable distance north in the central shelf area and then southeast to Bristol Bay. For example, a single pink salmon tagged at 62°N, 170°W in the summer of 1966 was recaptured in the Nushagak area of Bristol Bay (Yonemori 1967). This fish had actually bypassed the latitude of its home-river system by more than 200 km and migrated more than 800 km in a southeast directon from point of tagging to point of recapture. What proportion of the pink salmon of Bristol Bay origin undergo this rather extensive migration across the shelf is unknown.

Many of the streams and river systems entering Norton Sound produce pink salmon. The distribution and abundance of pink salmon noted in the central Bering Sea shelf area suggest that they are probably bound for streams and rivers entering Norton and probably Kotzebue Sounds. Pink salmon captured in research gillnets south

of St. Lawrence Island were moving eastward (Yonemori 1967) and probably destined for the streams of Norton and Kotzebue Sounds. The few pink salmon captured in research gillnets west and northwest of St. Lawrence Island (Hokkaido University, Faculty of Fisheries 1965 and 1968) were probably moving north and northeastward, also destined for Kotzebue and Norton Sounds. Pink salmon captured in the Gulf of Anadyr were moving northward (Yonemori 1967) and most probably destined for the Anadyr River.

- Spawning Migration, Chinook Salmon -- Maturing chinook salmon have been captured throughout the Bering Sea shelf during spawning migration, but little information is available to verify their direction of migration at this time. Information on the distribution and direction of migration for sockeye, chum, and pink salmon in the central, western, and southeastern shelf areas, respectively, suggests they are primarily bound for rivers and streams of the Alaska Peninsula, Bristol Bay, the Gulf of Anadyr, and Norton and Kotzebue Sounds (see Figs. 2, 3 and 4). If chinook salmon are responding similarly to the same environmental cues as sockeye, chum, and pink salmon to guide them during spawning migration, they should follow migration routes similar to these species. Based on this assumption, the probable directions of migration for chinook salmon captured in various areas of the Bering Sea shelf are shown in Figure 5.

Chinook salmon were captured most frequently in Bristol Bay where research fishing concentrated on the sockeye salmon runs to

this area and were generally captured in greater abundance and farther north offshore than sockeye salmon (see Figs. 2 and 5). This distribution is probably related to the size of the chinook salmon population migrating to specific river systems in Bristol Bay because they are produced in far greater abundance in streams entering the north side of Bristol Bay. Catches in fishing districts located on the north side of Bristol Bay (i.e., Nushagak and Togiak Bays) have composed over 80% of the total Bristol Bay catch of this species. Chinook salmon are also abundant in the Kuskokwim River, north of Bristol Bay.

- Spawning Migration, Coho Salmon -- Coho salmon have only been captured at a few locations on the Bering Sea shelf (Fig. 6) primarily because of the lack of exploratory fishing from late July to late August when they would be most abundant on the shelf (see Table III). Coho salmon have been captured most frequently in the southeastern Bering Sea shelf area. In this area, research fishing has concentrated on the sockeye salmon migration bound for the river and stream systems tributary to the Alaska Peninsula and Bristol Bay.

The same rationale used to show the probable migration route for chinook salmon in the shelf area is used to show the migration routes for coho salmon. There is little direct evidence, however, to verify these migration routes.

- General Seaward Migration -- The seaward migration of Pacific salmon begins in spring when the juveniles enter the shelf area

from their rivers or streams of origin. The seasonal timing of this migration is species and stock specific and variable due to annual differences in environmental conditions, e.g., time of ice breakup on lakes, streams, and rivers and the warming of these waters. Exploratory fishing for juvenile salmon (NMFS, ABL 1966 and 1967 data) and casual observations by biologists (Mike Nelson, ADF&G personal communication) in Bristol Bay indicate that chinook salmon are the first juvenile salmon to enter the bay in mid-to late May followed in order by sockeye, chum, pink, and coho salmon from late May to late July.

After entry into the Bering Sea, juvenile salmon remain in the nearshore waters for varying lengths of time during the initial few months of seaward migration (Hartt et al. 1967b, Straty 1974, and Barton 1979). Coastal movement during the initial few months of seaward migration appears to be typical behavior for Pacific salmon throughout their range based on observations in the Gulf of Alaska (Hartt et al. 1967a; Hartt and Dell 1976), along the south side of the Alaska Peninsula and eastern Aleutian Islands (Hartt and Dell 1976), and in the western North Pacific Ocean and Okhotsk Sea (French et al. 1976).

As the seaward migration of salmon progresses from early summer to late fall, the fish rapidly increase in size and ultimately vacate the nearshore waters and move offshore to more pelagic regions (Straty 1974 and Barton 1979). The seasonal timing of this offshore movement of juvenile salmon is species specific and variable due to annual differences in their time of entry into the

Bering Sea. For example, in years when environmental conditions (i.e., ice breakup and warming of water), favor the early seaward migration of juvenile salmon, offshore movement would be expected to occur earlier in the season and vice versa. The location and timing of offshore movement in a given year is probably a function of time of entry into the Bering Sea and growing conditions. The more rapidly juvenile salmon increase their size, the sooner offshore movement may be expected. Information is only fragmentary on the shelf distribution of juvenile salmon after they vacate the coastal waters.

Of the five species of juvenile Pacific salmon inhabiting the shelf, only the sockeye salmon of Bristol Bay has been studied sufficiently to describe in some detail characteristics of the seaward migration through the southern shelf area. Information on the seaward migration of the other species of salmon across the shelf is fragmentary and largely the result of the sockeye salmon studies of Hartt et al. (1964, 1967a and b), Straty (1974) and Straty and Jaenicke (In press) and of finfish surveys conducted in Norton and Kotzebue Sounds (Barton 1979). Much of what was learned about the behavior of juvenile sockeye salmon during seaward migration through Bristol Bay probably applies, in varying degree, to the other species of juvenile salmon.

- Seaward Migration, Juvenile Sockeye Salmon -- What is known of the distribution migration routes and ecology of juvenile sockeye salmon in the southeastern shelf area of Bristol Bay has been described in some detail by Straty (1974) and Straty and Jaenicke (In

press). Only the major points with respect to the juvenile sockeye salmon distribution and migration routes across the shelf area between late May and late September are summarized here.

Juvenile sockeye salmon from all river systems entering Bristol Bay, including those along the north side of the Alaska Peninsula, apparently follow the same seaward migration route regardless of the specific geographic location of their river systems of origin (i.e., whether the river enters on the north or south side of Bristol Bay - Straty 1974). This route is coastal along the north side of the Alaska Peninsula (Fig. 7). From late May to late September, juvenile sockeye salmon are most abundant between the coast and 48 km offshore. The fact that all stocks of juvenile sockeye salmon and apparently other species of juvenile salmon follow this seaward route suggests they are responding to the same environmental factor(s) that function to guide them seaward across the shelf and along this side of Bristol Bay.

Virtually nothing is known of the distribution and seaward migration routes of juvenile sockeye salmon originating in rivers north and northwest of Bristol Bay (i.e., those entering Kuskokwin Bay, Norton and Kotzebue Sounds, and the Gulf of Anadyr). Based on the apparent typical coastal movement of juvenile salmon throughout their range during the initial period of seaward migration, the probable seaward migration routes for juvenile sockeye salmon from these river systems is illustrated in Figure 7. As with Bristol Bay sockeye salmon, these fish probably would also vacate the nearshore waters and move offshore after an undetermined period of time.

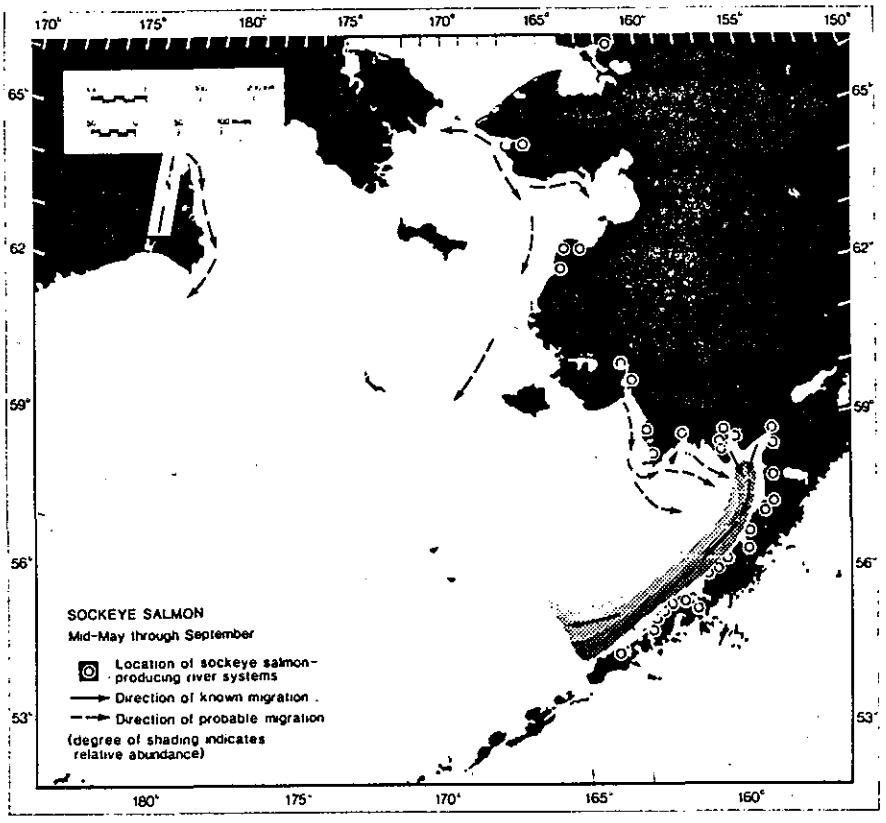

FIG. 7 Distribution of sockeye salmon during seaward migration, mid-May through September. (Adapted from Straty 1974; Straty and Haight 1979.)

Juvenile sockeye salmon originating in the various rivers of Bristol Bay, and most probably rivers in other areas as well, enter the sea at different times during late spring and early summer (Straty 1974; Rogers 1977). Sockeye salmon migrating from Bristol Bay lake systems with only one or two lakes enter earlier and over a shorter period of time than those migrating from multi-lake systems. In addition, the travel distances of juvenile sockeye salmon from lake outlet to Bristol Bay are different for each of the river systems. As a result, the individual major river stocks are somewhat separated from one another during the initial few weeks of seaward migration. Also contributing to this initial separation are the differences in their age and size at the time of entry into Bristol Bay. As mentioned earlier, Age 2.0 sockeye salmon precede Age 1.0 sockeye salmon in order of seaward migration. Since Age 2.0 fish from a given river system are larger than Age 1.0 fish, they may be expected to migrate seaward at a faster rate than Age 1.0 fish. The overall result of the difference in time of entry into Bristol Bay and fish size is that juvenile sockeye salmon are distributed throughout most of the area encompassing the seaward migration route from late May through late July.

Although the major stocks of Bristol Bay sockeye salmon may be segregated during the initial period of seaward migration, mixing of stocks takes place after the fish have been at sea a few months (Straty 1974). This most likely results from a decrease in the seaward migration rate of those fish that have entered the more seaward

areas of Bristol Bay where food is apparently more abundant than initially encountered in the inner bay.

From late May and early June through early August in years when more normal environmental conditions prevail, (e.g., mainly sea temperature), the greatest biomass of juvenile sockeye salmon will be present along the coast of inner Bristol Bay (northeast of 159°W) (Straty 1974). Early seaward-migrating sockeye salmon will be more abundant farther seaward in this area than later entrants into the bay. After early August, the greatest biomass of juvenile sockeye salmon apparently occurs in the outer bay or seaward of 159°W. Little is known about the distribution and migration route of juvenile sockeye salmon in Bristol Bay after late September when most studies were terminated.

The seasonal distribution and abundance of juvenile sockeye salmon in the shelf area of Bristol Bay may show considerable annual variation. For example, in 1971, which was characterized by anomalously cold sea temperatures from spring through fall (Straty and Jaenicke, In press), juvenile sockeye salmon were virtually absent in outer Bristol Bay in early July whereas they were abundant in this area in 1967 (a year with warm sea temperatures) in early to mid-June. Such annual variations in the seasonal distribution of juvenile salmon can probably be expected to occur in other areas of the shelf as well, resulting in annual variations in the time juvenile salmon are residents of the shelf and their time of entry into the North Pacific Ocean.

A final point which should be mentioned about the behavior of juvenile sockeye salmon during seaward migration concerns their vertical distribution. Juvenile sockeye salmon were found to be schooled and most abundant in the upper 5 m of water (Straty 1974). They displayed diurnal changes in depth, being most abundant at night in the upper 1 m of water and during daylight hours at a depth of 2 m.

- Seaward Migration, Juvenile Chum Salmon and Pink Salmon -- Except in Bristol Bay and Norton Sound, there is little known about the shelf distribution of juvenile chum and pink salmon. In Bristol Bay, both species have been captured during research fishing at various times from early summer to early fall in the area encompassing the seaward migration route of the juvenile sockeye salmon (see Fig.

7) (NMFS, ABL 1966 and 1969-72 data). There have been few juvenile chum and pink salmon captured outside this area. In Norton Sound (primarily Golovin Bay), juvenile chum and pink salmon were captured by beach seines in the nearshore littoral areas between the onset of ice breakup on June 9 and July 9, 1977 (Barton 1979).

In Bristol Bay, small numbers of chum salmon were captured by purse seine in the coastal waters as early as mid-June 1967. However, they did not become abundant in these waters until after mid-July in 1967 and 1969. Juvenile chum salmon remained abundant along the southeastern coast of Bristol Bay seaward of 159°W through August and until at least mid-September in 1969 and 1970

(NMFS, ABL 1969 and 1970 data). Juvenile pink salmon have not been captured in Bristol Bay in the area encompassing the seaward migration route of the juvenile sockeye salmon until after late June (NMFS, ABL 1966 data). They have been captured primarily in the coastal areas of inner Bristol Bay northeast of 159°W. Their abundance in this area increased from late June through mid-August of 1969. Presumably, they did not reach the coastal areas of the outer bay seaward of 159°W until late August and September. A few juvenile pink salmon were captured near Port Moller in outer Bristol Bay (at 56°12'N, 161°00'W) on August 25, 1969. These were the only juvenile pink salmon captured seaward of 159°W during the various years of intensive research fishing in the area by ABL.

In Norton Sound, juvenile chum and pink salmon captured in the nearshore littoral areas during June and early July were less than half the size (32-59 mm mean fork length) of those captured between late June and mid-September in Bristol Bay. No juvenile chum or pink salmon of the larger size captured in Bristol Bay were taken in the littoral or offshore area of Norton Sound after early July 1977. Barton (1979) concluded that juvenile chum and pink salmon vacated the nearshore littoral areas of Norton Sound and moved offshore to more pelagic areas; however, gillnets and tow nets were used to sample juvenile salmon in these areas. The author has found this type of gear to be much less efficient than round haul or purse seines for sampling juvenile salmonids in Bristol Bay. It is very likely that the small juvenile chum and pink salmon that had been present in the littoral areas of Norton Sound during June

and early July were missed by or avoided the fishing gear which was used to sample them offshore. After their movement offshore, they would have been larger in size and more dispersed, making them more difficult to sample. It seems likely that juvenile salmon of the small size reported by Barton (1979) would have migrated into distant deep offshore waters. This behavior is inconsistent with that observed for juvenile Pacific salmon throughout their range in North America.

In Bristol Bay just the opposite situation occurred. No juvenile chum or pink salmon of the small size sampled in Norton Sound were captured during research fishing by ABL. However, in Bristol Bay the littoral areas less than 16-18 m deep were not sampled for juvenile salmon. The mesh size of the purse seine used to sample juvenile salmon was capable of retaining fish as small as 60-70 mm. Therefore, it is likely that the smaller-sized juvenile chum and pink salmon were present in the littoral water of Bristol Bay during early June but were not sampled. After increasing in size and moving progressively offshore, they would have become available to the fishing gear used.

Both chum and pink salmon enter the estuaries shortly after emerging from the gravel (see Table II) and at a size considerably smaller (25-30 mm) than juvenile sockeye, chinook, and coho salmon. However, as indicated above, few of this size have been captured in Bristol Bay, which seems attributable to lack of sampling the areas where they most likely occur. Lending support to their probable residence in littoral areas are observations of

juvenile pink salmon in this size range milling around cannery docks in Bristol Bay in early June noted earlier. The implied behavior of juvenile chum and pink salmon during seaward migration in the shelf area would seem to be one of progressive offshore movement with increasing size.

- Seaward Migration, Juvenile Chinook Salmon and Coho Salmon -- Juvenile chinook and coho salmon have been captured along with juvenile sockeye salmon during research fishing in the shelf area of Bristol Bay. Similar in distribution to juvenile sockeye, chum, and pink salmon, they were found to be most abundant along the southeastern coast of Bristol Bay (see Fig. 7). A few juvenile coho salmon were captured during finfish surveys of Golovin Bay in Norton Sound (Barton 1979), but no mention is made concerning their distribution or movements.

In Bristol Bay, only small numbers of juvenile chinook salmon have been captured during research fishing conducted by the ABL in 1966, 1967, 1969, and 1970. These fish were caught in the inner bay northeast of 159°W in early June 1966. No juvenile chinook salmon have been captured in the shelf area of the bay beyond June. A few juvenile chinook salmon were reported taken during research fishing farther seaward in the eastern Bering Sea between June and August (Hartt and Dell 1976).

The lack of juvenile chinook salmon in the shelf areas of Bristol Bay after early June indicates that the majority of the chinook salmon had either entered the bay earlier before intensive fishing began or, for some unexplained reason, were missed by the

fishing gear. In the Salcha River drainage of the Yukon River, the peak downstream migration of chinook salmon occurred between the latter half of May and early June (Trasky 1974). The seaward migration of chinook salmon from Bristol Bay river systems probably also occurs during May and early June. The lack of juvenile chinook salmon in the shelf area of Bristol Bay beyond June also implies that these fish migrate seaward at a much faster rate than juvenile sockeye, chum, pink, and coho salmon. These species enter the bay later in the spring and summer than the juvenile chinook salmon and are present in the shelf area at least through mid-September; juvenile pink salmon are probably present in the shelf area into October.

Based on their time of appearance and magnitude of abundance indicated by fish catches made in the coastal waters of Bristol Bay, juvenile coho salmon are the latest species of Pacific salmon to enter the shelf. Although they have been captured along the southeastern coast of Bristol Bay as early as mid-June, research fishing indicates they do not occur in any abundance until late June or early July (NMFS, ABL 1966, 1967, 1969, and 1970 data). They appear to remain abundant in this area of the shelf throughout July and August and were still present in mid-September of 1970.

- Synopsis: Timing of Migration and Distribution -- Exploratory and research fishing and tagging experiments have shown that sockeye, chum, pink, chinook, and coho salmon are widely distributed throughout the Bering Sea shelf during spawning migration. They are more abundant in offshore waters than in coastal waters until

they reach the vicinity of their home-river/stream systems. Adult salmon are most abundant in the shelf area between mid-May and early September with the peak of abundance somewhat different for each species (see Table III).

Adult sockeye, chum, and pink salmon, and probably chinook and coho salmon, appear segregated to a varying degree according to the general geographic location of their home-river/stream systems at the time they enter the Bering Sea shelf. Salmon bound for the Yukon River, Norton and Kotzebue Sounds, and the arctic coast appear to be more prevalent in the central shelf area. Those bound for the rivers of the Gulf of Anadyr appear more prevalent in the western shelf area and in the case of chum salmon, in the western and central shelf areas. Salmon bound for rivers and streams in Bristol and Kuskokwin Bays and along the Alaska Peninsula appear more abundant in the eastern shelf area. The general similarities in the shelf distributions of sockeye, chum, and pink salmon bound for streams or rivers located in specific geographic areas, e.g., Bristol Bay, suggest that these species, and most probaby chinook and coho salmon as well, are responding inherently to the same environmental cues to guide them across the shelf to their rivers or streams of origin. Acceptance of this hypothesis implies that the spawning migration of salmon in the shelf area is directed along broad but specific routes which must be similar for all species.

As the spawning migration of salmon proceeds across the shelf in the general direction of their rivers of origin, salmon stocks

progressively segregate according to the specific location of their home-river/stream systems, such as the Nushagak River in Bristol Bay. This segregation of sockeye salmon stocks of Bristol Bay origin begins when the fish are still in the offshore waters and as much as 200 km from the mouths of home-river systems (Straty 1975).

The timing of the seaward migration of juvenile Pacific salmon across the shelf is similar to that of the adult spawning migration, (i.e., juvenile salmon are most abundant on the shelf between early to mid-May and late September). Although both juvenile and adult salmon are present on the shelf at the same time, their distributions and migration routes are quite different. As indicated above, adult salmon appear to remain in the offshore waters of the shelf until within the vicinity of the coastal area or the estuary containing their home river or stream. Juvenile sockeye, chum, pink, and coho salmon, however, appear to migrate seaward along the coast during the initial two months or so of seaward migration. Therefore, although the shelf is occupied by both juvenile and adult salmon, at the same time of the year, they remain separated from one another except, perhaps, in the vicinity of the mouths of their home rivers or streams. Little information is available on the distribution in the shelf area. The small number of juvenile chinook salmon caught in inner Bristol Bay suggest the seaward migration route of this species is also along the coast.

The principal factor insuring that juvenile salmon remain largely separated from the adults during seaward migration is the difference in their migration rates. For example, the majority of the

adult sockeye salmon bound for Bristol Bay river systems, cross the shelf in about 15 days (see Table III). Juvenile sockeye salmon, and most probably juvenile chum, pink, and coho salmon, however, appear to be confined to the coastal waters for at least 60 days during seaward migration. As a result, adult salmon have crossed the shelf offshore well before the juvenile salmon begin to move into that area.

Observations in Bristol Bay, Norton Sound, and the Gulf of Alaska indicate that juvenile salmon eventually move from the coastal waters farther offshore to more pelagic waters as their size increases. In Bristol Bay, the larger-sized juvenile sockeye salmon seem to be the first to move offshore (Ogi 1973; NMFS, ABL 1967, 1969 and 1970 data). If offshore movement of juvenile salmon is size dependent, its timing can be expected to display annual and seasonal variations. These variations would result from annual variations in environmental factors such as sea temperature and food abundance, which influence growth.

ENVIRONMENTAL FACTORS INFLUENCING THE MOVEMENTS AND DYNAMICS OF PACIFIC SALMON ON THE BERING SEA

Fishery scientists generally agree that environmental factors such as water temperature, food abundance, salinity, currents, etc., influence the distribution, movements, growth, and survival of salmon. To make a comprehensive synopsis of the movements and dynamics of Pacific salmon, one must understand how environmental factors and their variability affect the behavior of salmon residing on the shelf.

Considerable experimental research has been conducted in the laboratory on the influence of environmental factors on the physiology and behavior of salmon, but application of results to explain occurrences at sea has been limited. The published results of numerous studies conducted in Bristol Bay have focused on the apparent responses of sockeye salmon to certain environmental factors and their variability (Ogi 1973; Straty 1974; Nishiyama 1974; Fujii et al. 1974; Fujii 1975; Straty and Haight 1979; and Straty and Jaenicke, In press). Below is a summary of the results of these studies and the inferences made therefrom concerning probable movements and dynamics of Pacific salmon of the shelf.

Probable Influence of Temperature on the Distribution, Growth, and Survival of Pacific Salmon

Because of its influence on metabolism, environmental temperature has profound effects on the life processes of fish. Temperature sets limits to their metabolic rate within which the fish are free to perform, regulates their rate of growth and development, and acts as a directive factor resulting in the aggregation of fish within thermal ranges or movement to new environmental conditions (Brett 1956).

The studies of Manzer et al. (1965) have illustrated the relationship between the distribution of salmon and sea-surface temperature in the Bering Sea and North Pacific Ocean. These studies have shown that the range of tolerable and preferred sea surface temperature is different for each species and that these ranges change from spring through fall. The salmon species, in order of preferred sea temperatures (from colder to warmer), are sockeye,

chum, pink, chinook, and coho salmon (Table IV). Sockeye and chum salmon preferred the lowest temperature range; pink salmon, the intermediate range; and chinook and coho salmon, the highest range. From May through July and August, all salmon species preferred increasingly higher temperatures. In September, salmon again preferred colder waters. In spring and early summer, maturing salmon were associated with slightly colder sea temperatures than immature salmon. In late summer and fall, maturing salmon tended to be associated with higher temperatures. These seasonal changes in sea surface temperature preferences corresponded to the seasonal warming of surface waters.

