

FRI-UW-8411
December 1984

Fisheries Research Institute
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University of Washington
Seattle, Washington 98195

PROJECTED EFFECTS OF CO₂-INDUCED CLIMATE CHANGE
ON THE ALASKA POLLOCK (Theragra chalcogramma) FISHERY
IN THE EASTERN BERING SEA AND GULF OF ALASKA

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Final Report

to

Lawrence Berkeley Laboratory
Contract No. 4524910
1 October 1983 to 30 September 1984

Submitted: 28 December 1984

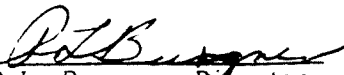
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1.0 INTRODUCTION

The carbon dioxide (CO₂) content of the earth's atmosphere, estimated to have been 270-290 parts per million in preindustrial times, is currently projected to increase to about 600 ppm during the 21st century, primarily as a result of burning of fossil fuels (National Research Council (NRC) 1983). A major direct effect anticipated from this increase is a 2-4°C rise in global mean surface atmospheric temperature. By means of this warming CO₂ may indirectly affect the environment and society in a number of ways, having impacts on health, agriculture, forestry, water resources, and fisheries. This report is one of a series that examines possible effects of warming on fisheries.

In recent years increasing attention has been paid to interactions between climate and fisheries (e.g. Cushing 1982). This report series evaluates the climate dependencies of single fisheries, as case studies against which other fisheries may be compared and from which global projections may be extrapolated. Other reports in this series examine British Columbia herring (Grosse and Sibley 1984), Alaska pink shrimp (Walline and Sibley 1984), and eastern Bering Sea yellowfin sole (Horrocks et al. in prep.). A synthesis of these results and a general discussion of the mechanisms and problems in evaluating the effects of climate on fisheries is in preparation.

Alaska (walleye) pollock, Theragra chalcogramma (Pallas), was chosen for this case study for several reasons. It is currently the world's largest single-species fishery by weight, with an annual catch of nearly five million metric tons, or about nine percent of global finfish catch (Bakkala et al. 1983). About a quarter of this is taken in U.S. water (Anonymous 1983). Pollock is the most commercially important member of the gadid (cod) family, contributing over 50% of the world gadid catch by weight (Talley 1982), and a value of \$3 billion after processing (Anonymous 1983). The gadid family is the world's second most important commercial fish family in terms of catch tonnage (after the clupeid, or herring family), and the most important for direct human consumption (Ryan 1979). Pollock is thus an important nutritional and economic resource, with a landed value of over \$1 billion per year (Talley 1982). Pollock also is a major prey of several important or endangered bird and mammal species in northern waters.

Pollock is distributed throughout the neritic north Pacific and adjacent seas north of approximately 35° N. Commercial concentrations are located on the Pacific coasts of British Columbia and Japan, in the Gulf of Alaska and along the Aleutians, and in the Bering, Okhotsk, and Japan Seas (Figure 1), with one or more distinct breeding stocks in each location. Commercial concentrations in U.S. waters are located between about 54° N and 60° N. Nearly 90% of world pollock catch is taken equally by Japan and the USSR, with smaller quantities taken by North and South Korea, Poland, West Germany, China, and joint ventures of U.S. vessels with foreign processors (Bakkala et al. 1979, 1983; Bakkala and Wespestad 1983; Alton and Deriso 1983a). The bulk of the catch is consumed in Asia. U.S. consumption of pollock is about 36 thousand metric tons per year, virtually all imported as frozen blocks or fillets at a total cost of about \$80 million per year (Talley 1982). Pollock contributed about 25% of all frozen block fish imports to the U.S. in 1976 (Ryan 1979). Total pollock catch in U.S. waters currently is about 1.2 million metric tons per year, about 90% of which is in the Bering Sea. Pollock accounts for about 80% of the finfish catch in the eastern Bering Sea (Bakkala et al. 1979) and about 65% in the Gulf of Alaska (Alton and Deriso 1983a).

Pollock in Alaska waters may be particularly useful as an ecological indicator of the effects of climate change due to unique habitat and life

cycle characteristics. Pollock is commonly referred to as a semi-demersal species; that is, it is oriented to but not exclusively associated with the bottom. As adults pollock are observed near the bottom and in midwater over the middle and outer continental shelf and upper slope, with some midwater populations in deep oceanic waters. Adults appear to undergo temperature-related seasonal vertical and horizontal migrations. Eggs, larvae, and juveniles are pelagic in the upper water column over the shelf. This breadth of habitat maximizes the likelihood both that some part of the pollock life cycle will exhibit sensitivity to climate change, and that pollock as a species will have the biological adaptability required to survive.

The habitat of pollock also is representative of major subarctic coastal fishery zones, including the northwest Pacific and northeast and northwest Atlantic. Each of these regions is characterized by an extensive area of continental shelf, which supports rich fisheries targeted on pelagic species (those caught with surface nets or midwater trawls, such as salmon and herring), and on groundfish (those caught with bottom trawls). Groundfish yields in the Bering Sea and northeast Pacific are comparable to those of the productive Atlantic fisheries (Table 1). Alaskan waters encompass two very different physical regimes: the Gulf of Alaska has cool and relatively constant temperate conditions, while the eastern Bering Sea experiences severe polar cold and extensive ice cover in winter. Thus Alaska waters represent a microcosm of climatic conditions in other major northern continental shelf fishery regions at similar latitudes, such as the relatively temperate northeast Atlantic and the ice-affected northwest Atlantic (Figure 2). Data records on the oceanography and fisheries of the northeast Pacific and Bering Sea are of relatively short duration compared to those in the North Atlantic, but intensive studies in recent years have furnished some uniquely detailed insights that aid in evaluating potential climatic impacts.

TABLE 1
Comparative Groundfish Yield of Northern Coastal Fishery Zones
(after Bakkala et al. 1976)

Location	Area (million km ²)	Mean annual catch of groundfish, 1970-73 (million metric tons)	Catch per area (metric tons km ⁻²)
E. Bering Sea	0.7	2.1	2.9
N.E. Pacific	0.3	0.4	1.6
N.W. Atlantic	1.3	2.1	1.7
N.E. Atlantic	2.6	3.2	1.2
North Sea	0.6	2.0	3.3

The comparison between adjacent warmer and colder environments should provide a useful contrast of climatic effects. Differing climatic conditions at a given latitude in these regions reflect differences in the relative importance of heat exchange across the air-sea interface, and heat transport due to currents. These mechanisms may respond differently to climatic warming. An environment such as the Bering Sea, which is transitional between temperate and polar conditions, should be the most sensitive to and provide the most visible evidence of climate change. The Bering Sea has the largest interannual variability in seasonal sea ice extent of any northern sea (Niebauer 1980). In addition, climatic changes resulting from increased atmospheric CO₂ are projected to be greatest at high latitudes.

This report will review aspects of the physical, biological, and pollock

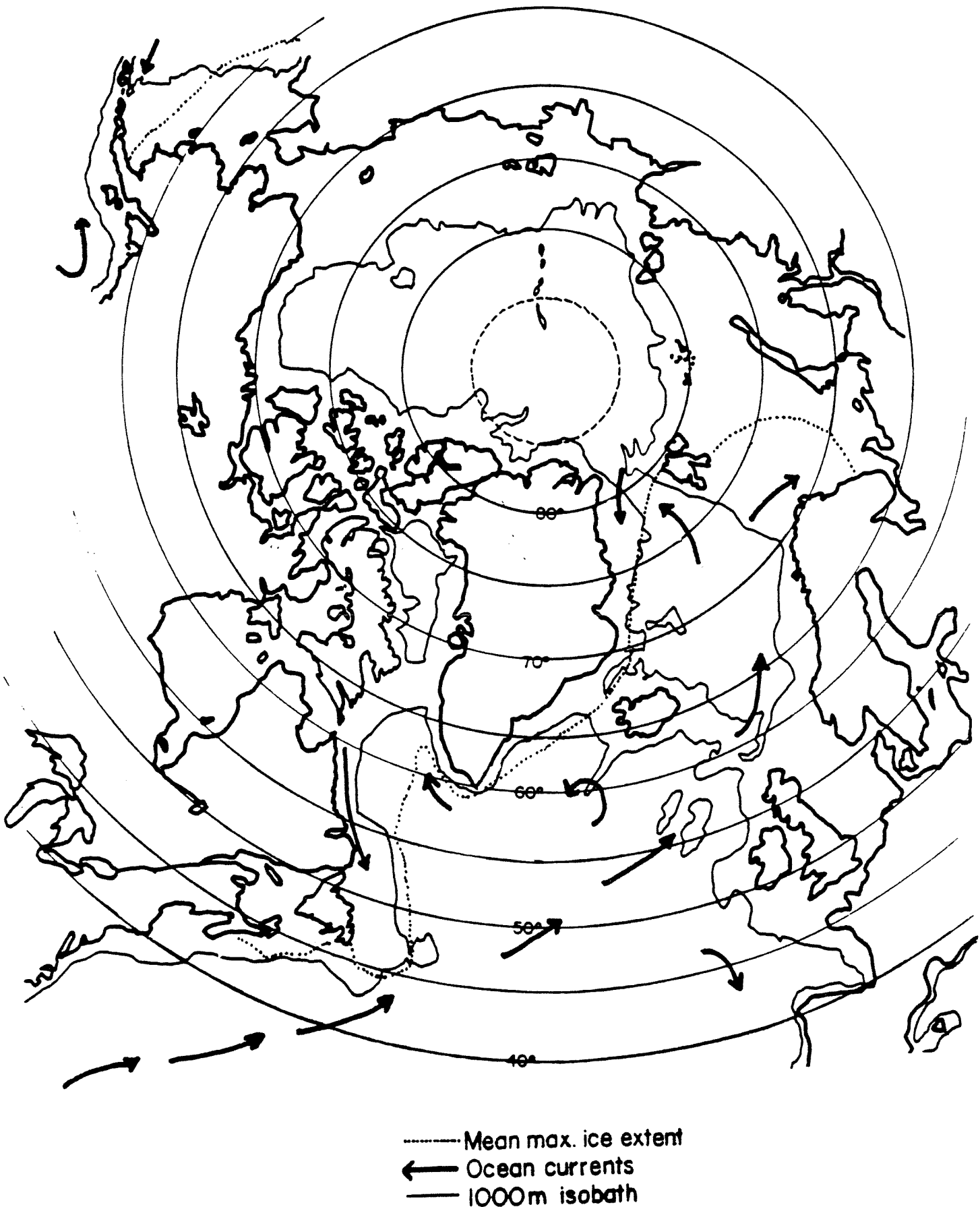


Figure 2. Latitudes, shelf width, ice extent, and general circulation of north circumpolar region (after Dietrich and Ulrich 1968).

fishery oceanographic characteristics of the eastern Bering Sea and Gulf of Alaska. A discussion section will review the climatic sensitivities of the environment and the fishery, and will evaluate possible changes due to climatic warming as well as commenting on the reliability of such forecasts and projecting future research needs. The state of knowledge of this area is evolving rapidly, and this report does not include some potentially valuable recent unanalyzed data, particularly on possible effects of the 1982-83 "El Nino". El Nino refers to a quasi-periodic set of Pacific-wide meteorological and oceanographic perturbations that includes warming of surface waters, reduced upwelling, and associated disruptions of plankton and fish production. Analysis of data from this most recent occurrence might shed some light on the potential effects of ocean warming in the future.

2.0 THE BERING SEA

2.1 PHYSICAL OCEANOGRAPHY

The Bering Sea (Figure 3) is bounded on the north and west by the Siberian and Kamchatkan coast of the USSR, on the east by Alaska, and on the south by the Alaska Peninsula and Aleutian Islands. The Bering connects to the Chukchi Sea and Arctic Ocean to the north via the Bering Strait, and to the Pacific Ocean to the south through Aleutian Island passes. The northeastern half of the Bering Sea overlies a broad (wider than 500 km) continental shelf that extends to a depth of roughly 180 m, and is fringed by a steep continental slope. The remaining deep waters (excluding the USSR continental shelf) are referred to as the Bering Sea basin or Aleutian basin.

2.1.1 Oceanic Domain

The circulation of the Aleutian basin is characterized by a large-scale cyclonic (counterclockwise) gyre (Figure 4). Pacific water enters the eastern Basin through Aleutian passes, and exits via a persistent northerly flow through the Strait, and through the much greater mass transport of the southerly East Kamchatka Current at the western edge of the basin (Favorite et al. 1976). There is a long-term mean net flow of coastal Pacific water from the Gulf of Alaska into the coastal domain of the eastern Bering Sea shelf through Unimak Pass (Schumacher et al. 1982). This transport is driven by a persistent baroclinic pressure gradient associated with the Kenai Current (Section 3.1). Upwelling associated with bathymetry and subsurface convergence at Amukta and Samalga Passes farther west, inferred from surface temperature, salinity, and pH, and nutrient, oxygen, and carbon dioxide concentrations characteristic of deeper water (Hood and Kelley 1974, Swift and Aagaard 1976). Weak upwelling also is inferred along the Gulf of Alaska coast east of Unimak Pass during summer (Section 3.1). The transport of water through these passes, although small compared to that in the Bering Sea gyre, influences the hydrographic characteristics of the shelf region (especially temperatures and nutrient concentrations), and therefore is of biological importance (Hattori and Goering 1981). Transport onto and northward along the shelf is required to supply the northward outflow through the Bering Strait (Coachman et al. 1975). Earlier assumptions were that transport onto the shelf might occur uniformly along its length, producing significant upwelling that could be biologically important (Coachman and Takenouti 1974). Recent surveys have demonstrated, however, that most of this transport occurs over the northern shelf, away from major fishery areas (Salo et al. 1983).

2.1.2 Shelf Domain

The physical oceanography of the southeastern Bering Sea shelf has recently been reviewed in detail by Kinder and Schumacher (1981a, 1981b), Allen et al. (1983), and Coachman (in press). These waters are discriminated into four domains: 1) the coastal domain, from the Alaskan coast to roughly the 50 m isobath; 2) the middle shelf domain, roughly between the 50 and 100 m isobaths; 3) the outer shelf domain, from the 100 m isobath to the shelf break at 150-200 m; 4) and oceanic waters over the slope and basin (Figure 5). In all domains the dominant currents, contributing at least 80% of the kinetic energy, are tidal currents with typical mean speeds of 20-25 cm sec⁻¹. Residual mean currents in all domains generally follow the bathymetry and parallel the northwestward flow of the eastern gyre. These currents are coupled to the basin circulation only over the outer shelf and upper slope, however.

A persistent 5-15 cm sec⁻¹ current, the Bering Slope Current (Kinder et

al. 1975), is observed over the upper slope. This current transports relatively warm water northward, and affects winter ice cover over the northern outer shelf (see below), and also produces some flux of heat and salt onto the southeastern outer shelf (Coachman 1983). Weaker net transport is observed in the coastal and outer shelf domains. Currents over the outer shelf are concentrated near the 100 m isobath and range in speed from 4-10 cm sec^{-1} along the shelf, with a smaller onshore component (Coachman 1982, Schumacher and Kinder 1983). The 1-5 cm sec^{-1} current in the coastal domain is associated with inflow from the Gulf of Alaska and alongshore rectification of tidal currents along the Alaska Peninsula, and with freshwater input from rivers along the Alaskan mainland. Energy from these currents is apparently not propagated into the middle shelf domain, where residual mean currents are less than 1 cm sec^{-1} . As a result the residence time of water in this domain is very long, up to two years.

Considerable low-frequency variability is superimposed on these mean patterns. The speed and direction of the Bering Slope Current fluctuate in association with transient 50-200 km eddies over time scales of weeks to years (Kinder et al. 1981). These eddies appear to originate in the southeastern sector, and may result from an interaction of variable meteorological and hydrographic forcing (including planetary waves) with fixed bathymetry, especially major submarine canyons north and south of the Pribilof Islands (Kinder and Coachman 1979). Wind-driven current pulses reach 15-30 cm sec^{-1} in all domains during 2-10 day storm events, but due to rotating wind vectors these storms generally produce little net mass transport (Schumacher and Kinder 1983). These events are least frequent and weakest during summer. Wind forcing is of greatest absolute magnitude on the slope and outer shelf, but is of greater relative importance in the middle and inner shelf domains where mean flow is weaker. Schumacher and Reed (1983) noted little interannual variability in currents on the eastern Bering Sea shelf, with the only major variability observed in the Bering Slope Current. However, even small interannual fluctuations in such weak transport patterns could have biological significance.

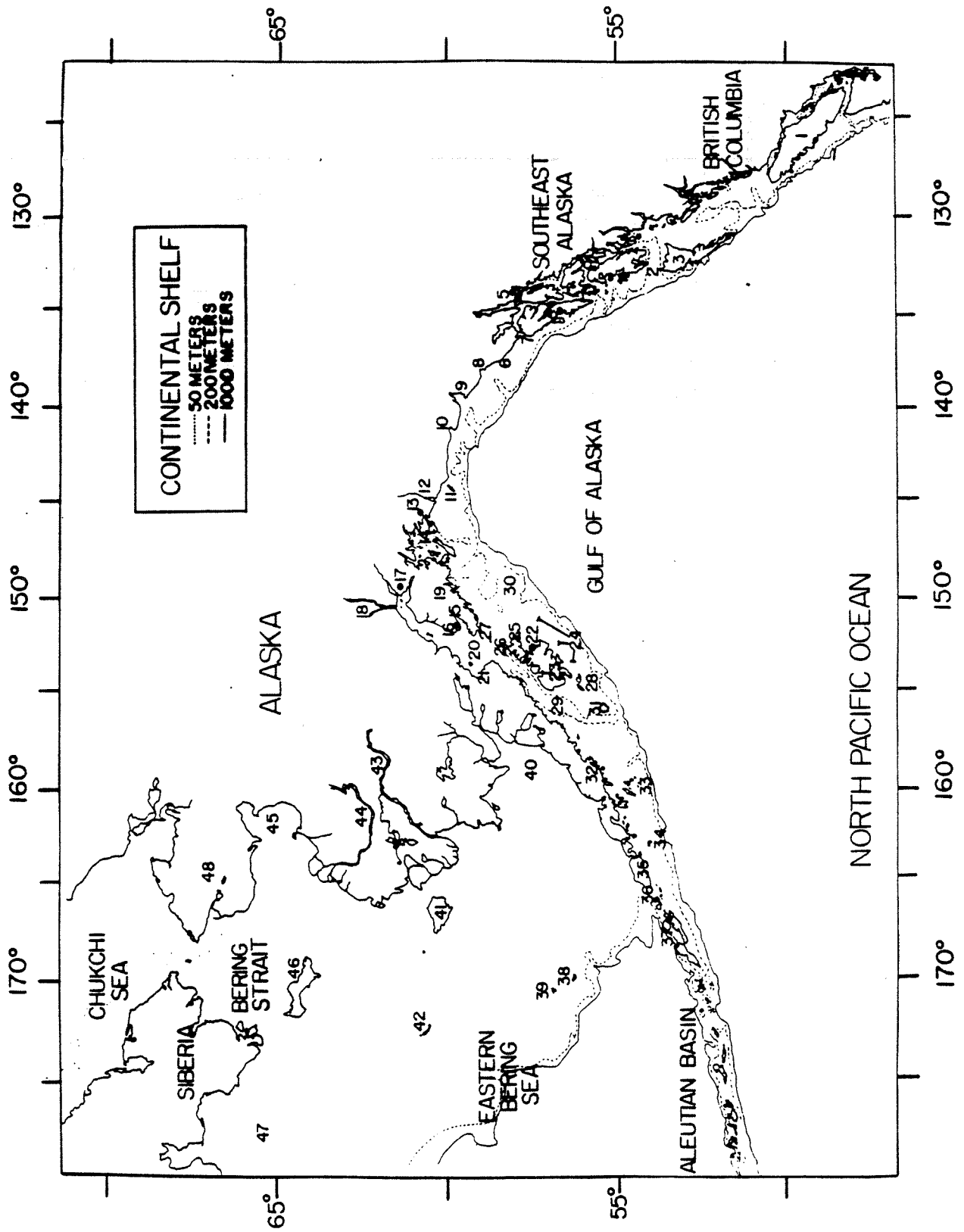
The four domains of the eastern Bering Sea are separated by three persistent transition zones resembling oceanographic fronts that overlie the 50, 100, and 180 m isobaths. These are broad regions of convergence discontinuity in hydrographic properties, and restricted exchange of water, salt, heat, and nutrients (Coachman and Charnell 1979; Coachman and Walsh 1981). Mixing coefficients are estimated to be ten times larger within domains than across fronts (Hattori and Goering 1981). The outer shelf break front appears to mark a shoreward transition to increased dominance of tidal over advective energy over the shelf, and also defines the zone of interaction between oceanic and middle shelf water masses (Kinder and Coachman 1978). The middle shelf water mass has lower salinity than the oceanic water mass of the basin due to ice formation and freshwater input, and also has greater seasonal temperature variability due to greater relative atmospheric exposure and weaker advection and mixing (Kinder and Schumacher 1981a). The middle front is a zone of subsurface convergence associated with variable onshore transport along the bottom from the outer shelf domain (Coachman 1982). This transport appears to be coherent with regional-scale atmospheric forcing. The upper 30 m of the middle frontal zone is less distinct, there is slow offshore transport, and weak upwelling is inferred. The inner front appears as a discontinuity between the vertically stratified middle shelf domain and the vertically homogeneous inner shelf domain (Schumacher et al. 1979). Waters in the coastal domain constitutes a separate water mass, distinguished by lower salinities due to freshwater input/land from Alaska.

All three shelf domains are mixed from above by winds and from below by tides. In the coastal domain, these two mixing forces overlap and generally

Figure 3.

Base map of eastern Bering Sea and Gulf of Alaska.

- | | |
|---------------------------------|-----------------------------------|
| 1. Vancouver Island | 2. Dixon Entrance |
| 3. Queen Charlotte Island | 4. Sitka |
| 5. Juneau | 6. Cape Fairweather |
| 7. Cross Sound | 8. Dry Bay |
| 9. Yakutat Bay | 10. Icy Bay |
| 11. Kayak Island | 12. Copper River |
| 13. Cordova | 14. Prince William Sound |
| 15. Kachemak Bay | 16. Homer |
| 17. Anchorage | 18. Susitna River |
| 19. Kenai Peninsula | 20. Cook Inlet |
| 21. Kamishak Bay | 22. Kodiak |
| 23. Kodiak Island | 24. Albatross Banks |
| 25. Afognak Island | 26. Stevenson Entrance |
| 27. Kennedy Entrance | 28. Trinity Islands |
| 29. Shelikof Strait | 30. Portlock Bank |
| 31. Chirikof Island | 32. Alaska Peninsula |
| 33. Shumagin Islands | 34. Sanak Island |
| 35. Unimak Island | 36. Unimak Pass |
| 37. Dutch Harbor | 38. St. George Island (Pribilofs) |
| 39. St. Paul Island (Pribilofs) | 40. Bristol Bay |
| 41. Nunivak Island | 42. St. Matthews Island |
| 43. Kuskokwim River | 44. Yukon River |
| 45. Norton Sound | 46. St. Lawrence Island |
| 47. Gulf of Anadyr | 48. Seward Peninsula |



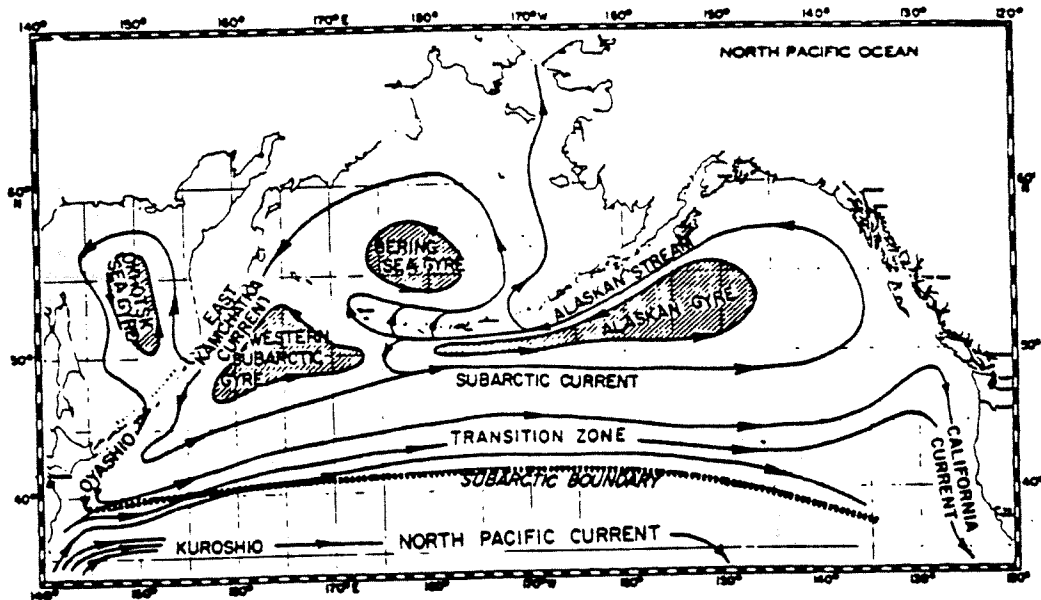


Figure 4. General circulation pattern of the northern North Pacific Ocean and adjacent seas (from Favorite et al. 1977).

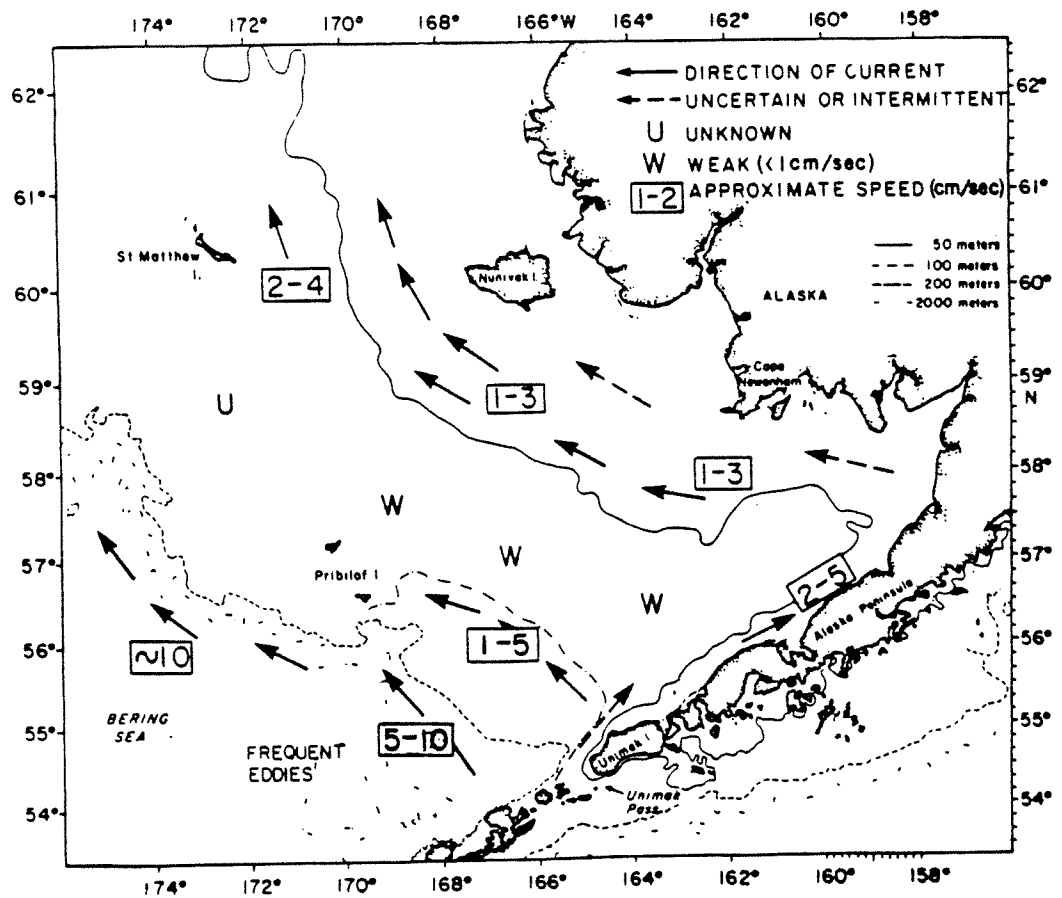


Figure 5. Mean net current patterns (neglecting tidal currents) in the eastern Bering Sea (from Kinder and Schumacher 1981b).

produce a vertically homogeneous water column (Figure 6). In the middle shelf domain, where transports due to advection and tidal diffusion are weak and most heat transfer occurs through the air/sea interface, heating of surface icemelt during the spring and summer isolates a 50 m warmer, fresher surface water layer from a residual core of deep cold water on the bottom of the middle shelf domain (Figure 7). In winter, when the two shallower domains are normally ice-covered, convection induced by cooling and freezing disrupts the vertical water column stability in middle shelf domain, and the inner front is less distinct (Schumacher and Kinder 1983, Coachman 1983). In the outer domain there is a persistent three-layer vertical stratification. On the bottom is tidally-driven intrusion of oceanic basin water that transports heat, salt and nutrients onshore. Between that and the surface wind-mixed layer is a stratum characterized by vertical "fine structure," believed to be an interleaving of oceanic waters with seaward-flowing middle shelf water of similar density (Coachman and Charnell 1979). The major physical processes controlling hydrographic properties in the three domains are a combination of advection and tidal diffusion over the outer and inner shelf, and diffusion over the middle shelf.

The mean meteorological pattern of the Bering Sea is one of a continental high pressure system over Siberia and a marine low pressure system over the Aleutians (Figure 8). The northern Bering Sea on the average is characterized by a relatively cold, clear, stable and dry polar climate, and northerly winds produced by the Siberian high (Overland 1981). The southern Bering Sea on the average is characterized by a warmer, cloudier, moister climate with no net wind direction, but rather a series of wind progressions associated with the passage of storms along the Aleutians. The relative extent of these weather systems varies seasonally and interannually. During winter winds are stronger, and the high pressure system dominates the Bering. Ice covers most of the shelf in winter, its extent varying over short and long time scales, depending on air temperature and wind direction. The broken and mobile ice front advances southward from the Bering Strait and Norton Sound region beginning in October-November, and reaches its maximum extent in March. Retreat usually begins in April, and the Strait is completely open by August (Figure 9). During summer the Bering is increasingly influenced by the Aleutian low, and the climatic boundary shifts northward so that the southern Bering experiences a net increase in southwesterly winds and storm tracks (Figure 8).

The strongest interannual variations in shelf conditions in the eastern Bering Sea are in water temperature and ice extent (Schumacher and Reed 1983). Distributions of water temperatures and ice extent in recent years are presented in Figures 10 and 11. Warm and cold years are linked to interannual variations in the relative positions of the high and low pressure systems and the associated winds (Niebauer 1980, 1983). The late 1950's and early 1970's were cold periods, which Takenouti (1974) associated with periods of maximum solar activity. The late 1960's and late 1970's were relatively warm periods. Some relationship between Bering Sea surface water temperatures and larger scale temperature anomalies in the Pacific have been noted (Niebauer 1981a), but most interannual water temperature variations are coupled directly to interaction with the atmosphere (Reed 1978). The summer temperature of bottom water in the midshelf domain is negatively correlated with the freezing-degree days of the previous winter: that is, midshelf bottom water is colder after cold winters (Coachman and Charnell 1979). Due to the long residence time of water over the middle shelf, temperature deviations from long-term mean can persist for up to two years (Niebauer 1980). Water temperature anomalies are not necessarily in phase over the entire shelf; Ingraham (1981) noted that in 1976, while most of the Bering Sea was abnormally cold, northerly winds blew the ice field offshore and inner Bristol Bay actually warmed earlier than average.

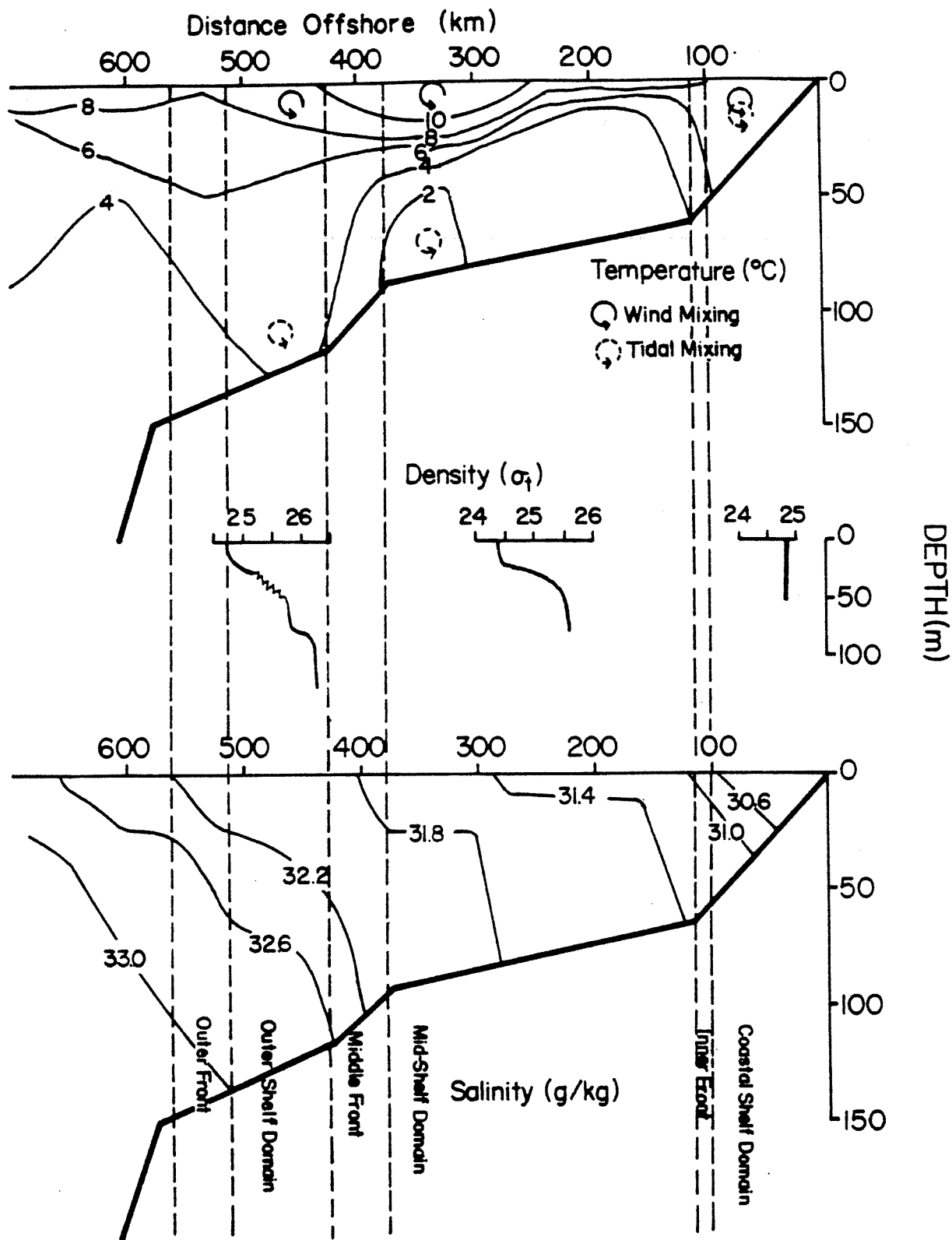


Figure 6. Representative vertical profiles of summer temperature, salinity, and density conditions in the eastern Bering Sea (after Schumacher 1981; and Schumacher and Kinder 1983).

