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Proceedings of the Workshop on Walleye Pollock and its Ecosystem in the Eastern Bering Sea

Edited by
Daniel H. Ito

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PROCEEDINGS
OF THE WORKSHOP ON WALLEYE POLLOCK AND ITS ECOSYSTEM
IN THE EASTERN BERING SEA

Northwest and Alaska Fisheries Center
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INTRODUCTION

by

James W. Balsiger[1]

The 1982 National Marine Fisheries Service Strategic Plan states that the mission of the National Marine Fisheries Service (NMFS) is to: "Achieve a continued optimum utilization of living marine resources for the benefit of the nation." It goes on to state that: "In carrying out our mission, we are building for the long term. One of our most important tasks is maintaining a proper balance between short-term performance and investment for maintaining strength in the future." Under National Objective 1, the plan states that NMFS should "establish or maintain research programs that reduce critical information gaps in our understanding of marine ecosystems." The plan further states that, among other things, the Northwest and Alaska Fisheries Center (NWAFC) should:

(a) "Conduct status of stocks, bioeconomics, and ecosystem analyses required to establish Optimum Yields (OY's) for multispecies fisheries;

(b) "Conduct multispecies ecosystem research to achieve increased understanding of species interactions and effects of perturbations, including fishing, on abundance;

(c) "For important commercial species in the Alaska fishery conservation zone (FCZ) conduct multispecies research on causes underlying recruitment variations in ecosystems;

(d) "Accelerate work on (the) fur seal sub-element in (the) ecosystem model in order to determine (the) magnitude of other factors impacting (the) fur seal population."

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Thus, it is within the goals and objectives of the NMFS and the NWAFC to conduct long-term ecosystem research which is directed at improving our ability to develop and evaluate current and future fishery management options in a multispecies context.

To further these goals, the NWAFC has encouraged all researchers to conduct their analyses in an ecosystem context and has promoted interaction among its researchers examining the functional interactions that constitute ecosystem analysis. In 1981 an Ecosystem Working Group was formed to enhance communication among NWAFC researchers.

The Ecosystem Working Group proposed that a Pollock Ecosystem Review Workshop be held to undertake two main tasks to initiate work on ecosystem-oriented problems involving walleye pollock in the eastern Bering Sea. The two tasks were:

1) identify and document significant ecosystem-oriented scientific and/or management problems; and
2) design a procedure to enhance a better and broader understanding of various alternative solutions of these problems.

This report describes the results of the Pollock Ecosystem Review Workshop and evaluates the progress made by the project.

The workshop, hosted by the Northwest and Alaska Fisheries Center, was held 2-4 May 1983, and was attended by participants (see Appendix 1) from Washington, Alaska, and Japan. Expertise embodied in this group ranged from physical oceanography to the biology and distribution of plankton, fish and marine mammals, fisheries, and economics. Most participants were research scientists; however, a number of individuals from management and policy development also attended. The objectives of this workshop were to:

1) enhance communication between individuals and groups engaged in pollock ecosystem research;
2) develop a conceptual model of the biophysical and fisheries systems in order to focus discussion;
3) identify gaps in conceptual understanding and existing data; and
4) expose NWAFC scientists to the potential of this type of workshop for guiding the analysis of ecosystem research and management problems.

The approach used to facilitate the 3-day workshop was taken from a series of techniques and procedures collectively termed Adaptive Environmental Assessment and Management (AEAM) (Holling 1978). A commercial firm (Environmental and Social Systems Analysts Ltd.) was contracted to conduct the workshop. This introductory chapter contains portions of their final report[2] required under the contract.

Central to this approach was the development of a model of the system of concern. Development of a model forces specialists to view their area of interest in the context of the whole system and promotes an interdisciplinary understanding of the system.

To conduct the workshop, a set of structured exercises was used. The first step was to clearly define and bound the problem. Lists were generated of the alternatives available to management (actions) and those measures of system performance (indicators) which managers use to evaluate success. The next step was to define the spatial extent and resolution required to adequately represent the system. Similarily, the temporal horizon and resolution required

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[2] Bunnell, P., R. Everitt, and T. Webb. 1983. Report on the pollock ecosystem review workshop. Unpub. manuscr., 41 p. Environmental and Social Systems Analysts Ltd., 678 W. Broadway, Vancouver, British Columbia, V5Z 1G6, Canada.

were agreed upon. Together, these exercises defined the conceptual limits of the model.

Within these conceptual limits, the system was divided into manageable components, or subsystems. To direct interdisciplinary understanding, the focus of the next exercise was the interactions between subsystems. Rather than listing all the variables within a subsystem, the "looking outward" exercise required specialists to define exactly what information they needed from other subsystems in order to adequately represent the dynamics of their subsystem. The result of this exercise was a delineation of how each discipline is linked to the other disciplines and how each can be used to define and describe the ecosystem.

The above exercises set the stage for more detailed technical work conducted by subgroups for each subsystem. They developed a description of their submodel and identified conceptual and data gaps relevant to the understanding of the whole system.

Bounding the Problem

No model can accommodate all the elements that may influence a fisheries resource. For example, the pollock ecosystem is part of an international fisheries system, of the national economy, and of the Bering Sea biophysical system. Important decisions in defining a conceptual model include those which identify what will and what will not be included in the model. In the pollock workshop, these decisions were facilitated by defining actions and indicators (management alternatives and measures for evaluating their effects) and by determining a manageable spatial and temporal framework.

Actions

Actions were defined as human interventions which change the dynamics of a system. Actions were defined specifically so that the response of each component of the system could be predicted. For example, catch restrictions were specified in terms of species, nation, vessels, size of catch, location, or quota.

Actions identified during the workshop were primarily related to fisheries management, either in terms of restrictions of fish caught or concerns for the management of other species such as marine mammals. Habitat protection and the manipulation of demand for the catch were also considered.

Following is a list of the actions identified during the workshop:

- Catch restrictions
  - Quota by species by nation; size limits by species; closure, time and area; gear restrictions; boat number restrictions; boat access, areas and trips
- Incentives and disincentives
  - Subsidies and loan guarantees; purchase contract; royalty fees
- Management of other species
  - Prohibited species; penalty fees; protection of marine mammals; competing species (yellowfin sole, king crab); and predators (marine mammals)
- Monitoring
  - Self reporting
- Demand
  - Marketing; processing technology; location of processors

Habitat

Protection and pollution control.

Indicators

Indicators were defined as those measurements used to evaluate the state, or health of a system. As in the set of actions, most of the indicators pertained to fisheries, economics, and social facets; however, a number of ecological indicators were also specified.

The indicators identified were

Ecological

Abundance and variability of fish species by age and sex, marine mammals and birds, and prey species;

Recruitment of fish; and

Habitat - extent and quality (e.g., spawning)

Economic

Catch by species, age, size, gear type; variability in catch; catch per effort; profit by gear type, vessel class, nation; and price by species

Fishery potential

Fleet diversity; gear type and technology; processing capacity; and infrastructure

Social

Employment; disposable income; resident population size; and returns to processors.

Space

For the conceptual model being developed at the workshop, the extent of the Bering Sea pollock system was determined by a combination of political and natural boundaries. The western boundary was taken as the international boarder, the eastern edge as the Alaska land mass, and the southern as the Aleutian archipelago. Subdivisions within this area were chosed from potential physiographic variables to reflect biologically significant differences and are discussed in the chapter on oceanography.

Time

Since the model for this workshop was conceptual in nature, the time dimension was somewhat loose. In terms of how far into the future one might wish to project (time horizon), the concern was in the 20- to 50-year range. This is long enough to project population trends of the longer lived organisms and to examine potential changes in fisheries dynamics.

Within each year, a seasonal time step was specified. Although some processes, particularly oceanographic and planktonic, occur with much shorter dynamics, the data available are best suited to integrating these on a seasonal basis. Other processes, such as large mammal population dynamics and fisheries, are best represented with a seasonal increment.

Subsystems and Interactions

In order to develop the conceptual model, the pollock ecosystem was divided into subsystems. These divisions paralleled established disciplinary areas: physical oceanography, plankton, marine fishes, mammals and birds, and the study of fisheries and economics. In order to better reflect the intent of this workshop, that is the focus on walleye pollock, that species was isolated for special consideration in a subgroup leaving a second marine fish subgroup to develop a conceptual model of other fish and squid. Since the larval stages of the pollock intermix with other plankton, they were allocated as the responsibility of the plankton subgroup. Marine mammals and birds were combined into a subsystem, the apex predators, so that a total of six subsystems were defined for six subgroups to consider:

1) physical oceanography;
2) plankton;
3) pollock;
4) other fish and squid;
5) apex predators; and
6) fisheries and economics.

Directives for the development of these six conceptual submodels were partially defined by the bounding exercises described above; what remained was an explicit definition of the information linkages between the submodels. This was accomplished with a "looking outward" exercise which specified the pieces of information each subsystem required from all other subsystems in order to predict how that subsystem will behave dynamically. The product of this exercise was an interaction matrix, with columns specifying the information needs and the rows specifying the information responsibiliites of each subsystem (Fig. 1). The diagonal of the matrix in Figure 1 represents the internal dynamics of each subsystem, which will be examined by the subgroups.

The looking outward matrix revealed that the physical oceanography subsystem has no information requirements from the other subystems. Thus,

TO FROM	PLANKTON	POLLOCK	OTHER FISH	APEX PREDATORS	FISHERIES & ECONOMICS
OCEAN	.sediment .wind speed .location of ice edge .depth of mixed layer .surface light .nutrients (N,P,Si) .horizontal transport	.temperature profile .horizontal transport .location of fronts .% bottom > 0°, 2° .location of ice edge	.temperature profile .horizontal transport .location of fronts .% bottom > 0° .location of ice edge	.location of ice edge .temperature profile .location of fronts .(wind & air temperature)	.location of ice edge .No. fishable days
PLANKTON		.turbidity (patchiness) .prey No. by: species classes depth, diel .larvae recruited to post-larvae time of recruitment	.turbidity .prey No. by size, depth (bethnic prey)	.No. by species classes and depth (planktonic stages of parasites)	
POLLOCK	.No. plankton consumed-species classes, eggs and larvae .No. eggs spawned (quality and size)		.No. pollock by age, size .No. other fish consumed by age, size	.No. pollock by age, depth (1, 10, 100, 100+ m) (micro level spatial distribution)	.No. pollock by age, size, sex, depth .spawning time .roe content, condition .parasites/g tissue .% area occupied
OTHER FISH	.No. plankton consumed-species classes, eggs and larvae .No. eggs spawned (quality and size)	.No. prey species by size classes .No. pollock consumed by size, age (behavorial exclusion)		.No. prey species by size classes depth for fish<25cm	.No. fish by species classes, size and age
APEX PREDATORS	.No. plankton consumed-species classes	.No. pollock consumed by age, size (micro level spatial) (number mammalian hosts)	.No. other fished by species groups and size		.No. mammals and birds
FISHERIES & ECONOMICS		.No. pollock caught by age, size, sex (including No. thrown back)	.No. fish caught by species and size	.No. incidental catch by species .gear loss & discard .offal	

Figure 1.--The looking outward matrix developed at the pollock ecosystem workshop.

the role of this submodel was contributory, and the participants with oceanographic expertise were allocated to the other subgroups.

The Conceptual Model

Each subgroup was given the charge of developing a conceptual model of their subsystem, and of listing the major conceptual and data gaps. The groups were also asked to prioritize the data gaps and develop a list of research needs. Each of the subgroups produced a diagrammatic description of the conceptual model, and some groups were able to elucidate the nature of the processes which were a part of the conceptual structure. Most groups generated a list, prioritized by some selectivity, of the major conceptual and data gaps. This information is contained in the individual chapters of this report.

Follow-up to the Workshop

Following the workshop, the subgroup leaders met with other interested researchers to identify and prioritize management questions that arose from the pollock workshop proceedings. The five principal questions that were identified are listed below:

1) What are the relative impacts of biotic and abiotic factors on pollock fisheries production?
2) Are eastern Bering Sea pollock best managed as a single production unit?
3) Can the three legislative acts (Marine Mammal Protection Act, Endangered Species Act, Fisheries Conservation and Management Act) be implemented simultaneously, and if so, how?

4) What bioeconomic factors cause shifts in effort between fisheries (including foreign and domestic) and how might these be used to better manage the fishery system?

5) What are the consequences to the eastern Bering Sea ecosystem and fisheries of various pollock population levels, including its extinction?

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OCEANOGRAPHY

by

James D. Schumacher[1]

ABSTRACT

Results are synthesized from studies of the atmosphere, ice cover, water properties, circulation, and biological-physical interactions for the eastern Bering Sea. Meteorological conditions are dominated by storms. These events govern the formation and advection of ice and provide energy for mixing. Exchange of heat with the atmosphere determines magnitude and extent of colder bottom waters over the middle shelf, and winds generate current pulses. Water over this shelf is partitioned zonally by a system of fronts which separate three hydrographic domains. These domains are distinguishable primarily by depth (Z) and seasonal changes in vertical density structure: coastal ($Z < 50$ m), middle shelf ($50 < Z < 100$ m) and outer shelf ($100 < Z < 170$ m). There is also a more subtle north-south temperature difference with decreasing temperatures toward the north. The hydrographic domains are nearly coincident with current regimes and are distinguishable by their distribution of horizontal kinetic energy and mean flow. Although there were great advances in our knowledge of the abiotic environment of this shelf in the past decade, many gaps still remain in both observational coverage and understanding; these are presented for future consideration.

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INTRODUCTION

The largest continental shelf of the World Ocean, outside that of the Arctic, lies contiguous to the west coast of Alaska in the eastern Bering Sea (Fig. 1). This shelf, which is bounded on the south by the Alaska Peninsula and on the north by Alaska and Siberia, subtends 11° of latitude and exceeds 500 km in width at its narrowest point. The shelf deepens gradually from the shore to about 170 m at the shelf break, which is indented by several huge canyons. The shelf is connected with the Gulf of Alaska by Unimak Pass and with the Arctic Ocean through the Bering Strait. Averaged over a year, a significant volume of water (about 1×10^6 m^3/s) flows northward through the Bering Strait (Coachman et al. 1975; Coachman and Aagaard 1981), and a lesser volume (0.15×10^6 m^3/s) flows from the Gulf of Alaska through Unimak Pass (Schumacher et al. 1982). Shelf waters receive an excess of precipitation over evaporation (Reed and Elliott 1979); river discharge, principally from the Kvichak, Kuskokwim, and Yukon Rivers, adds about 1.5×10^4 m^3/s (Roden 1967; Favorite et al. 1976). Apparently much of the remaining transport required to make up the Bering Strait outflow comes across the shelf south of Cape Navarin. Among the unique features of the eastern Bering Sea shelf are its vast size, its "leak" on the northern boundary, and the seasonal production of ice.

Recently, scientific interest has focused on relationships between ocean climate variability and the variability of fish stocks (e.g., Bakun et al. 1982; Sullivan 1982). Among the key abiotic parameters in the sea are turbulence (which affects patchiness and stability), transport, and temperature; variations in these can be important, particularly to early stages of the life cycle of marine organisms. These oceanographic parameters are linked to the atmosphere which provides fluxes of momentum, heat, and moisture. Furthermore, transport and turbulence are also important for nutrient fluxes and,

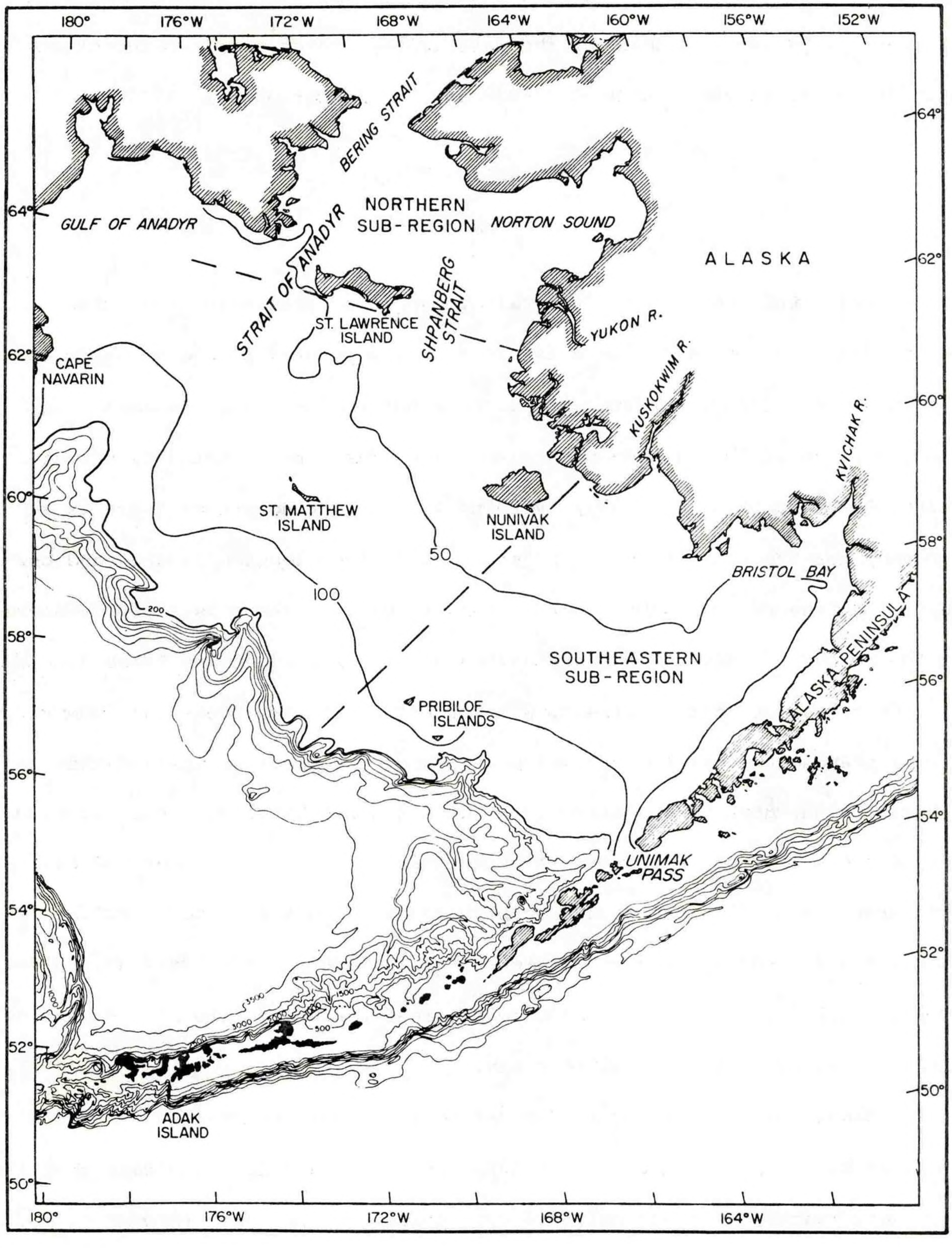

Figure 1.--Bathymetry and geographic names of the eastern Bering Sea (from Schumacher et al. 1983b).

given that light is not a limiting factor, primary production. In the following chapter, I review salient features of the abiotic environment of the eastern Bering Sea; much of the material was taken from two recent review articles by Schumacher and Reed (1983) and Schumacher et al. (1983b).

BACKGROUND REVIEW

Climatology

A major influence on the general atmospheric circulation over the Bering Sea is a region of low pressure normally located in the vicinity of the Aleutian Islands, referred to as the Aleutian low. This feature is a manifestation of the passage of storms, which dominate climatology of the Bering Sea (Brower et al. 1977; Overland 1981). During winter there is a tendency for two storm tracks, one parallel to the Aleutian Islands and one curving northward along the Siberian coast; however, there is always a decrease in the number of storms with increasing latitude (Overland and Pease 1982).

Outbreaks of cold polar air, which continue for 1-2 weeks, are common winter phenomena. Due to the juxtaposition of the Aleutian low and the Siberian high, mean winter winds over the eastern Bering Sea shelf are from the northeast. These winds are stronger than those during summer and have an interannual signal which influences both sea surface temperature (McClain and Favorite 1976) and ice coverage (Niebauer 1980, 1981, 1983; Overland and Pease 1982). During summer, storms tend to progress northward into the Bering Sea with mean winds arising from the south.

Because the meteorology is dominated by storms, vector-mean winds tend to be weak. Direct observations of wind on St. Paul Island indicate that the strongest monthly mean was only 3.4 m/s toward the southwest (Brower et al. 1977). Furthermore, since most of the outer- and middle-shelf waters are farther than a Rossby radius of deformation from the coast, they respond by following the rotating winds rather than as rectilinear coastal currents induced by Ekman divergence. Thus, while winds generate current pulses, they contribute little to generation of mean current in any of the regimes.

Ice

Ice cover is a seasonal feature of the eastern Bering Sea shelf, varying from none in summer to greater than 80% coverage during maximum extent in March (Niebauer 1980; Pease 1980). Fay (1974), Muench and Ahlnas (1976), Pease (1980), McNutt (1980, 1981) and Aagaard et al. (1981) have discussed the importance of the northern Bering Sea as an area where ice is produced along south-facing coasts because of wind-driven surface divergence. The ice produced in polynyas (areas of open water) is transported southwestward under prevailing northeasterly winds, eventually melting at the southwestern marginal ice zone. Salinization during freezing has a measurable effect on both flow and water properties in the vicinity of polynyas such as those on the leeward side of St. Lawrence and Nunivak Islands (Schumacher et al. 1983a). At the ice edge, bands of ice which accelerate away from the pack have been identified in satellite photographs (Muench and Charnell 1977; McNutt 1980, 1981). The melting ice causes a vertical stratification in the water column, and may produce a baroclinic geostrophic flow along the marginal ice zone (Niebauer 1982; Muench 1983).

Niebauer (1980, 1981) and Overland and Pease (1982) showed that the interannual variations in ice extent can be hundreds of kilometers, and these variations are generally correlated with either the wind field or the location of storm tracks. For example, the anomalous winds from the north during the winter of 1975-76 were correlated with extremes of 2°C below normal sea surface temperatures (SST), 20% above normal ice cover, and 400 degree days (DD) above normal conditions (Fig. 2). Note that SST is representative of temperature throughout the water column in the coastal (Z <50 m) domain. While the linkage between upper air pressure patterns and surface wind, SST, ice cover, and DDs seems straightforward, note that from October 1980 to February 1981 mean monthly winds were the most extreme; DDs and SST were above normal, while ice cover was far below (~30%) normal. The strong winds from the north, which did not cause much cooling or ice production in 1980-81, can be explained by the nature of upper air patterns which resulted in warmer air being pumped into the Siberian high (Niebauer 1983).

Hydrographic Features

Prior to 1975, some Japanese, Soviet, and American oceanographic research was conducted. Results from these studies, based primarily on broad hydrographic surveys, are summarized by Dodimead et al. (1963), Arsenev (1967), Ohtani (1973), Takenouti and Ohtani (1974), Favorite et al. (1976), and Ingraham (1981a). Since 1975 there has been a notable increase in the amount of research devoted to study of subregions of the shelf or specific oceanographic phenomena; this is a response to the possibility of petroleum development, the substantial harvests of pollock and crab, and the need to predict ice movement. Research has focused on the southeastern shelf and on that portion of the shelf around and north of St. Lawrence Island, including Norton Sound.

Kinder and Schumacher (1981a) synthesized recent hydrographic work over the southeastern shelf. The shelf is divided into distinct domains, delineated by water depths (Z), and separated by fronts (Figs. 3, 4). Within the coastal domain, Z <50 m, tidal mixing exceeds buoyancy input (away from the direct influence of river discharge) and the water is mixed vertically. In

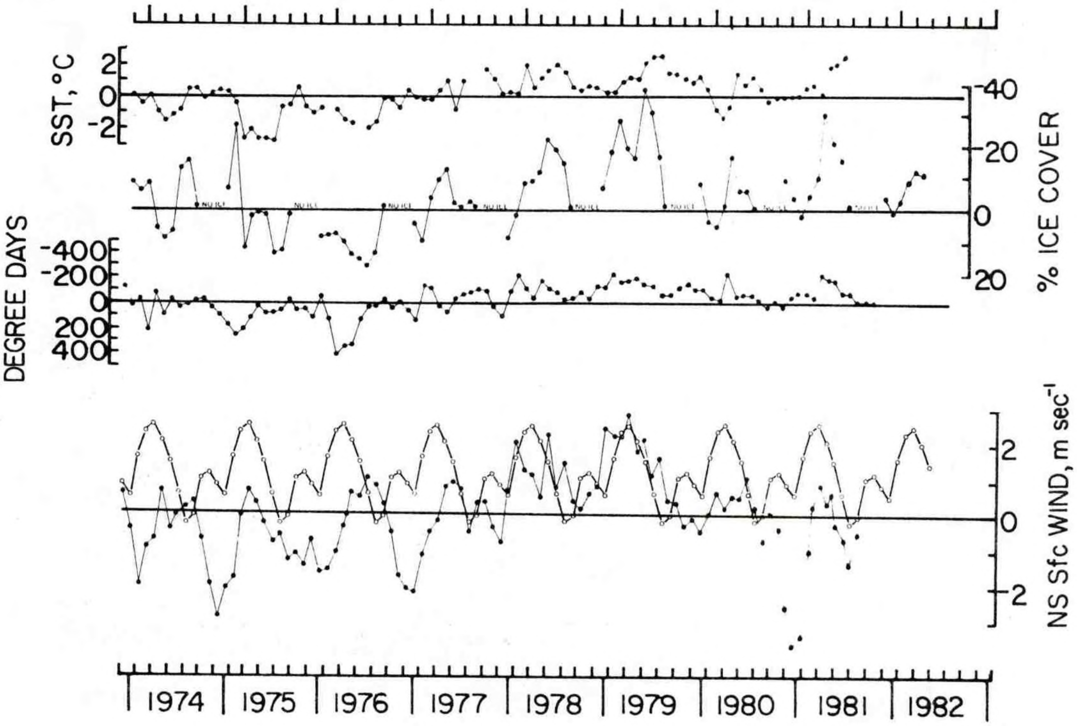

Figure 2.--Departures from monthly mean ice, sea surface temperature (SST), degree-days (DD), and north-south components of the surface wind (solid line with solid circles) from the eastern Bering Sea. In the wind panel, open circles with solid lines are seasonal mean winds plotted such that, for a given month, when wind anomalies (solid dots) fall below the seasonal mean (open dots), the wind is actually from the north regardless of the sign of the anomaly. When the anomaly rises above, the wind is from the south. Wind data have been smoothed by a 3 mo running mean (from Niebauer 1983).

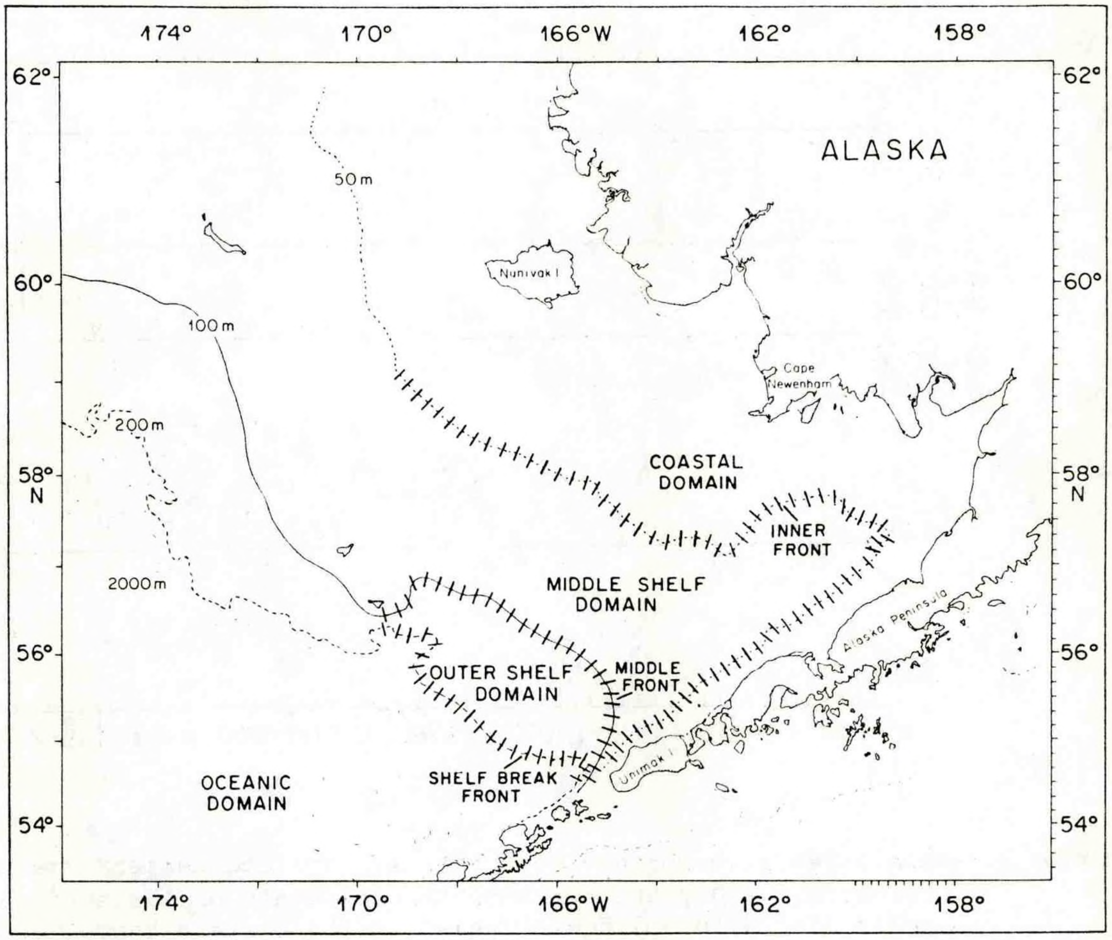

Figure 3.--Approximate locations of hydrographic domains and fronts over the southeastern Bering Sea shelf (from Schumacher et al. 1983b).

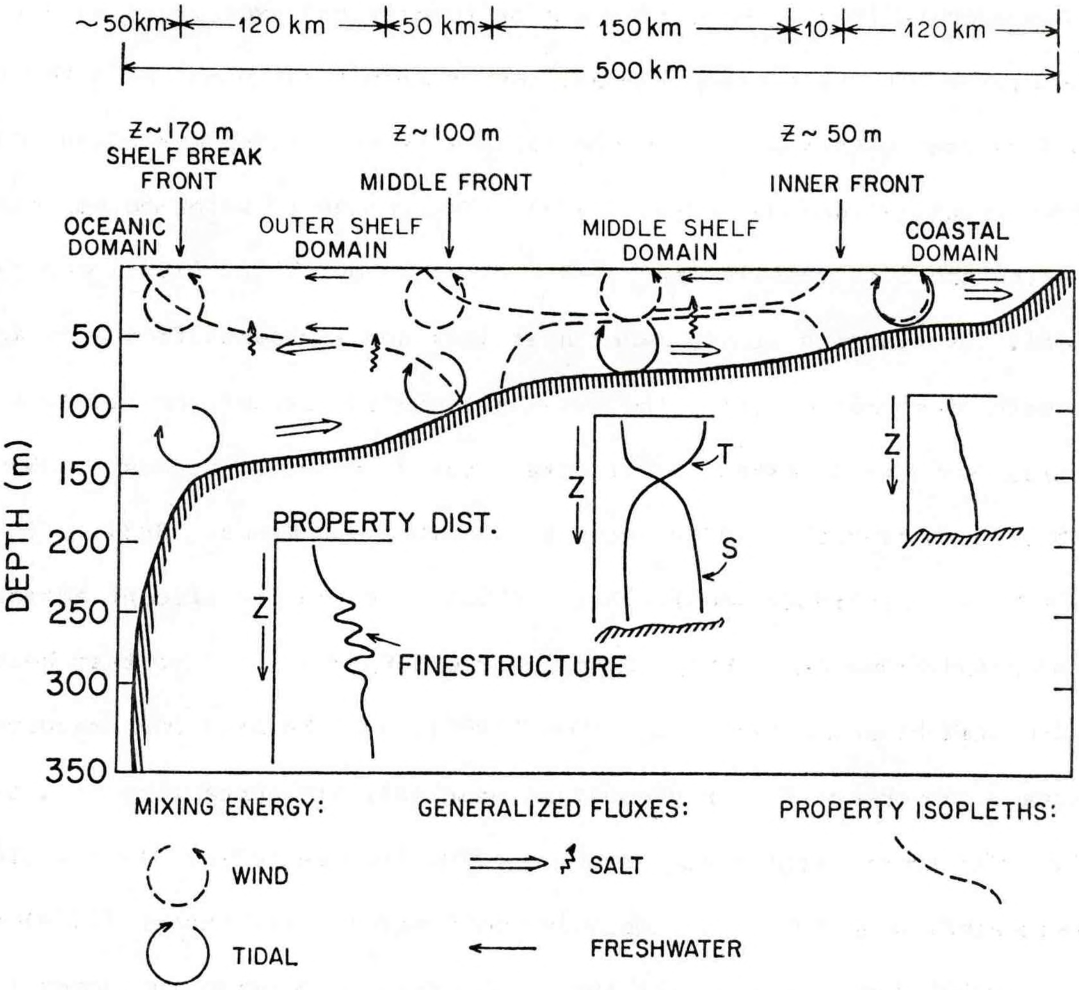

Figure 4.--A schematic interpretation on the cross-shelf plane of energy balance, fresh- and saltwater fluxes, and vertical structure; note that the middle shelf domain becomes mixed either during periods of surface cooling (winter) or during extreme storms (from Schumacher et al. 1983b)

the middle shelf domain, 50 m $\leq Z \leq$ 100 m, when the seasonally varying input of buoyancy (either from melting ice or insolation) exceeds tidal mixing, a two-layered structure predominates. Separating these domains is the inner front, a zone of transition in the balance between tidal mixing and buoyant energy input (Schumacher et al. 1979). The change in water column structure crossing the 50 m isobath was noted previously by Ohtani (1973) and by Muench (1976). Even during winter, when heat loss and increased frequency and strength of storms destroys the two-layered structure of the middle shelf waters, there is a stronger horizontal density gradient across the 50 m isobath than over the middle shelf (Schumacher and Kinder 1983).