TABLE IV

Probable Tolerable and Preferred Sea-Surface Temperatures for Pacific Salmon (From Manzer et al. 1965)

Species of Salmon	Tolerable range (C)	Preferred range (C)	Reference months for Preferred range
Sockeye	1-15	2,3-9	May, September
Chum	1-15	2,3-11	May, September
Pink	3-15	4-11	May, June
Coho	5-15	7-12	May, June, July
Chinook	2-13	7-10	July, August, September

The studies of Manzer et al. (1965) lend credence to the hypothesis, first advanced by Kaganovsky (1949) with respect to pink salmon, that in general, salmon avoid waters of near-freezing surface temperatures and vacate the Bering Sea and northwestern Pacific

Ocean in winter and move southward and eastward where water temperatures are more favorable. Winter temperatures of less than 3 C prevail over much of the Bering Sea and northwestern Pacific Ocean as indicated by long-term mean conditions (Laviolette and Seim 1969). Fujii (1975) concluded that sockeye salmon of western Alaska origin are prevented from entering the Bering Sea through passes in the Aleutian Islands until low temperatures and high salinities of surface water in the passes disappears. Manzer et al. (1965) speculated that in years when water temperatures are relatively high, sockeye and chum salmon may be present in the southern Bering Sea throughout the winter months because of their lower preferred temperature range. Sockeye salmon were, in fact, captured by gillnetting in January in the central Bering Sea along 180° and 175°E (Hunter and Larkins 1963).

If sea temperature is a dominant environmental factor regulating the seasonal distribution of Pacific salmon, the proportion of juvenile and immature salmon overwintering in the Bering Sea should be correlated with the extent to which winter sea temperatures exceed the species' minimum preferred temperatures.

Little information is available on the winter distribution of juvenile and maturing salmon on the shelf. Since salmon are present in the Bering Sea in winter, they might also be expected to enter the shelf, particularly in years characterized by anomalously warm winter sea temperatures. As mentioned earlier, juvenile chinook salmon were taken in bottom trawls in mid-winter near the shelf edge. The temperature at their depth of capture must have

exceeded the minimum tolerable temperature of 2 C for this species (see Table IV).

There is some evidence that the depth distribution of some species of Pacific salmon is restricted by sea temperature (INPFC 1963; Manzer 1964). Japanese investigators reported that in the early part of the season when a thermocline had not developed, salmon were scattered vertically whereas after establishment of a thermocline, salmon tended to concentrate in the surface layer (INPFC 1963). Manzer (1964) reported that sockeye and chum salmon differ in behavior toward the thermocline. A well-produced thermocline appears to present a physical barrier through which sockeye salmon do not migrate. Chum salmon, however, reacted this way to the thermocline only during hours of darkness. We do not know to what extent vertical movements of salmon are restricted by development of a thermocline on the shelf during summer.

In addition to its restrictive influence on the seasonal and vertical movements of immature and maturing salmon, sea temperature may also influence the width of the seaward migration route of salmon across the shelf (Straty 1974). Sea temperatures of coastal waters on the southeastern side of Bristol Bay are generally a few degrees warmer than adjacent waters offshore (i.e., isotherms parallel the coast). As a result, during seaward migration through this area, juvenile salmon are afforded a range of temperatures which may include those best suited to their thermal requirements at the time. Evidence offered by Straty (1974) suggests that juvenile sockeye salmon avoid the colder offshore waters during

seaward migration, particularly in years (e.g., 1971) when anomalously cold sea temperatures prevail. In 1971, juvenile sockeye salmon were captured during research fishing by ABL only at locations nearest the coast and in the shallowest water that could be fished.

Sea temperature not only restricts the seasonal movements of salmon on the shelf but also modifies their movements through its influence on growth and swimming speed (Straty 1974, Straty and Haight 1979; Straty and Jaenicke, In press). Year-to-year sea temperature differences of 6 C between May and December have occurred in Bristol Bay (Fig. 8).

Laboratory experiments have shown that changes in sea temperature of this magnitude profoundly affect the swimming speed of young sockeye and coho salmon (Brett et al. 1958). As temperature increased from 2-10 C, swimming speed of juvenile sockeye salmon increased over 80%. Juvenile coho salmon showed a similar increase in swimming speed between 4 C and about 12 C. Annual variations in sea temperature of the magnitude shown in Figure 8 should result in significant annual differences in swimming speed and, in turn, the seaward migration rate of juvenile salmon across the shelf. As a result, annual differences can be expected in the shelf distribution of juvenile salmon and in their time of entry into the offshelf regions of the Bering Sea and the North Pacific Ocean. Annual differences in the seasonal distribution of juvenile sockeye salmon have been observed in Bristol Bay and attributed, in part, to these extreme variations in sea temperature (Straty 1974; Straty and Haight 1979).

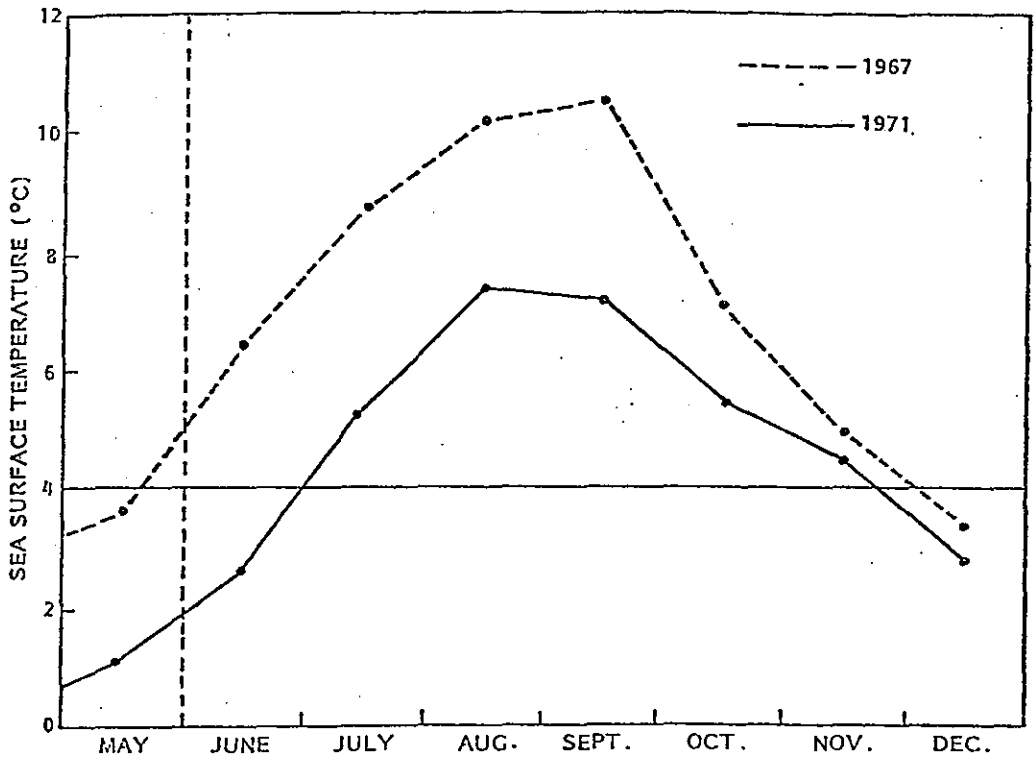

FIG. 8 Average monthly sea surface temperatures at 57°N 163°W in Bristol Bay during May-December 1967 and 1971. Vertical line represents time of peak migration of sockeye salmon from Bristol Bay rivers. (From Straty and Jaenicke, In press.)

Sea temperature may also influence the rate of seaward migration[4/], and possibly survival, through its influence on growth (Straty 1974, Straty and Haight 1979 and Straty and Jaenicke, In press). Donaldson and Foster (1940) found that young sockeye salmon did not grow at temperatures below 4 C. Low temperatures apparently reduce the rate of digestion which, in turn, reduces consumption and growth (Brett and Higgs 1970). Growth and food utilization were highest at approximately 10 C. It is apparent (see Fig. 8) that juvenile salmon migrating seaward through Bristol Bay experienced significantly different growing seasons[5/] in 1967 and 1971. The growth pattern of scales of sockeye salmon from several river stocks of Bristol Bay which migrated seawards in 1967 and 1971 were found to be significantly different, reflecting the effects of sea temperature in these two years (Straty and Jaenicke, In press). As a result of annual variations in sea temperature, the size of juvenile salmon crossing the shelf and at completion of their first summer growing season can also be expected to display annual variation.

Annual variations in the size of seaward migrating salmon may be of significance in terms of their survival. For example, a number of studies have shown that the survival rate of juvenile salmon increases with increased size (Ricker 1962; Foerster 1954;

4/ Swimming speed is a function of water temperature and fish length.

5/ Growing season, which has been defined as the degree and duration of sea temperatures exceeding 4 C, influences the amount of growth a juvenile salmon attains during the first year of ocean life (Straty and Jaenicke, In press).

Manzer 1972; Pella and Jaenicke 1978). This concept of an increased survival with increased size suggests that environmental factors such as high sea temperature and abundant food, which result in rapid growth, are conducive to high early marine survival of juvenile salmon. Straty and Jaenicke (In press) have discussed in some detail the probable survival advantages and disadvantages of annual variations in the size of juvenile sockeye salmon during seaward migration across the shelf. These include, for example: 1) the advantage of a rapid increase in size in reducing the period during which juvenile salmon are subjected to size-dependent predation by fish and marine birds and mammals, 2) the probable increased rate of seaward migration resulting from increased size and earlier entrance into the North Pacific Ocean, and 3) changes in the food habits of juvenile salmon accompanying changes in fish size which will influence the extent of competition for similar food items exploited by other fish and marine birds.

Juvenile salmon reside a considerably longer period of time on the shelf than maturing salmon. As a result, annual variations in sea temperature may be expected to have more pronounced and measurable effects on the distribution, growth, and abundance of juvenile salmon while they cross the shelf than on maturing salmon. Data presented by Nishiyama (1974), however, illustrate the apparent influence differences in sea temperature have on the growth rate of maturing Bristol Bay sockeye salmon during the peak period (June 18-July 2) of their migration across the shelf (Table V). The rate of growth per day (%) and increment of growth in 1967, a year

when high sea temperatures occurred (Fig. 8) was 60% greater than in 1971 when cold sea temperatures prevailed.

TABLE V

Rate of Growth per Day and Increment of Growth of Age 2.2 Yr Bristol Bay Sockeye Salmon in 1967 and 1971 (Data from Nishiyama 1974)

Year	Sea surface temperature (°C)	Sex	Body weight (g) Initial	End	Mean	Rate of growth per day (%)	Increment of growth
1967	8.5±1.02	Female	2106	2412	2259	0.753	17.00
		Male	2426	2750	2588	0.696	18.00
1971	4.6±0.74	Female	2086	2156	2121	0.471	9.98
		Male	2343	2413	2378	0.438	10.41

In conclusion, it seems obvious that annual variations in sea temperature of the magnitude occurring in Bristol Bay will have significant effects on the distribution and growth of maturing and juvenile Pacific salmon while they are residents of the shelf. Annual variations in sea temperature may also indirectly influence the survival rate of juvenile salmon through its influence on growth rate.

Influence of Abundance and Type of Food on Growth and Distribution

In addition to being a function of environmental temperature, growth in salmon is a function of the amount and type of food consumed. The potential energy available to salmon for maintenance and growth is quite different for each type of food organism eaten

(Nishiyama 1974). Annual, seasonal, and areal variations in abundance and type of food eaten by salmon residing on the shelf have been reported by Dell (1963); Nishiyama (1974); Straty (1974); Carlson (1976); Straty and Jaenicke (In press). Studies of juvenile sockeye salmon in Bristol Bay suggest that variations in food type and abundance may result in corresponding variations in the distribution, growth, and, therefore, survival of juvenile salmon.

In the shelf area of Bristol Bay, zooplankton (the food of juvenile salmon) were found to be considerably more abundant along the migration route of juvenile sockeye salmon (see Fig. 7) seaward of 159°W (Straty and Jaenicke, In press). This difference was maintained from June through August. In addition, the coastal water of the bay (less than 37 m deep) contained a significantly lower abundance of zooplankton than the offshore waters (deeper than 37 m). A comparison of the fullness of the stomachs of juvenile sockeye salmon sampled in these areas reflected these differences in zooplankton abundance. The volume of their stomach contents showed that juvenile sockeye salmon generally consumed more food farther seaward and farther offshore.

The response of juvenile sockeye salmon to greater food abundance in the more seaward portion of the Bristol Bay shelf area was clearly evident in the size of the fish and growth patterns of their scales. Generally, fish sampled seaward of 159°W were larger than those in the inner bay northeast of 159°W. The appearance of widely-spaced marine-type circuli on the scales of these fish also showed that initial marine growth did not occur or accelerate until

the juvenile sockeye salmon had entered outer Bristol Bay seaward of 159°W (Straty 1974). Juvenile sockeye salmon usually take from 4-6 weeks to reach the outer bay although this may vary annually. After these fish enter the outer bay, where food is more abundant, they apparently spend more time feeding and move seaward at a more leisurely pace than through the inner bay.

Not only was the food of juvenile sockeye salmon more abundant in outer Bristol Bay, but larger forms of food items occurred there. Straty and Jaenicke (In press) offer evidence that suggests the increased growth rate of juvenile sockeye salmon observed in outer Bristol Bay may also be due to the increased size of food items occurring there.

Variations in food type and abundance must also influence the distribution and/or growth of maturing salmon crossing the shelf but such relationships have not been described. The annual differences in the rate of growth per day shown for maturing Bristol Bay sockeye salmon during late June and early July of 1967 and 1971 (see Table V) (Nishiyama 1974) are probably due to the combined effects of annual variations in sea temperature and the type and abundance of food consumed.

Influence of Salinity

As shown in Figure 7, the seaward migration route of juvenile sockeye salmon from major Bristol Bay river systems is from the river mouths to the southeastern side of inner Bristol Bay. This movement is through the area of the most pronounced salinity

gradients (Straty 1974; Straty and Jaenicke, In press) and it supports the experimental conclusions of McInerney (1964) whose experiments showed that the juveniles of the five species of Pacific salmon occurring in the shelf area were able to use estuarial salinity gradients as one of the directive cues in their seaward migration. Juvenile salmon displayed a temporal progression of salinity preference changes which parallel the salinity gradients typical of river outflows experienced by young salmon on their way to the ocean. The terminal salinity preference shown by young salmon was for water of open-ocean concentration.

The apparent response of juvenile sockeye salmon to salinity gradients in Bristol Bay was best exemplified by the direction of movement of fish migrating seaward from the Wood River system. These fish left the Wood River on the northern side of inner Bristol Bay and migrated across the bay to the southeastern side (Straty and Jaenicke, In press) experiencing a horizontal change in salinity of 30°/oo in a distance of 120 km. This route is their most direct route through the turbid water of the inner bay to the clearer waters of higher salinity in the outer bay. If salinity gradients are the principal environmental factors directing the initial movement of juvenile salmon after they enter the shelf, environmental events, such as prolonged periods of higher wind which cause shifts in the position of river outflows, may result in short-term changes in distributions.

The distribution of maturing Bristol Bay sockeye salmon during migration across the shelf (see Fig. 2) may also be influenced

by the distribution of salinity. Fujii (1975) has implied that the spawning migration route of sockeye salmon in this area is related to the position of water of high salinity flowing eastward into Bristol Bay. This water appears as a wedge of high salinity water which extends well into inner Bristol Bay northeast of 58°N, 158°W (Straty 1974) and is distinguished from coastal water in the outer bay by the 32.0°/oo isohaline (Fujii 1975). The position of this water mass occurs between 56-57°N latitude in outer Bristol Bay but was found to vary in position from year to year. Assuming maturing sockeye salmon prefer or are confined to this water mass, the position of their main migration route may also be expected to display annual variations.

SYNOPSIS: INADEQUACY OF EXISTING KNOWLEDGE ON PACIFIC SALMON OF THE BERING SEA SHELF

Deficiencies in our knowledge of the distribution, movements and abundance of Pacific salmon while residents of the shelf are apparent in the foregoing discussion. The intensive investigations carried out in the southeastern shelf area and adjacent river system have permitted a more complete description of salmon distribution, movements, and abundance here than for the central, western, and northern shelf areas. These investigations have focused mainly on sockeye salmon of Bristol Bay. As a byproduct of these investigations, some information has also been obtained on the timing of migrations and distribution of maturing and juvenile chum, pink, chinook, and coho salmon in the southeastern shelf area. Investigations of salmon in the central, western, and northern shelf areas

have been minimal. As a result, the timing of migrations and distribution and movements of salmon in these areas are based on few studies or have been inferred from the results of salmon investigations in the southeastern shelf area. Most investigations of salmon that have been conducted on the shelf occurred between May and September. Therefore, our knowledge of the occurrence and movements of salmon on the shelf before and after this period is grossly deficient. Major gaps existing in our knowledge of Pacific salmon of the shelf are summarized below.

Fall-Spring Occurrence of Salmon

The species composition, distribution, abundance, and movements of salmon on the shelf between November and April is largely unknown. The occurrence of juvenile chinook salmon in bottom trawls near the shelf edge in mid-winter suggests the possibility that other salmon species may also occur here during the winter. This may occur in years when winter sea temperature exceeds the minimum preferred temperatures of the species.

In Bristol Bay, where the only intensive studies on juvenile salmon have been conducted, virtually nothing is known of their distribution and movements after late September. They are probably present on the shelf well after this date, particularly the smaller pink salmon and the later seaward migrating coho salmon. Juvenile salmon migrating from rivers and streams located in the northern shelf area, e.g., Kotzebue and Norton Sounds, may be present in the coastal and offshore areas of the shelf even later than those migrating seaward from Bristol Bay rivers.

Distribution of Maturing Salmon

The timing of migration, general distribution, and movements of maturing sockeye salmon and, to a lesser extent chum salmon, of Bristol Bay origin have been well defined. This is because research fishing and tagging studies have taken place largely between mid-June and July when these species are most abundant. Significantly less is known of the distribution and movements of maturing pink, chinook and coho salmon in the southeastern shelf area.

Even less is known about the distribution and movements of maturing salmon of all species in the central, western, and northern shelf areas. Few tagging experiments have been conducted on the shelf west of 168°W and north of 59°N. As a result, the direction of movement of a salmon species in a given area in some cases is based on the recapture of a single tagged fish. Additional systematic research fishing and salmon tagging are required in the central, western, and northern shelf areas between early May and early October to more precisely define the distribution, movements, and geographic area of origin of maturing Pacific salmon occurring there. To derive the greatest benefit from such investigations, they should be conducted west of 168°W between the shelf edge north of 56°N and 66°N.

Distribution of Juvenile Salmon

The only salmon species of Bristol Bay origin whose juveniles have been investigated to any extent is the sockeye salmon, for which there have been studies on timing of migration, distribution and abundance. As a result of these studies, some information has

been obtained on the distribution of juvenile chum, pink and coho salmon in the southeastern shelf area. Because these investigations were conducted between early June and late September, little has been learned of the distribution and movements of juvenile chinook salmon in this area. Chinook salmon apparently enter the shelf earlier than early June and few have been captured in Bristol Bay. Little is known also of the distribution and movements of juvenile pink salmon seaward of 159°W in Bristol Bay and after early August. Because of their smaller size during the initial period of seaward migration, juvenile pink salmon apparently migrate seaward at a slower rate than the other salmon species, and few were captured before investigations were terminated in late September. The distribution and movements of all species of juvenile salmon in the southeastern shelf area beyond late September remain open to speculation.

Virtually nothing is known about the time of migration and shelf distribution of juvenile salmon originating in rivers and streams north and west of Bristol Bay. Based on the observed distribution of juvenile salmon in Bristol Bay and throughout their range in the North Pacific Ocean, it seems safe to assume that fish from these areas will initially migrate seaward along the coast. They would also be expected to move offshore as their size increases. This offshore movement may occur well before they cross the shelf, resulting in a significant population of Age .0 salmon in the offshore waters of the shelf in late summer and fall. Verification of such an occurrence awaits the results of additional research.

One final point concerning the seaward movements of juvenile salmon is the direction of movement of those fish originating in rivers north of Bering Strait (e.g., in Kotzebue Sound and along the Siberian and North American arctic coasts. Do they migrate seaward initially along the coast on the east or west side of the shelf or through the offshore waters? The answer to this question is open to conjecture.

Estimates of the Abundance

Estimates of the annual abundance of maturing sockeye, chum, pink, chinook, and coho salmon returning to Bristol Bay between 1951 and 1976 inclusive have been made by Rogers (1977). Estimates of the average total abundance of each species returning to rivers and streams in Bristol Bay and along the northern side of the Alaska Peninsula have also been made by Stern et al. (1976). Similar estimates have not been made for maturing salmon returning to other western Alaska rivers and streams entering the shelf north of Bristol Bay. In addition, estimates are not available for the total abundance of each species of salmon returning to rivers and streams entering the Gulf of Anadyr and along the Siberian and North American arctic coasts. Assuming the catch statistics in Table I indicate the relative contribution of each area to the total population of maturing salmon entering the shelf each year, the areas north and west of Bristol Bay contribute 14.2% of this population. The reliability of this figure, however, can only be determined through improved estimates of the commercial and subsistence catches and escapement of maturing salmon in these areas.

On the basis of available data and several assumptions listed below, the possible range in the total number and biomass (weight) of maturing salmon entering the shelf each year is between 5.5-65.9 million fish or 15,125-181,225 mt. The assumptions in making this estimate are:

1. The catch statistics given in Table I indicate the contribution of each area of the shelf to the total shelf population of maturing salmon.
2. Annual fluctuations in the abundance of salmon produced in all rivers and streams entering the shelf follow those for Bristol Bay between 1951 and 1976 inclusive (Rogers 1977).
3. 2.75 kg per fish (Table II) is assumed to be the mean weight of all salmon species combined.

The estimate is derived by multiplying the low and peak estimates (4.5 and 54 million fish) of the numbers of maturing salmon returning to Bristol Bay between 1951 and 1976 inclusive by the mean proportion of salmon (0.82) Bristol Bay contributes to total shelf population of salmon each year (see Table I).

Estimates have also been made of the numbers of juvenile sockeye, chum and pink salmon entering Bristol Bay each year between 1950-1974 inclusive (Rogers 1977). In addition, the average and peak estimates of all species of juvenile salmon entering the shelf from Bristol Bay and streams along the northern side of the Alaska Peninsula for 1955-1975 inclusive have been made by Stern et al. (1976). Estimates of juvenile salmon entering the shelf from areas

north and west of Bristol Bay have not been made. The average and peak estimate of juvenile salmon migrating seaward from Bristol Bay for 1955-1975 numbered 461.6 and 1,374.5 million fish, respectively. If the same rationale used above to calculate the abundance of maturing salmon is applied to these figures, the annual probable mean and peak number of juvenile salmon entering the shelf are 566 and 1,676 million, respectively.

Variability in Environmental Factors

Additional research to better define the distribution and movements of salmon on the shelf must also aim at providing a better understanding of salmon distribution in relation to variations in the physical and biological features of this area. Some subjects that should receive attention include: 1) the relationship between salmon distribution and growth and annual fluctuations in the abundance and distribution of preferred food types, e.g., euphausiids, fish larvae; 2) identification of the sources and magnitude of food competition occurring between juvenile salmon and other pelagic components of the shelf and possible effects on their growth; 3) the impact on zooplankton abundance in the offshore waters of the shelf caused by the passage of a large population of maturing salmon and possible influence on juvenile salmon growth; 4) the impact on the available food supply and growth of late-migrating juvenile salmon resulting from the passage of an abundant stock of early-migrating juvenile salmon; and 5) the effect of annual variations in sea temperature on the distribution and growth of salmon should continue to be monitored.

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FINFISH AND THE ENVIRONMENT

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ABSTRACT

Characteristic features of the eastern Bering Sea shelf ecosystem are summarized and an annual chronology of monthly mean environmental conditions and events as well as distributions and spawning areas of halibut, pollock, herring and yellowfin sole is presented for the purpose of providing a synthesis of the foregoing Chapters of this Section and indicating some aspects of the ecosystem dynamics of the area. The inadequacies of existing information on species behavior, multispecies interactions and environmental relations are discussed and a number of specific fisheries oceanography studies are recommended. It is suggested that a more complete listing of sequences of resource-environment events be attempted and more multidisciplinary studies be conducted. When conditions, processes and interactions are understood, the area should be considered as a potential site for shelf-ranching, i.e. selective protection, development and harvesting of specific resources.