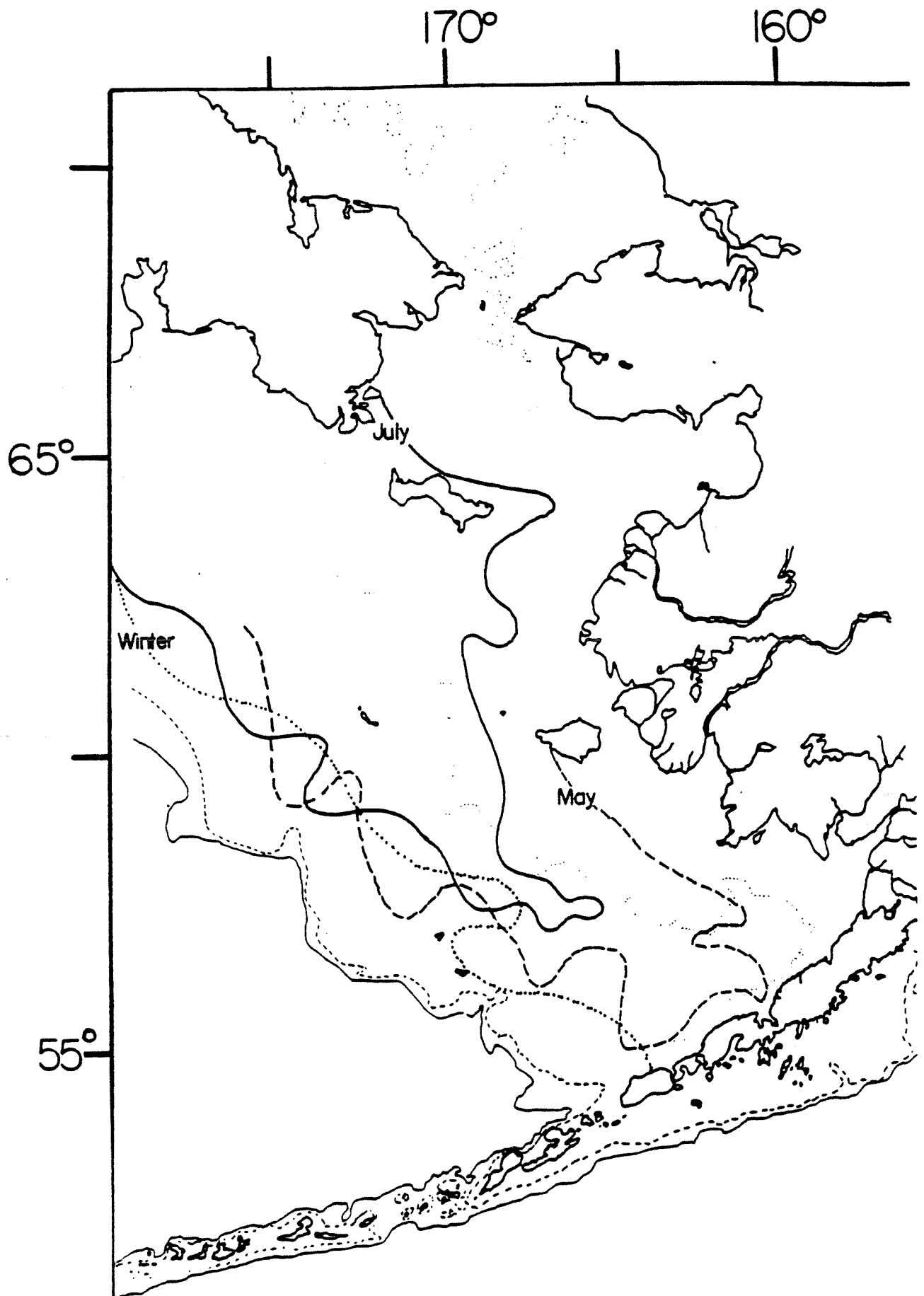


Figure 7. Mean seasonal areal extent of 1° C bottom temperature isotherm on the eastern Bering Sea shelf (after Ingraham 1981).

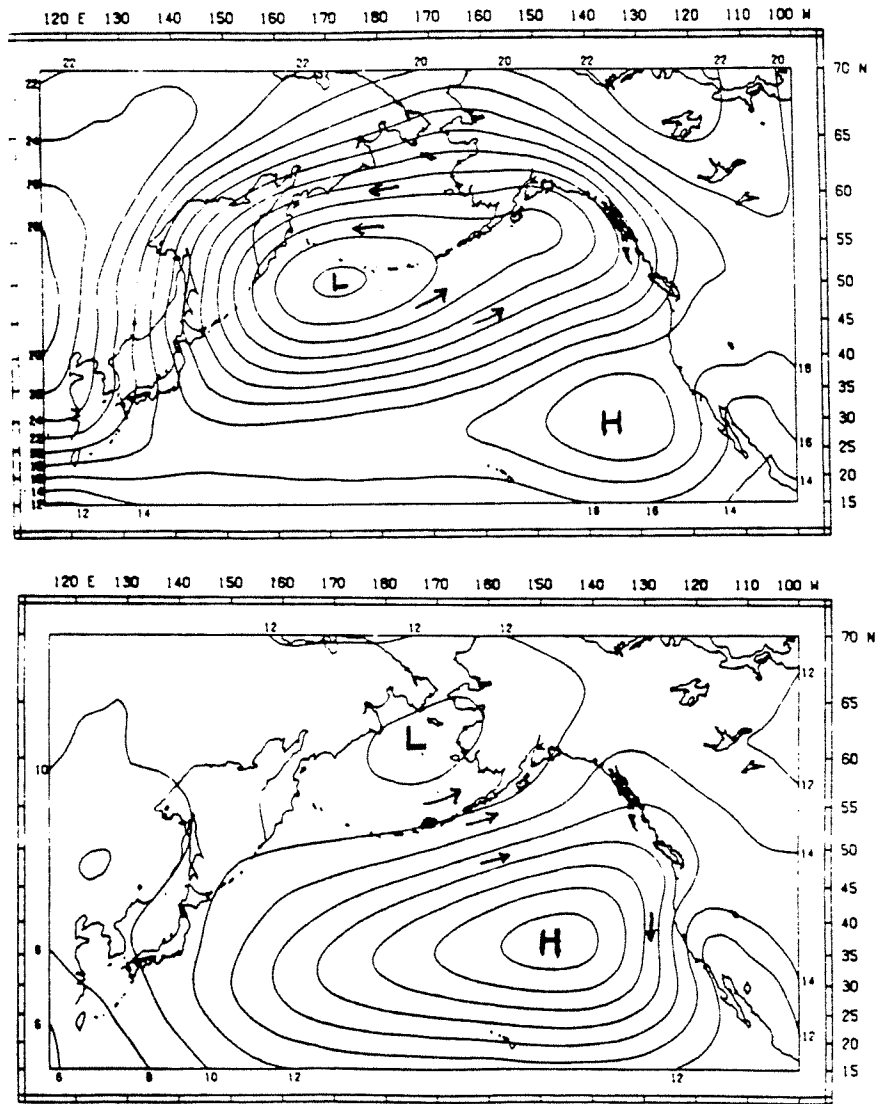


Figure 8. Mean atmospheric pressure and wind patterns in the North Pacific Ocean and Bering Sea in winter (top) and summer (bottom) (after Favorite et al. 1977).

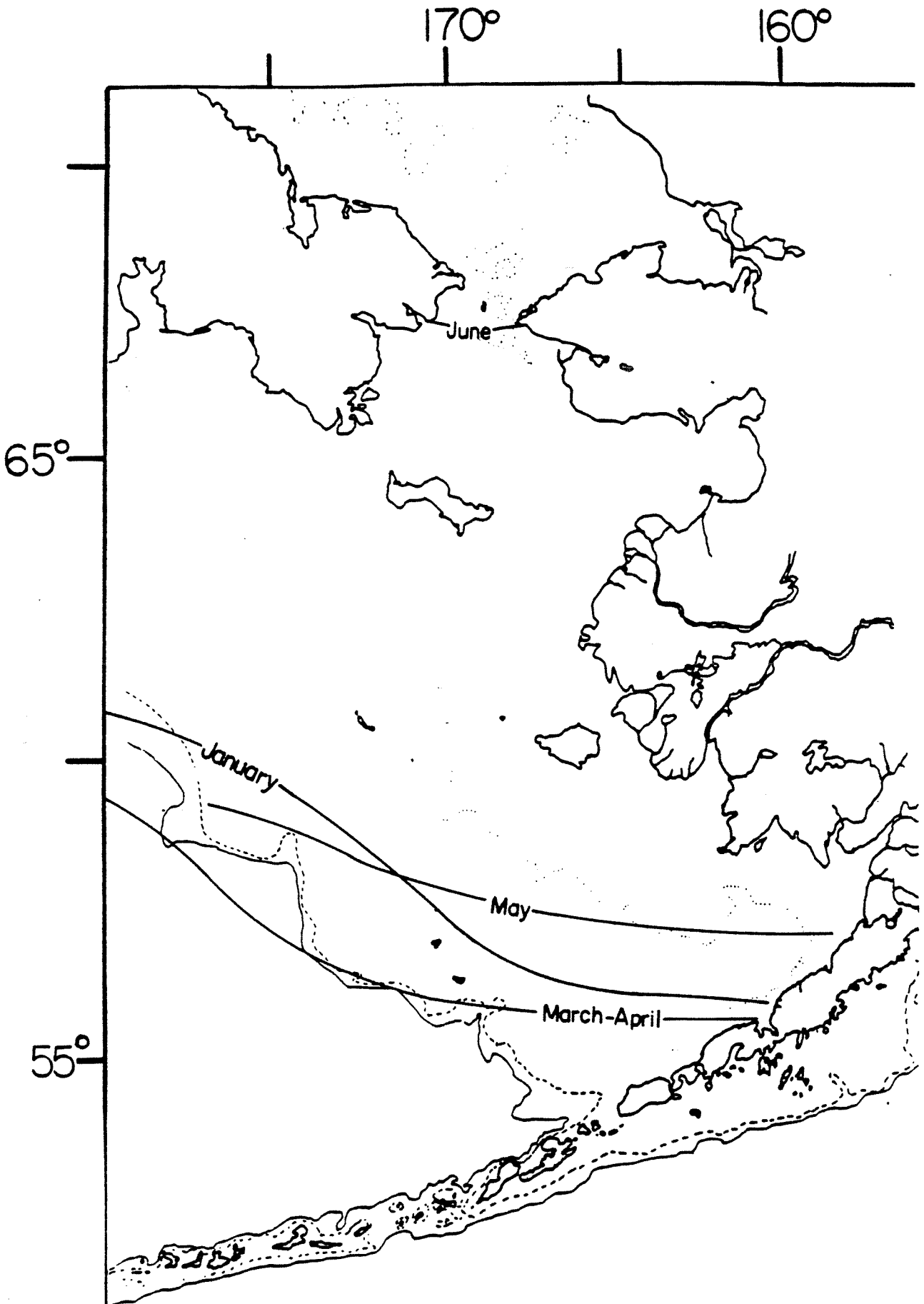


Figure 9. Mean seasonal ice edge extent in the eastern Bering Sea (after Ingraham 1981).

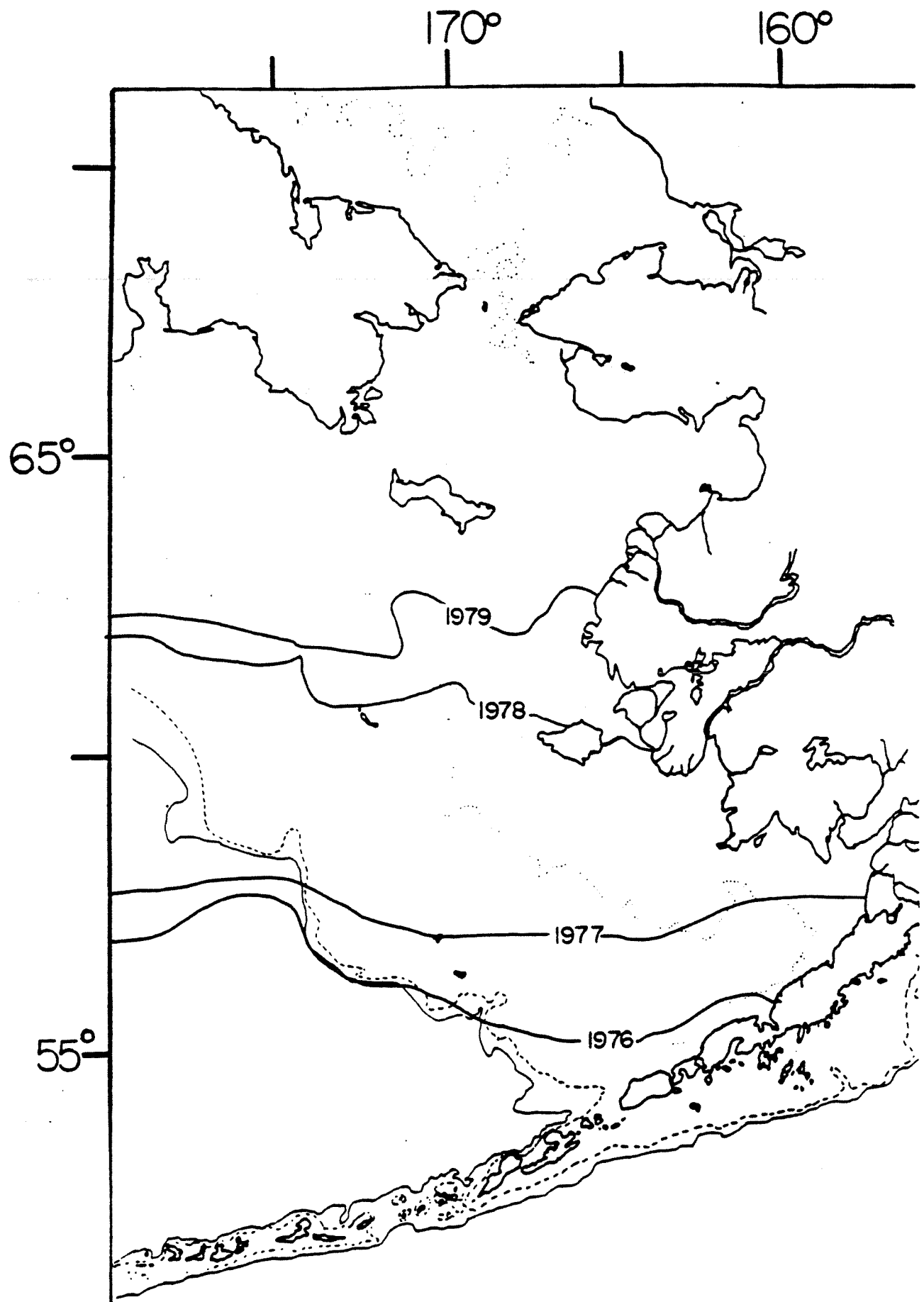


Figure 11. Recent interannual variability of maximum (March-April) ice edge extent in the eastern Bering Sea (after Ingraham 1981).

2.2 PLANKTON PRODUCTION

2.2.1 Primary Production

Portions of the eastern Bering Sea continental shelf are comparable in annual primary production to other productive subarctic shelf regions such as the Grand Banks and the North Sea (Coachman and Walsh 1981; Sambrotto et al. 1984). The high productivity has been attributed to strong vertical stratification and to the high nutrient content of the source water that originates from the Bering Sea basin and the North Pacific. There are few data on productivity in oceanic waters, but high productivity has been observed in the western Bering Strait region where oceanic waters are transported over the shelf (Sambrotto et al. 1984). However, since most commercial fish yield is taken from the southeastern shelf region, more intensive data on lower trophic levels have been collected from that region.

Primary productivity patterns in the southeastern shelf region vary seasonally and in the different domains (Table 2). Primary productivity is uniformly low in the coastal domain due to the strong mixing present there throughout the ice-free season. In waters that are ice-free all year (which usually include much of the outer shelf and some of the middle shelf domain), a spring increase in phytoplankton growth ("bloom") begins at the onset of thermal stratification in late March (Sambrotto and Goering 1983). This growth is supported by high concentrations of nutrients mixed into the surface later by winter storm winds. The peak of the bloom occurs in late April and May (Coachman and Walsh 1981; Smith and Vidal 1984), associated with the seasonal decline in storminess, and the amount of production during this period is fairly constant year to year.

After the initial spring outburst of growth, further production over the shelf is regulated by processes controlling nutrient supply. The source of nutrients for the shelf is diffusive transport from the deep waters overlying the continental slope, and due to the frontal structure and lack of advection this supply is greatly restricted (Coachman and Walsh 1981). The vertical flux of nutrients is estimated to be 1-2 orders of magnitude less than that on other productive continental shelf regions such as Peru or Georges Bank (Walsh 1983). With the onset of strong surface stratification in late May and June, especially in the middle shelf domain, there is little additional supply of nutrients (Hattori and Goering 1981), causing a decline in primary productivity, with a maximum at a subsurface depth (Iverson et al. 1979a). After spring, 10 - 50% of primary production in both the outer and middle shelf domains may be supported by ammonium regenerated by grazers (Coachman and Walsh 1981). During late spring and through the summer, this stable pattern may be punctuated by intermittent storms that mix nutrients into the surface layer and stimulate bursts of production. The additional production generated by these mixing events varies interannually, and may contribute 10 - 50% (average 37%) of spring production. Niebauer et al. (1981a) estimated that production from April through June (including ice-edge production, below) contributed 65% of annual production.

Where winter ice cover is present an earlier bloom is observed, associated with the very stable surface layer of low-salinity meltwater (Alexander and Niebauer 1981). An ice-edge bloom can begin as early as February, as much as a month before the same species bloom in open water. Ninety-nine percent of the production during this bloom is believed associated with free-floating microalgae, rather than with the flora embedded in or on the ice (Alexander and Chapman 1981). Blooms associated with icemelt also can occur during fall or winter if ice is blown southward and melts in warmer water, especially when ice breakup is accelerated by storm winds. The most

intense blooms, occurring in areas of open water within the ice field, follow the retreating ice edge northward, and peak in late May after blooms have passed in open waters to the south and west (Figure 12). Instantaneous productivity can reach $25 \text{ mg-C m}^{-3} \text{ hr}^{-1}$ and $600\text{-}700 \text{ mg-C m}^{-2} \text{ hr}^{-1}$, and standing stocks can exceed $20 \text{ mg-Chl a m}^{-3}$ (Niebauer et al. 1981a). Alexander and Niebauer (1981) inferred possible upwelling and resulting additional nutrient supply and productivity under conditions of northerly winds blowing parallel to the ice edge. The ice edge bloom may be 50 to 100 km wide and last up to three weeks, finally terminated by nutrient exhaustion (Alexander 1981).

There is some uncertainty about the relative importance of open-water and ice-edge blooms to total annual production of the shelf region. In principle, an open-water bloom should follow the ice-edge bloom at a given location (Figure 12), but its intensity may be decreased by prior nutrient depletion (Alexander and Niebauer 1981). However, Sambrotto and Goering (1983) noted that on the southeastern shelf, where ice cover is usually less extensive and where meltback occurs during the windier conditions of April, ice-edge blooms may not affect the occurrence of a later open-water bloom. Present survey data have inadequate spatial and temporal coverage to assess the course of the spring blooms in a typical year, or to observe differences among years that result from interannual variations in ice cover and storminess. Production associated with the ice-edge spring bloom decreases in warm years, due to the reduced spatial and temporal extent of icemelt and resultant weaker stability, and due to greater separation from nutrient-rich slope water (Niebauer et al. 1981a). However, open-water production may compensate for this deficit, since it would begin earlier in the season (Coachman and Walsh 1981) and might be associated with greater wind-mixed nutrient input (Sambrotto and Goering 1983). Open-water blooms (and storm-induced mixing) thus would be relatively more important under warm conditions (Sambrotto et al. 1984). The proximity of the ice-edge to the shelf break also can affect the consumption of plant production by herbivores (see below).

The pattern of phytoplankton standing stock also varies across the shelf. Standing stocks are low in the coastal domain due to low productivity. High chlorophyll *a* concentrations have been observed over the shelf break on the Bering Sea side of Unimak Pass, associated with bathymetrically-induced upwelling and input of high-nutrient Pacific water (Koike et al. 1982). Iverson et al. (1979a) observed a persistent band of high chlorophyll about 15 km wide coincident with the shelf break front between Unimak Pass and the Pribilof Islands. The middle front also is a region of increased phytoplankton standing stock (Iverson et al. 1979b), possibly supported by an increased vertical nutrient flux associated with weak subsurface convergence and upwelling (Coachman 1982).

The differences between the four eastern Bering Sea domains also are reflected in the phytoplankton species composition (Goering and Iverson 1981). In winter the shelf phytoplankton "assemblage," consists of flagellates (Schandelmeier and Alexander 1981), with very low standing stocks and productivity due to low light intensities and strong vertical convection under the ice. The spring bloom in late March and early April is composed of boreal chain-forming centric diatoms such as *Thalassiosira* spp. and *Chaetoceros* spp. Sancetta (1981a) and Schandelmeier and Alexander (1981) associated certain species of *Nitzschia* and *Thalassiosira* closely with ice melt blooms in the middle shelf domain. Over the slope and outer shelf the phytoplankton assemblage is dominated by the large colonial flagellate *Phaeocystis pouchetii* (Goering and Iverson 1981). This species does not require silicon, and higher silicate concentrations are observed in this domain than in the

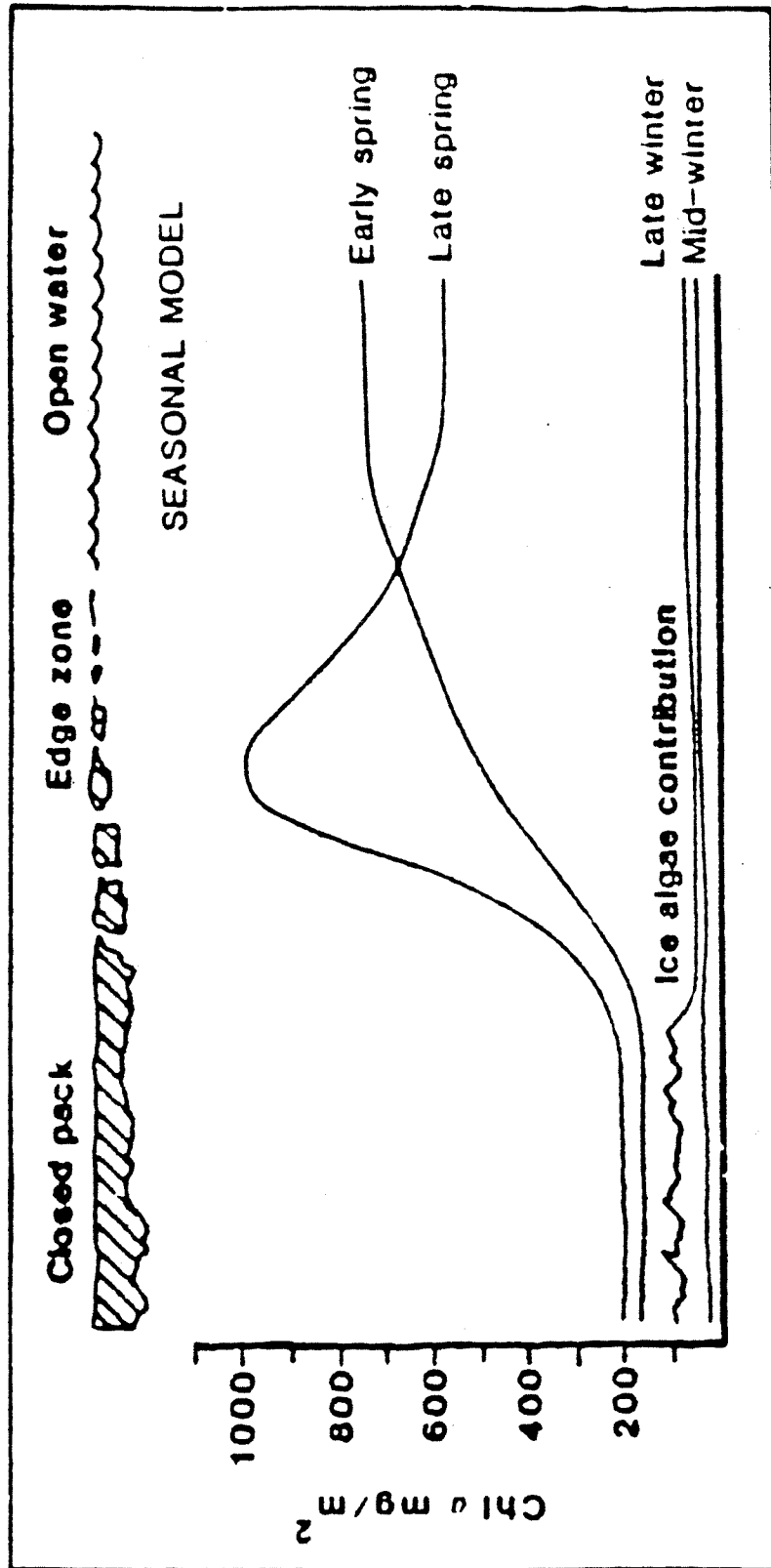


Figure 12. Schematic diagram of differences in seasonal phytoplankton standing stocks relative to the ice edge in the eastern Bering Sea (from Niebauer et al. 1981a).

diatom-dominated middle shelf domain (Iverson et al. 1979b). Part of this cross-shelf difference also may be caused by differential grazing pressure (see below). As waters warm and nutrient depletion begins over the midshelf in May and June, the diatom species assemblage shifts to more southerly species of Rhizosolenia, Nitzschia, Chaetoceros spp., and Corethron spp. (Iverson et al. 1979b). The summer midshelf diatom assemblage is dominated by Rhizosolenia alata, a pennate diatom with a reduced silica requirement, that subsists on recycled nitrogen (Goering and Iverson 1981). Apparently few data are available, however, on summer abundance of flagellates, which often can be the dominant phytoplankton in strongly stratified neritic waters (e.g. Parsons et al. 1978).

Differences between domains also are reflected in the species of phytoplankton found in sediments, although differential grazing, sinking, and dissolution can cause the species assemblage of the sediment to differ from that of the water column. In particular, flagellates are not preserved in sediments, so that the most useful indicator species are the more heavily silicified species of diatoms and radiolarians (Sancetta 1981a, b; Morley and Hays 1983). The diatoms Denticulopsis spp. and Coscinodiscus spp. dominate the sediments of the Bering Sea basin, and are indicative of warmer, higher-salinity oceanic and Pacific waters (Sancetta 1981a, b; Katamani 1983). Tests and cysts of certain species of Thalassiosira and Chaetoceros are associated with colder, lower-salinity, and more productive shelf waters, and especially with ice-edge blooms (Sancetta 1981a, b). Sancetta (1979; 1983) correlated fossil and recent sediments and observed the southward and seaward propagation of the cold-water species during glacial periods.

High productivity over the eastern Bering Sea shelf removes dissolved CO_2 from seawater, resulting in increased pH values. Significant pH anomalies have been observed in waters of the southeastern Bering Sea shelf by Codispoti et al. (1982), and near Unimak Pass and the Bering Strait by Koike et al. (1982). The elevated pH values may reach 8.44 (versus 7.6 in deep water), and CO_2 concentrations may be as low as 125 microatmospheres, versus 336 microatmospheres in the atmosphere and up to 1300 microatmospheres in deep water (Park et al. 1974). CO_2 concentrations are positively correlated with nutrient concentrations, and negatively correlated with chlorophyll *a* concentrations and oxygen supersaturation (Hood 1981; Koike et al. 1982). pH and CO_2 anomalies persist over the southeastern shelf throughout the summer until eliminated by winter mixing and overturn. Surface water stability fostering high primary productivity over the shelf also restricts the replenishment of CO_2 removed from seawater by photosynthesis. Walsh (1983) postulated that sequestering of CO_2 by phytoplankton over the eastern Bering Sea and other continental shelf regions and subsequent subsurface offshore transport and burial in the sediments may account for a significant sink for atmospheric CO_2 .

2.2.2 Secondary Production

There are significant differences in the standing stocks, productivity, and species composition of zooplankton with distance from land in the eastern Bering Sea. Figure 13 shows estimated mean zooplankton biomass distribution, with a maximum along the shelf break front near the Pribilof Islands. Mean zooplankton biomass for the entire Bering Sea has been estimated at 37 g wet weight m^{-2} (Motoda and Minoda 1974). In contrast to primary production, secondary production (Table 2) is highest in the outer shelf domain. This paradox results from physical constraints on zooplankton species composition, and has significant implications for the food web.

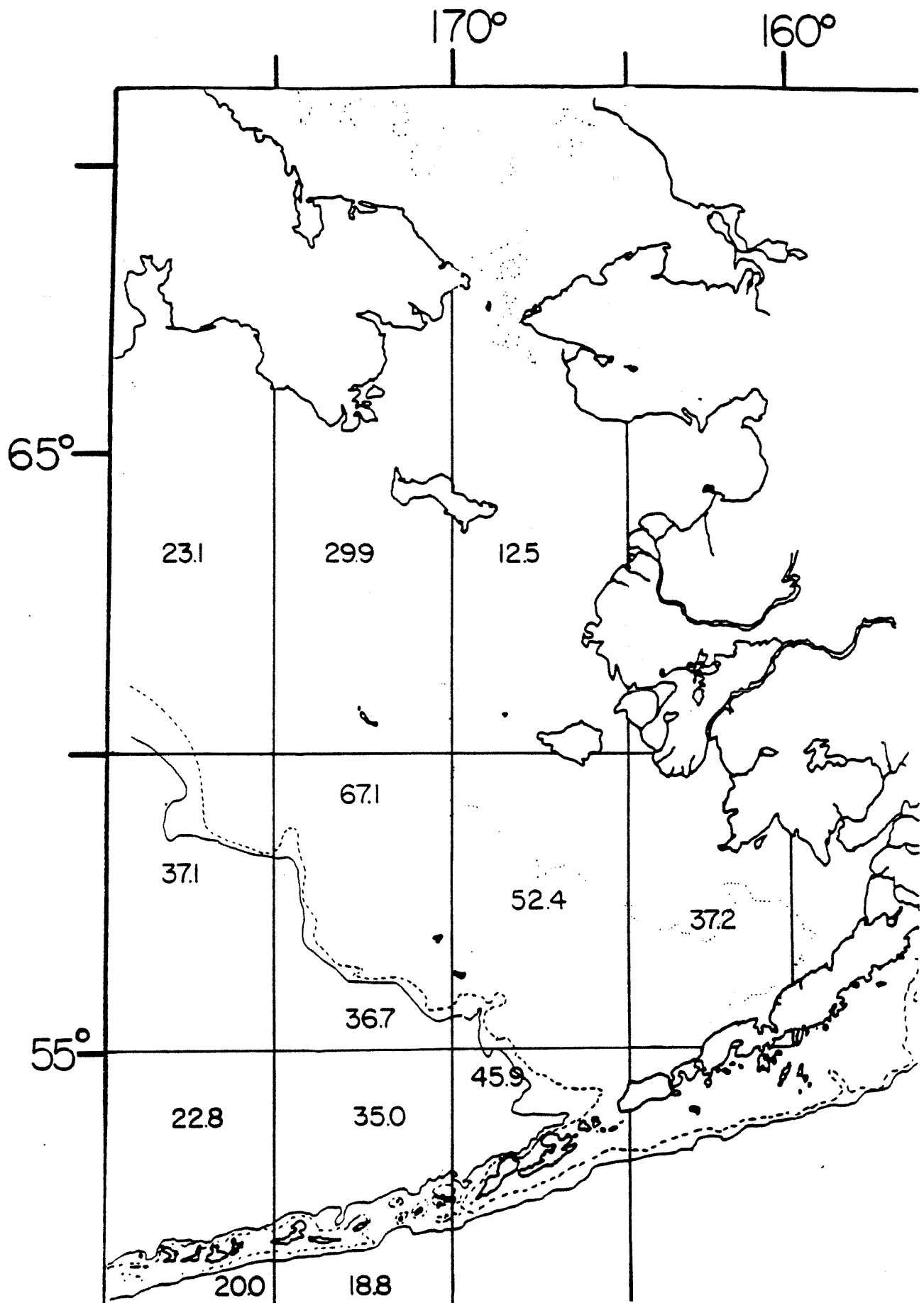


Figure 13. Estimated mean (1956-1970) areal distribution of summer zooplankton biomass (g wet weight m⁻², 0-80 m) in the eastern Bering Sea (after Motoda and Minoda 1974).

TABLE 2
Primary and Secondary Production in the Eastern Bering Sea
(Cooney 1981)

Area	Primary production (gC m ⁻² yr ⁻¹)	Secondary production (gC m ⁻² yr ⁻¹)	Transfer Efficiency
Basin	90	13	14%
Outer Shelf Domain	200	64	16%
Midshelf Domain	400	7-10	2%
Coastal Domain	120	2-6	3%

Dominating the biomass of the outer shelf and slope zooplankton assemblage are the large copepods Neocalanus spp., and Eucalanus sp. (Cooney and Coyle 1982), having a standing stock of 20 to 40 grams m⁻² (dry weight) along the shelf break front during spring. Numerically dominant but with standing stock less than 10 g m⁻² are smaller copepods (Metridia sp., Pseudocalanus spp., and Oithona spp.), and euphausiids (Thysanoessa and Euphausia spp.) (Cooney 1981; Cooney and Coyle 1982; Dagg et al. 1982; Smith and Vidal 1984). Zooplankton stocks occur in patches of 5-15 km extent, concentrating especially in frontal regions of high primary productivity (Iverson et al. 1979b; Woodby 1984). Little direct information is available on life cycles of these organisms in the eastern Bering Sea, but some inferences can be made using data from the Gulf of Alaska (Frost et al. 1983; Miller et al. 1984). Neocalanus adults remain in deep water (below 300 m) without feeding, and release eggs that float toward the surface. Immature stages feed in surface waters through the summer, then return to deeper water to overwinter and reach sexual maturity. The middle front over the shelf is believed to constitute a barrier that the outer shelf large copepod assemblage does not penetrate (Iverson et al. 1979b), so that these animals essentially are restricted to the outer shelf and oceanic domains.

The abundance of euphausiids and smaller copepods (Acartia sp., Pseudocalanus spp., Oithona spp., and Calanus spp.) over the middle shelf appears to be roughly similar to that over the outer shelf, but in the absence of the larger copepods, these become the dominant zooplankton (Dagg et al. 1982; Smith and Vidal 1984). However, the importance of euphausiids may be underestimated. Most euphausiids at the surface appear to be juveniles, but adults are poorly sampled by nets (Incze et al. 1984). Using acoustic techniques, Woodby (1984) observed euphausiid standing stocks ten times higher on the outer shelf than on the middle shelf. Furthermore, even on the outer shelf where large zooplankton species are abundant, the euphausiids and smaller zooplankton are estimated to consume 70% or more of the phytoplankton (Cooney and Coyle 1982).