Within the middle shelf, there is little or no significant advection (Kinder and Schumacher 1981b; Schumacher and Kinder 1983) so that heat content is dictated by air-sea exchange (Reed 1978), and the salt flux required to maintain the observed nearly constant mean salinity appears to be a tidally driven diffusion (Kinder and Coachman 1978; Coachman et al. 1980). These recent studies support the suggestion by Takenouti and Ohtani (1974) that the cold (<0°-3°C) bottom layer of the middle domain observed in summer is primarily formed in situ. Coachman and Charnell (1979) found a high correlation ($r = -0.96$, $n = 12$) between mean lower-layer temperatures in June over the middle shelf and degree days of frost during the preceding winters. At the seaward edge of this domain (about 100 m shelf depth), the slope of the bottom becomes five times greater than is typical for the majority of the shelf. Here the water columns undergo a change over a broad (about 50 km wide) transition zone, the middle front.

The outer domain, 100 m $\leq Z \leq$ 170 m, is characterized by well mixed, upper and lower layers separated by an intermediate layer containing fine structure. The outer shelf is bathed by slope waters which are warmer and more saline than the waters of the middle shelf. This juxtaposition of water masses of slightly different densities results in lateral interactions with layering of water masses occurring at vertical scales of 1-25 m within the mid-water column (Coachman and Charnell 1977, 1979). In general, the outer shelf waters intrude shoreward near the bottom while middle shelf waters extrude seaward above them. Within the middle front, vertical fluxes of salt, heat, and nutrients appear to be enhanced (Coachman et al. 1980; Coachman and Walsh 1981).

Kinder and Coachman (1978) described the shelf break front, which separates the outer shelf from the oceanic domain, and recognized its essentially saline character; it is the zone of relatively steep upper layer salinity gradients (about 0.5 g/kg in 50 km) dividing upper layer shelf water from the upper layer water of the Bering Slope Current. This current, which parallels the shelf break from near Unimak Pass to near Cape Navarin, transports about 5×10^6 m^3/s northwestward (Kinder et al. 1975). The oceanic region immediately seaward of the shelf break front is replete with mesoscale eddies (Kinder and Coachman 1977; Kinder et al. 1980). Using adjusted sea level observations, Kihara (1982) inferred that the warm saline Alaska stream extension waters (Bering Slope Current inflow along the northern side of the Aleutians) were most prevalent between 1965 and 1969 but weakened after 1970. The changes in inflow were correlated with changes of mean bottom water temperature over the outer portion of the southeastern shelf. Interannual signals in Bering Slope Current transport exist which impact the outer shelf water properties and perhaps transport in this domain.

The other subregion of the eastern Bering Sea shelf which has been recently studied in some detail is the northern shelf (north of about 62°N lat.) including Norton Sound. Coachman et al. (1975) reported three identifiable water masses; the most saline water mass (Anadyr) lies west of St. Lawrence Island and on the west side of Bering Strait, the least saline waters (Alaskan Coastal) lie contiguous to the Alaskan coast on the east, and between these a separately definable water mass of intermediate salinity (Bering Shelf) is present. More recent studies (Aagaard et al. 1981; Schumacher et al. 1983a) support the observations of the zonal salinity gradients differentiating these water masses. These studies also show that during ice formation in some local areas, brine rejection results in salinity values as high as 35 g/kg.

The large region of the eastern Bering Sea shelf that lies between the southeastern and northern subregions has been the subject of only limited studies. However, hydrographic data collected during summer (Kitani and Kawasaki 1978) and winter (Bourke and Paquette 1981; Salo et al. 1980; Muench 1983) suggest that the three domains present over the southeastern shelf extend northward to the vicinity of St. Lawrence Island, and the three separate water masses of the northern region are identifiable with these domains.

Although the east-west or zonal differences were stressed because domain characteristics are so clear, north-south or latitudinal differences also exist. For example, in Figure 5 the temperature of the coldest water is shown for summer 1967. It is evident that waters in the southeastern subregion between the 50 and 100 m isobaths are 2°-3°C warmer than those between St. Lawrence and St. Matthews Island. This latitudinal difference appears to be a typical feature of middle shelf bottom water temperatures as shown in Ingraham (1981b).

Currents

Over the southeastern shelf, tides dominate the kinetic energy of the water, often comprising 90% or more of the fluctuating kinetic energy. Further

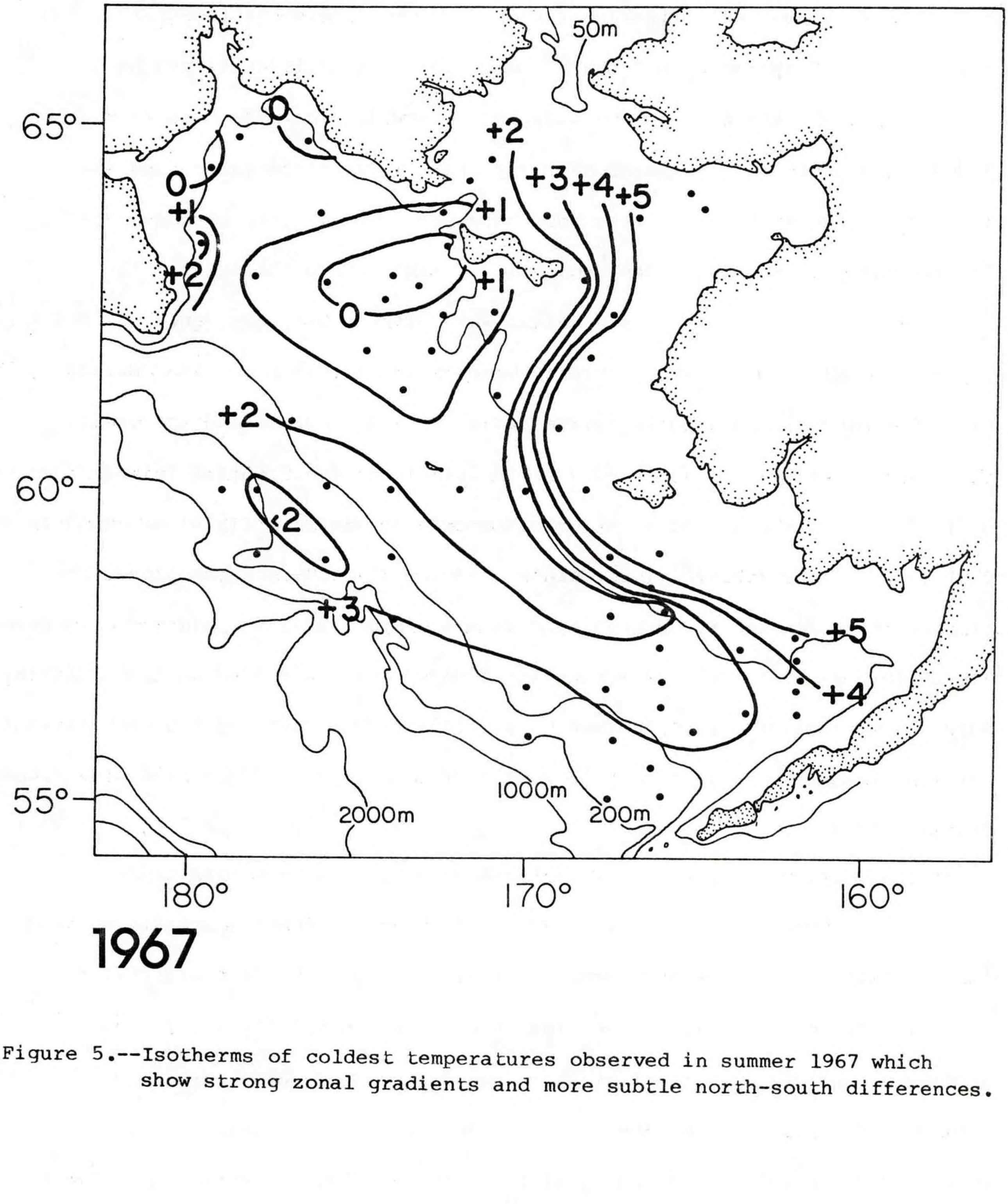

Figure 5.--Isotherms of coldest temperatures observed in summer 1967 which show strong zonal gradients and more subtle north-south differences.

north, however, the tides become less energetic and comprise a much smaller percentage (<10%) of the total fluctuating kinetic energy. Pearson et al. (1981) examined current and water pressure records from the eastern Bering Sea shelf and produced cotidal charts of tidal current constituents (M_2, N_2, K_1, and O_1). They found that the M_2 constituents (the largest) are as high as 35 cm/s along the Alaska Peninsula and as low as 3 cm/s or less in Norton Sound where there is an amphidrome. The tidal wave enters the Bering Sea from the North Pacific Ocean through the central and western passages of the Aleutian Island chain and then propagates eastward onto the shelf. The semidiurnal tide propagates as a Kelvin wave along the Alaska Peninsula but appears to be converted to a Sverdrup wave upon reflection in inner Bristol Bay. The diurnal tides co-oscillate between the deep basin and the shelf with amphidromes located between Nunivak Island and the Pribilof Islands and west of Norton Sound. Recent numerical models by Hastings (1976) and Sunderman (1977), which are vertically integrated models of the M_2 component over the entire Bering Sea shelf, and by Leendertse and Liu (1977) and Liu and Leendertse (1978, 1979), which are three-dimensional models of all significant constituents, have all predicted tides. Pearson et al. (1981) found generally good agreement between field observations and the models of Sunderman (1977) and of Leendertse and Liu (1977).

More than 20 years of direct current measurements have been collected over the southeastern shelf since 1975, with somewhat fewer observations from the northern shelf and Norton Sound. Three mean and low-frequency current regimes have been identified over the southeastern shelf (Fig. 6); these regimes are nearly coincident with the previously described hydrographic domains (Kinder and Schumacher 1981a, b; Schumacher and Kinder 1983). Coastal waters from the Gulf of Alaska shelf flow into the Bering Sea through Unimak Pass and then apparently continue northeastward along the Alaska Peninsula

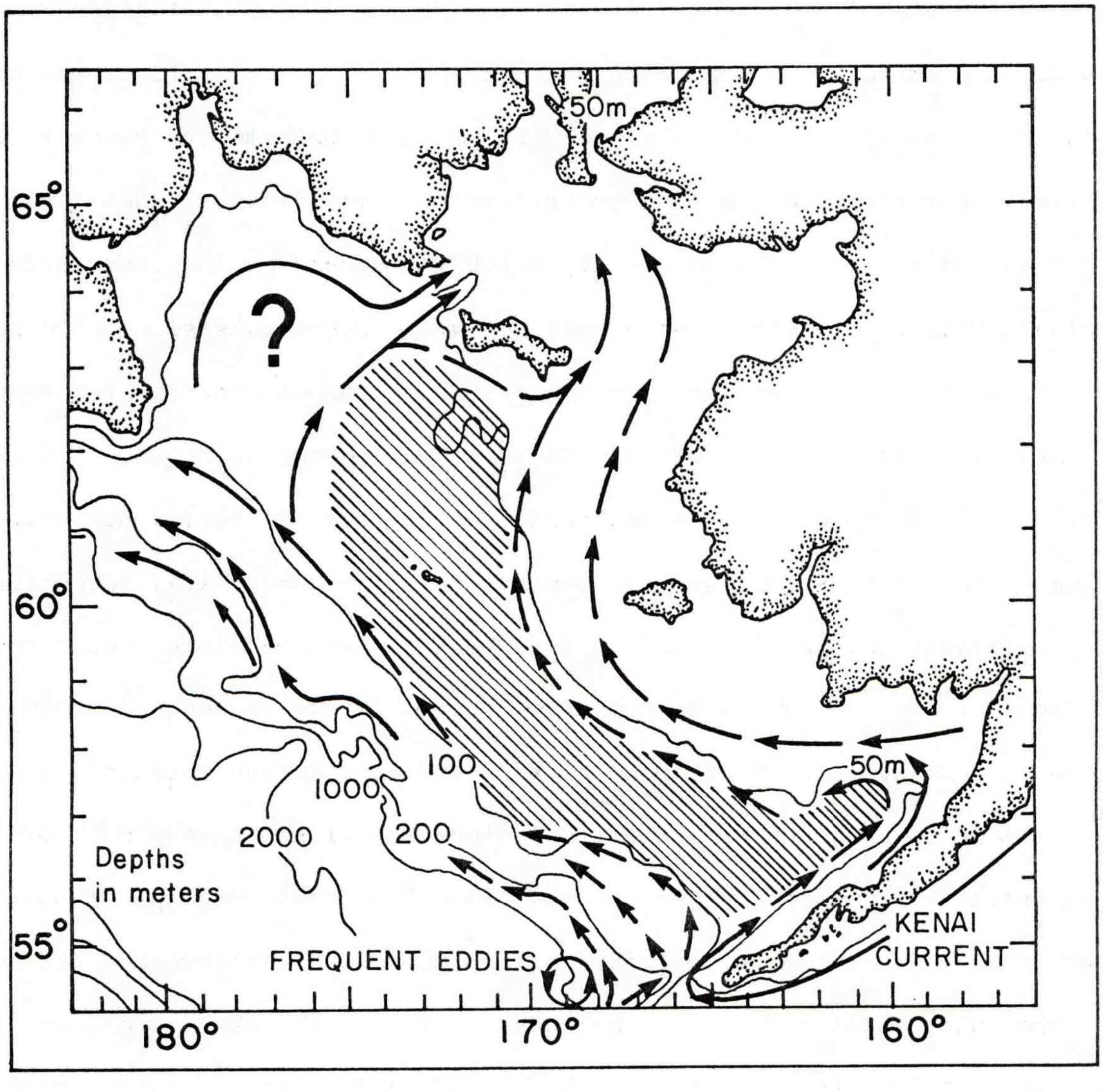

Figure 6.--Schematic of long-term mean circulation based on direction measurements, inferred baroclinic flow, water properties, and model results (from Schumacher and Reed 1983).

(Schumacher et al. 1982; Schumacher and Moen 1983). Within Bristol Bay, the flow becomes counterclockwise and then follows the 50 m isobath northward past Nunivak Island. Currents appear to be strongest near the inner front, paralleling this feature at speeds between 1 and 6 cm/s, with the highest speeds occurring in winter. Although fluctuating kinetic energy is dominated by tides (about 96%), there are significant pulses of flow which are wind driven. A combination of baroclinic-geostrophic flow and residual current produced by the interaction of tides with shoaling bathymetry, however, appears to account for the observed mean velocities (Schumacher and Kinder 1983).

The middle shelf current regime, which is bounded by the inner and middle fronts, is a region where there are wind-driven pulses, but the mean current (<1 cm/s) is statistically insignificant except near the regime boundaries. Kinetic energy at periods which correspond to meteorological forcing (2-10 d) is of similar magnitude to that of the coastal domain. Due to the great width of this shelf, however, there are no coastal boundaries within a Rossby deformation radius, and Ekman divergence at the coast does not appear to be an important mechanism for generating currents in this regime. Instead, currents respond to the wind as rotating vectors. It is this lack of organized flow (advection), together with the seasonal development of an upper layer which acts as an insulating lid, that permits the bottom layer of the middle domain to retain its cold signature throughout the summer.

The outer shelf regime lies between the middle and shelf break fronts. Vector mean flow here is statistically significant, with along-isobathic speeds between 1 and 10 cm/s (northwestward) and across-isobathic speeds between 1 and 5 cm/s (northeastward). Unlike the two shoreward regimes, the higher speeds are not necessarily a winter feature. Because the cross-shelf flow does not typically extend onto the middle shelf, the middle front is often a region of convergence; in the outer domain, advection is equal to or more important than tidal diffusion in achieving cross-shelf fluxes (Coachman 1982). Estimates of baroclinic geostrophic speeds and those generated by topographic rectification of tides on the enhanced bottom slope under the middle front are similar to the observed along-isobathic flow (Schumacher and Kinder 1983). The outer regime is richer than the two other regimes in kinetic energy at periods greater than 10 d. This may result from propagation of energy and eddies from the Bering Slope Current landward across the outer shelf. Like the Bering Slope Current, month-to-month and lower frequency aperiodic variations in along-shelf transport are likely to be common.

The Bering Slope Current is rich in baroclinic structure and eddies. This current is a mixture of Alaska Stream and Bering Sea water (Takenouti and Ohtani 1974; Favorite et al. 1976), with the former source entering the Bering Sea through passes in the western Aleutian Islands (Reed 1971; Favorite 1974; Swift and Aagaard 1976; Sayles et al. 1979). Measured and inferred current speeds (Kinder et al. 1980) and modeled currents (Han and Galt 1979) suggest an along-slope flow that averages 5-15 cm/s toward the northwest.

Circulation over the northern shelf is dominated by a generally northward flow of water bound for the Arctic Ocean. This pattern can be temporarily reversed because of large-scale meteorological forcing, particularly in early winter (Coachman and Aagaard 1981). Recent current measurements have shown that mean and low-frequency flow is usually aligned with isobaths both east and west of St. Lawrence Island; through the Bering Strait, mean flow often reaches 10-25 cm/s or more (Coachman et al. 1975; Schumacher et al. 1983a; Salo et al. 1983). South and southwest of St. Lawrence Island the flow is much weaker. The few direct measurements made between the southeastern and northern subregions of this shelf appear to confirm delineation of the flow field into three regimes, as on the southeastern shelf. Baroclinic currents resulting from melting ice may be statistically significant, however, so that relatively strong mean flow (5-10 cm/s) could exist over the middle shelf associated with ice cover. The flow associated with the middle front appears to be continuous over the outer shelf, flowing seaward from the Pribilof Islands and northwestward to the vicinity of Cape Navarin. Here, some portion of the flow appears to follow the 80 m isobath toward the northeast, exiting the region through Anadyr Strait at speeds of 10-20 cm/s.

Relations Between Abiotic and Biotic Environments

Studies of biological processes of the southeastern Bering Sea and in the vicinity of the ice edge have contributed to an understanding of the physical processes in these areas. Hattori and Goering (1981) studied nutrient distributions and primary production and found a zonation that was congruent with the three hydrographic domains. Iverson et al. (1979, 1980) and Goering and Iverson (1981) demonstrated that the phytoplankton and zooplankton communities of the ecosystem were organized by the system of fronts and domains. In quantitative assessments, they inferred relative rates of diffusion and advection of the biological variables based on physical hypotheses about the vertical and horizontal rates of diffusion. Coachman and Walsh (1981) constructed a diffusion model for cross-shelf fluxes of nutrients using a combination of physical, chemical, and biological data. Kinder et al. (1983) showed that the location of tidal fronts around the Pribilof Islands was correlated with the distribution of feeding seabirds.

Nishiyama et al. (1982) used the term "nursery layer" for that portion of the water column in which physiological and ecological conditions are advantageous for the survival and growth of early life stages of walleye pollock, Theragra chalcogramma. The existence of this layer depends on the influx of buoyancy and mixing. In the early spring, the source of buoyancy is ice melt, and momentum transferred from winds provides mixing energy. The presence of ice also depends on exchange with the atmosphere for both formation and advection. The stability and inherent primary productivity of the upper mixed layer seem to be important for the success of other species (e.g., larvae of snow (Tanner) crab Chionoecetes spp.: Incze 1983).

Other relations between abiotic and biotic environments have been reported. Interactions between ice and biota occur in several ways. Ice melt creates local stability, frontal features, and baroclinic geostrophic transport, and under certain conditions, upwelling occurs at the ice edge (Muench 1983; Niebauer et al. 1981; Niebauer 1982). Alexander and Niebauer (1982) show that primary production is enhanced in the marginal ice zone MIZ). They note that the location of the MIZ may be critical; when ice cover is extensive, it approaches the shelf break in the proximity of nutrient-rich waters. If such waters are made available through upwelling, then phytoplankton blooms can be of longer duration. Cross-shelf transport of Bering Slope waters, however, could also provide a mechanism for a richer nutrient supply near the ice edge without extreme ice cover. McLain and Favorite (1976) have noted the impact of anomalously cold winters on fisheries in the Bering Sea. Walters and McPhail (1982) used cluster analysis techniques to examine some qualitative characteristics of demersal fish and invertebrate community structure. Their results indicated large-scale patterns of community organization which are consistent with the hydrographic domains.

RESULTS OF MEETING

The primary goal of the Pollock Ecosystem Workshop was to enhance communication among scientists whose expertise spanned many facets of the rich Bering

Sea ecosystem. The focus was on walleye pollock, whose management is part of the National Oceanic and Atmospheric Administration's (NOAA) mission. The workshop utilized the Adaptive Environmental Assessment technique (Holling 1978) and was conducted by consultants from Environmental and Social Systems Analysts Ltd. (ESSA). In this technique, subgroups are established and information required from and by other subgroups is identified by input from all participants. As this procedure was applied, it became clear that oceanography was to be a source of abiotic information with little or no information required from the other subgroups. (One could envision scenarios where information would be required; e.g., if concentrations of spawning pollock were sufficiently high, then pollock could be a nutrient source and the oceanography subgroup would require information on time, location, and concentration of chemicals supplied.) Thus, results from the oceanography subgroup are all under the category of "gaps in information or understanding." Prior to elucidating these, however, I noted that the eastern Bering Sea is partitioned into eight subregions (Fig. 7). Unfortunately, this spatial decomposition of the eastern Bering Sea does not account for the fact that waters around the Pribilof Islands are shallower than 50 m. There is a front around the islands which is analogous to the inner front and has an impact on the distribution of feeding birds (Kinder et al. 1983). The large marine mammal populations also make the Pribilof Island a unique biome.

Most of the lack of understanding of transport, turbulence, and temperature characteristics results from a paucity of field observations, particularly in regions 5 through 8 (Fig. 7). The Bering Slope Current has received little investigation and its impact on cross-shelf fluxes and along-shelf transport is not known. Francis and Bailey (1983) hypothesize that year-to-year changes in recruitment to the group of pollock northwest of the Pribilof Islands

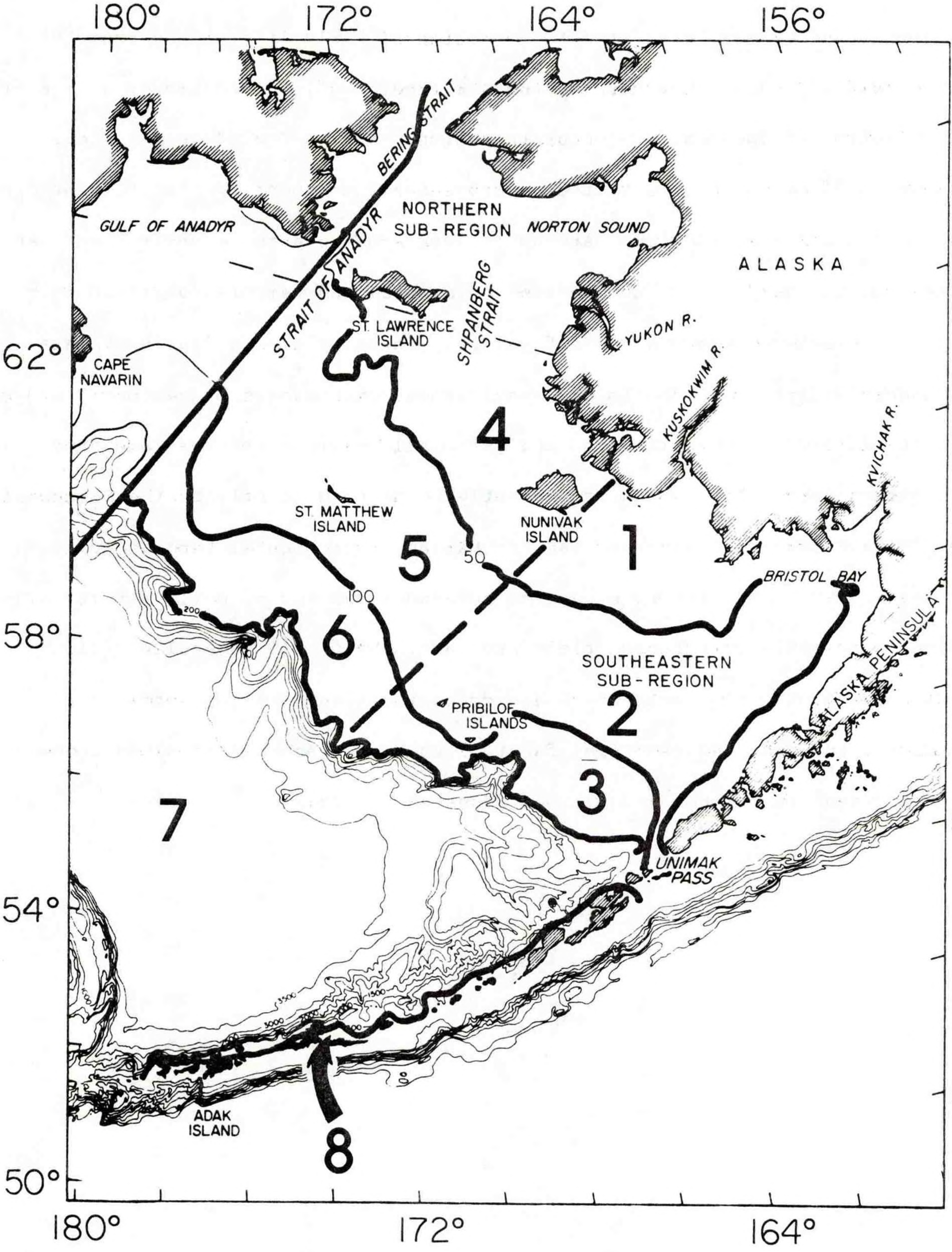

Figure 7.--Subregions of the eastern Bering Sea used for discussions during the workshop.

(regions 5 and 6) may be related to advection of early life stages from the outer shelf of the southeastern Bering Sea (region 3). Furthermore, a greater concentration of spawning may occur in region 3 during "cold" years; i.e., spawning pollock may be restricted in cross-shelf movement by the 2°C isotherm. Before such complex relations between pollock and the abiotic environment can be tested, we must measure and understand spatial and temporal variations in the linkage between slope and shelf waters. There is also a dearth of data and understanding about the abiotic environment encompassed by regions 7 and 8.

In addition to compiling and analyzing all previous observations from the eastern Bering Sea (which is presently being done jointly by the Northwest and Alaska Fisheries Center and Pacific Marine Environmental Laboratory), the next logical step toward enhancing our understanding of pollock in this region is to begin coordinated field programs. This will hopefully yield abiotic and biotic data sets which are concomitant and are collected with coanalysis in mind. An essential facet of such studies will be close cooperation between disciplines and various research groups.

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JUVENILE AND ADULT WALLEYE POLLOCK OF THE EASTERN BERING SEA: LITERATURE REVIEW AND RESULTS OF ECOSYSTEM WORKSHOP

by

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ABSTRACT

A literature review of the biology of walleye pollock, Theragra chalcogramma, from the eastern Bering Sea is presented which emphasizes results of recent hydroacoustic-midwater trawl surveys and studies of growth and feeding. Regional and temporal differences exist in the diet, growth, fecundity, predation mortality, and spawning and feeding behavior of pollock. An emergent theme is that hydrographic conditions, especially temperature, influence the distribution of juvenile and adult pollock, areally and within the water column. The spatial distribution in turn affects fisheries production through the above processes as well as contributing to regional differences in recruitment.

A number of hypotheses were expressed during the ecosystem workshop concerning the influence of hydrographic conditions on the spatial distribution and regional production of pollock, including the following:

1) During years when thermal stratification continues later into the autumn, 0-age juveniles occupy the upper water column for a longer period of time than in years when the stratification breaks down early. Cannibalism is therefore low, but predation by marine birds is high.

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2) Adult pollock avoid water colder than about 2.0°C. During years when residual cold water of 2.0°C or less remains over the middle shelf:

   a) the middle shelf may serve juvenile pollock as a refuge from cannibalism,

   b) adults are more concentrated on the outer shelf resulting in higher catch rates by the commercial fishery and higher predation by marine mammals, and

   c) spawning does not extend as far onto the shelf as in years of warmer bottom temperatures.

3. Pollock spawned over the southeast slope recruit primarily to the northwest, due to the northwestward flow of the Bering Slope current. Pollock spawned over the middle shelf experience little or no net transport.

INTRODUCTION

Walleye pollock, Theragra chalcogramma, is distributed throughout the North Pacific Basin. It supports intensive multinational fisheries in the western Pacific Ocean, the Sea of Okhotsk, the Sea of Japan, the Bering Sea, and the northeastern Pacific Ocean. Pollock currently ranks as the most productive single species fishery in the world (Food and Agriculture Organization 1977, 1978, 1979, 1980; Bakkala and Wespestad 1983) with total annual harvests averaging about 5.1 million metric tons (t) since 1971.

Pollock is the dominant fish species, by weight, over the outer shelf and slope of the eastern Bering Sea and in the Aleutian Basin areas. The commercial catch from these areas has averaged nearly 1.3 million t since 1970, although recent harvests have been limited, partly by catch restrictions, to just under 1 million t (Bakkala and Wespestad 1983). Because of its importance to commercial fisheries and the dynamics of the eastern Bering Sea ecosystem, pollock has been the focus of a number of recent research efforts including the present pollock ecosystem workshop.

This paper consists of two parts. The first part reviews the literature on the biology of walleye pollock from the eastern Bering Sea with emphasis on recent results of hydroacoustic-midwater trawl and plankton surveys, and studies of growth and feeding. New concepts of spawning behavior, recruitment, growth, and survival resulting from these studies are discussed. The second part summarizes the results of the pollock ecosystem workshop. This section presents a conceptual ecosystem model of juvenile and adult pollock and summarizes potential mathematical model formulations. The data necessary for these formulations are compared with available data, and an attempt is made to document gaps in current knowledge.

PART I. LITERATURE REVIEW

Juveniles

Approximately 50 d after hatching (depending on ambient water temperature), larval pollock complete their fin ray development and enter the juvenile phase, which includes fish of about 20-250 mm fork length (Smith 1981; Walline 1980, 1983) (Fig. 1). Pollock larvae usually metamorphose in late June or early July and grow to about 100 mm by December and to 200 mm by the end of the following year, although variability in spawning and hatching dates results in a broad distribution of lengths within an age group (Walline 1981).

Distribution

In summer, young-of-the-year pollock primarily occupy the upper 40 m of the water column (Walline 1981; Nishiyama and Haryu 1981; Nishiyama et al. 1982). Hydroacoustic-midwater trawl surveys have revealed that the depth distribution of 0-age juveniles may be controlled by the presence or absence of a sharp seasonal thermocline (Fig. 2). These surveys have also found large concentrations of age-1 and age-2 pollock above the strata sampled by demersal gear (Bakkala et al. 1983).

There is a general trend towards semidemersal behavior with increasing age. Although age-1 fish are often found in the upper water column, especially when a strong thermocline exists, many are taken during demersal trawl surveys. By age 4, however, most fish over the shelf and slope are found within 50 m of the bottom (Bakkala et al. 1983). Figure 3 is a conceptual diagram of the distribution of pollock within the water column over their life history.

The geographic distribution of juvenile pollock is widespread over the eastern Bering Sea shelf. Apparently their occurrence over the Aleutian Basin

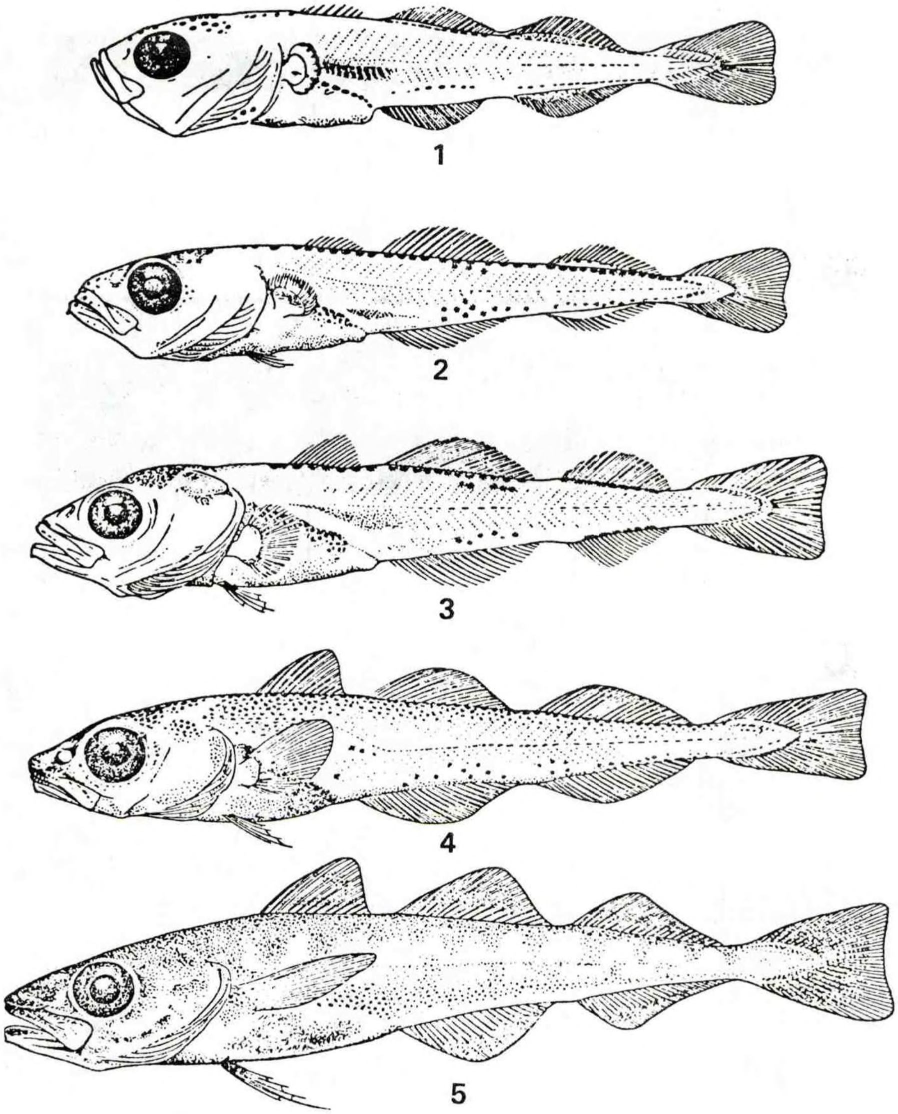

Figure 1.--Larval and juvenile walleye pollock, Theragra chalcogramma, from the eastern Bering Sea. 1) 10.7 mm, 2) 21.3 mm, 3) 30 mm, 4) 40 mm, 5) 100 mm (from Gorbunova 1954).