INTRODUCTION

The general guidelines for the previous papers on halibut, herring, pollock, yellowfin sole and salmon were to present a brief review of the biology of the individual fish, discuss real or apparent environmental relations and list future research requirements. As indicated earlier (see Overview) this information was largely derived from studies designed to assess specific commercial stocks for management purposes. The original purpose of this Chapter was merely to summarize the fish distributions in order to place them in clearer focus, and by permitting inspection of temporal and spatial separations and overlaps, to show the potential value of multispecies and ecosystem studies over present approaches to fisheries management and oil pollution studies. However, it became apparent that although annual NWAFC and other research cruises, usually in late spring and early summer may provide adequate data for resource management and even inferences pertaining to warm and cold years, they afforded few specific environmental indices, and information on fish distributions during other parts of the year was fragmentary. Because assessments of potential dangers from oil spills require knowledge of year-round distributions and activities of living marine resources, we have constructed an annual chronology of monthly conditions and events that not only reflects the paucity of knowledge in respect to the effects of the environment on fish but also gives additional insight into potential relations. And, in this vein, we have also posed sixteen questions that could provide the basis for various fisheries

oceanography studies. It should be pointed out again that unlike some other Sections of this Volume in which investigators are reporting results of specific studies planned, approved and funded by OCSEAP (i.e. physical oceanography and fisheries biology which have been conducted independently), here we have attempted to synthesize fragmentary pieces together into an overall dynamic system. The information available and space permitted has been inadequate for such a task and clearly demonstrates the reason why most investigators wisely limit their focus to one idea or concept. But the eastern Bering Sea shelf should be viewed as a system and all studies should be considered as merely components of the whole if we are to advance our understanding of the area.

MONTHLY MEAN CONDITIONS AND EVENTS

There are a number of characteristic features of the eastern Bering Sea ecosystem that make it quite different from most other important fisheries areas (Table I), but discussions will be limited to monthly mean environmental conditions and movements of halibut, herring, pollock, yellowfin sole and salmon with the intent of supplementing information already presented.

Ice information presented stems largely from Potocsky (1975) and NESS satellite imagery. Oceanographic conditions are derived from monthly summaries compiled at NWAFC from acquired and extant NODC geofile data (see Shelf Environment) in which data from October to March are extremely limited. Fisheries information in the form of schematic diagrams has been extracted from the foregoing Chapters and discussions with authors.

TABLE I

Characteristic Features of the Eastern Bering Sea Shelf Ecosystem

Characteristic Features	Consequences
Physical Features	
Large continental shelf	High standing stocks of biota High fish production Large food resources for mammals
High latitude area	Nutrient replenishment with seasonal turnover Environmental distribution limits for many species Large seasonal changes Seasonal presence of ice Accumulation of generations
Large occasional changes	Seasonally changing growth Seasonal migrations Possibility of large anomalies
Ice	Presence of ice-related mammals Migration of biota (in and out) caused by ice Limited production in winter
Cold bottom water	Outmigration of biota Higher mortalities and lower growth of benthic and demersal biota Accumulation of generations
High runoff	Low salinities (near coasts) High turbidities Presence of eurohaline fauna
Sluggish circulation	Local biological production Local pelagic spawning
Biological Features	
High production and slow turnover	High standing stocks
Fewer species (than in lower latitudes)	Few species quantitatively very dominant
High amounts of marine mammals and birds	High predation by apex predators
Pronounced seasonal migrations	Great local space and time changes of abundance
Fisheries Resource Features	
Pollock dominant semidemersal species	Flexible feeding and breeding habits, especially environmental adaption
Yellowfin sole dominant demersal species	Abundant benthos food supply
Herring and capelin dominant pelagic species	Important forage species in the ecosystem
Abundant crab resources	Large, relatively shallow shelf Few predators on adults, especially environmental adaption
Abundant marine mammals	Abundant food supply, no enemies insignificant hunting. Competes with man on fishery resources
Man-related Features	
Fisheries development rather recent	Ecosystem in near-natural state, not yet fully adjusted to effects of extensive fishery
Little inhabited coasts	Ample space for breeding colonies for mammals and birds Very limited local fisheries, no pollution

January

Air temperatures range from near 0 C near the Alaska Peninsula to lower than -15 C near Bering Strait. The leading edge of drift ice extends over 300 km seaward trending NW/SE from the mid-Alaska Peninsula to Cape Navarin, passing between St. Matthew and the Pribilof Islands; driven by mean northerly winds, it advances 3-5 km/d. Water temperatures near -1.8 C (minimum temperature possible at existing salinities) extend from inside the ice edge shoreward and isothermal and isohaline conditions occur under the ice; within 100 km seaward of the ice edge bottom temperatures may be several degrees higher because complete overturn usually occurs only under the ice. Bottom temperatures at the shelf edge and upper slope, and particularly southward of the ice edge in the southern part of the shelf, are 3-4 C, thus 5-6 C higher than in the vast area under the ice.

At this time most fish have retreated seaward and southward aggregating over the outer shelf and upper slope between the Pribilof Islands and Alaska Peninsula: herring largely northward of the islands (but also to the northwest and southeast) over the outer shelf (100-200 m); pollock and yellowfin sole at similar depths south of the islands but pollock also extend out over the slope and basin; and halibut seaward of the shelf edge and down the slope (Fig. 1). An important event is halibut spawning, eggs are released at depths of 300-500 m and rise slowly in the water column, larval stages eventually seeking the shallow shelf areas required for survival. The conditions, behavior and migrations of herring, yellowfin sole and other fish that may overwinter in coastal areas is unknown.

February

Environmental conditions are largely similar to January except for slightly lower air temperatures. The seaward advance of the ice edge continues, except in the area northward of the Alaska Peninsula where the northeastward onshelf movement of warm water retards ice formation; however, northwestward of this area an advance of 1-3 km/d occurs and ice extends seaward of the Pribilof Islands. Under appropriate air, sea and wind conditions the ice edge may advance rapidly--the formation of thin surface ice may spread 50-100, or more kilometers in a day and thicken, or break up and melt, depending on subsequent weather conditions.

Halibut spawning is largely completed and eggs are dispersed by existing currents which are poorly defined and seemingly variable and complex (Hanson 1978). The existence of large and small eddies in this area may serve to retain eggs and larvae in the southwestern part of the shelf, but may also make them vulnerable longer to predation by the massive fish biomass in this area. As a result of a special study aboard the Miller Freeman in 1978, Waldron (1978) indicated that pollock spawning may commence in this area in late February; in contrast to halibut eggs, pollock eggs are concentrated in the surface layer. Apparently there is little change in the distribution of herring and of pollock and yellowfin sole as well, except perhaps a slight southward movement in the northern slope areas as water temperatures progressively decrease below 3 C.

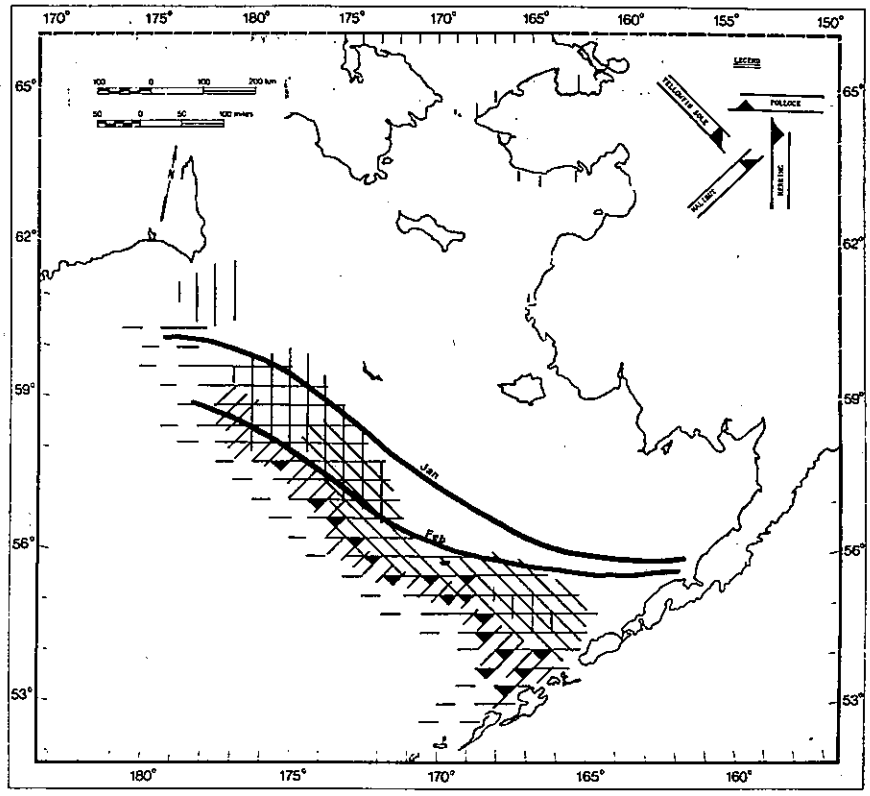

FIG. 1 Schematic diagram of January-February distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and broad line - ice edge).

March

Air temperatures begin to increase and ice extent approaches a maximum except for unusually cold years (e.g. 1956, 1971, 1976) when it occurs in April. Although sea surface temperatures show little change, the water column under the ice is isothermal at -1.8 C down to depths exceeding 100 m and greater depths (200 m) at the northwest extremity of the shelf edge where ice cover has existed since December. Cold water (0 to -1.8 C) in the midshelf area has nearly reached a maximum southward extent just northward of the central Alaska Peninsula, but the warm water (~3 C) area northward of the western edge of the Alaska Peninsula remains.

It is not known whether the progressive cooling of shelf edge and upper slope water (which continues until the ice edge retreats) or spawning behavior triggers a southward movement of various stocks, but increases are apparent in numbers of pollock southward of the Pribilof Islands and spawning continues in the area from the 100 m isobath seaward (Fig. 2). Why spawning does not occur farther inshore is not known. Halibut and yellowfin sole, present in the spawning area, are about to commence shoreward migrations. Herring north of the Pribilof Islands commence shoreward migrations to coastal spawning sites and to what extent the ice cover effects these migrations is not known, except that herring have over-wintered northward of Norton Sound under the ice (as in Gulf of Bothnia and Gulf of Finland).

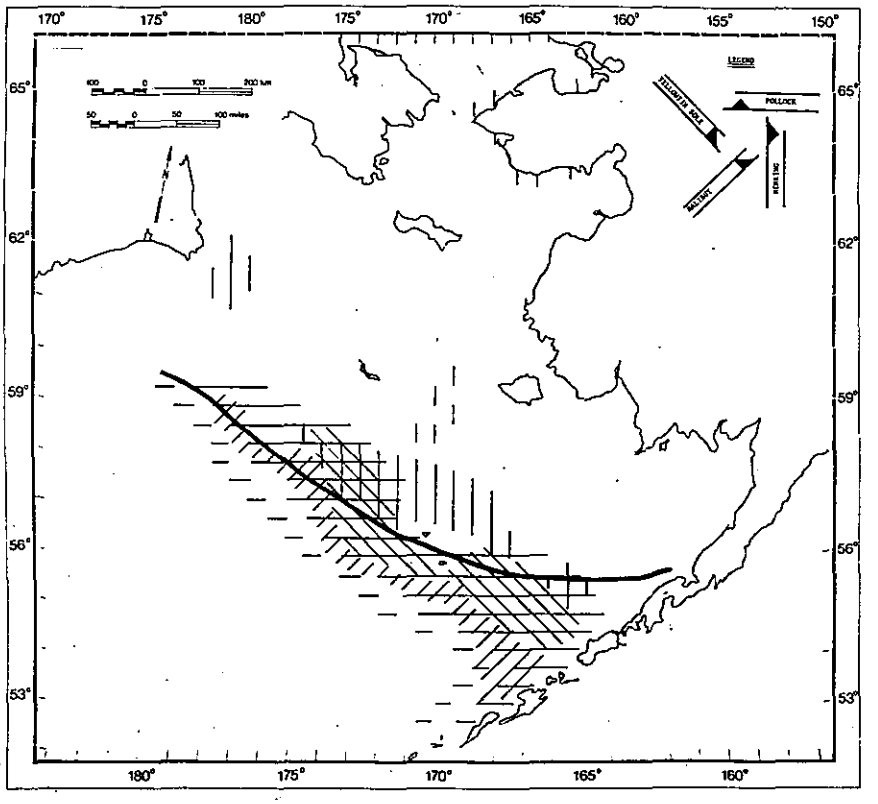

FIG. 2 Schematic diagram of March distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and broad line - ice edge).

April

Air temperatures begin to rise above 0 C immediately northward of the Alaska Peninsula but are below freezing throughout the rest of the area. Although in cold years the ice edge may still be advancing slowly southwestward and sections of it may be driven to the coast of the Alaska Peninsula as far west as Unimak Pass (e.g. 1956), usually a corridor remains ice free north of the western half of the peninsula. Ice over the southern half of the shelf reaches maximum thickness--~90 cm inshore near Nunivak and 45 cm near the Pribilof Islands. Isothermal conditions through the water column occur over most of the area as surface temperatures north of the peninsula rise above 3 C. In Bristol Bay where air temperatures over land have increased to 5 C, some runoff occurs and bottom temperatures rise from -1.8 to 0 C. However, northward along the coast winter water temperatures of -1.8 C prevail.

Pollock spawning continues seaward to the 100 m isobath with maximum concentrations of fish still north of Unimak Island (Fig. 3); though concentrations exist seaward of the shelf the abundance is not known. Herring are proceeding shoreward and the effect of the ice cover and the -1.8 C isothermal condition in the water column at midshelf is not known. In 1976, a cold year, spawning activity along the peninsula appeared to increase, but a maximum survey effort occurred; and in 1979, a warm year, early and extensive spawning occurred in the Togiak area. Yellowfin sole also begin easterly shoreward migrations from north and south of the Pribilof Islands, apparently in advance of halibut.

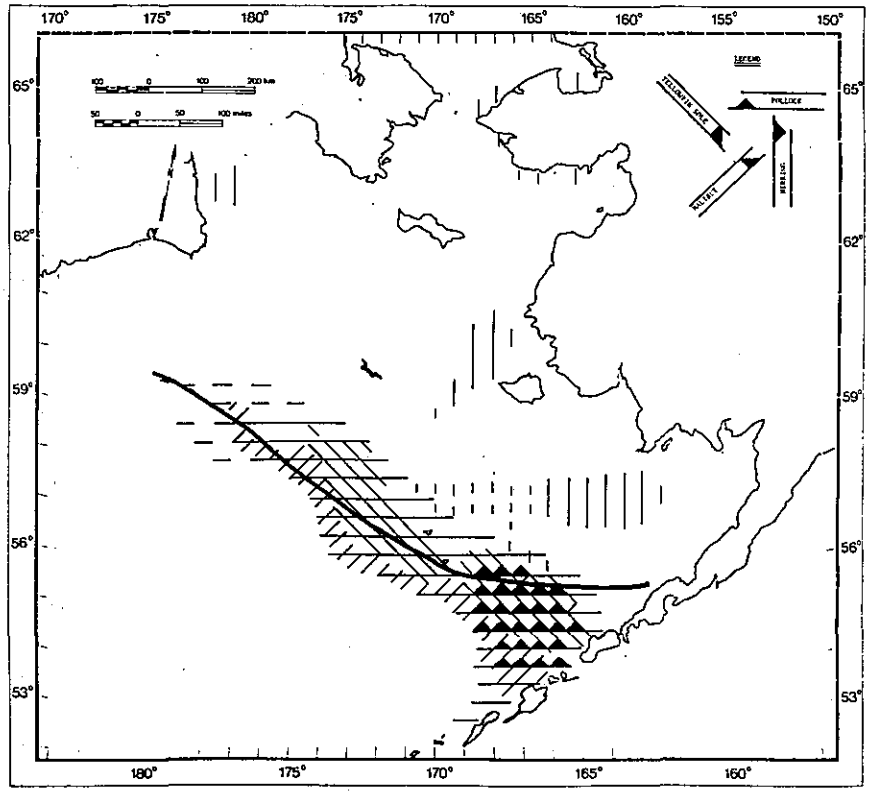

FIG. 3 Schematic diagram of April distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and broad line - ice edge).

May

Air temperatures rise rapidly, only generally northward of St. Lawrence Island do below 0 C conditions occur. Retreat of the ice edge is equally dramatic, reaching nearly 10 km/d in the central shelf area. There is little evidence yet of a surface layer, but surface temperatures above 4 C occur northward of Unimak Island, about 2 C in inner Bristol Bay and above 0 C northward along the coast to Norton Sound; but runoff is still limited and coastal salinities generally remain above 30°/oo.

Pollock spawning has reached a peak and adult concentrations shift northward along the outer shelf and slope; planktonic eggs and larvae largely concentrated near the surface are dispersed by currents off and across the shelf but primarily in a northwesterly direction along the shelf edge. Halibut extend into the midshelf area southeast of the Pribilof Islands, their northeasterly advance hindered or at least affected by the midshelf cold zone. Yellowfin sole commence easterly migrations along two paths, one north and the other south of the Pribilof Islands (although in May 1978 and 1979 warm years, yellowfin sole were observed feeding on herring spawn in northern Bristol Bay). Herring reach the coast from the Alaska Peninsula to Nunivak Island and spawning occurs in these areas (Fig. 4). Juvenile salmon appear along the coast and maturing salmon occur at the outer shelf. It is interesting to note that at this time the male fur seals, heavy predators, particularly on pollock and salmon have arrived at the Pribilof Islands.

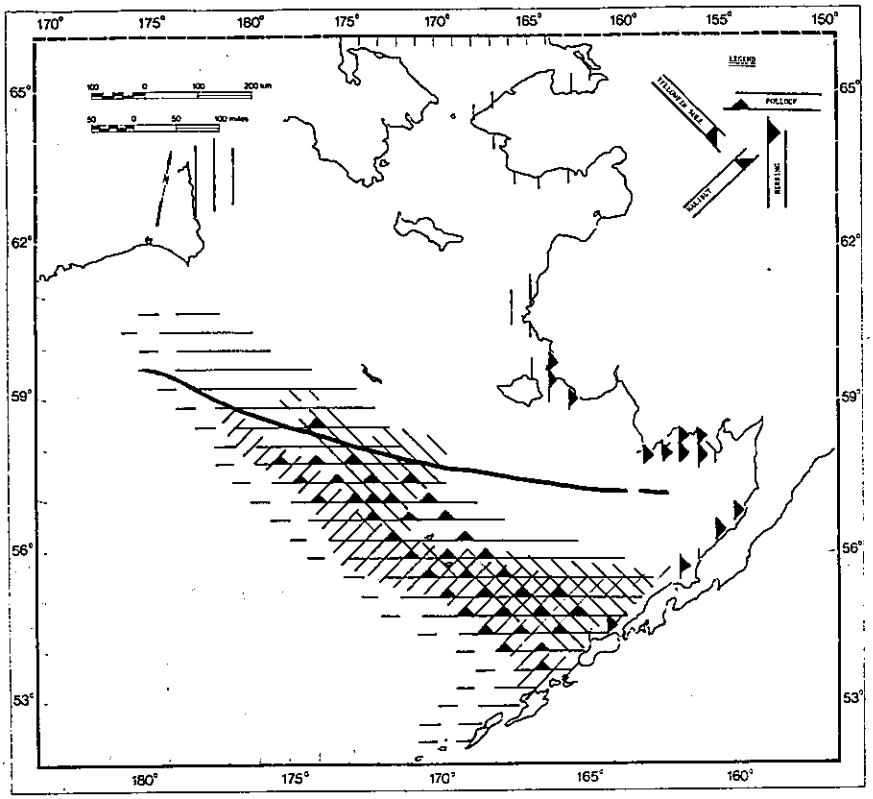

FIG. 4 Schematic diagram of May distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and broad line - ice edge). Some salmon are present.

June

Air temperatures (offshore) range from 3-8 C and the ice edge retreats rapidly (30 km/day) into the Chuckchi Sea, except at the western side of the Bering Strait and northern Gulf of Anadyr. Surface water temperatures throughout the area are above 0 C; 14 C in Norton Sound, 6 C north of the peninsula and in Bristol Bay; and 0-2 C in the midshelf area, between the 40 and 150 m isobaths north of the Pribilof Islands to the Gulf of Anadyr. Surface and inshore dilution from ice melt and runoff is first evident; coastal surface salinities reach a minimum in Norton Sound (16°/oo), which enhances surface warming.

Herring spawning occurs along the coast northward of Nunivak Island to Norton Sound; to the southward spawning is complete and herring disperse along the coast (Fig. 5). Pollock move shoreward to the 60-70 m isobaths east of the Pribilof Islands and northward to 60°N along the outer edge of the self; spawning has largely ceased, larvae have been transported northward along the shelf edge and juveniles extend inshore along the coast. Halibut extend into inshore areas as they conduct feeding migrations throughout the shelf area. Yellowfin sole continue to have two thrusts shoreward, one north of the Pribilof Islands and the other along the north side of the peninsula and northward in outer Bristol Bay where overwintering juveniles have an opportunity to accompany adults enroute to spawning grounds. Salmon occur throughout the southern part of the shelf area, king salmon reach the Yukon River mouth and the extensive sockeye salmon runs reach Bristol Bay prior to the end of the month.

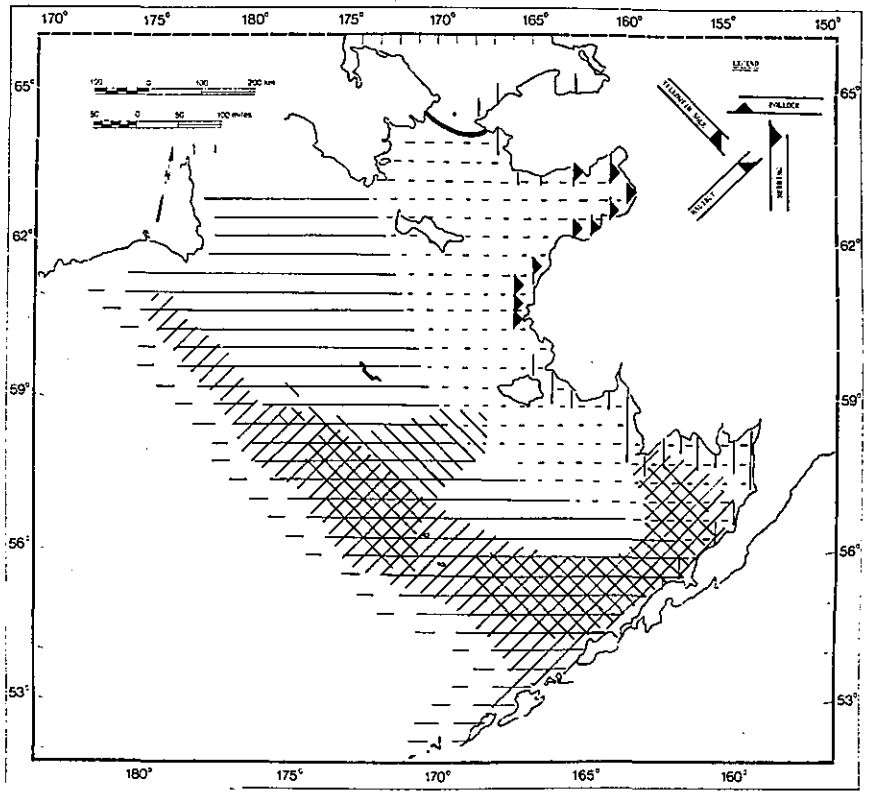

FIG. 5 Schematic diagram of June distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; short dashes - juvenile distribution, where known or different from adults; and broad line - ice edge). Salmon occur throughout the shelf area.

July

Air temperatures approach 10 C and sea surface temperatures of 10-12 C occur in the Gulf of Anadyr, 3-5 C at the west side and 5-7 C at the east side of Bering Strait, 14-16 C in inner Norton Sound, 10-12 C southward along the coast to Unimak Pass and 5-7 C in mid-shelf areas seaward over the basin. Bottom temperatures in the midshelf area from the Gulf of Anadyr to the Alaska Peninsula range from -1 to 1 C; in Bering Strait, 1-2 C; in inner Norton Sound, 5-9 C; along the coast from Norton Sound to Unimak Pass, 7-10 C; and along the shelf edge, 2-4 C. Offshore dilution due to river discharges along the Alaskan coast continues and minimum salinity values occur in outer Bristol Bay (28°/oo).

Herring spawning occurs along the coast northward of Norton Sound to Kotzebue Sound; no information is available on the Gulf of Anadyr stocks (Fig. 6). Yellowfin sole spawning commences northwest and southeast of Nunivak Island, the two stocks appear to remain separated; however, both spawning areas remain inshore of the mid-shelf cold front in an area of generally northerly flow. Pollock distribution remains the same as the previous month with adults generally seaward of the 50 m isobath but juvenile pollock and herring remain in inshore areas. Halibut continue to expand their range northward over the shelf. Salmon are generally ubiquitous, adults entering coastal areas and rivers from Cape Navarin to the Alaska Peninsula to spawn, and smolts becoming acclimated to the oceanic salinities and moving seaward across the shelf beginning the oceanic phase of their life cycle.