The different species and standing stocks of grazers over the middle and outer shelf domains have been connected to possible differences in the fate of the organic matter fixed by phytoplankton. Dagg et al. (1982) concluded that grazing intensity was insufficient to control phytoplankton growth over the outer shelf, or to affect the cross-shelf distribution of phytoplankton standing stock. Incze et al. (1984) hypothesized that the abundance of Neocalanus spp. on the outer shelf most likely was regulated by the supply of diatoms on which they feed, while temperature rather than food supply probably regulated the abundance of middle shelf copepods (Smith and Vidal 1984). If middle shelf copepods are not food limited, the poorly studied flagellate phytoplankton, the preferred food of small copepods, might be abundant in this domain. The large diatoms observed during the spring bloom

in the middle shelf domain cannot be grazed by small copepods, and on the outer shelf Phaeocystis pouchetii can be grazed only by euphausiids. Thus in both domains it appears that some phytoplankton species escape significant grazing (Iverson et al. 1979b).

The life cycle patterns of the dominant copepods also produce cross-shelf differences in the temporal pattern of grazing. The life cycle of Neocalanus spp., in which maximum biomass in the surface layer occurs in spring (Cooney and Coyle 1982), and in which reproduction takes place before and without need of the spring phytoplankton bloom (Miller et al. 1984), enables it to exploit early season primary production. In contrast, the smaller copepods that dominate the middle shelf domain must feed immediately before reproducing, and reach their maximum biomass in summer (Cooney 1981; Cooney and Coyle 1982; Smith and Vidal 1984). Thus over the middle shelf, a spring lag in onset of grazing stress is inferred that would permit a large fraction of the spring bloom to be ungrazed. This effect could be magnified by the greater sensitivity of the reproductive timing and growth of the smaller copepods to temperature (Smith and Vidal 1984; Dagg et al. 1984; Incze et al. 1984). Part of this difference also might arise because middle shelf copepods reside closer to the surface than those on the outer shelf (Sambrotto and Goering 1983). Sambrotto and Goering (1983) further speculated that wind mixing that stimulated phytoplankton production might increase secondary production on the outer shelf, but decrease it on the middle shelf due to disruption of subsurface phytoplankton aggregations to which small copepods might orient for feeding.

In both the outer and middle shelf domains, most primary production apparently is ungrazed. Cooney and Coyle (1982) estimated grazing of 20% or more of primary production in the outer shelf domain compared to less than 5% in the middle shelf. Dagg et al. (1982) estimated that about 20% is grazed in both domains. Walsh (1983) described interannual variations in grazing on the middle shelf, ranging from 3% in a cool year to 30% in a warm year. By any of these estimates, a greater mass of primary production is ungrazed in the middle shelf. In contrast, Katamani (1983) estimated that only 2% of primary production in the Bering Sea basin reached the bottom. Walsh (1983) estimated that an annual mean of $3 \text{ mg m}^{-2} \text{ day}^{-1}$ of carbon is ungrazed in the middle shelf domain, compared to 0.6 mg carbon on the outer shelf. The fate of this ungrazed carbon is uncertain but has important possible trophic implications.

2.2.3 Vertical Carbon Flux

The differences in percentage and absolute magnitude of primary production grazed in the outer and middle shelf domains of the eastern Bering Sea are believed to account for differences in the food web dynamics of these domains. Iverson et al. (1979b) suggested that the middle shelf supports predominantly benthic and demersal food web, since a large fraction of the carbon fixed in that domain is ungrazed and therefore must sink to the bottom. Likewise, because a greater proportion of primary production apparently is consumed on the outer shelf, a pelagic food web was inferred in that domain. Furthermore, Smith and Vidal (1984) estimated a 40-60% mortality of outer shelf copepods during April and May due to predation, compared to nearly zero mortality of middle shelf copepods.

This interpretation of differing food web patterns is supported by the observed pattern of standing stocks of invertebrate benthos and demersal fishes. On the southeastern shelf benthic biomass is greatest (about 100 g m^{-2}) in the midshelf domain (Alton 1974), and is dominated by epifauna such as crabs (Jewett and Feder 1981). Dense aggregations of bivalve infauna and crab epifauna in the midshelf domain at depths of about 75 m are believed to be supported by detritus derived from ungrazed sinking phytoplankton (McDonald

et al. 1981). The major bottomfish of the eastern Bering Sea shelf, yellowfin sole (Limanda aspera), also is most abundant in the middle shelf domain (Bakkala 1981).

Walsh (1983), however, argued that as much as 50% of primary production in both the outer and middle shelf domains may not be consumed at all. The organic carbon content of shelf sediments is quite low, and the appearance of ammonium maxima near the bottom of the middle shelf and in midwater in the outer shelf (Saino et al. 1983) suggests remineralization into the water column. Phytoplankton-derived sediments also may be resuspended by wind and tidal mixing. Walsh (1983) concluded that the sink for this missing production is the sediments on the continental slope.

2.3 FISHERY BIOLOGY OF POLLOCK

2.3.1 Life Cycle

Egg, Larval, and Juvenile Stages. Bering Sea pollock begin life as buoyant 1.5 mm eggs that are laid in midwater and float toward the surface (Nishiyama and Haryu 1981). Pollock eggs can be up to 97% of the planktonic eggs sampled during spring (Waldron and Vinter 1978). Eggs appear from February through June, but are most abundant from March to mid-May (Incze et al. 1984). Time to hatching depends on temperature; at a typical ambient temperature of 3°C hatch time is about 22 days. Some variability in egg size is observed; egg size is related to development rates in the laboratory, and this relationship could be used to infer effects of temperature on larval survival in the field (see below). No estimates of egg or larval mortality have been made in the field, but mortality rates are presumed to be very high.

Pollock larvae are 3.5 to 4.4 mm long at hatching. They live exclusively off their yolk sac for about one week, then begin feeding while still supported by the yolk sac for an additional week (Incze et al. 1984). At 7 to 7.5 mm the yolk sac is fully absorbed and the larvae are termed post-yolk sac. During this stage the mean growth rate is about 0.35 mm day⁻¹ (Walline 1983). At a length of about 20-30 mm the fin rays are fully developed and the larvae become age 0 juveniles (Haryu 1980); on the average this transition occurs in May-June, roughly 70 days after spawning (Walline 1983). Juveniles grow at a mean rate of 0.5 mm day⁻¹ (Walline 1983) and reach a length of 90-110 mm by December (Smith 1981). Pollock are considered age 1 juveniles on January 1 following hatching.

The vertical distributions of pollock eggs, larvae, and juveniles are better understood than their horizontal distributions. Eggs are distributed mostly in the upper 20 m (Nishiyama et al. 1983). Larvae are observed at depths from 10 to 40 m (Paul 1983; Nishiyama et al. 1983; Dagg et al. 1984). Larvae may be distributed uniformly in turbulent waters, or aggregated at the thermocline where one is present (Traynor 1984). Age 0 juveniles remain planktonic in the upper 40 m, apparently aggregating near the thermocline in stratified waters (Francis and Bailey 1983). Ages 1-2, juveniles are found progressively deeper in the water column and may be observed in midwater schools 5-20 m thick within 30 m of the bottom between the 90 and 160 m isobaths (Bakkala and Alton 1983; Traynor 1984). There is considerable interannual variability in the horizontal distribution of eggs, larvae, and juveniles, such that no generalizations can be drawn about the factors controlling those distributions (Incze et al. 1984). The spatial distributions of larvae do not always conform to those that would be predicted from known spawning locations and current patterns (Sherman et al. 1983). Egg distribution appears to be consistently centered over the outer shelf domain between the Pribilof Islands and Unimak Pass. A slow northwestward drift and dispersion of eggs and larvae from the locations of spawning on the outer shelf is inferred from the local currents. All immature stages are essentially confined to shelf waters and are rare in the Aleutian Basin. Smith (1981), Bakkala et al. (1982), Bakkala and Alton (1983), Francis and Bailey (1983), and Traynor (1984) have described various distributions of larvae and juveniles over the middle and outer shelf domains southeast and northwest of the Pribilof Islands in different years, but no mechanism has been demonstrated to account for these differences.

The factors controlling pollock year-class strength in the eastern Bering Sea, and the possible critical period during which those factors may act, have not been clearly identified. Growth and mortality rates of juvenile pollock are both higher than those of adults (Figure 14). Smith (1981) suggested that a minimum in natural mortality at ages 2-3, and an apparent low interannual variability of abundance of juveniles at age 2 compared to age 1, indicated that most winnowing of the year class is complete by that age, and that therefore age 1 might be the critical age for determining year-class strength. Walline (1983) posed the working hypothesis that year-class strength of eastern Bering Sea pollock is controlled by predation, especially

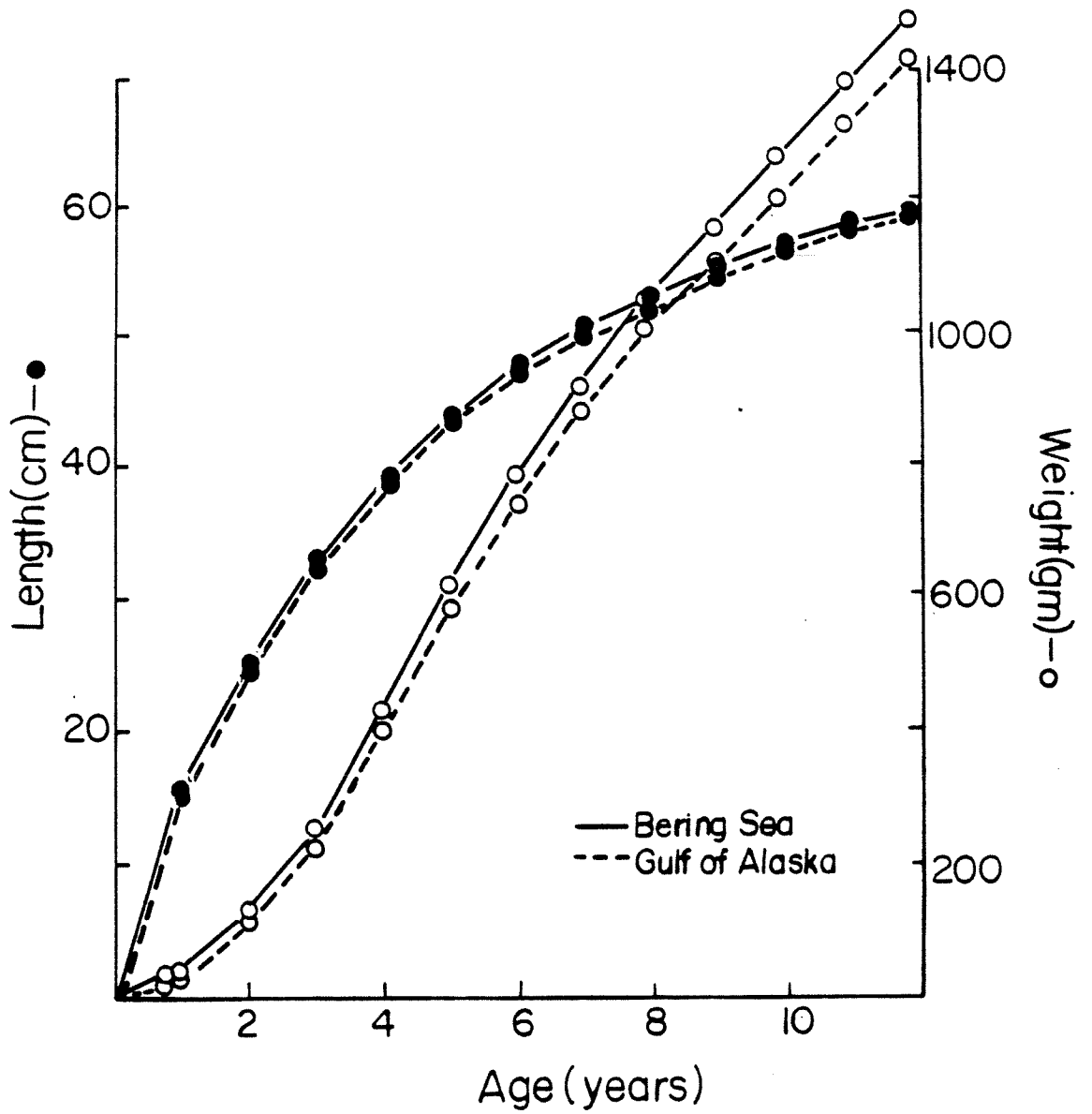


Figure 14a. Mean length- and weight-at-age of pollock in the eastern Bering Sea and Gulf of Alaska (after Niggol 1982).

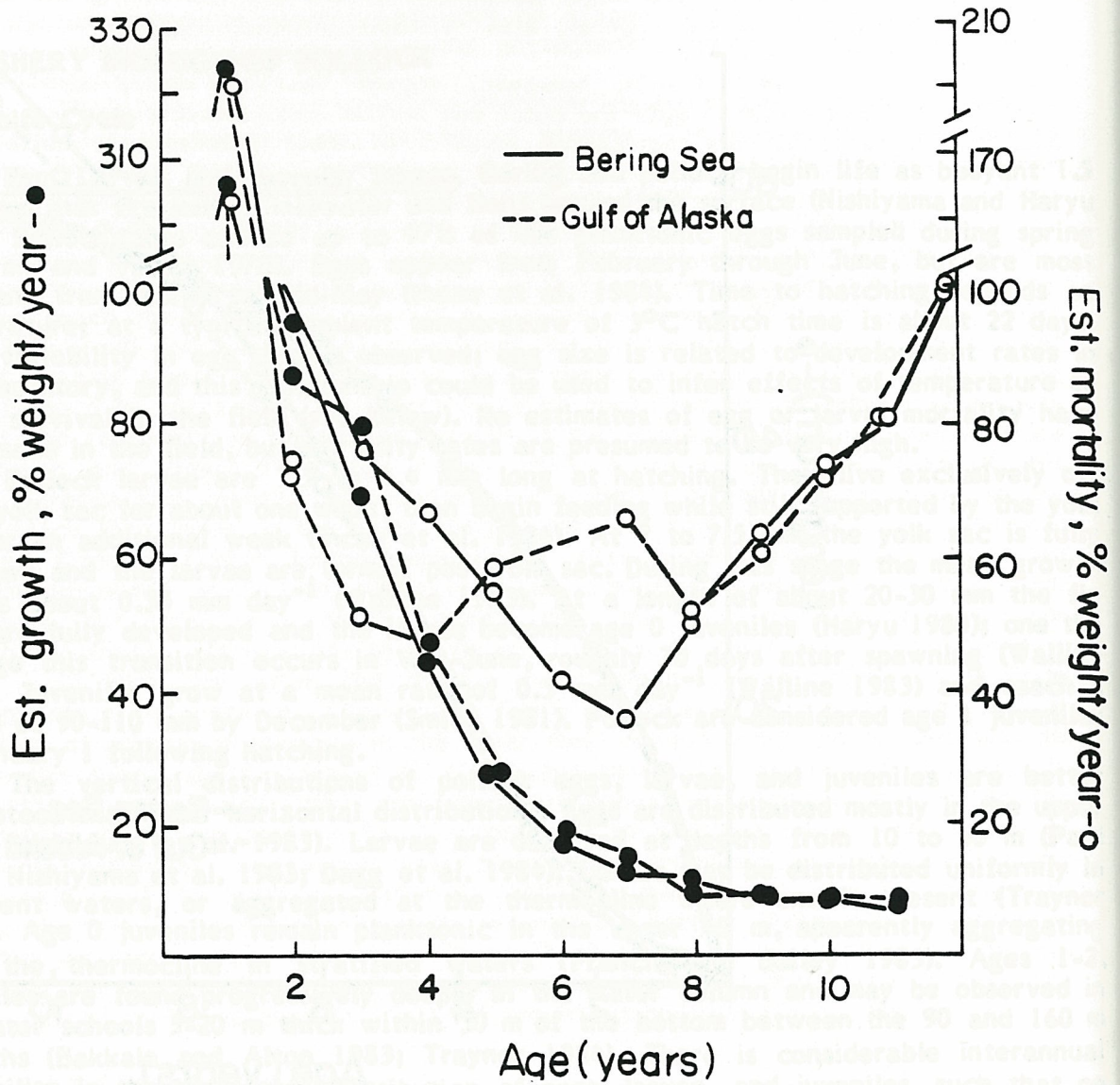


Figure 14b. Estimated mean gross growth and mortality rates (percent of total biomass per year) versus age of pollock in the eastern Bering Sea and Gulf of Alaska (after Niggol 1982).

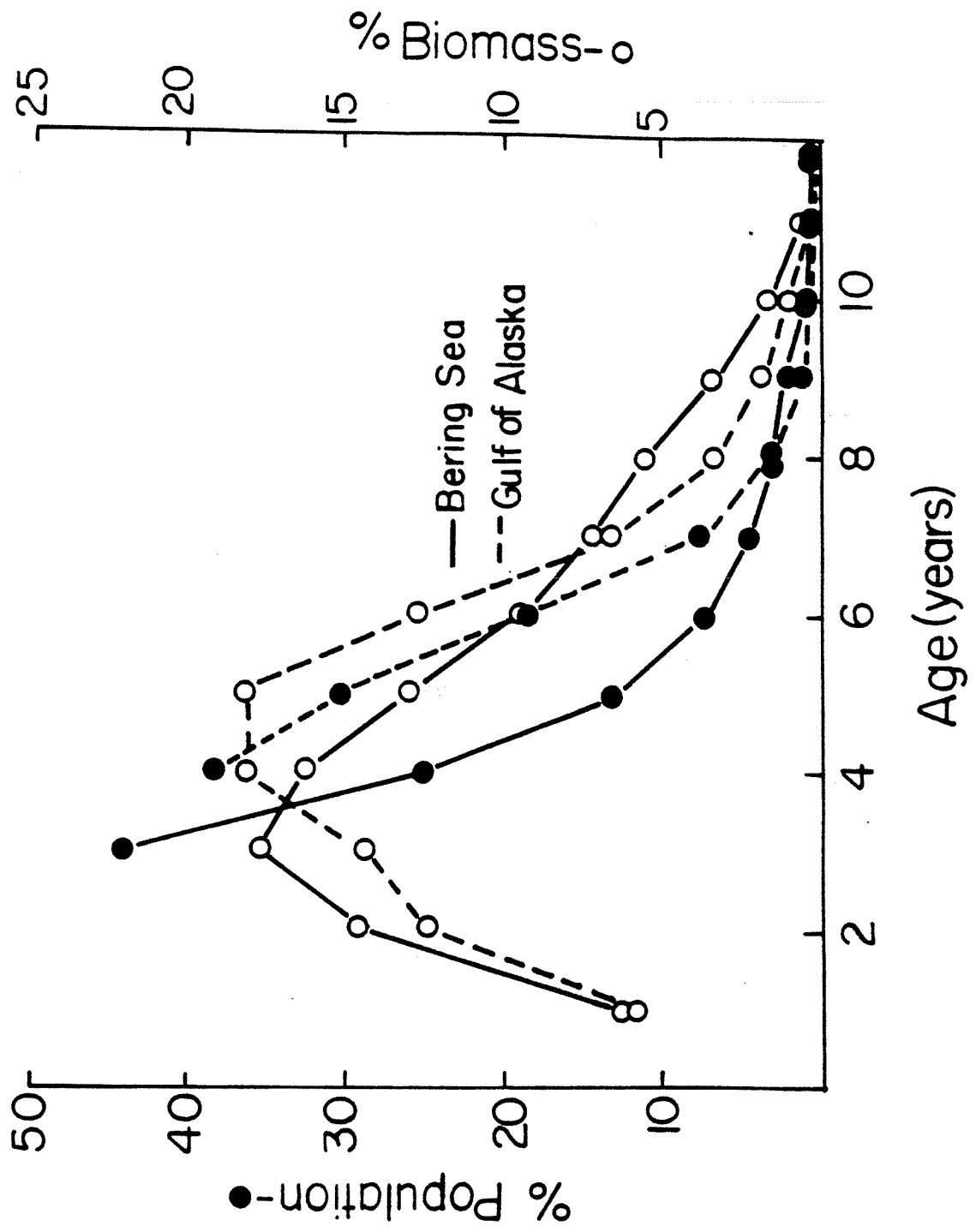


Figure 14c. Mean fraction of total pollock standing stock versus age of pollock in the eastern Bering Sea and Gulf of Alaska (after Niggol 1982).

cannibalism (see below), on age 1 juveniles. This conclusion is contrary to theories from other major fisheries (e.g., Lasker 1981) that larval first-feeding and starvation may limit year-class strength. Incze et al. (1984) argue, however, that Walline's data of 1978 and 1979 may present atypically good years for larval feeding in the southeast Bering Sea, and that the apparent importance of predation may be difficult to generalize. In addition, recent data (Alton and Bakkala 1983) indicate that previous methods of surveying year-class strengths were flawed and the data presented by Smith (1981) were biased, so that previous generalizations about the control of year-class strength were no longer valid.

Adult Stage. Attainment of sexual maturity takes place mostly at ages 3 and 4, at lengths from 32 to 40 cm (Salveson and Alton 1976, Bakkala and Smith 1978). Full adoption of the semi-demersal adult habitat and recruitment to the fishery occur mostly at ages 2-3 (Lynde 1984). More than 50% of adult pollock remain within 50 m of the bottom in dense schools 5-20 m thick and 20 to 50 km in breadth during the daytime, and disperse upward at night to feed (Alton and Bakkala 1983; Traynor 1984). Adults inhabit the middle and outer shelf domains and the upper slope between the 50 and 450 m isobaths, concentrated near the shelf break. Recent acoustic surveys also have located fully pelagic adult (age 4 and older) pollock populations over the Aleutian Basin at depths of 50 to 150 meters (Bakkala et al. 1983; Okada 1983). Adults appear to undergo seasonal migrations, spending the winter (October-February) at depths of 150-300 m in oceanic waters, and migrating onshore to spend spring and summer over the middle and outer shelf at depths of 90-140 m (Salveson and Alton 1976).

A consistent shift in maximum fishery yield from south to north of the Pribilof Islands in June (Figure 15; Salveson and Alton 1976) suggests a northward along-shelf migration of pollock during summer, thus creating a hypothetical counterclockwise annual adult migration pattern. However, the evidence also is consistent with the existence of two separate stocks that both overwinter in the Aleutian Basin but migrate separately to the northern and southern shelf during spring, with earlier migration to the south associated with earlier warming (see below). Little genetic difference between fish from the two regions can be detected (Grant and Utter 1980). However, length-at-age of adults is significantly greater in shelf populations south of the Pribilof Islands than in populations on the northern shelf or in the Aleutian Basin (Lynde 1984), suggesting either genetic differences or differences in temperature and feeding conditions. Furthermore, age structures and yields in the two regions have changed in different ways during the last decade (Francis and Bailey 1983), and length-at-age and other morphometric differences have been described (Lynde 1984), supporting the two-stock hypothesis.

The spawning period of pollock extends from February through June, and is concentrated from April to mid-May (Incze et al. 1984; Lynde 1984). Sexual maturity and spawning may take place later in more northerly shelf waters (Lynde 1984; Walline 1983), and the location of spawning appears to be very sensitive to bottom water temperature (see below). In an average year the principal spawning effort is first observed in February in midwater over the slope and shelf break between the Pribilof Islands and Unimak Pass (Figure 16), and appears to progress inshore later in the season, culminating in the middle shelf domain in May. Some spawning also is observed north of the Pribilof Islands and in the Aleutian Basin (Lynde 1984; Traynor 1984). Observed egg sizes decrease with time and distance onshore. Smaller eggs are laid by smaller (younger) females, and by females that have laid more than one clutch of eggs (batch spawners). The observed pattern is consistent with either smaller females laying eggs later in the season and farther inshore, or with repeated batch spawning of all females as they migrate onshore (Lynde 1984). The latter hypothesis is currently favored, although batch spawning has not been observed directly in Bering Sea pollock populations.

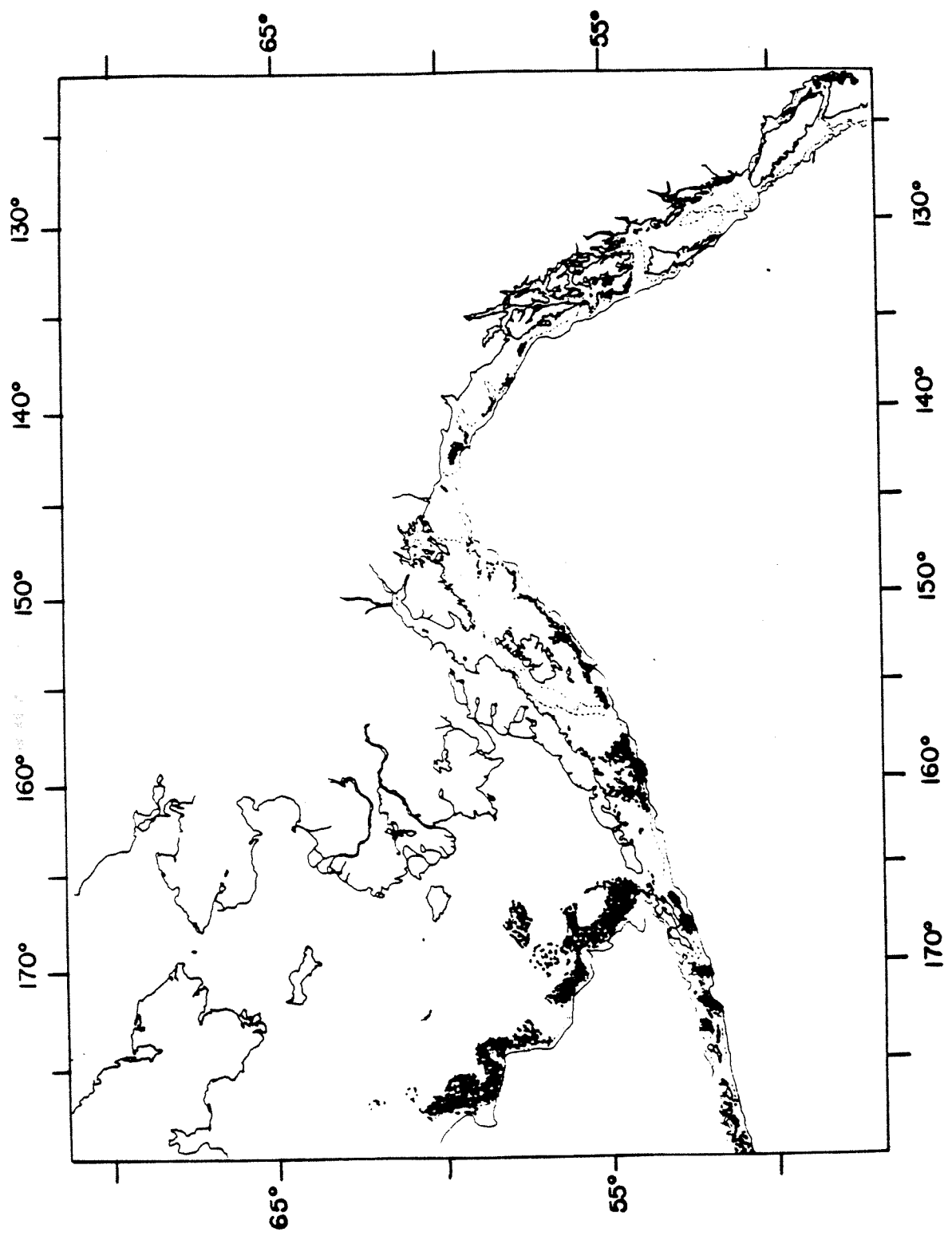


Figure 15. Distribution of pollock catch in the eastern Bering Sea and Gulf of Alaska. Recent fishery in Shelikof Strait not shown (after Smith et al. 1981).

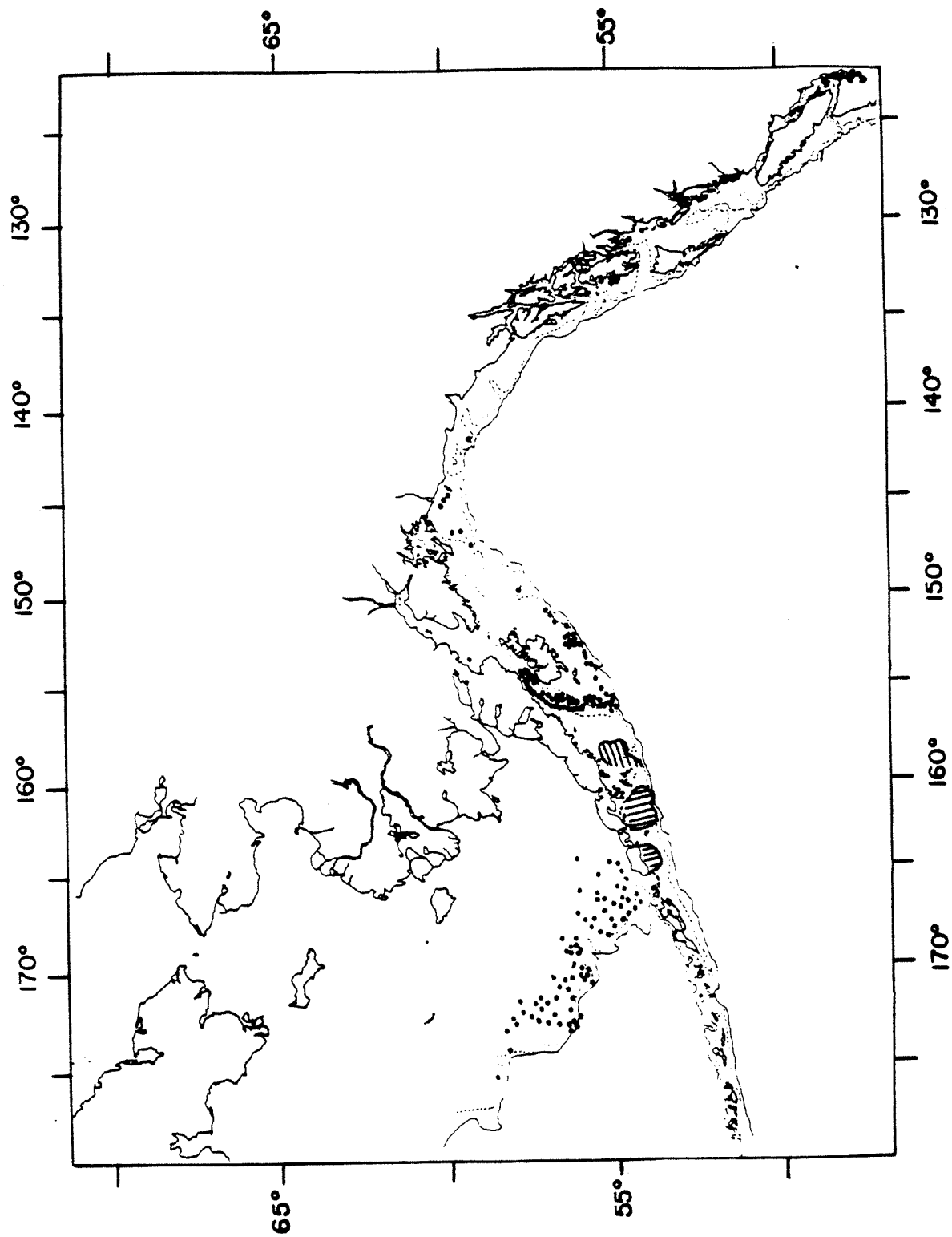


Figure 16. Observed distribution of pollock spawning in the eastern Bering Sea and Gulf of Alaska (after Hirschberger and Smith 1983; and Alton and Deriso 1983a).

2.3.2 Trophic Relationships

Prey. Larval and juvenile pollock feed almost exclusively on zooplankton. The diet of larvae consists primarily of eggs and nauplii of copepods (Incze et al. 1984). With increasing size, juveniles take increasingly larger prey, including copepodites and adults of small copepods such as *Oithona* spp., *Pseudocalanus* spp., and *Acartia* spp., and furcilia and calyptopis stages of euphausiids (Figure 17; Nishiyama and Hirano 1983, Lynde 1984). The food web supporting pollock in the eastern Bering Sea is depicted in Figure 18. Lynde (1984) has speculated that zooplankton stocks in the middle and outer shelf domains may not differ in their ability to support pollock larvae, because abundances of small copepods are believed to be similar in the two domains. However, the outer shelf may be superior for feeding of juveniles due to the presence of large copepods (relative abundances of euphausiids are uncertain and also should affect juvenile feeding). Growth rates of larval and juvenile pollock inferred from otolith rings by Walline (1983) showed no significant differences between middle and inner shelf domains. From this evidence Walline (1983) inferred that food supplies do not limit growth of larval or juvenile pollock on the eastern Bering Sea shelf. This conclusion is supported by laboratory data (reviewed by Incze et al. 1984) indicating that larvae can feed successfully at the ambient zooplankton concentrations present in this region. Dagg et al. (1984) also calculated that nauplii of small copepods were so numerous in the middle shelf domain that mortality due to pollock predation was insignificant to their abundance. Walline (1983) did derive significantly lower growth rates for larvae and juveniles sampled north of the Pribilof Islands. These differences were not associated with food supply and may have been related to temperature or to genetic variation (see below).

The principal prey of adult pollock are copepods, euphausiids, and small fishes (Bailey and Dunn 1979). Adults also prey to a small and variable extent upon crab, shrimp, and other benthic species (Feder and Jewett 1981). The adult diet varies seasonally and spatially (Dwyer 1984). Adults of all sizes consume mostly euphausiids during spring. During summer small (less than 30 cm) adults consume copepods and euphausiids, large (greater than 50 cm) adults consume predominantly small fishes, and other adults have a mixed diet of zooplankton and fishes. During the fall and winter a major portion of the diet of adults of all sizes is composed of small fishes. Pollock in the Aleutian Basin appear to consume primarily euphausiids at all times of year. The heavy consumption of zooplankton over the shelf during spring and summer, and all year in the Aleutian Basin, corresponds to the annual maximum in zooplankton abundance as pollock migrate onshore to the outer shelf in spring and the middle shelf in summer (see below). Pollock populations north of the Pribilof Islands and in the Aleutian Basin have consistently lower feeding and growth rates (Dwyer 1984; Traynor 1984) that suggest poorer feeding conditions in these areas, although genetic (see above) and temperature (below) differences also may be important.