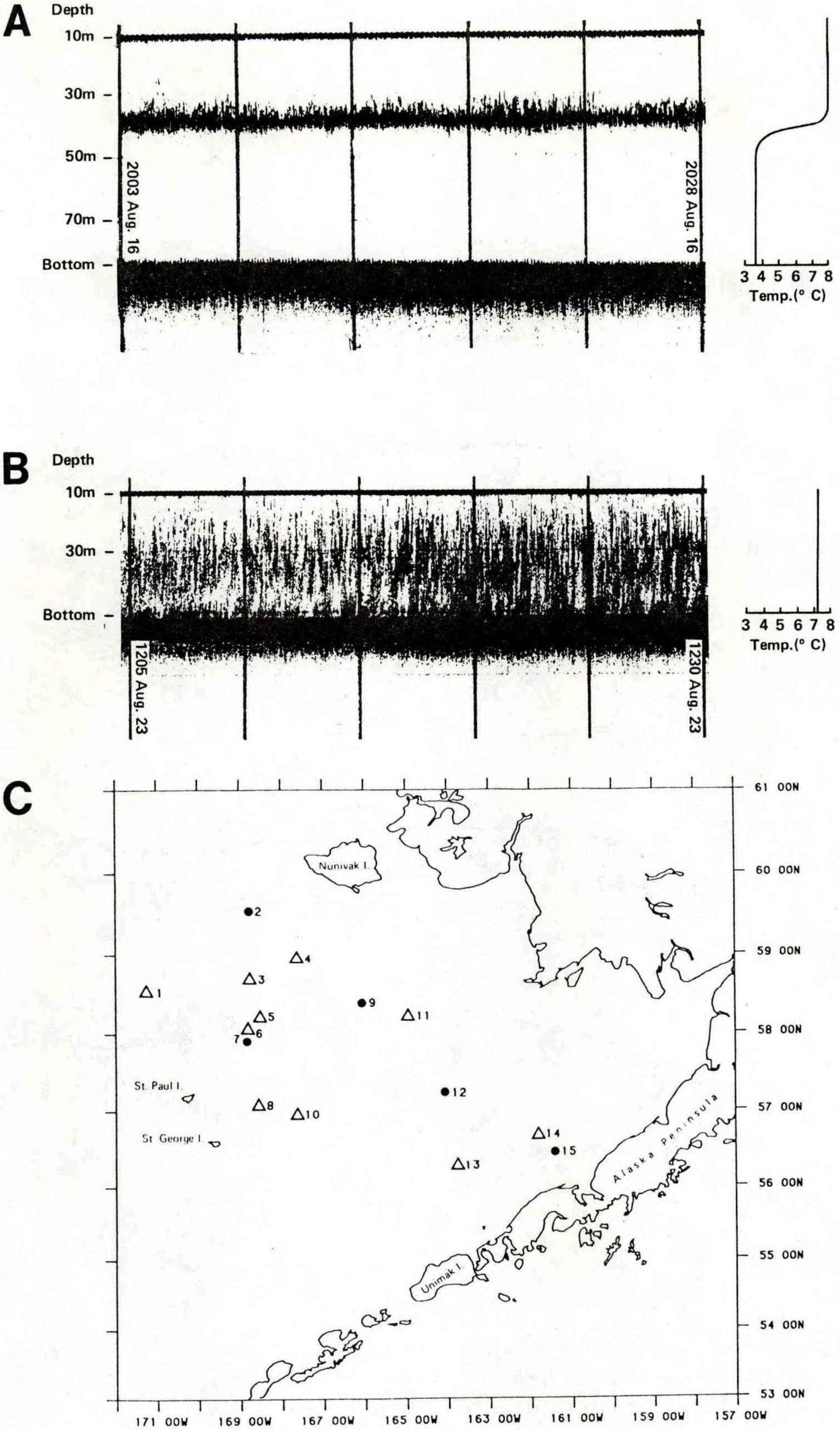

Figure 2.--Echograms of juvenile fish sign, along with water temperature profiles, A) prior to haul 10, B) prior to haul 11, <u>Chapman</u> Cruise 82-4, and C) location of trawl stations (from Francis and Bailey 1983; J. Traynor pers. commun. 1983).

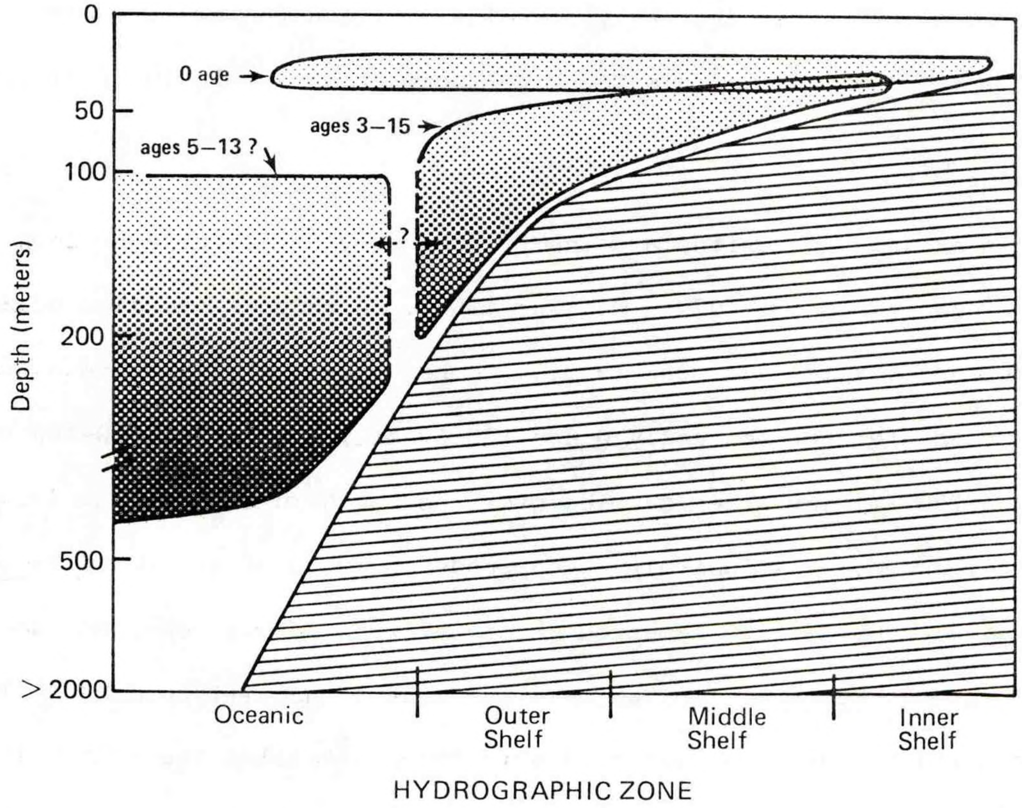

Figure 3.--Conceptual model of the vertical distribution of juvenile and adult walleye pollock across the eastern Bering Sea shelf and slope, and Aleutian Basin areas. Age-1 and age-2 pollock range throughout the water column over the outer, middle, and inner shelf domains.

is rare (Bakkala et al. 1983), although some 0-age specimens were taken there in 1979 (Walline 1983). The initial distribution of 0-age pollock depends on the distribution of spawning adults, egg and larval advection, and differential survival due to variability in feeding success and predation. Unfortunately, the influence of these factors is difficult to assess because the distribution of 0-age fish over time has not been observed. Some hypotheses concerning egg and larval transport and early juvenile distribution are presented in the article by Incze et al. in this Technical Memorandum and in the following sections.

Diet and Growth

Copepods and euphausiids are the primary prey of juvenile pollock (Takahashi and Yamaguchi 1972; Walline 1983). Amphipods are also occasionally important (Bailey and Dunn 1979). Cooney et al. (1980) found a distinct difference in diet between early 0 age (20-60 mm), late 0 age (60-100 mm), and age-1 (100-200 mm) juveniles sampled over the southern shelf (Fig. 4). Early juveniles fed almost exclusively on copepods and eggs of the genus *Pseudocalanus*. Larger 0-age juveniles supplemented this diet with larger copepods such as *Metridia* sp. and *Eucalanus* sp. as well as barnacle nauplii, pteropods, appendicularians, and unidentified fish. Age-1 juveniles fed primarily on large copepods and euphausiids. The larger, seasonally migrating copepods preferred by the larger juveniles do not occur in abundance inshore of the 80 m isobath (Cooney and Coyle 1980). This led Cooney et al. (1980) to suggest that older juveniles over the outer shelf and slope regions experience an advantage in growth and survival over their middle- and inner-shelf cohorts.

Walline (1983) examined the growth of individual juveniles by counting increments on otoliths presumed to be daily growth rings. A total of 30 juveniles, collected during 1978, 1979, and 1981, were examined from the

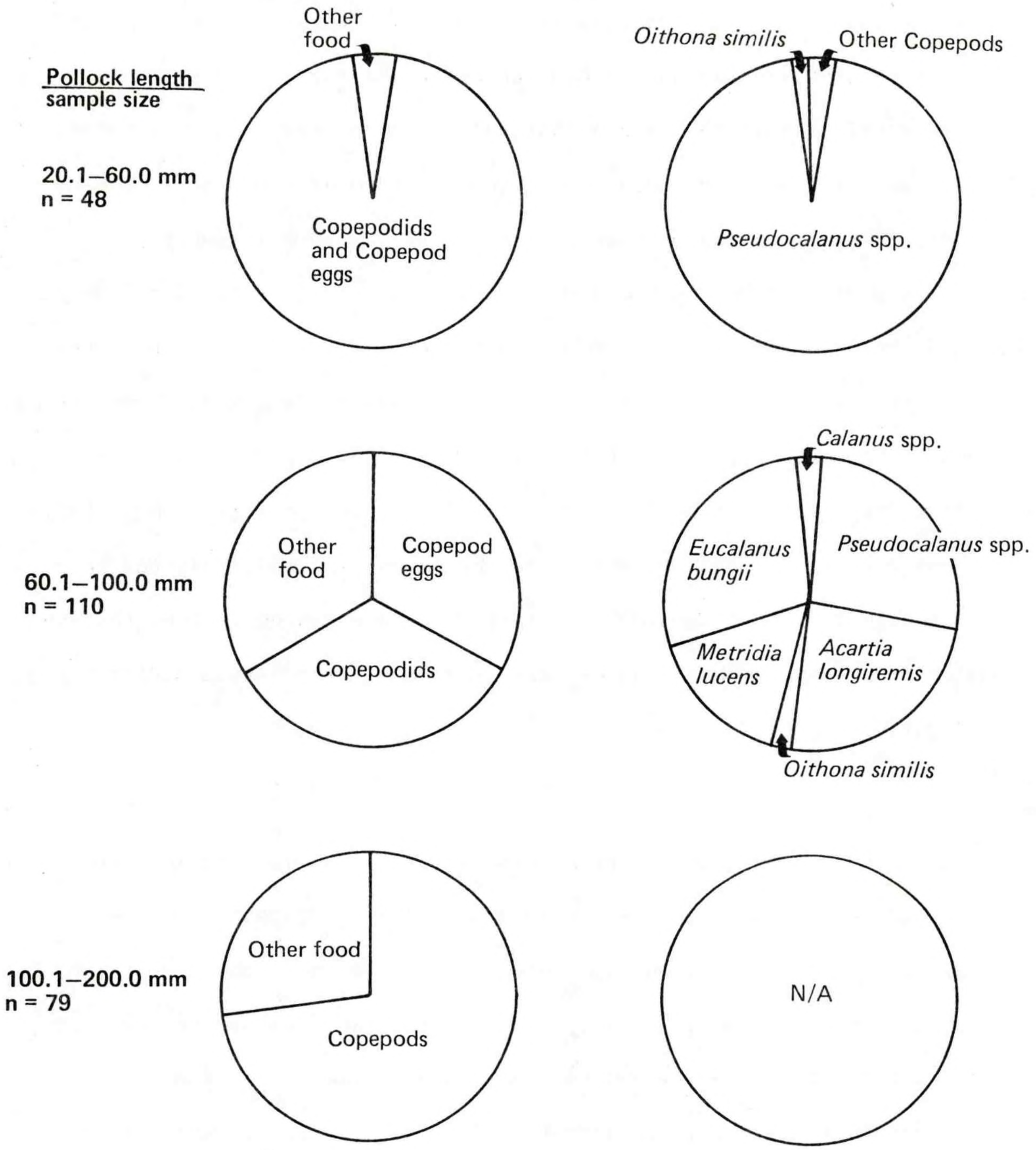

Figure 4.--Prey species composition for three size classes of juvenile walleye pollock from the southeastern Bering Sea slope areas during 1979 (from Cooney et al. 1980).

eastern Bering Sea. Although juvenile growth rates differed between sampling stations, the variability was not as high as one might expect. Juveniles seemed to be growing at roughly a constant rate, 0.55 mm per day. Nishiyama (1981) calculated the monthly average observed length over the period 1976-80 and estimated the food energy requirements of larval and 0-age juvenile pollock from the eastern Bering Sea shelf (Table 1). His results also indicate an average juvenile growth rate of about 0.5 mm per day. There was one notable exception, however. A few juveniles collected by Walline during 1978 apparently had hatched in the winter. These individuals exhibited significantly lower average growth rates than juveniles hatched in the spring or summer, but their survival caused Walline (1983) to speculate that timing of hatch may not be crucial to successful first feeding. This hypothesis was supported by the wide distribution of successful hatching dates as estimated from larval otoliths (Walline 1983).

Predation Mortality

Because of the seemingly uniform growth rate of juveniles and the broad distribution of successful larval hatching dates, Walline (1983) suggested that predation, rather then starvation, might be the primary factor determining year-class strength. As juveniles, pollock serve as a major food resource for a wide variety of species including adult pollock (see adult diet and growth sections in this article), other fish (in the article by Smith et al.), marine mammals and birds (in the article by Kajimura and Fowler), and man (in the article by Terry et al.) (Fig. 5).

I am aware of no published studies of predation on pollock eggs or larvae. Studies on other species, however, indicate that pelagic fishes (Hunter 1981) and invertebrate predators (Purcell 1981; Moller 1980; Bailey and Yen 1983) may have significant impact on the survival of these early life-history stages.

Table 1.--Average observed length of larval and juvenile walleye pollock and estimated food energy requirement by month (Nishiyama 1981).

Month	Average length (mm)	Average weight (mg)	Food Energy requirement (cal)
May	7.1	2	1.1
June	17.9	38	8.6
July	30.8	193	32.9
August	45.3	635	85.3
September	61.1	1582	188.9
October	78.0	3544	366.7

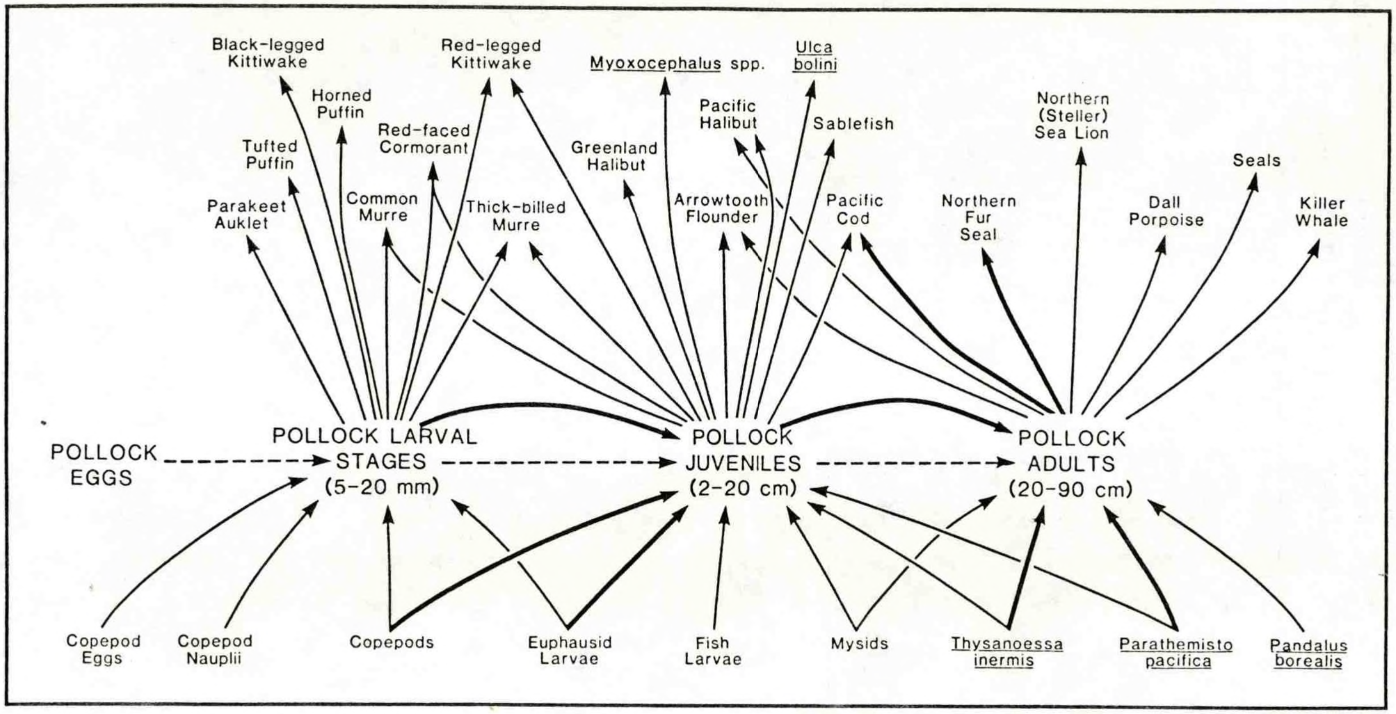

Figure 5.--Apparent food web based on walleye pollock in the eastern Bering Sea. Dotted lines indicate ontogeny. Solid lines show important feeding relationships, with arrowheads and line weights indicating the direction and magnitude of carbon flows (from Smith 1981).

Adults

Adult pollock primarily occur over the outer shelf and slope regions of the eastern Bering Sea, but also occupy pelagic waters of the Aleutian Basin. There appear to be fundamental differences between the Aleutian Basin population and the shelf and slope populations with respect to diet, growth, time of spawning, and distribution in the water column. Perhaps the most striking difference occurs in age distributions between the two areas (Fig. 6). Over the Aleutian Basin, there is a preponderance of older fish and few, if any, less than age 4 (34 cm), suggesting that adult fish recruit to the basin from other areas.

Unit Stocks

From the distribution of pollock eggs in ichthyoplankton surveys (Nishiyama and Haryu 1981; Bulatov 1979, 1981; and the article by Incze et al. in this Technical Memorandum) and the distribution of spawning adults in demersal and midwater trawl catches (Babayon 1981, Hirschberger and Smith 1983; Moiseev 1983; Fedeyev et al. 1983), it is apparent that the main spawning ground for the shelf population lies between the Pribilof Islands and Unimak Pass. It also appears that spawning occurs northwest of the Pribilof Islands (Fig. 7, see also the article by Incze et al. in this Technical Memorandum). Recent hydroacoustic-midwater trawl surveys have located spawning concentrations over the Aleutian Basin as well (Okada 1983). It is not known, however, how isolated these spawning populations are. There is a need for tagging studies to determine whether individuals return to the same areas to spawn.

Apparently there is enough genetic mixing to prevent the detection of significant regional differences in allelic frequencies using electrophoretic techniques (Grant and Utter 1980). Serobaba (1977), however, identified

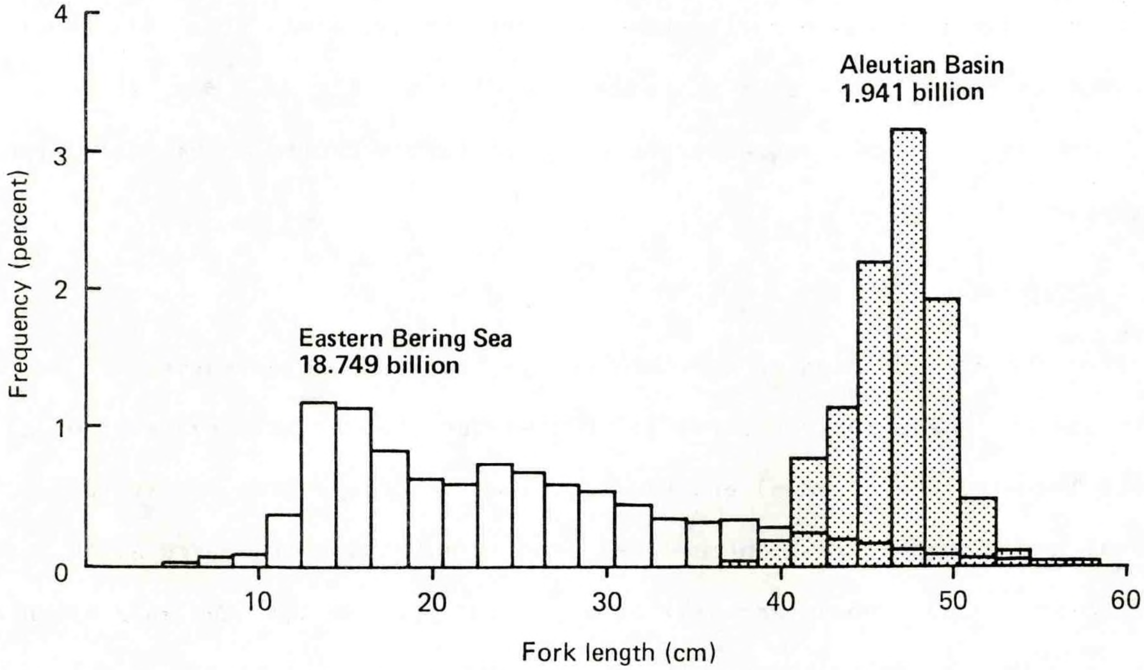

Figure 6.--Length frequency distributions of sample walleye pollock populations in the Aleutian Basin and on the eastern Bering Sea continental shelf as shown by the Japanese hydroacoustic-midwater trawl and Japan-U.S. demersal surveys during 1979. Numbers within the figures are population estimates derived from the two surveys (from Bakkala et al. 1983).

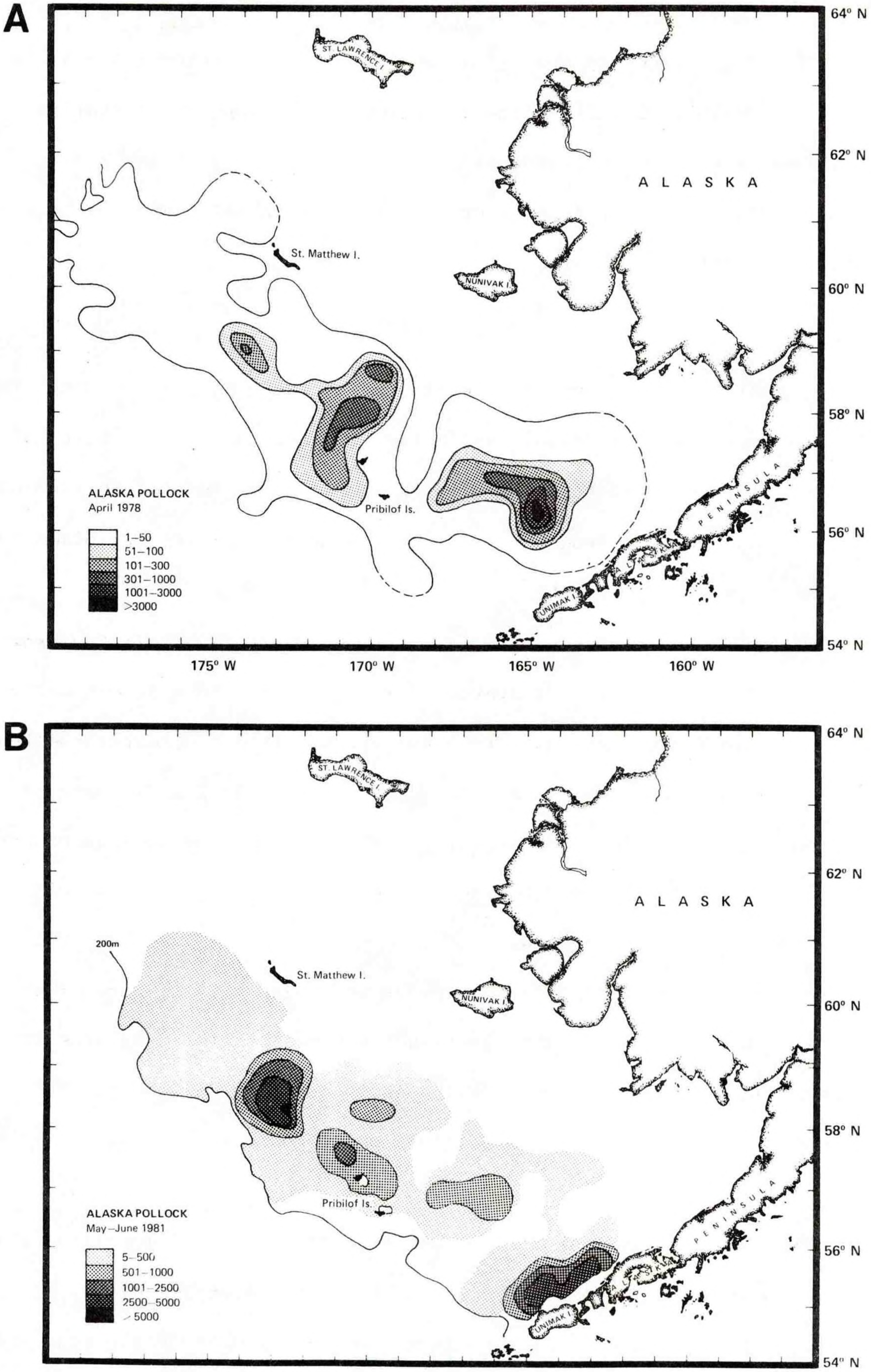

Figure 7.--A) Spatial distribution of walleye pollock eggs from ichthyoplankton surveys during April 1978 (adapted from Bulatov 1979), and B) distribution of adult pollock from midwater trawl surveys during May-June 1981 (adapted from Moiseev 1983).

morphometric differences between adult pollock caught northwest and southeast of the Pribilof Islands. Significant regional differences in larval (Walline 1983) and adult growth have also been observed. Undoubtedly these differences are due in part to environmental factors. Whether or not there are heritable differences is still in question.

Growth

Both otoliths and scales are used to estimate the age of pollock. The two techniques provide comparable estimates for ages up to about 5 yr, after which scale readings tend to underestimate age relative to otolith readings (Bakkala et al. 1983). Throughout this review, age estimates are based on otolith readings.

Smith (1981) fitted the generalized form of the von Bertalanffy growth function (Richards 1959) to the average size at age (in fork length and wet weight) of pollock from demersal trawl survey data from the eastern Bering Sea shelf and slope for the years 1973-78 (Fig. 8; Table 2). The lack of inflection points in these relationships indicates that the average growth rate of pollock in the eastern Bering Sea is highest for juveniles and decreases monotonically with age.

Okada and Yamaguchi (1983) and Traynor and Nelson (1983) noted that the average size of pollock from the Aleutian Basin was consistently less than that of pollock of the same age from the eastern Bering Sea shelf. Preliminary results of a statistical analysis of adult pollock growth indicate that the average size at age:

1) is significantly less for pollock from the northern slope area than for pollock from the shelf or southern slope areas,
2) is significantly less for pollock from the Aleutian Basin area than for pollock from the shelf areas, and

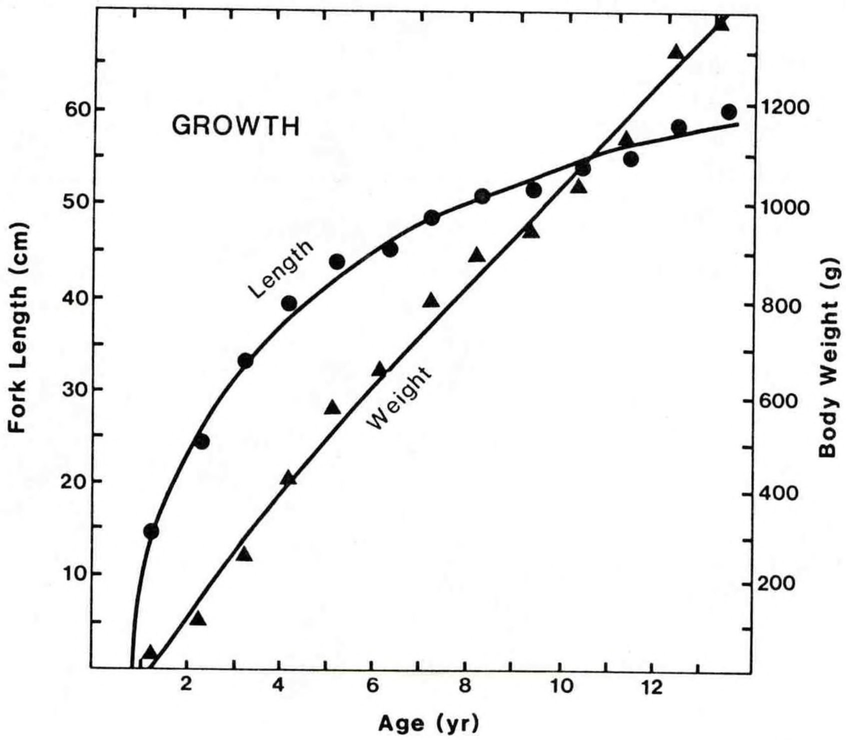

Figure 8.--Growth in length and weight, based on age-length data from walleye pollock sampled from the eastern Bering Sea shelf and slope during 1973-78 (from Smith 1981).

Table 2.--Generalized von Bertalanffy growth curve parameters for walleye pollock from the shelf and slope areas of the eastern Bering Sea during 1973-78.

	Y_∞	K	x_o	d
Growth in Length (Y = fork length (cm))	64.81	0.132	0.78	0.520
Growth in Weight (Y = weight (g))	7057	0.016	1.18	0.944

$Y_x = Y_\infty \ [1-e^{-K(x-x_o)}]^d$ (from Smith 1981).

3) does not always differ significantly between pollock from the northern slope and pollock from the Aleutian Basin.[1]

Regional differences in growth may be due to differences in environmental conditions, energy intake, or perhaps genetic differences between stocks. Some evidence exists for each of these factors. Differences in water temperature between the hydrographic domains (see the article by Schumacher in this Technical Memorandum) probably affect metabolic rates and thus growth. The prey composition, average weight of pollock stomach contents, and percent of stomachs that are empty also differ between regions, affecting growth (Dwyer et al. 1983). Finally, regional differences in the size of gill rakers and length of intestines (Serobaba 1977) may indicate genetic causes of growth differences.

There seems to be a higher degree of seasonal variability in average size at age for pollock from the southeastern slope than for pollock from other areas.[1] In some years, the average size at age for pollock from the southeastern slope area resembles that of pollock from the Aleutian Basin during the first quarter of the year, but resembles that of pollock from the shelf areas during the fourth quarter (Fig. 9). Perhaps this is an indication of local mixing or migration.