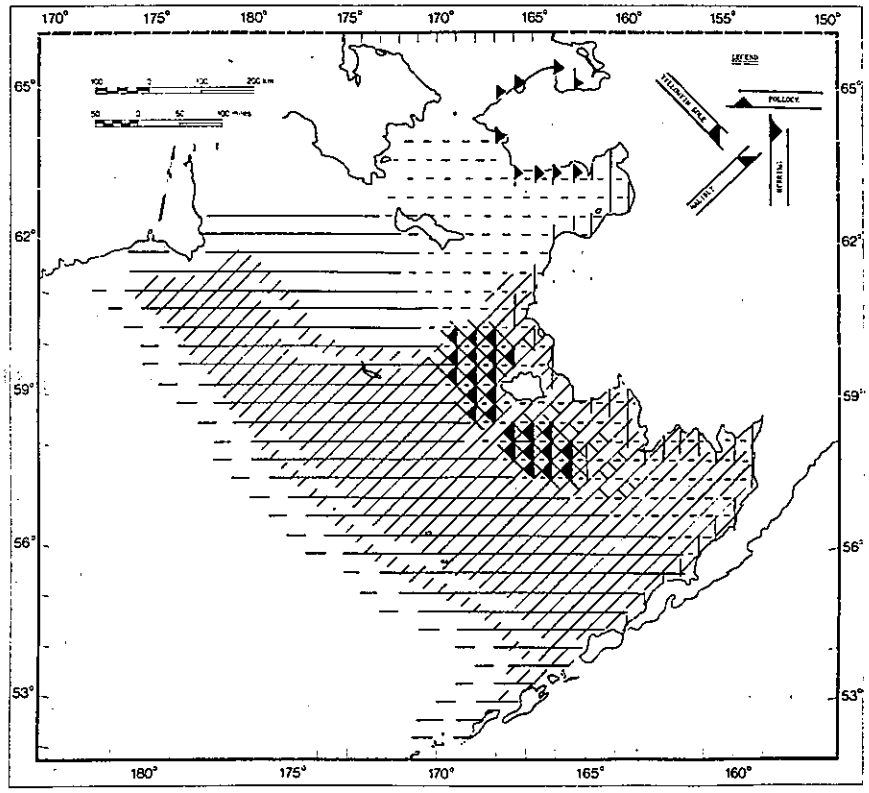

FIG. 6 Schematic diagram of July distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and short dashes - juvenile distribution, where known or different from adults. Salmon occur throughout the shelf area.

August

Air temperatures over the shelf have reached a maximum in July and commence to decline, but are still 5-10 C. However, along the coast sea surface temperatures continue to increase; maximum values (15 C) occur in Norton Sound but temperatures in excess of 10 C occur along the coast from the Alaska Peninsula to Bering Strait and even in Kotzebue Sound. On the western side of Bering Stait values of 2-4 C occur along the coast but these rise to 7 C along the eastern side of the Gulf of Anadyr and 13 C along the west. Mid-shelf values range from 7-9 C, but at the shelf edge they are 9-10 C. There is a marked difference in bottom temperatures which range from 9 C to -1 C northward to Bering Strait; whereas 10 C values generally occur along the coast from Bering Strait southward to the Alaska Peninsula. Values in mid-shelf range from -1 C in the north to 1 C in the south, and values of 3 C persist along the shelf edge. Maximum stability in the surface layer and maximum thermocline occurs in the mid-shelf area. Surface salinities in east Norton Sound have increased to 20°/oo, whereas dilution in inner Bristol Bay is still evident (26°/oo).

Yellowfin sole spawning is completed and these stocks disperse over the shelf (Fig. 7). Herring commence seaward migrations off Nunivak and Unimak Islands to wintering grounds, whereas the distribution of halibut and pollock remain largely unchanged. Most of the maturing salmon have reached spawning sites but smolts and juveniles continue moving seaward in undefined paths.

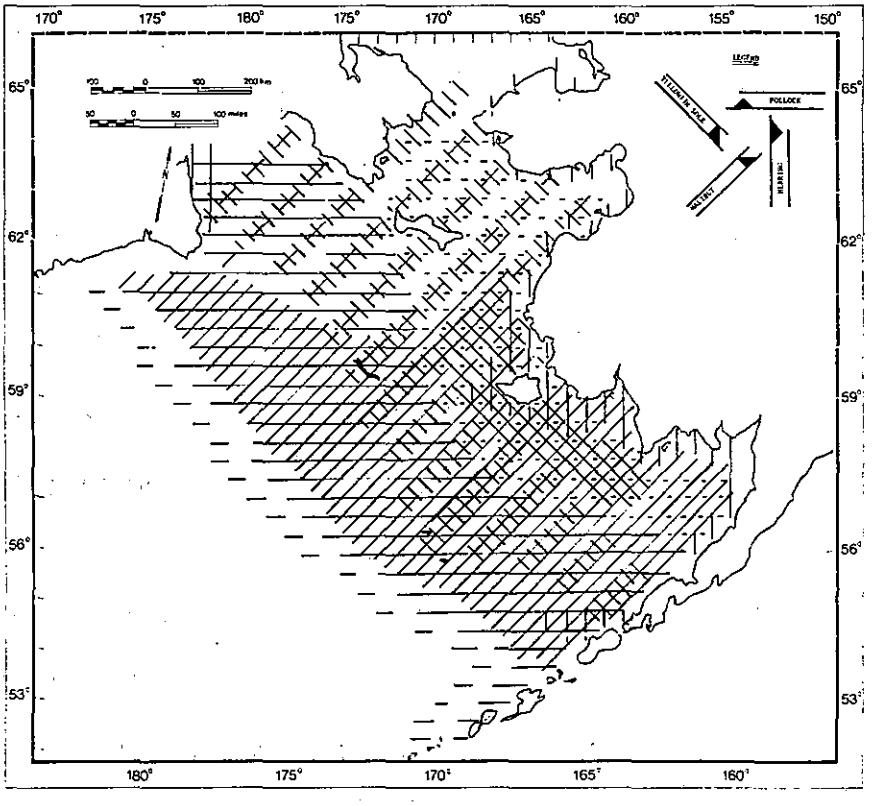

FIG. 7 Schematic diagram of August distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and short dashes - juvenile distribution, where known or different from adults. Salmon occur throughout the shelf area.

September

Air temperatures drop to 3-8 C and although maximum inshore sea surface temperatures of 10 C prevail from the Alaska Peninsula to Norton Sound, values of 6-8 C occur in the Gulf of Anadyr and 5-8 C in the mid-shelf area. Bottom temperatures remain relatively unchanged from August, the previous month, as do general salinity conditions.

Of particular interest at this time is the apparent seaward intrusion of warm, dilute, obviously coastal water, southwest of Nunivak Island (see Shelf Environment). If not an artifact caused by the averaging of data, this intrusion could have a pronounced effect on the return seaward of herring and yellowfin sole, possibly other stocks.

The offshore migrations of herring west of Nunivak Island and northwest of Unimak Island continue, and the dispersion of yellowfin sole from the spawning area off Nunivak Island commences (Fig. 8). Although it is apparent that yellowfin sole subsequently range over a large portion of the shelf, it is believed that the major concentrations remain west of Nunivak Island and it is from this location that the two major stocks commence seaward migrations to wintering grounds at the outer shelf. The timing of separation of juveniles that will overwinter in coastal areas is not clear. Halibut and pollock distributions are apparently unchanged. And, salmon stocks, both adult and juvenile, have largely cleared the shelf area by the end of the month, but stragglers may be present.

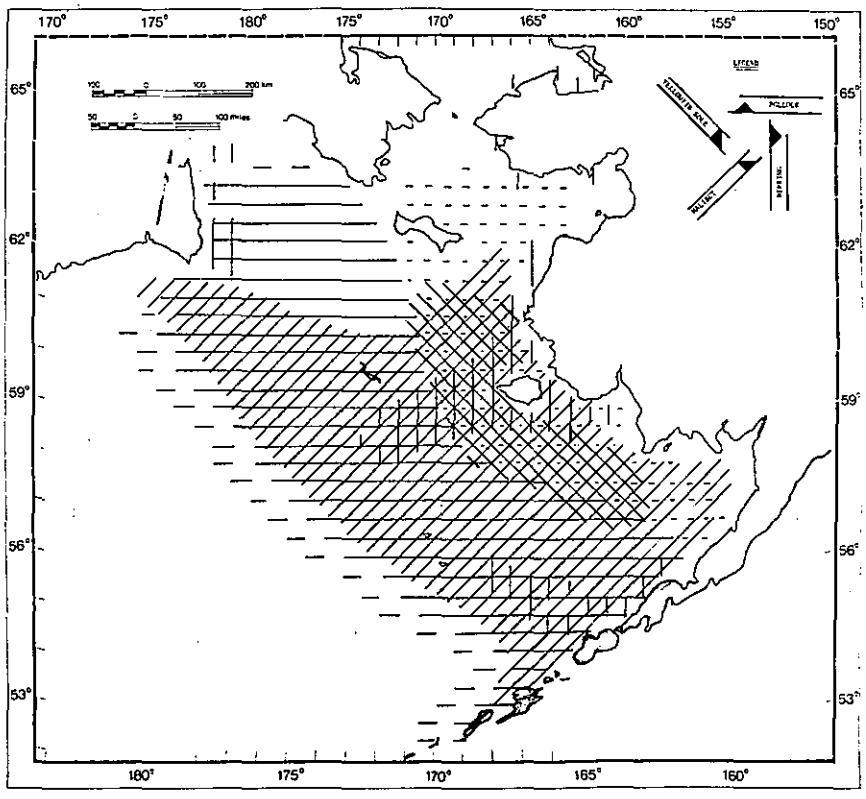

FIG. 8 Schematic diagram of September distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and short dashes - juvenile distribution, where known or different from adults. Salmon occur throughout the shelf area.

October

There is a marked further lowering of air temperatures and values below zero occur over the northern half of the shelf; ice begins to form in the Gulf of Anadyr, the west side of Bering Strait and east Norton Sound. Oceanographic data are too fragmentary to indicate mean conditions over the shelf but some features are apparent. Surface and bottom temperatures of 6-8 C occur along the coast from the Alaska Peninsula to Norton Sound. Mid-shelf surface temperatures of 5-7 C occur and bottom temperatures remain largely unchanged with only minor increases due to downward diffusion of heat but marked changes where seaward advection may occur. Coastal salinities increase above 30°/oo except in Norton Sound where values of 27-28°/oo occur.

Herring off Cape Navarin and Unimak Island have essentially reached wintering grounds and the main stock northwest of the Pribilof Islands occurs between the 50 and 100 m isobaths southward of St. Matthew Island (Fig. 9). Some juvenile yellowfin sole enter Bristol Bay where they will overwinter, but the two main adult stocks move southwestward and southward returning to winter grounds. Halibut and pollock stocks have begun retreating to the shelf edge. Why this occurs while even inshore coastal temperatures, particularly bottom temperatures are still in excess of those they will overwinter at (3-4 C), and no extensive offshore ice occurs is unknown. By the end of the month most of the fur seals will have left the Pribilof Islands and moved southward out of the Bering Sea.

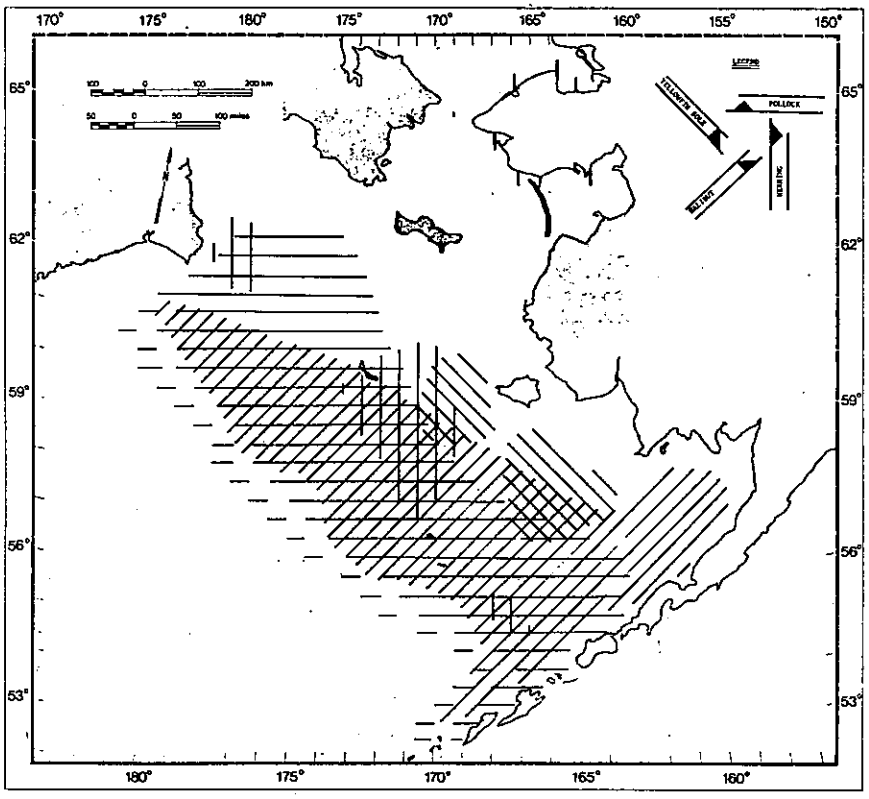

FIG. 9 Schematic diagram of October distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and broad line - ice edge).

November-December

Although essentially only air temperature (-10 to 3 C in November, and -15 to 0 C in December) and ice cover data are available, one can presume that the effects of the wind mixing and subsequent ice cover will quickly dominate any downward diffusion of residual heat in the water column. Both cooling effects will reach depths exceeding 100 m; the former taking place within a day or so, the amount of cooling depending on water temperatures in the surface layer; and, the latter requiring one to several weeks. However, it is prolonged ice cover that gradually results in bottom temperatures on the shelf lowering to -1.8 C and the freezing-out of fresh water results in higher salinities. Nevertheless, temperatures of 3-4 C occur at the bottom at the shelf edge and upper slope. The ice edge in November generally extends from Bristol Bay seaward of Nunivak and St. Lawrence Islands into the western Gulf of Anadyr. By December it extends from outer Bristol Bay, passing St. Matthew Island to Cape Navarin.

Herring and yellowfin sole are believed to reach offshore wintering grounds in November (Fig. 10). Herring overwintering in the Norton Sound area under the ice may experience temperatures higher than -1.8 C in the deeper areas if wind mixing did not establish neutral stability in the water column before ice cover was formed. Pollock retreat to the 100 m isobath by the end of December and at this time halibut have largely retreated seaward of the 200 m isobath.

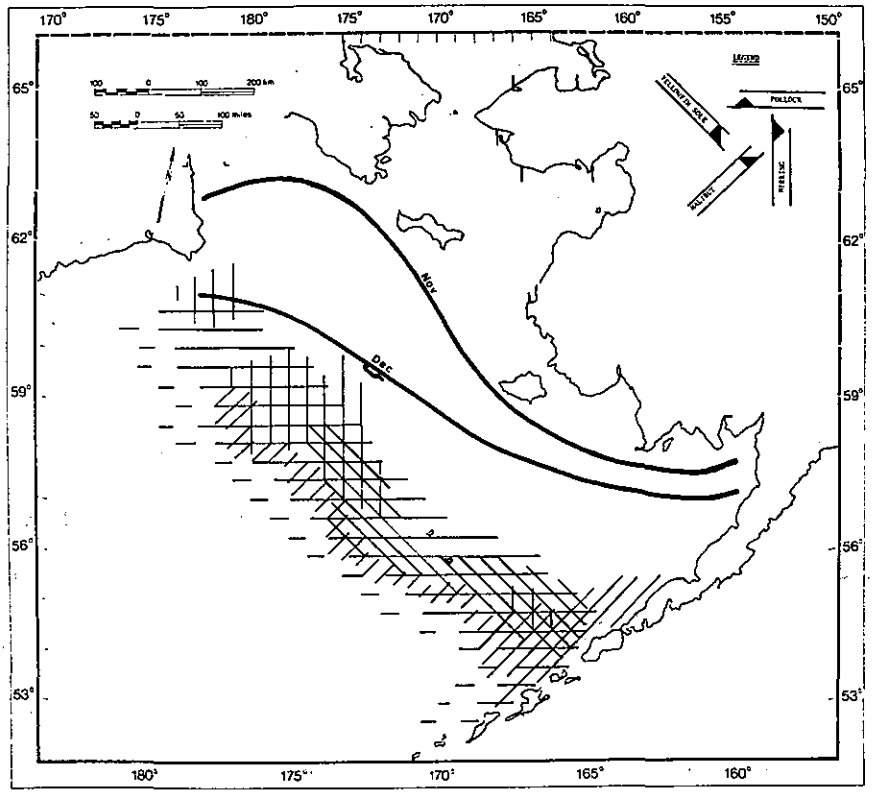

FIG. 10 Schematic diagram of November-December distribution of halibut, herring, pollock and yellowfin sole (solid triangles indicate - spawning areas; long dashes - probable extension of shelf range; and broad line - ice edge).

RESOURCE ENVIRONMENT RELATIONS

Before discussing fisheries oceanography studies that have been or should be conducted, it is useful to provide additional information on movements of the fish indicated. The life histories of these dominant (except for halibut) fish selected for discussion in this Section are quite diverse. Harden Jones (1977) suggests that fish movements can be summarized in the form of triangular patterns in which adult fish move between their spawning, feeding and wintering areas in a sequence which depends on the season in which they spawn: spring spawners (in our case, pollock and herring) follow a clockwise sequence of feeding-wintering-spawning, and autumn spawners (no representatives in this limited case) a counterclockwise sequence of feeding-spawning-wintering. Such a scheme does not provide for halibut which in our case spawn in winter in the wintering area, and yellowfin sole that spawn in the summer distant from the wintering area.

Plausible ranges and time scales of advection (passive transport) and migrations are shown schematically (Fig. 11). The average advection (~1 km/hr) and average migration (~3 km/hr) are indicated relating time to distance and periodic migrations such as semidiurnal and seasonal migration are also shown. The expected relative magnitudes of changes of biomass of a given species as a result of different periodic migrations as well as possible long-period "drift" within the system (which could result in long-period changes in abundance depending on transgressions of pelagic fish on and off the shelf and demersal fish into and out of the areas along

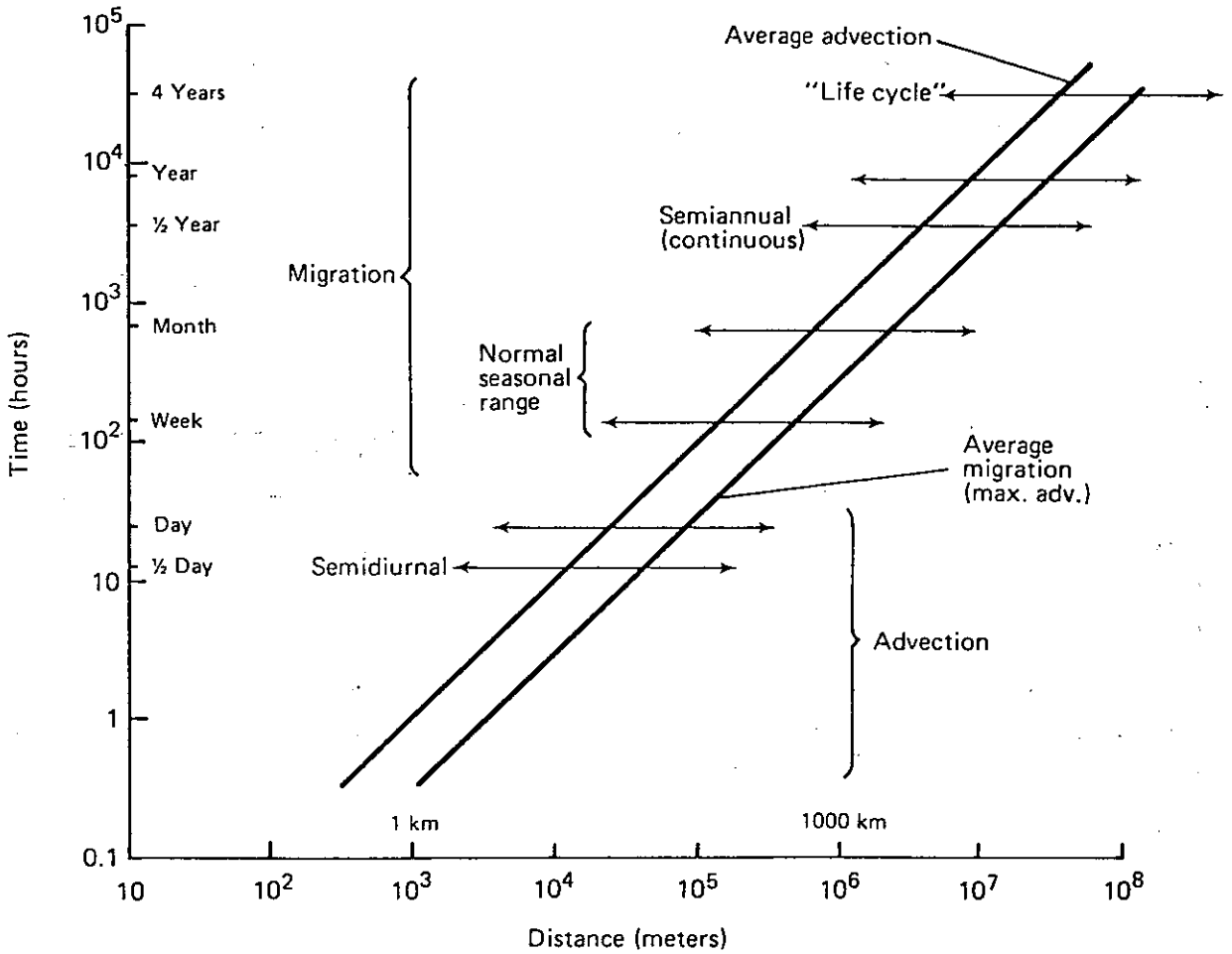

FIG. 11 Ranges of advection and migration of stocks in marine ecosystems.

the shelf (Fig. 12)). Migrations speeds are not known, except perhaps for Bristol Bay sockeye salmon, but some estimates of magnitudes of shelf distances traversed and required speeds for the eastern Bering sea have been compiled (Table II). Data for similar species in the North Sea indicate these estimated speeds are considerably lower than might be expected and Bering sea stocks may have considerably more mobility over the shelf than heretofore considered.