A distinctive attribute of pollock is the high incidence of cannibalism. Juvenile pollock are the dominant small fish in the diet of adult pollock, and adult pollock at times may be the most significant predators on juvenile pollock. Young-of-the-year appear to escape cannibalism during the summer, possibly due to vertical segregation between juveniles (retained in the upper 40 m by surface stability) and deeper-living adults (Francis and Bailey 1983). Age 0 juveniles may reach a critical size threshold in autumn, when they first begin appearing in adult stomachs (Dwyer 1984). This appearance coincides with the seasonal decline in zooplankton abundance and the breakdown of surface stratification in the autumn, however. Juveniles remain vulnerable to cannibalism through the winter, and are eaten by the largest adult pollock during the following summer at age 1. However, age 1 juveniles largely escape cannibalism during the spring, possibly due to the relative abundance of zooplankton or due to spatial segregation from adults by temperature barriers (see below). Dwyer (1984) and Walline (1983) speculated on the possible life cycle consequences and evolutionary advantages of cannibalism in pollock, but no clear conclusions have been

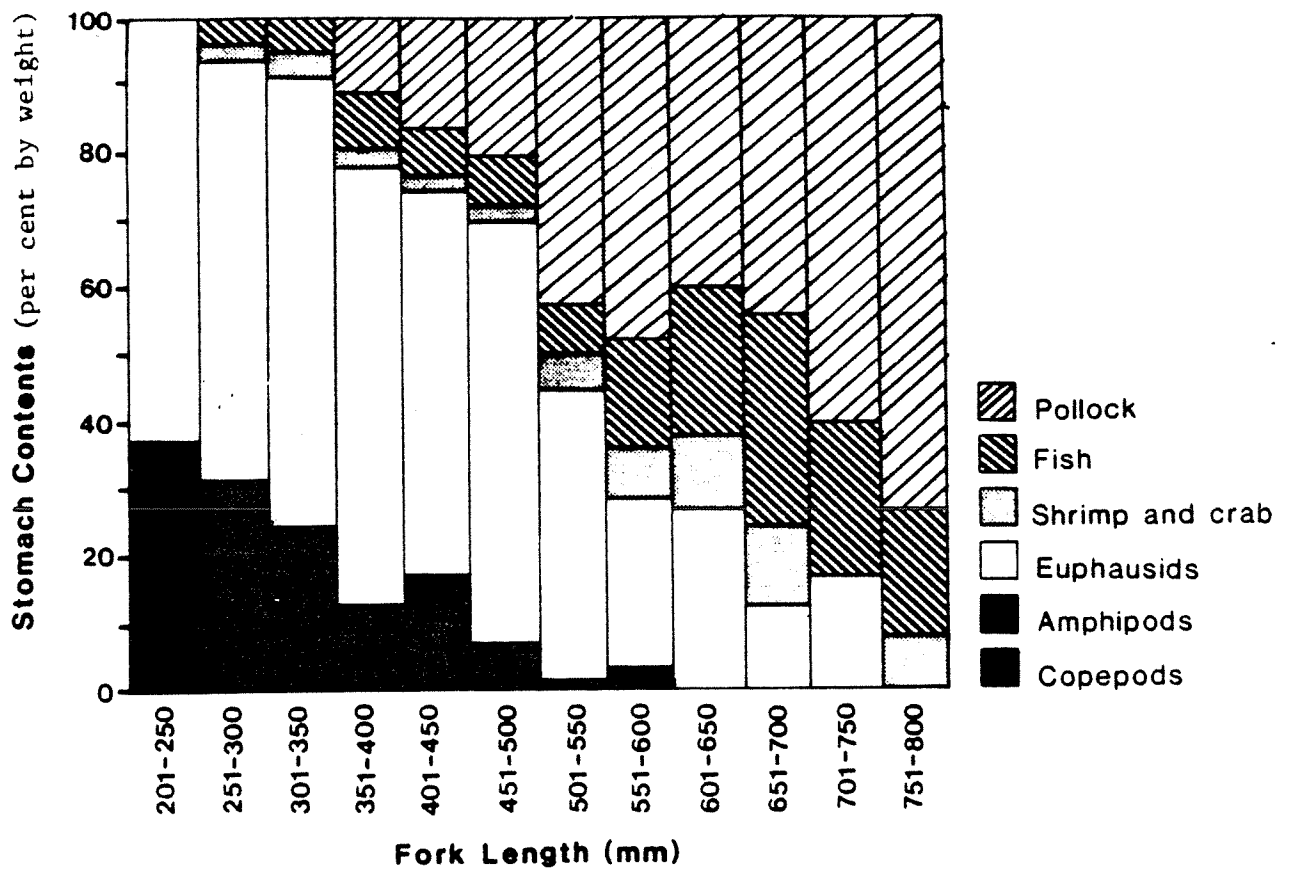


Figure 17. Prey spectrum of different sizes of pollock in the eastern Bering Sea (after Smith 1981).

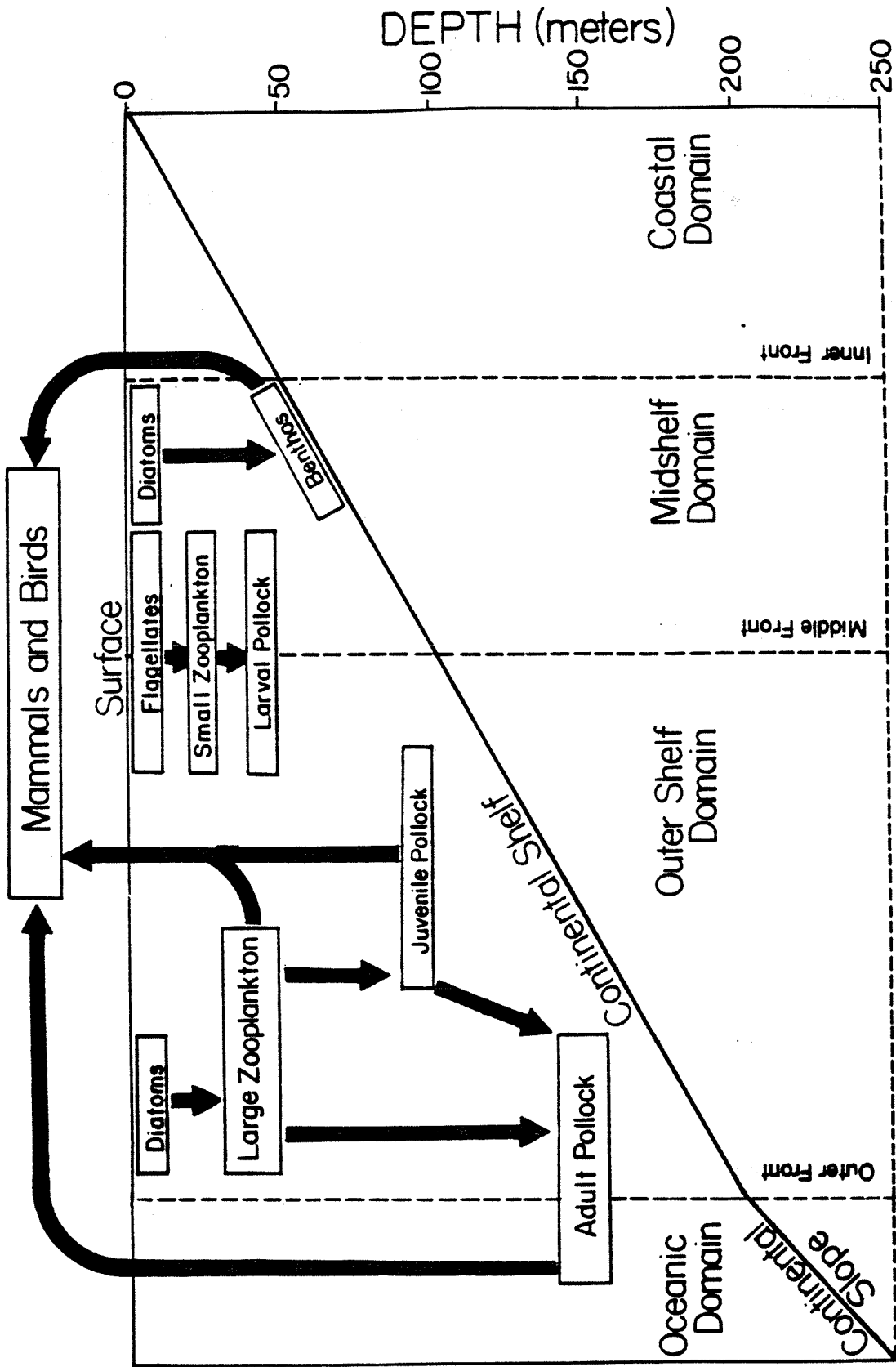


Figure 18. Schematic diagram of pollock food web in the eastern Bering Sea (after Smith 1981; Feder and Jewett 1981; and Cooney 1981).

reached. Cannibalism may enhance population stability, may permit adults to indirectly consume prey that grew in areas (such as the shelf in winter) that only their juveniles inhabit, or may simply represent exploitation of the most abundant prey.

Predators. The eastern Bering Sea supports high populations of apex predators, which dominate the structure of the food web (Laevastu and Favorite 1981). During the summer it has a higher population density of mammals than any other region of the ocean, and more marine birds than the remainder of the northern hemisphere. Most of these animals are migratory and enter the Bering Sea in summer for feeding and reproduction. The estimated consumption of fishes by birds and mammals has been estimated in excess of 3 million metric tons yr^{-1} , equalling or exceeding the total commercial fish catch (Laevastu and Favorite 1981; Harry and Hartley 1981; Ashwell-Erickson and Elsner 1981).

The identities of predators and the magnitude of predation pressure on pollock eggs and larvae in this region at present are unknown (Incze et al. 1984). Some fish species, e.g. Pacific cod (Gadus macrocephalus) are known to consume pollock but their quantitative significance has not been assessed (Smith et al. 1984). Kajimura and Fowler (1984) concluded that the most important pollock predator in the eastern Bering Sea is the northern fur seal (Callorhinus ursinus). Fur seals breed primarily on the Pribilof Islands and feed widely over the outer shelf and upper slope. Pollock compose about 40% of the diet of fur seals, which are capable of feeding on all sizes of juvenile and adult pollock but consume mainly those in the range 4-40 cm (1-4 years). The remainder of their diet consists of capelin, herring, and squid. Annual consumption of pollock by fur seals is estimated from 118,000 to 160,000 metric tons (Kajimura and Fowler 1984; Hood and Calder 1981; Harry and Hartley 1981; Ashwell-Erickson and Elsner 1981).

Several other species of marine mammals also consume pollock, mainly juveniles. These include seals (Phoca spp.), Steller sea lions (Eumetopias jubatus), baleen whales (Balaenoptera spp. and Megaptera sp.), toothed whales (Physeter sp. and Delphinapterus sp.), and porpoises (Phocoena sp. and Phocoenoides sp.) (Lowry and Frost 1981; Frost and Lowry 1981; Harry and Hartley 1981). These predators also consume zooplankton, herring, smelt, capelin, cod, squid, and some benthic invertebrates. Whales, fur seals, and sea lions migrate in open water and do not penetrate beneath the ice; harbor and ribbon seals and beluga whales reside at the ice edge, which they follow as it seasonally advances and retreats (Fay 1974). Of these species the most important pollock predators are believed to be sea lions, fin whales (Kajimura and Fowler 1984), and seals (Hood and Calder 1981; Harry and Hartley 1981; Ashwell-Erickson and Elsner 1981). Annual pollock consumption of these species together may equal that of fur seals.

Juvenile pollock also suffer significant predation from seabirds, estimated at 300,000 metric tons annually (Hunt et al. 1981a). The principal seabird predators are murre (Uria spp.) and kittiwakes (Rissa spp.), and of secondary importance, northern fulmars (Fulmaris sp.) and puffins (Lunda and Fratercula spp.) (Kajimura and Fowler 1984; Hunt et al. 1981a, b). Kittiwakes are surface feeders that take prey only in the upper 0.5 m, while murre dive to feed down to 125 m. All species take pollock in the 2-20 cm size range (age 0-1), and also feed on other small fishes and zooplankton. On broad scales and under mean conditions the standing stocks and consumption of seabirds appears to correlate with prey density. Murre and kittiwakes nest in coastal and island colonies in summer and fall but range widely over the shelf in spring (Hunt et al. 1981c). These species are most abundant over the middle and outer shelf, and mostly avoid the coastal domain and oceanic waters due to low prey populations (Hunt et al. 1981b). Schneider and Hunt (1982) and Woodby (1984) observed higher seabird populations in the outer shelf domain than in the middle shelf domain. There is uncertainty, however, about the correlation of seabirds and prey on smaller spatial scales. Schneider and Hunt (1982) observed little difference between domains in consumption by subsurface-feeding murre, but consumption by surface feeders

(kittiwakes and fulmars) was three times greater on the outer shelf. Woodby (1984), however, noted that murrens were more abundant on the outer shelf. Kinder et al. (1983) observed that murrens concentrated near frontal zones surrounding the Pribilof Islands, probably due to higher prey abundance, but Woodby (1984) could find no correlation of seabird and prey densities at such scales.

Most of the species mentioned above also may act as competitors with pollock for common prey. Other small or juvenile fishes (Smith et al. 1984), baleen whales, and especially seabirds prey on zooplankton in common with juvenile and adult pollock. Especially significant among these are shearwaters (*Puffinus* spp.), migratory surface-feeding seabirds as abundant as murrens (Hunt et al. 1981a, b). Predators on juvenile pollock potentially compete with cannibalistic adult pollock. Laevastu and Favorite (1978) used simulation modeling to infer that competitive interactions could partially explain the increase in pollock stocks during the early 1970's as herring stocks declined (Hood and Kelley 1974; Wespestad 1981). All of these relationships are likely to be complex interactions of competition and predation between different age classes, however, and very few data are available with which to examine their possible implications (Smith et al. 1984; Kajimura and Fowler 1984).

The carbon budgets constructed for the eastern Bering Sea shelf from currently available data do not balance well, and sometimes conflict. Walsh (1983) calculated that zooplankton may consume 25-50% of primary production on the outer shelf and 10-25% on the middle shelf. An additional 15-25% may be consumed by benthic organisms. Thus in the middle shelf domain about half of carbon fixed by phytoplankton would go to supporting fish or their prey. However, Walsh estimated that 50% of annual primary production may not be consumed by either the pelagic or benthic food web, and may be exported to slope sediments. According to his analysis (see also Table 2), consumption by pollock ($40 \text{ g carbon m}^{-2} \text{ yr}^{-1}$) would be the equivalent of about 20% of annual primary production, and yield about 5 metric tons km^{-2} ($0.4 \text{ g carbon m}^{-2} \text{ yr}^{-1}$) of fish catch, similar to values in the North Atlantic (Walsh et al. 1981; Coachman and Walsh 1981). However, according to earlier calculations of Smith (1981), pollock consume carbon equivalent to 2-4% of observed primary production. Both of these estimates require very high values of transfer efficiency and would severely limit the fraction of primary production available to other species known to have high standing stocks. Schneider and Hunt (1982) estimated the flux of carbon to seabirds at $0.05 \text{ g m}^{-2} \text{ yr}^{-1}$, or 0.03-0.05% of primary production. Other authors have estimated fluxes to seabirds three (Hunt et al. 1981a) to five (Favorite et al. 1977) times larger. Using such data, Hood and Calder (1981) estimated that pollock, infaunal benthos, epifaunal benthos, and commercial fisheries each seem to require over 100% of primary production, when transfer efficiency is considered. These discrepancies suggest that food requirements of pollock could be overestimated or may further support the speculation (Section 2.2) that some phytoplankton might have been overlooked in existing studies.

2.3.3 Fishery

The pollock fishery in the eastern Bering Sea began in the early 1960's when Japanese began retargeting their trawling effort after yield of yellowfin sole declined (Low 1974), and yield of pollock increased steadily until the 1970's. Strong pollock year-classes are believed to have been generated in 1964-67 and 1970 (poor year classes are thought to have occurred in 1957-60). Pollock has dominated the Japanese groundfish yield since, contributing over 80% of the catch during the 1970's. Trawl catch per effort (CPUE) increased from 1.94 to 5.99 metric tons hr^{-1} during the period 1964-1971 (Figure 19). This increase may or may not indicate an actual increase in pollock biomass. By correcting for retargeting on pollock and for unrecorded discards of incidental pollock catch, Low (1974) estimated that trawlable pollock biomass remained constant at about 5 million metric tons (mt) during this period. However, Wespestad and Terry (1984) considered the apparent increase in

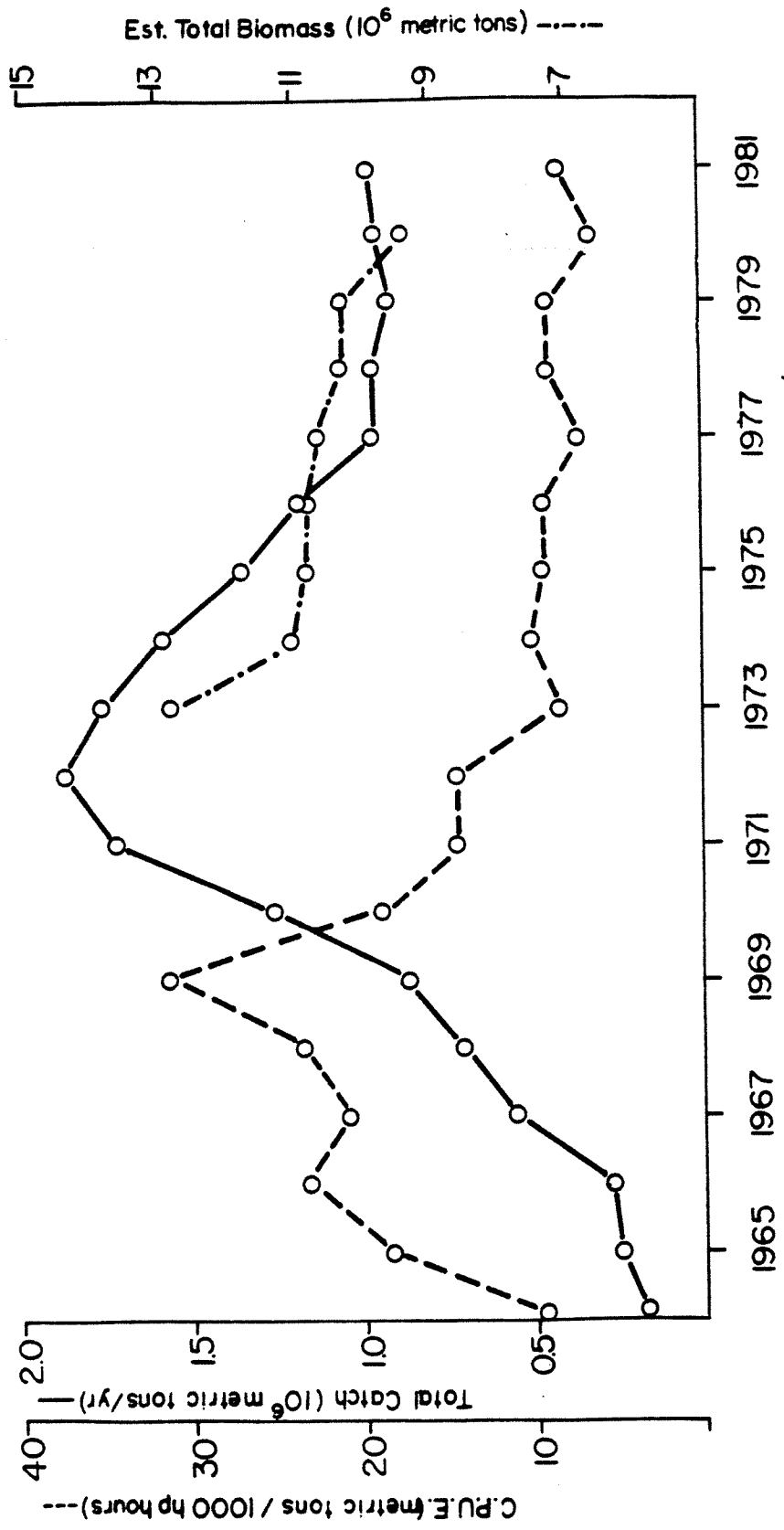


Figure 19. Pollock abundance trends in the eastern Bering Sea (total catch, catch per effort, and estimated total biomass, after Bakkala and Westestad 1983; and Berger 1983).

standing stock to be real.

Pollock yield peaked at over 2 million mt in 1971-73 (Figure 19), and indication of overfishing began to appear. Catch per effort began dropping in 1969, and at the same time the age distribution of the catch shifted from mainly 4-year olds (greater than 40 cm long) to mainly 2-3 year olds (less than 40 cm), where it has remained since (Smith 1981). Salvesson and Alton (1976) suggested that adult growth rates may have increased during the early 1970's, as a result of lower population density. On the basis of simulation modeling, Laevastu and Marasco (1982, 1983) suggested that the increase in the relative proportion of juveniles in the pollock population age structure indicated a reduction in cannibalism associated with overfishing. Swartzman and Haar (1983) noted that fur seals consumed a higher proportion of juvenile pollock during the early 1970's, possibly related to decreased cannibalism. These observations prompted speculation that intensive fishing of adults actually might increase fishery yield by reducing cannibalism. If true, this paradoxical property of the pollock fishery nevertheless ultimately would be limited by reduction in the reproductive potential of the adult population. Since there is a low incidence of sexual maturity in the 2-3 year old fish that now compose a significant fraction of the population, overfishing of adults combined with a failure of 1 or 2 year classes of juveniles could cause disastrous drops in reproductive potential (Smith et al. 1976). Furthermore, newer data on cannibalism (Dwyer 1984), migration patterns (Francis and Bailey 1983), and year-class strengths (Bakkala and Traynor 1984) complicate and cast doubt on the simplistic picture.

Upon initiation of the U.S. Fishery Management Conservation Zone in 1976, catches were restricted to the neighborhood of 1 million mt (Bakkala et al. 1981). Catch per effort has stabilized since 1975, suggesting that this catch is close to equilibrium yield (Bakkala and Traynor 1984). Thus 1971-73 catches may have exceeded equilibrium yield by a factor of two, and resulted in overfishing. However, Wespestad and Terry (1984) projected an equilibrium yield of 2.0 to 2.6 million mt. These analyses are currently under re-evaluation because of changes in the estimated biomass of pollock in the eastern Bering Sea. Total biomass of eastern Bering Sea pollock estimated by bottom trawling has varied widely from 0.6 to 8 million mt, probably due to variability of both sampling and abundance (Bakkala et al. 1981). Trawlable biomass estimates between 1963 and 1978 indicated a variability of 50% about the long-term mean (Smith 1981). The variability of pollock abundance and year-class strength appears to be much lower than that of other species (Francis and Bailey 1983; Wespestad and Terry 1984). Recent acoustic surveys have attempted to assess the sizes of midwater populations over both the shelf and the basin, which are undersampled by research trawls (Bakkala and Alton 1983; Traynor 1984). The addition of these pelagic stocks to previous trawl biomass assessments has brought present and hindcasted estimates of total pollock biomass in the eastern Bering Sea to the neighborhood of 10 million mt (Figure 19).

The present biomass of pollock in the eastern Bering Sea is estimated at about 8 million mt, down from an estimated peak of 11 million in 1979 (Bakkala and Traynor 1984). This decline is attributed to a succession of poor year-classes in 1979-81, and the decline is projected to continue as a result. Abundance should begin to increase again with recruitment of the stronger 1982 year-class. An additional pollock stock with an estimated biomass of 1 million mt and an equilibrium yield of $100,000 \text{ mt yr}^{-1}$ is present in the Aleutian Island region.

2.3.4 Temperature and Climate Relationships

Egg, Larval, and Juvenile Stages. The development times of eggs, larvae, and juveniles depend in part on temperature. Egg hatching times in the laboratory range from over 30 days at 0°C to 12 days at 10°C (Nakatani and Maeda 1984), with highest survival at 2°C (Hamai et al. 1971). Paul (1983), however, observed a greater incidence of successful first-feeding of larvae at 5.5°C than at 3°C . Larvae reared at

the higher temperature required more food. Similar observations have not been made in the field, however. Field evidence for temperature effects on larvae also is fragmentary. Larval growth rates inferred by Walline (1983) were significantly lower in colder water north of the Pribilof Islands in 1978-1979, and were not correlated with food availability (but could have arisen from genetic differences). Length-at-age of larvae was greater in 1977 than in 1976, a record cold year (Waldron and Vinter 1978), although no temperature-related spatial differences were observed within either year. However length-at-age was greater in more southerly juveniles in 1975-76 (Bakkala and Smith 1978). These disparities may be indirectly related to temperature by genetic differences, but are not thought to be related to food supplies (see below). Furthermore, Walline's (1983) data indicate little geographic difference in mean date of hatching, and no correlation of inferred growth rates with apparent hatch dates.

Incze et al. (1984) speculated that observed differences in egg size (smaller in shallower water) could affect survival rates of larvae at different temperatures. Larger eggs have more yolk and are associated with longer development times and larger larvae. Larger size might be advantageous at low temperatures or food abundances, by affording larvae greater food reserves and more time in which to acquire feeding skills. Smaller size might be advantageous at higher temperatures or greater of predation pressure, by allowing eggs and larvae to complete their most vulnerable life cycle stages more quickly. These hypothetical advantages could be applied to either spatial or interannual differences in larval survival and growth.

The movements of eggs and larvae with permanent and temporary wind-induced water motions may affect growth and survival. Walsh et al. (1981) used a simple current model to demonstrate that eggs hatching on different dates would encounter different mean wind regimes, and therefore would be transported in different directions. Egg survival in the model was dependent on the food supplies for eggs transported onto the shelf versus into the Aleutian Basin. According to Walsh et al. (1981), warm events with southwesterly winds would be most favorable for larval survival. However, Cooney et al. (1979) observed that survival of first-feeding larvae might be highest during water column stabilization events between the passage of storms. Such events are infrequent in April and May and are associated with high pressure and northerly winds. Cooney et al. (1979) theorized that stabilization would permit vertical aggregation of zooplankton prey and thus foster improved feeding conditions. There has been no verification of either of these hypotheses.

Juvenile pollock have a hypothetical temperature tolerance range of about 0° to 10°C (Lynde 1984). The upper and lower limits are inferred from the presence of juveniles in the surface layer of the middle shelf domain during summer, and their likely presence under shelf ice in winter. Walline (1983) found no correlation of temperature with inferred juvenile growth rates. Temperature effects on adults (see below) are speculated to have significant consequences for the distribution and survival of juveniles.

Adult Stage and Spawning. The potential effects of temperature on mature pollock has been reviewed by Lynde (1984). The principal effects appear to be regulation of the extent and timing of migration over the shelf during spring and summer. Adult pollock in the eastern Bering Sea are observed predominantly within the temperature range of 1.5-7.5°C, with an inferred optimum of about 3°. A large body of survey and catch data indicates that the onshore extent of the summer adult migration pattern is governed by temperature, with pollock remaining in deeper water farther offshore in cold years compared to warm years (Figure 20; Bakkala and Alton 1983). Adult pollock are hypothesized to remain mostly seaward of the 3°C bottom temperature isotherm. During spring the onshore movements of adult pollock would therefore be obstructed by the cold bottom water in the middle shelf domain, and would remain on the slope and outer shelf until this water warmed sufficiently. It appears that spawning occurs later north of the Pribilof Islands, in accord with the

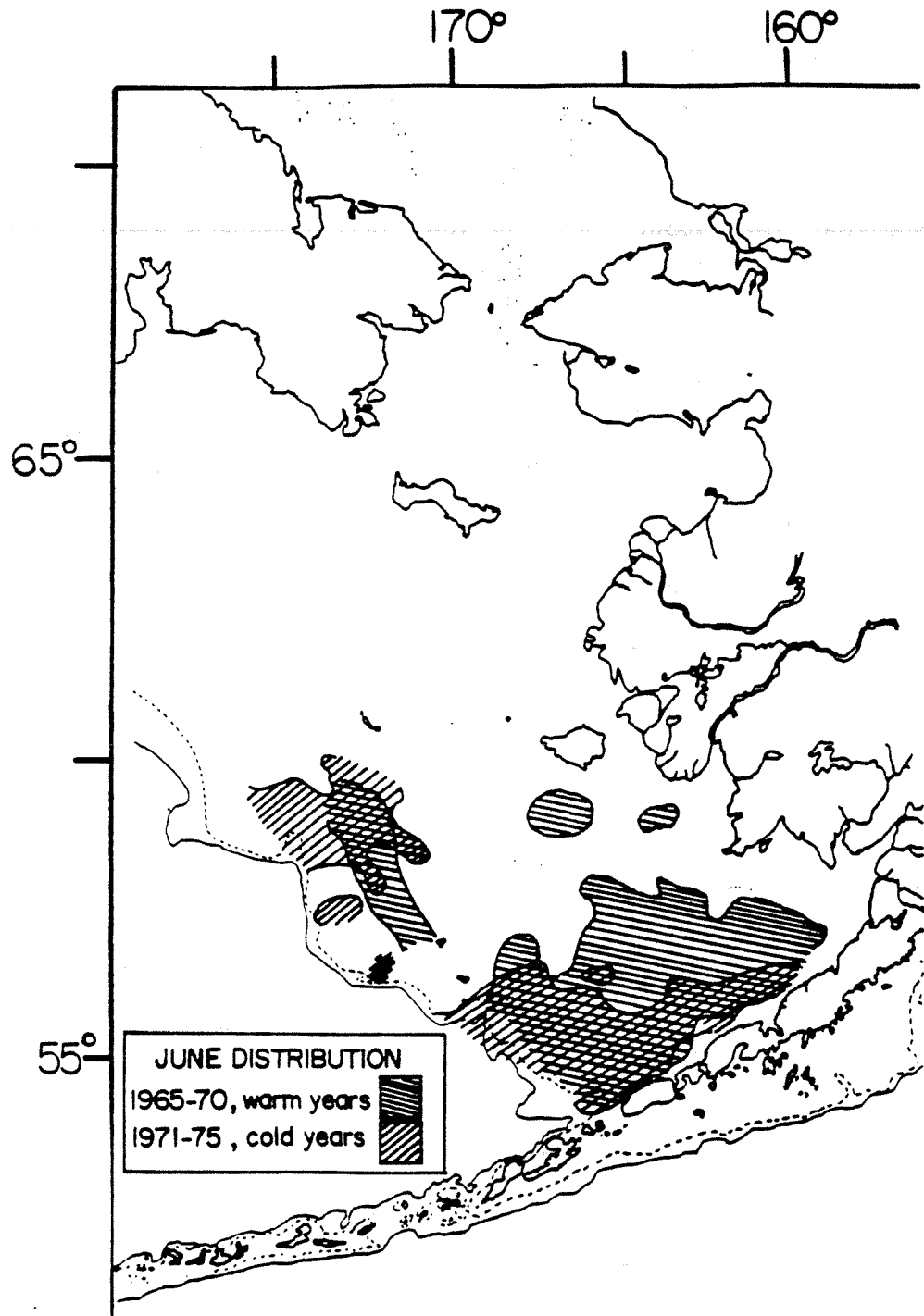


Figure 20. Distribution of pollock standing stocks in the eastern Bering Sea during warm and cold Junes (after Smith et al. 1976).

colder temperatures in that region. In a year such as 1976, in which bottom temperatures in the middle shelf remained anomalously low following a winter of record ice cover, pollock catch was low and was shifted into deeper water, and adults may have been excluded from the middle shelf domain all year (Bakkala and Smith 1978). In such years catch rates on the outer shelf might be expected to rise. Temperature may also be involved in the apparent northward shift of catch in summer. Similarly, the offshore migration of adults in the fall toward the slope and outer shelf, where bottom temperatures remain at 3°C all year, may be triggered by cooling of shallower water.

Other species also show the effects of distribution and interannual variability of temperature. Only about 17% of the total benthic standing stock on the eastern Bering Sea shelf is believed accessible to predation by commercial groundfish (Stoker 1981; Feder and Jewett 1981). The remainder inhabits northerly regions from which crab, mammal and demersal fish predators apparently are excluded by low bottom temperatures, a conclusion that is supported by data showing higher survivorship and greater seasonal biomass increases among northern shelf benthos (Alton 1974). Distributions and migrations of predatory flatfishes seem to be unaffected by interannual temperature variations, however (Smith et al. 1976; Bakkala 1981).

The distribution of pollock spawning also appears to be influenced by temperature effects on adult migration. Few eggs are found in the surface layer above regions where bottom temperatures are outside the range of 1.6° to 3°C (Nishiyama and Haryu 1981). Thus the initial distribution of eggs and larvae would be further offshore in colder springs. Francis and Bailey (1983) hypothesized that eggs and larvae would be transported northward in cold years (such as 1972-73) after being spawned over the slope and outer shelf where there are weak alongshelf currents, and subsequently would recruit to the adult population north of the Pribilof Islands. In contrast, in warmer years (such as 1977-78) larvae spawned early in the season would be transported northward, while those spawned later would remain in the southeastern middle shelf domain. This hypothesis was supported by data showing that catch rates declined south of the Pribilof Islands and increased north of the Pribilofs in the years following the cold period of 1972-1976. Validation of this hypothesis depends on resolving questions surrounding stock separations, adult migration patterns, and interannual variability of larval and juvenile distributions.

From the data available on the relative distributions of immature and mature pollock in the eastern Bering Sea, it is possible to construct hypothetical scenarios of the effects of spatial and temporal temperature variability on the possible incidence of cannibalism (Lynde 1984; Dwyer 1984). It is likely, for instance, that horizontal segregation between adults on the outer shelf and slope, and juveniles in colder water on the middle shelf in winter and spring, constrains the magnitude of cannibalism during those seasons. Vertical segregation between 0-age juveniles near the surface and adults near the bottom in stratified waters in summer also may reduce cannibalism (Francis and Bailey 1983). Interannual differences in cannibalism could depend on two-year couples of temperatures (Lynde 1984): e.g., if a warm spring preceded a cold spring, a year-class of age 1 juveniles that had been spawned on the middle shelf might be spared from cannibalism by the restriction of adults to the outer shelf. Likewise, juveniles on the northern shelf could experience less cannibalism in all years. Further field surveys are required to verify such hypotheses.

No simple relationship can be seen between interannual variations in temperature and pollock recruitment in the eastern Bering Sea. Previously it had been hypothesized that larval survival might be low in cold years and high in warm years, because strong year-classes were produced in the warm years from 1965-68, and weaker year-classes in the cold years of the early 1970's (Smith et al. 1976). Pollock also produced strong year-classes in the warm years 1977 and 1978 (Bakkala and Weststad 1983). However, stronger pollock year-classes were produced in the cold years 1972, 1973, and 1976 (Smith 1981), and weak year-classes were produced in the warm years 1979, 1980, and 1981 (Bakkala and Traynor 1984). The interannual

variability in mortality due to cannibalism and predation hypothesized above may account for part of this complexity. The cold year of 1976 caused reproductive difficulties among seabirds preying on larval and juvenile pollock, including kittiwakes, northern fulmars, and glaucous gulls (Larus hyperboreus), both near the shelf break in the eastern Bering Sea (Hunt et al. 1981b), and in the Chukchi Sea (Springer et al. 1984). Storminess patterns, associated with warming (see Section 2.1) also may affect the feeding and predation mortality of pollock (e.g. Cooney et al. 1979) and other predators. Poor survival of Tanner crab (Chionoecetes spp.) larvae (Incze 1983) and kittiwakes (Lynde 1984) in 1980 have been attributed to storm-induced turbulence that hampered feeding. Despite greater mean abundance of their juvenile pollock prey in waters of the southern Bering Sea, reproductive success of black-legged kittiwakes (R. tridactyla) is consistently lower than in northern waters, due to greater storminess (Hunt et al. 1981b). Surface-feeding birds (such as kittiwakes, shearwaters, and fulmars) are certainly sensitive to storminess, but Woodby (1984) suggested that diving murrens also are vulnerable.