Fecundity

Both male and female pollock begin to attain sexual maturity at about 25 cm fork length, and 50% are mature by 31-34 cm (3-4 yr of age; Fig. 10) (Bakkala and Smith 1978). Maturity occurs at a later age in the north, however

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[1] Lynde, C. M., M. VanHouten, and R. C. Francis. (In prep.). Regional and temporal differences in the growth of walleye pollock, <u>Theragra chalcogramma</u>, from the eastern Bering Sea, with implications for fisheries management. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

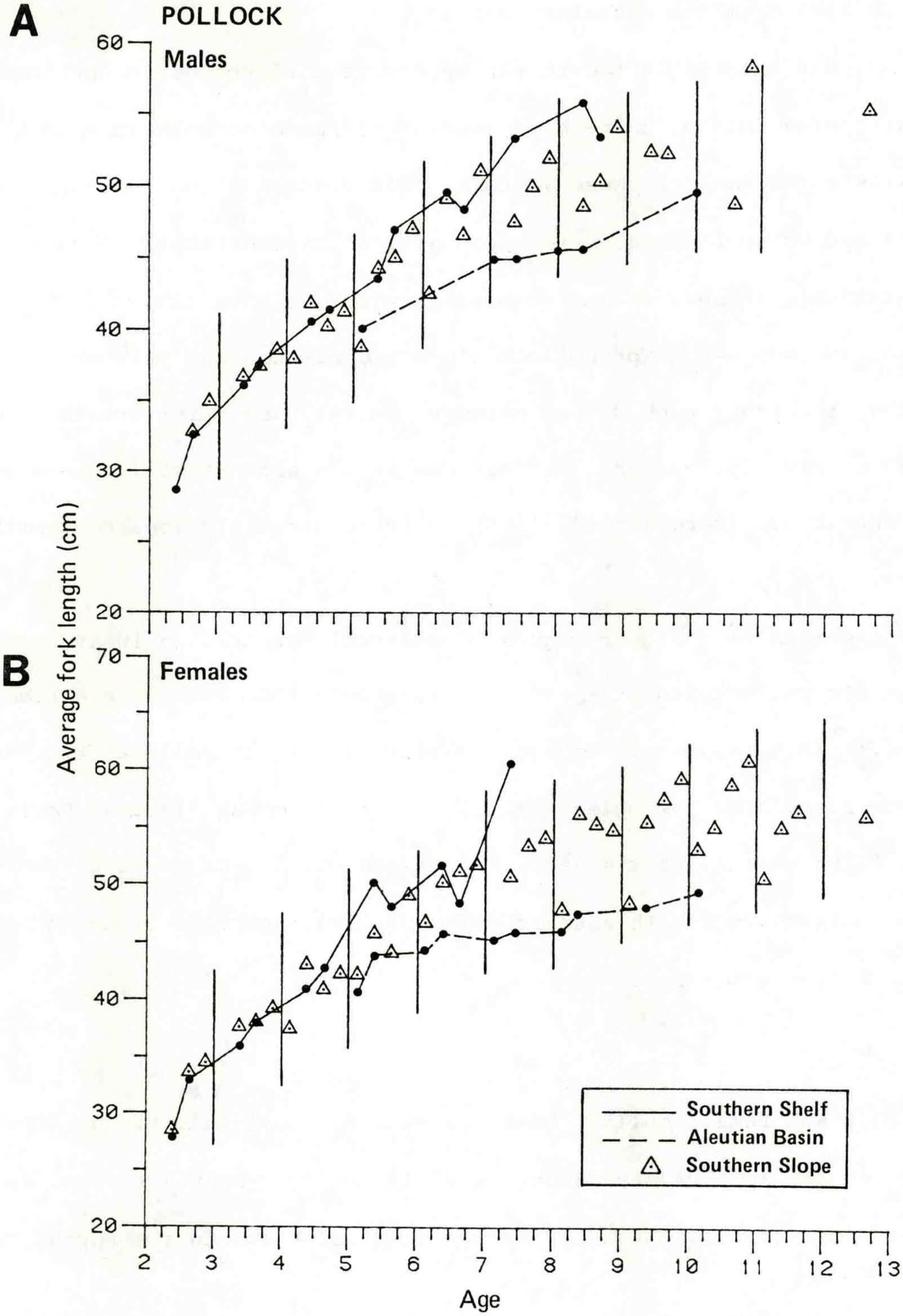

Figure 9.--Average length at age of male (A), and female (B) walleye pollock from the eastern Aleutian Basin, and the southern slope, and southern middle shelf areas of the eastern Bering Sea during 1981.

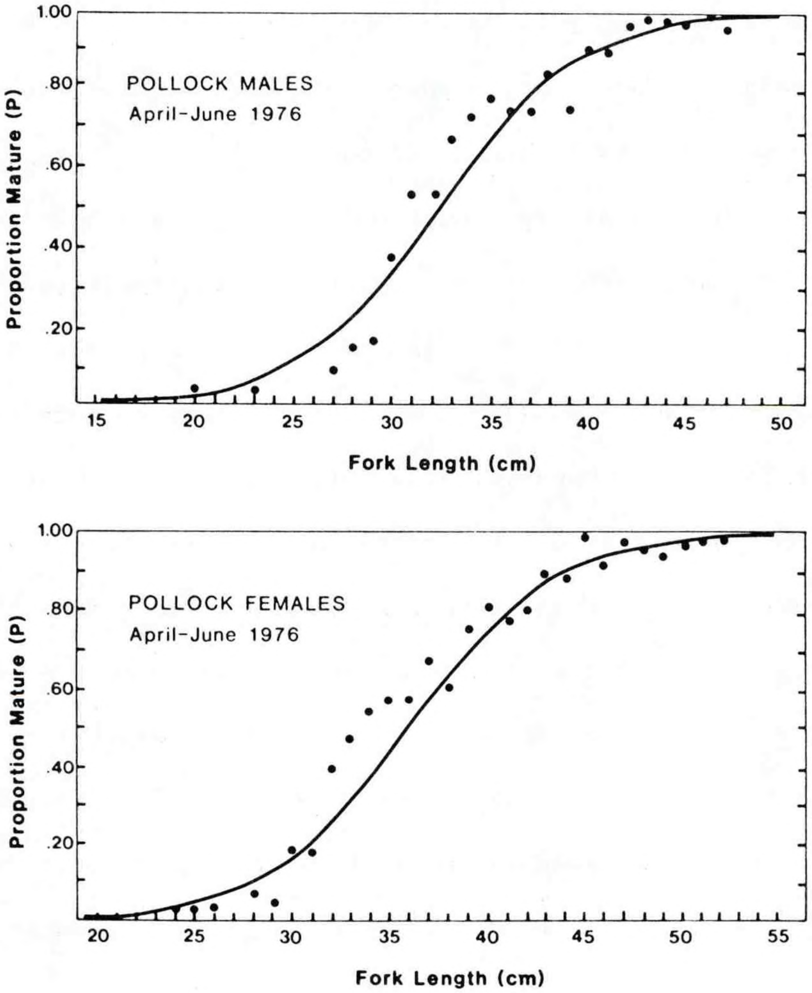

Figure 10.--Length-maturity relationships observed from walleye pollock taken during the April-June 1976 demersal trawl survey in the eastern Bering Sea (from Smith 1981; Bakkala and Smith 1978).

(K. M. Bailey, Northwest and Alaska Fisheries Center, Seattle, WA 98112. pers. commun.). The estimated numbers of eggs spawned per year range between 222,400 and 487,900 for a 50 cm female (Table 3). Observations have ranged as high as 1,389,000 for a 75 cm female (Serobaba 1971). There is considerable uncertainty in the estimated average fecundity at length, since the percentage of developing oocytes released per year has not been fully quantified by field and laboratory studies, although studies are currently being planned to compare the fecundity of pollock from the Bering Sea and Gulf of Alaska. In a preliminary study, Shew (1978) described two general size classes of oocytes: large (>0.59 mm diameter) and small (<0.59 mm diameter). She calculated two separate fecundity-length relationships assuming 1) only large oocytes are released, and 2) all oocytes are spawned each year. Gorbunova (1954) and Serobaba (1971), however, delineated three classes of developing oocytes, of which two were said to be released each year in batches. Zver'kova (1977) also described batch developement of ova in pollock from the Sea of Japan. Recently, Yoon (1982) completed a detailed study of the reproductive ecology of walleye pollock from Funka Bay, Hokkaido in which the fecundity estimates at length were higher than those of Shew (1978). Yoon found that pollock raised in captivity spawned in 2-5 batches over a period of 18 d and he estimated that animals in the field may spawn 10 or more times per year.

Spawning Behavior and Migration

Pollock have a protracted spawning period in the eastern Bering Sea, extending from February through July (Yamaguchi and Takahashi 1972; Hirschberger and Smith 1983; Okada 1983). In places where bottom depth exceeds 100 m, active spawners were observed in midwater shoals with inactive spawners segregated at lower depths (Serobaba 1974; Yoon 1982). The centers of distribution of eggs usually occur over areas of 2.0-3.5°C bottom water

Table 3.--Walleye pollock fecundity estimates by area.

Area	Source	Parameter estimates of the fecundity-length relationship (Eq. 10, Appen. 1) a	b	Predicted fecundity by length 30 cm	40 cm	50 cm
EBS[c]	Serobaba 1971	2.89	2.93	60,900	141,500	271,900
EBS	Shew 1978[a]	0.292	3.462	37,900	102,700	222,400
EBS	Shew 1978[b]	0.376	3.536	62,800	173,800	382,600
NE Sea of Jpn	Zver'kova 1977	0.16	3.72	50,000	145,800	334,400
Funka Bay Jpn	Yoon 1982	0.0837	3.982	63,800	200,600	487,900

[a] Assuming only large (>0.59 mm of diameter) oocytes are released each year.

[b] Assuming all oocytes are released.

[c] Eastern Bering Sea.

and eggs are very seldom found over areas where bottom water temperatures are less than 1°C (Gorbunova 1954; Serobaba 1968, 1974; Bulatov 1979, 1981, 1982; Moiseev 1983; Nishiyama and Haryu 1981). The layers of water in which stage I eggs were primarily distributed were also found to have high oxygen concentration (Serobaba 1974). Serobaba suggested that these properties were important for mobility of spermatozoa and fertilization of ova.

Spawning appears to proceed shoreward across the shelf during the spawning period (Serobaba 1974; Nishiyama and Haryu 1981; M. E. Clark, University of California, La Jolla, CA 92093. Pers. commun.), perhaps in response to warming water temperatures in the middle shelf domain. Over the Aleutian Basin, spawning apparently occurs in February and March (Okada 1983). Along the slope and outer shelf, peak spawning occurs in March and April, whereas the middle shelf peak is in April and May (Fig. 11).

Maeda (1976) noted that near Funka Bay, Hokkaido, pollock congregate at the front separating the Oyashio cold water mass from the Tsugaru warm current before spawning. He conjectured that the seaward side of the front was used as a spawning ground and that the location of the front varied from year to year depending on oceanographic conditions. A similar situation may exist in the eastern Bering Sea with spawning pollock following the 3°C isotherm as it recedes landward and to the north from the outer shelf.

Serobaba (1968) and Nishiyama and Haryu (1981) noted that within a given area the average egg diameter tended to decrease over time. Since average egg size does not change with developmental stage (Gorbunova 1954; Nishiyama and Haryu 1981), these differences have been attributed to differences in the size of spawning females, with smaller females spawning smaller eggs later in the season. Such is the case with other species of marine fishes (Bagenal 1971). However, Yoon (1982) noted that the average egg size also decreases

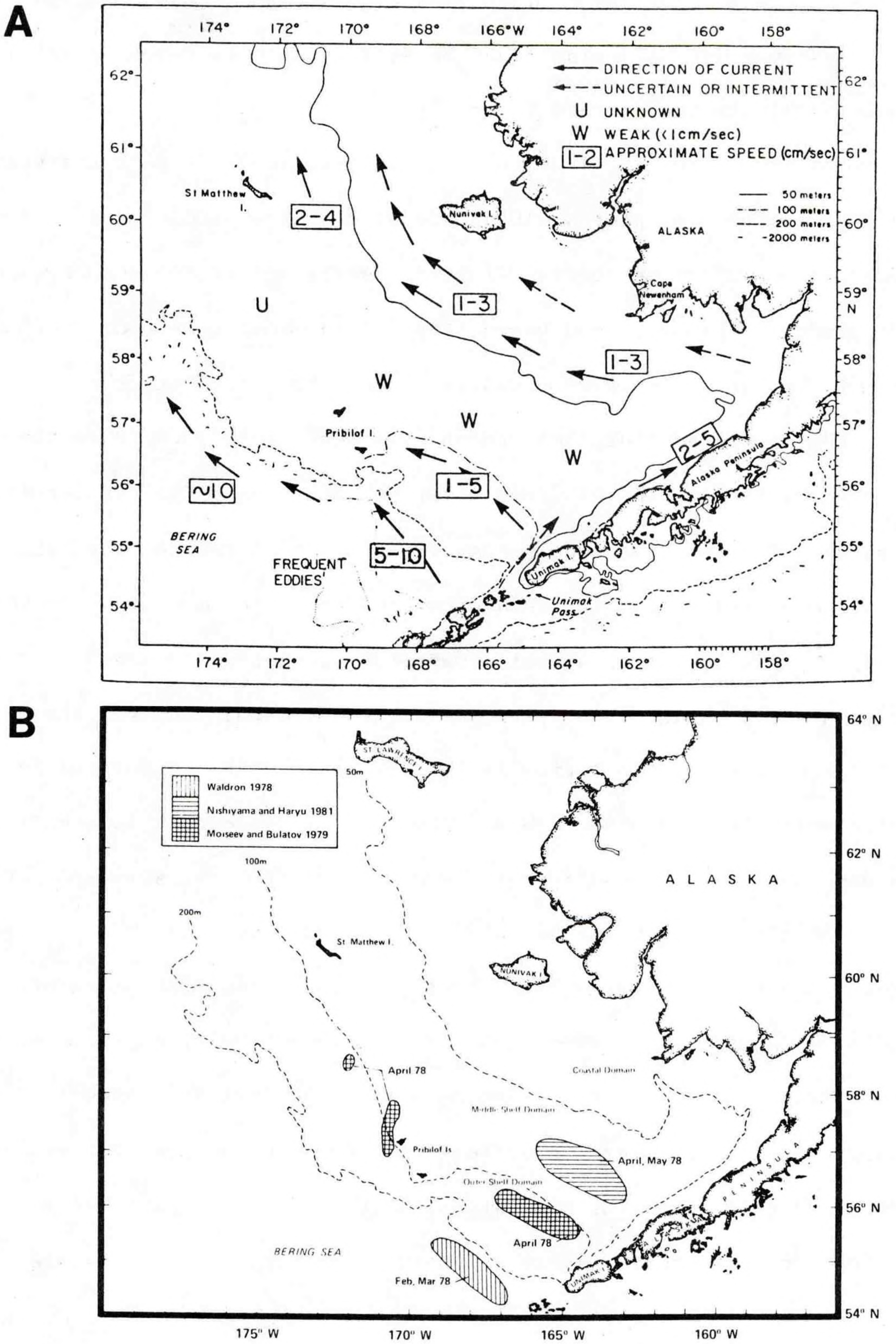

Figure 11.--Estimated net circulation by hydrographic domain during 1981 (A), and location of spawning walleye pollock during 1978 (B) (from Francis and Bailey 1983; Waldron 1978; Nishiyama and Haryu 1981; Moiseev and Bulatov 1979).

with each subsequent batch for a given female. Therefore, the observed decrease in average egg size also might be attributable to batch spawning, assuming it occurs in the eastern Bering Sea.

Nishiyama and Haryu (1981) and others proposed that the same individuals initially spawn over the outer shelf and later over the middle shelf. Regional differences in egg diameter observed in the eastern Bering Sea lend credence to this argument. Nishiyama and Haryu (1981) found that eggs from the northern middle shelf area were significantly larger than those from other areas, and Serobaba (1974) reported that the largest eggs were usually found at the landward ends of their transect lines (over the middle shelf). If larger pollock spawn first and individuals spawn in only one location, the later spawned eggs of the middle shelf should be smaller on the average. On the other hand, if individuals spawn while migrating inshore, the larger, faster swimming fish would be expected to be the vanguard, accounting for the larger eggs over the middle shelf. During two of the years that regional differences in egg size were observed (1968, 1972), there is evidence that larger fish were present in the middle shelf areas immediately after the spawning period (Fig. 12) (Takahashi and Yamaguchi 1972; Maeda 1972; Serobaba 1974).

These concepts could be explored by tagging spawning fish; however, the trauma of such handling may affect behavior. Alternatively, repetitive cross shelf-slope transects during the spawning season may indicate changes in length composition of spawners in different areas. Research is currently being conducted to examine the size at age of different spawning groups sampled from the commercial fishery in order to determine if stocks are mixing during spawning.

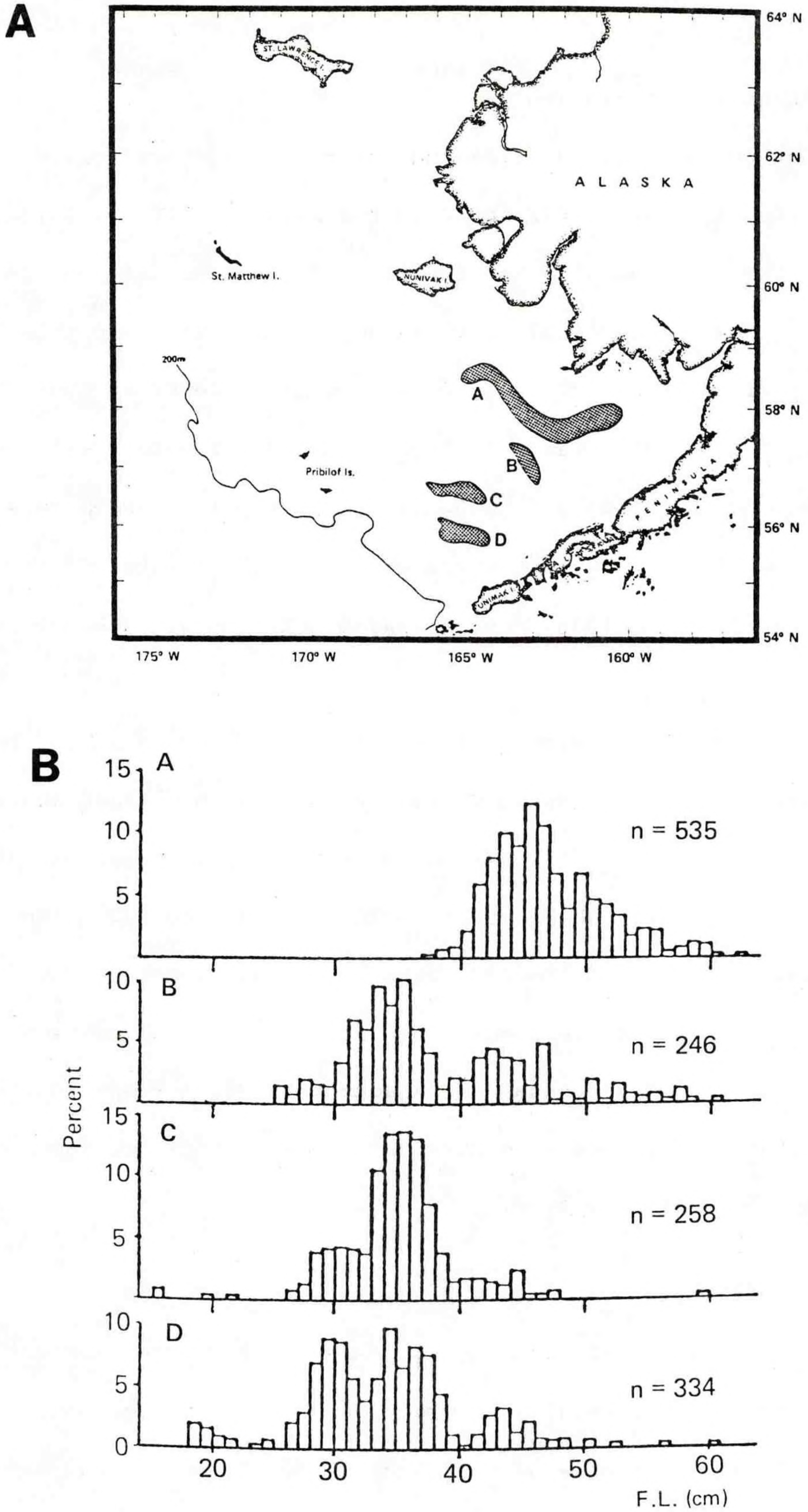

Figure 12.--Sampling areas for walleye pollock within the eastern Bering Sea during June 1968 (A), and frequency distributions of pollock lengths in each sampling area (B) (adapted from Maeda 1972).

Feeding and Wintering Migration

After (or perhaps during) spawning, there is a general dispersal of adults from the slope and outer shelf to the middle shelf domain, and in some years inner shelf domain, for feeding. These observations are based on commercial catches and demersal trawl surveys. The extent of this inshore movement of pollock apparently depends on the presence or absence of the cold (-1.0°-2.0°C) bottom water mass of the middle shelf domain (Bailey and Francis 1983; Bakkala and Alton 1983). Concentrations of pollock were primarily located in outer shelf waters in years when the bottom water of the middle shelf was cold (1975 and 1976), but extended onto the middle shelf in warm years (1979 and 1981; Fig. 13).

With the onset of the winter season, the shelf population of pollock retreats from the cold (-1.5°-0.0°C) bottom water on the inner and middle shelf to the warmer (ca. 3°C) water of the outer shelf (Serobaba 1968; Shimada et al. 1983). This outer shelf water is tempered by the intrusion of oceanic water (see the article by Schumacher in this Technical Memorandum). In contrast, most of the Aleutian Basin population probably remains over the basin throughout the year (Okada and Yamaguchi 1983), perhaps benefitting from more uniform and moderate temperature conditions at the apparent expense of a reduction in available food.

Diet and Cannibalism

As pollock increase in size, there is an increasing preference for larger prey items. The relative dietary importance of copepods decreases while the relative importance of fish increases. Takahashi and Yamaguchi 1972; Mito 1974; Bailey and Dunn 1979). Fish prey species include myctophids, herring, gadoids, cottids, hexagrammids, and zoarcids (Bailey

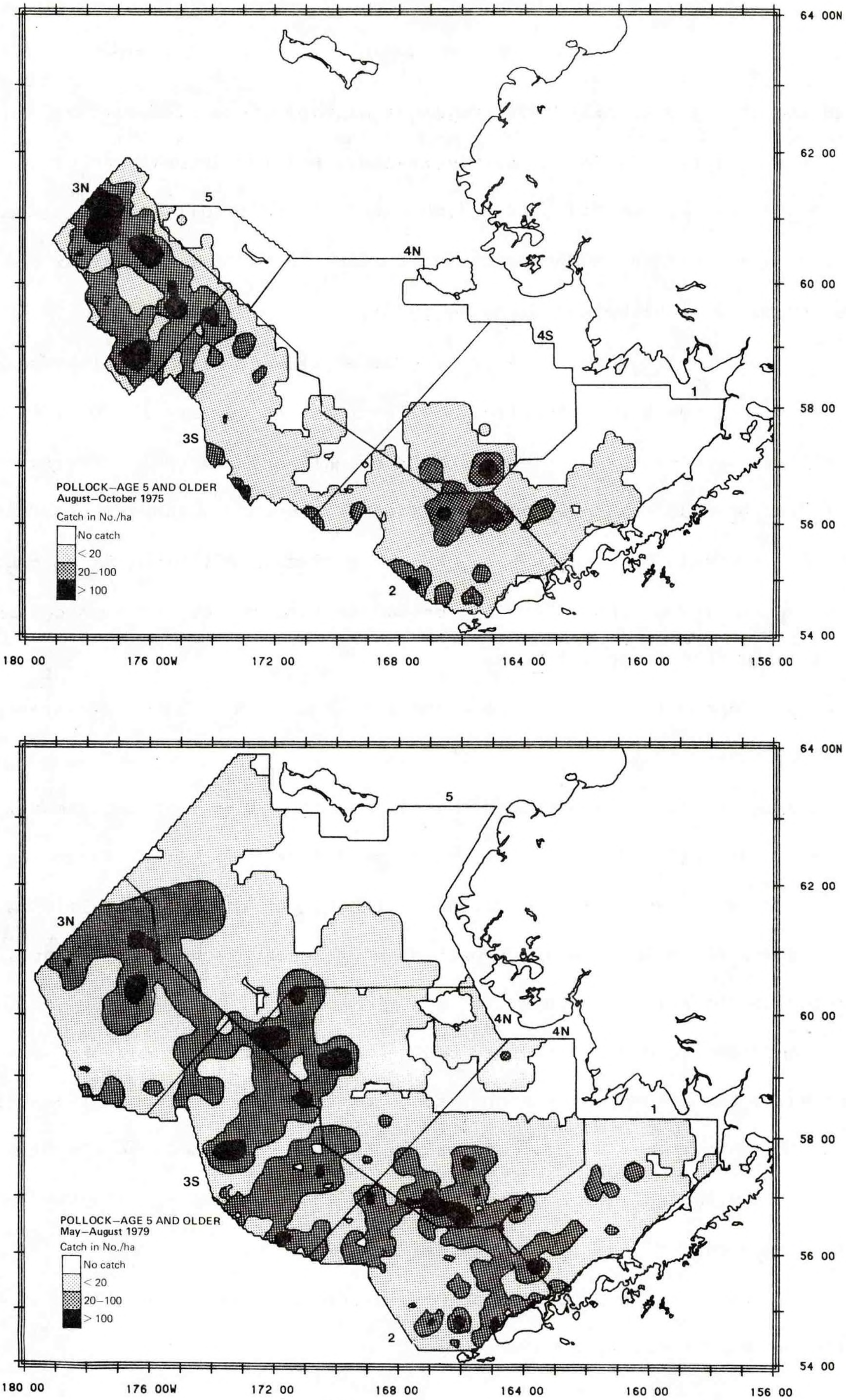

Figure 13.--Distribution of population numbers of age-5 and older walleye pollock in the eastern Bering Sea in the relatively cold year of 1975 and relatively warm year of 1979 as shown by Northwest and Alaska Fisheries Center demersal trawl survey data (from Bakkala and Alton 1983).

and Dunn 1979; Wespestad 1979; Dwyer et al. 1983; see also the article by Smith et al. in this Technical Memorandum), but the largest proportion (often more than 75% by weight) of the fish eaten by adult pollock over the eastern Bering Sea shelf and slope consists of juvenile pollock (Takahashi and Yamaguchi 1972; Francis and Bailey 1983).

From a preliminary analysis of pollock stomach samples collected aboard research and commercial fishing vessels since the summer of 1981 (Dwyer et al. 1983), it appears that there are both seasonal and regional differences in the diet of adult walleye pollock. Table 4 presents a summary of adult stomach contents by area, season, and size class. Although the data are sketchy in places, the following generalizations can be drawn concerning the diet of the shelf population:

1) Euphausiids are an important food source for all size-classes during the spring and summer;

2) copepods are important to small adults (<35 cm) in the summer;

3) juvenile pollock are important to the smaller adults in the fall (although they may be less important northwest of the Pribilof Islands); and

4) juvenile pollock are important components of the diet of the larger adults in the fall and winter.

Apparently, 0-age juveniles begin to settle out of the upper water column in the autumn with the breakdown of the seasonal pycnocline. At this time they are vulnerable to cannibalism by most adult pollock (Dwyer et al. 1983). By the following winter or spring their increased size renders them vulnerable only to the larger adults.

Cannibalism may offer certain evolutionary advantages related to density dependency (Fox 1975), such as:

1) increased population stability and persistence,

2) increased growth for adults and surviving juveniles, and

3) increased survival and reproduction for adults.

Fox (1975) suggests that cannibalism may be an evolved behavior in some species. For pollock, however, it may be strictly a function of the encounter rate between opportunistic adult predators and vulnerable prey-sized juveniles. As noted by Fox, "many fish grow faster on larger food items and their own species may be the...most available prey."

Within the Aleutian Basin, fish are much less prevalent in the diet of large adult pollock and cannibalism is rare. This is due to the low availability of small fishes in general and juvenile pollock in particular. Instead, the diet consists primarily of zooplankton such as copepods, euphausiids, amphipods, appendicularians, and occasionally fish (primarily myctophids) and squid (Okada 1979; Okada and Yamaguchi 1983).

Natural Mortality

Estimates of the instantaneous rate of natural mortality range from about 0.3 (R. Francis, Northwest and Alaska Fisheries Center, Seattle, WA 98112. Pers. commun.) to 0.65 (Chang 1974). Francis used Pauly's (1979) method of estimating natural mortality from growth parameters and ambient water temperature. He estimated natural mortality rates of 0.34 and 0.31 for pollock from the northwest and southeast areas of the eastern Bering Sea, respectively. I used a method of estimating population abundance and natural mortality rates from catch and effort data (Bledsoe and Lynde 1982). In this analysis the average natural mortality was estimated to be 0.5 overall. Bakkala and Wespestad (1983) applied Pope's (1972) cohort analysis technique to catch-at-age data for pollock from the eastern Bering Sea for the period 1973-80. By adjusting the natural mortality rate until the estimated

Table 4.--Predominant food category by weight in the diet of adult walleye pollock by season, area, and length category for the years 1981, 1982 (Dwyer et al. 1983).

Area	Size class (cm fork length)	Season			
		Winter	Spring	Summer	Fall
Southeast of Pribilof Islands	<35	Insuf. data	Euphausiids	Copepods Euphausiids Fish (other than pollock)	Fish (mostly pollock)
	35-50	Insuf. data	Euphausiids	Euphausiids	Fish (mostly pollock)
	>50	Fish (mostly pollock)	Euphausiids Fish (other than pollock)	Euphausiids	Fish (mostly pollock)
Northwest of Pribilof Islands	<35	Euphausiids Fish (other than pollock)	Euphausiids	Copepods Euphausiids	Euphausiids
	35-50	Euphausiids Fish (other than pollock)	Euphausiids	Euphausiids Fish (mostly pollock)	Fish (Pollock in '81 myctophids in '82)
	>50	Fish (mostly pollock)	Fish (mostly pollock)	Euphausiids Fish (mostly pollock)	Fish (Pollock in '81 myctophids in '82)
Aleutian Basin	<35	-	-	-	-
	35-50	Euphausiids	Insuf. data	Copepods Misc.	Euphausiids Fish (myctophids)
	>50	Euphausiids Misc.	Insuf. data	Euphausiids Misc.	Fish (other than pollock) Shrimp Misc.

population structure approximated that of the demersal and hydroacoustic surveys, they obtained age-specific natural mortality rates of 0.85 and 0.45 for ages 1 and 2, 0.30 for ages 3 through 10, and gradually increasing mortality rates for older ages. The overall average mortality rate was estimated to be 0.41.

Abundance Estimates and Recruitment

Table 5 lists the estimated abundance of pollock of ages 1 through 7 over the shelf and slope areas during the period 1973-80. Also shown are the estimates for the same areas during 1979 derived by Bakkala et al. (1983) from demersal trawl and hydroacoustic-midwater trawl survey data, and by Bakkala and Wespestad (1983) from cohort analysis. The various estimates differ substantially. Of the two survey methods, the demersal trawl survey underestimates the abundance of age-1 and age-2 pollock since the majority are above the portion of the water column sampled by demersal trawls. On the other hand, the hydroacoustic survey probably underestimates the abundance of older ages. The combined demersal trawl and hydroacoustic-midwater trawl survey results may more accurately reflect the true age distribution of the population. Relative to the combined survey results, the cohort analyses appear to underestimate the abundance of younger ages and overestimate the abundance of older ages.

Estimates of biomass for 1979 obtained from the surveys and cohort analyses are more comparable, totaling 10.3 million t based on the cohort analysis (Bakkala and Wespestad 1983) and 11.1 million t based on the combined survey results (Bakkala et al. 1983). For the period 1973-79, biomass estimates based on cohort analysis ranged from 12.8 to 10.3 million t.

Table 5.--Estimated numbers (billions) of walleye pollock from the eastern Bering Sea for the years 1974-81, based on cohort analysis and pair trawl effort (Lynde unpubl. data), and estimated numbers during 1979 based on survey data (Bakkala et al. 1983) and Pope's (1972) cohort analysis (Bakkala and Wespestad 1983).

Age/Year	1974	1975	1976	1977	1978	1979	1980	1981
1	32.9	23.9	32.8	26.5	32.1	46.1	6.5	-
2	32.4	19.8	14.4	19.9	16.0	19.4	27.8	3.9
3	8.1	17.5	11.4	8.6	11.3	9.3	11.1	16.1
4	2.1	4.1	8.4	5.8	4.0	6.2	4.8	6.0
5	2.5	1.1	2.4	4.4	2.8	2.0	3.3	2.6
6	1.2	1.2	0.6	1.3	2.4	1.4	0.8	1.8
7	0.7	0.6	0.6	0.3	0.7	1.3	0.7	0.4

	1979				
	Survey			Cohort Analysis	
Age	Demersal	Hydroac.	Total	Method A[a]	Method B[b]
1	7.7	69.1	76.9	20.5	46.1
2	5.7	41.1	46.8	14.2	19.5
3	2.4	3.9	6.3	5.2	9.3
4	1.2	0.4	1.6	3.9	6.2
5	0.8	0.5	1.3	2.4	2.0
6	0.4	0.1	0.5	1.1	1.4
7	0.2	0.0	0.2	1.0	1.3

[a] Cohort analysis technique as in Bledsoe and Lynde (1982), source: Lynde (unpub. data).

[b] Cohort analysis technique as in Pope (1972), source: Bakkala and Wespestad (1983).

Recruitment estimates (numbers of age 1 fish) from the two catch-at-age analyses by Bakkala and Wespestad (1983) and Lynde (unpubl. data) were similar for 1973-78, but diverged in 1979 (Fig. 14). The 1979 year class (age 1 in 1980) appears to be much less abundant than previous year classes. The low abundance of the 1979 year class has also been indicated by the analyses of Francis and Bailey (1983) and Traynor (1983), and survey results (Bakkala and Wespestad 1983). As an example of the importance of pollock to the ecosystem, the failure of the 1979 year class may have had adverse effects on the breeding success of marine birds, such as kittiwakes, nesting on the Pribilof Islands. Black-legged and red-legged kittiwakes feed heavily on 1-yr-old pollock in the summer and young-of-the-year pollock in the fall (Hunt et al. 1981). McRoy and Walsh (1981) hypothesized that poor production of food during 1980 caused the nesting failure of St. George Island kittiwakes in 1981 (Fig. 14).