TABLE II

Speeds of Migrating Fish

Species	Speed (km/d)
Sole[1]	7-16
Plaice[1]	1-7
Herring[1]	4-30
Salmon (sockeye)[2]	54
Salmon (chum)[2]	48
Halibut[3]	6
Herring[4]	25
Yellowfin Sole[4]	3-7

[1]Harden Jones (1977) - North Sea area
[2]Kondo et al. (1965) - E. Bering Sea shelf
[3]Novikov (1970) - E. Bering Sea shelf
[4]Estimated from spawning migration - E. Bering Sea shelf

Another point that has been established here is that although environmental conditions are variable and stock distributions fluctuate, there are apparently no environmentally related indices, other than generally defined warm or cold years, that could be or

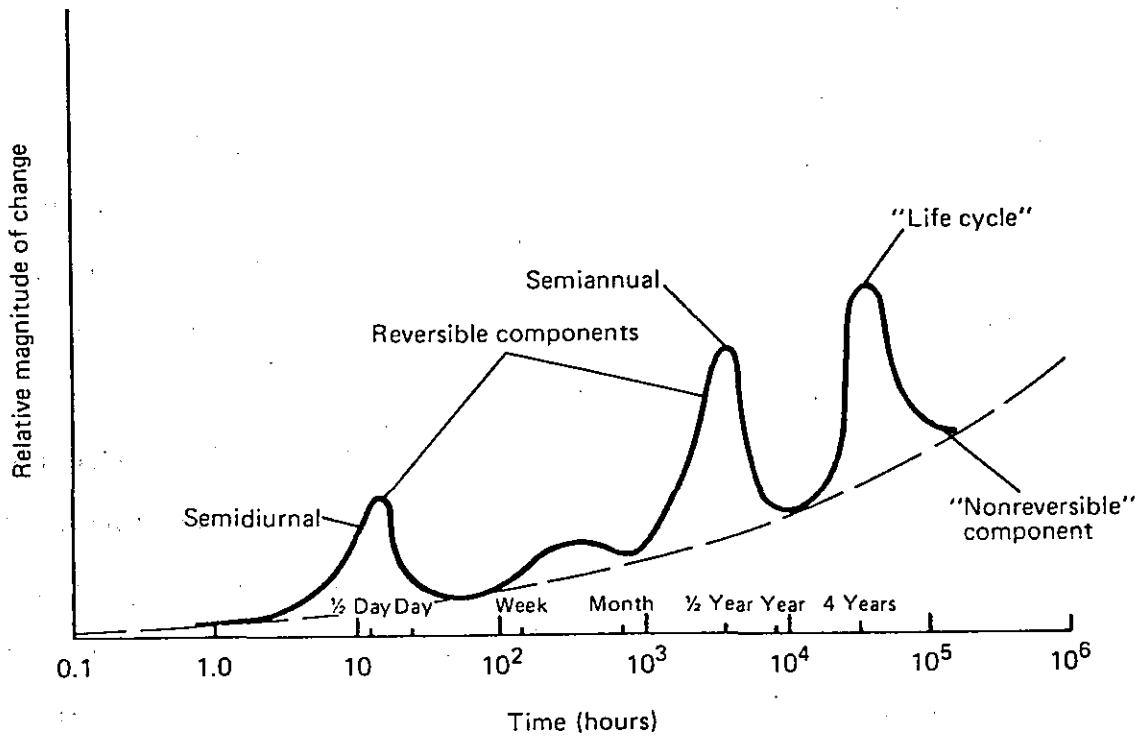

FIG. 12 Relative changes in abundance of stocks due to advection and migration.

are used to forecast successful or unsuccessful spawning or year-class strengths, anomalous distributions or migration paths, and fluctuations in annual abundances. Even though in the foregoing summaries of monthly events only mean conditions were considered, and events could be advanced or delayed as much as a month as a result of warm or cold conditions, the initial primary considerations for determining distributions were largely depth and season; for example, halibut occur in winter seaward of the 200 m isobath; adult pollock are generally seaward of 100 m in winter regardless of the position of the ice edge and seaward of 50 m in summer; juvenile pollock in summer are found shoreward of the 100 m isobath; the yellowfin sole wintering area is largely between the 100 to 200 m isobath but juveniles overwinter in inner Bristol Bay under the ice where the shallow depths assure that the water temperature will be -1.8 C; herring overwinter largely between 100-200 isobaths again apparently without any regard to the ice edge and some inshore stocks overwinter in ice-covered coastal regime. In only a few instances are there specific evidences of environmental influences. Yet if one approaches these conditions or events from a fishery oceanographer's or environmentalist's viewpoint rather than from that of a management biologist's, another perspective is evident and a number of instances are discussed.

Winter

Most discussions of productivity deal with aspects of the roughly million square kilometers of shelf yet it is obvious that in winter most of the biomass (excluding mammals) is restricted to

a small fraction (less than a fifth) of the total shelf area for nearly half of the year, November to April. Although one might argue that feeding in winter is usually drastically reduced, it should be obvious that bottom temperatures at the shelf edge (3-4 C) during this period are several degrees higher than in the mid-shelf area throughout the summer (-1 to 2 C), even though inshore temperatures may reach 10-15 C. Predator and prey are crowded together and there is evidence at other times and places that halibut consume yellowfin sole; and pollock are primarily cannibalistic (Takahashi and Yamaguchi 1972). (1) What effects do changes in the continuity and extent of the anomalous 3-4 C bottom temperatures on the outer shelf and upper slope have on species and biomass distributions, and to what extent does predation and growth occur during winter in this narrow zone?

Halibut spawn in January at depth and environmental conditions in the southeastern corner of the Bering Sea basin can be considered relatively constant. The prolonged period from egg release to when food is no longer provided by the yolk sac eliminates the availability of forage as a critical factor until early spring. (2) Does the success of a halibut year-class in this area depend on a predominance of onshelf flow along the shelf edge, possibly entrainment of larvae in local eddies, or is this stock maintained by transport of eggs and larvae from the North Pacific Ocean through Aleutian Island passes and spawning in this area provides the basis for stocks on the Asian (Cape Navarin-Cape Olyutorski) coast? Of course for management purposes one can wait until individual year-

classes are recruited into the fishery, but unless this question is resolved one will not be able to assess the effect of oil or oil spills on halibut (and other groundfish with similar behavior) recruitment in specific areas.

Herring are shown to have possibly 3 offshore wintering grounds largely associated with equivalent bottom topographies, however these represent 3 areas with distinct environmental conditions. The stock indicated for the area south of Cape Navarin spends a large part if not the entire winter under the ice at -1.8 C; the major wintering ground north of the Pribilof Islands may have ice cover only in March or April, this is not sufficient time to establish -1.8 C conditions and temperatures of 0-2 C prevail; the possible winter concentration between Unimak Island and the Pribilof Islands will encounter temperatures of 2-4 C and experience ice cover and colder conditions only in extremely cold years. (3) Are the 3 different winter temperature regimes critical to the isolation of these 3 stocks and if so, do the stocks have broader distributions than indicated and do the locations of the stocks change with environmental conditions? It should be pointed out that attempts by NWAFC to sample herring in the major wintering ground in February 1978 failed, (winter 1978 can be classified as warmer than normal).

Spring

The herring are the first to leave the area of concentrated biomass in winter, and spawning migrations commence in March. This

may be an instinctive movement because ice cover is relatively constant, at depths in excess of 100 m temperature regimes do not change (-1.8 C, 0-2 C and 2-4 C) and relative darkness at depth does not provide any signal or impetus. The primary factors here must be increasing light evident in upper layers and the presence or absence of ice. (4) Since the extent of mean ice cover usually reaches a maximum in April, are shoreward migrations from wintering grounds near the shelf edge that commence in March conducted under the ice, or do herring migrate southward (or await retreat of the ice edge) and proceed to the coast in open water? If the former is true, herring would arrive in spawning areas on schedule but in cold years they would have to wait until the coast was free of ice to spawn. Although rafting can occur the ice edge is usually composed of soft ice (vessels have easily penetrated 50-100 km) and such observations could be made and indices established because spring distributions and shoreward migration routes could then be ascertained by analyses of satellite imagery of ice cover.

Certainly pollock spawning in spring is a dominant event, although at this time it is difficult to compare this to the effects of sculpin spawning. The abundance of adults increases in spring north of Unimak Island (Low and Akada 1978). (5) Does the progressive cooling of shelf edge and upper slope water north of the Pribilof Islands into April as a result of prolonged ice cover, cause a southward retreat of adult pollock or is this a spawning migration?

As might be expected of a successful species, spawning is protracted. Waldron (1978) found that pollock larvae were present near the shelf edge northward of Unimak Island in March and if development occurred locally, spawning would have commenced in February. However, the larvae were found in a northward protruding tongue of temperature maxima (4 C) and it's possible that they were advected into the area from south of the Alaska Peninsula where conditions can be much warmer at this time of the year. Unlike halibut, pollock eggs and larvae occur in the surface layer and are exposed to the vicissitudes of weather from March to July. In spring 1976 eggs were found within the ice edge when an unusual southward thrust of ice occurred, and violent spring storms are the general rule rather than the exception. (6) What are the effects of stormy vs calm weather, ice vs no ice, and early (February-March) vs late (May-June) spawning on pollock year classes? A simple device that would not only assist in determining answers but also permit prompt verification and evaluation of conditions would be a moored biological buoy that would sample organisms in the water column (5 m to bottom) at weekly (or shorter) time intervals from February to late spring when the data would be recovered and evaluated.

Further, pollock spawning apears to be largely restricted to the area seaward of the 100 m isobath, thus in close proximity of the Pribilof Islands and the million or so fur seal predators. (7) What are factors environmental or otherwise that appear to confine adult pollock seaward of the 100 m isobath before, during and after spawning?

It is not clear whether halibut or yellowfin sole are first to commence shoreward migrations, but the latter have a spawning incentive. (8) Do halibut follow yellowfin sole shoreward to assure a source of food or is their shoreward migration and subsequent consumption of benthic organisms simply the result of a seasonal feeding behavior pattern?

In respect to both inshore migrations Hardin Jones' (1977) selective tidal transport hypothesis may be quite applicable. His studies indicate that plaice in European waters move into midwater to take advantage of tidal flow in the direction of overall purposeful movement, but return to the bottom at the turn of the tide. This movement is aided by a gliding (or sail-planing) afforded by lift forces provided by their shape and permits spending half their time in midwater. Such a behavior in the stock between the Unimak and Pribilof Islands would permit considerable enhancement of migrations because current data (Dodimead et al. 1963) and tidal model studies at NWAFC (Hastings 1975) indicate a general NE/SW oscillation northward of the Alaska Peninsula particularly in Bristol Bay that would aid migrations from the shelf edge into Bristol Bay and a change in oscillation that would aid a subsequent general northward movement over the shelf, the benefit from such tidal sequences also aiding return movement to the southwestern part of the shelf in fall. (9) Does selective tidal transport give halibut, yellowfin sole and other flatfish considerably more mobility and migration speed than currently envisioned (~3-6 km/d)?

When one seeks resource-environment relations, the onshore delay or aggregation of halibut and yellowfin sole at the cold front north of the Alaska Peninsula (see Halibut Ecology and Population Characteristics and Ecology of Yellowfin Sole) is a convincing example. But the northerly movement of halibut proposed by Natarov and Novikof (1970) and the eastward movement of the yellowfin sole stock north of the Pribilof Islands indicated here raises some doubts as to the absolute validity of this phenomenon; although U.S.S.R. studies in the Grand Banks off the east coast have indicated that hunger transcends discomfort and fish will at times intrude into areas having environmental conditions normally avoided. (10) What is the role of selective tidal transport and the ability of halibut and yellowfin sole not only to move quickly but to rise easily into the water column in their penetration of the cold, midshelf zone? Studies of benthos and possible relations to fish in this area are the subject of another Section of this Volume.

In regard to salmon movements, over 40 years ago Moulton (1939), in a foreword of a symposium concerning the migrations of salmon, noted that in the problem of accounting for the migration of salmon one enters a field in which science and romance appear to meet. This was because in spite of environmental and tagging studies the story of what takes place in the apparently super-natural migrations, wherein mature fish return after several years at sea to precisely the stream of their birth, was far from being complete and explanations of such migrations were equally open to

question. Although considerable information on oceanic distributions and migrations has been forthcoming from studies conducted since 1953 under the aegis of the INPFC, how salmon find their way in the ocean remains a major and interesting fisheries oceanography problem. Coastal migrations and their explanations are subject to the same inadequacies as ocean migrations. Less than a decade ago at another salmon symposium Larkin (1975), after reviewing information on how salmon navigate, postulated that they might have a system of collectivizing judgment that could provide a school with remarkable navigational accuracy, and if schooling was due to an ability to detect their conferees by scent this would permit effective schooling of adults in the ocean as well as the detection by adults of coastal regimes carrying the scent of juveniles that had commenced seaward migrations. Although such ideas are perhaps more intuitive than scientific, there are numerous examples of extraordinary salmon behavior other than the fact that mature individuals return to natal streams annually and arrive at the coast with consistent and appropriate timing. Such punctuality might be considered supernatural if it were not for their mobility; for example, king salmon migrate over 2400 km up the Yukon River in 3.5 weeks advancing at an average speed of 110 cm/sec or about 85 km/d without consideration of opposing river flow (Gilbert and O'Malley 1922), and disregarding any potential to swim shorter distances at higher speeds they could transit the shelf area in much less than a week although shelf migration speeds of only 50 km/d are reported (see Table II). Although there is scant knowledge as to the

nature of such movements, there is an apparent order to the sequences of arrivals at river mouths of all species.

Large incidences of king salmon in trawl catches in winter 1979 near Zemchug Canyon came as a surprise to biologists who have studied salmon migrations for decades. Since this canyon is believed to have been cut across the shelf during periods of lower sea level (land bridge) by the Yukon River, if these salmon can be shown to be of Yukon River origin one is inclined to believe that salmon homing instincts have strong environmental imprints. But it is apparent (see Trans-shelf Movements of Pacific Salmon) that movement of Yukon River, Norton Sound, and Gulf of Anadyr salmon, and those that eventually pass through Bering Strait are largely unknown. Questions concerning the movement of salmon in the eastern Bering Sea in relation to environmental factors are too numerous to list only one or two but obviously little is known about movements northward of the Pribilof Islands. (11) What are the migration routes over the shelf of adult and juvenile salmon from Gulf of Anadyr, Arctic Ocean, Norton Sound and Yukon River areas? Obviously extensive environmental studies must accompany any distributional or tagging problems.

There are numerous evidences that Pacific salmon respond to environmental factors (Favorite et al. 1978) and it is apparent that migrations of various species and stocks through the various lease areas (e.g. St. George Basin, Navrin Basin, Norton Sound) cannot be ascertained or predicted until more information is obtained on relations of environmental factors on shoreward migrating

adults and seaward migrating smolts (juveniles) in this area. The effects of oil contamination of river mouths could affect upstream migrations of sockeye, coho and king salmon and coastal spawning of chum and pink salmon; and spills at offshore sites could greatly affect migrations of salmon of U. S. and U.S.S.R. origin (spills in spring and summer would also be disastrous to herring because spawning beds are intertidal).

Summer

It has been pointed out that adult pollock are cannibalistic, preying extensively on juveniles and, in summer, juveniles occur largely within the area between the 100 m isobath and the coast; whereas the adults are largely confined seaward of 100 m. (12) Is the presence of juveniles in inshore areas where warm conditions occur a response to environmental factors including forage or are they found there because it is the only area where predation by adults does not occur, and what factors confine adult pollock seaward of the mid-shelf area?

Herring spawning occurs in northernmost areas in summer reflecting a northerly sequence with time and perhaps a direct relation to temperature and ice, also possibly to the effects of coastal dilution which is also delayed from that in more southerly areas. (13) Can the time of herring spawning at various areas along the coast, which can vary from a week to a month, be defined by temperature or salinity conditions, and does advanced or delayed spawning periods affect the success of year classes, or contribute to reduced or excessive predation on spawners?

One of the dominant summer events is the spawning of yellowfin sole in the area off Nunivak Island. This occurs inside one of the sharpest frontal zones on the shelf, between the mid-shelf and coastal sub-domains. Temperatures in the frontal zone at this time increase sharply shoreward, from -1 to 10 C. Thus, spawning occurs in the warmest area of the eastern part of the shelf that does not have excessive dilution and high turbidity due to local rivers (such as inner Bristol Bay and Norton Sound) and in an area that has a broad extent of shallow depths (unlike the northern coast of the Alaska Peninsula). The length of time required for larvae to obtain mobility or drop to the sea floor is not known but a northerly flow in this area of 25 cm/sec ($\sim$0.5 kt) would transport them through Bering Strait in about 20 days unless caught in eddies in Norton Sound. (14) What mechanism prevents the dispersal of yellowfin sole larvae into the Arctic Ocean?

It is apparent in the monthly mean distributions of properties for September that there is a marked seaward intrusion of coastal water in the Nunivak Island area that could have a major effect not only on circulation, but on movements of larvae of yellowfin sole, and juvenile pollock and herring. (15) Is this trans-shelf intrusion real or an artifact of averaging data and what is its effect on conditions and events in this area?

Fall

Although little is known concerning precise fall distributions of fishes, it is generally believed that most commence a retreat southward and seaward to the shelf edge by October. Although air

temperatures have lowered, mean sea surface temperatures have not decreased substantially. Water temperatures in coastal areas have lowered a few degrees but are still high (~8 C); and ice appears only in eastern Norton Sound and along the shore. Thus there is little evidence of drastic environmental changes other than light duration and intensity, until November. (16) What factors trigger fall seaward movements of fish to the shelf edge and what is the nature and relative timing of movements of individual stocks?

CONCLUSIONS

The eastern Bering Sea ecosystem encompasses a vast renewable resource of great potential and value that should be carefully protected and developed but one about which we have very little basic understanding. Although the NWAFC in conjunction with the North Pacific Fisheries Council are expending great efforts to estimate the various individual resources for management purposes, there should be an equal thrust to understand conditions and processes as well as periodic and aperiodic events and their causes and effects. This can come about only through cooperative, interdisciplinary research. Basic research and resource assessment should continue but fisheries oceanography studies combine both of these aspects and provide an integrative focus that is badly needed as exploitation of individual resources of commercial value accelerates.

Nearly a decade ago when congressional support for fisheries studies was wanting, one argument put forth justifying limited support for marine research was that marine fisheries were a common

property resource, couldn't be protected and posed real problems in regard to development. The ideal example given was a plot of trees that could be clearly defined spatially, containing a crop that could be protected (from man and diseases), selectively harvested on demand, and selectively reseeded to provide a continuing resource. The eastern Bering Sea shelf, relatively isolated from the broad sweep of ocean currents, is a unique place to consider development of a major marine habitat that can be protected and developed when we have a basic understanding of requirements of individual species and stocks, interactions among them and their place in the ecosystem. The economic justification is obvious, the value of fisheries products extracted in 1978 was roughly half a billion dollars and the problem of protection is answered by the recent FCMA.

We hope that it is apparent from the limited discussion presented that the merit in multispecies and ecosystem approaches to investigating and understanding conditions and processes is readily apparent and such a focus will be considered in all future studies. Because this requires extensive accountability of species interactions and environmental effects one is at a loss to handle the multiplicity of factors involved without formulation of some sort of modeling or simulation techniques. A great deal of preliminary work has been accomplished along these lines at NWAFC and a summary of an existing simulation model (DYNUMES) that presents the quantifications of biomasses omitted in this Chapter is presented in the following, and concluding, one. Such studies also permit independent

assessments of movements in relation to environmental factors such as temperature and forage requirements.

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ECOSYSTEM DYNAMICS IN THE EASTERN BERING SEA

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ABSTRACT

The spatial and temporal dynamic aspects of the marine ecosystem in the eastern Bering Sea were investigated with the ecosystem model DYNUMES III. Equilibrium biomasses of major species and ecological groups are presented together with their annual consumption. The latter represents a major portion of the "natural mortality" which removes a major part of the annual production of biomass, especially of forage species and faster growing juveniles of other (larger) species. Examples of the dynamics of the biomasses of some species, with certain restraints on recruitment variations, over a four-year period are also given.

Marine mammals, as apex predators, remove a considerable part of the fish production and the effect of their predation on the marine ecosystem is in many respects similar to that of the fishery.

Some validation of the results of simulation model computations is provided by comparisons with survey results, adjusted by catchability factors.

INTRODUCTION

In the past it has been customary to consider the marine ecosystem and the living resources in it as a quasi-steady state system. This has been effected mainly by averaging the quantity of resources over large regions, such as the eastern Bering Sea, and over long time units, such as a year or more. However, conditions in marine ecosystems are not stable in space and time, but are subject to various seasonal changes (e.g. feeding and spawning migrations, etc.) and by environmental anomalies (e.g. varying extent of ice cover); all of which are rather pronounced in the Bering Sea.

The objectives of this study were to investigate the effects, and spatial and temporal magnitudes, of the dynamics of the Bering Sea ecosystem, including the source and sink areas of biomasses of various species and the seasonal changes of these sources and sinks as well as the changing predator-prey relations.

The eastern Bering Sea contains large numbers of marine mammals as apex predators whose numbers vary seasonally. Their effects on the ecosystem were also investigated and are briefly reported.

The predetermined length of this paper does not permit the presentation of all supporting data and details, which have been and are continuingly being reported in various NWAFC Processed Reports. Furthermore, as instructed, only key references have been cited.

MAJOR PROCESSES IN THE MARINE ECOSYSTEM AND A REVIEW OF THE ECOSYSTEM SIMULATION MODEL DYNUMES III.

The major dynamic processes in any marine ecosystem which affect the abundance and distribution of species are listed (Fig. 1) together with the major factors affecting these processes and their results.

The most difficult to reproduce quantitatively are the results from the spawning process (i.e., the larval recruitment and the early mortalities of larvae). After many decades of intensive research on stock-recruitment problems, we now know that no simple relation exists between the spawning stock size and the recruitment size to an exploitable stock. It can only be stated in general terms that proportionally larger recruitment can result from small spawning stock and proportionally smaller recruitment can result from a large spawning stock. The numerous hypotheses on proper food availability to larvae and subsequent effects on recruitment size have not been proven either. Many fisheries scientists are inclined to believe now that factors affecting recruitment sizes to exploitable stocks seem to be controlled mostly by predation in larval and juvenile stages (Hempel 1978; Rothschild and Forney 1979) and that recruitment might be largely influenced by environmental anomalies (Garrod and Colebrook 1978).

The factors affecting growth and reduction of species biomasses are generally known, although refinement of knowledge on the small variations in the growth of individual species is continuing.

Predation has been included traditionally in an all-encompassing term "natural mortality", of which predation constitutes the

A. Biomass abundance affecting processes

Main process	Major affecting factors
SPAWNING (reproduction, larval recruitment)	Spawning biomass size (including fecundity) Predation on eggs and larvae Availability of food (including starvation) Environmental factors (including advection)
GROWTH	Age Temperature (anomalies) Food availability
PREDATION (mortality)	Vulnerability (sp. size) Predator abundance
MORTALITIES	Senescent mortality Spawning stress mortality Disease mortality

(SPAWNING)

B. Biomass distribution affecting processes

SOURCE-SINK AREAS (Differences in abundance affecting factors in space and time)	Growth Predation Other mortalities
MIGRATIONS	
Seasonal	Feeding migration Search for optimum environment
Life cycle dependent	Spawning migrations Predation avoidance migrations Feeding migrations
Environment dependent	Search for optimum environment Advection by currents

(APEX PREDATORS AND FISHERY)

FIG. 1 Major dynamic processes in the marine ecosystem.

major portion in most species. In order to remedy this shortcoming the predation mortality is computed within ecosystem models in great detail, using data on food requirements for growth and maintenance and space and time variable food composition. Very few fish stomach analysis studies have been accomplished on Bering Sea stocks. Those available largely list only the frequency of occurrences of food items in the stomach, making these studies absolutely useless exercises. Fortunately recent European studies of fish feeding habits (e.g., Daan 1973) have established that feeding in the marine environment is largely both food size/fish size, and food availability dependent; and this knowledge has been incorporated in our DYNUMES (Dynamical Numerical Marine Ecosystem) model. In addition, special studies at NWAFC have quantitatively ascertained the age-dependent spawning stress and senescent mortalities (Granfeldt 1979a), and these also have been included in the DYNUMES model.

Due to spatial changes in factors affecting growth and in predator and prey distributions, considerable spatial and temporal differences in the growth and decline of biomasses occur (these are described later). All of these interactions are nonlinear and therefore can be evaluated quantitatively only with three or four dimensional ecosystem models such as DYNUMES. Few epibenthic organisms are sessile during most of their lives. Most species undertake migrations for various reasons, seasonal migrations are connected most often with seasonal changes in the environment, both

in relation to the availability of food and to the search for optimum environmental conditions (e.g., temperature). In addition, pelagic organisms are advected with seasonally changing currents. Life-cycle dependent migrations are for spawning, feeding, and/or predation avoidance. Very little is known on the migrations of fish and especially of the distribution of juveniles in the eastern Bering Sea. In this respect the fisheries research in the Bering Sea and in the Gulf of Alaska is at least many years behind fisheries research in the North Atlantic. Only the seasonal migrations of some flatfishes are approximately known in the North Pacific (Alverson 1960), however, North Atlantic studies have a longer history and more intensive research efforts.

The static conditions usually implied in past studies of ecosystem productivity as well as in respect to the effects of fishing will not give quantitative answers when prey is quasi-stationary and predators migrate or vice versa. Some of these migration effects are shown schematically (Fig. 2). Consider that there is a given benthos biomass as a fish food resource at the section a-b. Under stationary conditions this benthos biomass is grazed by the stationary predator biomass (a-b) at this location. However, if the predator moves with a speed C through this section, the "up-migration" of biomass A can prey on the same standing stock of benthos at the section a-b during migration. If the speed is doubled, the biomass A+B can prey on the same benthos biomass (time factor must also be considered above). This applies also to fishing: in the stationary case, the fish is caught (and sampled) as

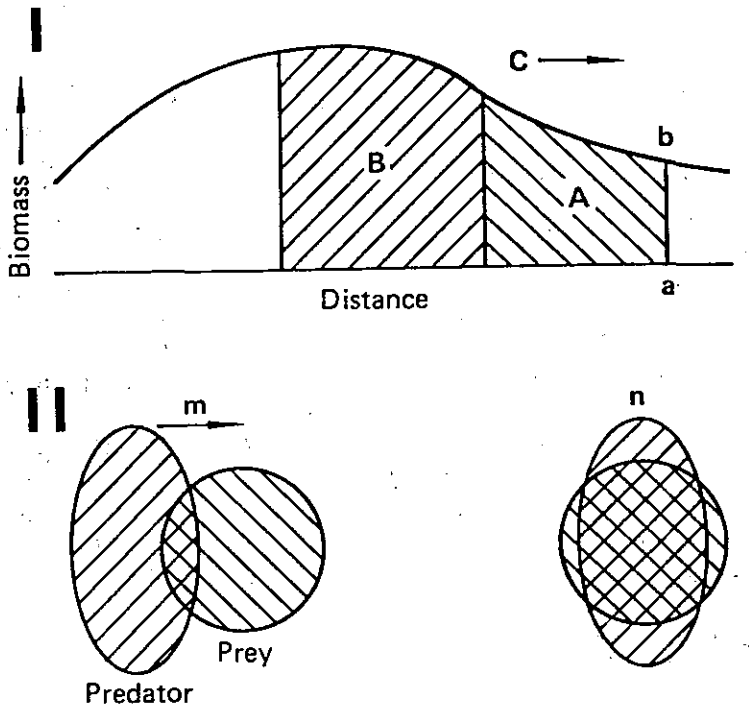


FIG. 2 Schematic presentation of two effects of migration.