3.0 THE GULF OF ALASKA

3.1 PHYSICAL OCEANOGRAPHY

The Gulf of Alaska is defined as waters roughly circumscribed by the Alaskan coast from British Columbia to the western end of the Alaska Peninsula at Unimak Pass, north of about 54°N . (Figure 3). The Gulf may be separated into an oceanic domain and several coastal domains: 1) the coast of southeast Alaska, with a narrow shelf and a highly indented and sheltered shoreline; 2) the open coast from Cross Sound to Kayak Island with a narrow (70-90 km) shelf; 3) the wider (240 km) shelf from Cordova to the Shumagin Islands, with major embayments including Prince William Sound (depth exceeding 700 m) and Cook Inlet, and the major complex of Kodiak and Afognak Islands; and 4) the narrower shelf south of the Alaska Peninsula that tapers westward beyond the Gulf along the Aleutian chain. Shoreward of Kodiak Island on the central shelf is Shelikof Strait, a 300 meter deep submerged valley enclosed by sills of depths about 200 m, and seaward of the Island are shallow (50 m) banks separated by troughs of 100 m depth. Total shelf area is $15,500 \text{ km}^2$, and shelf break depth ranges from 150-160 m off Kodiak to 120-130 m off Unimak Island (Arctic Environmental Information and Data Center [AEIDC] 1974). Winter ice cover in the Gulf is restricted to the more enclosed and fresher nearshore waters of Cook Inlet and Kodiak Island bays. Interannual variability in ice extent is governed by air temperature, freshwater input, and heat transport by coastal currents (Poole and Hufford 1982).

3.1.1 Oceanic Domain

The oceanic circulation pattern of the Gulf of Alaska is characterized by a cyclonic (counterclockwise) gyre centered at about 55°N and 140°W , believed to be driven by the winds in the North Pacific (Aleutian) low pressure system (Ingraham et al. 1976; Figures 4 and 8). Water enters the gyre from the south via the Subarctic Pacific current, which is fed a varying mixture of western Pacific waters from the Kuroshio and Oyashio currents, together with a certain amount of recirculated gyre water, possibly from the neighborhood of 165°W (Favorite et al. 1976; Tabata 1975). On encountering the continental shelf off the North American coast, the Subarctic Pacific current is believed to be diverted northward to form the Alaska Current. The current is further constrained by the Alaskan shelf, and is known as the Alaskan Stream as it flows westward past Kodiak Island and along the Alaska Peninsula and Aleutian Islands.

The gross current structure of the gyre appears consistent with a long-term hydrographic adjustment to the presence of the Aleutian Low over the gyre center in winter (Ingraham et al. 1976; Schumacher and Reed 1983). The Low actually is an atmospheric pressure trough that forms a trajectory for eastbound cyclones of high wind velocity (mean 25 kt or 13 m sec^{-1}) and 5 to 7 day duration (the dominant time scale in the energy spectrum) between November and February. This pattern produces mean winds roughly paralleling the coast in the northeastern Gulf (Livingstone and Royer 1980). During summer the Aleutian Low shifts northwestward into the southern Bering Sea (Figure 8) and prevailing winds in the Gulf are weaker and more southwesterly. Formerly this shift was believed to seasonally reduce mass transport in the gyre, but recent evidence suggests that only surface layers

are affected and that total mass transport is relatively constant (Reed et al. 1980).

At the center of the gyre is a belt of surface water divergence underlying the mean position of the Aleutian Low, at latitudes of 50-55° N in winter and 55-60° N in summer (Favorite et al. 1976), with maximum intensity in winter. The gyre induces a net outward Ekman transport that produces surface convergence along most of the Alaskan coast during most of the year. Weak coastal surface divergence is inferred south of the Aleutians and Alaska Peninsula during summer from the large-scale pattern of southwesterly winds parallel to the coast (Figures 8 and 21). However, Livingstone and Royer (1980) found significant differences between these predicted winds and observed winds offshore, and coastal winds can be even more anomalous due to topographic effects.

At the gyre center, divergence produces gradual upwelling and an upward and northward transport of deep old Pacific Intermediate water high in salinity and nutrients and low in dissolved oxygen, generating a hydrographic structure called the Ridge Domain (Favorite et al. 1977). Surface waters in the northern Gulf are relatively fresh due to runoff from the continent, and Tully and Barber (1960) have compared the entire Gulf system to an estuary, with deep landward flow and surface seaward flow. There is a permanent halocline at a depth of 100-200 m (roughly the depth of the shelf break). A seasonal summer halocline is present at about 50 m, although it may be disrupted by mixing over the shelf. Summer surface temperatures in oceanic waters typically reach 13-14°C (Tabata 1965, Royer 1976). In winter water is commonly isothermal at 3-4°C to a depth of 75-100 m due to mixing and convective overturn. A temperature maximum of 5°C at about 300 m in winter is stable due to its higher salinity (Favorite et al. 1977).

The Alaska Current is broad, with speeds of 10-30 cm sec⁻¹ in the northeastern Gulf (Royer 1975; Schumacher and Reed 1983). Weak (5 cm sec⁻¹) currents at the shelf break appear to be driven by the Alaska Current (Hayes 1979). Seasonal fluctuations in current speed are small, but low-frequency (2-10 day) variability and reversals are common and of greater intensity in winter (Lagerloef et al. 1981). This variability is poorly coupled to wind forcing, and has been attributed to the passage of eddies and meanders of scales from 100 to 300 km. Hydrographic structures consistent with this interpretation have been described by Royer and Muench (1977), Royer et al. (1979), Ingraham (1979), and Reed (1980). Tabata (1982) described a large-scale persistent eddy offshore from Sitka with speeds significantly higher than those of the mean Alaska Current. Willmot and Mysak (1980) and Tabata (1982) have hypothesized that such eddies may be generated by the interaction of atmospherically-generated planetary waves with bathymetry.

The dominant oceanic current of the northern and western Gulf is the Alaska Stream (Reed 1984). Current speeds reach 100 cm sec⁻¹ over the shelf break near Kodiak Island, and most transport is confined within 60 km of the shelf (Royer 1981a; Niebauer et al. 1981b). The Stream extends deep into the water column over the slope, with maximum surface current speeds of over 100 cm sec⁻¹. The intensification of the Stream in comparison to the broader and more diffuse Alaska Current has been attributed to the constraining influence of the coast and shelf of the western Gulf. A decrease in Stream speeds and transport in summer might be inferred from the weakening of the Aleutian Low and its associated changes in wind speed and direction, but there are differing interpretations of current meter data. Royer (1981a)

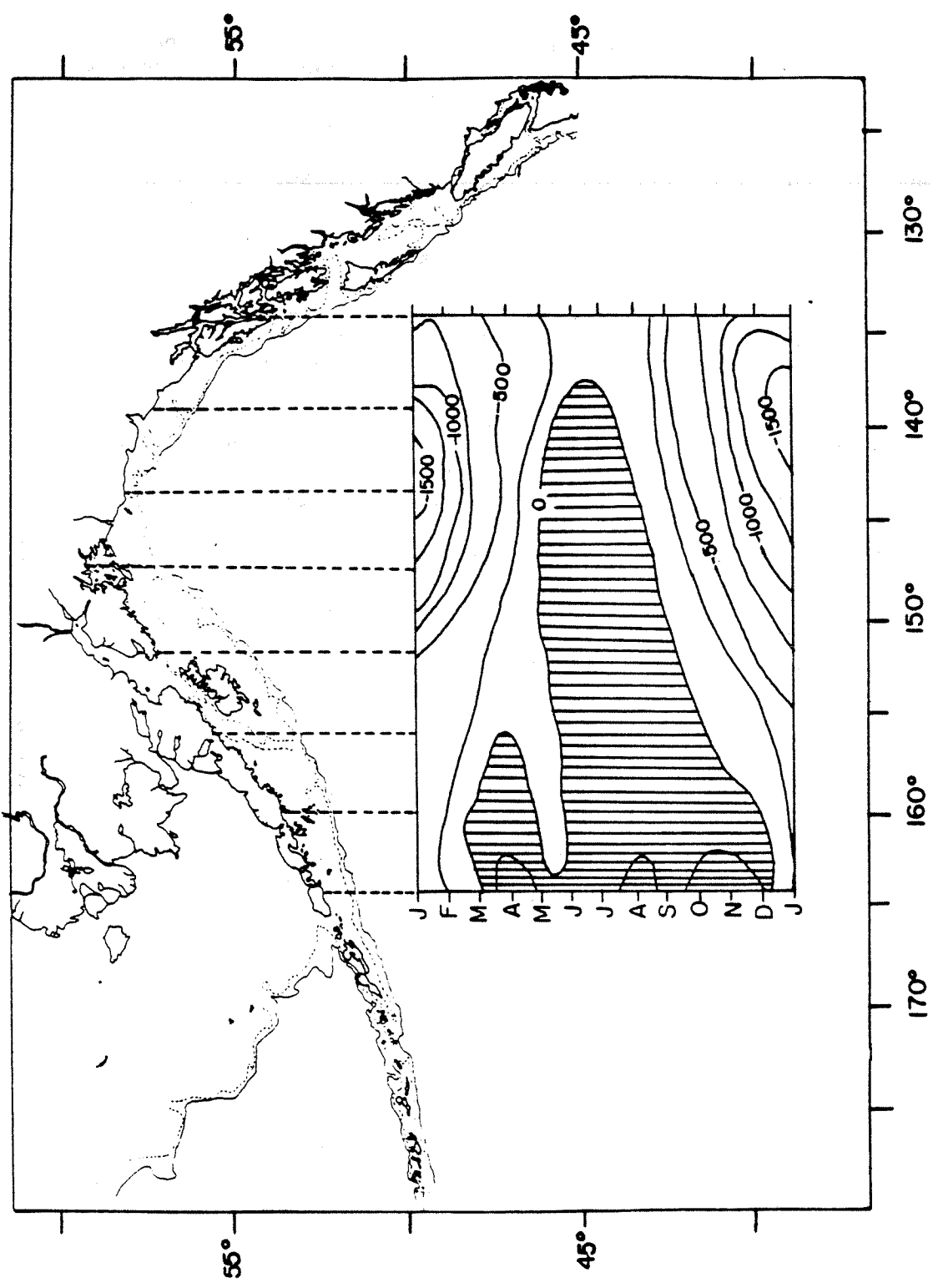


Figure 21. Monthly distribution of coastal upwelling and downwelling ($m \text{ sec}^{-1} \text{ km}^{-1}$ of coast) in the Gulf of Alaska. Positive values (shaded) denote upwelling (after Ingraham et al. 1976).

concluded that transport is greatest in spring, probably due to forcing by winds and coastal freshwater input. However, Reed et al. (1980) and Reed (1984) concluded that no consistent seasonal signal can be demonstrated, although there may be fluctuations in wind-driven currents in the surface layer. Low-frequency (2-10 day and interannual) variability in the speed and direction of the Stream, including periods of weak flow (Schumacher and Reed 1983) and surface shelf break reversals, have been attributed by Reed et al. (1981) to the passage of eddies and meanders. Anticyclonic eddies of the scale of tens to a hundred kilometers have been observed in the Stream by Royer and Muench (1977), Reed et al. (1980), and Niebauer et al. (1981b). Schumacher and Reed (1983) and Reed (1984) also suggested possible splitting of the Alaska Current and large-scale atmospheric and planetary wave patterns as possible mechanisms for interannual fluctuations in the Alaska Stream.

Favorite et al. (1976) traced the Alaska Stream along the Alaska Peninsula and Aleutian Islands as far west as 165°E . The Stream was described as compressed into a narrow band 18 to 55 km offshore with highest velocities in summer; in winter the velocities in the Stream were said to decrease to about 10 cm sec^{-1} and to disperse 100 to 300 km offshore. At that time eastward countercurrents and sharp fronts were observed inshore of the Stream associated with the boundaries between Pacific and Bering Sea water masses. Favorite et al. (1976) inferred a divergence of the Stream in the vicinity of Unimak Pass (165°W), with roughly 40% of its volume recirculated eastward back into the gyre. Another 40% of the Stream volume was judged to enter the Bering Sea at 170°E . However, Schumacher et al. (1982) determined that transport through Unimak Pass into the Bering Sea is derived from coastal sources, rather than from the Alaska Stream. Reed (1980) and Wright (1981) have confirmed the recirculation pattern at 175°W to 180° .

3.1.2 Alaska Coastal Current

Over most of the northern Gulf of Alaska shelf there is significant flow close to the coast distinct from the Alaska Current and Stream, but the magnitude of the current and its causes appear to vary. In the northeastern Gulf coastal zone, current speeds are greater than those at the shelf break, and appear to be regulated by different processes, primarily winds (Hayes 1979; Lagerloef et al. 1981). Lagerloef et al. (1981) and Hayes (1979) observed mean alongshore currents at all depths over the shelf off Yakutat and Icy Bay, with a weak seasonal signal (average speeds of 12 cm sec^{-1} in summer and 20 cm sec^{-1} in winter). The primary seasonal fluctuation was observed in current variance, which was high all year but much greater in winter. The winter increase was associated with wind intensification. Reed et al. (1981) and Royer (1981b) concluded that freshwater input and seasonal warming had only a limited effect on the coastal current in this region, and Reed and Schumacher (1980) linked seasonal variations in the current to winds. However, Hayes (1979) and Lagerloef et al. (1981) presented current meter evidence of aperiodic current fluctuations that occur at all times of year, at time scales from roughly weekly to interannual. This variability was decoupled from fluctuations in the local wind field and of greater relative importance in summer when wind forcing is weaker (Hayes and Schumacher 1976). The fluctuations commonly took the form of rotations and reversals that suggested transient eddies. The greatest fluctuations were observed at the shelf break, however it was not clear whether eddies over the shelf

might have been propagated from those observed at the shelf break. The presence of such eddies and the associated current speeds have been confirmed using drogues and drifters and satellite photos (Royer et al. 1979; Feely et al. 1979). Muench et al. (1981) observed an eddy off Icy Bay that they linked to steering of currents by an offshore submarine canyon.

The westward coastal current pattern is altered beginning in the vicinity of Prince William Sound. Persistent eddies are observed associated with Kayak Island (Royer and Muench 1977; Royer et al. 1979, Feely et al. 1979). Freshwater input also appears to increase west of Yakutat (Royer 1979), generating a low-salinity coastal current that is driven more by salinity gradients and freshwater forcing than by winds (Livingstone and Royer 1980; Royer 1981b, 1982) or by energy propagated from the Alaska Current. Royer (1981b, 1982) described the coastal current off the Kenai Peninsula as a narrow (less than 25 km), high-velocity (greater than 10 cm sec^{-1}) jet based on geostrophic calculations. The maximum speed and transport were observed in autumn and the minimum in early summer, in phase with the seasonal pattern of freshwater input, and out of phase with the seasonal wind maximum in winter. The major effect of wind is hypothesized to be in confining the current to a narrow jet rather than a broad current with an offshore component but similar mass transport (Royer 1983a, b; Schumacher and Reed 1980).

Schumacher and Reed (1980) gave the name Kenai Current to the segment of the coastal current that continues westward, passing over sills that partially disrupt its vertical stratification, crossing the mouth of Cook Inlet (Muench et al. 1978) and turning southwestward through Shelikof Strait. Their findings reinforced those of Royer: the current was restricted to the western coast of the Strait and marked by a salinity minimum, with surface speeds ranging from 100 cm sec^{-1} in winter to $20\text{-}30 \text{ cm sec}^{-1}$ in early summer, and both seasonal and interannual fluctuations correlated primarily with freshwater input and secondarily with winds. Mysak et al. (1981) observed mean surface currents ranging from a maximum of 50 cm sec^{-1} in autumn to 10 cm sec^{-1} in early summer, with a decrease deeper in the water. Part of the transport in the Strait is contributed by low-salinity transport along western Cook Inlet (Poole and Hufford 1982) that can reach 50 cm sec^{-1} (Muench et al. 1978). The resulting winter residence time of surface water behind Afognak and Kodiak Islands was approximately ten days (Schumacher et al. 1978). Little is known about the Kenai Current west of Shelikof Strait, but a weaker ($5\text{-}12 \text{ cm sec}^{-1}$) extension of it has been traced to Unimak Pass and into the Bering Sea (Schumacher et al. 1982).

The general pattern of seasonal and low-frequency fluctuations in currents and mass transport in Shelikof Strait is not believed to be directly driven by local meteorology (Schumacher and Reed 1980). Mysak et al. (1981) described quasi-periodic 3-6 day fluctuations in currents in the Strait that they attributed to wave-like baroclinic instabilities that propagated downstream at $20\text{-}30 \text{ km}^{-1}/\text{day}$ and were independent of winds. However, winds may be important for generation of current fluctuations in the upper few meters of the water column. Two to seven day reversals in surface currents are observed frequently in the summer (Schumacher and Reed 1980; Poole and Hufford 1982), associated with a shifting of large-scale monthly mean wind patterns from northeasterly to southwesterly (Ingraham et al. 1976). Analysis of empirical data by Muench et al. (1980) indicates that due to topographic steering, local winds predominantly follow the long axis of the Strait, and are mostly from the northeast in winter and from the

southwest in summer; on an annual basis winds blow up the Strait 60% of the time (Figure 22). These winds might be expected to offset the effects of freshwater forcing close to the surface. Schleuter and Rauw (1981) used the analysis of Muench et al. (1980) to develop scenarios for the transport of spilled oil in Cook Inlet and Shelikof Strait. They concluded that because of the tidal null, winds (which blow from the south 72% of the time during this period) dominate surface transport in Shelikof Strait in summer (April to September) when the Kenai Current is at its annual minimum strength. They projected that trajectories of oil (and therefore by implication surface water) in the Strait would be mostly northeastward during summer.

A greater residence time of surface water in the Strait during the summer also can be inferred from the seasonal pattern of surface currents. The residence time of water in Shelikof Strait is further governed by tidal currents, which are weaker in the center of the Strait than at its entrances. Muench et al. (1980) analyzed tidal currents and amplitudes in the neighborhood of Kodiak Island and determined that although there was strong tidal action over the shoals to the northeast and southwest of the island, with mean maximum tidal excursions of 12-20 km, tidal excursions in Shelikof Strait were only 1.5-8 km due to the baffling effect of the Island (Figure 22). Tides intrude into Shelikof Strait around both ends of Kodiak Island, and form a standing wave (antinode) at its center. Tidal ranges and currents are smallest during March and September, and greatest during June and December (Harris 1981). Thus due to the shelter of Kodiak Island and the reversal of winds, Shelikof Strait (especially at the surface during spring and summer) appears to be a location of relative shelter from the rapid transport of shelf water by tides and the Kenai Current.

Significant cross-shelf transport in the surface and bottom layers over the northern Gulf shelf is associated with the large- and small-scale seasonal pattern of winds and currents. In the northeastern Gulf, coastal downwelling is inferred throughout the year from large-scale mean winds, with a weakening in summer (Hayes and Schumacher 1976; Ingraham et al. 1976), but local winds may correspond poorly with large-scale predictions (Livingstone and Royer 1980). Hayes (1979) observed significant onshore flow at all depths at the shelf break, but suggested that this flow was decoupled from coastal processes. Feely et al. (1979) inferred downwelling in early spring from surface onshore transport and near-bottom offshore transport, and associated this pattern with cooling of nearshore and subsequent bottom waters on the shelf. However, Royer et al. (1979) observed consistent subsurface onshore flow during summer that was attributed to entrainment by surface offshore flow, which implied coastal upwelling. In the central Gulf, Royer (1975) observed that bottom water salinities on the shelf increased during summer as surface salinities decreased, and that renewal of deep water in fjords also occurred at this time. Favorite and Ingraham (1977) observed generally onshore and westward movement of bottom water off Kodiak in winter. Shelikof Strait also exhibits two-layer circulation. In response to the surface current, deep higher-salinity offshore water intrudes along the bottom of the Strait, entering over the sill at the southern mouth of the Strait. Thus the Strait resembles a large estuarine system, with maximum stratification at its southern end (Mysak et al. 1981). Schumacher and Reed (1980, 1983) described increased winter bottom salinities in the Strait and in Amatuli Trough, which they attributed to increased entrainment of deep water from the slope during the seasonal maximum of the Kenai Current. Thus it appears that onshore entrainment of

offshore bottom water may occur throughout the year on the central Gulf shelf, driven by upwelling in summer and by the Kenai Current in winter.

3.1.3 Kodiak Shelf

The hydrographic and current structures of the waters on the outer continental shelf off the Kenai Peninsula and Kodiak Island differ from those of the adjacent coastal and Alaska Stream domains, and are significantly affected by shelf bathymetry. The shelf is indented with several troughs that communicate with continental slope water and separate shallow Portlock and Albatross Banks (Figure 22). Although their proximity to the coast makes these waters fresher than those offshore, they are not as stratified as Kenai Current or Alaska Stream waters. Surface temperatures on the inner shelf range from 0-1°C in winter to 12-15°C in summer (Royer 1975; Royer and Muench 1977). This range is greater than that on the outer shelf because of air-sea heat exchange with a shallow surface stratified layer created by the low-salinity Kenai Current (Schumacher and Reed 1980). Over shallow banks, mixing reduces the seasonal surface temperature range to 1-2°C in winter and about 11°C in summer (Schumacher and Reed 1980), with weak stratification in summer and mixing to 80-100 m in winter. The oceanic subsurface temperature maximum layer, seasonally relatively constant at 3-5°C, impinges on the shelf break at depths of 200-300 m (Figure 23). Some of this denser slope water intrudes onto the shelf into troughs and the Shelikof Strait (Royer 1975; Schumacher and Reed 1980; Reed 1984). During winter bottom water in these troughs remains warmer and more saline than surface water, for which it is a source of heat and salt (Figure 23; Royer and Muench 1977; Schumacher and Reed 1980; Reed et al. 1980). Bottom temperatures in troughs remain at similar temperatures through the summer. Slope waters appear to be cooler (3.5°C or lower) in the western Gulf (Marlowe and Miller 1975).

Currents generally are weaker and more variable over the shelf off Kodiak Island than in the Alaska Stream or the Kenai Current (Figure 22), with many eddies and countercurrents (Reed et al. 1980; Reed and Schumacher 1981). Dominating the energy spectrum over most of the shelf are 50 cm sec⁻¹ tidal currents with variable direction (AEIDC 1974). These currents are weaker over the banks southeast of Kodiak Island than at the entrances to Shelikof Strait. Mean residual surface currents over the shelf are southwestward, and have been measured to range from 2-3 cm sec⁻¹ in March to 5 cm sec⁻¹ in summer and 15-30 cm sec⁻¹ in November (Schumacher et al. 1978; Muench et al. 1980; Wright 1981; Lagerloef 1983). Variability in these currents is associated in part with surface salinity distributions. Royer and Muench (1977) and Schumacher and Reed (1980) described persistent countercurrents associated with warm low-salinity "filaments" near the shelf break. Low-salinity bands may be frontal zones experiencing surface convergence, around which anticyclonic geostrophic reversals would be inferred (Favorite and Ingraham 1977). The source of this low-salinity water may be diffuse freshwater input all along the coast (Ingraham 1979), or in autumn may result from a splitting of the coastal current before it enters Shelikof Strait (Schumacher and Reed 1980). Ingraham (1979) and Wright (1981) also have described intrusions of oceanic water over the shelf that add to the complexity of hydrographic and current patterns.

Another significant source of variability is the generation of eddies by interactions of currents with bathymetry. Favorite and Ingraham (1977) described eddies over shallow banks associated with increased surface

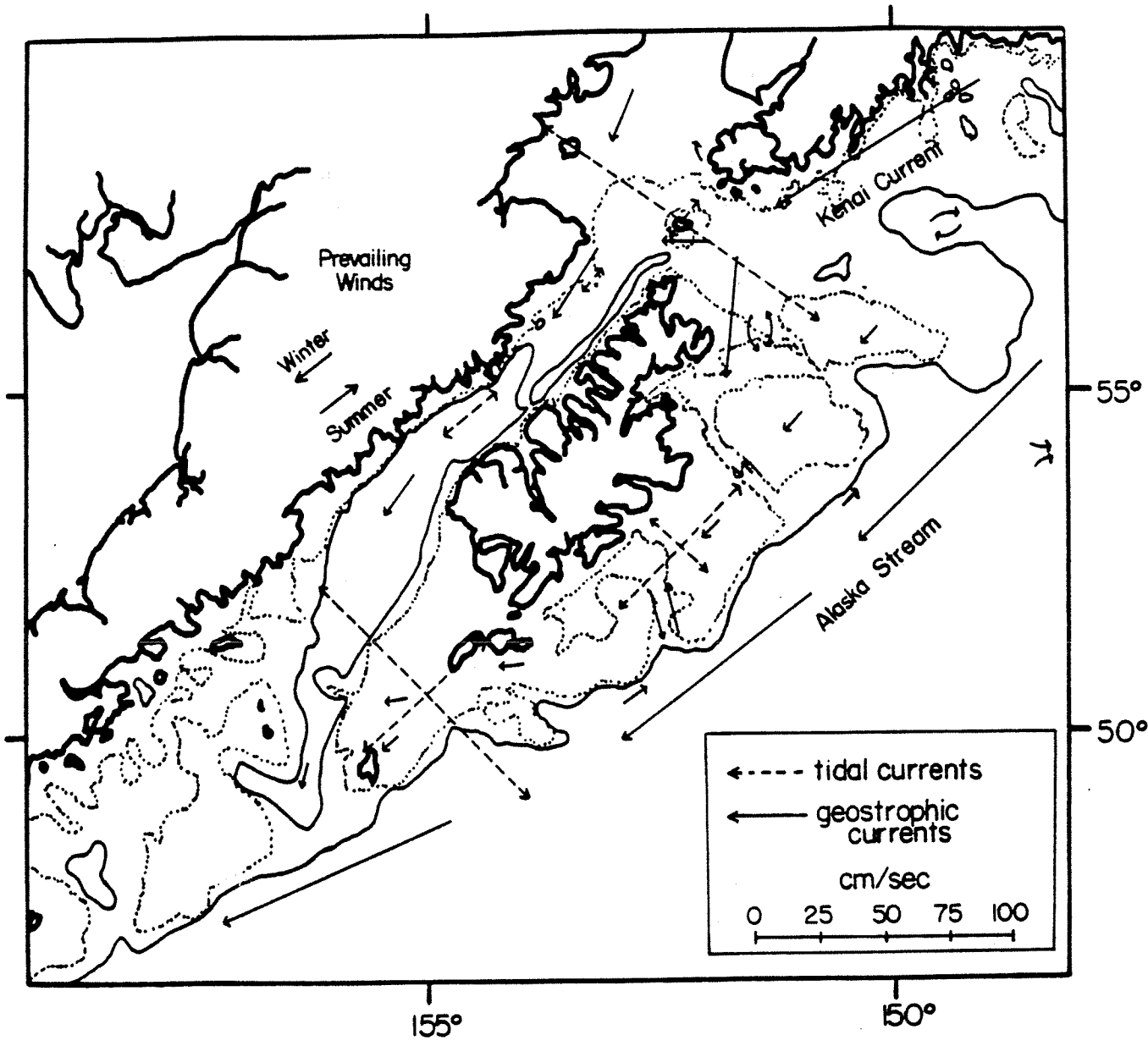


Figure 22. Detailed geostrophic and tidal current distribution near Kodiak Island (after Favorite et al. 1977; Ingraham 1979; Kendall et al. 1980b; Muench et al. 1980; Schleuter and Rauw 1981; and Schumacher et al. 1978 and 1979).

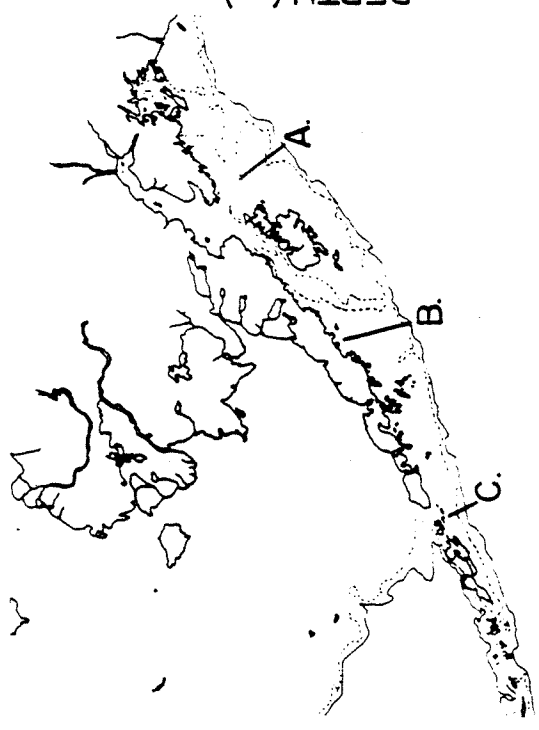
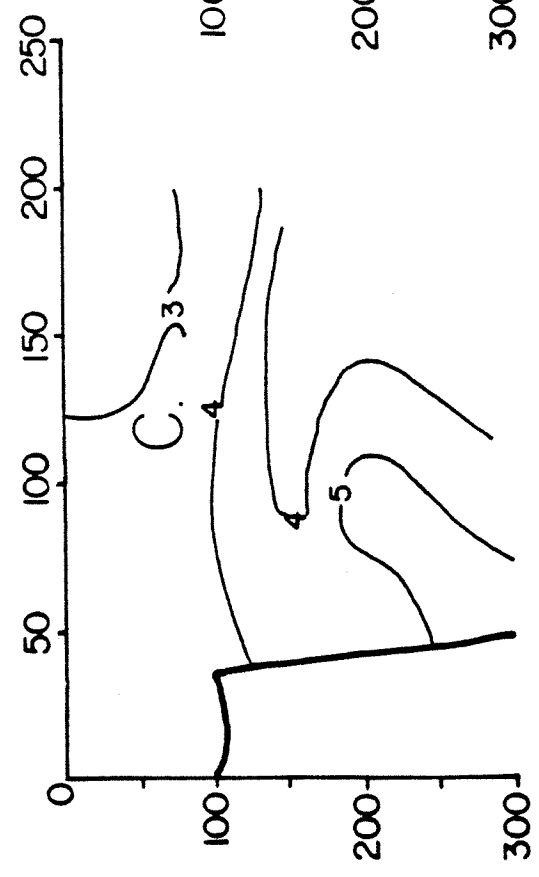
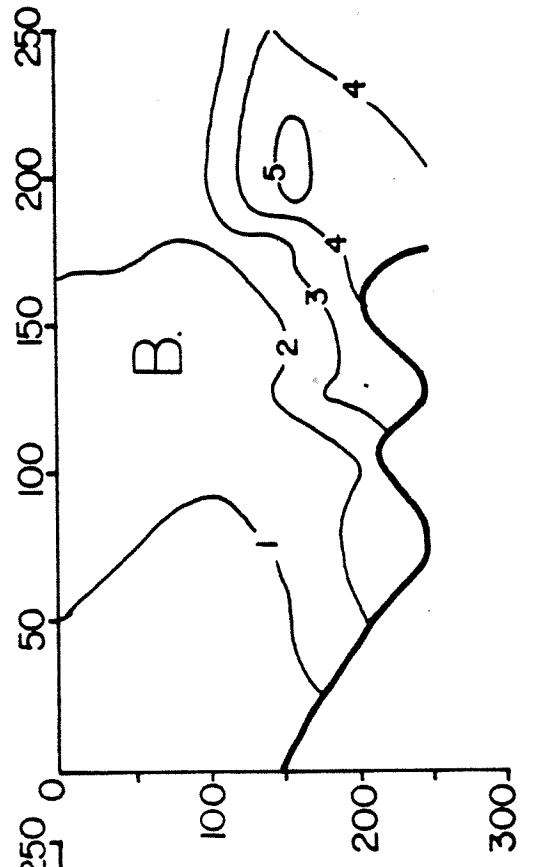
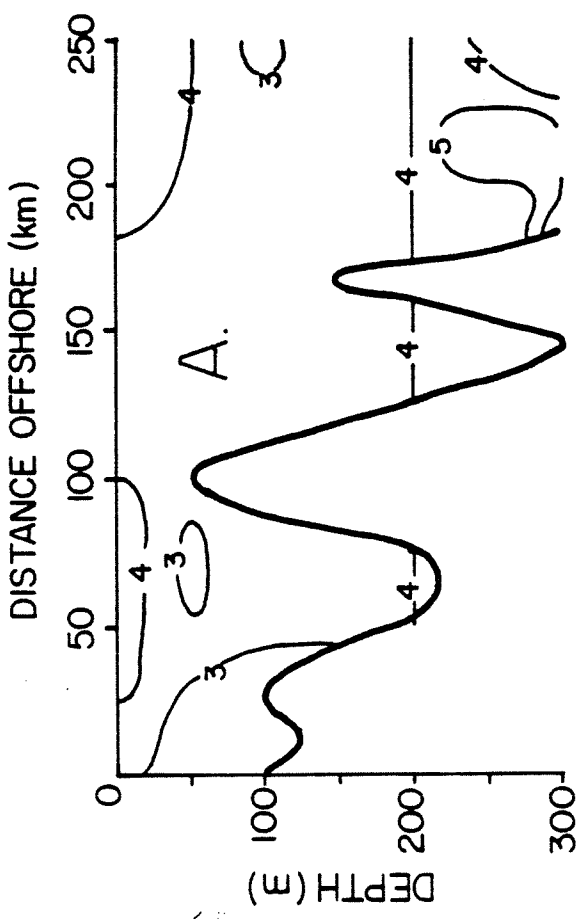


Figure 23. Vertical temperature distribution on the outer shelf and slope in the central Gulf of Alaska in May 1972 (after Favorite et al. 1977), and in the western Gulf of Alaska in February 1980 (after Wright 1981).

salinities, divergence, and vertical mixing. Persistent eddies frequently have been observed over troughs (Schumacher and Reed 1980; Reed et al. 1980; Muench et al. 1980; Wright 1981). Lagerloef (1983) described the steering of currents along the walls of troughs, at speeds of 5-20 cm sec⁻¹, to produce eddies that were visible on satellite photographs. Additional eddy generation over the shelf may be caused by wind distributions (Royer and Muench 1977; Lagerloef 1983) and by propagation of eddies onshore from the Alaska Stream (Reed et al. 1980; Niebauer et al. 1981b). These would affect currents, kinetic energy, and hydrographic distributions over the shelf.

3.2 PLANKTON PRODUCTION

3.2.1 Primary Production

Oceanic Domain. Most data on primary production in eastern subarctic Pacific oceanic waters (including the Gulf of Alaska) come from Canadian weather Station P (50°N , 145°W), in the Subarctic Pacific Current on the southern boundary of the Gulf. There is weak divergence and upwelling at this station, and as in oceanic waters throughout the Gulf vertical mixing extends to the permanent halocline (100 m) in winter and to the seasonal thermocline (20-30 m) in summer (Ingraham et al. 1976).