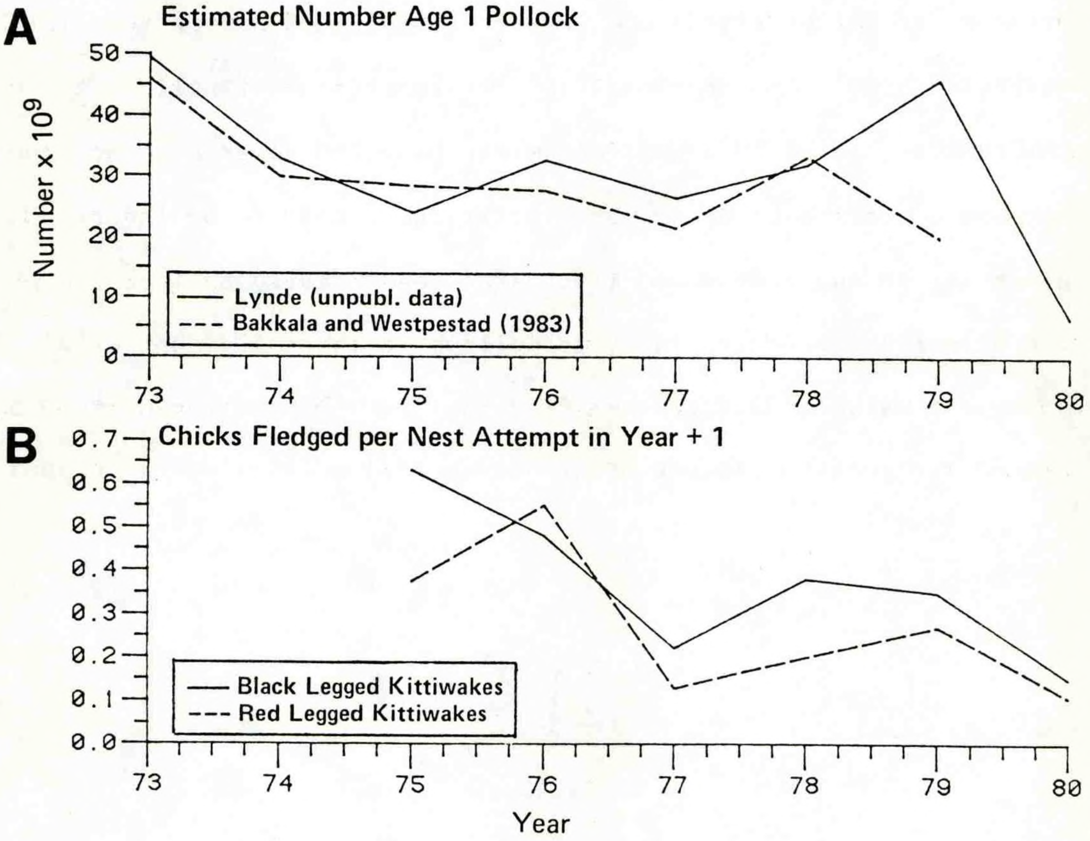

Figure 14.--Estimated number of age-1 walleye pollock by year during 1973-80 (A) (Bakkala and Wespestad 1983; Lynde unpubl. data), and the number of kittiwake chicks fledged per nest attempt on St. George Island during 1973-80 (B) (from McRoy and Walsh 1981).

PART II. RESULTS OF WORKSHOP

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Two questions formed the basis for discussion during the workshop sessions:

1) If we were to model the juvenile and adult components of the eastern Bering Sea walleye pollock ecosystem, how would we go about it based on what we now know, and

2) what further information would be required?

Although an actual working model was not the intent, the modeling approach served as a conceptual framework and provided common grounds for discussion.

With this in mind, the tasks of the juvenile and adult pollock subgroup were:

1) to list the major components and important biological processes within the juvenile and adult pollock subsystem,

2) to state the functional relationships assumed to describe or govern the processes within the subsystem,

3) to identify areas where the functional relationships are not known (conceptual gaps),

4) to identify the types of data needed to quantify those relationships that are known, and

5) to suggest potential areas of future research needed to bridge data and conceptual gaps.

Model Boundaries, Constraints, and Level of Resolution

During the first day of the workshop, areal boundaries for the model were established. Boundaries were chosen to reflect the four distinct hydrographic domains in the eastern Bering Sea (see figure 3 in the article by Schumacher in this Technical Memorandum) with an additional differentiation based on a line from the Pribilof Islands to Cape Avinof. A time horizon of 20-50 yr was established for simulation with an annual resolution for some variables, such as catch, and a seasonal resolution for others, such as consumption and growth.

Indicators and Actions

A number of variables were identified as important indicators of the state of the system. It was suggested that a model of the juvenile and adult pollock subsystem should track the following variables over time: 1) level of pollock recruitment, 2) pollock abundance by age or size class, 3) areal distribution and, especially, the extent of spawning grounds.

A number of potential management actions were also identified. These would attempt to control or alter the state of the system through fishing regulations or incentives (see article by Terry et al. in this Technical Memorandum).

Information Flow between Subsystems

An important product of the workshop was a matrix of information that each subgroup would require from the other subgroups. Table 6 lists the information that the juvenile and adult pollock subgroup should provide to, and receive from, each of the other subgroups.

Table 6.--Juvenile and adult walleye pollock subgroup information requirements. All information is dimensioned by time and area.

Subsystem	To juvenile and adult pollock	From juvenile and adult pollock
Oceanography	Temp. profile Horizontal transport vectors % bottom area <0°C, <2°C Location of ice edge Location of fronts	
Plankton	Turbidity Prey no. by species group, by depth, diel No. surviving pollock postlarvae	No. pollock eggs produced Size & condition of eggs Biom. of plankton eaten by sp. group and size class
Other fish and invertebrates	No. prey by sp. group, size class No. pollock eaten by age Abundance of sp. interacting with pol. other than through predation, i.e. behavioral exclusion	No. pollock by age or size class No. other fish eaten by sp. group and size class
Apex predators	No. pollock eaten by age or size class	No. pollock by age, size, depth microdistribution (patchiness of pollock)
Fisheries and economics	No. pollock caught by age, size and sex (including incidental mortality)	No. pollock by age, size, sex, depth Roe content at time of spawning Condition index of pollock Parasitism levels % of area occupied

Components, Processes and Conceptual Model

Because food requirements, fishing success, reproductive potential, timing and location of spawning, and mortality rates depend on the size of the pollock, it was decided that a model of the eastern Bering Sea pollock ecosystem should include the age and size structure of the pollock population. This could be handled by a limited number of age groups or size stanzas with similar production characteristics. We suggest treating each age or cohort separately until at least age 7 after which survivors could be pooled.

Although the components of our subsystem are simple and well defined, the processes affecting the flow of biomass between components and subsystems are numerous, complex, and for the most part poorly understood. Table 7 lists the most important processes and the factors believed to influence the dynamics of the juvenile and adult pollock subsystem. Figure 15 illustrates our conceptual model in which the components, processes, and biomass flow are delineated.

Most of the discussion in the juvenile and adult pollock subgroup centered around the processes affecting biomass flow. These were categorized as: 1) processes for which the functional forms are known and estimates of the rates (i.e., parameters of the functional relationships) exist or are attainable from present data; 2) processes for which the functional forms are known from theory, but the data are insufficient to estimate the rates (i.e., data gap); or 3) processes for which the functional forms are either unknown or a number of alternative forms are possible (i.e., conceptual gap). It is disconcerting to note that most of the processes fall into the latter two categories.

Table 7.--Biological and physical processes important in the dynamics of juvenile and adult walleye pollock.

Process	Component or relation	Functional forms	Equation number (Appen. 1)
Consumption	energy intake vs. prey density	Ivlev	1
		Holling disk	2
	prey selection	size selective feeding	
		selectivity matrix	
		optimal foraging	
	intake vs. energy demands	(see Growth, Repro., Migr.)	
Growth	growth rate vs. size	von Bertalanffy	3a, 3b
		explicity energy intake	4
		biomass based	5
	vs. temperature	explicit anabolic, catab.	6
		biomass based	7
		parabolic	8
Reproduction	% mature vs. size	double exponential	9
	fecundity vs. size	power function	10
	fecundity vs. energy intake	explicit conversion to egg	11
	bottom temp., loc. of fronts	(see migration)	
Migration - Spatial Distr.	transfer rate between areas	gradient times velocity	12
	velocity vs. body length		
	seasonal migration	input matrix	
		simple oscillation	13
	temperature preference	isotherm model	
	advection/transportation	transport. coef.	14
	search for food	modified trans. coef.	15
Mortality	cannibalism		
	starvation	required vs. actual consum.	16, 17
	disease, parasitism	constant rate	
		modified by pollock and/or marine mammal abundance	

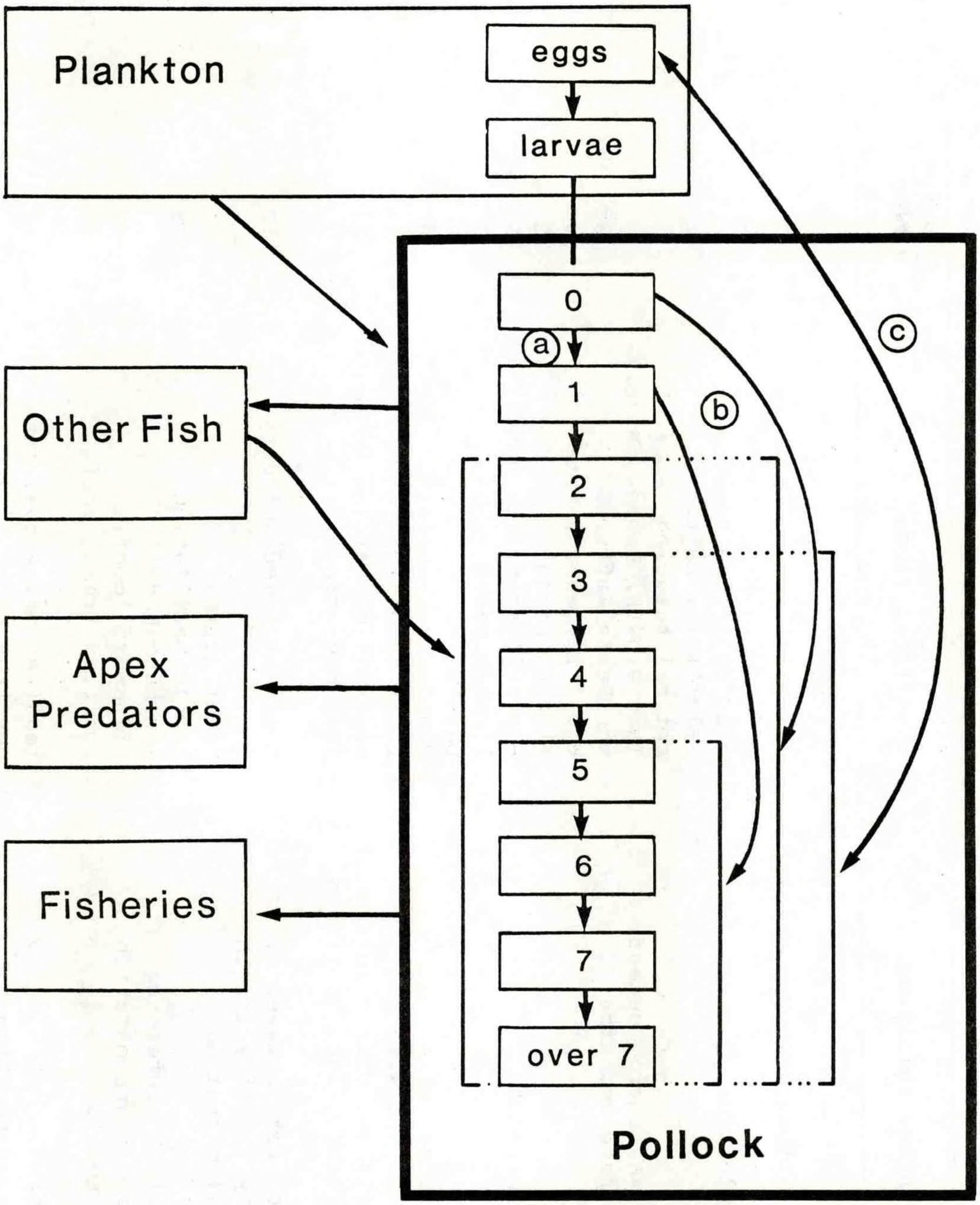

Figure 15.--Conceptual ecosystem model for the juvenile and adult walleye pollock subsystem.

a) processes linking age classes include growth, aging, and natural mortality;

b) cannibalism;

c) percent maturity, fecundity, and migration.

Consumption

The rate of food consumption by pollock depends on seasonal energy demands and on the perceived density and desirability of each potential prey item. The seasonal energy demands could be determined from growth, migration, and reproductive processes. Perceived prey densities depend on prey abundance and the degree of spatial and temporal co-occurrence. Holling (1959) and Ivlev (1961) functions (Eq. 1, 2; Appendix 1) are most often used to relate ingestion to prey density. We are not aware of any empirically derived parameter estimates for this relationship for juvenile or adult pollock.

Prey desirability depends on prey size, ease of capture, and nutritional content. Studies have been conducted on the size specific feeding relationships of other gadoids (e.g., Daan 1973). Estimates of prey consumption by region, season, and size class are available for pollock based on a recent study of pollock stomach samples (Dwyer et al. 1983). Estimates of prey abundance are also needed by region and season in order to calculate prey selectivity indices. Reasonable estimates of copepod biomass exist, but estimates of euphausiid abundance have in the past been highly variable (see article by Incze et al. in this Technical Memorandum).

Growth

The rate of somatic growth depends on body size, rate of energy intake, and environmental factors such as temperature. Functions commonly used to relate growth rate to body size are those of von Bertalanffy (1938), Chapman (1961) and Richards (1959) (Eq. 3a, 3b; Appendix 1). Parameter estimates for the von Bertalanffy relationship have been made for pollock by region and season (unpubl. data of the author) and these could be incorporated in the model. Such an approach ignores the causes of regional variability, however, which may include differences in energy intake or environmental conditions. A growth function such as Eq. 4 (Appendix 1) relates anabolic processes to energy intake and catabolic processes to weight (Parrish 1975; Bledsoe 1979), allowing for the explicit calculation of energy intake via Holling or Ivlev functions. Parameter estimates for Eq. 4 might be obtainable from data on other gadoid species (Jones and Hislop 1978). More specific estimates for pollock could be derived through laboratory studies of ration and growth.

The effects of temperature on growth might be modeled by a simple parabolic or polynomial function (Fig. 16; Eq. 8, Appendix 1). Based on the work of Dr. Nishiyama and others, the following hypotheses were expressed: 1) the optimum water temperature for adults is about 3°C, 2) the upper and lower limits are about 7.5°C and -1.5°C, respectively, for adults, and 3) the upper limit for juveniles is probably greater than for adults, because juveniles are distributed in the upper layers of the middle and inner shelf domains where upper temperature extremes are greater.

Reproduction

The number of viable fertilized eggs produced depends on the number, size, condition, and the sex ratio of mature adults. The percent of fish that are sexually mature usually varies with length in a sigmoidal fashion. Bakkala and Smith (1978) found that a double exponential curve (Eq. 9, Appendix 1) provided a good fit to data on pollock from the eastern Bering Sea (Fig. 10).

The fecundity-size relationship is usually expressed as a power function of length (Eq. 10, Appendix 1). Fecundity is probably more closely related to weight than length, however, since fecundity-at-length may vary with somatic condition. Estimates of the parameters of the fecundity-length relationship exist for pollock (Table 3), but estimates differ substantially.

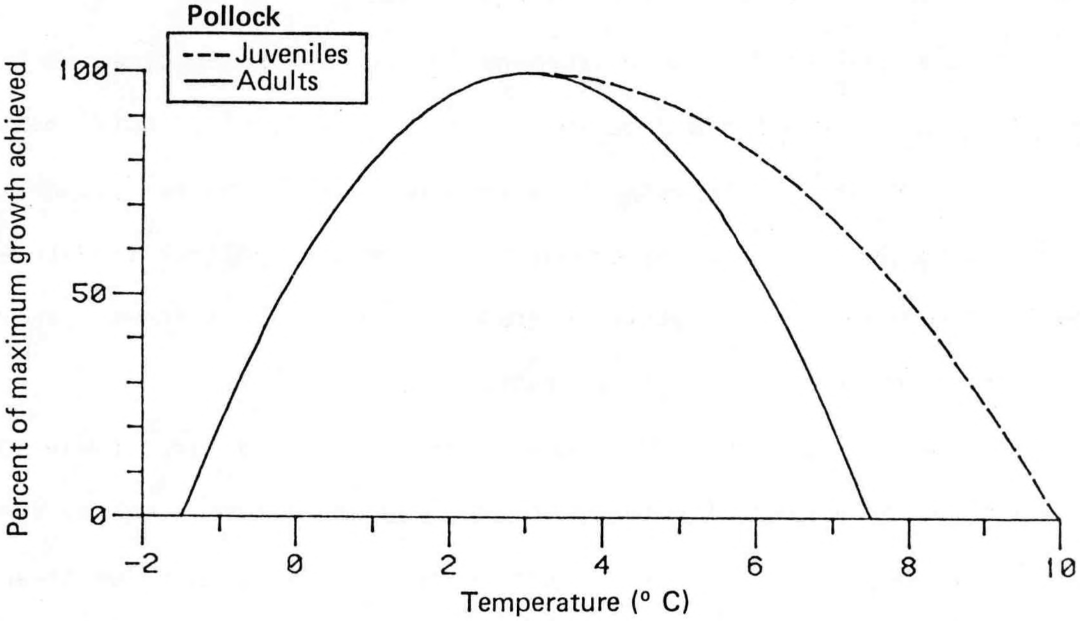

Figure 16.--Hypothetical relationship between ambient water temperature and percent maximum growth of juvenile and adult walleye pollock.

The uncertain percentage of the total oocytes released each year is a problem that has not been resolved.

Migration and Spatial Distribution

The spatial and temporal distribution of pollock in the eastern Bering Sea is influenced by advection and dispersion due to currents, tides, and wind stress; migration due to environmental gradients in temperature and food abundance; and aggregation-dispersion due to spawning and foraging behavior. This is a difficult, yet important, process to model. The eastern Bering Sea is clearly not a homogeneous system and, as a result, pollock tend to exhibit regional differences in production characteristics such as growth, recruitment, diet, and probably fecundity and mortality as well.

Because of the model's rather coarse spatial resolution, it was suggested that a measure of aggregation be calculated. This measure, such as the percentage of area occupied, would reflect the degree of aggregation due to spawning and cold water avoidance, or dispersion due to foraging.

One approach to modeling the transfer of biomass or numbers between areas is to define the rate of transfer as a function of velocity and gradient vectors (Laevastu and Larkins 1981; Kume and Bartoo 1981)(Eq. 12, Appendix 1). The velocity should be a function of body size (Fry and Cox 1970). The gradient field should be the summation of gradients due to 1) advection, dispersion, and turbulence (as calculated by an oceanography submodel); 2) seasonal migration (input gradients empirically determined from average survey and commercial catch distributions); and 3) temperature preference and food availability.

The relative importance of each of these components is unknown. The following hypotheses were expressed during the workshop concerning the ramifications of environmental and behavioral influences on the spatial distribution of pollock.

1) Adult pollock avoid water colder than about 2°C.

2) Juveniles do not avoid, or at least occur in, water as cold as 0°C.

3) Spawning occurs at or near the 2-3°C isotherm.

4a) Individuals spawn in batches, migrating as they spawn in response to the movement of the 2-3°C isotherm, and

  i) females spawn first over the Aleutian Basin, then over the southeast slope, and finally over the shelf as they migrate, or,

  ii) basin fish do not move onto the shelf, but shelf populations migrate landward while spawning, or

4b) batch spawning does not occur; individuals spawn in one location only.

5) Pollock spawned over the southeast slope recruit primarily to the northwest, due to the net northwestward circulation, while pollock spawned over the middle shelf experience little transport.

6) During years when thermal stratification extends later into autumn, 0-age juveniles occupy the upper water column for a longer period of time than years when stratification breaks down early. Cannibalism is therefore low, but predation by marine birds is high.

7) During cold years,

  a) the middle and inner shelf domains may serve a refuge from cannibalism, since adults may be excluded by the cold bottom water mass,

  b) adults are more aggregated since there is less water of a suitable temperature, therefore commercial catch rates and predation by marine mammals should increase, and

c) spawning does not proceed as far onto the shelf; recruitment occurs primarily to the northwest.

Mortality

The causes of mortality include fishing, predation, starvation, disease, parasitism, spawning stress, and senescence. Mortality through predation and fishing would be handled explicitly in this conceptual model. All but cannibalism would be calculated in other submodels, such as those developed by the "fisheries-economics" and "other fish" subgroups. Within the juvenile and adult pollock submodel, small pollock would be treated as any other pollock prey. Some factors which are hypothesized to affect the extent of cannibalism are listed above. One approach to modeling mortality due to starvation, suggested by Bledsoe (1979), is to equate the differential form of the von Bertalanffy equation with Eq. 4, and solve for the energy intake rate (EV) needed to grow as predicted by von Bertalanffy parameters. The probability of starvation increases if the actual energy intake rate is consistently less than EV (Eq. 16, Appendix 1). Growth curves fitted to individual growth histories by digitizing photographs of scale or otolith surfaces (Hirschhorn and Small 1981) might be used to calculate the minimum observed growth rate which could then be used as a threshhold in the above relationship.

Mortality rates due to disease, parasitism, spawning stress, and senescence are difficult, if not impossible, to measure. Disease and parasitism may not account for a large direct mortality, but they may significantly increase susceptibility to predation. Parasitism of pollock is also important for other reasons: 1) it adversely affects the fishing industry by lowering the quality of the product, 2) pollock might serve as intermediate hosts for certain helminthic parasites that may ultimately be detrimental to marine mammals (which are the definitive hosts), and 3) differences in parasite populations sometimes make it possible to differentiate unit stocks. This technique may be useful for separation of pollock stocks. To date, however, few studies have been conducted on the parasite population of pollock from the Bering Sea (Mamaev et al. 1965; Love and Moser 1983).

Data and Conceptual Gaps and Suggested Future Research

Initial attempts to model any complex system are usually hampered by lack of information concerning the processes which control the dynamics of the system. The initial phase of the modeling process is nevertheless important because it leads to the identification of information gaps, and it clarifies the need and direction for future research. A number of data and conceptual gaps were identified during the pollock ecosystem workshop. Those pertaining to the juvenile and adult pollock subgroup are listed in Table 8. In order to better understand the pollock ecosystem, research should be conducted to bridge these gaps. We suggest a combination of field, laboratory, and other research.

Field research could include: 1) continued plankton and hydroacoustic-midwater trawl surveys designed to describe the distribution of juvenile pollock (especially 0-age juveniles) and potential prey over time by area, 2) repetitive cross-shelf transects during the spawning season to collect samples for fecundity analysis and to identify the degree of mixing between northwest, southeast and Basin populations based on size-age distributions, and 3) continued collection of stomachs from pollock taken in the foreign fishery and during research cruises, with emphasis on broad seasonal and areal coverage, to describe regional and seasonal differences in pollock diet.

Table 8.--Data and conceptual gaps in the knowledge of juvenile and adult walleye pollock from the eastern Bering Sea.

Data gaps	Conceptual gaps
-Distribution of 0-age juveniles over time	Relative influences of advection, temp., migration, predation on distribution
-Distribution of spawning adults over time	
-Fecundity/length relationship	
-% of total oocytes released per year	
-Abundance by age and area	Factors influencing migration
-Juvenile diet by area, season	
-Prey abundance by area, season	Prey desirability
-Degree of mixing between NW/SE/Basin	Stock structure
-Nature and degree of parasitism by area	Causes of fluctuations in parasite load
-Growth rate vs. temperature	
-Growth rate vs. prey density	
-Regional recruitment patterns	Factors affecting recruitment

Laboratory research could include: 1) histological and perhaps, laboratory rearing studies of spawning adults to determine fecundity by size and the degree of batch spawning, 2) studies of parasite populations associated with pollock in order to estimate the impact on fishery production and marine mammal populations, and possibly to aid in stock separation, 3) laboratory or field enclosure studies of prey selection and growth vs. temperature and ration, 4) continued electrophoretic studies to aid in the separation of stocks, and 5) analysis of individual growth by digitizing images of scale or otolith patterns, to estimate individual growth histories (i.e., minimum, maximum, and variance by area and time), and to investigate the feasibility of using discriminant analysis as an aid in stock separation.

Other research could involve translating pertinent Japanese and Soviet literature, such as Yoon's (1982) thesis, and developing alternative statistical or modeling techniques, such as cohort analysis by region, to improve estimates of regional abundance.

The above list is certainly incomplete and no attempt has been made to prioritize the research according to the expected benefits vs. cost of obtaining such information. However, we hope that this list will stimulate discussion and contribute in some small way to the goal of better understanding the pollock ecosystem of the eastern Bering Sea.

ACKNOWLEDGEMENTS

This chapter is the product of all the members of the juvenile and adult walleye pollock subgroup, whose insights greatly increased the scope of the background review, and whose enthusiastic cooperation helped make the workshop a success. I am also especially indebted to Robert Francis, Lewis Incze, Richard Bakkala, Kevin Bailey, and Gerald Hornof of the Northwest and Alaska Fisheries Center for their helpful reviews.

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Appendix 1

POTENTIAL MATHEMATICAL FORMULATIONS OF BIOLOGICAL PROCESSES WITHIN THE JUVENILE AND ADULT WALLEYE POLLOCK SUBMODEL

Consumption

Energy intake vs. prey density

Ivlev (1961)

$$R = R_{max}\,[1. - e^{-k_i X}] \qquad (1)$$

Holling (1959)

$$R = \frac{k_2 X}{k_3 + X} \qquad (2)$$

where: R = ingestion rate,
R_{max} = maximum ingestion rate,
X = prey abundance level,
k_i = parameters

Growth

Growth rate vs. body size

Ursin (1967)

$$dW/dt = h\,W^m - k\,W^n \qquad (3)$$

von Bertalanffy (1938)

$$dW/dt = h\,W^{2/3} - k\,W \qquad (3a)$$

Richards (1959), Chapman (1961)

$$dW/dt = h\,W^m - k\,W \qquad (3b)$$

where: W = weight
h = coefficient of catabolism
k = coefficient of anabolism
m = catabolic exponent
n = anabolic exponent

Catabolism a function of energy intake; anabolism a function of body size

Parrish (1975), Bledsoe (1979)

$$dW/dt = a\,E - k\,W^m, \tag{4}$$

where: E = energy intake rate
a = coefficient of assimilation
(includes specific dynamic action)

Biomass based growth

Laevastu and Larkins (1981)

$$dB/dt = B\,e^g - B, \tag{5}$$

where: B = biomass
g = instantaneous rate of change due to growth

Growth rate vs. temperature

Ursin (1967)

$$dW/dt = h\,W^m - k\,W^n, \tag{6}$$

where: $h = (p_1 e^{p_2 T} - p_3 e^{p_4 T})$,
$k = p_5 e^{p_6 T}$
$P_1\text{-}P_6$ = parameters

Laevastu and Larkins (1981) (biomass based)

$$dB/dt = B\,e^g - B\ , \tag{7}$$

where: $g = ce^{\left(\frac{1}{T_0} - \frac{1}{T}\right)}$,
c = parameter,
T = ambient temperature,
T_0 = optimum temperature

Simple parabolic function (Fig. 16)

$$P = a + b\,T + c\,T^2, \tag{8}$$

where: P = growth correction factor,
T = temperature,
a,b,c = parameters

Reproduction

Percent maturity vs. body length

Sigmoidal - double exponential (Bakkala and Smith 1978)

$$M = e^{-ae^{-bL}} \tag{9}$$

where: M = percent mature,
L = body length,
a,b = parameters
e = natural antilog

Fecundity vs. body length

Power function of body length

$$F = a\,L^{b} \tag{10}$$

where: F = fecundity,
L = body length,
a,b = parameters

Fecundity vs. energy intake

Explicit conversion to eggs (Bledsoe 1979)

$$F = \begin{cases} 0 & \text{, if } E < EV \quad \text{(see Eq. 16)} \\ a\,(E - EV) & \text{, if } E \geq EV \end{cases} \tag{11}$$

where: E = energy intake rate,
EV = energy intake rate necessary to grow according to von Bertalanffy eq.,
a = parameter

Migration - Spatial distribution

Transfer rate between areas

Product of gradient and velocity

$$dX_i/dt = \sum_{j=1}^{2 \text{ or } 3} [(dX_i/dL_j)\ (dL_j/dt)\ dt] \qquad (12)$$

where: X = biomass or numbers in i^{th} compartment,
j = index of direction, either 1) N/S, 2) E/W, or 3) Up/Down,
dt = time step
L_j = distance between compartments in j^{th} direction,

examples: Laevastu and Larkins (1981) (biomass based)
Kume and Bartoo (1981) (numbers)

Time dependent gradient

Seasonal oscillation (Kume and Bartoo 1981)

$$dX_i/dt = X_i \frac{A_{max}}{\sqrt{2\pi\sigma}} e^{-\frac{1}{2}[(t-t_o)/\sigma]^2} \qquad (13)$$

where: A_{max} = maximum migration rate,
t = time of year
t_o = time of year when maximum migration is expected
σ = standard deviation of time

Simple transportation coefficient (Beverton and Holt 1957)

$$dX_i/dt = A_{ij}\ X_i, \qquad (14)$$

where: A = coefficient of transportation or migration in direction j

Trans. coefficient modified by food availability (Beverton and Holt 1957)

$$\frac{1}{A} = \frac{1}{d}\left(\frac{1}{V} + \frac{t}{d}\right) \qquad (15)$$

where: d = average distance between food patches,
V = swimming velocity,
t = time spent feeding (not swimming)

Mortality

Starvation (Bledsoe 1979)

$$S_i = \begin{cases} 0 & , \text{ if } (W^*_i/W_i) > a/b \\ a\ (W^*_i/W_i) - b, & \text{ if } (W^*_i/W_i) < a/b \end{cases} \tag{16}$$

where: S_i = starvation mortality rate of i^{th} age group,

W_i = weight of i^{th} age group,

W^*_i = weight expected of i^{th} age group if growing according to von Bertalanffy (see Eq. 3a, 4)

a,b = parameters

EGGS AND LARVAE OF WALLEYE POLLOCK AND RELATIONSHIPS TO THE PLANKTONIC ENVIRONMENT

by

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ABSTRACT

In the eastern Bering Sea, eggs of walleye pollock, Theragra chalcogramma, are spawned during a migration which begins early in March over the continental slope and continues through June into shallower shelf sea waters. Peak spawning appears to occur from about middle March to middle May. Pollock eggs are planktonic and require about 22 d to hatch at upper mixed layer temperatures of 3.0-3.5°C. Eggs hatch into yolk sac larvae that are about 4 mm in length. The yolk-sac larval stage lasts about 15 d, but larvae start feeding at 5-9 d. First feeding yolk-sac larvae prey on copepod eggs and nauplii. Thereafter, increasingly larger zooplankton prey are consumed as the larvae grow, but the lower size limit of prey taken remains unchanged. A marked shift towards larger prey, copepodids and eventually copepods, occurs at yolk-sac absorption at a larval length of approximately 7 mm. Larval growth rates based on measurements of preserved specimens are about 0.20 mm body length per day during yolk-sac stage and about 0.35 mm d^{-1} during post-yolk

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larval development. A slower growth rate of post-yolk larvae north of the Pribilof Islands has been observed. First-feeding larvae appear to be capable of capturing nauplii at prey concentrations frequently observed in the southeastern Bering Sea. The primary prey items of older larvae have been identified, but the prey densities required for feeding at levels which support average rates of metabolism and growth are not known. The shift in prey types at yolk absorption may be a "critical period" in larval life history of this species. Average daily ingested ration needed to support observed growth of larvae from 5 to 22 mm body length has been estimated with a preliminary carbon budget. Egg mortality rates and major predators of eggs and larvae are unknown. Spatial and interannual variations in primary and secondary production of the southeastern Bering Sea and potential relationships to year-class success are discussed.

INTRODUCTION

The eggs and larvae of walleye pollock, Theragra chalcogramma, generally inhabit the upper 30-40 m of the water column in the eastern Bering Sea during late winter and spring. The survival of these early developmental stages depends in part on interactions with other components of the planktonic community (invertebrate predators and prey) and with avian and nektonic predators. The abundance of these other organisms varies spatially and temporally in the environment where pollock spawn, but the quantitative effects of such variability on the early life history stages of pollock are not presently known.

In addition to its basic vertical structure, the plankton community has spatial scales of variability which range in size from small patches to much larger areas, such as the hydrographic domains of the eastern Bering Sea (Iverson et al. 1979; see also the article by Schumacher in this Technical Memorandum for delineation and names of the hydrographic domains). Temporally, the planktonic system can vary on scales of minutes or hours (patches); it can vary over periods of days (wind forcing and mixing); it varies seasonally in terms of community development; and it varies interannually in terms of temporal patterns and abundance of organisms.

The specific organisms and the within-year time and space scales of most significance to survival of pollock eggs and larvae are not well known. Biological interactions during egg and larval stages clearly take place at small spatial scales, but the small-scale conditions are affected by large-scale processes which have regional, seasonal, and event scale characteristics. Those patterns of events, processes, and conditions which lead to abundant year-classes of pollock by way of comparatively high survival of eggs and larvae have not been identified.

Variations in production dynamics of the plankton probably have both direct and indirect effects on early life history stages of pollock . Direct effects include the availability of prey and the temporal and spatial patterns of distribution and abundance of major predators. Indirect effects include the abundance of organisms which may be preyed upon instead of pollock eggs and larvae, thereby reducing predatory losses of pollock. Variations in planktonic production may also directly affect juvenile pollock, which feed heavily on euphausiids and copepods (Takahashi and Yamaguchi 1972; Bailey and Dunn 1979; Walline 1981; Dwyer et al. in press).

It is generally accepted that small differences in survivorship of larvae, because of their large numbers, can ultimately result in great differences in adult populations several years later. Differences in larval survivorship are difficult to detect, however, because they usually represent small changes in absolute mortality rates which are high. Investigators therefore usually focus on conditions which affect eggs and larvae, thereby hoping to formulate mechanistic explanations for year-class abundance which may be tested in the field. Understanding cause-effect relationships begins with knowledge of egg and larval physiology, larval feeding ecology, and variability of critical components of the pelagic environment--including the dynamics of predator and prey populations.