I. With a given migration speed c the biomass A passes through the section a-b. Doubling either the speed or time, biomasses A+B pass through the same section.

II. Schematic example of the migration of predator into the region of a given prey.

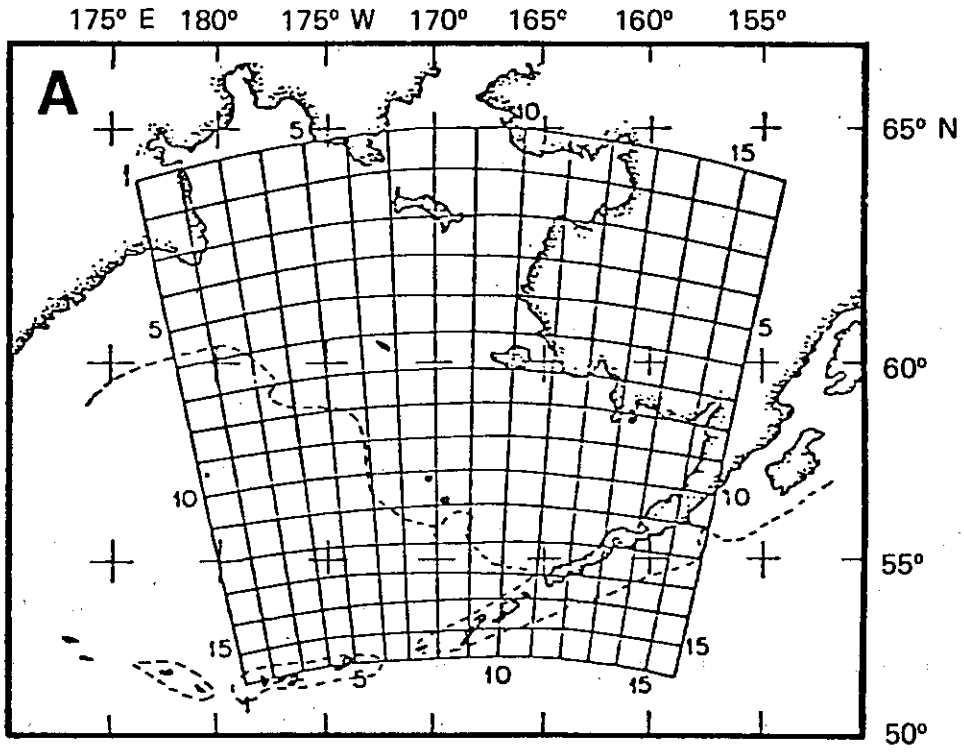
representing the biomass present at all times. However, with varying migration speeds and quantities of biomass passing through the section, the effect of a constant fishery for different segments of the population would be different. This difference becomes more complex if the biomass age composition also varies with time as the fish biomass moves through section a-b. The second part of the Figure shows the self-explanatory effect of predation caused by separation and/or overlap of predator and prey. These concepts are simulated numerically in the model.

The extensive and relatively complex ecosystem simulation model DYNUMES has been described elsewhere (Laevastu and Favorite 1978a, In Press). All necessary species-specific data, such as growth rate, temperature preference, food item preference, etc., are obtained from available empirical data and introduced into the model. The initial distributions of species (groups of species) are prescribed at each grid point in a geographically oriented grid (Fig. 3A), together with other necessary space and time dependent data such as depth, monthly surface and bottom temperatures, ice cover, migration speed (u and v components), etc.

The numerous computations are accomplished at each grid point at each time step (e.g., monthly). There are four basic formulas and a great number of auxiliary computations. The first basic formula is the biomass balance formula:

$$B_{i,t,n,m} = B_{i,t-1,n,m}(2 - e^{-g_{i,t,n,m}})\, e^{-m} - C_{i,t-1,n,m} \qquad (1)$$

where: $B_{i,t-1,n,m}$ is the biomass of species i in previous time



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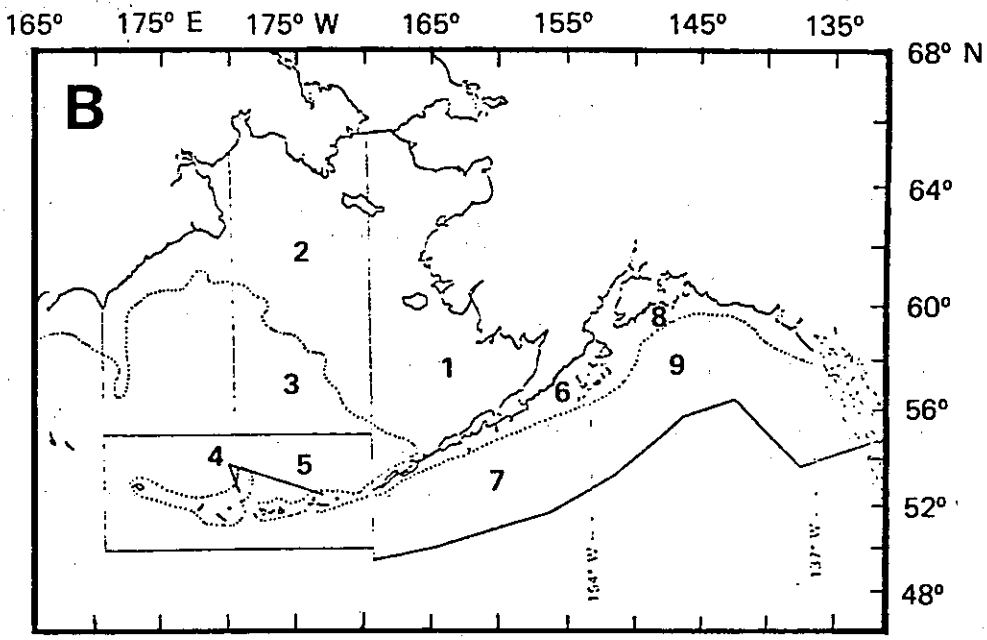


B

FIG. 3 Computation grid of DYNUMES for the eastern Bering Sea (A) and the fisheries management and statistical areas (B).

step (t-1) at the location n,m; g is the growth coefficient which is a function of temperature, season, and availability of food; m is a mortality coefficient (senescent mortality and spawning stress mortality), and C is predation (mortality) as computed in previous time step:

$$C_{i,t,n,m} = \sum_j C_{i,j,n,m} \text{ and} \quad (2)$$

$$C_{i,j} = R_{j,t,n,m} \Pi_{j,i,t,n,m} \quad (3)$$

where $R_{j,t,n,m}$ is the total food requirement of species j and $\Pi_{j,i,t,n,m}$ is the fraction of food of species j which consists of species i. This fraction varies in space and time (t,n,m) depending on the availability of suitable food items.

The migrations are computed with an "upmigration" interpolation finite difference formula:

$$B_{t,n,m} = B_{t-1,n,m} - (t_d | U_{t,n,m} | UT_{n,m}) - (t_d | V_{t,n,m} | VT_{n,m}) \quad (4)$$

where: t_d is the length of time step, U and V are migration speed components, and UT and VT are migration gradients of biomass.

EQUILIBRIUM BIOMASSES IN THE EASTERN BERING SEA AND THEIR LONG-TERM DYNAMICS

If the growth of all individual biomasses in a given ecosystem equals the removal of them by predation, mortalities, and fishery, we can talk about equilibrium biomasses which can be sustained in this given ecosystem. These equilibrium biomasses can be determined under certain conditions: by ignoring migration effects and using the Bulk Biomass Model for given areas (Laevastu and Favorite 1978b), and by finding a unique solution for equations (1) to (3), provided part of the consumption (C) is predetermined.

The predetermined consumption for the eastern Bering Sea has been obtained by computing the consumption by marine mammals as the first step in the computations, using predescribed monthly numbers of mammals and keeping their food requirements and food consumption constant. Despite a number of other minor limitations of the Bulk Biomass model (e.g. the food composition can vary only to a limited extent), the error of the results of this model does not exceed ± 30% of the given value of the biomass. The equilibrium biomasses in NWAFC Statistical and Management Areas 1, 2, and 3 (Fig. 3B) are given in Table I. These biomasses are the "minimum sustainable equilibrium biomasses" (Laevastu and Favorite 1978a) obtained by using the highest plausible growth rates and the lowest plausible food requirements. The equilibrium biomasses (Fig. 4) are grouped by three different regimes (pelagic, semidemersal, and demersal). The semidemersal species dominate all other ecological groups (12 million mt), mainly due to their more flexible feeding habits. The biomasses of pelagic and demersal species are about equal (ca 7.5 million mt each). The most abundant species is pollock (ca 9 million mt), followed by cottids and other smaller, noncommercial demersal species (4 million mt), and capelin, other smelts, and sand lance (3.5 million mt). Salmon, which occur seasonally are not included in Table I and Figure 4.

The biomasses of demersal stocks decrease more than one order of magnitude from Area 1 to the deep ocean regime, Area 3, whereas there is little relative change in the biomasses in the pelagic species between the continental shelf and deep ocean regimes. The

TABLE I.

Equilibrium Biomasses and Ecosystem Internal Consumption of some Species/Groups of Species in the Eastern Bering Sea (in 1,000 tons)

Species or Groups of Species	Total biomass, in 1,000 tons				% Exploitable Biomass	Total Exploitable Biomass	Consumption, in 1,000 tons				Annual Turnover Rate
	Area 1	Area 2	Area 3	Eastern Bering Sea			Area 1	Area 2	Area 3	Eastern Bering Sea	
Halibut, turbot	260.5	142.1	8.8	411.3	54	222.1	66.9	31.7	2.8	101.4	0.25
Flathead sole, arrowtooth flounder	945.1	236.4	17.0	698.4	54	377.1	147.7	69.6	7.0	224.3	0.32
Yellowfin sole, rock sole	661.8	444.7	24.0	1,130.5	45	508.7	174.1	87.6	9.2	270.9	0.24
Other flatfish	492.3	363.5	26.5	882.3	28	247.1	220.2	111.2	14.3	345.7	0.39
Cottids	2,478.1	1,450.0	189.5	4,117.6			1,347.2	664.7	115.8	2,127.7	0.52
Cods	593.9	391.5	50.6	1,036.0	72	745.9	301.2	168.6	31.5	501.3	0.48
Sablefish	71.3	37.7	18.0	127.0	40	50.8	18.6	10.2	1.4	30.2	0.24
Pollock	5,513.4	2,997.3	702.5	9,213.2	70	6,449.2	2,390.9	1,135.2	464.2	3,990.3	0.43
Rockfishes	1,009.9	477.3	139.0	1,626.3	30	487.9	445.2	210.9	65.8	721.9	0.44
Herring	1,219.1	578.5	171.4	1,968.9	30	590.7	832.9	399.1	125.6	1,357.6	0.69
Capelin, sand lance	2,165.8	1,047.8	292.3	3,505.8			1,550.7	749.5	219.2	2,519.4	0.72
Mackerel	701.3	330.4	131.9	1,163.6	45	523.6	387.9	183.0	78.3	649.2	0.56
Squid	523.3	248.4	498.3	1,270.1			621.5	307.5	668.1	1,597.1	1.26
Crab	522.2	309.9	14.3	846.4	40	338.6	180.0	93.1	5.9	279.0	0.33
Shrimp	427.3	479.9	24.3	931.5	65	605.5	350.0	187.8	14.2	552.0	0.59
Predatory benthos	466.6	378.0	41.7	886.3			198.0	138.4	20.8	357.2	0.40
Infauna	13,401.3	10,517.4	443.3	24,362.0			13,813.0	9,085.9	546.4	23,445.3	0.96
Epifauna	10,433.3	7,006.9	452.0	17,89.2			6,471.8	3,845.4	305.0	10,622.2	0.59

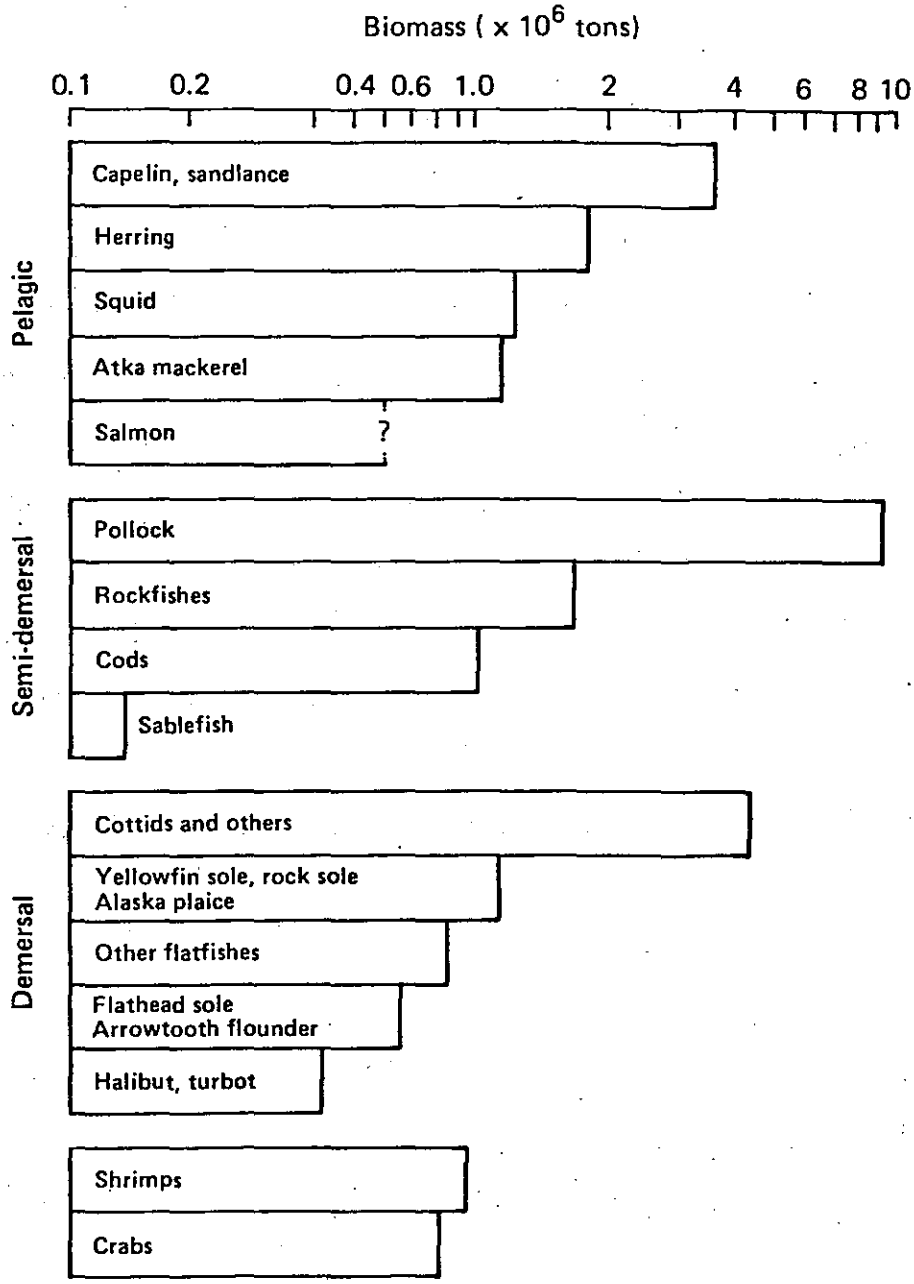


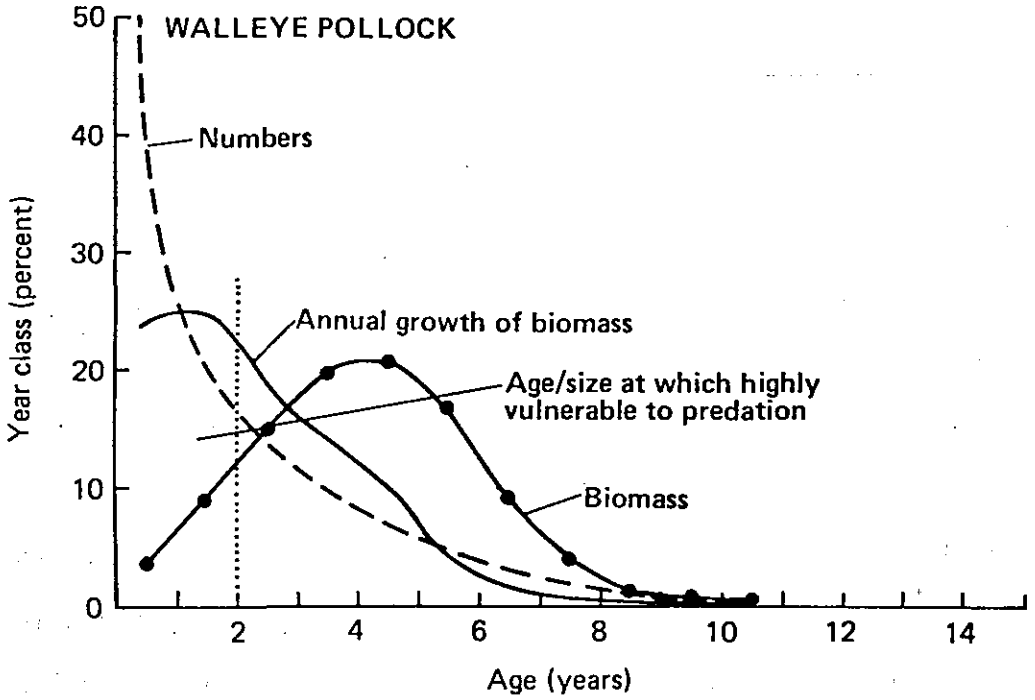
FIG. 4 Equilibrium biomasses of three different regimes in the eastern Bering Sea.

biomasses of semidemersal stocks also decrease from the continental shelf regime to the deep ocean regime, mainly due to the disappearance of the benthic food resource. The semidemersal species live a pelagic life and consume pelagic food over the deep water.

Very little is known about the benthos. The total equilibrium biomasses require about 50 g/m^2 standing stock of benthos. The existence of this standing stock is entirely possible if we compare the eastern Bering Sea with the wellinvestigated Barents Sea.

Quantitative zooplankton data from the eastern Bering Sea is also nearly absent. Soviet studies in the early 1960's were quantitatively deficient, giving only the minimum standing stocks of copepods and no quantitative data on abundant euphausids (Laevastu, Favorite and Dunn 1976). The total equilibrium biomasses consume about 50 g/m^2 of zooplankton, thus the annual production of zooplankton must be at least this amount.

The annual turnover rate (last column in Table I) (turnover rate = annual consumption/mean standing stock) provides information on the predation and other mortalities of the species or groups of species. Due to prevailing size-dependent predation in the marine ecosystem, the younger, smaller organisms are most vulnerable to predation. The growth rate of the biomass is highest at the younger ages. Thus the growth rates determine the length of the period during which a given species is most vulnerable to predation. The distribution of biomass with age and the predation-vulnerability (Fig. 5) is shown for two species as an example.



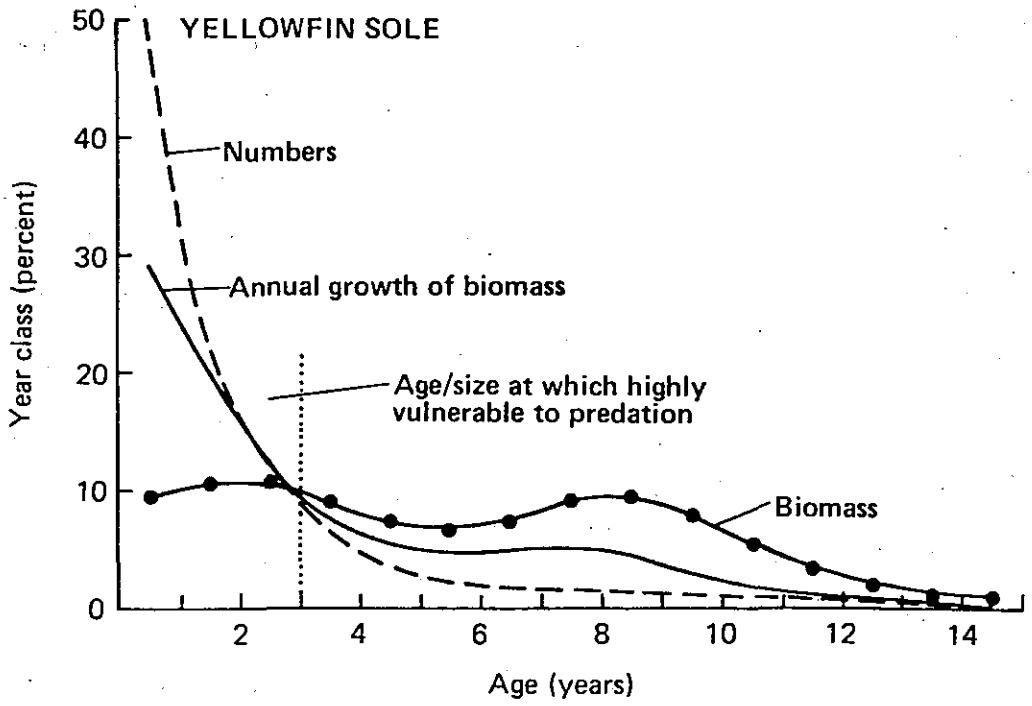


FIG. 5 Mean biomass and its annual production distribution with age in pollock and yellowfin sole. The portion of biomass highly vulnerable is indicated.

The long-term dynamics of the biomasses in the marine ecosystem can be studied with the DYNUMES and BBM models after determination of the equilibrium biomasses by introducing a cause for change in behavior or abundance of any species in the ecosystem. The results of such studies have limited reliability beyond a few years because of the uncertainty in predicting the recruitment (spawning success). An example of the change in biomasses of a few species in Area 1 (see Fig. 3B) over four years assuming that larval recruitment was made directly proportional to the spawning biomass present, rather than a function of the relation between equilibrium biomass and actual biomass (i.e. as conventionally assumed that large spawning biomasses produce proportionally smaller recruitment and vice versa) is shown in Figure 6. The interactions of the biomass fluctuations are rather complex and would take too much space to analyze here, but computer printouts are available for this study. It should, however, be pointed out that there are "natural", quasiperiodic fluctuations of biomasses in the marine ecosystem which have considerable magnitudes. The periods can be from a few years to more than a few decades and the magnitudes can be of a considerable extent (e.g. the biomass can be a fraction of a few tenths to several times its longterm mean value). The causes for these fluctuations can be manifold and not necessarily caused by man (fishing). These fluctuations can, to a certain extent, be studied with ecosystem models.