The dominant characteristic of phytoplankton dynamics in subarctic Pacific oceanic waters, of which Station P is representative, is the relative lack of seasonal variation in phytoplankton standing stocks. According to Hobson (1980), compensation depth for phytoplankton growth (the depth at which net photosynthesis is zero) deepens with increasing light intensity from 40 m in winter to 60 m in summer in subarctic waters at 52°N . Phytoplankton blooms should begin when the decreasing mixed depth equals the "critical depth" (the depth over which depth-integrated net photosynthesis is zero; it is deeper than the compensation depth). Parsons et al. (1968) calculated that, on the average, blooms should begin in March in the coastal waters of Washington and Oregon and propagate northward and seaward, reaching the center of the Alaska gyre by May.

Mean monthly primary productivity estimates at Station P increase as predicted to a June maximum (Table 3). Although Clemons and Miller (1984) report a 50% increase in phytoplankton standing stocks in August, this is a weak trend, and it may be more appropriate to say that mean chlorophyll *a* concentrations remain roughly constant all year, with greater variance in summer than in winter. The discrepancy between increased productivity but constant biomass is believed due to consumption by zooplankton (Figure 24). As a result of relatively weak stratification, persistent vertical mixing, and the low phytoplankton biomass, mean surface nitrate concentrations, which reach 17 micromolar in winter, remain above 7 micromolar in summer and are not believed to limit phytoplankton growth (Anderson et al. 1977). The relatively shallow permanent halocline is believed to restrict vertical mixing during winter, permitting some net production during that time that would further obscure seasonal trends (Clemons and Miller 1984).

Higher standing stocks and daily and annual production rates are estimated for waters south of the Aleutians than for Station P (Table 3). Anderson et al. (1977) noted some variability of annual production at Station P, but both interannual and geographic variability in available data from the subarctic oceanic domain were of smaller scale than intraannual variability in which occasional bloom "events" were observed. Variability in production on all time scales showed little relationship with changes in upwelling rate or herbivore populations.

Several studies provide some conflicting accounts of the dominant species of primary producers in the oceanic Gulf of Alaska. Although most data on phytoplankton species composition in this region have focussed on the more easily studied large taxa, especially diatoms, there have been indications that very small organisms (cyanobacteria and flagellates) may contribute as much to primary productivity, and recent studies are beginning to enumerate these species. Karohji (1972) stated that the oceanic Gulf phytoplankton is dominated by the diatoms *Nitzschia* sp., *Rhizosolenia* sp., and by *Phaeocystis* sp., the same genera said to dominate in the Bering Sea. Booth (1975) found that large diatoms and dinoflagellates contributed 74% of the biomass in enrichment cultures from the oceanic subarctic Pacific. Dominant

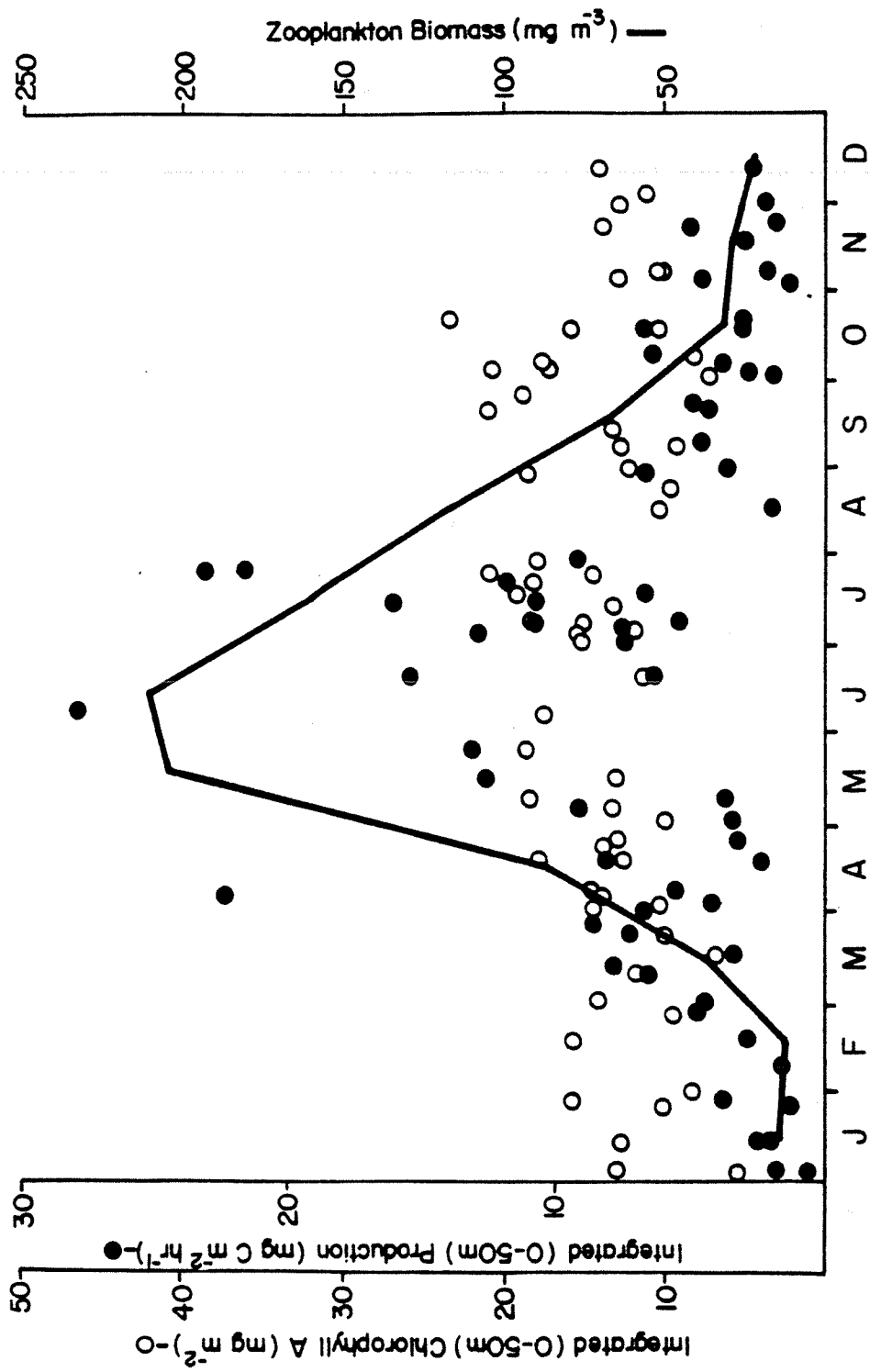


Figure 24. Mean seasonal pattern of zooplankton biomass compared to seasonal data on phytoplankton biomass and productivity at Station P (after Frost 1983).

diatom genera were Corethron, Thalassiosira, Denticula, Fragilaria, and Rhizosolenia. Booth (1981) enumerated phytoplankton larger than 20 micrometers, and found that in addition to the above such genera as the diatoms Ethmodiscus sp., Cylindrotheca sp., dinoflagellates, and coccolithophorids ranked most abundant. She noted, however, that smaller species comprised 96% of biomass at some stations. In addition, Parsons (1972) observed that a high proportion of primary productivity was attributable to small phytoplankton. Larrance et al. (1977) concluded that the oceanic phytoplankton is dominated by species less than 20 micrometers in diameter, especially coccolithophorids. Clemons and Miller (1984) observed that although large diatoms (especially Corethron sp., Thalassiothrix sp., Chaetoceros sp., and Rhizosolenia sp.) could be locally abundant at times, on the average more than 75% of particles were smaller than 20 micrometers. Taylor and Waters (1982) enumerated some of the small flagellate species (e.g., Gymnodinium sp., Micromonas sp.), which they described to be dominant in subarctic Pacific areas of low phytoplankton standing stock such as the Gulf of Alaska. Booth et al. (1982) found the most abundant small phytoplankton to be Phaeocystis sp. (non-colonial form), the diatoms Minidiscus sp. and Nitzschia sp., and two Cryptomonas spp. During the "El Nino" summer of 1983 the dominant phytoplankton at Station P were cyanobacteria (blue-green algae), a group conventionally associated with oligotrophic tropical waters (Booth, personal communication.)

TABLE 3
Phytoplankton Abundance in the Gulf of Alaska

LOCATION	PRIMARY PRODUCTIVITY (MASS OF CARBON M ⁻² TIME ⁻¹)	STANDING STOCK (MG-CHL a)
Oceanic	48-70 g yr ⁻¹ (a,b,c)	
Station P (a,b)	30-100 mg day ⁻¹ winter 600-700 mg day ⁻¹ June mean 350 mg day ⁻¹ summer	0.3-0.4 m ⁻³ (surface) 10-20 m ⁻² all year
Aleutians (a,b,c)	90 mg day ⁻¹ winter 410 mg day ⁻¹ summer 100 g yr ⁻¹	>1 m ⁻³ (surface), >60 m ⁻² spring
NE Gulf Fall 1975 (c)		33 m ⁻²
Neritic (a,d)	80-240 g yr ⁻¹	1-2 m ⁻³ (surface)
Peninsula (e)	400 g yr ⁻¹	
P. Wm. Sound (c)	185 g yr ⁻¹	
Fall 1975	2.9 g day ⁻¹	
NE Gulf (c)	mean 141 mg day ⁻¹ east of PWS mean 522 mg day ⁻¹ west of PWS	18 m ⁻²
Fall 1975		
Kachemak Bay	7.7 g day ⁻¹ May 1976	
Cook Inlet	4.9 g day ⁻¹ May 1976	

(a) Anderson et al. (1977), Hobson (1980); (b) Ichimura (1980);
(c) Larrance et al. (1977); (d) Cooney (1972); (e) AEIDC (1974)

Shelf Domain. Data from continental shelf waters are much sparser than those from Station P. Annual productivity estimates are higher than those for the Aleutian oceanic region, and are especially high along the northwestern Gulf shelf, possibly as a result of coastal upwelling from April to August. In

contrast to oceanic conditions, data reviewed by Anderson et al. (1977) demonstrate the marked seasonality of neritic waters in the Gulf. Spring and summer mean neritic chlorophyll a concentrations at neritic stations were higher than oceanic concentrations, and mean surface nitrate concentrations in summer were "substantially reduced, especially in the northeastern Gulf" where little upwelling is observed. Neritic conditions were described as extending well beyond the shelf break. In the neritic zone primary productivity peaked in spring (March-May), and in summer in the oceanic zone. Few samples were available from shelf waters, however. Mentioned as neritic inhabitants were the diatoms Chaetoceros spp., Melosira spp., and Stephanopyxis spp., as well as the colonial flagellate Phaeocystis sp. The diatoms Rhizosolenia alata and Thalassiosira sp., important components of the Bering Sea shelf flora, were classed as oceanic inhabitants.

The only recent study comparing neritic and oceanic productivity in the Gulf of Alaska was conducted by Larrance et al. (1977) in autumn 1975 and summer 1976. Flagellates dominated on the shelf off the Copper River during its seasonal runoff peak in October-November, and their distribution was extremely patchy because of physical inhomogeneity. Biomass, productivity, and nutrient concentrations generally increased offshore. Integrated chlorophyll a concentrations were lower over the shelf than offshore (Table 3); surface nitrate concentrations ranged from 3 micromolar inshore to 12 offshore. During the same period mean productivity over the shelf was greater within and west of Prince William Sound than east of the Sound. A diatom bloom (Skeletonema costatum, 8 mg m^{-2} chlorophyll a, $2.9 \text{ g-C m}^{-2} \text{ day}^{-1}$) was observed in the Sound, where annual productivity was observed to peak in the spring. Surface nitrate concentrations were less than 5 micromolar, but there was no evidence that they limited phytoplankton growth.

Larrance et al. (1977) also surveyed conditions in Cook Inlet and Kachemak Bay from April to August 1976. Previous studies had established a pattern for inshore waters such as Port Valdez (Goering et al. 1973) and Auke Bay (Iverson et al. 1974): vigorous diatom blooms during spring followed by thermal stratification and dominance of flagellates during summer, except when wind mixing events stimulated diatom outbursts. In April 1976 low phytoplankton biomass was observed in Cook Inlet, while a bloom was observed in Prince William Sound. In early May stratification and a diatom bloom began in Kachemak Bay and a flagellate bloom had begun in oceanic waters. By late May productivity and biomass in the Sound had increased 2 to 4 fold compared to April. Blooms appeared to propagate seaward from Kachemak Bay, where a strong pycnocline was present at 10-20 m depth. Surface nitrate depletion and the formation of a subsurface phytoplankton maximum began at this time and persisted into August. At times during the season productivity and biomass in Kachemak Bay were ten times higher than in Kamishak Bay (on the opposite side of Cook Inlet), and one hundred times higher than in the well-mixed center of the Inlet, especially in the turbid upper inlet. Biomass peaked in Kachemak Bay in May, and in the Sound and Cook Inlet in July, and declined to winter levels at all locations by late August. Flagellates dominated phytoplankton inshore during late summer, and phytoplankton biomass was higher in the oceanic zone at that time. At the oceanic station (continental slope, depth 1500 m) the euphotic zone was deep (28-35 m), production increased rapidly (but biomass increased only gradually) beginning in spring but was reduced by surface nutrient depletion in July and by increased vertical mixing in August. Similar results were observed in 1978 by Chester and Larrance (1981).

A general depletion of CO_2 in surface waters has been observed in summer south of the Peninsula and in Prince William Sound, with anomalies approaching 100 microatmospheres (Longerich and Hood 1972). Surface pH

values of 8.2-8.4 were observed on the shelf, compared to values of 7.7 in deep water. At all locations a strong positive correlation of CO_2 and nutrient concentrations was observed. CO_2 concentrations slightly in excess of atmospheric equilibrium (+30 microatmospheres) were observed south of Unimak Pass and in the center of the Alaska Gyre, and are considered indicative of upwelling. Miyake et al. (1974) reported that CO_2 concentrations in oceanic waters of the northern northeast Pacific were very close to equilibrium with the atmosphere. Hobson (1980) speculated that diatoms may dominate under bloom conditions in the subarctic Pacific because they may possess the enzyme phosphoenolpyruvate carboxylase (PEP-Case) that utilizes HCO_3^- rather than CO_2 as the substrate for carbon fixation in the photosynthetic dark reaction. A plant possessing this metabolic mechanism might have an advantage over one using the ribulose biphosphate carboxylase (RuBP-Case) pathway under bloom conditions in which surface water CO_2 concentrations might become depleted. Little experimental work has been done, however, to determine the photosynthetic pathways of different marine phytoplankton species, (Holm-Hansen 1982), or the CO_2 concentrations at which potential advantages of one species over another might come into play (Goldman et al. 1982).

3.2.2 Secondary Production

Oceanic Domain. Most of the data on Subarctic Pacific secondary production were obtained from Canadian studies at weather Station P. Conditions at this station appear to be very representative of those in the subarctic Pacific over scales of hundreds of kilometers (Miller et al. 1984). The record of macrozooplankton abundance at this station is in fact one of the most extensive in the world, covering over 24 years continuously from 1956 to 1980 (Frost 1983). The zooplankton assemblage was sampled with nets, and on the average was composed of 90% copepods by weight. The mean annual maximum zooplankton biomass during this period (Table 4) was about 30 g wet weight m^{-2} , comparable to estimates in the oceanic Bering Sea basin (Motoda and Minoda 1974). Cooney (1972) estimated secondary production at 13-16 g-C $\text{m}^{-2} \text{yr}^{-1}$ and transfer 20% efficiency in the oceanic Gulf of Alaska; both values are similar to Cooney's (1981) estimates for the outer shelf domain of the Bering Sea.

Frost (1983) analyzed some Station P data to demonstrate that interannual variability in annual zooplankton biomass maxima exceeds a factor of two, and discussed the lack of adequate hypotheses to account for this variability. Anderson et al. (1977) and Wickett (1967) associated some changes in zooplankton composition and standing stock with variations in salinity at Station P and northerly intrusions of temperate "transition" water masses, but much of the variability could not be explained by these mechanisms. There is potential for further such analysis if the data analyzed by Frost (1983) were to be compared to climatological data such as that presented in McLain and Ingraham (1980).

The annual pattern of plankton growth at Station P is characterized by the failure of phytoplankton standing stocks to increase in proportion to the spring increase in primary productivity. This discrepancy is attributed to consumption by zooplankton species with unique life cycles. The primary grazers at this time of year are believed to be immature stages of large copepods of the genus Neocalanus. Frost et al. (1983) determined that Neocalanus spp. dominate the oceanic zooplankton community during spring due to morphological adaptations that permit them to feed on an extremely broad range of phytoplankton sizes and concentrations. Furthermore, reproduction in these species is supported by stored energy from previous

feeding rather than from feeding on the spring increase in primary production. Therefore large populations of immature feeding stages are present at the surface to consume the surplus phytoplankton biomass generated by increased spring growth (Miller et al. 1984). Adult Neocalanus reproduce at depths below 250 m through most of the year, with a peak in late fall to winter. Feeding copepodite stages are present at the surface for much of the year, each individual returning to deep water to mature without additional feeding. Maximum copepodite biomass (Figure 24) and grazing pressure are observed in spring, in phase with the seasonal maximum of primary production. Feeding appears to be reduced during summer, possibly due to high temperatures, but increases again in fall, and may be sustained by the persistence of phytoplankton growth through the winter (Clemons and Miller 1984). Neocalanus spp. can vary their feeding rate widely in response to changes in food supply, and thus are effective at maintaining constant low standing stocks of phytoplankton (Frost et al. 1983). The same Neocalanus spp. and a similar relationship to primary production have been observed in outer shelf and oceanic waters of the Bering Sea (Cooney and Coyle 1982).

TABLE 4
Zooplankton Abundance in the Gulf of Alaska

<u>LOCATION</u>	<u>STANDING STOCKS</u>
Oceanic	
Station P	Interannual and vertical means 10 g wet weight 1000 m ⁻³ (winter) to 200 (May-June), 0-150 m (a) Range 250-1250 ml 1000 m ⁻³ , 0-100 m (July 1971) (b)

Neritic	
Unimak Island	Vertical means 20-400 ml 1000 m ⁻³ (c)
Peninsula	Vertical means 100-1600 ml 1000 m ⁻³ (c)
Shumagin/Kodiak	Vertical means 200-400 ml 1000 m ⁻³ (c)
P. Wm. Sound	Integrated mean 1100-1500 ml m ⁻² , 0-730 m (Fall 1975) (d) Range 0.1-7.4 ml m ⁻³ , 0-25 m (d)
NE Gulf	Mean 1.2 ml m ⁻³ , 55-200 m (d)
Cook Inlet	Integrated mean 43-1000 ml m ⁻² , 0-75 m (d)
Kodiak Slope	Integrated mean 500-1200 ml m ⁻² , 0-1500 m (d)
Kodiak Shelf	Vertical means 30-180 ml 1000 m ⁻³ (fall-spring) and 450-820 (summer), surface to bottom (1977-79) (e)

(a) Frost (1983); (b) Marlowe and Miller (1975); (c) AEIDC (1974);
(d) Damkaer and Dey (1977); (e) Kendall et al. (1980b)

Dominating the net zooplankton community later in the season, according to July 1971 data of Marlowe and Miller (1975), are the copepods Eucalanus bungii, Microcalanus sp., Oithona sp., and Metridia sp. About one third of the zooplankton biomass throughout the year appears to be contributed by small (less than 0.3 mm) zooplankton (Miller et al. 1984). Eucalanus contributes about 20% of the biomass during spring and has a definite grazing impact. However, the life cycle of this species (and probably the others) requires feeding phytoplankton just prior to reproduction, and therefore would be less effective in maintaining constant plant stocks. Also present are the amphipod Parathemisto pacifica, chaetognaths (Sagitta spp.), and euphausiids

(Euphausia pacifica and Thysanoessa spp.). Maximum populations of copepod and micronekton species in the upper 100 m ranged from 10^3 to 10^4 per m^3 , and 10^2 to 10^3 per m^3 , respectively. Marlowe and Miller (1975) and Miller et al. (1984) also reported some data on diel vertical migrations of zooplankton species. Using coarse-meshed (6.35 mm) nets during July 1973-75, Frost and McCrone (1979) observed sparser euphausiid populations of less than 0.1 per m^3 (1-15 per m^2), dominated by E. pacifica.

Shelf Domain. The data record on zooplankton over the Gulf of Alaska shelf is much smaller than that from Station P. Comparisons of neritic and oceanic data are complicated by reporting of data over different depth intervals and in different units (Table 4). The evidence indicates that zooplankton standing stocks generally are higher over the shelf, as would be expected, and that some species differences are observed as well.

One review (AEIDC 1974) placed peak zooplankton biomass between Kodiak Island and Unimak Island at two to eight times that of Station P. Kendall et al. (1980b) summarized the results of sampling off Kodiak Island from fall 1977 to spring 1979, and found that during summer standing stocks of zooplankton per m^2 of sea surface (vertically integrated) were generally similar to those at Station P, but that standing stocks per m^3 of volume were two to four times greater in the shallower waters over the shelf. Vertically integrated biomass showed less seasonal variation over the shelf than at Station P, and remained about double the oceanic value. There was some evidence that similar biomasses of zooplankton per m^3 over banks and troughs produced greater vertically integrated biomass over the deeper troughs. Kendall et al. (1980b) also concluded that mean copepod populations were highest over the slope in winter, nearshore and over the midshelf in spring and summer, and nearshore in fall.

Damkaer and Dey (1977) found still higher zooplankton standing stocks at inner shelf stations associated with Prince William Sound and Cook Inlet. Vertically integrated biomass in Prince William Sound during October-November, 1975 was five to ten times the spring maximum at Station P. During April to August, 1976 they observed a seaward propagation of seasonally maximal zooplankton biomasses beginning in Kachemak Bay in May (a surface maximum of about $30 \text{ ml } m^{-3}$ at that location may have been contaminated by phytoplankton), and reaching open Cook Inlet and the Kodiak shelf in June and July (surface maxima of about $10 \text{ ml } m^{-3}$). Damkaer and Dey (1977) also noted that vertically integrated biomass was slightly higher over a slope station than in Cook Inlet due to the greater depth of the former (1500 m vs. 75 m), similar to the findings of Kendall et al. (1980b). The highest overall standing stocks in this study were found in Prince William Sound, however.

AEIDC (1974), Damkaer and Dey (1977), and Kendall et al. (1980b) all reported that copepods dominated the zooplankton community of neritic waters. The most abundant copepods in the latter studies were smaller near-surface copepods such as Pseudocalanus sp., Calanus sp., Oithona sp., and Acartia sp. Mean populations of copepod species were in the range of 10^3 animals m^{-3} . Damkaer and Dey (1977) noted a few individuals of Neocalanus spp. in Cook Inlet and especially over a deep (730 m) hole in Prince William Sound, but stated that on the whole these larger copepods were excluded from shelf waters by their need for greater depths. Damkaer and Dey (1977) also reported data on vertical migration of zooplankton species; a few large individuals of Euchaeta sp. and Metridia sp. caused significant increases in surface biomass during their nocturnal migrations.

Second in importance to copepods in the above studies were micronekton, especially euphausiids, hyperiid amphipods, and chaetognaths. Thysanoessa

spp. were the dominant euphausiids over the shelf, and the presence of E. pacifica was associated by Kendall et al. (1980b) with the intrusion of oceanic water into troughs. In an earlier report on Kodiak shelf data, Dunn et al. (1979) stated that euphausiid populations of about 5 per m³ were similar to those found at Station P by Frost and McCrone (1979), but again were denser on a per m³ basis due to shallower water. Kendall et al. (1980b) later reported Kodiak shelf euphausiid populations approaching 10² per m³ in summer.

3.2.3 Vertical Carbon Flux

Most of the food supplies for benthic invertebrates and demersal fishes are believed to originate from sinking of plankton and its by-products. Although few studies are available from the Gulf of Alaska, data indicate that organic matter input to the benthos both as absolute mass and as fraction of primary production is significantly higher in neritic areas than in oceanic areas. Thus higher benthic production and standing stock should be observed in areas of greater input from the water column. Lorenzen et al. (1983) found that only 7% of daily primary production sank out of the surface layer of the oceanic subarctic Pacific, and only 3.7% reached the bottom (using the data of Table 3). This yields an estimated maximum flux of 3-7 g-C m⁻² yr⁻¹ to the benthos. In Cook Inlet, however, Chester and Larrance (1981) calculated that an average of 12% of daily primary production reached the bottom, and that a flux of 60 g-C m⁻² yr⁻¹ reached the benthos in Kachemak Bay, a highly productive inlet supporting intensive groundfisheries. This difference between oceanic and shelf sedimentation is consistent with the relative magnitudes of primary production, and with the apparently more intensive grazing pressure in oceanic waters, which would retain and utilize a greater fraction of plant production in the water column. However, Lorenzen et al. (1983) found evidence of significant sinking of ungrazed phytoplankton, and did not observe the high incidence of zooplankton fecal material in suspended matter that would be expected from this hypothesis. Furthermore, little of the vertical carbon flux in Cook Inlet was judged to originate from direct sinking of phytoplankton, and a mean of 86% was in the form of zooplankton fecal pellets at all times of year (Chester and Larrance 1981). Thus, the dynamics of the differences between shallow and deep water organic sedimentation in the Gulf of Alaska are still uncertain.

There is circumstantial evidence, however, that further relates continental shelf benthic production to the inferred patterns of primary production in overlying waters. Feder et al. (1980) reported that overall mean benthic standing stocks on the Gulf of Alaska shelf were lowest in the northeastern Gulf (1.7 g m⁻²), higher in Prince William Sound (2.6 g m⁻²), and highest on the Kodiak shelf (3-4 g m⁻²) where they were comparable to those on the southeastern Bering Sea shelf (3.3-5 g m⁻²). Feder (1979a) located the highest benthos and demersal fish standing stocks in the northeast Gulf off the Copper River delta, and speculated that riverborne nutrients and trapping of plankton in eddies could enhance vertical carbon flux at that location. This pattern roughly resembles the distribution of coastal upwelling (Figure 21), neritic plankton abundance, and pollock abundance (see below) and supports the hypothesis that benthic production is related to planktonic production. Feder (1979a), however, found that a large portion of the organic carbon in Cook Inlet sediments originated as detritus from nearshore macrophytic algae, suggesting that unlike that on the Bering Sea shelf, benthic production on the Gulf shelf may not be regulated by planktonic production alone.

3.3 FISHERY BIOLOGY OF POLLOCK

3.3.1 Life Cycle

Egg, Larval and Juvenile Stages. Pollock eggs may be observed in small quantities throughout the Gulf of Alaska during most of the year (Alton and Deriso 1983a). Most of the standing stock of eggs, however, appears to occur in discrete intense aggregations. The principal egg concentration that has been located occurs regularly in Shelikof Strait in late March and early April (Rogers et al. 1980). Bates and Clark (1983) observed that pollock eggs were the dominant eggs in both the neuston and water column off Kodiak Island and the Alaska Peninsula from March through May of 1981. Highest egg abundances (over 10^4 eggs m^{-2}) were observed in southwestern Shelikof Strait in early April. These concentrations are ten times those reported from the southeastern Bering Sea shelf (Walline 1983). Lesser concentrations of eggs also have been observed at the shelf break south of the Trinity Islands in late April. Bates and Clark (1983) inferred that egg abundance increased rapidly beginning in the third week of March, peaked around the beginning of April, then dropped to a lower sustained level through May. Dunn and Naplin (1974) also reported concentrations exceeding 10^4 eggs m^{-2} in lower Shelikof Strait in April 1972, when they comprised 97% of all eggs caught in bongo nets. Sherman et al. (1983) described eggs in this vicinity as occurring mainly at depths from 20 to 50 m.

Some surveys also have located lesser concentrations of pollock eggs southeast of Kodiak Island. Rogers et al. (1979) surveyed egg abundance in Kodiak bays (depths to 171 m) in 1978 and 1979. Eggs were less abundant (maximum 0.1 eggs m^{-3} in bongo hauls and 0.8 eggs m^{-3} in neuston hauls) than in Shelikof Strait, with a similar pattern of seasonal abundance. Pollock eggs were dominant in April, but contributed only 1% of total egg catch from Kodiak Bays on an annual mean, with flatfish eggs very abundant from June through August. Kendall et al. (1980a) surveyed the open Kodiak shelf from fall 1977 through spring 1979, and noted persistent egg concentrations, with a maximum in excess of 10^3 eggs m^{-2} , over Kiliuda trough in spring. Half the pollock eggs were said to be neustonic, and the remaining half were evenly distributed through the vertically mixed 120 m water column.

Pollock eggs in these locations are subject to potential advective transport to the southwest by the Kenai Current and the Alaska Stream. Sherman et al. (1983) described eggs and larvae as generally drifting southwestward along the Alaska Peninsula during the two weeks until hatching and the six to eight weeks as ichthyoplankton during April and May. In late April 1981, Bates and Clark (1983) observed an aggregation of 10^4 larvae m^{-2} 100 km southwest of the egg aggregation they had observed in early April. The seasonal maximum of larval pollock abundance occurred in late April to early May, and a constant minimum size of sampled larvae suggested continuous hatching prior to this period. Pollock larvae dominated the water column ichthyoplankton through May. Pollock comprised 62% on pelagic fish larvae over the Kodiak shelf in May 1972 (Dunn and Naplin 1974), reaching a maximum of over 10^3 larvae m^{-2} in bongo tows. Rogers et al. (1979) found low larval concentrations not exceeding 0.1 larvae m^{-3} in bongo tows in Kodiak bays. Kendall et al. (1980a) reported pollock larvae were concentrated in spring in the same areas as eggs: in Shelikof Strait, southwest of Kodiak Island, and over Kiliuda Trough. Both Bates and Clark (1983) and Kendall et al. (1980a) reported that pollock larvae were scarce in neuston tows.

Almost no information is available on the juvenile stage of pollock in the Gulf. Alton (1981) described juvenile pollock as remaining in the upper 50 m near shore and in straits. There are several incidental reports of midwater populations of small pollock in shallow and inshore waters: on Kodiak banks (Hughes and Alton 1974; Feldman and Rose 1981); in inside waters of southeast Alaska (Carlson et al. 1982); in Prince William Sound (Parks and Zenger 1979); and in Cook Inlet (Blackburn 1979b). These reports usually associated increasing pollock size with increasing depth. Blackburn

(1979a) and Rogers et al. (1979, 1980) observed young of the year entering Kodiak Island bays beginning in September. Alton (1981) suggested that Gulf of Alaska pollock rear in straits and nearshore areas, and Janusz (1983) observed tentatively that recruitment of age 1 juveniles was occurring in the Chirikof region at the mouth of Shelikof Strait, but not farther west in the Shumagin region. It thus appears that when searching for the mechanisms controlling recruitment of Gulf of Alaska pollock, it would be wisest to examine factors that might contribute to retention of eggs, larvae, and juveniles near the areas where they were spawned.

Adult Stage. The average growth pattern of Gulf of Alaska pollock is shown in Figure 14. Locations of commercial pollock catch in the Gulf of Alaska are shown in Figure 15. Relative abundance of pollock in different areas and depths of the Gulf, as compared also to the Bering Sea, are shown in Figure 25. The western region of the Gulf compares favorably with the recent overall mean total groundfish catch of 9.8 metric tons km^{-2} in the North Sea (Andersen and Ursin 1977), while abundance is clearly lower in the eastern Gulf. According to Hughes and Hirschhorn (1979) and Alton and Deriso (1983a), 90% of the present exploitable biomass of pollock in the Gulf is found west of Kodiak Island. Highest population densities observed by Hughes and Hirschhorn (1979) were on the continental slope in the Sanak region and on the outer shelf in the Kodiak region, and highest total biomass was found in the Chirikof region. Adult pollock are less common in inshore waters, such as inner Cook Inlet at depths of less than 75 m (Blackburn 1979a), and Kodiak Bays (Blackburn 1979b). Parks and Zenger (1978) found a very low exploitable biomass of pollock on the northeast Gulf coast off Yakutat. Higher standing stocks were observed in southeast Alaska. Parks and Zenger (1979) found low abundance of all trawled species in Prince William Sound. Feldman and Rose (1981) found pollock to be only 1-2% of the trawl catch in the Yakutat and southeast Alaska area. Carlson et al. (1982), however, estimated that pollock had the largest biomass of any single species in southeast Alaska. There is insufficient information at this time to account for this distribution, but there is some evidence on the possible influences of temperature, advection, food supply, and bathymetry.

The vertical distribution of pollock in the Gulf is similar to that in the Bering Sea. Hughes and Hirschhorn (1979) reported that pollock in the western Gulf were associated with the shelf-break depths of 100-300 m, especially near troughs and submarine valleys. Pollock school near the bottom during the daytime, and to disperse upward in the water column at night to feed, although sometimes this diel vertical migration pattern may be absent (Alton 1981; Alton and Deriso 1983a). Hughes and Alton (1974) found few indications of midwater pollock concentrations on the Kodiak shelf in May-June 1973, with a low catch of small individuals taken from a scattering layer at about 100 m depth in 150-200 m of water. More extensive midwater populations of small pollock were observed in the Shelikof and Shumagin regions. Hughes and Alton (1974) noted that adult abundance appeared to increase with depth and distance from shore, and that adults did leave the bottom at night.

Horizontal migration patterns of pollock in the Gulf of Alaska are virtually unknown, except for those during the brief period of spawning (see below). No tagging experiments have been performed. Alton (1981) stated that bottomfish in the Gulf generally migrate onshore in summer and offshore in winter, corresponding with the general pattern of bottom currents on the shelf. Pollock appear to migrate offshore in winter to remain within the relative temperature maximum at the shelf break and slope (Favorite et al. 1977), but there are no data on alongshore migrations.