This chapter reviews those aspects of egg and larval physiology and ecology which are thought to be important to survival of larval pollock, and it briefly summarizes what is known about variability of the planktonic environment of the southeastern Bering Sea. A simple model emphasizing relationships between the planktonic community; larval, juvenile and adult pollock; and potential nektonic predators is presented. Prominent gaps in knowledge are identified. General concepts of plankton-larva interactions are not reviewed in this paper; the reader is referred instead to recent discussions by Hunter (1981, 1982), Houde (1982), Laurence (1982), and Blaxter and Hunter (1982).

POLLOCK EGGS

Pollock eggs are spawned at depth and ascend to the upper pelagial zone. In the eastern Bering Sea, most are found in the upper 20 m of the water column (Serobaba 1974). Fewer than 1% were found in the neuston layer (upper 0.25 m) in a survey by Waldron and Vinter (1978). In spring, the eggs and larvae of pollock can dominate the ichthyoplankton of the southeastern Bering Sea, constituting in one study 55% of fish larvae and 97% of fish eggs sampled during April (Waldron and Vinter 1978).

Pollock eggs have been found from February to July in the eastern Bering Sea, but are most abundant from middle March to middle May (Serobaba 1968; Waldron 1981). In the southern and southeastern Bering Sea, eggs are found first in oceanic waters over the Aleutian Basin and continental slope, and later over the shelf (Nishiyama and Haryu 1981). This spatial and temporal trend reflects an onshore spawning migration which is thought to be strongly influenced by bottom water temperature (Nishiyama and Haryu 1981; Francis and Bailey 1983). In the southeastern Bering Sea, spawning at the shelf break generally begins in early March, over the outer shelf in early April, and over the middle shelf sometime later, depending on temperature. The onshore spawning migration appears to be limited by water less than 2.5°C (Nishiyama and Haryu 1981, and references cited therein). Following cold winters, migration apparently does not extend far into the middle shelf domain (Francis and Bailey 1983).

Pollock eggs average about 1.5 mm diameter. Nishiyama and Haryu (1981) examined eggs from the neuston layer and found a range of diameters from 1.3 to 1.9 mm. Differences in egg size are not related to developmental stage of the egg (Gorbonuva 1954; Nishiyama and Haryu 1981), but vary with season and geographic location. Spatial patterns of distribution of egg size may vary from year to year (see the article by Lynde in this Technical Memorandum), and the reasons for these patterns remain unclear. One possible explanation is that egg size decreases with successive spawnings of individual fish (cf. Blaxter and Hunter 1982; Yoon 1982), and that spatial patterns of egg size result from spatial and temporal aspects of the spawning migration. Alternatively, Serobaba (1968) suggested that patterns of egg size may result from differences in the sizes of fish spawning over different areas of the shelf.

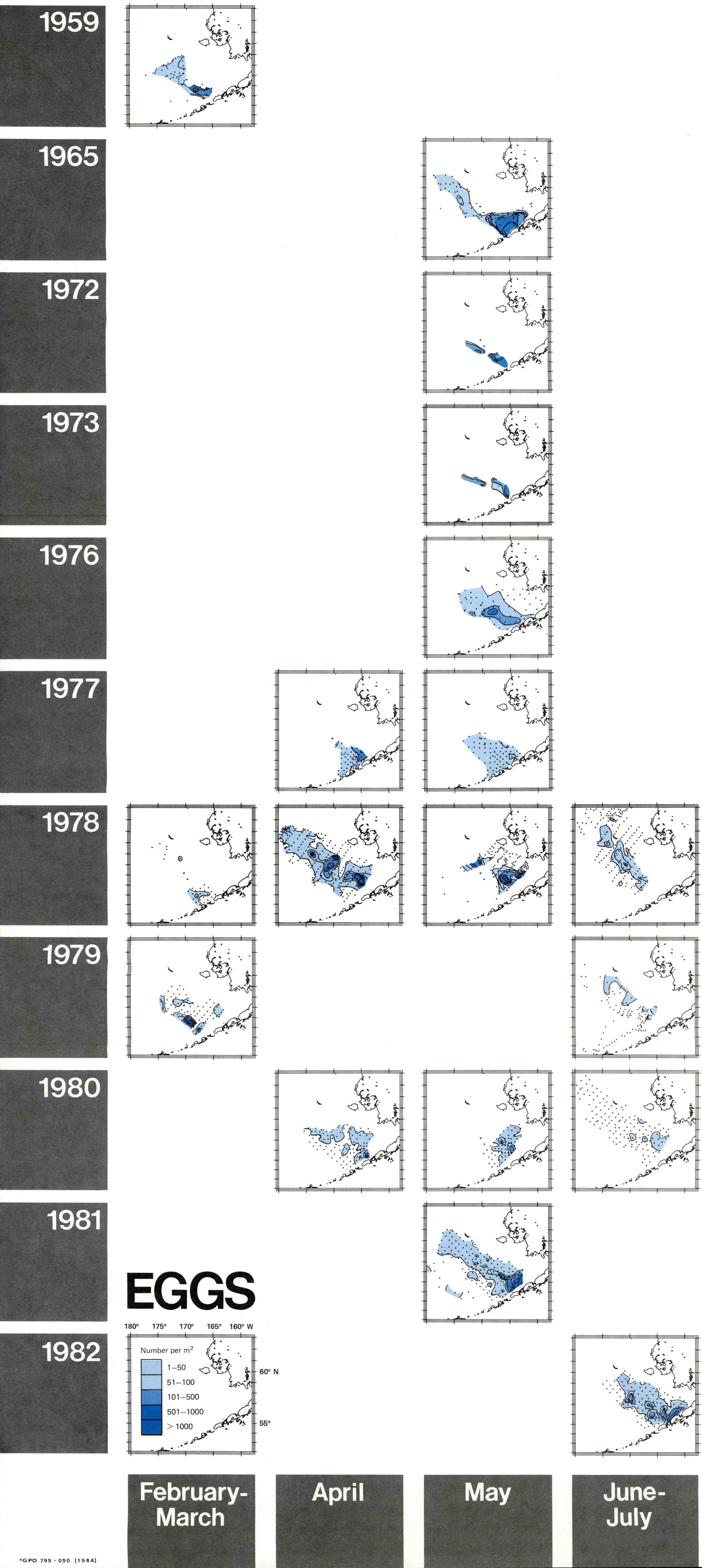
Differences in egg size may have important consequences in early life history. Larger eggs generally give rise to larger larvae (Hamai et al. 1971; Ware 1975) which may be functionally better predators at first feeding and may be generally more fit. Larger eggs also produce larger yolk reserves and a longer duration of the yolk-sac larval stage (Blaxter and Hempel 1963). T. Nishiyama (unpubl. data, see Nishiyama and Haryu 1981:1008) estimates that the largest pollock eggs he observed (1.9 mm diameter) are about 2.5 times the dry weight of the smallest observed (1.3 mm). It is not clear whether larger yolks are an advantage or a disadvantage, for while larger yolk reserves delay the requirement for feeding, they prolong a stage which may be particularly vulnerable to predation. Ware (1975) argues that at lower temperatures the advantage is probably with larger eggs because of the longer development times, whereas the converse is probably true at higher temperatures. Different egg sizes also may show selective advantages depending on the relative abundance of predators and prey in a given area and year. For instance, larger yolk reserves may be an advantage to larvae when zooplankton prey are comparatively scarce. Rates of reproduction and growth of small copepods (prey of pollock larvae) in the southeastern Bering Sea appear to be significantly reduced by cold temperatures (see later discussion), and larger yolks would appear to be favored under such conditions. However, because large yolks may impede swimming and escape response, they may be a disadvantage when predators are abundant. The relative importance of egg size to survival of pollock larvae thus remains unanswered.

Comparatively little sampling for eggs and larvae has been conducted north of the Pribilof Islands, so the timing and extent of spawning in this region is not well known. The results of Soviet surveys conducted during 1978 indicate roughly similar spawning times over the outer shelf northwest and southeast of the Pribilof Islands in that year (Fig. 1), but Haryu (1980) indicates that spawning can occur later in the north. Data on egg and larval abundance from numerous cruises to the eastern Bering Sea are graphically summarized in Figures 1 and 2. The information provided in some of the reports used in constructing these figures did not permit separate months to be analyzed. Consequently, some data, particularly for 1965 and 1981, had to be combined and represented for a single month (see Table 1 for details). There are some difficulties in interpreting survey data when a sufficient time series is lacking. Specifically, some of the illustrated patterns of abundance may be biased by earlier or later sampling in one region or another. Nonetheless, these figures provide an indication of the interannual differences in spatial distribution and abundance of pollock eggs and larvae.

Development time of eggs from spawning to hatching ranges from about 14 d at 5°C to about 25 d at 2°C (Hamai et al. 1971). The eggs of pollock in the

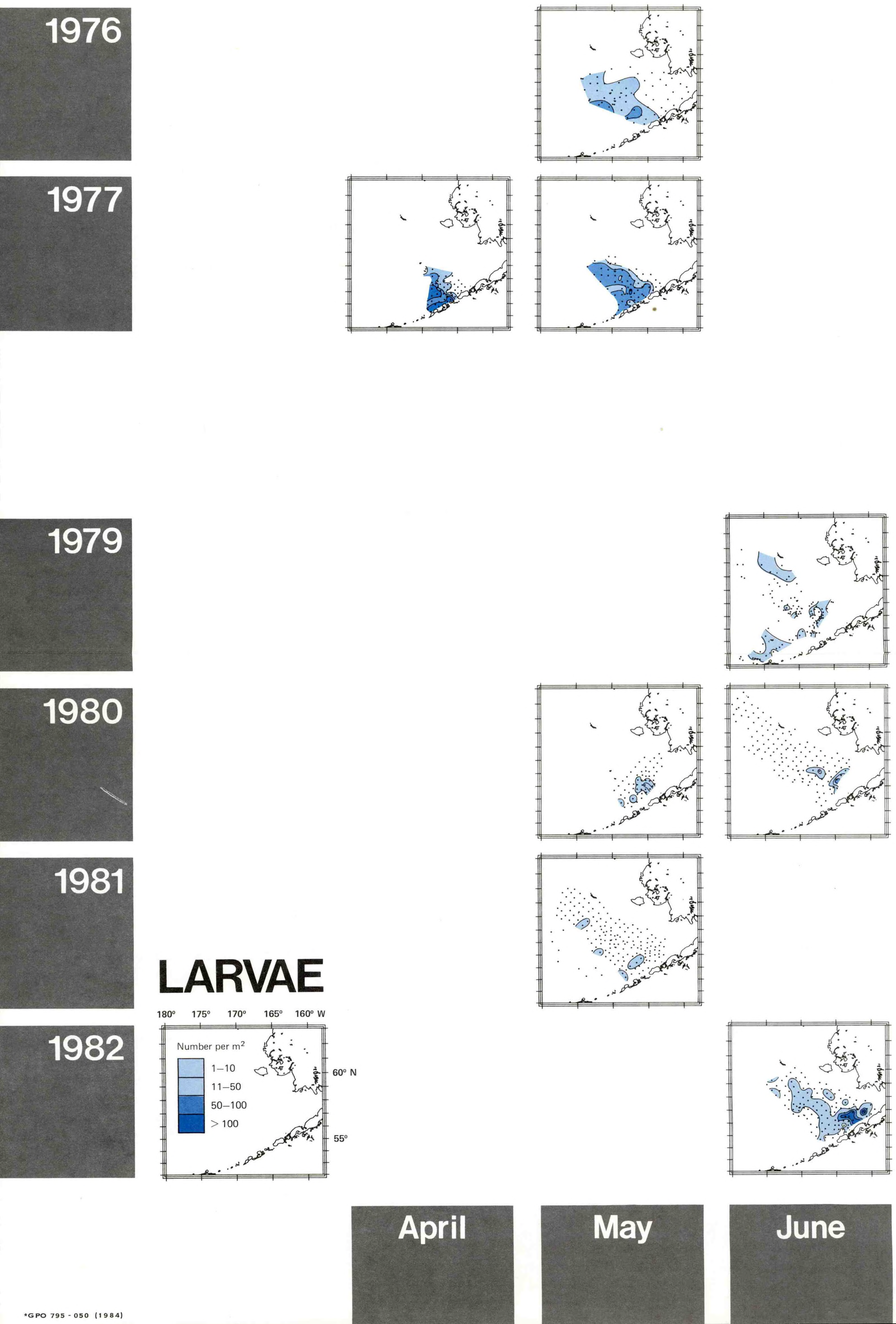
Figure 1.--Distribution and abundance of walleye pollock eggs sampled in the eastern Bering Sea. Sources of data are summarized in Table 1 (compiled by A. W. Kendall, Jr. and B. M. Vinter).

Figure 2.--Distribution and abundance of larval walleye pollock sampled in the eastern Bering Sea. Sources of data are summarized in Table 1. Note that the contoured intervals are for lower abundances than shown in Figure 1. (compiled by A. W. Kendall, Jr. and B. M. Vinter).



*GPO 795 - 050 (1984)

LARVAE



*GPO 795 - 050 (1984)

Table 1.--Sources of data on abundance of walleye pollock eggs and larvae depicted in Figures 1-2. Information provided includes author's citation, dates of sampling, and life history stages reported.

1959	Musienko (1968), 3-29 March, eggs
1965	Serobaba (1968), March-May, eggs (data all included in Fig. 1 for May; author cites May as peak of spawning, low abundance region to the northwest may be the result of earlier sampling)
1972	Maeda and Hirakawa (1977), 21 April-29 May, eggs (data all included in Fig. 1 for May)
1973	____________________, 16 April-30 May, eggs (data all included in Fig. 1 for May)
1976	Waldron and Favorite (1977), 26 April-31 May, eggs and larvae (data all included in Figs. 1 and 2 for May)
1977	Waldron and Vinter (1978), 19-27 April, eggs and larvae ____________________, 3-15 May, eggs and larvae
1978	Waldron (1978), 11 February-16 March, eggs
	Bulatov (1979), 10 April-3 May, eggs (data all included in Fig. 1 for April)
	____________________, 10-20 May, eggs
	____________________, ?-27 June, eggs
1979	Bulatov (1981), 27 February-12 March, eggs
	Walline (1981), 1 June-23 July, eggs and larvae
1980	Bulatov (1981), 6 April-2 May, eggs (all data included in Fig. 1 for April)
	____________________, 5-20 May, eggs and larvae
	____________________, 4 June-19 July, eggs and larvae
1981	Bulatov (1982), 25 March-4 June, eggs and larvae (data all included in Figs. 1 and 2 for May; author cites end of April as peak of spawning, low abundance estimates may therefore represent earlier sampling)
1982	Fedeyev et al. (1983), 3-21 June, eggs and larvae

southeastern Bering Sea are usually exposed to temperatures of about 3.0-3.5°C, and an estimate of 22 d for hatch is reasonable.

Pollock eggs have a tough chorion, and laboratory observations indicate that larvae experience considerable mortality at hatching (A.J. Paul and M.E. Clarke pers. obs.). This mortality has not been quantified or verified at sea. Little is known about predation on fish eggs. Mortality between eggs at spawning and early larval stages is high in most fishes (Hunter 1981), but how this mortality is apportioned betweeen predation and other causes such as hatching mortality is not known. The effects of parental nutrition, age, fecundity, and stress on egg survival also are not well known.

POLLOCK LARVAE

Larvae of pollock can be distinguished from other northern Pacific gadoids following the descriptions of Matarese et al. (1981) and Dunn and Vinter (1984). At hatch, a yolk-sac larva averaging about 4 mm standard length (SL: anterior tip to end of the notochord) emerges from the egg. At 5°C this stage lasts about 15 d (Hamai et al. 1971). Yolk-sac larvae begin to feed at 5 d at 5°C and 9 d at 3°C (Paul 1983). Feeding during yolk-sac stage apparently contributes to growth. Larvae from the field and feeding laboratory-reared larvae show otolith increments significantly larger than those of larvae maintained in the laboratory without food (Clarke in prep.). In addition, it is reasonable to assume that feeding yolk-sac larvae gain experience as predators and must be better prepared to cope with their environment at yolk absorption, when they become completely dependent on exogenous sources of food.

After yolk absorption at about day 15, post-yolk larvae continue to grow without marked morphological changes until they acquire the full complement of dorsal fin rays. This occurs at an average SL of approximately 22 mm

(Haryu 1980) and requires about 36 d (Walline 1983). At this point, about 50 d after egg hatch and 73 d after spawning, the pollock is considered a juvenile (Haryu 1980).

Walline (1983) used the method of enumerating growth structures, which he interpreted to be daily increments, on the otoliths of larval and small juvenile ($\leq$30 mm) pollock to establish their age from hatching. By taking the length of these fish, subtracting the average hatching length of 4 mm, and dividing by the estimated age in days, he estimated the average daily growth rate achieved by fish of various sizes. These estimates are probably conservative, as they were based on lengths of preserved specimens and were not corrected for possible shrinkage (cf., Theilacker 1980; Bailey 1982; Fowler and Smith 1983). Walline (1983) found a constant growth rate (measured as average daily increments of body length) of fish from 4 to 7 mm and from 7 to 30 mm. Larval growth rates in the southeastern Bering Sea in 1978 and 1979 (the only years sampled in Walline's study) averaged 0.20 mm d^{-1} before yolk-sac absorption (7 mm) and 0.35 mm d^{-1} from 7 mm to juvenile stage. Post-yolk-sac larvae caught north of the Pribilof Islands had an estimated average growth rate of 0.30 mm d^{-1}. A schematic of spawning, egg development, larval growth rate (body length), and time for the oceanic and shelf sea environments is provided in Figure 3. Larval growth rates expressed in terms of dry weight and carbon are presented later in this paper.

In his studies, Walline (1983) specifically looked for differences in larval growth rate which might be related to environmental conditions. He compared larvae 1) from the middle and outer shelf domains and the oceanic domain west of the eastern Bering Sea shelf break; 2) from north and south of the Pribilof Islands; 3) from a variety of egg hatching dates (back-calculated from otolith increments); and 4) from two different years, 1978 and 1979. As mentioned above, he found small, but statistically significant

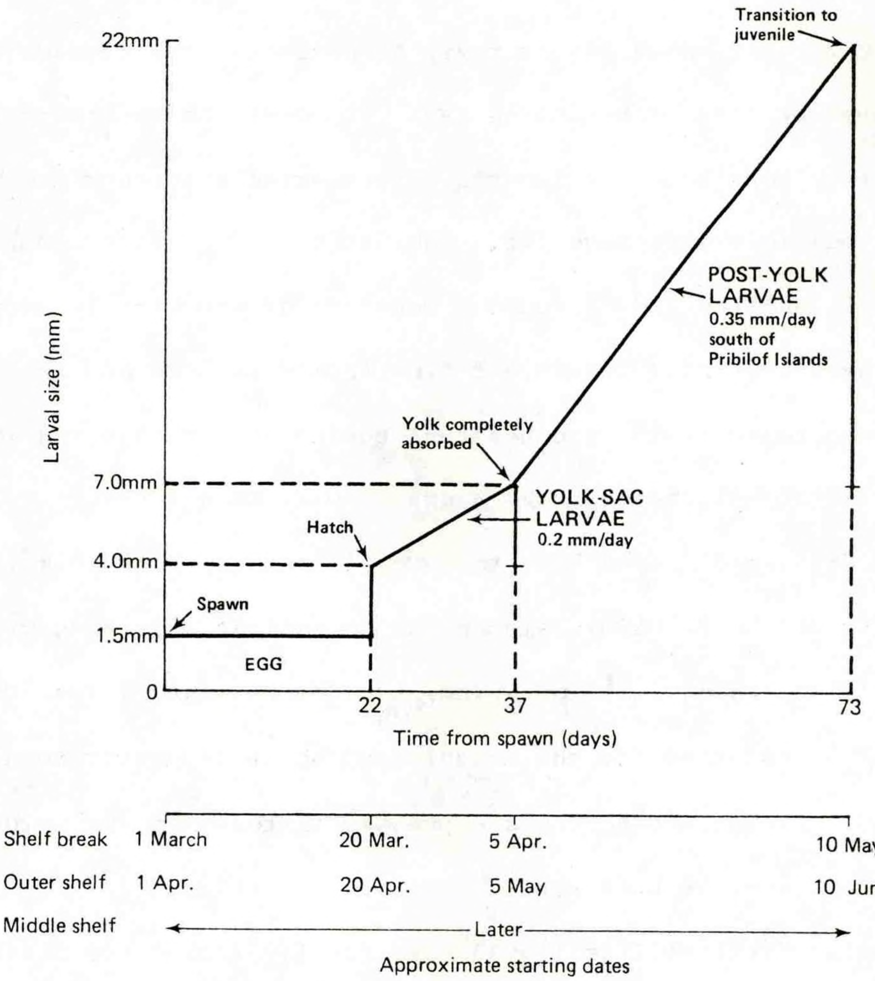


Figure 3. Development and growth of walleye pollock eggs and larvae in the southeastern Bering Sea and approximate dates for the beginning of each stage over the shelf break and outer shelf. Events over the middle shelf occur later; they depend on temperature and can vary significantly from year to year (see text for details).

differences in growth of larvae collected north and south of the Pribilof Islands, but no major differences among the other comparisons. He concluded that the surviving larvae from all areas and hatching dates had encountered sufficient food and that there was no narrow "critical time window" with respect to larval survival in either year. An implicit corollary to this conclusion is that food was, on the average, more abundant than required by the larvae. It is likely that larval growth rates could be the same only if food concentrations were saturating over relatively short time and space scales. These findings led Walline to further conclude that predation was probably the primary factor influencing year-class abundance of pollock.

It should be cautioned that Walline's conclusions apply only to the survivors of 2 particular years, and the months of April, May, and June of those 2 years may have presented comparatively salubrious conditions for pollock larvae. Incze (1983) found marked differences in larval year-class strength of a brachyuran crab which hatches in April in the same area studied by Walline (but mostly over the middle shelf, not outer shelf). These crab larvae, which are found primarily in the upper 20 m, were abundant in 1978 and 1979, but rare (one to two orders of magnitude less abundant) in 1980 and 1981. Incze (unpubl. data) found that the differences in larval crab abundance over part of the middle shelf appeared to be due to post-hatching events and probably to feeding failure. Although pollock larvae may forage with greater efficiency than crab larvae, it is perhaps premature to discount the possibility that food availability sometimes limits the success of larval pollock year-classes. Decreased standing stock of zooplankton prey may influence larval year classes via a "critical period" in larval development or may add to losses (to predators and other causes) due to slowed growth rate. The latter condition assumes that instantaneous rates of mortality remain at some appreciable level throughout larval development, and that prolongation of the larval period results in lower survivorship. It will be pointed out later that zooplankton reproduction and growth appear to be more variable over the middle shelf than outer shelf (see section on zooplankton dynamics); consequently, larval year-class success may be more variable over the middle shelf.

Larval growth rates for 1980 and 1981 are being estimated by Clarke (unpubl. data) and will soon be available for comparison with the results of Walline's study of 1978 and 1979 year-classes. Neither Walline's nor Clarke's studies were designed to estimate larval year-class abundance.

Hunter (1981) and others point out that physiological mortality (starvation) is itself probably not a major, direct source of mortality in the sea. It is more likely that poorly fed individuals succumb to predation due to prolonged duration at small size and decreased capacity to avoid predators. Problems caused by poor feeding conditions may be compounded by increased predation pressure in a sparse zooplankton community. These factors may decrease the likelihood of finding larvae with histories of significantly reduced growth.

Experiments by Paul (1983) support Walline's conclusion that larvae were not food limited at first feeding in 1978 or 1979. Using first-feeding (yolk-sac) larvae, Paul was able to get 10% of the larvae to feed on 100-300 μm diameter nauplii (collected from coastal plankton) at prey concentrations of 10 liter^{-1}. This is a reasonable representation of natural conditions with respect to prey concentrations in the southeastern Bering Sea. Bottle casts by Cooney et al. (1978), Cooney (1979) and Clarke (unpubl. data for 1980) usually gave naupliar concentrations of about 10 liter^{-1} at 20-30 m depth over the shelf in April and May. The concentrations observed in 1980 ranged from 1 to 24 liter^{-1}, while some samples from the previous 2 years provided much higher concentrations. Paul (1983) increased naupliar concentrations up to 50 liter^{-1}, but did not observe a marked increase in the percentage of larval pollock that initiated feeding in his laboratory studies. Clarke (unpubl. data) found that up to 40% of pollock larvae would feed at concentrations of 30 nauplii per liter in feeding experiments conducted at sea using laboratory reared larvae. Differences in the results of these two studies may be due to differences in experimental temperature (Paul 1983), or condition, age or size of the larvae used.

Dagg et al. (in press) looked at vertical distributions of nauplii (mostly 150-250 μm width) and pollock larvae ($\overline{x}$ = 5.2 mm length) during a 48-h drogue study over the outer shelf during May 1981. They found 10 or more nauplii per liter at 20 m depth in most of their samples. This was also the depth of maximum abundance of pollock larvae, approximately 0.4 m^{-3} between 10 and 20 m depth. The estimated impact of larval predation was less than 1.0% of the estimated daily naupliar production. According to these estimated rates of larval predation, prey abundance, and prey production, as well as other data on standing stocks of nauplii, it appears that 1) pollock larvae do not have a significant impact on the abundance of their naupliar prey, and 2) food may not commonly be limiting for first-feeding larval pollock. It is generally assumed that fish larvae become increasingly adept predators as they increase in size, so these results would at first indicate that there also should be no subsequent difficulty in capturing prey. However, this does not consider the fact that the diet of larval pollock changes with size (see below).

Walline (1983) examined vertical distributions of slightly larger pollock larvae during two 48-h periods in the middle and outer shelf domains in June 1979. Sampled larvae were between 4 and 25 mm and 4 and 14 mm length at the outer and middle shelf stations, respectively. This size range included both yolk-sac and post-yolk larvae. Most larvae were found at a depth between 10 and 30 m; few were in the upper 10 m. Larvae tended to be more dispersed and slightly deeper at night, but the vertical shifts were only on the order of 10 m. For example, the maximum at 10-20 m during the day might become a more generalized distribution from 10 to 30 m at night. These data indicate that the first-feeding and post yolk-sac larvae share essentially the same habitat. Conditions within the 10-30 m depth range during stratified conditions (spring and early summer) can thus be a focus of field studies examining larva-plankton interactions with this species in the southeastern Bering Sea. M. E. Clarke is currently examining the effects of major mixing events (storms) on the distribution of naupliar prey at these depths.

The stomach contents of larval pollock have been examined numerically (Clarke 1978) and on the basis of biomass (Nishiyama in prep.). Figure 4 shows the numerical composition of stomach contents of 697 larval pollock ranging in length from 4.8 to 17.7 mm. Copepod nauplii, copepod eggs, and the small cyclopoid copepod *Oithona similis* were numerically the most abundant food items taken. Growth of larvae was accompanied by a steady increase in the upper size of prey taken, but not the lower size. Figure 5 shows that this does not change with time; small larvae continue to take primarily nauplii and metanauplii even later in the spring. Incidence of feeding was 100% for larvae longer than 7.7 mm. It is not known if the lower incidence of feeding of smaller larvae was due to trauma from sampling.

T. Nishiyama (unpubl. data) examined the importance of various taxa on the basis of biomass contributions to larval diet. He found that as soon as larvae start taking larger copepods and copepodids, the quantitative nutritional importance of eggs, nauplii, and the small *Oithona* sp. diminishes rapidly despite the fact that they are still taken in high numbers (Fig. 6). The

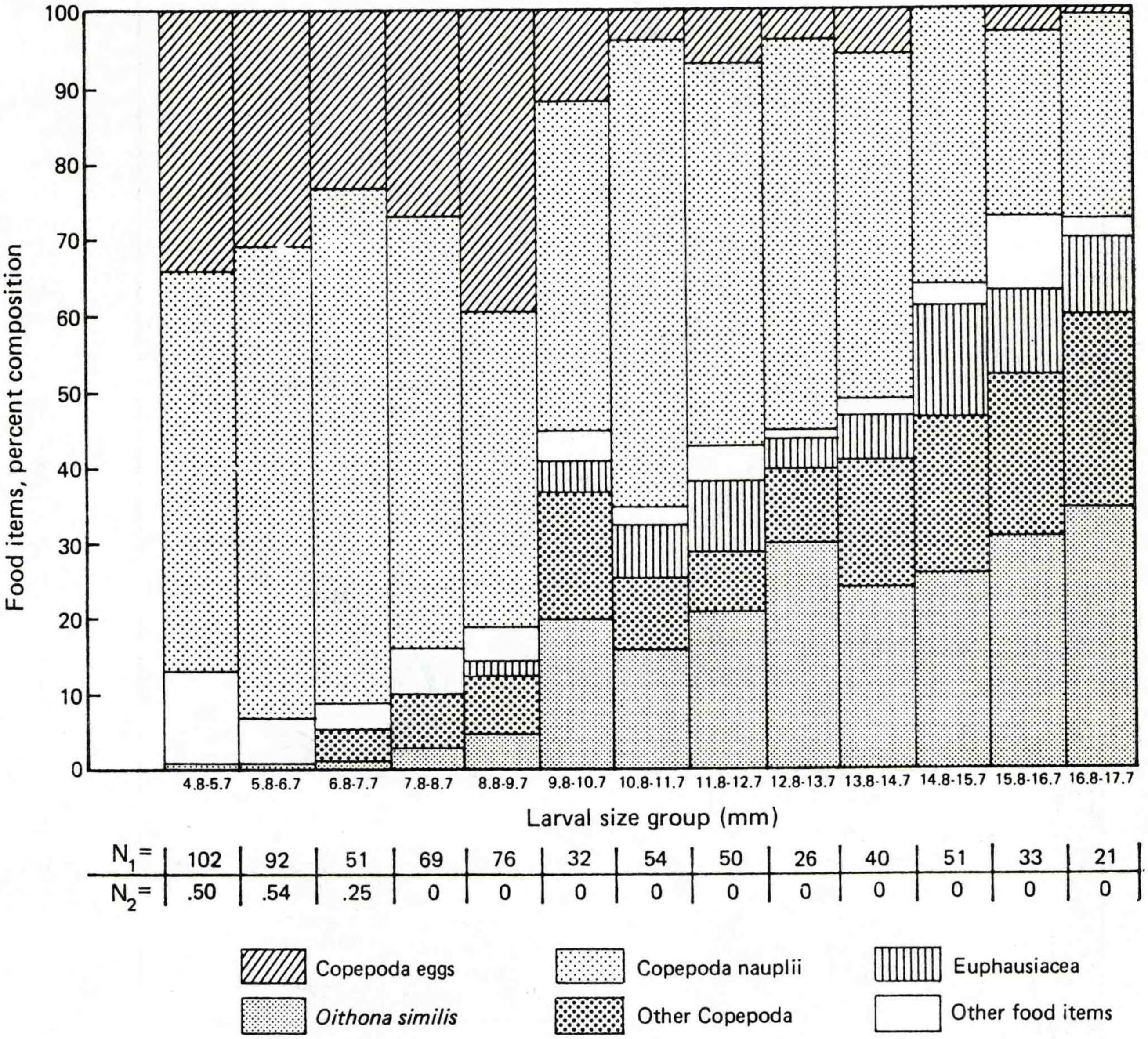


Figure 4. Numerical composition of food items found in the stomachs of larval walleye pollock in the southeastern Bering Sea during 1977. "Other Copepoda" includes juvenile and adult stages of small copepod genera (e.g., Pseudocalanus spp.) and juveniles (copepodids) of the larger genera (e.g., Eucalanus spp.). "Euphausiacea" includes only the juvenile stages (nauplius, metanauplius, calyptopis, furcilia). N_1 = the number of larvae examined; N_2 = the proportion of larvae without food in the stomachs. Figure and data are from Clarke (1978).

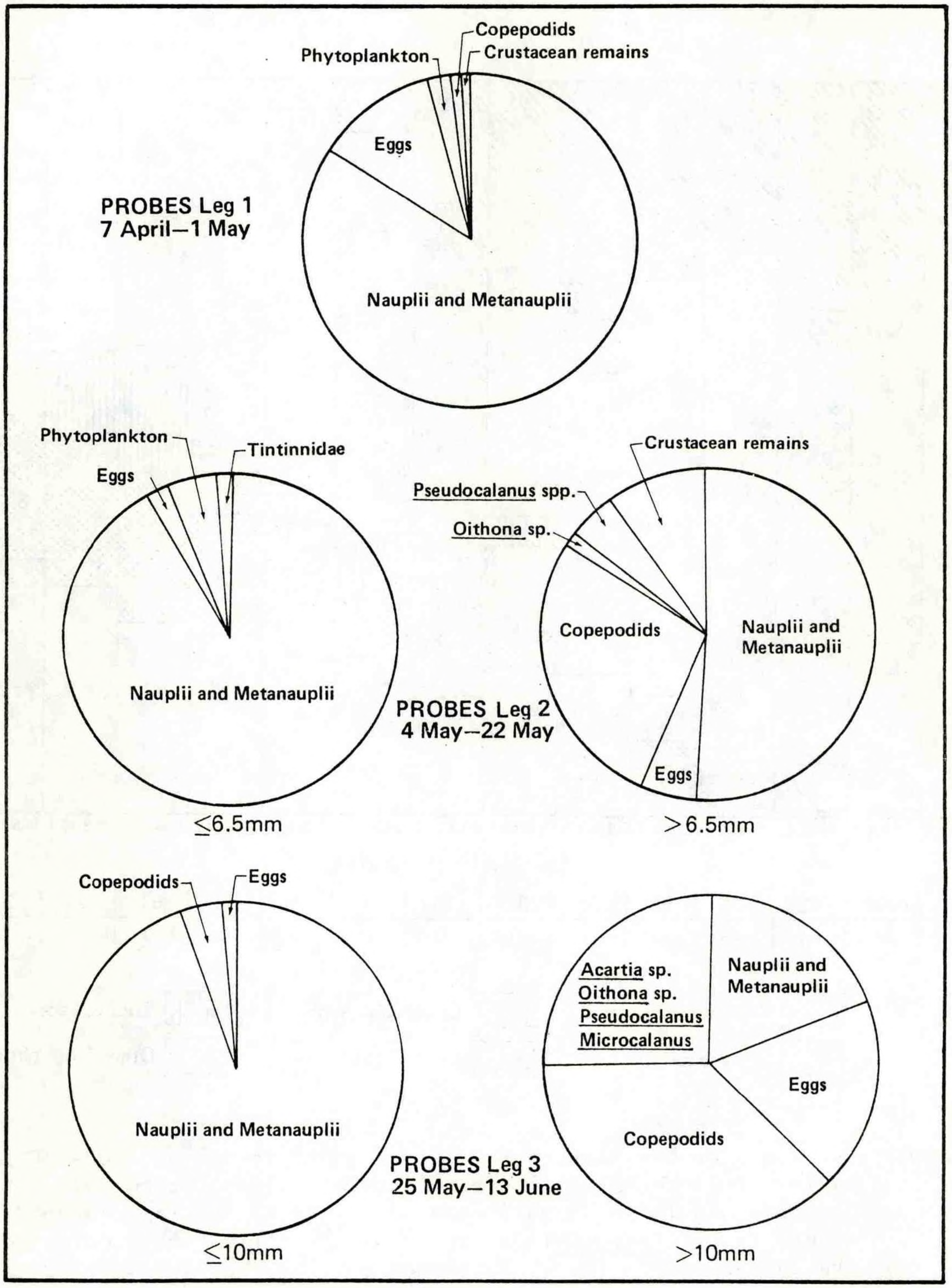


Figure 5. Numerical composition of stomach contents of larval walleye pollock during Legs I through III of the PROBES cruise of 1978 (research vessel T. G. Thompson cruise TT139). Note that the diet of small pollock (≤10 mm length) does not change appreciably through time (from Cooney et al. 1978).