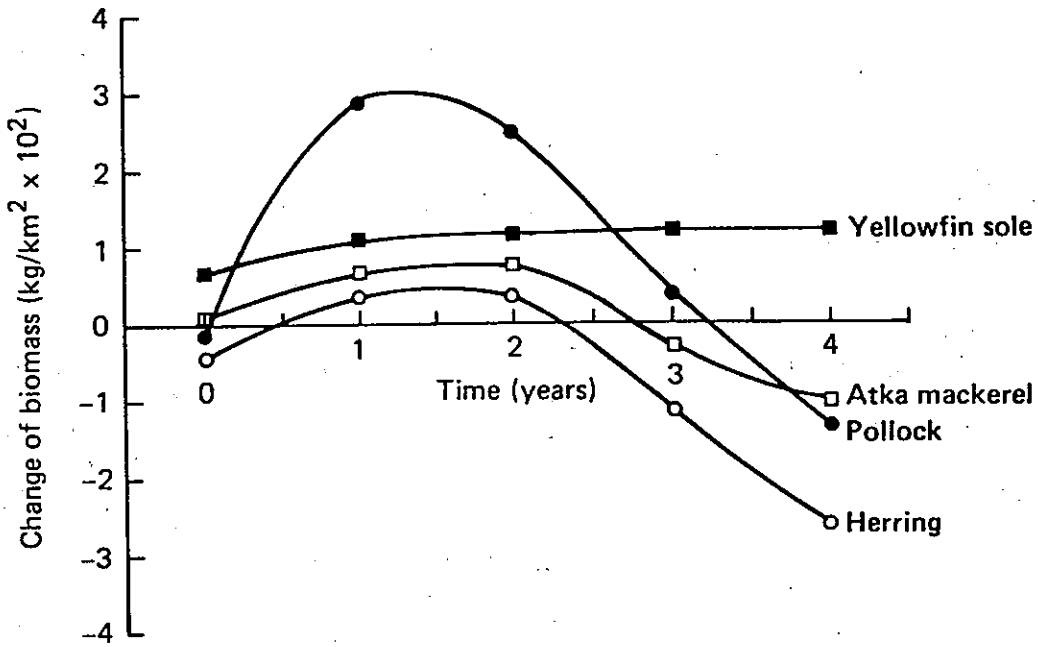


FIG. 6 "Natural" changes of biomasses of yellowfin sole, Atka mackerel, pollock, and herring in the fisheries management Area 1 in the eastern Bering Sea.

SEASONAL DYNAMICS OF THE BERING SEA ECOSYSTEM

There are two basically different causes for seasonal spatial and temporal changes in the biomasses. The changes in abundance are caused by seasonally changing growth, predation (and other mortalities), and production and release of eggs and milt; the changes in distribution are caused by seasonal migrations of species and environmental interactions. The results of both major causes of seasonal dynamics must be viewed spatially. Unfortunately little consideration has been given to the spatial aspects of biomass (and ecosystem) dynamics in the past, mainly due to difficulties in its empirical study by nonsynoptic resource surveys. However, the gridded ecosystem models with spatial resolution such as DYNUMES make such studies possible.

Examples of spatial and temporal aspects of biomass dynamics (Figs. 7 and 8) depict the biomass sources and sinks in February and August of two different-sized groups of pollock (juveniles, $<$22 cm, and maturing pollock 22 and 45 cm) -- source refers to the area where biomass growth in a given time interval (month) exceeds its losses by predation, fishery, and other mortalities; sink refers to the opposite condition, i.e. losses exceed growth. The sources and sinks of older pollock (45 cm) are not shown because this size group has only sinks (large senescence and spawning mortality, fishery, and small growth rate) which are roughly proportional to biomass present.

The sources and sinks of all species change due to spatial and temporal changes of the processes which cause them. There is usually

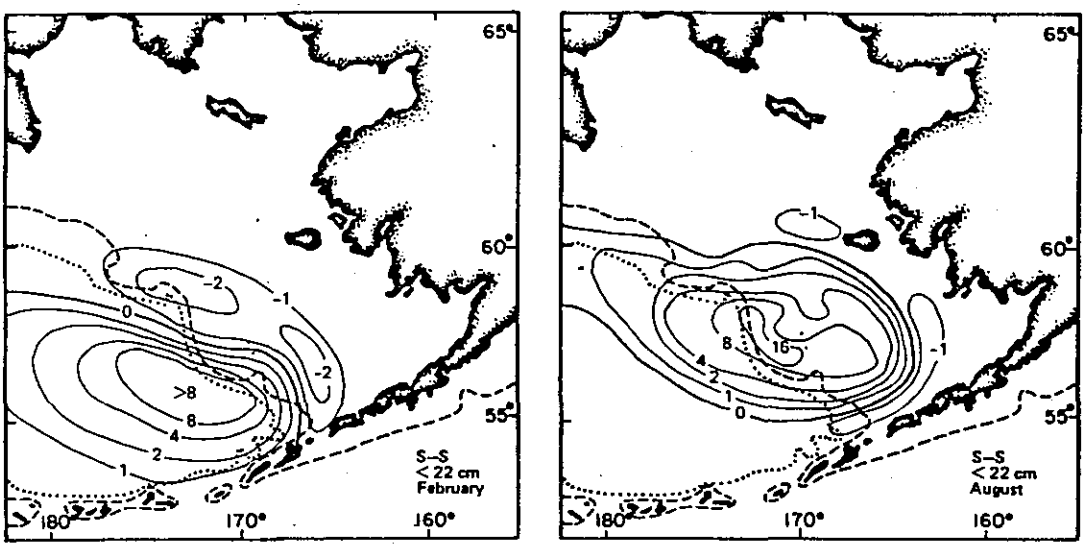


FIG. 7 Sources and sinks of juvenile pollock (<22 cm long) in February and in August in the eastern Bering Sea (in 100 kg/km^2).

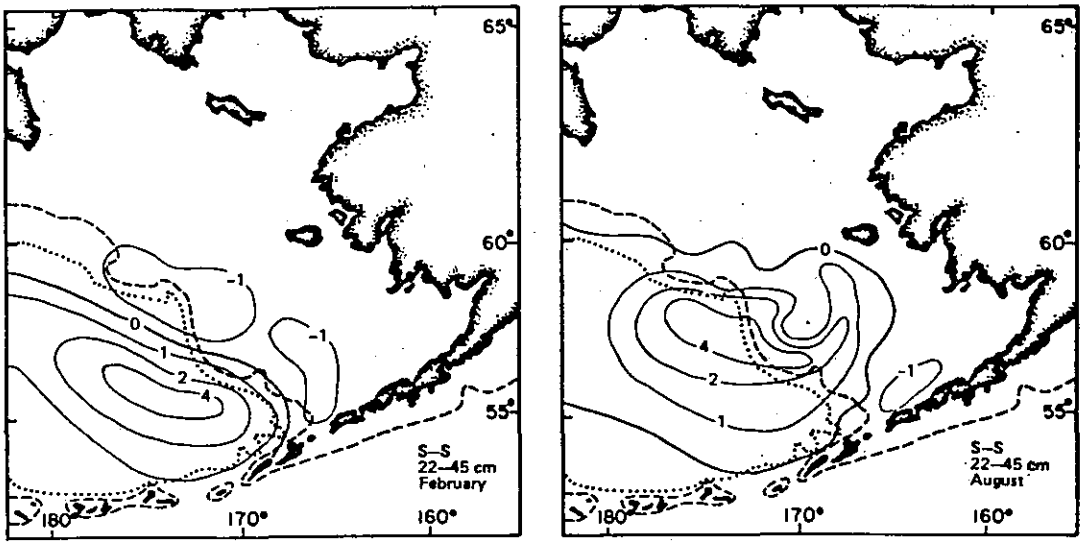


FIG. 8 Sources and sinks of maturing pollock (22 to 45 cm long) in February and in August in the eastern Bering Sea (in 100 kg/km^2).

a sink at the periphery of the distribution of the biomass. This sink is usually compensated by outmigration from the center of main distribution (spreading). There is a quasicontinuous source of pollock off the continental slope over the deep water and during winter this source area is displaced southwest where the temperature of the water is higher, allowing higher growth rates.

The distribution of the three different age groups of pollock in August is shown (Figs. 9, 10 and 11). A partial separation of juvenile and old pollock is brought about by cannibalistic predation of older pollock on its own juveniles. The highest concentration of biomass of older pollock is found off the continental slope, whereas the juveniles are found mainly on the continental shelf.

The effects of seasonal depth-migrations of yellowfin sole on its distribution changes are shown (Figs. 12, 13 and 14). The seasonal depth migrations of flatfish were investigated by Alverson (1960) and on the basis of his work it was assumed that yellowfin sole migrate from deep water into shallow water during May and June (Fig. 12) and back into deep water in October and November (Fig. 13). A migration speed of 3 km/day was assumed in the model. It is not always possible to determine a single cause for seasonal migrations, which can be spawning migration, search for food, or search for acceptable or optimum environmental conditions, etc.

This resulting monthly change of biomass can be considerable in an area where active and extensive migrations occur (see Figs. 12 and 13). These seasonal migrations have profound effects on

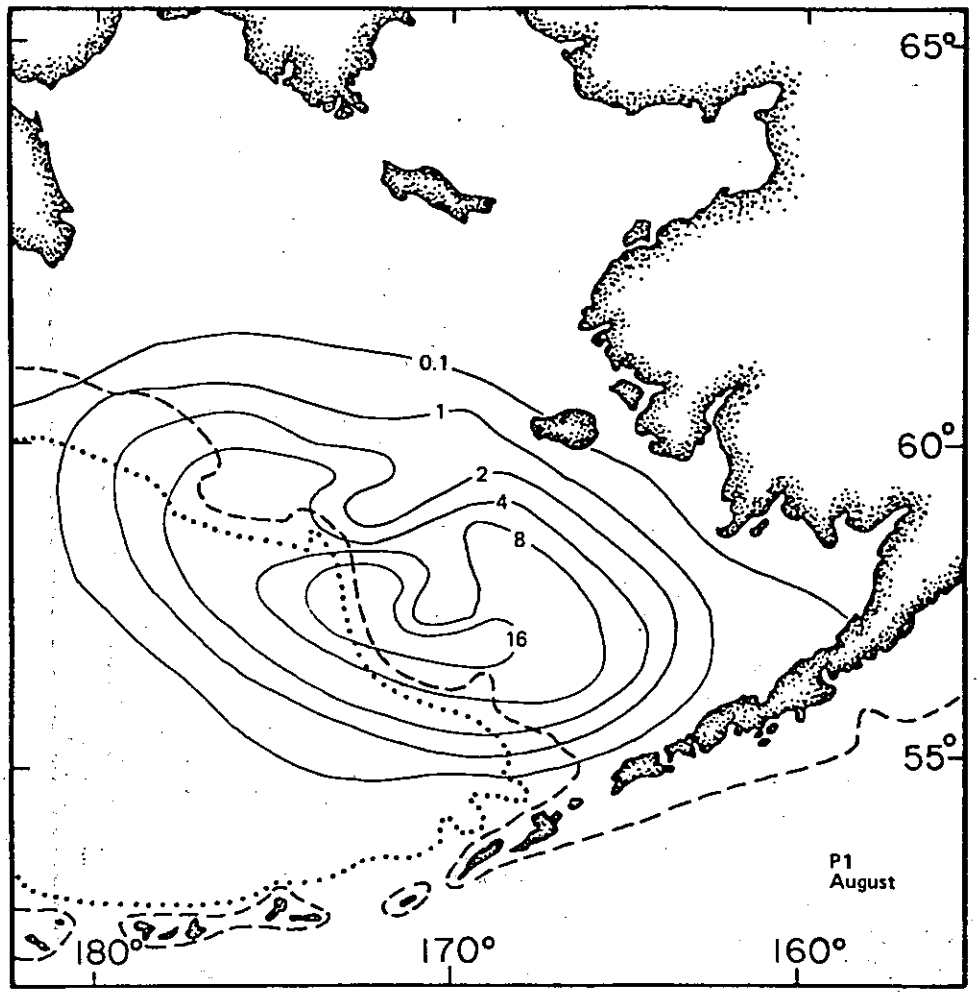


FIG. 9 Distribution of juvenile pollock (<22 cm long) in August in the eastern Bering Sea (tons/km^2).

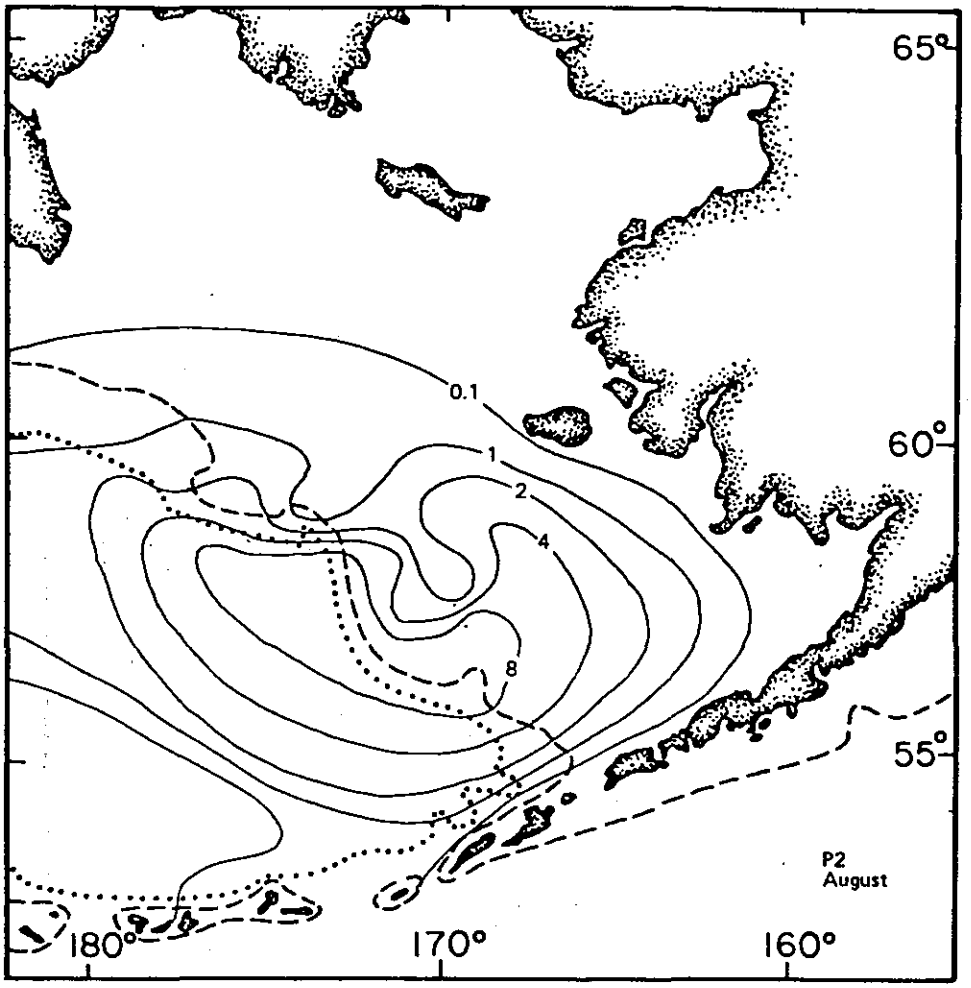


FIG. 10 Distribution of "maturing pollock" (22 to 45 cm long) in August in the eastern Bering Sea (tons/km^2).

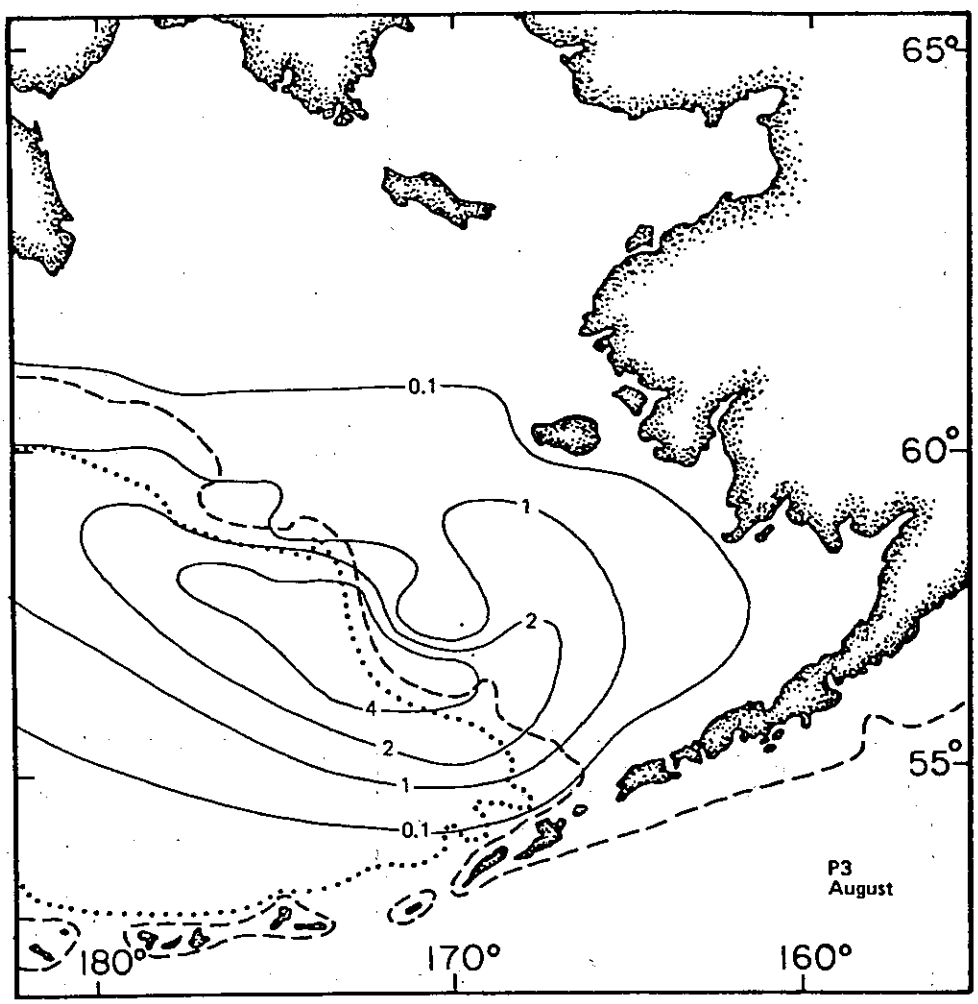


FIG. 11 Distribution of "old pollock" (>45 cm long) in August in the eastern Bering Sea (tons/km^2).

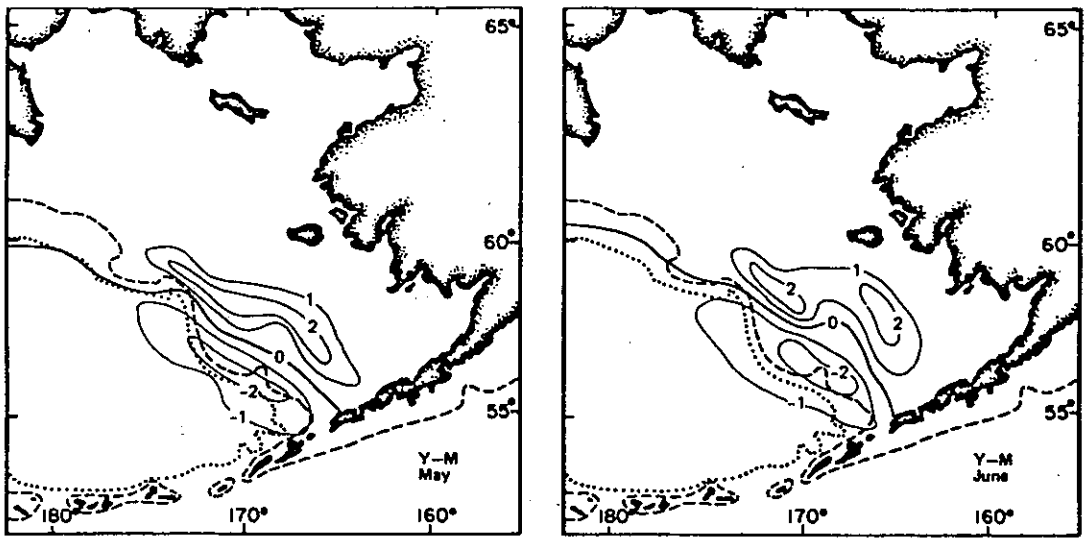


FIG. 12 Change of yellowfin sole biomass distribution due to migration in May and June in the eastern Bering Sea (tons/km^2).

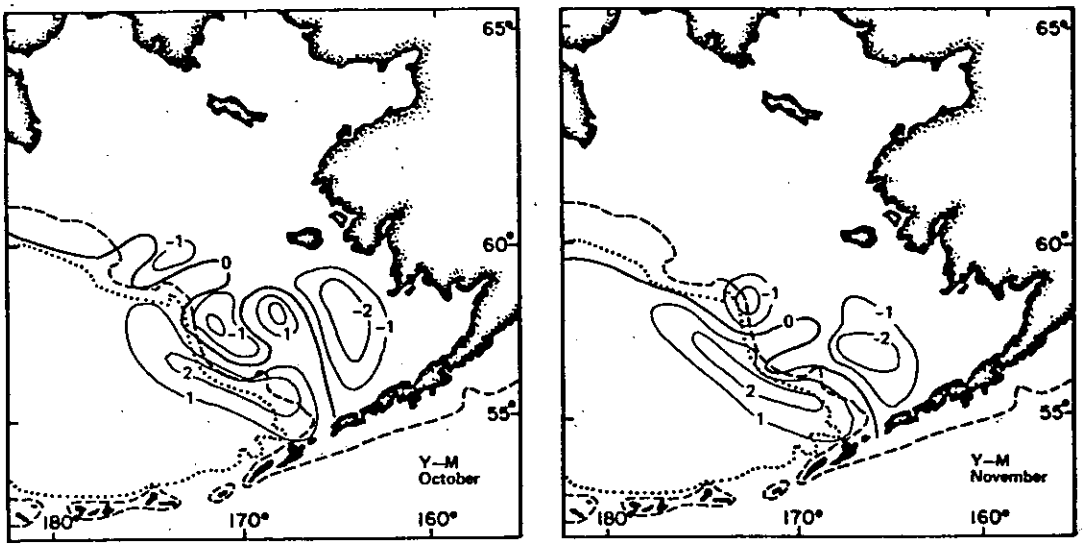


FIG. 13 Change of yellowfin sole biomass distribution due to migration in October and November in the eastern Bering Sea (tons/km^2).

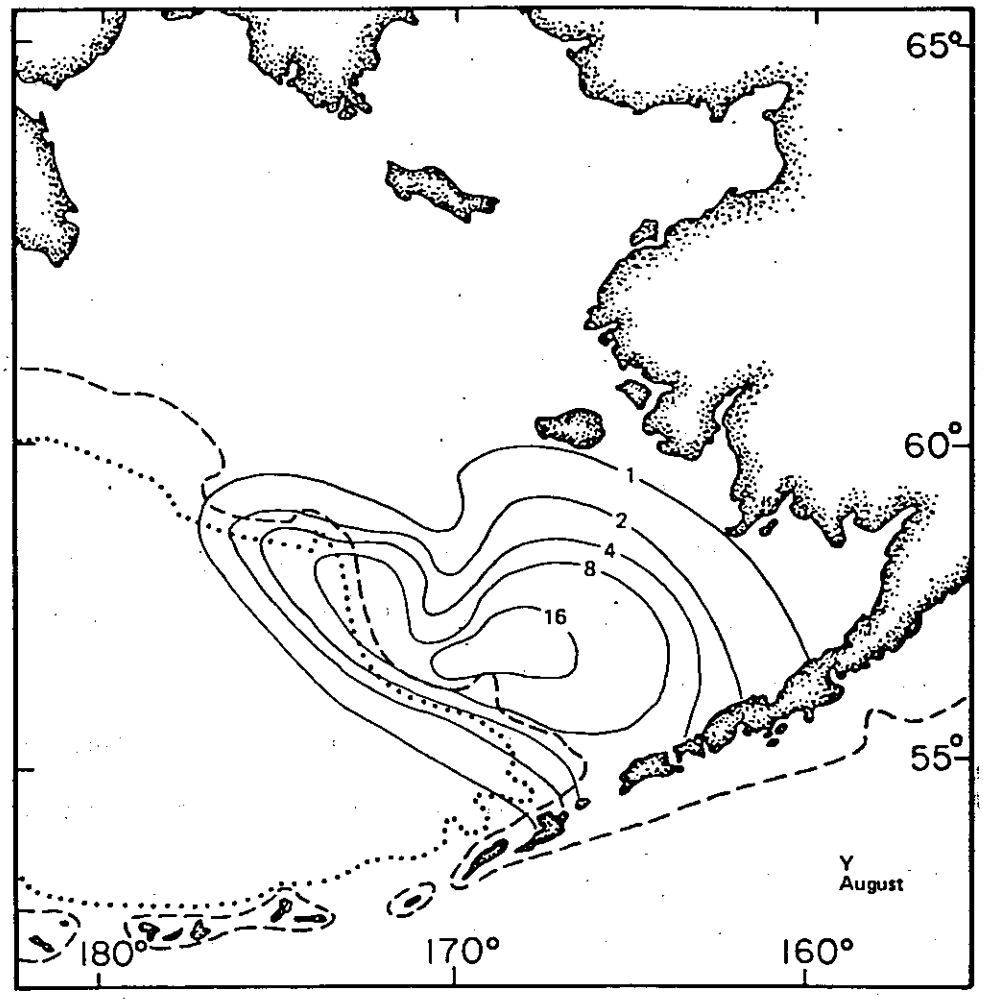
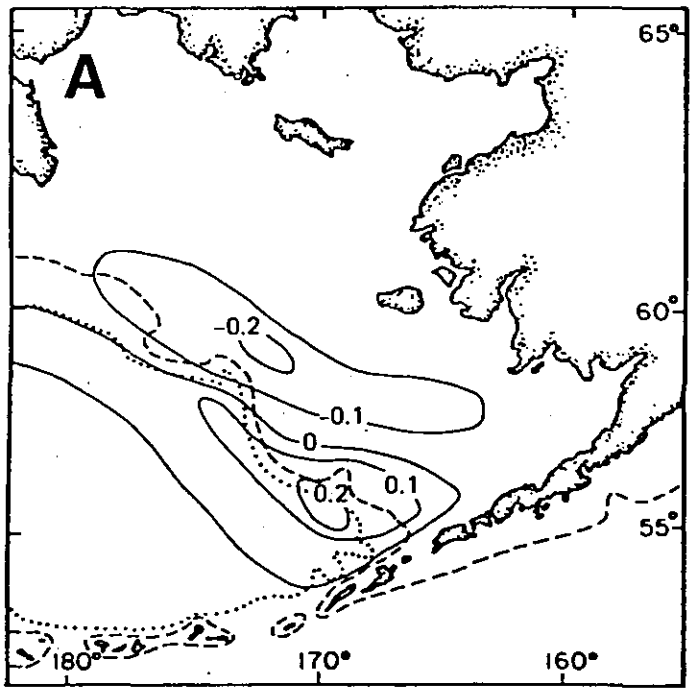


FIG. 14 Distribution of yellowfin sole in August in the eastern Bering Sea (tons/km^2).

other biota as well as on the evaluation of fishery resources with trawling surveys. For example, flatfish are dependent on benthos as a food source and migrations cause heavy grazing of benthos in some areas during some seasons, allowing a "recovery period" during other seasons. A proper trawling survey evaluation must account for seasonal migration to avoid erroneous results.