During summer adult pollock standing stocks are highest in the 100-300 m depth stratum (Hughes and Hirschhorn 1979). Alton (1981) inferred that pollock are most commonly associated with soft bottom areas, and so were more common in sheltered troughs than in more exposed advective environments with coarser bottom material, such as the sand and gravel banks on the western Gulf shelf. Several trawl surveys (e.g., Pereyra and Ronholt 1976; Hughes and Alton 1974; Feldman and Rose 1981) have confirmed that off Kodiak Island and in the Chirikof region adult pollock are least

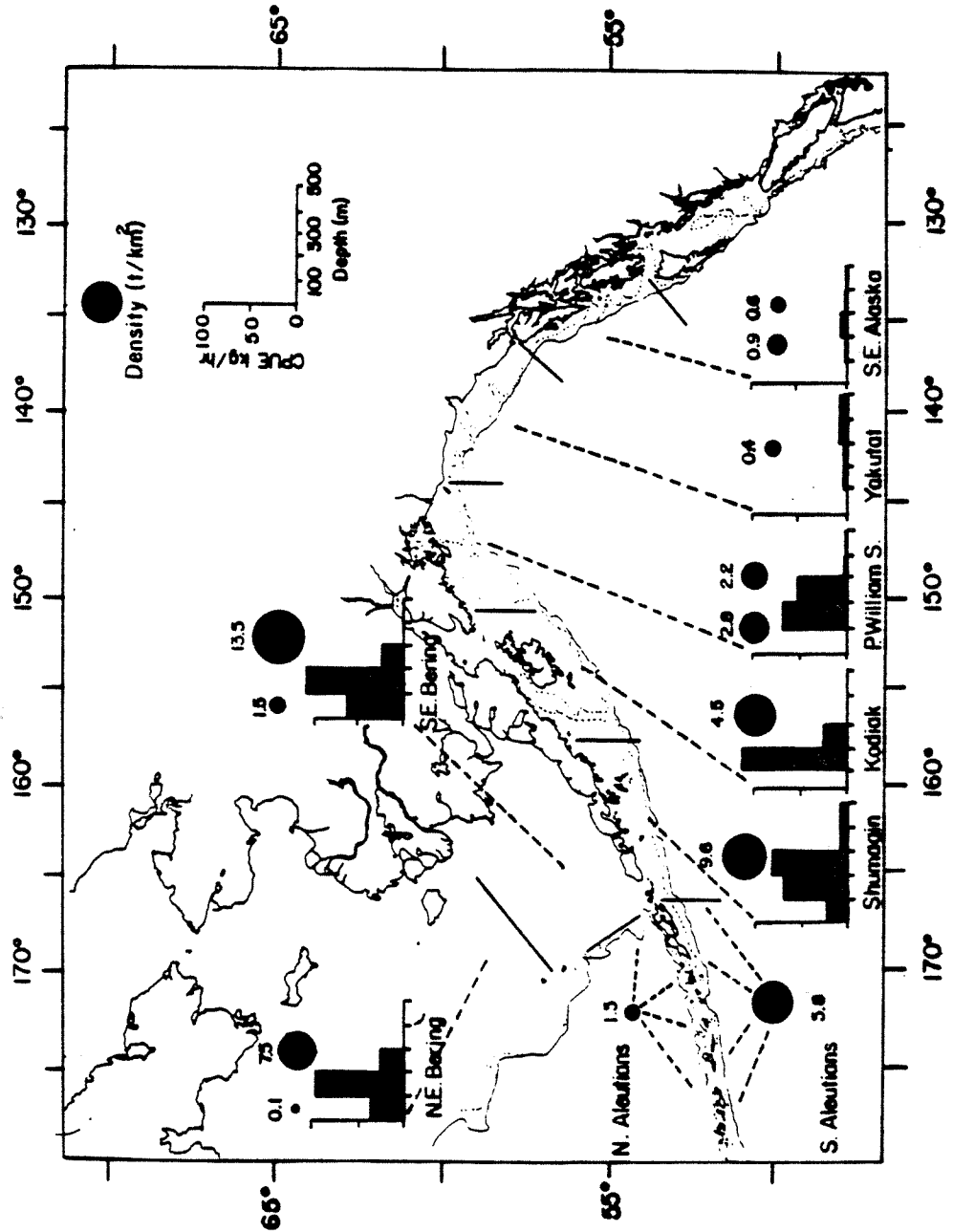


Figure 25. Catch per effort versus depth and mean estimated biomass density of pollock in regions of the eastern Bering Sea and Gulf of Alaska (after Alton 1981; Alton and Deriso 1983; Bakkala et al. 1982; and Ronholt et al. 1982).

abundant in the shallow waters over banks, and most abundant in troughs and on the outer shelf break. Parks and Zenger (1978), Feldman and Rose (1981), and Carlson et al. (1982) also observed pollock associated with troughs and sheltered waters in the eastern Gulf.

Spawning. Adult pollock reach sexual maturity mostly at age 3, at lengths of 29-32 cm (males) and 30-35 cm (females) (Hughes and Hirschhorn 1979). Spawning activity, like egg appearances, have been reported over a wide range of locations and times of year in the Gulf of Alaska (Alton and Deriso 1983a). Locations of reported spawning are shown in Figure 16. The major spawning event that has been observed in the Gulf is an intense aggregation in western Shelikof Strait over a concentrated period in late March and early April (Alton and Deriso 1983b). During spawning midwater schools segregated by sex are located approximately 80 m off the bottom in the deepest portion of the Strait (depth about 300 m) (Nunnallee et al. 1982), and a smaller biomass of adults is found at the bottom (Alton and Deriso 1983b). Spawners do not feed during this period. Alton and Deriso (1983a) speculated that this spawning event may be synchronized with food supplies or currents favorable to larval survival, and noted that there was no evidence for any major spawning aggregation east of Kodiak. Migration of pre-spawners into the Strait has been observed in January, and dispersal of post-spawners occurs rapidly after mid-April (Nunnallee et al. 1982). Present biomass of this migratory population was estimated at 2.5 million metric tons, comparable to the total known adult standing stock from Kodiak to the Shumagin area (Sherman et al. 1983; Alton and Deriso 1983b). Maximum summer pollock catches are taken to the west of Shelikof Strait. This pattern suggests a single spawning stock that migrates upstream in winter to spawn, and swims or is carried downstream in spring and summer.

Alternatively, possible separate large-scale spawning aggregations have been suggested in the Shumagin, Chirikof, and Kodiak regions by Alton and Deriso (1983a) and Brown and Rose (1983b) based on large Soviet trawl catches in March-April 1980-1981, and in the Unimak Pass and Kenai Peninsula areas based on U.S. research surveys (Alton and Deriso 1983b). There is evidence that there may be separate eastern and western spawning stocks, bounded roughly by Shelikof Strait. Walline (1983) determined that estimated hatching dates of pollock larvae south of the Alaska Peninsula in 1980 were later toward the west-- from about March 25 in the vicinity of the Trinity Islands to about May 2 near Unimak Island. This is the opposite of the pattern that would be expected from southwestward transport of larvae along the Alaska Stream, and suggests a stock that spawns later south of the Peninsula. There also are apparent differences in size-at-age and year-class strength east and west of Kodiak Island. Hughes and Hirschhorn (1979) noted that strong year-classes occurred in 1967 west of Kodiak and in 1970 east of Kodiak; that the mean length-at-age of the 1973-74 year classes was larger in the Chirikof and Sanak regions than in the Kodiak and Shelikof regions; and that older fish dominated the population in the Sanak region. Janusz (1983) observed the reverse pattern in 1981: mean size was larger in the Chirikof region than in the Shumagin region, but there were more older individuals in the latter area; age 2 fish at Chirikof were smaller but growing more quickly, implying later hatch dates but better growth conditions; and there were distinct unexplained differences in sex ratios between the two areas. The mechanisms causing these conflicting observations are not clear, but these data support the notion of separate populations. Grant and Utter (1980) performed electrophoretic studies on Pacific pollock and concluded that only eastern and western Pacific stocks could be clearly distinguished genetically. Slight differences were observed between the Bering Sea and Gulf of Alaska, and between the eastern and western Gulf.

3.3.2 Trophic Relationships

Prey. Less information is available about the position of pollock in the food web

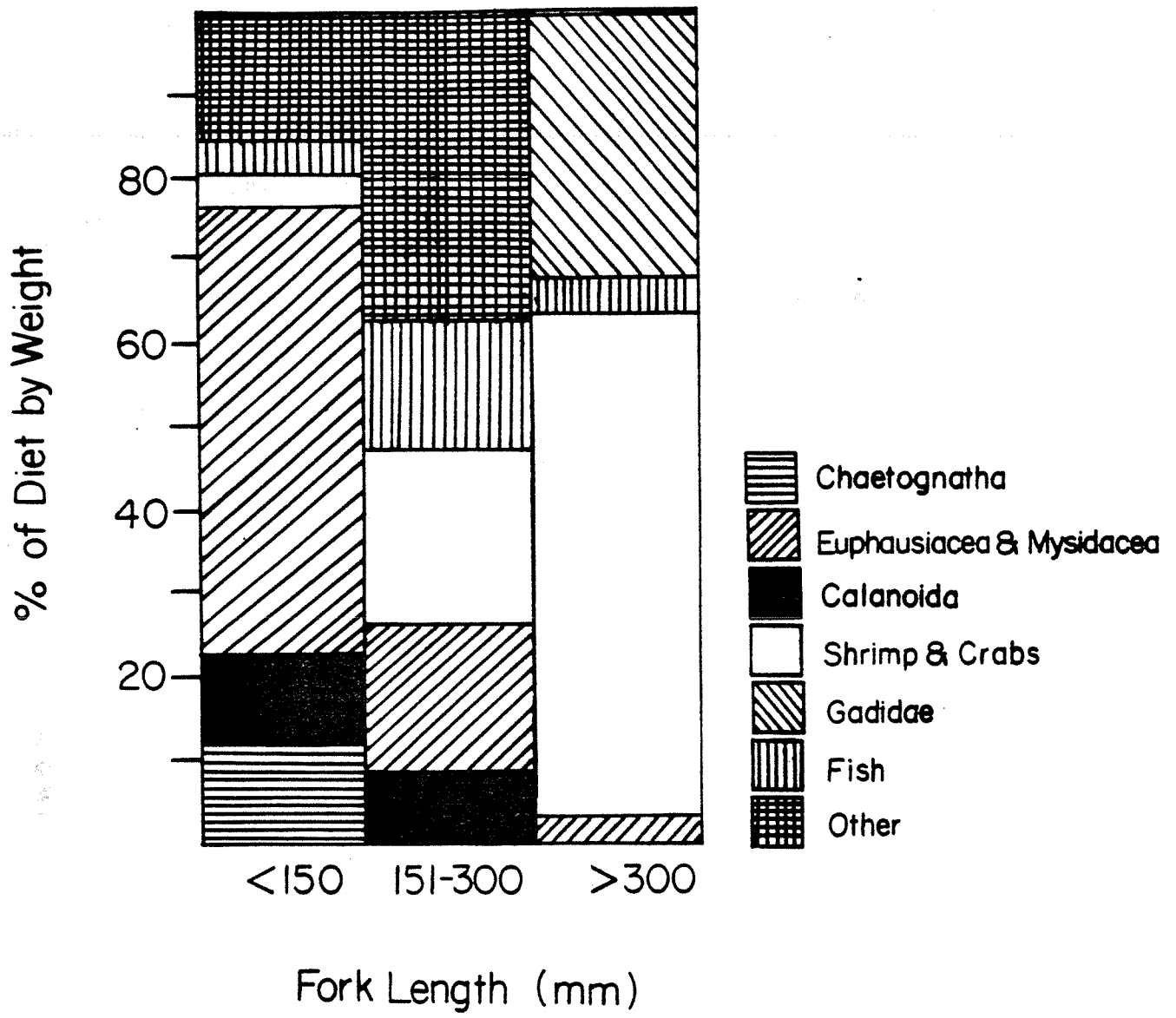


Figure 26. Prey spectrum of different sizes of pollock in the Gulf of Alaska (after Rogers et al. 1979).

of the Gulf of Alaska than for the Bering Sea. The information available generally resembles that from the Bering Sea (Figures 17, 18 and 26), but seems to indicate a higher proportion of benthic prey of adult pollock in the Gulf. This judgement may be biased, however, because much of the data comes from individuals sampled in nearshore habitats that may be atypical of the population as a whole.

Few data are available on the prey of larval or juvenile pollock in Gulf of Alaska. Blackburn (1979a) and Rogers et al. (1979, 1980) observed low concentrations of juvenile pollock in midwater in Kodiak Bays feeding on copepods, chaetognaths, mysids and euphausiids, with a high proportion of empty stomachs in winter. Rogers et al. (1980) observed that juvenile pollock trawled in Kodiak Bays in summer (mean weight 138 g) ate almost exclusively shrimp, while smaller juveniles trawled in autumn (mean weight 44 g) ate equal amounts of shrimp and fishes, of which 68% were pollock. The latter data may be poorly representative of conditions on the open shelf, however, since they come from juveniles trawled in an area where they are mostly in midwater, where shrimp are most abundant, and where pollock were only the seventh most abundant trawled species, rather than the most abundant as observed elsewhere.

Alton (1981) stated that adult pollock in the Gulf of Alaska feed primarily on zooplankton and small fishes, and are cannibalistic at times. Rogers et al. (1979) observed that pollock longer than 30 cm sampled from Kodiak Bays consumed as their primary prey roughly equal quantities of shrimp and fishes. The principal fish prey were juvenile gadids, consistent with a possible importance of cannibalism. However, these data also may not be representative of conditions on the open shelf. Feder (1979a, b) and Feder et al. (1980) observed that pollock (size unspecified) consumed mainly shrimp and euphausiids in Kodiak bays, over the Kodiak shelf, and in the northeastern Gulf, and consumed juvenile salmon as well as shrimp and zooplankton in the Aleutian Island region. Pollock examined by Simenstad (1979) from the Kodiak shelf consumed 25% shrimp and 48% fishes, while those sampled in Cook Inlet had a diet consisting of 90% benthic mysids. Simenstad (1979) concluded that although pollock were usually considered at least facultative planktivores, his data showed a very low incidence of planktonic prey.

Predators. Also on the basis of more limited data, predators on Gulf of Alaska pollock seem to be the same as in the Bering Sea. Possibly the predator spectrum in the Gulf is more diverse, since there are smaller known populations of seabirds and fur seals, two of the major predators in the Bering Sea (Morris et al. 1983). The role of adult cannibals as predators on juvenile pollock in the Gulf also is poorly known.

Alton (1981) termed marine mammals, especially fur seals and sea lions, the probable main predators on Gulf of Alaska bottomfish. Birds and baleen whales were thought to be of unknown importance as predators on juveniles, and sperm whales were also cited as possible important predators. Pitcher (1980, 1981) observed that pollock comprised over 50% of the diets of northern sea lions (Eumetopias jubatus) and harbor seals (Phoca vitulina richardsii) in the Gulf of Alaska. Fiscus (1979) discussed mammal predation on a similar gadid, Pacific hake (Merluccius productus) in more southerly waters. Jewett (1978) observed that Pacific cod (Gadus macrocephalus) preyed mainly on fishes, especially pollock, in the Gulf of Alaska. Feder (1979b) also observed predation on pollock by Pacific cod and by arrowtooth flounder (Atherestes sp.). Livingston (1977) used a simulation model to estimate that the principal predation pressure on Gulf pollock came from Odontocete (toothed) whales, with a secondary removal by fur seals and sea lions, and only a small role of seabirds. Total pollock consumption by marine mammals was estimated at 300,000 metric tons yr^{-1} , and total predation at 1,100,000 metric tons yr^{-1} . Mean lifetime mortality of Gulf pollock was estimated at 0.2-0.4 yr^{-1} by Hughes and Hirschhorn (1979).

3.3.3 Fishery

The harvest of pollock in the Gulf of Alaska is an order of magnitude smaller

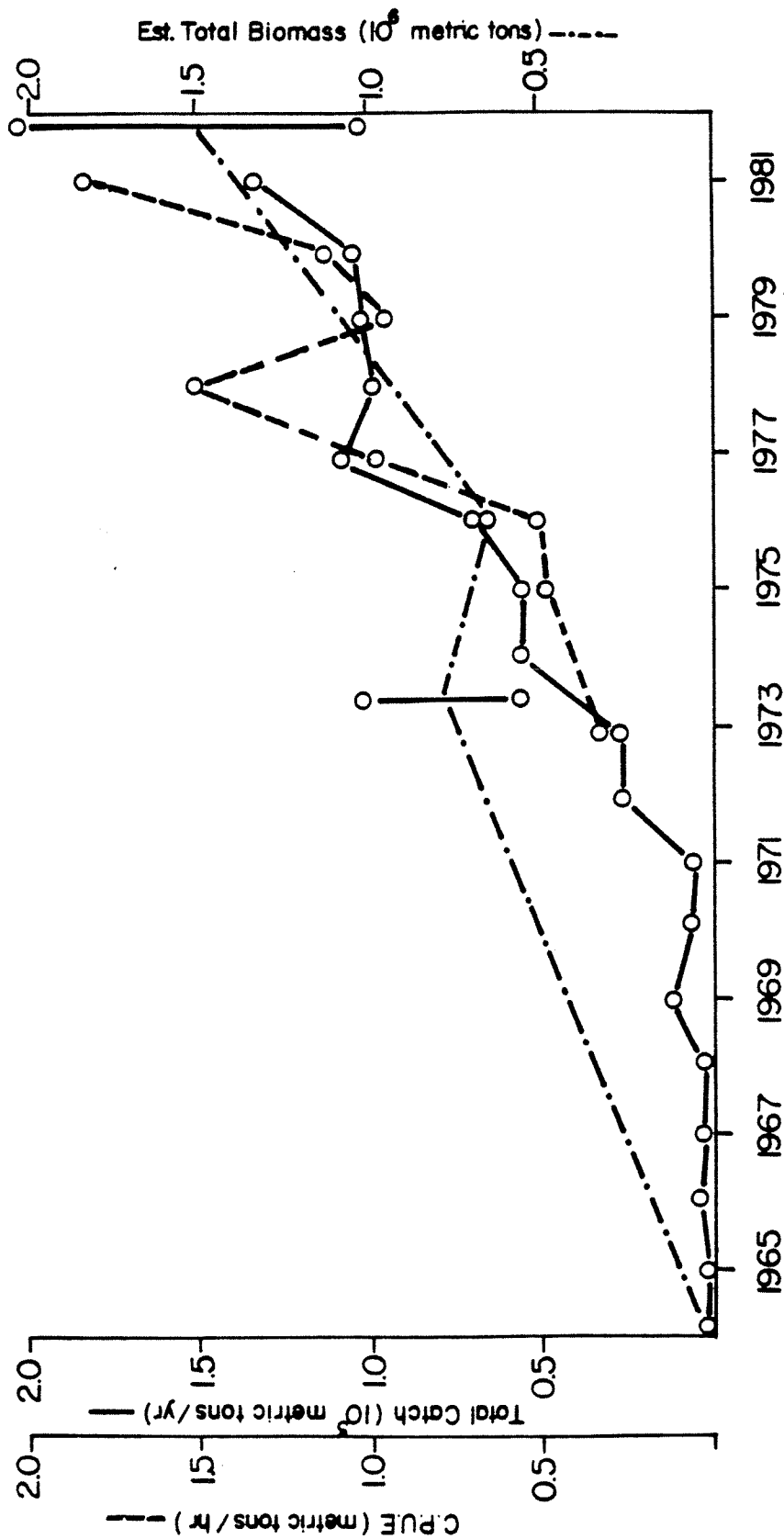


Figure 27. Pollock abundance trends in the Gulf of Alaska as measured by total catch, catch per effort, and estimated total biomass (after Alton and Deriso 1983a; and Ronholt et al. 1978).

that that in the Bering Sea, and yields per unit area generally are lower also (Figure 26). However, the Gulf pollock fishery also is younger than that in the Bering Sea and has been expanding rapidly in recent years (Figure 27). This growth is believed to result from an actual increase in exploitable pollock biomass rather than simply from retargeting or another form of enhanced catchability, and that long-term increase may still be continuing (Alton and Deriso 1983a). Pollock historically were not considered a major constituent of the Gulf of Alaska fishery or community (Bakkala et al. 1979). Alverson (1967) and Reeves (1972) cited Pacific cod and Pacific Ocean perch (*Sebastes alutus*) as the major roundfish in the trawl fishery, although there were suspicions of large unfished stocks of pollock. Flatfishes then accounted for over 50% of the total trawl catch. The recent increase in standing stocks of pollock in the Gulf of Alaska has been thoroughly documented from research trawl data standardized for vessel and gear type (Figure 28). This increase was evident in all areas and in all depth strata (see below). Estimated total biomass and overall mean CPUE increased roughly ninefold (Pereyra and Ronholt 1976).

There is no accepted explanation for this dramatic change. Alton (1981) associated it with overfishing of Pacific Ocean perch, which has a depth distribution and prey spectrum similar to pollock, and may be a competitor, a predator, or both. Annual catch of this species dropped from 350,000 mt out of a record total groundfish catch of 394,000 mt in 1965, to less than 12,000 of a total of 200,000 mt in 1979 (Wall et al. 1981), while pollock catch increased from less than 1% to about 59% of the total trawl catch (Feldman and Rose 1981). Mean CPUE of Pacific Ocean perch in the Gulf dropped from 36.8 kg hr⁻¹ in 1961-62 to 12.7 kg hr⁻¹ in 1973-76 (Ronholt et al. 1978).

Total estimated pollock biomass in the Gulf peaked in 1981 at 3.8 million mt (it may have been higher in 1982 when no survey was made), and has since declined to 2.6 million tons in 1983 because of poor recruitment of the 1980 year class (Alton and Deriso 1983b). The fishery traditionally has been dominated by the foreign catch in the Shumagin Island area during summer (Alton 1983). However, small joint ventures with U.S. fishermen are expanding, and a major fishery is developing during spawning season in Shelikof Strait. Most fish taken are in the range of 35-55 cm in length (3-5 years old), and a significant proportion are females from which roe is harvested (Alton and Deriso 1983a). 1983 roe yield was about 5500 mt and was valued at \$45 million, comparable to the value of the catch for fish flesh (Alton and Deriso 1983b).

The pollock that spawn in Shelikof Strait, treated as a distinct stock for management purposes, produced strong year-classes in five consecutive years, 1975-1979 (Alton and Deriso 1983b). Weak year-classes were produced in 1973-1974 and again in 1980. Estimates of exploitable biomass of this stock have risen from 700,000 mt in 1976 to 2.5 million mt in 1982 (Nunnallee et al. 1982; Alton and Deriso 1983b). The Alaska Groundfish Management Plan set optimal yield for the western Gulf at 169,000-338,000 mt yr⁻¹, compared to a 1979 catch of 103,000 mt (Alton 1981). During the period 1979-1982 harvestable production has been estimated at 500,000 mt yr⁻¹ compared to annual catches ranging between 103,000 and 166,000 mt (Alton and Deriso 1983b). The Gulf of Alaska pollock fishery may thus be considered "immature" in the sense that the resource is underexploited and surplus biomass is available. Furthermore, explorations still are underway to locate fishable concentrations and spawning aggregations of pollock in the Gulf, and to obtain baseline data on the whereabouts of both juveniles and adults following spawning.

3.3.4 Temperature and Climate Relationships

The habitat and environmental conditions preferred by adult pollock in the Gulf of Alaska appear similar to those in the Bering Sea, except that Gulf pollock inhabit slightly higher temperatures. Gulf pollock have a variable depth distribution, controlled, according to Reeves (1972), by a temperature optimum of 2-5°C. Hughes and Alton (1974) observed adult pollock in trawls within the temperature range of 4.4-6.2°C; warmer waters, in which no pollock were found, were generally shallow and

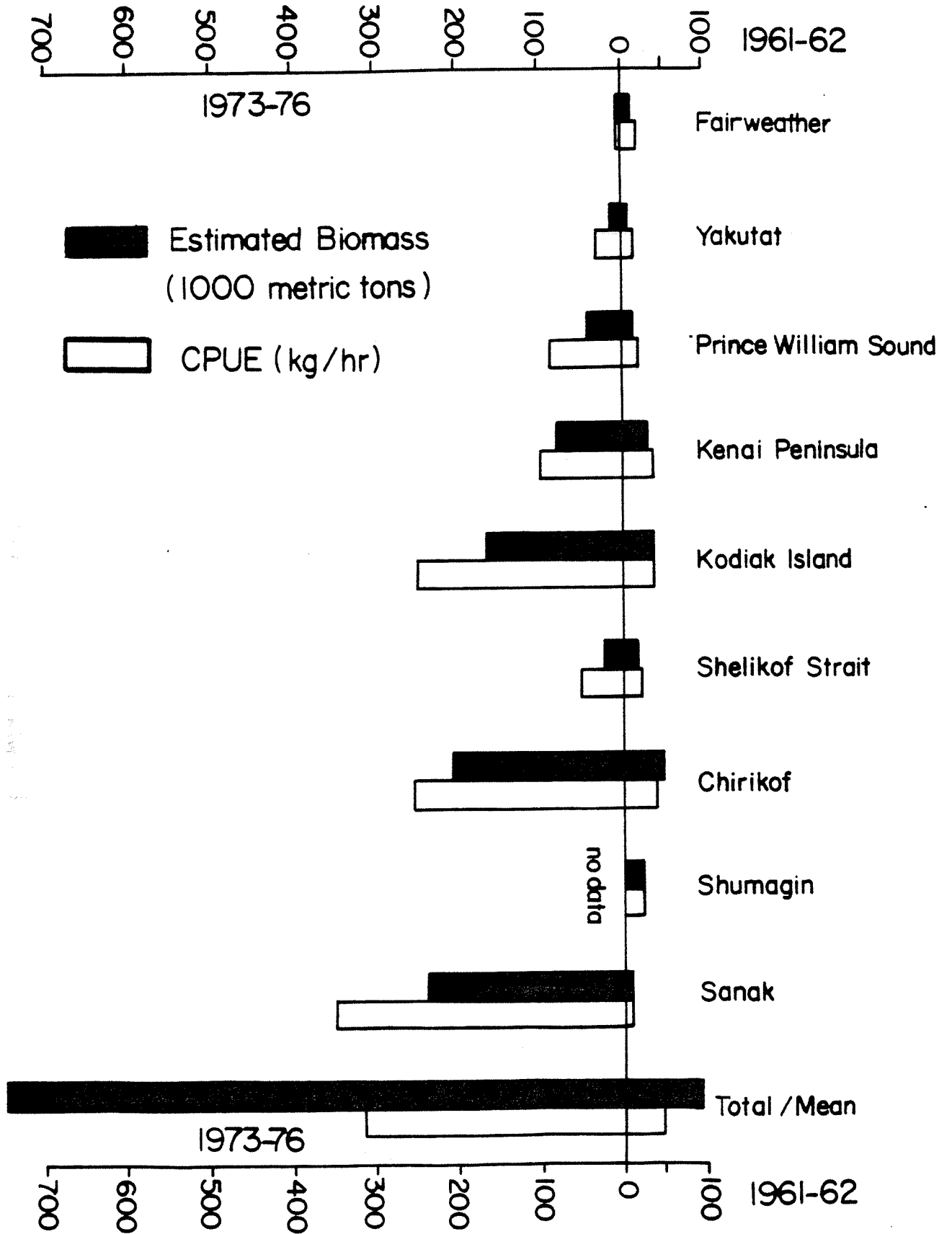


Figure 28. Changes in catch per effort and estimated biomass of pollock in the Gulf of Alaska between 1961-62 and 1973-76, by area and overall (after Ronholt et al. 1978).

strongly mixed. Known spawning activities of Gulf of Alaska pollock occur in midwater where temperatures are uniform with depth at about 5-6°C, below a surface layer with temperatures of 2-5°C (Nunnallee et al. 1982; Brown 1983). Sherman et al. (1983) described intrusions of warm oceanic water into Shelikof Strait during the spawning period in March. Haynes and Ignell (1983) observed pollock eggs in the laboratory to range from 23 days at 2°C to 6.6 days at 11°C; thus most eggs would hatch in about 14 days at 5°C. Except for the 1-2°C temperature difference, these conditions resemble the spawning conditions in the eastern Bering Sea. The Gulf is unique, however, because most pollock spawning appears to be concentrated at a single place and time.

A major unanswered question about the early life history of pollock, therefore, is whether larvae are advected by currents to rearing and recruiting areas significant distances from where they were spawned, and thus whether major upstream migrations of spawning adults must occur, as observed in Pacific hake (Merluccius productus) off the continental U.S. (Francis and Bailey 1983), and as suggested for Gulf of Alaska sablefish (Anoplopoma fimbria) by Balsiger (1982). Avoidance of currents has been shown to influence the life history strategies of several north Pacific coastal fishes (Parrish et al. 1981). Favorite et al. (1977) raised the possibility that larvae of species spawned in the northern Gulf may be transported around the entire Alaska Gyre for a period of 1-3 years before being recruited and spawning near their waters of origin. LeBrasseur (1970), however, reported no gadid larvae ever were sampled in long-term Canadian studies of the oceanic northeast Pacific. Furthermore, the feeding environment for larval and juvenile pollock, which probably consume zooplankton, would be much less favorable in oceanic waters of the Gulf (although the region south of the Aleutians might be quite a favorable one). Thus large-scale transport of pollock larvae does not appear likely.

An alternative hypothesis, that larval and juvenile pollock remain near their spawning grounds, can be formed by examining recent data on the fine structure of currents in the vicinity of Kodiak Island and Shelikof Strait (Figure 22). The velocity of the Alaska Stream is greatly reduced, and at least one persistent countercurrent has been identified, shoreward of the shelf break; wind and surface current reversals have been documented off Kodiak Island and in Shelikof Strait; several intermittent or persistent eddies have been observed that are produced in part by irregularities in coastline and bathymetry; and subsurface cyclonic flow has been documented within troughs. These perturbations reduce both the scalar and vector mean transport over the shelf. Tidal currents also are greatly reduced northwest and southeast of Kodiak Island. Furthermore, the seasonal onset of the mean southwesterly wind pattern and coastal upwelling in the Shelikof region, coincident with the spring minimum in the Kenai Current and the March minimum in tidal ranges and currents, would tend to retard advective losses at that time, especially near the surface. These observations suggest that reductions in strength of the Kenai Current are favorable for survival of juvenile pollock.

A complementary hypothesis has been presented regarding Pacific halibut (Hippoglossus stenolepis). Halibut spawn on the bottom at the shelf break, their larvae drift shoreward and surfaceward, and juveniles rear in shallow bays. Parker and Schumacher (1984) found increased halibut year-class strength in years when the Kenai Current was stronger. From this they inferred that stronger onshore transport of bottom water associated with intensification of the Kenai Current favored the retention of halibut larvae in nearshore rearing habitats. There is insufficient information with which to adequately assess the magnitude and importance of these effects in relation to spawning habitat and year-class strength of pollock, but clearly these data provide a fruitful avenue for further inquiry. The hypothesis that availability of advective refuge at least partly determines sites of successful spawning concentrations in the Gulf of Alaska should be examined in relation to other possible spawning sites such as the Shumagin area and Prince William Sound. In addition, interannual variations in year-class strength of Gulf pollock should be compared to the

corresponding variations in temperature and transport, especially by the Kenai Current.

The overall pattern of adult pollock distribution in the Gulf of Alaska shows highest abundances at shelf break depths (100-300 m) in regions with indented or sheltered areas of continental shelf bathymetry such as the Kodiak shelf, and lowest abundances in such exposed areas as the Yakutat shelf. More irregular areas may offer optimal and stable temperatures, more plentiful food or other beneficial conditions and refuge from advection (for juveniles or adults, or both). Troughs provide increased shelf break length, have current patterns that tend to reduce advective removal, and experience intrusions of slope water that remains at 3-5°C all year. In addition, the indented shelf bathymetry of the Gulf near Kodiak Island and elsewhere provides an increased distance over which pollock may find proper conditions of depth, temperature, and low advection well inshore of the shelf break, where currents are reduced.

There also is a distinct similarity between the longitudinal distributions of pollock and inferred coastal upwelling in the Gulf (Figures 21 and 25). Such upwelling could benefit pollock by means of a reduction in summer water temperatures, and could be linked as well to the apparent enrichment of planktonic food supplies in the western Gulf. Upwelling could have a negative effect of transporting pollock eggs and larvae offshore away from favorable nursery areas, but that effect could be offset by a simultaneous reduction in southwestward transport of surface water. Some support for the hypothesis that food supplies may limit pollock in the Gulf of Alaska is seen in the data of Hughes and Hirschhorn (1979), Brown and Rose (1983a), and Janusz (1983), who attributed smaller individual sizes and growth rates in the strong year-classes of 1967, 1970, 1972, 1975, and 1976 to possible density dependence of growth. Strong year-classes have been observed in the Shelikof Strait pollock population for at least five consecutive years, 1975-79, with the strongest classes in the latter years of that period. Comparison of these data to physical data on temperatures and transport could provide insights into the mechanisms controlling pollock abundance in this region.

4.0 CLIMATE EFFECTS ON POLLOCK: ANALYSIS

At the present time there is no clear understanding of how pollock abundance is regulated by the environment. Anticipating the effects of climate change on pollock must therefore be an exercise in uncertainty. It is not possible to hindcast the pollock response to past climates, so it could not be possible to forecast the pollock response even to a known future climate. This report outlines the major mechanisms, according to present knowledge, that should govern that response.

There are two major limitations on this analysis. First, quantitative relationships between pollock and its environment generally are lacking, so only qualitative descriptions of processes can be made. Second, there is no basis on which to assess possible interactions between the various mechanisms described below. Multiple pathways of environmental influence are possible, but in the absence of direct observations or quantitative relationships their relative importance is difficult to establish. This report mainly discusses the possible mechanisms and attempts to ascertain which of them are the most appropriate as subjects of further research.

4.1 FACTORS REGULATING POLLOCK ABUNDANCE

To understand the causes of fluctuations in pollock abundance in the Bering Sea and Gulf of Alaska, it is necessary to look at more than simple changes in total biomass or fishery yield. It is necessary to examine the populations in terms of their age structures. The population sizes and biomasses of cohorts of pollock spawned in successive years-- the strengths of successive year-classes-- are not constant; instead, variations in year-class strength cause the age structure of pollock stocks to vary. Single strong year-classes, interspersed among weaker year-classes, can dominate the fishery catch for several years. Substantial and prolonged increases or decreases in the exploitable biomass of pollock result from series of successive strong or weak year-classes, as were observed during the late 1970's in both the Gulf of Alaska and the eastern Bering Sea. The central exercise in determining the relationship between environmental factors and pollock abundance, therefore, is to isolate and identify the factors controlling year-class strength.

A practical problem with studying dependence of year-class strength on the environment is that surveying abundance of pollock (especially juvenile stages) is time-consuming, expensive, and not necessarily reliable. Currently year-class strength is not reliably known until the age of recruitment to the fishery (that is, the age when fish of the year-class begin appearing in the commercial catch), which ranges from two to six years after spawning. Unfortunately, the determinants of year-class strength occur before recruitment to the fishery, during periods of the life cycle that are not closely monitored. Consequently we do not directly observe the factors that determine year-class strength. Pollock mortality rates are very high and variable during the egg and larval stages, and drop significantly and stabilize during the juvenile phase. Thus it appears that environmental conditions at some stage of immaturity must control the quantity of fish that will become available to enter the fishery. Therefore, analysis of possible effects of climate change will focus on environmental influences to which pollock appear to be most sensitive during this critical period. Both the exact age and the particular environmental conditions that are of importance are poorly known, however, and may vary in different locations and times.

No dominant mechanism has been demonstrated to control pollock year-class strength in the eastern Bering Sea. Predation and cannibalism have been investigated as possible control processes, but recent evidence suggests that food supplies also may be important. The climate-related properties of the abiotic environment that affect these biotic processes include surface and bottom temperature, currents, vertical stability, ice cover, and frontal structures. Surface temperature affects growth and development rates of early life history stages of pollock, and of their prey. Currents influence the areal dispersion of pollock eggs and larvae. Vertical stability affects both

primary productivity and the feeding abilities of pollock and their predators. Ice cover and bottom temperature distributions limit the northward and shoreward penetration of adults and evidently determine the geographic distributions of spawning, and so of eggs and larvae. All of these factors may affect the spatial distribution of juvenile pollock relative to predatory seabirds, mammals, and adult pollock.