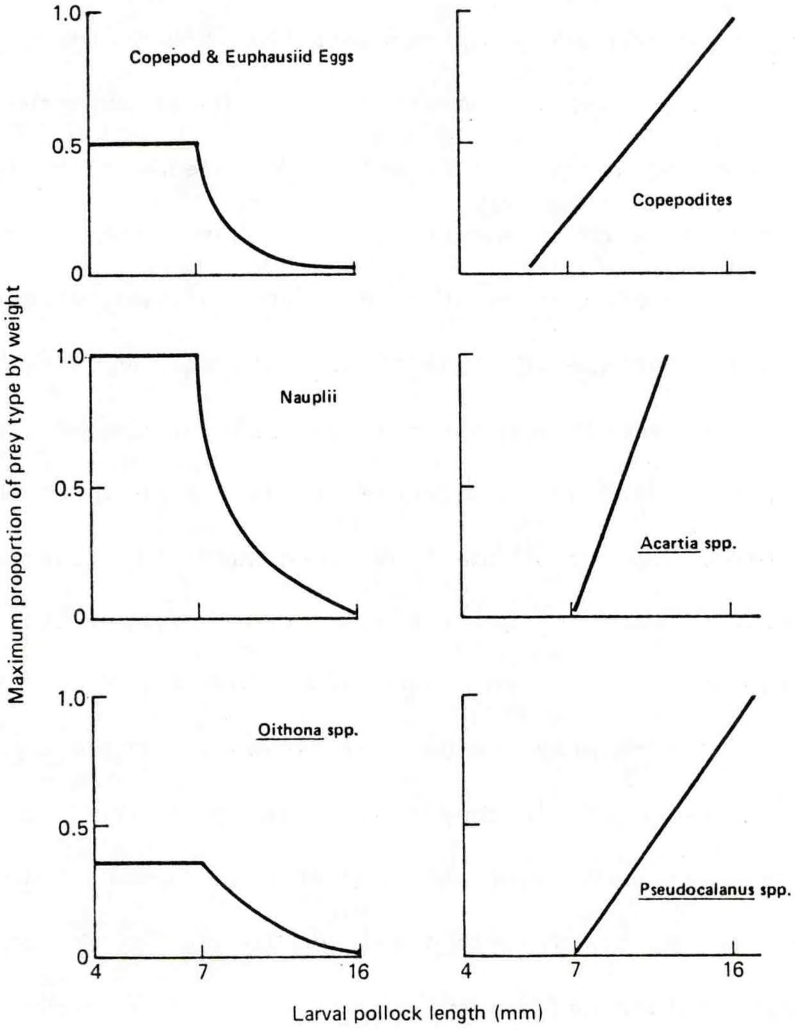


Figure 6. Contribution of various zooplankters to the ingested ration (biomass) of larval walleye pollock of various lengths. Percent weight denotes the maximum proportion of biomass of the stomach contents of a single larva contributed by a prey type. Note change at about 7 mm larval length. In post-yolk larvae (>7 mm), eggs, nauplii, and Oithona spp. constitute rapidly declining portions of the ingested ration in terms of biomass. Trends are from data of T. Nishiyama.

most prominent break in the pattern of prey contribution to biomass (and presumably energy) occurs when larvae reach about 7 mm body length, which is the length at yolk-sac absorption (age 15 d). The ingestion of larger prey is accompanied by a 50% increase in the mean daily growth rate measured as increments in body length (Fig. 3). From the viewpoint of larval energetics, the abundance of Acartia spp. and Pseudocalanus spp. copepods and unidentified copepodites becomes much more important than the abundance of the small prey required by younger larvae. Assessment of the relationship between planktonic conditions and the success of larval feeding relative to total energy needs therefore must take these species into account for the period after yolk absorption. Several species of copepod show strong interannual differences in timing and magnitude of production, particularly over the middle shelf, but prey density requirements for successful feeding of post yolk-sac larvae have not been studied and, therefore, it is not known whether these changes have measurable impacts on the growth and survival of larval pollock.

While a distinct change in the pattern of prey contribution to the ingested ration occurs at yolk sac absorption, Clarke (1978) points out that the number of larger prey consumed by larvae undergoes a gradual, rather than sudden, increase. This is consistent with the gradual attainment of anatomical features which presumably affect predation on larger organisms, including the development of maxillary teeth (11-12 mm larval length) and ossification of the vertebral column and caudaul fin rays (11-16 mm larval length, G. Dunn and R. Bates, NWAFC, National Marine Fisheries Service, Seattle, WA 98112, unpubl. ms.).

As a basis for future studies, the carbon budget of larval pollock can be compared with the carbon content of predominant prey species to estimate the number of prey which must be consumed to meet basal metabolic and growth requirements. The following is a preliminary analysis of this sort. Because growth in terms of carbon was estimated from larval lengths which were not corrected for possible shrinkage due to preservation, the estimated growth rate (% body C d^{-1}) might be low. Respiration rates used in this analysis were made on quiescent larvae and were considered to represent "routine" or "resting" metabolism, in which case these data also are conservative estimates of energy expended in the field. It is not presently known to what extent field and laboratory metabolism differ. Clarke (unpubl. data) and Nishiyama and Harris (unpubl. data) are currently completing much more detailed analyses based on measurements of stomach contents of individual fish from the southeastern Bering Sea.

Nishiyama (1981) compared body length to wet body weight of larval pollock in the size range 4.1-18.5 mm. The allometric equation relating these two parameters yielded an r^2 of 0.99:

$$W = aL^b \qquad (1)$$

where: $a = 0.0023$,

$b = 3.4$,

W = wet weight (mg), and

L = length (mm).[1]

Dry body weight averages about 18.8% of wet body weight of larvae (using data from Nishiyama 1981: Table 9), so the above equation may be rewritten to provide a direct estimate of dry body weight for larvae of a given length:

$$W = 0.188\ (0.0023 \cdot L^{3.4}) \qquad (2)$$

$$= 4.324 \cdot 10^{-4} \times L^{3.4}. \qquad (3)$$

---

[1] The values of constants "a" and "b" were derived from samples collected in May. Samples from June provided different values of a and b, but these were based on a larger range of fish lengths (7.0-34.0 mm), and are therefore not used here.

Approximately 44% of dry body weight is carbon (data for pollock from 3.5 to 39.0 mm body length from Fukuchi 1976, quoted by Nishiyama 1981:295). Using this conversion factor and Eq. 3, the carbon weight of larval pollock can be determined for any body length. Table 2 provides these estimates by 1 mm increments from 5 to 22 mm.

Dry weight data (Table 2) can be fitted to the exponential growth equation to estimate the specific growth rate of larvae (Warren 1971:139):

$$W_2 = W_1 \cdot e^{k(t_2 - t_1)} \qquad (4)$$

where: W_2 = dry weight (mg) at time 2,
W_1 = dry weight (mg) at time 1,
t_1 = time 1 (days),
t_2 = time 2 (days), and
k = specific growth rate.

Rewriting the equation gives:

$$k = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}\text{, and} \qquad (5)$$

$$(e^k - 1) \times 100 = \%\text{ dry weight increase per day.} \qquad (6)$$

Larval growth should then be divided into at least two phases before calculating the average daily growth rate: one phase before yolk sac absorption and one phase after absorption. This division is based on the observed change in average daily growth rate measured as length (Walline 1983; see earlier discussion). The increase in larval size during yolk-sac stage is comparatively small and the assumption of a constant growth rate during this period is probably reasonable. For post-yolk larvae the range of growth is much greater. Since specific growth rate must decrease with time (as a function of body size), the assumption of a constant growth rate leads to a probable underestimate for small larvae and an overestimate for larger larvae. This problem cannot be

Table 2.--Estimated dry weight and carbon content of larval walleye pollock.

Length (L) (mm)	Estimated dry body weight (mg)[a]	Estimated carbon (mg)[b]
5.0	0.103	0.045
6.0	0.191	0.084
7.0	0.323	0.142
8.0	0.509	0.224
9.0	0.759	0.333
10.0	1.086	0.478
11.0	1.502	0.661
12.0	2.019	0.888
13.0	2.650	1.166
14.0	3.409	1.499
15.0	4.311	1.897
16.0	5.369	2.362
17.0	6.598	2.903
18.0	8.013	3.526
19.0	9.630	4.237
20.0	11.465	5.045
21.0	13.534	5.955
22.0	15.853	6.975

[a] Estimated dry body weight = $4.324 \cdot 10^{-4} \times L^{3.4}$

[b] Estimated carbon weight = 0.44 x estimated dry body weight

corrected with the data presently available. For both stages, temporal variations in growth rate due to environmental conditions, such as patchiness in food supply, and individual differences in growth rate cannot be accounted for.

Larvae are about 4.4 mm body length at hatching (approximately 0.067 mg dry weight using Eq. 3) and grow to approximately 7.4 mm (0.390 mg) in 15 d. The daily increase in dry body weight over this period is thus 12.5% (Eq. 6). Post yolk-sac larvae grow from 7.4 mm length (0.390 mg) to 22 mm (15.853 mg) in about 51 d, an increase in dry body weight of 7.5% d^{-1}. Carbon appears to be a nearly constant proportion of dry body weight over this size range, so these estimates represent the daily carbon-specific growth requirements of the larvae, namely: 12.5% and 7.5% body carbon d^{-1} for yolk-sac and post-yolk larvae, respectively.

Nishiyama (1981) measured routine (resting) metabolism of pollock and related this to body length and wet weight. He provides data for two larval lengths, 7.1 ($8.5\ \mu l\ d^{-1}$) and 17.9 mm ($0.286\ ml\ d^{-1}$). Using his measurements of metabolic rate (= oxygen consumption rate = VO_2) and converting to dry weight measurement of body size, it is possible to express VO_2 (metabolism) in terms of body carbon respired:

$$\text{Respired carbon } (\mu g\ C) = VO_2 \cdot RQ \cdot \frac{0.536\ \mu g\ C}{\mu l\ CO_2} \cdot W$$

where: $VO_2 = \mu l\ O_2 \cdot mg\ dry\ wt^{-1}\ d^{-1}$,

RQ = Respiratory Quotient,

$= \dfrac{\mu l\ CO_2}{\mu l\ O_2}$,

= 0.75 for a high protein diet (Giese 1973),

W = mg dry weight.

Relating respired carbon ($\mu g\ C\ ind^{-1}\ d^{-1}$) to individual carbon weight estimates the percentage of body carbon respired per day. A respiration rate (metabolic demand) of 2.3% and 3.3% body C ind^{-1} d^{-1} is indicated for larvae of 7.1 and 17.9 mm length, respectively. The average of the two calculations gives a mean respiration rate of approximately 2.8% body C d^{-1}. This is probably a conservative estimate, as it is based on measurements of routine, and not active, metabolism. For small larvae (90-120 μg dry wt) the lowest measurements of VO_2 indicate "resting" respiration values of about 3% body C ind^{-1} d^{-1}; however, some values about twice this rate also have been observed (respiration data of Clarke listed in Theilacker and Dorsey 1980:126).

The daily ration required to support post-yolk larval growth observed in the southeastern Bering Sea can now be estimated using the average daily growth (7.5% body C ind^{-1} d^{-1}) and reasonable assumptions about the efficiencies of growth and assimilation. First, assume that the sum of carbon required for metabolism and other energetic losses equals 7.5%. This appears reasonable since respiratory demand has been measured at about 3-6% body C ind^{-1} d^{-1}, and additional carbon losses due to excretion of nitrogenous compounds must be expected. The total carbon requirement, including that needed for growth, is thus estimated as 15% of body carbon per day, and the net growth efficiency (growth ÷ assimilated ration) is 50%. Second, assume that the ingested ration is assimilated at 70% efficiency, providing a gross growth efficiency (growth ÷ ingested ration) of 35% (0.50 x 0.70 = 0.35; cf. Theilacker and Dorsey 1980:131). The resulting estimates of daily ration for larvae of various sizes (Table 3) indicate that post-yolk larvae consume, on the average, approximately 21.5% of their body weight per day. The estimated rations were calculated for larvae of 20 and 22 mm length for comparative purposes only. That these probably are overestimates should be re-emphasized. The systematic decrease in specific growth rate with increasing size is not accounted for by the estimated average used in the calculations, and the

Table 3.--Estimated ration required to support metabolism and growth of walleye pollock larvae in the southeastern Bering Sea.

Body length (mm)	Body weight of carbon (mg)	Required ration[a] μg C d^{-1}
7	0.142	30.4
10	0.478	102.4
12	0.888	190.3
14	1.499	321.2
16	2.362	506.1
18	3.526	755.6
20	5.045	1,081.1
22	6.975	1,494.6

[a] Calculated as required ingested ration = $\frac{[\text{body weight of carbon } (\mu g) \times 0.15]}{0.70}$

length-to-weight relationship data which were used extended only up to larvae of 18 mm length.

The estimated required daily ration (Table 3) can be compared to the carbon values of various prey (Table 4) to predict the number of prey required (Table 5). It is obvious from the data presented in Table 5 that increasing reliance on larger prey is necessary, as the number of smaller prey required per day becomes excessive as larvae grow. The number of *Pseudocalanus* spp. and *Acartia* spp. adult copepods required per day also becomes quite high for larger pollock larvae (approximately 280 d^{-1} for 20 mm larvae), but fish larvae of this size often have a high strike-capture efficiency and are probably capable of preying at this rate (G. Laurence, Northeast Fish. Ctr., Narragansett Lab., Narragansett, R. I. 02882, pers. commun.: results of experiments with Atlantic gadoid larvae of similar size). Again, the probable overestimate of specific growth rate, and therefore of dietary needs, of larger larvae is stressed.

Data of Nishiyama (in prep.) indicate that *Pseudocalanus* spp. and *Acartia* spp. copepodids and copepods are the major prey of pollock larvae larger than about 10 mm (Nishiyama's data included larvae up to about 16 mm, Fig. 6). However, these species of copepod are subject to large interannual differences in abundance, particularly over the middle shelf (Smith and Vidal in prep.), and these differences may affect the feeding success of the larger pollock larvae.

The juvenile stages of euphausiids also may be an important contributor to the diet of late larval stage pollock. This is not indicated in Figure 6, but is suggested by their size, abundance, and published data of Clarke (1978). The calyptopis stages of euphausiids all contain more carbon per individual than the adult *Acartia* spp. or *Pseudocalanus* spp. copepods. The

Table 4.--Estimated carbon content of potential prey of larval walleye pollock in the southeastern Bering Sea: N, naupliar stages; C, copepodid stages; A, adult; F, female; M, male.[a,b]

Species/Stage	Carbon Content (μg·ind^{-1})
Oithona eggs/NI	0.01
Pseudocalanus spp. eggs/NI	0.054
Acartia spp. eggs/NI	0.4
Oithona spp. AF	0.5
Calanus marshallae NI	0.9
Pseudocalanus CIII	1.1
Acartia spp. copepodites (mean)	
Euphausiid (*Thysanoessa raschii*) eggs/NI	2.3-2.6
C. marshallae CI and CIII (mean)	5.0
Pseudocalanus spp. AF	5.5
Acartia spp. AF	<5.5
Euphausiid NII	6.7
Euphausiid metanauplius	8.6
Euphausiid calyptopis I	7.2[c]
Euphausiid calyptopis II	9.8
Euphausiid calyptopis III	16.8
C. marshallae CIII	19.4
C. marshallae CIV	58.4
C. marshallae CV	147.1
Neocalanus plumchrus CIII	15.0
N. plumchrus CIV	55.0
N. cristatus CIII	30.0
N. cristatus CIV	120.0

[a] The list is not inclusive of all species found in the southeastern Bering Sea, only those which are abundant and *may* be preyed upon by pollock larvae.

[b] Carbon was estimated as 45% of dry weight except for *N. plumchrus* (50%) and *N. cristatus* (60%). Estimates for eggs/NI are based on measurements of eggs. Data are from Vidal and Smith (in press) and Smith (unpubl. data) (1983) except for *T. raschii* eggs/NI, *C. marshallae* CI and *Pseudocalanus* AF, which were also taken from Incze (1983).

[c] Calyptopis I dry weights were less than metanaupliar weights at two stations where samples for weight determination were collected.

Table 5.--Selected potential prey and approximate number required to satisfy carbon requirements of growing walleye pollock larvae assuming that total energy needs are equal to twice the growth requirement and assimilation efficiency is 70% (Table 3), and assuming that only a single taxon is ingested (latter assumption made for comparative purposes only). Abbreviations are same as those used in Table 4.

	NUMBER PREY REQUIRED PER DAY								
Larval length (mm)	*Oithona* spp. eggs/NI	*Pseudocalanus*/ *Acartia* spp. eggs/NI	*Oithona* spp. AF	*Pseudo-calanus* spp. CIII	Euphausiid eggs/NI	*Pseudo-calanus* spp. AF	Euphausiid Calyptopis I-III (mean)	*C. mar-shallae* CIII	*N. plum-chrus* CIII
7	4343	803	109	49	18				
10		2709	367	163	61				
12		5034	681	302	111	50			
14			1147	511	188	85			
16			1807	804	296	133	64		
18				1200	440	198	96		
20				1716	632	280	137	79	56
22					806	389	190	111	72

calyptopis III contains more than three times the carbon of the adult copepods, yet its total length (approximately 2 mm: S. L. Smith, Oceanographic Sciences Division, Brookhaven National Lab., Upton, NY 11973, unpubl. data) is only slightly greater than that of *Acartia* spp. adults (approx. 1.2 mm total length: Cooney et al. 1978) and similar to *Pseudocalanus* spp. (2 mm total length). An increase in the average number of calyptopes was found by Clarke (1978) in pollock larvae longer than about 15 mm, and an analysis of the contribution of calyptopes to ingested ration relative to the total contribution of *Acartia* spp. and *Pseudocalanus* spp. copepods is given in Table 6. This analysis indicates that the calyptopes probably contribute about as much as copepods (*Pseudocalanus* spp. and *Acartia* spp.) to the ingested ration of pollock larvae of this size.

The calyptopis stages of euphausiids probably can be sampled quite reliably using ordinary zooplankton sampling gear. Incze (unpubl. data) examined the catches of euphausiid nauplii, calyptopes, and furciliae from PROBES (Processes and Resources of the Bering Sea Shelf) zooplankton collections of 1980 (Smith et al. 1982). Estimates of naupliar abundance showed erratic patterns probably related to patchiness in the distribution of this stage. Furciliae also showed erratic patterns of abundance and usually very low numbers, possibly because they begin strong vertical migrations similar to the adults (M. Macauley, pers. commun.). The estimates of abundance of calyptopis stages I, II and III combined, however, showed very consistent patterns of horizontal and vertical distribution. Calyptopes may be as abundant or more abundant than adults of *Pseudocalanus* spp. and *Acartia* spp. (Incze unpubl. analysis of PROBES data). This suggests that juvenile euphausiids may be very important for the late larvae of pollock, providing prey of intermediate size and catchability between the small, abundant copepods and the larger, faster

Table 6.--Number of calyptopis stage euphausiids and total number of *Pseudocalanus* and *Acartia* spp. copepods, (copepodids and adults) in larval walleye pollock from 8.8 to 17.7 mm body length (data from Clarke 1978 for larvae collected in the southeastern Bering Sea). An approximation of carbon from calyptopes was made using the mean carbon content of the three stages (11.3 μg C ind^{-1}). The approximation for copepods assumed that all *Pseudocalanus* and *Acartia* spp. were adults and that each contributed 5.5 μg C (Table 4). An overestimate of the carbon contributed by these copepods and an underestimate of the relative contributions of calyptopes most probably results from these assumptions. Comparisons are made for larvae longer than 14.8 mm, at which length the average number of calyptopes per larva increased markedly in Clarke's (1978) data.

Size category of larvae (mm) body length	8.8-9.7	9.8-10.7	10.8-11.7	11.8-12.7	12.8-13.7	13.8-14.7	14.8-15.7	15.8-16.7	16.8-17.7
No. of Larvae Examined	76	32	54	50	26	40	51	33	21
No. of calyptopes	5	5	14	14	1	7	44	37	21
Mean No. of calyptopes larva^{-1}	.06	.16	.26	.28	.04	.17	.86	1.12	1.0
No. of *Pseudocalanus* and *Acartia* spp.	22	23	68	38	35	119	103	94	53
Mean No. *Pseudocalanus* and *Acartia* spp. larva^{-1}	.29	.72	1.26	0.76	1.35	2.98	2.02	2.85	2.52
Mean μg C from calyptopes[a]							9.7	12.6	11.3
Mean μg C from copepods[a]							11.1	15.7	13.9
C from calyptopes: C from copepods							0.9	0.8	0.8

[a] See assumptions in Table heading

copepods and older stages of euphausiids. The size at which pollock larvae begin consistently to capture prey larger than the calyptopes or *Acartia* spp. and *Pseudocalanus* spp. is unknown.

The larger species of copepod in the southeastern Bering Sea are not uniformly abundant over the shelf (Cooney et al. 1980; Cooney and Coyle 1982; Vidal and Smith in press; Smith and Vidal in press). The most striking difference between plankton of the middle shelf and the outer shelf and slope is the presence of large oceanic copepods, primarily *Neocalanus plumchrus*, *N. cristatus*, and *Eucalanus bungii* over the outer shelf and slope. These are bathypelagic species whose copepodids migrate to the upper ocean in March, and whose presence in the outer shelf domain is thought to result from onshore mixing due to sporadic meteorological forcing (Vidal and Smith in press). The abundance of these copepodids steadily decreases landward of the slope, and very few are found landward of the middle front (100 m isobath). The only large copepod whose center of abundance is the middle shelf domain is *Calanus marshallae*. This species is smaller than either *Neocalanus* spp. or *E. bungii*, but it may be as abundant as the outer shelf populations of *Neocalanus* spp. Euphausiids, however, appear to be found in similar numbers across the shelf (both middle and outer shelf domains). While the species differ (*Thyssanoessa inermis*, outer; *T. raschii*, middle), they are of similar size and may go through the same development stages at approximately the same time of year (Smith and Vidal unpubl. data). They thus appear to present a common food resource of similar abundance over both shelf areas where pollock may spawn. It is not yet known to what extent the timing of production or the abundance of euphausiids varies from year to year in the southeastern Bering Sea.

PREDATORS

Understanding the impact of predation on pollock eggs and larvae requires much more information than currently exists. Virtually nothing is known about which natural predators take pollock eggs and larvae in significant numbers or how predation rates on pollock are affected by the availability of other prey (e.g., Kuhlmann 1977 cited in Hunter 1981). In addition, the gelatinous zooplankters, which may be important predators depending on their timing (e.g., Bailey and Batty 1983), have not been extensively and quantitatively sampled in the southeastern Bering Sea. The importance of various nektonic predators is also unknown. Small fish escape most sampling gear, and larvae are known to disintegrate too rapidly in the stomachs of larger fish to enable stomach content analyses to provide even a rough estimate of predation rates (Kendall, pers. commun.). Despite these difficulties, predation on eggs and larvae requires study. If the sources and relative importance of predatory losses were known, then the potential for interannual differences in predation pressure could be assessed as a factor contributing to fluctuations in year-class abundance of pollock.

THE PLANKTONIC ENVIRONMENT

Since the planktonic predators of pollock eggs and larvae are not known, this section focuses on production of the plankton community primarily as it affects the abundance of food for larval and juvenile pollock. It should be remembered, however, that planktonic production also may indirectly influence predation on pollock larvae by affecting the abundance of alternate prey.

The lowest trophic level of direct consequence to pollock life history is the zooplankton. Even in first feeding larvae (4.8 to 5.7 mm length), the incidence of phytoplankton in stomachs is low (Kamba 1977, Clarke 1978) and probably represents a minor energetic contribution to the larvae. The timing and abundance of phytoplankton, however, have an impact on zooplankton production, so the following discussion begins with patterns of primary production.

The temporal development of the spring phytoplankton (diatom) bloom over the southeastern Bering Sea shelf and slope can be divided into a pre-bloom, light-limited phase; a post-bloom, nutrient-limited phase; and an intervening peak bloom period characterized by the surface spring chlorophyll maximum (Sambrotto et al., Univ. of Alaska, Fairbanks, AK 99701, unpubl. data). Maximum standing stock of phytoplankton is lower over the slope and outer shelf than the middle shelf due to early grazing pressure by oceanic copepods (Vidal and Smith in press; Heinrich 1962).

Water column light conditions in the southeastern Bering Sea usually are adequate for phytoplankton growth during March, when a reduction in nitrate from wintertime levels is already observed (Sambrotto et al. unpubl. data). The spring phytoplankton bloom, however, does not occur in this region until late April or early May (see Figs. 32, 33 of Walsh 1983). During the PROBES studies of 1979-81, surface blooms were observed only when the ratio of the upper mixed layer depth to the critical depth became less than 0.3 (Sambrotto et al. unpubl. data). This occurs at early stages of water column stabilization when the seasonal pycnocline is still easily eroded by wind mixing; initiation of the bloom was therefore associated with a hiatus in wind mixing events during each of the years studied. This hiatus was caused in these 3 years by stagnation of a low pressure system over the southeastern Bering Sea. The chlorophyll maximum in the surface layer was reached no sooner than about 20 April and no later than about 10 May during the period 1978-81. The difference in timing between middle shelf and outer shelf was as great as the differences between years and showed no systematic trend (Walsh 1983: Figs. 31, 32).

In addition to timing, there is considerable interannual variation in phytoplankton production during the spring bloom period. Of the approximately 700 mg-at $NO_3^- m^{-2}$ uptake during the spring bloom, an average of about 320 mg-at m^{-2} is accounted for during the high growth period leading to exhaustion of nitrate from the upper mixed layer. Nitrate uptake before water column stabilization accounts for about 30-60 mg-at $NO_3^- m^{-2}$, while post-bloom diffusive flux can account for an additional 50-70 mg-at m^{-2}. The enhancement of new production (nitrate uptake) by vertical mixing and exchange of nutrients from below the pycnocline is responsible for the average remaining 260 mg-at m^{-2} of nitrate uptake, or about 37% of the average annual spring bloom total. However, the contribution of nitrate uptake related to wind mixing can vary considerably; for example, from about 10% in 1981 to about 50% in 1979 (Sambrotto and Goering 1983). This resulted in nearly 1.7 times the nitrate uptake over the middle shelf in 1979 compared to 1980 when integrated from the surface to 77 m (water column depth at the location for which the estimate was made) for the period 25 April-2 June (Sambrotto and Goering 1983). Estimates based on ^{15}N uptake and nitrogen depletion rates in the middle domain placed 1980 production at about 1.4 times that of 1981. For the outer shelf, an estimate based on measured ^{15}N uptake rates during the spring bloom integrated over the 0.1% photic zone gave 2.5 times the nitrate uptake in 1980 compared to 1981.

The effect which these interannual differences in primary production have on the zooplankton community varies with domain. Over the middle shelf, primary production appears always to exceed grazing capacity, with the result that much of the spring bloom production of this region sinks to the bottom (Iverson et al. 1979; Cooney and Coyle 1982; Dagg et al. 1982). The impact on abundance of zooplankton in this domain should thus be negligible. In fact, a major influence on zooplankton production over the middle shelf appears to be temperature; despite higher primary production during the spring bloom in 1980, cold temperatures yielded lower zooplankton biomass than 1981 (calculated for the end of May in both years using unpubl. data of Smith and Vidal). Also, 1980 had much lower zooplankton biomass than 1979 despite only slightly lower primary production (Walsh 1983). The effect of temperature was probably mediated by a slowing of growth and reproduction of the small species of copepods which dominate the middle shelf domain (Vidal 1980a, b; Vidal and Smith, in press). However, other factors also may be involved. For instance, zooplankton production was higher over the middle shelf in 1979 than in 1981, despite similar temperatures and surplus production of phytoplankton (Walsh 1983 for 1979-80 comparison; Incze 1983 for 1980-81 comparison using data from Smith et al. 1982 and Smith unpubl. data). The time series of observations is too short to evaluate possible underlying reasons for this difference, but possible explanations include the effect that sporadic mixing has on species composition of phytoplankton and the effect that this may have on feeding and reproduction in small copepods (Cahoon 1981).

Over the outer shelf, interannual differences in primary production appear to have direct effects on zooplankton production, at least with the larger species of copepod. Smith and Vidal (in press) showed that growth rate of Neocalanus plumchrus copepodids was greater in 1980 than in 1981, despite cooler temperatures. Presumably, this difference in growth rate was due to differences in abundance or type of food. There also may be interannual differences in abundance of these copepodids due to variations in reproductive output from the previous year's population and differences in on-shelf mixing during late winter (mostly March: Vidal and Smith in press). The copepodids of Neocalanus spp. are too large to be preyed on by larval pollock, but are a significant part of the diet of juvenile pollock 30-35 cm length (Dwyer et al. in press; see also the article by Lynde in this Technical Memorandum). Consequently, interannual differences in primary production over the outer shelf and slope, and lagged effects of reproduction of large oceanic copepods and on-shelf mixing of copepodids may have measurable impacts on feeding and growth, and hence survival and production, of year-classes of young pollock living in these regions. It is not known if similar patterns exist for planktonic production and pollock feeding over deeper water of the Aleutian Basin or northwest along the Bering Sea outer shelf and slope.

Among planktonic organisms, euphausiids also play an important role as food items in juvenile pollock of 30-35 cm length and also may be a significant component in the diet of smaller, including 0-age, juveniles. However, estimates of abundance of euphausiids are prone to severe sampling problems, and comparatively little is known about interannual differences in their numbers in the eastern Bering Sea (rough estimates of abundance have been made by Smith and Vidal for 1980 and 1981, in press). It may be possible to base future estimates of euphausiid populations on quantitative sampling of calyptopis stages (see previous discussion). This requires that the fecundity and sex ratio of adults and the duration of calyptopis stages be known (Incze and Smith unpubl. data).

SUMMARY

A simple schematic diagram of interactions between pollock eggs, pollock larvae, and other components of the pelagic environment (Fig. 7) should help to summarize the relationships discussed above. This diagram does not attempt to illustrate all possible interactions; instead, it focuses on the principal

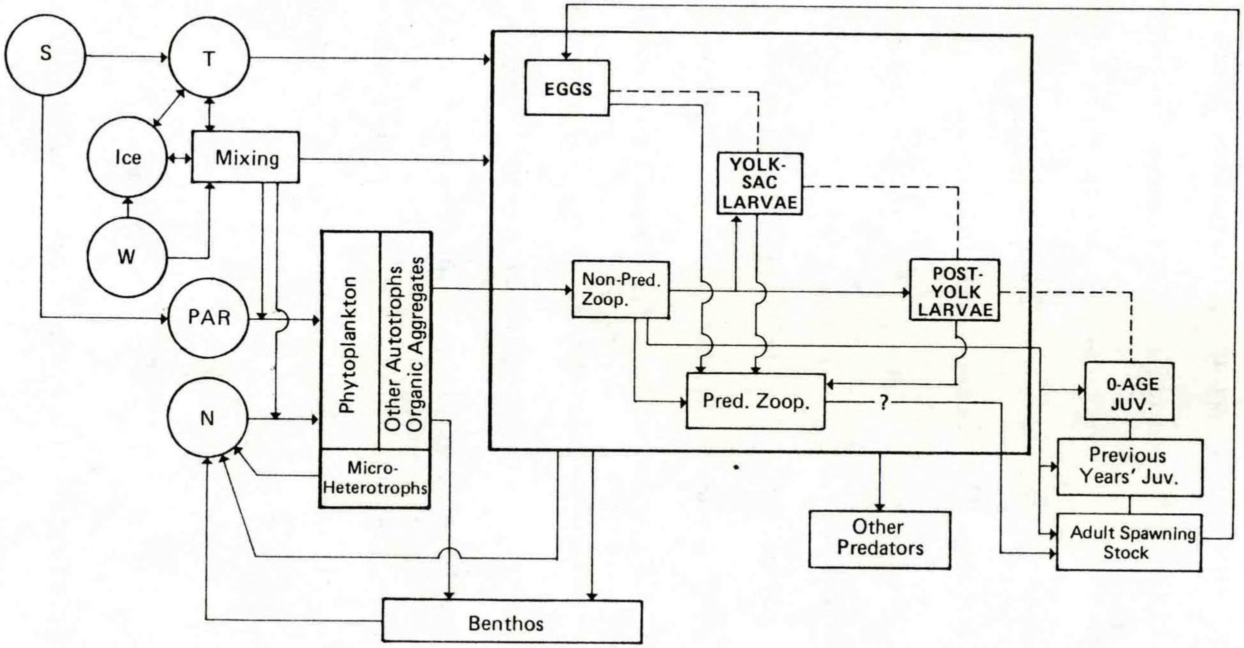


Figure 7. Schema of major influences on the survival of walleye pollock eggs and larvae to the juvenile stage. Planktonic organisms are in the heavily bordered boxes. Predatory (Pred.) and non-predatory zooplankton (Zoop.) are separated. Material flows and abiotic influences on the planktonic environment of pollock are indicated by arrows. The development of pollock from eggs to 0-age juveniles (Juv.) is shown by broken lines. Interrogation mark indicates a flow of questionable importance. Only interactions of direct consequences are modeled. Symbols represent: S, solar radiation; T, temperature; W, wind stress; PAR, photosynthetically active radiation; N, nutrients.

pathways of abiotic influences and flows of biogenic materials which influence the early life history of pollock.