Seasonal migrations are affected by various environmental anomalies and, especially at high latitudes such as in the Bering Sea, water temperature anomalies are usually the most pronounced and the easiest to observe. Furthermore, more is known of the effects of temperature on the species than of the effects of other environmental variables. Two dynamic effects of temperature anomalies are included in the DYNUMES model: the "forced" migration of most species out of areas with subzero bottom temperatures (including a slightly increased mortality), and the effect of temperature on food uptake and growth.

An example of the effect of water temperature anomalies on the growth of the herring biomass is given in Figure 15, showing the sources and sinks of the biomass for a February with average or normal water temperature, and for a February with 1.5 C positive temperature anomaly. The growth of biomass is considerably enhanced in the latter case, especially in the southern, warmer part of the area. It should be noted that the effects of cold anomalies on growth are less than the effects of warm anomalies, as growth is nearly arrested at low temperatures. However, temperature anomalies of cold bottom water have considerable effect on seasonal



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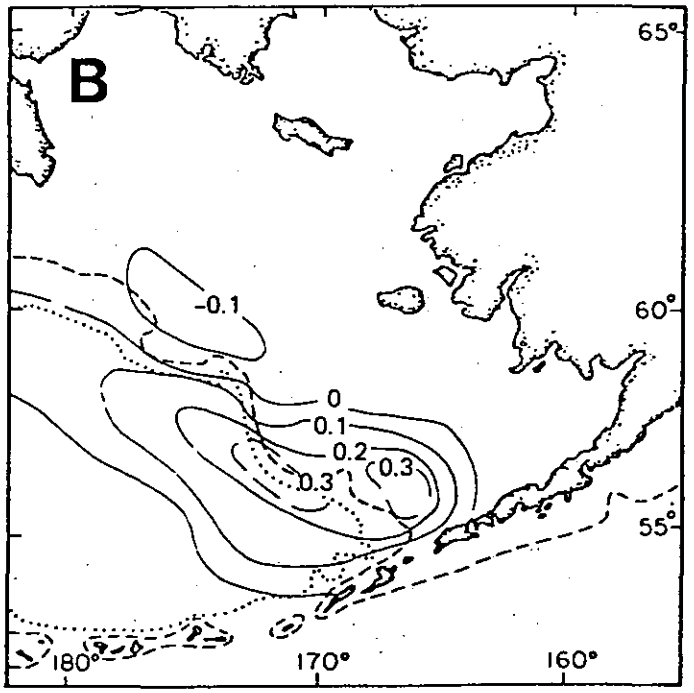

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FIG. 15 Effect of temperature anomaly on the source and sink of herring in February in the eastern Bering Sea (A-"normal" February, B-February with a +1.5°C temperature anomaly).

migrations of flatfishes to feeding and spawning grounds in shallower water. In years with extensive cold bottom water formation on the shelf in the winter, the spring migrations of flatfishes to shallower water can be considerably delayed (Best 1979).

EFFECTS OF SPACE-TIME VARIATIONS IN THE DISTRIBUTION OF PREDATOR AND PREY

Predation in any marine ecosystem is largely controlled by predator-prey size relations and the availability and suitability of prey. Thus if some "normal" and/or preferred prey items are not available, substitution with other, comparably sized food items is made. This process is included in the DYNUMES model. There can also be areas and times when not enough food is available, thus starvation with several of its consequences will occur, the first of which is usually a delay of sex products development.

Some of the dynamic aspects of predator-prey "overlap", pertaining especially to benthos and to seasonal migrations of flatfish, have been presented (see Fig. 2). The effects of spatial distribution of different prey items on the composition of food of a predator are schematically shown in Figure 16, which depicts a vertical section with predator-prey distribution. Not only does the food composition of the predator vary in space, but the predation pressure on the prey varies as well.

The various possible types of responses of predator and prey biomasses are shown (Fig. 17) and although these responses can be classified into some defined types, there is considerable overlap of these responses in the real nature due to various predator-

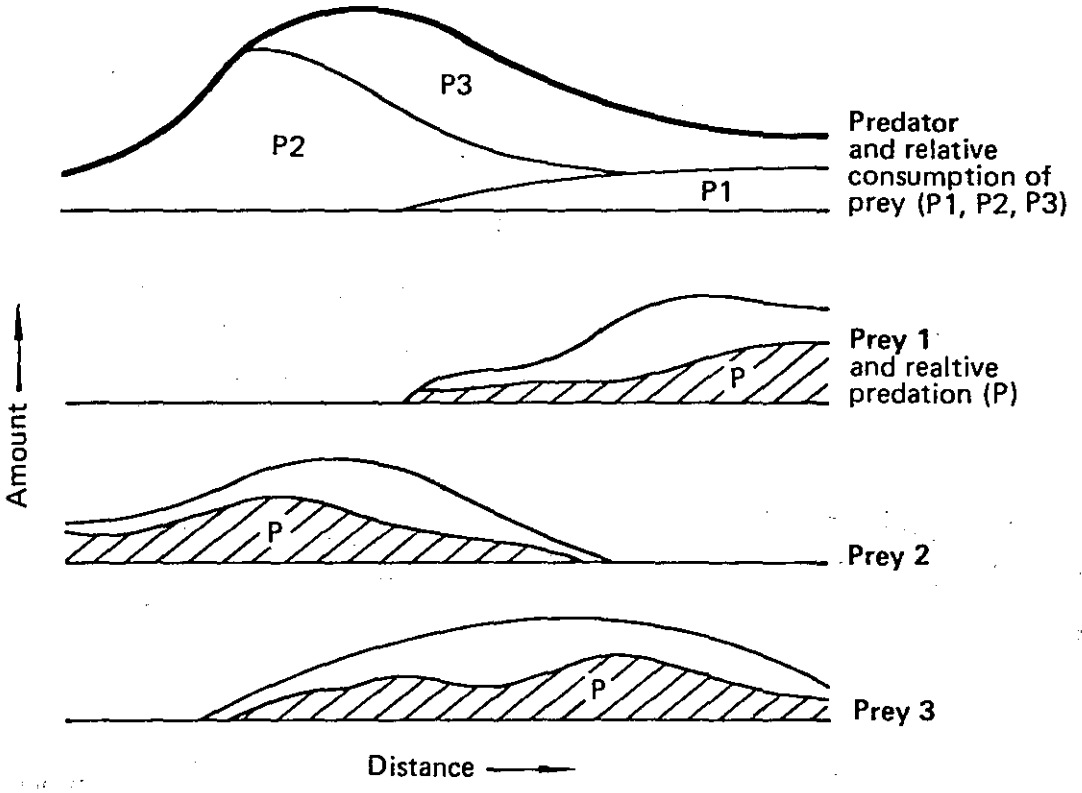

FIG. 16 Schematic presentation of the predation by one predator on three prey items with different spatial distributions (presented as a section).

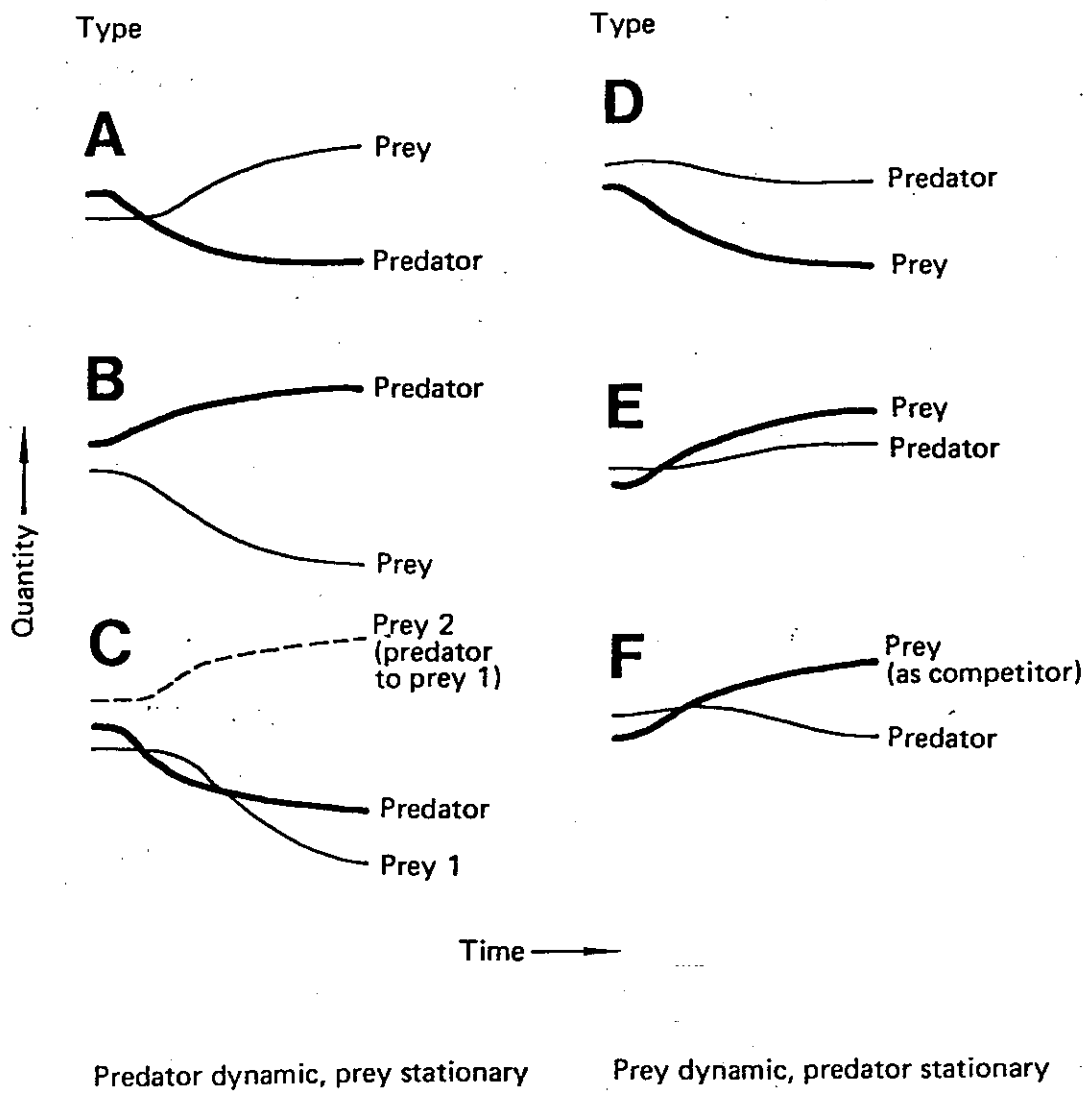

FIG. 17 Types of responses to biomass changes in predator-prey controlled ecosystem.

prey dynamic processes (i.e. changes in space and time). Some of the response types are as follows: when the predator biomass decreases (e.g. because of outmigration), local prey abundance increases (type A), and when predator biomass increases, prey decreases (type B). In the case when the secondary prey is predator to primary prey (i.e. secondary prey is competitor to primary predator), the predator biomass decreases (types C and F). If the prey is mobile and decreases (e.g. by outmigration), the predator biomass might decrease as well (e.g. forced outmigration in search of food and/ or because of starvation) (type D) and vice versa (type E).

The percent of mean monthly zooplankton standing stock consumed per month in the eastern Bering Sea is given (Fig. 18). Zooplankton and benthos are the main food resource buffers in the marine ecosystem. The monthly mean zooplankton standing crop was simulated in the model using past quantitative knowledge on its abundance and seasonal changes. The simulated zooplankton standing stock was made to vary spatially and temporally between 400 and 800 mg/m^3. The areas of high zooplankton consumption changed from month to month as affected by the distribution of consumers. This spatial and temporal change of high consumption would allow replenishment by growth and advection in previously heavily grazed areas. It can be assumed that fish eggs and larvae are consumed at the same rate as zooplankton. Thus, if a high zooplankton consumption area coincides with high abundance of pelagic eggs and larvae, low larval survival and low recruitment can be expected of the given

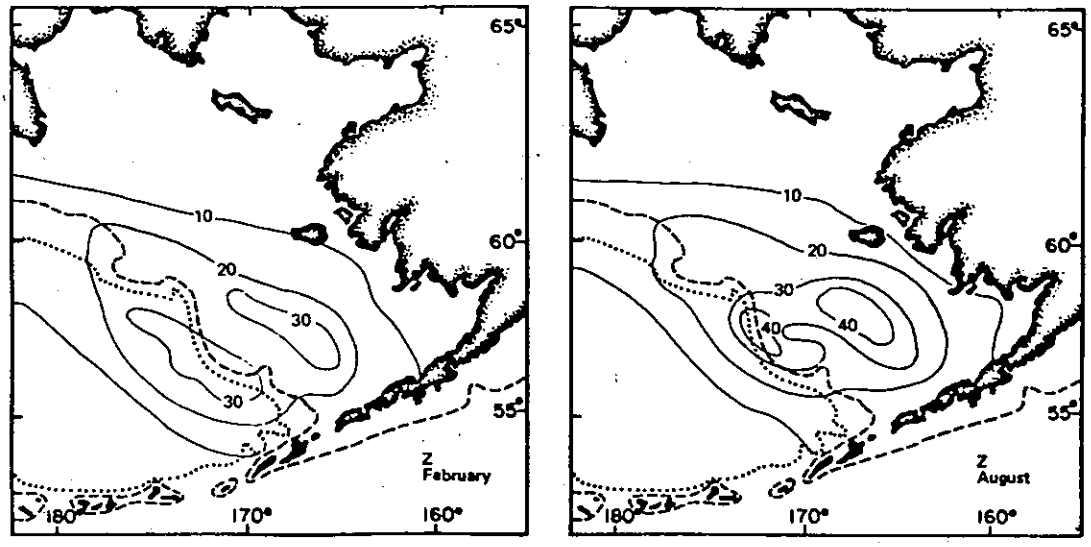

FIG. 18 Percent of monthly mean zooplankton standing stock consumed in February and in August in the eastern Bering Sea.

species. The zooplankton consumption in the northern part of the area is low, thus a great part of the deceased zooplankton can settle to the bottom providing food (detritus) for the abundant benthos. The consumption of benthos is also low in the northern part of the area although its standing crop is high ("accumulation of generations" in the sense of Spärk). Thus the benthic biomass (or zooplankton biomass) cannot be proportional to the production of fish in all areas.

The consumption of zooplankton near the shelf edge is quite high (see Fig. 18) and this raises several questions about the possible source of zooplankton there. First, the zooplankton simulation in the model for this area might be too low despite the fact that considerably higher quantities were simulated than indicated in the literature, because present quantitative zooplankton catching methods are obviously deficient (Laevastu, Favorite and Dunn 1976). Second, the zooplankton, especially euphausiids, might be transported by currents to the convergence at the continental slope.

EFFECTS OF MAMMALS AS APEX PREDATORS ON THE ECOSYSTEM

During summer the Bering Sea contains more mammals per unit area than any other ocean area. Furthermore, during summer the numbers of marine birds in the region (over 40 million) exceed those in the rest of the northern hemisphere. Both mammals and birds are apex predators, their effect on the ecosystem being similar to the effect of fishing by man.

The occurrence of mammals is seasonal and their distribution uneven, in addition, their mobility creates various temporal and spatial dynamic effects on the rest of the ecosystem. Estimates of numbers of marine mammals present varies considerably from one source to another. It is apparent that some of the estimates have little to do with reality.

There are three types of seasonal occurrence of mammals -- the winter visitors (e.g. "ice" seal and bowhead whale), summer visitors (e.g. fur seal, sea lion, shearwaters, and sperm whale), and year around residents (e.g. belukha whale).

The estimates of daily food requirements by marine mammals are also quite variable in the literature. The more conservative estimates are between 4-8 percent body weight daily, depending on the species, and these estimates were used in the model. A feeling for the massive consumption by mammals can be obtained when one considers that values for the month of September indicate that fur seals alone are responsible for one-third of the total consumption.

Seasonal changes of some marine mammals and birds are shown (Fig. 19) and these estimates are believed to be the best and most realistic estimates, found from various, more reliable sources in the literature.

The consumption of fish by marine mammals and birds in the area is about 3 million mt, which is about twice the total area catch by the fishery of all nations. The effect on the ecosystem of consumption by marine mammals is similar to the effect of the fishery -- continual removal of biomass without providing much of a

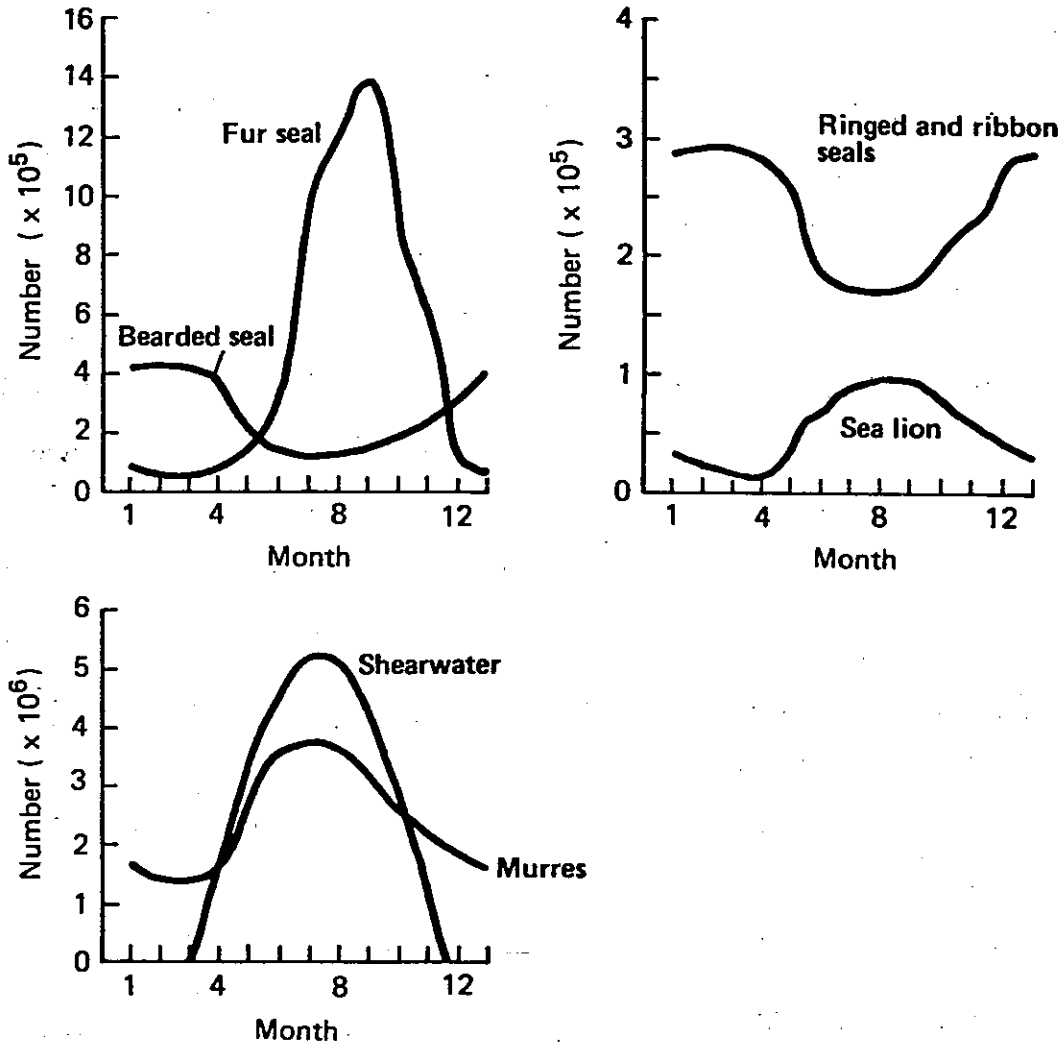

FIG. 19 Monthly numbers of some mammals and birds in the eastern Bering Sea.

return in the form of food for other biota in the ecosystem. Considering the magnitude of consumption by mammals in relation to harvest by the regulated fishery, it becomes obvious that fisheries management measures will have a limited effect on fishery resources without simultaneous management of marine mammals as well. Furthermore, the seasonal and selective predation by many mammal species will have considerable adverse effects on several fishery resources important for man (e.g. the predation on returning salmon by the belukha whale, fur seal and sea lion).

VERIFICATION AND VALIDATION OF ECOSYSTEM MODEL RESULTS

Verification of the ecosystem simulation model (DYNUMES III) has been done by insuring that the formulas used in the model reproduce known effects and behaviors. Furthermore, verification has been done by simulating events which are known to produce given changes in the ecosystem. Thus the evaluation of sensitivity in large ecosystem models becomes a continuing study of the response of the ecosystem to changes in various rate and state parameters.

Although the dynamic aspects of the Bering Sea ecosystem are difficult to validate empirically due to the absence of data, particularly from extensive time-series and behavioral studies, the validation of general abundance and distribution results is possible by comparing the computed abundance and distribution of biomasses with independently obtained empirical data such as those obtained from fisheries surveys. This comparison is rewarding only provided the latter are properly converted using catchability coefficients (Granfeldt 1976b). Examples of this validation are

given in Table II for the species which are more reliably reported quantitatively in the resource surveys. In general, resource surveys are considered accurate only to about ± 50% (Grosslein 1976), whereas the error in the model computation results does not exceed ± 30% of the reported value.

Qualitative validation of the simulation models can be provided by occasional special fisheries surveys. The following serves as an example. In the early stage of the Bering Sea ecosystem modeling, it became obvious that there must be a considerable amount of pollock (and some other fish species) over the deep water in the Bering Sea. However, pollock were never caught over deep water and the model results were severely criticized until a

TABLE II

Comparison of Exploitable Biomasses of some Species in the Eastern Bering Sea as Obtained by Surveys and as Computed with PROBUB Model (in 1,000 mt)

Species/Groups of Species	Mean 1975, 1976 Surveys (Converted) from Bakkala and Smith (1978)	Equilibrium Exploitable Biomass from PROBUB Model	Catch 1975
Greenland turbot, halibut	176	222	65
Flathead sole, arrowtooth flounder	206	377	26
Yellowfin and rock sole, Alaska plaice	2,716	509	74
Pollock	3,698	6,449	1,285
Cod	233	746	57

recent Japanese survey showed considerable amounts of older (larger) pollock over deep water. Furthermore, the deep water areas turned out to be source areas of biomass for many pelagic and semipelagic species at least part of the year. The abundant euphausids in this area provide an ample food source. However, no extensive schooling occurs over deep water, making the fishery less profitable there than over the continental shelf.

A multitude of processes can be quantitatively studied with ecosystem simulation models. The above paper provides only a general review of some of the major dynamic processes and their results in the marine ecosystem in the eastern Bering Sea.

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