It is more difficult to evaluate the biological and climatic factors controlling pollock year-class strength in the Gulf of Alaska, where there is no significant ice cover, and bottom temperatures are less variable than in the eastern Bering Sea. Warm temperatures or resource competition at the southern end of the Gulf may set a boundary on the geographic extent of commercially exploitable pollock populations. There are few data on the importance of prey, predators, or cannibalism. The most pressing questions concerning control of pollock year-class strength in the Gulf center around the influence of wind stress, runoff, and advection on the distribution of juvenile pollock and their food supplies in the western Gulf.

Pollock of all ages can thrive only within a specific range of environmental conditions such as temperature, pH, and salinity. Temperatures below or above optimum retard the growth and development rates of very young fish, and also may impair their abilities to capture food and avoid predation. Growth rates of adult and to some extent juvenile fish are less affected, due to their mobility to seek waters of optimal temperature, but resulting alterations of migration patterns can themselves have biological consequences. Temperature also can affect pollock by altering other properties of its environment. Sensitivity to climate change involves more than simply physiological responses of fish to water quality; temperature-related changes in the physical and biological organization of the environment appear an equally likely avenue by which the impacts of climatic change will be felt. Climatic effects on pollock (which are in fact indirect effects of increasing atmospheric CO₂) that are mediated through changes in water motions, food supplies, competition, and predation are more complex and therefore more difficult to predict, but may be equally important.

These factors and their anticipated impacts on eastern Bering Sea and Gulf of Alaska pollock are summarized in Table 5. Impacts to which pollock are judged to be most sensitive are indicated. As a gross generalization, recent series of strong pollock year-classes in both areas have been associated with multi-year warming periods, prompting speculation about improved fishing under climatic warming. To clarify the possible mechanisms of climatic effects on pollock, the intermediate effects on the physical and biological environments are treated separately below.

4.2 PROJECTED ABIOTIC EFFECTS OF CLIMATE CHANGE IN THE STUDY AREA

4.2.1 Water Temperature

Prediction of the range of water temperatures to be encountered within the study area under a climatic warming scenario is beyond the scope of this report. Estimates of air temperature increases at high latitudes as a result of a doubling of atmospheric CO₂ concentrations are in the range of 8°-10°C (NRC 1983). Surface water temperature increases would be lower due to the higher heat capacity of water, and deep water temperature increases would be smaller still, at least over the same time scale. Revelle (1983) projected equilibrium increases in zonal mean ocean temperatures for a doubling of atmospheric CO₂ (half of the temperature increase for a CO₂ doubling and increased trace gases). At the latitudes of the southeastern Bering Sea and northern Gulf of Alaska these increases are roughly 3.5°C at the surface and 2.5°C at 200 m. However, dynamic considerations such as alteration of current and turbulence patterns would complicate the response of water temperature to atmospheric warming.

Revelle's estimates may be more applicable to the Bering Sea shelf, where temperatures are regulated mostly by air/sea heat exchange, than to the Gulf of

TABLE 5. Projected Climate Effects on Bering Sea and Gulf of Alaska Pollock

CLIMATIC STIMULI AND ABIOTIC EFFECTS	BERING SEA BIOLOGICAL EFFECT	EFFECT ON BERING SEA POLLOCK	GULF OF ALASKA BIOLOGICAL EFFECT	EFFECT ON GULF OF ALASKA POLLOCK
Increased Water Temperature	Increased growth and development rates of all species	<u>Northward expansion of habitat</u> Increased exploitable population; earlier spawning; reduced stock difference	Increased growth and development rates of all species	Northward contraction of habitat Possible reduction of southern stocks, replacement by hake
Surface temperature		Possible enhanced feeding and predator avoidance	Same	Same
Bottom temperature		Earlier onshore and northerly migration, broader spawning	Negligible	Negligible
Decreased Ice Cover	<u>Increased bird and mammal predation</u>	Decreased yield	Not applicable	Not applicable
Decreased surface stability	Middle shelf: Plankton growth decrease in spring, increase in summer	<u>Reduced juvenile refuge from cannibalism</u> Possible increased larval food supply, possible decreased feeding ability	Not applicable	Not applicable
Increased Surface Stability	Outer shelf: Earlier and greater plankton growth	Increased juvenile and adult food supply and feeding ability	Same	Same
Increased Precipitation and Freshwater Addition	Negligible	Increased juvenile refuge from cannibalism	<u>Increased coastal current strength and larval transport</u>	? Uncertain effects on larval survival

TABLE 5 (continued). Projected Climate Effects on Bering Sea and Gulf of Alaska Pollock

CLIMATIC STIMULI AND ABIOTIC EFFECTS	BERING SEA BIOLOGICAL EFFECT	EFFECT ON BERING SEA POLLOCK	GULF OF ALASKA BIOLOGICAL EFFECT	EFFECT ON GULF OF ALASKA POLLOCK
Northward Shift of Storm Track Decreased stability	Dispersal of prey aggregations for larval, juvenile, and adult pollock, cannibals and predators	Increased cannibalism but decreased predation and feeding	Not applicable	Not applicable
	Outer shelf: Decreased and later plankton growth	Reduced juvenile and adult food supply		
	Middle shelf: Plankton growth decrease in spring, increase in summer	Possible increased larval food supply		
Increased stability	Not applicable	Not applicable	Increased and earlier plankton growth	Increased larval, juvenile, and adult food supply
Net southwest winds	Disruption of fronts and plankton aggregations?	Disruption of food supply?	<u>Decreased downstream transport of larvae</u>	Uncertain effects on larval survival
		Transport out of nursery habitat?	<u>Increased upwelling, offshore larval transport, and plankton growth</u>	Increased larval, juvenile, and adult food supply; uncertain effects on larval survival
DOMINANT FACTORS Reduced stability	Effects on plankton growth and prey aggregation	Effects on cannibalism and predation offset by habitat expansion and fishery	Not applicable	Not applicable
Decreased currents	Not applicable	Not applicable	Changes in larval transport	Effects on retention in nursery habitat

Underlining indicates probable dominant effects.

Note: This table indicates only partial effects of individual climate-fishery mechanisms. Interactions between these processes are unknown.

Alaska shelf, which is significantly affected by currents. In both environments such changes could occur rapidly, since mean summer surface temperatures in both areas have fluctuated over a range of 4°C during the last decade (Niebauer 1983; Xiong and Royer 1984). In the eastern Bering Sea, increased air temperatures also would affect the seasonal and areal magnitude of sea ice cover. Ice extent is highly variable interannually, with virtually the entire shelf frozen in cold years and almost none in warm years under present climatic conditions. It must be assumed that seasonal ice cover in the Bering Sea would be drastically reduced or even eliminated in response to climatic warming. Incze (1983) has called ice extent the most climate-sensitive aspect of the physical environment of the Bering Sea.

4.2.2 Water Motions

Water motions relevant to biological processes can be categorized as organized (advective) motions that cause a net transport of water, and chaotic (turbulent) motions that cause no net transport. These motions may be horizontal or vertical. Net horizontal motions (currents) are induced by wind stress of consistent direction, and by lateral pressure gradients associated with temperature and salinity distributions. Net vertical motions (upwelling and downwelling) are associated with divergence and convergence of horizontal currents. Both horizontal and vertical motions also may be associated with the passage of planetary waves propagated from wind forcing at remote locations. Turbulence may be caused by instability (vertical convective instability occurs under surface cooling conditions, and flow instability may occur both vertically and horizontally). Turbulence also results from mixing due to energy transfer from winds. Resistance to vertical turbulence is offered by vertical stability, resulting from buoyant surface heat or freshwater input. Each of these types of motion has differing biological effects.

Turbulence. Under present mean conditions, weak vertical water column stability characterizes most of the oceanic and neritic waters of the Bering Sea and Gulf of Alaska for most of the year. The middle shelf domain of the eastern Bering Sea is strongly stable during spring and summer due to surface icemelt. Seasonally strong surface stability also occurs in nearshore regions of the Gulf of Alaska due to surface heating in summer (e.g., Kachemak Bay) or freshwater addition (e.g., Cook Inlet and Kenai Current). In general climatic warming, together with glacial melting and increased net precipitation, would increase stability in all these areas. However, in the middle shelf domain of the Eastern Bering Sea, reduction in ice cover associated with warming should increase spring and summer surface salinities and thus decrease vertical stability.

The present pattern of vertical stability also could be altered by changes in wind patterns. Strong turbulence is imparted by the passage of storms, and regions experiencing increased storminess would be destabilized, while regions of decreased storminess would stabilize. Climatic warming might be expected to shift present atmospheric pressure patterns and the associated storm tracks northward, and possibly to decrease latitudinal pressure gradients and so decrease the intensity of storms. According to this scenario the Gulf of Alaska would experience a decrease in storm frequency and intensity that would reinforce thermal stabilization. The eastern Bering Sea would experience an increase in storm frequency (if not intensity) that would cause destabilization, counteracting thermal effects over most of the area but reinforcing them in the middle shelf domain. The projection that storm tracks might shift northward as a result of climatic warming is not verified, however, and must be tested against theoretical analysis and empirical evidence.

Horizontal perturbations in flow patterns, usually taking the form of eddies, have numerous causes. These include instabilities in currents, bathymetric steering, complexity of hydrographic structure, and interactions of all these factors with planetary waves. Eddies may be most common in regions of strong horizontal current

shear, and may be transported along or across the mean flow pattern. No general relationships exist from which to project the possible responses of eddy generation mechanisms to large-scale changes in temperature, wind speed and direction, or freshwater addition associated with climate change.

Currents. At the present time current patterns in the eastern Bering Sea and the Gulf of Alaska are consistent with the mean wind patterns, especially as reflected by the positions of storm tracks that pass over the central Gulf in winter and the Aleutian region in summer. Near the centers of storms tracks, changes in wind direction as a storm passes do not generate consistent net lateral motion of surface water. This is the present situation on the southeastern Bering Sea shelf (Overland 1981). At some distance from storm tracks, prevailing winds induce currents that may be modified by land masses and bathymetry, as observed in the Gulf of Alaska. Under climatic warming and northward translation of atmospheric pressure patterns, the summer storm track would persist for a greater portion of the year. This would induce a net increase in frequency of southwesterly winds, which might be expected to weaken mean currents in the Gulf and possibly to increase them in the Bering. Changes in large-scale mean current patterns would be gradual over a period of years, due to slow readjustment of the hydrographic structure in the upper 1000-1500 m of the water column. Changes in wind-driven currents over the shelf would respond much more quickly, however, over time scales of days to weeks. Since mean currents on the southeastern Bering Sea shelf are weak under present conditions, the potential for significant change exists. A possible induction of net northeastward currents might disrupt the existing frontal structures over the shelf, with physical consequences that are difficult to foresee.

The increases in precipitation and freshwater input projected for higher latitudes (NRC 1983) also could affect currents in the coastal domains of the study area. These factors might increase the strength and reduce the seasonal variability of freshwater-driven currents, principally the coastal Kenai Current in the Gulf of Alaska. This increase would interfere with the projected reduction in wind-driven currents on the shelf. An increase in the frequency (if not the intensity) of southwesterly winds should affect larval and juvenile pollock spawned in Shelikof Strait, but until the distribution of these life stages and their relationship to present advection patterns is known, only speculation is possible. However, more frequent southwesterly winds should increase the seasonal extent and possibly the intensity of coastal upwelling south of the Alaska Peninsula, and also should increase the residence time of surface water in Shelikof Strait (Ingraham et al. 1976). This tendency also would be opposed by intensification of the Kenai Current, but such freshwater effects probably would not extend off the shelf to the Alaska Stream. Although it is not certain whether relaxation and increased frequency of southwesterly winds under present summer conditions cause a decrease in transport in the Alaska Gyre, theoretical calculations predicting such an effect (e.g. Favorite et al. 1976) may be used to infer a decrease under climatic warming.

4.3 PROJECTED BIOTIC EFFECTS OF CLIMATE CHANGE IN THE STUDY AREA

4.3.1 Effects of Water Temperature

Effects on pollock. The geographic range of pollock in the north Pacific and adjacent seas appears to be strongly influenced by temperature. Inada (1983) theorized that pollock spread to the Pacific from the Atlantic via the Arctic Ocean and the Bering Strait during a warmer period in the Pleistocene epoch. He also suggested that the warmer-water gadid Pacific hake (Merluccius productus) colonized the Pacific during the Miocene era when the Central American isthmus was open. The present boundary between ranges of the two species in the eastern Pacific may result from differing temperature tolerances, or from competition in the neighborhood of

Washington and British Columbia. Pollock extend farther south in the western Pacific (Figure 1), possibly due to the absence of hake, which may have been obstructed in its geographic spread along the continental shelf by the presence of pollock. Gong and Zhang (1983) related the southernmost extent of pollock in the western Pacific to a cold current from the north that maintains 2-5°C conditions along the east coast of Korea.

Commercial concentrations of pollock are found in the northeast Pacific and eastern Bering Sea mostly within the temperature ranges of approximately 1-14°C (surface) and 1-6°C (bottom). 2.0-3.5°C appears to be the range of optimal bottom temperature for spawners in the eastern Bering Sea (Lynde 1984). A higher optimal temperature range for the Shelikof Strait spawning aggregation in the Gulf of Alaska may be inferred from the ambient 5-6°C temperatures (e.g. Brown 1983). Commercial concentrations of pollock may be excluded from northern shelf areas of the western Bering Sea by very cold temperatures associated with the Okhotsk Sea and the East Kamchatka Current. North of about 60°N in the eastern Bering Sea, winter and spring temperatures become inhibitory to adults and lower larval growth rates are observed (although not necessarily as a direct result of temperature). Summer surface temperatures are relatively high over much of this region, however, due to vertical stability. Although the Gulf of Alaska is situated at similar latitudes to the Bering Sea, winter temperatures are warmer and more uniform around its perimeter as a result of strong advective input of more southerly Pacific water. East of roughly Shelikof Strait, water temperatures may be above optimal for pollock, since abundance declines beyond this point and fishable concentrations are associated with deep canyons and straits.

It thus would be anticipated that climatic warming would cause a shrinkage of the southern end of the range of Alaska pollock. A possible replacement of pollock by Pacific hake (Francis and Bailey 1983) also could be hypothesized. The distribution of pollock in the northeast Pacific generally coincides with the extent of the Alaska Gyre, and a northward shift of the Gyre system (including the Subarctic Current) associated with warming would likely bring an influx of unfavorable warm Transition Zone water (Favorite et al. 1977). Such a shift may have occurred temporarily during the "El Nino" summer of 1983, and study of 1983 conditions might provide a preview of consequences of CO₂-induced warming. Shrinkage of range might be less in the western Pacific due to cooling by the Oyashio Current from the north. The replacement of pollock by hake, should it occur, might at least partially mitigate impacts on overall fishery yield.

Potential northward expansion of the pollock range in the Bering Sea would be regulated principally by reductions in winter ice cover. The areal extent of bottom temperatures that are inhospitable to adult pollock is closely linked, in the absence of bottom currents, to ice extent. The sensitivity of pollock migrations to interannual temperature differences as mediated by ice extent could make this ecosystem an ideal one for monitoring climatic impacts on fisheries.

Under ice-free conditions, adult pollock might inhabit the entire length of the shelf break and upper slope of the eastern Bering Sea in winter, and spawn over the entire outer and middle shelf domains. Removal of bottom water temperature limitations thus could as much as double the effective habitat for eastern Bering Sea pollock, without displacement of other commercial species. Associated with this expansion would be more uniform in growth rates and stock structures between northern and southern areas. The concomitant increase in standing stocks, however, would depend on associated biotic effects that are not easily determined. Logistics of fishery operations could be aided by warmer temperatures and reduced problems with vessel icing. However, warming could have a slight compensating effect that would tend to reduce availability of pollock to fishing vessels. Both fishing and predation are most efficient when the prey are concentrated over a small area. Under present conditions adults can be observed to concentrate near the shelf break during cold springs, making them more accessible to fishing (Lynde 1984). With the broader

dispersal of adults due to warming, greater effort might be required of predators and fishermen to locate and take the same pollock catch.

The western Bering Sea and Okhotsk Sea shelves, which are colder than the southeastern Bering Sea shelf (Sancetta 1983), might become hospitable for commercial pollock stocks due to climatic warming. It is also possible that pollock could colonize waters north of the Bering Strait, as inferred for the Pleistocene by Inada (1983). Although the Strait may be too shallow to be inhabited by adults, advection of juveniles could provide a seed population. The extent to which such colonization might be possible would depend on the extent of Arctic ice cover over the preferred adult depth habitat, the outer shelf and upper slope. Since ice advances landward in the Arctic Ocean (rather than seaward as in the Bering Sea), it appears that adults could become established only if seasonal ice and the associated bottom temperatures extended no farther inshore than the 100 m isobath, and more likely the 200 m or 300 m isobath. These requirements make colonization more likely in the Beaufort Sea, with a narrower shelf, than in the Chukchi Sea.

Surface water warming would accelerate the development rates of pollock eggs, larvae, and juveniles in both the eastern Bering Sea and the Gulf of Alaska. This acceleration might enhance the abilities of larvae and juveniles to feed and to avoid predation, but such effects have not been demonstrated in the laboratory (Incze et al. 1984). Faster development causes reduced length at a given life cycle stage and higher mortalities of pollock larvae have been observed at temperatures above 2°C in the laboratory (Hamai et al. 1971). The effects of accelerated larval growth rates on pollock year-class strength cannot be fully assessed without knowledge of the effects of warming on prey and predators (including cannibals). Furthermore, changes in timing and distribution of feeding and predation could be as important as simple changes in biomass.

Effects on prey. Climatic warming could affect the food supplies of pollock both by altering the mean abundance of prey and by altering their spatial and temporal distributions. These factors could in turn be controlled by the effects of both temperature and water motions. Although there is not yet direct evidence that pollock year-class strength in the study area is affected by existing fluctuations in prey abundance, major reductions in plankton production or spatial/temporal availability could have serious consequences. Larval and juvenile pollock consume mainly zooplankton (copepods and euphausiids) and other crustaceans larvae. These organisms in turn consume phytoplankton. Increasing surface water temperature will accelerate growth and development processes of plankton as much as they do those of pollock. Eppley (1972) estimated that maximum phytoplankton growth rates double with a 10°C temperature increase. Vidal (1980) recently obtained extensive laboratory data documenting accelerated development of North Pacific copepods with increasing temperatures. If there is an adequate phytoplankton food supply this acceleration should increase pollock food supplies.

Temperature effects are different on different plankton species, and shifts to more southerly species assemblages are a possible result of climatic warming. However, within the variability of existing data no temperature-related areal differences in plankton species composition are evident within the study area. We might assume, therefore, that latitudinal shifts in plankton communities related to water temperature above would arise only from major hydrographic alterations of the sort that also would by themselves alter the latitudinal range of Alaska pollock.

It is possible that warming could upset the present synchronization of the seasonal pollock life cycle with those of zooplankton, or that of zooplankton with the seasonal abundance of phytoplankton, by accelerating one more than the other. Such desynchronization could disrupt the pollock food chain, by producing food when it is not needed or causing reduced food availability during critical periods. Seasonal life cycles of the dominant zooplankton on the eastern Bering Sea and Gulf of Alaska oceanic and outer shelf domains-- euphausiids and the large copepods Neocalanus spp.--

are ontogenetically programmed like those of pollock, with one generation per year in the spring, overwintering in deep water, and reproductive effort dependent on past nutrition. Alteration of the timing of life cycles, and disruption of the synchronization would be much less likely among these animals than among smaller organisms which have more plastic seasonal reproductive patterns and remain closer to the surface all year. Seasonal patterns of spawning and abundance of smaller middle shelf copepods (such as Pseudocalanus spp. and Acartia spp.) are dependent on temperature and abundance of phytoplankton within the previous several weeks, and phytoplankton production is highly variable on meteorological time scales of a few days to a month. Therefore the greatest potential for desynchronization of juvenile pollock food supplies lies in the inner and middle shelf domains in the spring and summer. The possibilities for desynchronization will be determined by changes in stability and advection in addition to simple physiological temperature responses.

Effects on predation and cannibalism. Few data are available on field responses to warming of adult fishes or marine birds and mammals of the northeast Pacific and Bering Sea. Many of the bird and mammal species are among the most migratory animals in the world, and this adaptability could provide resistance to climatic change. Some ice-dependent animals such as the walrus could be displaced northward, but the dominant predators on juvenile pollock-- murre, kittiwake, and fur seal-- probably would be affected less. Possibly the major factors affecting these predators would be changes in abundance of pollock and other prey, rather than physiological effects of temperature. There are several ways in which warming could distinctly change the availability of juvenile and adult pollock to predators.

The most significant climate-related change affecting predation on juvenile pollock would likely be reduction of ice cover. Ice excludes air-breathing bird and mammal predators, and the cold water that persists below ice even after it has melted appears to exclude cannibalistic adult pollock. Thus ice cover is believed to be an important source of refuge from predation for juvenile pollock in the eastern Bering Sea, and its elimination could significantly increase both the geographic and the seasonal extent of predation pressure there. Expansion of predation would likely parallel whatever areal expansion of pollock habitat might occur as a result of warming. Such a potential increase in predation pressure could at least partially offset any increase in pollock standing stocks generated by expansion of habitat.

The effects of warming on predation in the Gulf of Alaska are more difficult to speculate upon due to lack of data, but would probably be less dramatic than in the Bering due to the absence of ice effects. The lack of information, especially on the incidence of cannibalism, is unfortunate since it could provide a useful contrast and a guideline for the role of predation in an ice-free environment.

4.3.2 Effects of Currents

Effects on prey. Currents affect pollock food supplies mainly by means of coastal upwelling, which stimulates phytoplankton production. Such a stimulation would accompany the projected increase in upwelling south of the Alaska Peninsula in the Gulf of Alaska. This increase might take the form of an earlier onset and longer duration of seasonal production rather than a higher peak intensity. Increased primary production should support increased populations of zooplankton of all sizes. Whatever the relationship between currents and pollock year-class strength in this region, increased food supplies should improve the fitness of those juveniles that successfully reach nursery waters.

In the southeastern Bering Sea the relationship between currents and plankton abundance is not so clear. Net southwesterly winds and the resulting coastal downwelling would seem to have little effect on primary production of open waters over the shelf. The greatest potential advective alteration could result if the frontal system were disrupted, possibly permitting Neocalanus spp. to reach middle shelf

waters. Such an intrusion could increase middle shelf zooplankton standing stocks and reduce carbon flux to the benthos. It is not clear, however, that Neocalanus could complete its life cycle in the shallow waters of the middle shelf domain, and thus it might not become established in significant numbers.

Effects on pollock. Transport of pollock and eggs and larvae away from suitable nursery waters is one of the principal hypothetical mechanisms thought to control year-class strength of marine fishes (e.g. Wooster 1983). Although such a mechanism has not been conclusively demonstrated to affect larval survival in the study area, attention has been focussed on the implications of the weak currents on the southeastern Bering Sea shelf and the strong currents in Shelikof Strait for pollock life cycles. It is reasonable to expect that major alterations in advective conditions in these environments could have important effects on pollock survival. If any change were to occur in Bering Sea currents as a result of warming, it would most likely be increased northward flow on the southeastern shelf. The possible effects of the resulting northward displacement of pollock larvae can only be speculated upon. As a first approximation it might be assumed that warming would cause environmental conditions on the northern shelf to resemble present conditions on the southern shelf, so that the principal effect would be habitat expansion. However, the actual outcome would depend on relative effects on prey and predators and spawning distributions.

Both the relationship of current strength to larval survival and the possible change in current strength under warming in Shelikof Strait are uncertain. Reduced westward advection associated with a net increase in southwesterly winds would seem to favor larval retention near nursery areas, but associated coastal upwelling could prevent the shoreward transport that might be necessary. The same advective changes could introduce colder western and deep waters into the western Gulf shelf, that would probably correspond more closely to inferred optimal temperatures for pollock, especially under a warming scenario. Increased Kenai Current transport caused by increased freshwater addition could increase downstream losses but also could favor retention close to shore. Resolution of advective effects on larval survival would appear to be the most critical climate-related question to be answered about Gulf of Alaska pollock.

The linkage of planetary waves to biological phenomena in the ocean is just beginning to be recognized. Mysak et al. (1982) correlated pink salmon and herring yield with long-period wave patterns off British Columbia, and Barber and Chavez (1983) described in more detail the biological effects of waves associated with "El Nino" off Peru. These waves are propagated over ocean basin spatial scales from their points of origin, and changes in existing wave patterns could contribute significantly to the effects of climate change on fisheries.

Effects on predation and cannibalism. Large pollock predators such as birds, mammals, and adult fishes are not themselves affected by currents although they could be affected indirectly through changes in food supply. However, changes in current patterns could affect pollock year-class strength if eggs, larvae, or juveniles were transported into waters providing a greater or lesser degree of refuge from predation and cannibalism. Francis and Bailey (1983) speculated that in some years under present conditions larvae in the eastern Bering Sea may be transported into shallow or cold waters from which cannibalistic adults are excluded. If enhanced northward currents associated with climate change were to increase such transport (and especially if bottom water temperatures remained low), survival could be increased. Another potential effect would be disruption of the frontal system over the eastern Bering Sea shelf, which by dispersing pollock aggregations might reduce losses to seabirds (Kinder et al. 1983) and possibly other predators. Altered advection in the Gulf of Alaska also might change predatory losses by affecting dispersal of larval and juvenile pollock.

4.3.3 Effects of Water Turbulence

Effects on prey. Vertical mixing and stability are opposing influences that are both necessary for primary production. With an optimal balance between the two, stability maintains phytoplankton in bright light near the surface while mixing provides a continuous supply of nutrients from below (Strickland 1983). Weak stability disperses phytoplankton deep in the water, reducing available light for photosynthesis. Strong stability, although very favorable (particularly for production of flagellates) as long as nutrient supplies last, leads to nutrient exhaustion and reduced productivity when prolonged.

In most Gulf of Alaska and eastern Bering Sea waters, which are weakly stable, primary production would increase and begin earlier in the season as a result of the stabilizing influence of warming and increased freshwater input. In inshore areas of the Gulf such as Kachemak Bay, earlier production would be observed along with earlier nutrient depletion, so that annual production might not change significantly. Dramatic effects on primary production would be expected in the strongly stable middle shelf domain of the eastern Bering Sea, caused by reduction in icemelt and the associated vertical stability. The vigorous spring diatom bloom now observed would be reduced in magnitude, but primary production would be sustained over a longer period, and mean annual primary production might even increase. The projected increased frequency of storms could likewise reduce spring primary productivity, but increase summer and perhaps annual production (Sambrotto and Goering 1983).

The principal effect of these changes in phytoplankton production and temperature on zooplankton would be increased production of small copepods, especially in the Bering middle shelf. This increase would generally improve food supplies for larval pollock, rather than disrupting synchronization in the pelagic food chain. Reduction or delay of the spring diatom bloom on the already weakly stable outer shelf of the Bering Sea by reduced icemelt and increased storminess could decrease production of larger zooplankton, especially of the large copepods Neocalanus spp. that feed mostly early in the season. This decrease could reduce food supplies for juvenile pollock. In the middle shelf domain, however, curtailment of the ungrazed spring bloom would reduce the loss of fixed carbon to the benthos, and divert part of it into the pelagic food chain later in the season. That is, primary production on the middle shelf could come to resemble the present condition of the outer shelf. Although beneficial for pollock, this diversion might be detrimental to demersal fish and shellfish production.

Effects on pollock. Potentially as important as zooplankton standing stocks for juvenile pollock nutrition is the spatial distribution of prey. Predators in the sea are generally believed to feed more effectively when prey are aggregated in "patches," and turbulence reduces effective prey availability by dispersing these aggregations. Incze (1983) associated poor year-classes of tanner crabs (Chionoecetes spp.) in the eastern Bering Sea with storm-induced vertical mixing during a critical spring feeding period in warm years such as 1980. Cooney et al. (1979) also associated a strong 1977 year class of pollock with calm conditions in April of that year. Thus the predicted destabilization and increased storminess in the eastern Bering Sea might hamper feeding of juvenile pollock, while increased stability in the Gulf of Alaska should improve feeding conditions.

Eddy perturbations in horizontal currents have the effect of reducing vector mean transport of suspended fish eggs and larvae. Such eddies may be a major factor in the retention of pollock within nursery areas during maturation, especially in the Shelikof Strait and Kodiak Shelf regions of the Gulf of Alaska. Although they are difficult to identify with the present state of knowledge, any climatic changes that might increase eddy generation in the study area would be expected to increase larval retention and consequent survival.

Effects on predation and cannibalism. The balance between vertical stability and turbulence, in addition to affecting the abundance and availability of pollock prey, also affects the availability of juvenile pollock to predators and cannibals. Storm-induced turbulence that disperses aggregations of juvenile pollock has been observed to hamper the feeding and the consequent reproductive success of surface-feeding predators such as kittiwakes. It is uncertain whether effects of changes in predation pressure on juvenile pollock associated with changes in turbulence would be offset by changes in the degree of aggregation and availability of zooplankton prey.

Recent data from the middle shelf domain of the eastern Bering Sea indicate, however, that vertical stability in summer may provide a refuge from cannibalism by retaining age 0 pollock in the upper water column where they are unavailable to adults (Dwyer et al. 1983). Breakdown of stratification in autumn appears to be associated with onset of cannibalism on young-of-the-year, although attainment of a critical minimum size by juveniles cannot be excluded as the trigger for cannibalism. Therefore increased turbulence in this domain might shift mortality of juvenile pollock away from predation and toward cannibalism. The effects of changes in turbulence on patterns of predation and cannibalism in the Gulf of Alaska would probably be smaller than those in the Bering Sea. The increase in stability projected for this region would seem to favor bird and mammal predation over cannibalism as a source of mortality.

5.0 SUMMARY AND CONCLUSIONS

The eastern Bering Sea shelf region is an intensely seasonal environment characterized by ice cover and extreme low temperatures in winter, and weak currents and strong vertical stability over the middle shelf in summer. Available data indicate that food supplies have been adequate in the years that have been studied, so that pollock year-class strength appeared to be controlled by effects of predation (including cannibalism). The abiotic conditions and alterations to which pollock year-class strength seems most sensitive are: ice cover and cold bottom temperatures that exclude predators and cannibals for much of the year from shelf waters inhabited by juveniles; and vertical stability of surface water, which provides juvenile pollock both an hospitable feeding environment and refuge from deeper-living cannibalistic adults. Warming, with a possible corresponding increase in frequency of storms, would greatly reduce ice cover and the associated vertical stability. These changes would probably permit increased predation and cannibalism, which would adversely affect abundance of pollock per unit area. At the same time a northward expansion of pollock habitat, and a possible stimulation of summer plankton growth in the middle shelf domain, could compensate for this decline and maintain the total exploitable pollock biomass and fishery yield at close to present levels.

The Gulf of Alaska, at similar latitudes to the southeastern Bering Sea, is warmer, less seasonal and essentially ice-free due to a strong influx of Pacific water from the south. Unlike the eastern Bering Sea middle shelf it is weakly stable and highly advective. Insufficient information is available to do more than speculate on factors controlling pollock abundance, which has been increasing steadily for two decades. The most important question regarding pollock abundance is how year-class strength is maintained in such an advective environment; that is, where hospitable nursery waters are located and how eggs, larvae, and juveniles reach and are retained within them. Increased precipitation and coastal freshwater input could strengthen the coastal Kenai Current that governs residence time of surface water in the Shelikof Strait spawning area. A global decrease in wind speeds associated with reduced thermal gradients in the atmosphere might weaken the Alaska Stream at the shelf break but have little effect on the Kenai Current. However, warming might retard currents in the Gulf by increasing the incidence of southwesterly winds that oppose the direction of the dominant Alaska Stream and Kenai Current. Such winds would favor coastal upwelling and increased food supply in the spawning area, but the potential effects of altered lateral transport on pollock year-class strength are not clear.

These projections are highly speculative. More definitive answers will require substantial additional research on the abiotic environment and its effects on life cycle stages of pollock and their prey and predators. In both the eastern Bering Sea and the Gulf of Alaska, pollock abundance as determined by interannual differences in juvenile year-class strength clearly is dependent on a great diversity of climate-related environmental interactions. In most cases the dependence of biological processes on temperature is unknown or poorly parameterized, so that quantitative predictions of effects of climate change cannot be made. The most difficult aspect of such predictions, however, is weighing the relative impacts of counteracting processes to evaluate which are most significant even under present conditions. Thus the lack of quantitative data makes it unreliable even to predict qualitatively the directions of responses to climatic changes, much less their magnitudes.

Predictions of effects of climate change on Alaska pollock fisheries ultimately can be improved only through increased basic scientific knowledge of the environment and its organisms. The foremost data gaps in both the eastern Bering Sea and the Gulf of Alaska concern the locations and abundance of eggs, larvae, and juveniles, the abundance and spatial and temporal distribution of prey, and the importance of predation and cannibalism.

Greater understanding of the processes controlling fluctuations in pollock abundance can be gained only by combining two major efforts. First, large-scale

synoptic surveys should be made of as many variables as possible, to establish instantaneous oceanographic and fishery conditions over crucial areas such as the Pribilof-Unimak region of the eastern Bering Sea and the Shelikof Strait region of the Gulf of Alaska. These surveys should be supplemented by appropriate laboratory observations that attempt to represent biological conditions (such as the effects of small-scale prey distributions) that cannot be observed directly in the field. Second, there should be long-term baseline monitoring of key variables that can be used effectively to monitor interannual variability, especially during periods when intensive surveys are lacking.

One additional useful tool for analyzing climate scenarios is simulation modeling. The veracity of simulation models always depends on the quality of data and conceptual relationships employed in their construction. When the state of knowledge reaches a point at which critical ecological processes may be quantified with reasonable parameters, models provide a means for exploring the theoretical implications of various hypotheses and assumptions. Such exercises feedback to invigorate field and laboratory studies. Simulation, though its abilities are limited, is the only tool now available for sorting out the relative importance of various postulated climatic effects on the total fishery ecosystem.

Some models have already been developed that might be adapted for orderly numerical speculation about climate effects on pollock. DYNUMES (Laevastu and Larkins 1981) includes a spatial grid of the study area, multiple fisheries and predators, and the effects of cannibalism on pollock. It has not yet been employed to examine possible effects of climate change. Certain important aspects of the environment are not considered in this model, such as currents, stability, ice cover, and plankton production, and temperature is included only implicitly in the choice of certain rate and transfer coefficients. Another model (Knechtel and Bledsoe 1981, 1983) does include plankton, but not predators nor spatial variability. Despite its simplifications, DYNUMES in its present form seems to create a recognizable caricature of the eastern Bering Sea ecosystem. It could be used to make simple climatic predictions (e.g. Laevastu and Marasco 1982), and with some modification might be tailored to meet the needs of the present project more precisely. Such models could provide an overall organizational structure into which further data and theoretical insight could be incorporated.

ACKNOWLEDGEMENTS

This report benefitted from thorough and careful reviews by K. Bailey, D. Grosse, D. Gunderson, S. Kim, and J. Schumacher. Additional discussions with L. Incze, and K. Parker were helpful. Figures were prepared by F. Ghatan and typing was performed by S. Roloff. This report was prepared under contract #4524910 to T.H. Sibley from the Lawrence Berkeley Laboratory, University of California, as part of the Indirect Effects of CO₂ Program of the U.S. Department of Energy.

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