In this schema, yolk-sac and post-yolk larvae are separated because they appear to rely on quite different sources of prey to satisfy bulk energy requirements. The zooplankton community has been separated into two functional groups--predatory and nonpredatory. Here, predators are treated as strictly predatory because this is their main impact on the system. The fact that some also may consume phytoplankton is not modeled. An organism should be included in the predator box only if its predatory impact on eggs, larvae, or the food or predators of larvae is significant. For similar reasons, there is no flow indicated from predatory zooplankton to pollock larvae, because the major suppliers of larval food (nauplii through adult copepods) are the nonpredatory zooplankton, especially *Pseudocalanus* spp., *Acartia* spp. and juvenile euphausiids. Some species may have early life history stages which are prey, but later stages which are predators. These can be accommodated by placing the different stages in the corresponding functional groups with respect to interactions with pollock larvae. Values for such things as temperature, phytoplankton abundance, etc. are not provided because they change interannually and with domain.

The purpose of Figure 7 is to divide certain planktonic processes into categories which can be studied. These fall into two gross levels. First, the conditions which directly affect eggs and larvae (temperature, food, predators); and second, those variables which control temperature, food, and predators (such as winter-spring ice cover, wind mixing, populations of overwintering zooplankton and predators). The schema emphasizes those linkages which may be critical to success of the egg and larval stages of recruitment. This should provide a framework for formulating research questions central to ultimately understanding causes of variations in recruitment to the exploitable stage. Based on this model and the discussions provided above, the following points summarize those steps in egg and larval development of pollock which are least understood and which may be important determinants of year-class strength:

1) Effect of maternal physiology (nutritional history, stress, etc.) on fecundity, egg size, and egg and larval survival.
2) Effect of egg size on larval survival under various conditions of temperature and prey availability.
3) Natural hatching mortality.
4) The identity of natural predators and rates of predation under varying conditions of planktonic richness.
5) Feeding rates and prey density requirements of early and late post yolk-sac larvae (7-22 mm body length) at various temperatures.

Some of the above questions are experimentally more tractable than others. For instance, it is quite feasible to estimate rates of predation by predatory zooplankton, but more difficult to do the same with planktivorous fish, such as herring. Similarly, experimental estimation of larval mortality rates due to causes other than predation (i.e., failure to develop and function adequately) is never free of the question of artifact from handling and rearing. Nonetheless, knowledge of these processes is required to advance our understanding of principal mechanisms affecting year-class abundance of pollock.

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RELATIONSHIPS BETWEEN WALLEYE POLLOCK, OTHER FISH, AND SQUID IN THE EASTERN BERING SEA

by

Gary B. Smith[1], M. James Allen[2], and Gary E. Walters[1]

ABSTRACT

The ecosystem of walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea includes a large number of other fish and invertebrate species that are ecologically linked to pollock as community associates, prey, predators, or competitors, or economically linked to pollock through the multispecies trawl fisheries. Community associates include the characteristic demersal and pelagic fishes and squid that live with pollock in different parts of its oceanic and neritic environments. Most fish species that have feeding relationships with pollock interact with pollock in different ways as they grow, often serving as prey when small, potential food competitors when larger, and predators when fully grown. Economic linkages exist between pollock and other species that are alternative targets in the trawl fishery, taken incidentally in the bycatch, or jointly affected by fishery management regulations.

A conceptual model is developed for these interactions of pollock with other fishes and squid, based on four major functional groups: pollock, pollock prey, pollock predators, and potential pollock competitors. Species in these groups are classified into four ecological types on the basis of their body size, position in the water column, and foraging behavior: small pelagics, large pelagics, benthopelagics, and benthic fishes. Because species

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may have multiple trophic roles with pollock at different stages in their life histories, as they grow and change habitats and behavior, they may be members of more than one functional group.

Important gaps in our knowledge of other fish and squid include the limited seasonal coverage of population sizes and distributions, and limited availability of biological data for species of low commercial interest. The kinds of information needed are more data on size and age, reproduction, birth and mortality rates, feeding biology, growth, and responses to environmental conditions.

INTRODUCTION

Although walleye pollock, Theragra chalcogramma, is one of the central components of the Bering Sea food web (Smith 1981), its extended ecosystem is a complex multispecies environment composed of numerous invertebrates, fishes, seabirds, and marine mammals. The largest subset of ecologically related species is the group of associates that are often found living with pollock, either epipelagically in the open ocean or over the continental shelf and slope, as members of the same communities. The next largest subset is the group of species that share connections in the food web with pollock (i.e., that have prey or predators in common). A smaller subset, but probably the most important, is composed of those species that have direct biological interactions with pollock in feeding relationships as predators or prey. This latter group includes a few major types of zooplankton and pelagic fish prey, and a wide variety of primarily upper trophic level predators (Fig. 1).

In addition to these biological interactions, a number of species are also related economically to pollock through the commercial fisheries. Large multispecies trawl fisheries in the eastern Bering Sea and Aleutian Islands regions harvest approximately 1,300,000 metric tons (t) of fish annually (Bakkala et al. 1979 and Fig. 2). Although pollock is the primary target species and has accounted for 74-78% of the total catch in recent years, about 30 other fish species are also important. These species are linked economically with pollock because they affect the value of the species mix obtained from trawling. Some are more highly valued alternative target species; whereas others are important because of resource conservation issues.

This paper describes the ecological and economic interactions of these species with pollock in more detail and identifies gaps in our knowledge of these relationships. Before going further, it may be helpful to review some

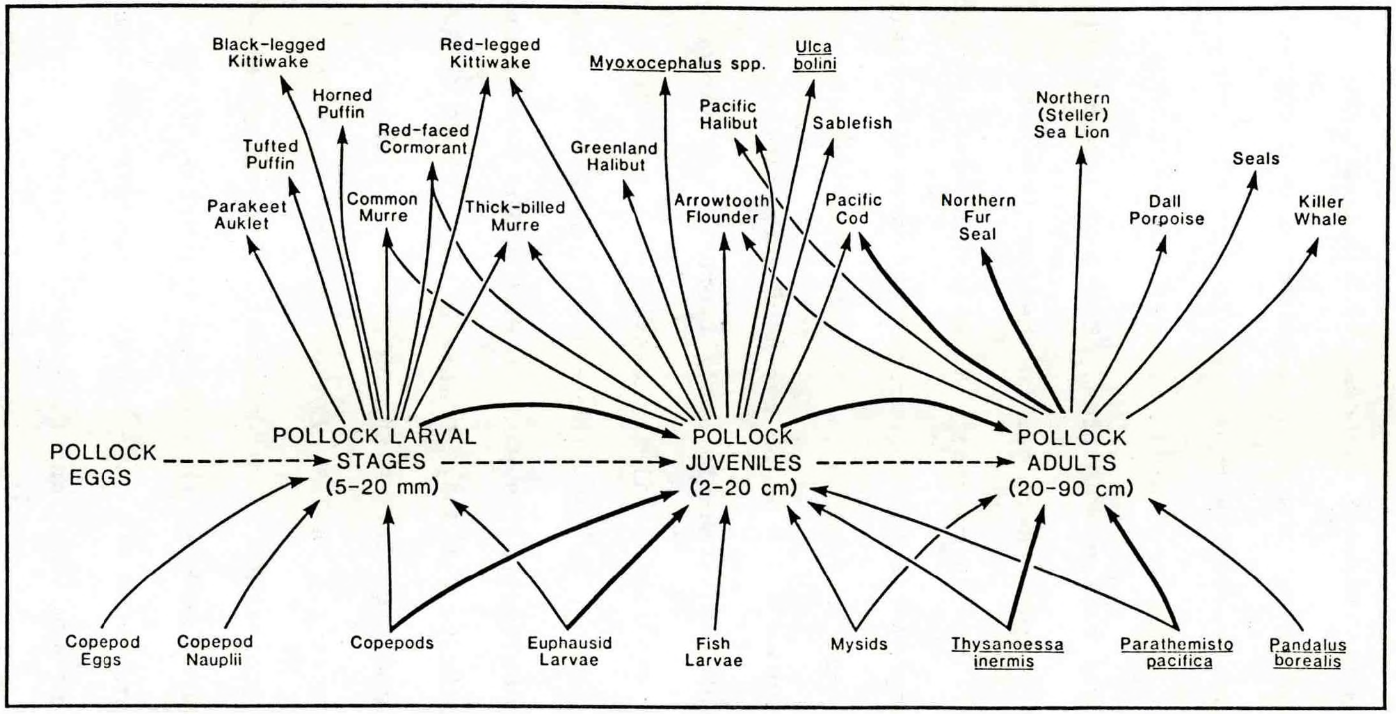

Figure 1.--The apparent food web based on walleye pollock over the eastern Bering Sea continental shelf (from Smith 1981). Dotted lines indicate pollock ontogeny. Solid lines show the direction and relative magnitude of carbon flows.

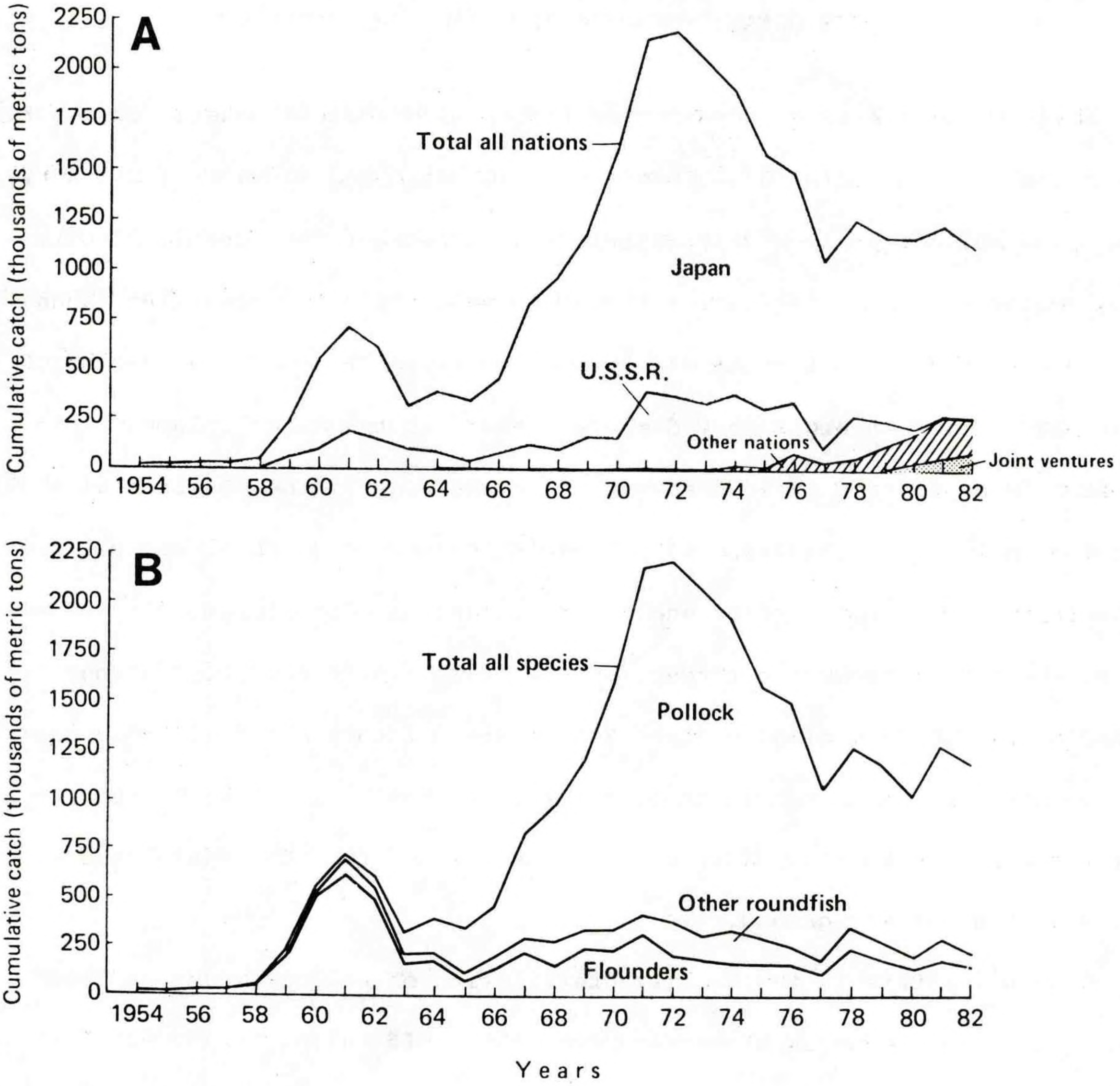

Figure 2.--Groundfish catches in the eastern Bering Sea (east of long. 180°): A) by nation; and B) by species group (modified from Bakkala et al. 1979).

of the fundamental characteristics of the apparent distribution and behavior of pollock in the Bering Sea.

MODEL FOR OCEANIC-NERITIC DISTRIBUTION OF POLLOCK

Walleye pollock is an oceanic-neritic species that is densely concentrated near the shelf edge (Fig. 3). Recent hydroacoustic and midwater trawl surveys have found pollock to be widely distributed throughout the oceanic Aleutian Basin region of the Bering Sea, although at relatively low densities (Nunnallee 1978; Okada 1979). During the day these fish concentrate between depths of 50 and 150 m, and at night they disperse upward in the water column. This low-density population extends seaward from the edge of the continental shelf. Over the continental shelf and slope, adult pollock form dense, semipelagic concentrations along the outer shelf between depths of approximately 150 and 250 m, where they provide a target for the trawl fisheries. Populations of juvenile pollock (age-classes 1 and 2 yr) extend into the middle shelf region and are distributed higher in the water column than adults (Smith 1981). Spawning occurs primarily along the shelf edge, and the continental shelf serves as the nursery ground.

Seasonal shifts in the density distribution of pollock occur as they move to the shelf edge in winter and onto the shelf during spring and summer (Favorite and Laevastu 1981). The timing and extent of these seasonal migrations are probably strongly influenced by ocean climate.

BIOLOGICAL INTERACTIONS WITH POLLOCK

Oceanic Environment

Little is known about the biology of pollock in the Bering Sea oceanic environment, and most of the available information has come from recent fish

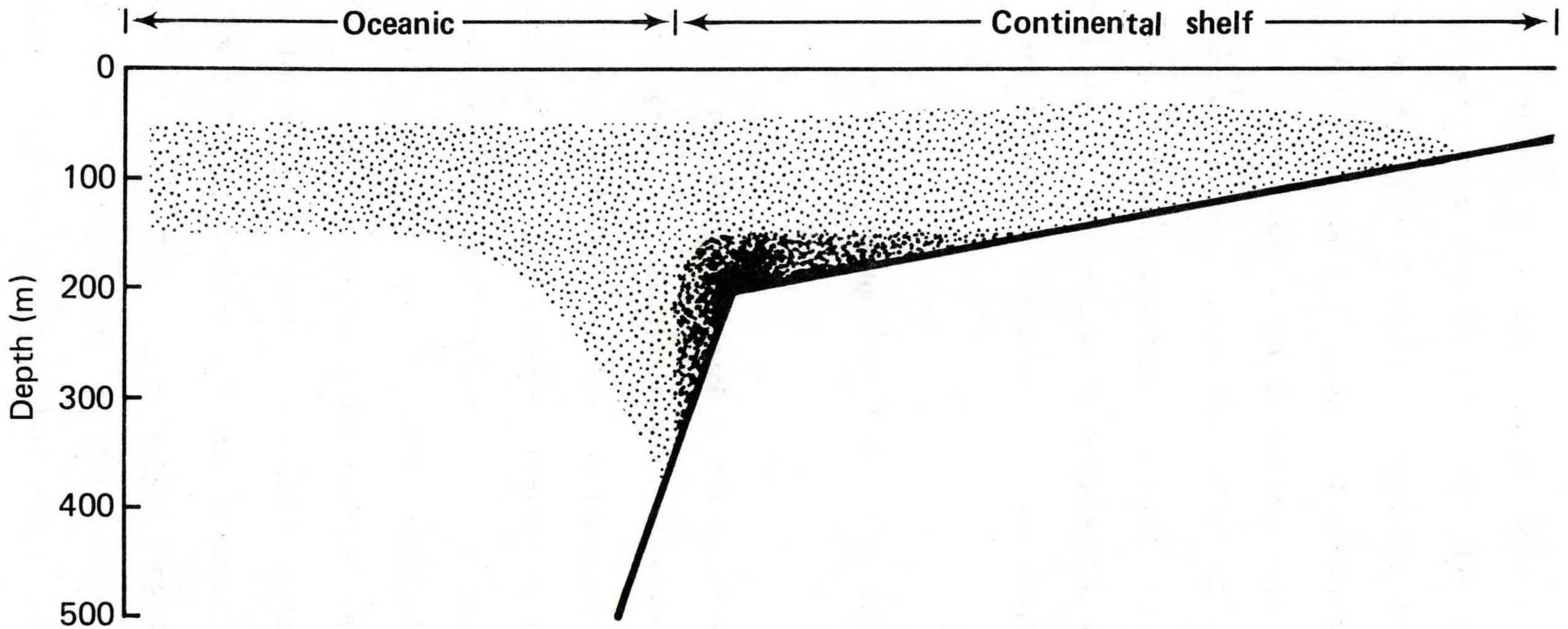

Figure 3.--A simple conceptual model for the oceanic-neritic distribution of walleye pollock in the eastern Bering Sea and their interaction with the continental shelf. Shading indicates relative population densities.

surveys. A peculiar characteristic of this oceanic population is its unusually narrow size range. During an acoustic and midwater trawl survey of the Aleutian Basin in June-July 1978, 82% of the pollock taken were between 44 and 50 cm fork length, and no fish were found smaller than 36 cm (Nunnallee 1978). Similar size distributions have been observed in other years (Okada 1979).

Pollock prey in this region are better known than are pollock predators. Major food items of pollock in the oceanic region include copepods, euphausiids, and larvaceans (Okada 1979); in addition, myctophids, other mesopelagic fishes, and small squid may be taken. Predators of pollock in this environment are poorly understood, but probably include pinnipeds, toothed whales, and large squid.

Continental Shelf Environment

Community Associations

Pollock are a dominant component of both the middle and outer shelf fish faunas of the eastern Bering Sea continental shelf. The geographic and bathymetric organization of the fish and macroinvertebrate faunas on the shelf shows similarity to, and is apparently largely affected by, an oceanographic system of three principal hydrographic domains (Kinder and Schumacher 1981; Walters and McPhail 1982; Walters 1983).

The characteristic outer continental shelf fauna (Fig. 4), found between approximately the 70 and 260 m isobaths, is dominated by the following species (in order of decreasing relative abundance): pollock; Pacific cod, Gadus macrocephalus; Greenland turbot, Reinhardtius hippoglossoides; flathead sole, Hippoglossoides elassodon; skates, Rajidae; arrowtooth flounder, Atheresthes stomias; eelpouts, Lycodes; and sablefish, Anoplopoma fimbria (Walters and McPhail 1982: Tables A-7, B-9, C-11 and D-7).

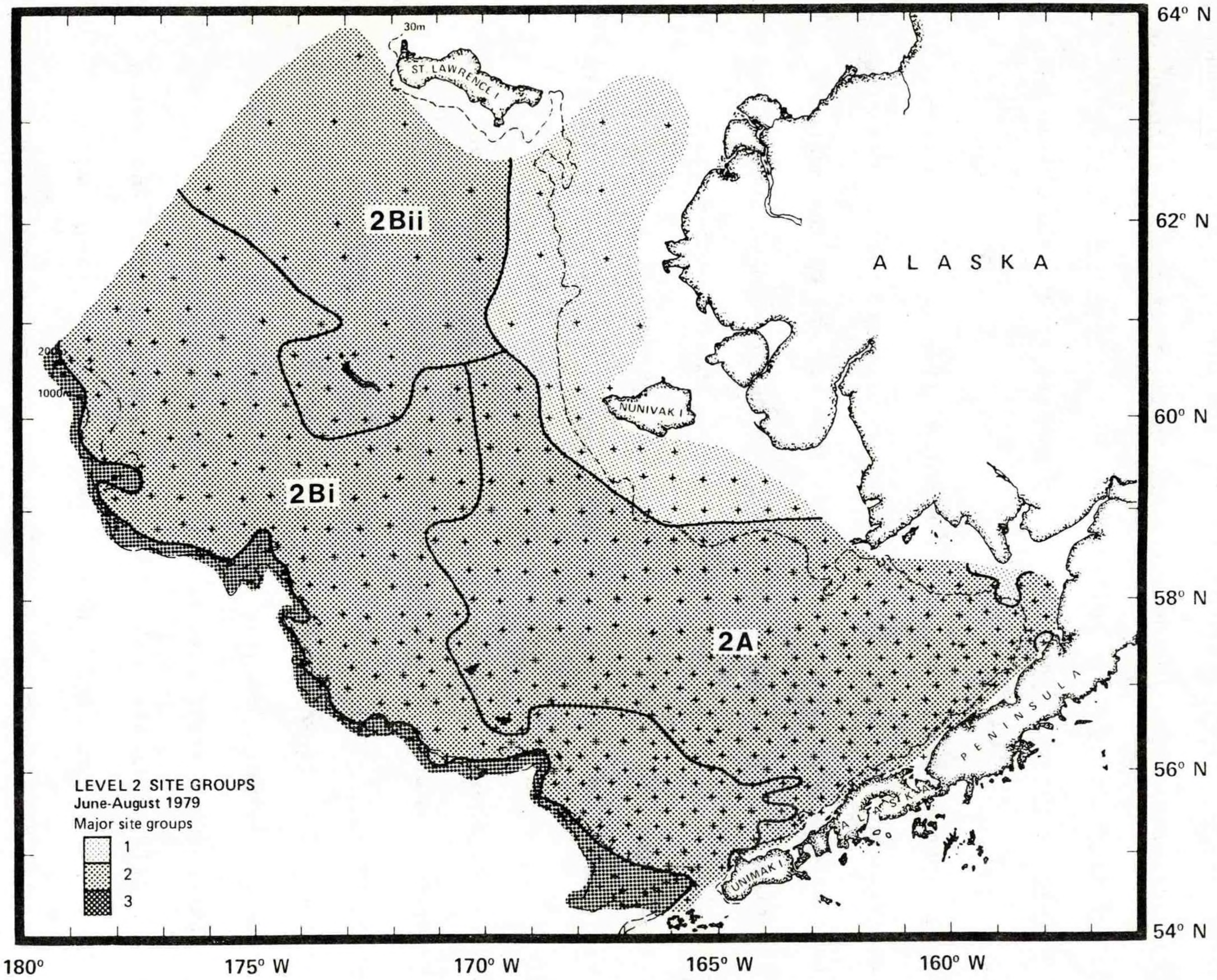

Figure 4.--Example of major geographic assemblages observed for the crab and groundfish faunas of the eastern Bering Sea continental shelf, based upon a 1979 trawl survey (from Walters and McPhail 1982). The five major assemblages shown are: group 1, a northern coast fauna; group 2A, a middle shelf fauna; group 2Bii, a St. Matthew Island (northern) fauna; group 2Bi, an outer shelf fauna; and group 3, a continental slope fauna.

The characteristic middle shelf fauna (demersal and semipelagic), found between the 25 and 100 m isobaths, is dominated by the following species: yellowfin sole, *Limanda aspera*; pollock; Pacific cod; Alaska plaice, *Pleuronectes quadrituberculatus*; rock sole, *Lepidopsetta bilineata*; *Myoxocephalus* spp.; flathead sole; *Hemilepidotus* spp.; wattled eelpout, *Lycodes palearis*; and longhead dab, *Limanda proboscidea* (Walters and McPhail 1982: Tables A-3, B-3, C-3 and D-2).

Biological associations of neritic fishes that live over the eastern shelf are less well known, partly because of the mobile and dynamic characteristics of the various populations. Pollock is probably one of the dominant members of the midwater community because of its widespread distribution and abundance over the outer and middle shelf regions. About 10 other fish species are also important as resident or transient members of the neritic system, either because of their relative abundance or population migrations through different regions.

Five species of Pacific salmon--sockeye salmon, *Oncorhynchus nerka*; chum salmon, *O. keta*; pink salmon, *O. gorbuscha*; chinook salmon, *O. tshawytscha*; and coho salmon, *O. kisutch*--all spend a portion of their juvenile and adult lives as residents of shelf waters (Straty 1981). Because of their high abundance, these species are probably important components of the midwater system during their trans-shelf seaward and spawning migrations.

Nonsalmonid pelagic fishes that are relatively abundant over the Bering Sea shelf include Pacific herring, *Clupea harengus pallasi* (Wespestad and Barton 1981; Wespestad 1978); capelin, *Mallotus villosus*; rainbow smelt, *Osmerus mordax*; and eulachon, *Thaleichthys pacificus* (Macy et al. 1978). Pacific sand lance, *Ammodytes hexapterus*, a benthopelagic species, is also important in some areas. However, these five species are generally restricted to particular areas of the shelf at different times of the year. Herring in the eastern Bering Sea spawn along the Alaska coast between the Yukon and Kuskokwim Rivers in spring, with major spawning grounds occurring in the Togiak Bay area of Bristol Bay, then migrate to a major wintering ground northwest of the Pribilof Islands (Wespestad and Barton 1981). Capelin, rainbow smelt, eulachon, and Pacific sand lance are most abundant in nearshore areas, where their local densities can sometimes be very high; they are also observed in low densities at scattered locations over most of the eastern shelf.

At least one squid species, Berryteuthis magister, is important in the shelf midwater community, although its distribution is largely restricted to the shelf edge (Wilson and Gorham 1982).

Pollock Prey

The major food resources of pollock vary with body size, regional location, and time of year. Juveniles (2-20 cm) feed on zooplankton--primarily copepods, euphausiids, and amphipods (Bailey and Dunn 1979). At larger sizes, fish and other nektonic organisms become increasingly important components of the diet, and cannibalism is common (Fig. 5).

In a study of the stomach contents of 497 juvenile and adult pollock collected during spring and summer 1977, Bailey and Dunn (1979) found that fish constituted 26-29% of the food biomass. The taxonomic composition of the fish fraction, based on a different collection of pollock stomach samples from summer 1974, was found to be 89% pollock by weight; other fish identified were gadids, cottids, hexagrammids, and zoarcids. Dwyer et al. (1983) found major seasonal changes in the contents of 2,857 pollock stomachs examined over a 2-yr period. Euphausiids dominated the diets of small (16-39 cm) and large (40-78 cm) pollock during the spring. During the summer, copepods and euphausiids were most important to small fish, and small pollock was the

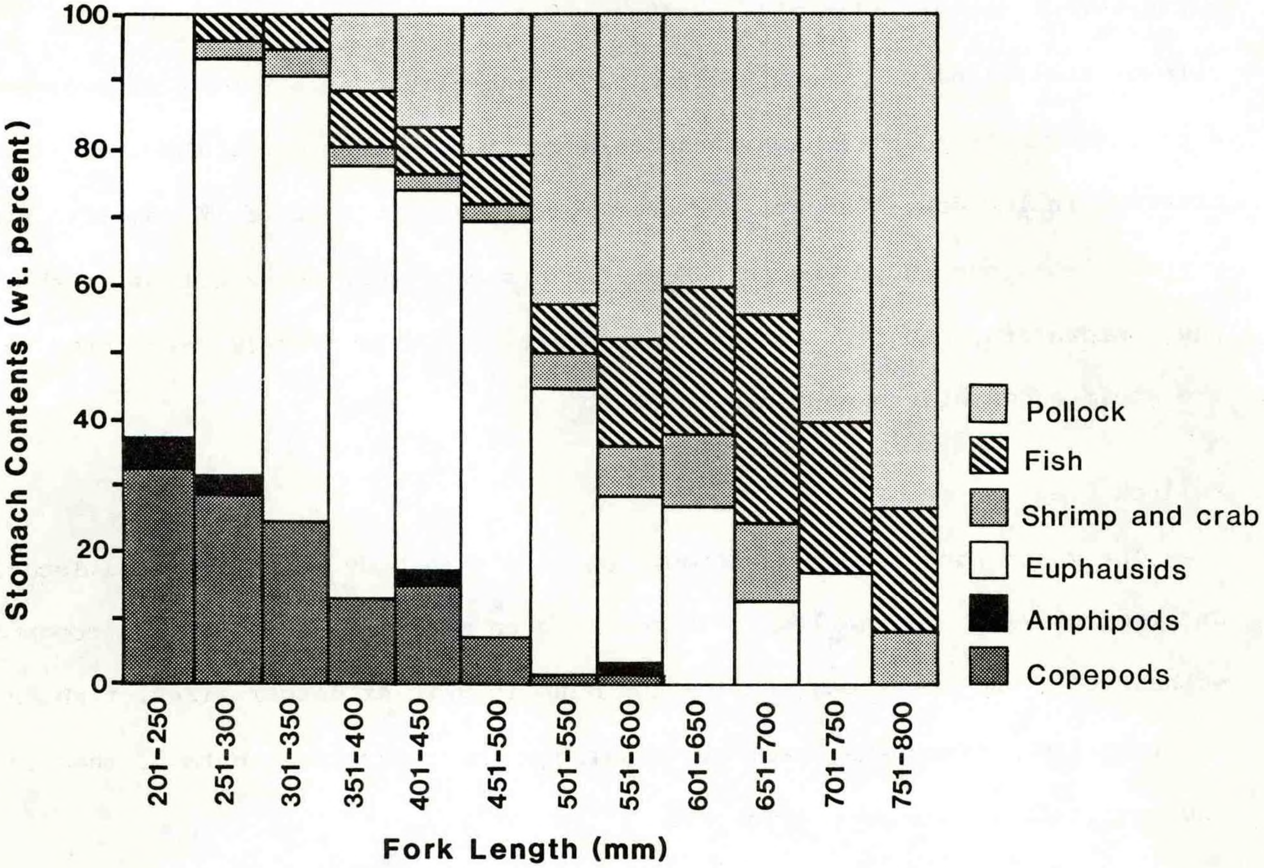

Figure 5.--Changes in composition of pollock prey with size (from Takahashi and Yamaguchi 1972).

major food of large fish. Age-0 pollock was the major food of both small and large pollock during the winter. Although juvenile pollock remained important to large pollock during the winter, small pollock fed on other fish (such as myctophids) during this time.

Other fish and nektonic prey that have been cited include Pacific herring (which represented 6.9% of the food volume of pollock collected from the shelf edge in winter 1978; Wespestad 1978), squid (Mito 1974; Wespestad 1978), and capelin and Pacific sand lance (Feder 1978). In southeastern Alaska, Armstrong and Winslow (1968) observed pollock feeding on young coho, pink, and chum salmon in the size range 30-65 mm. Because pollock dominates the midwater fish community in many areas, it may be an important predator of the osmerids and of the larval and juvenile stages of other fish species that occur in this environment.

Pollock Predators

A wide variety of fishes, seabirds, and marine mammals feed upon the different life history stages of pollock (Fig. 1). In addition to the intraspecific predation of pollock on smaller pollock, which is probably a principal source of pollock mortality, at least 16 other fish predators have been reported (Mito 1974; Nishiyama 1974; Feder 1978; Smith 1981). These include pelagic fishes fishes that feed on pollock in the water column, large-mouthed semipelagic fishes that school and mix with pollock, and large-mouthed benthic fishes that ambush prey or make feeding forays from the bottom.

Following spring spawning, one would expect pollock larvae, postlarvae, and early juveniles to be available to, and actively fed on by large-mouthed planktivores in the midwater fish community. Nishiyama (1974) found that fish larvae formed a significant part of the diet of sockeye salmon during their early summer migrations into Bristol Bay in 1964-69. Principal larvae eaten were pollock, Pacific sand lance, and cottids.

In their first year, juvenile pollock (22-120 mm long) are generally a superabundant prey resource utilized by a large number of species over the entire continental shelf. Mito (1974) described eight fish species that took 0-group pollock as abundant prey items. These included larger pollock; flathead sole; arrowtooth flounder; Pacific cod; spinyhead sculpin, *Dasycottus setiger*; yellow Irish lord, *Hemilepidotus jordani*; thorny sculpin, *Icelus spiniger*; and Atka mackerel, *Pleurogrammus monopterygius*.

Because of their relative abundance (Bakkala et al. 1982), Pacific cod, Greenland turbot, arrowtooth flounder, and Pacific halibut are important predators of pollock in the outer shelf region (Mito 1974). Pacific cod mixes and schools with pollock. Mito (1974) found that shrimp, crab, and pollock accounted for nearly 80% by weight of the food organisms found in Pacific cod, and the fraction represented by pollock increased with length (Dunn 1979). Cod larger than 65 cm fed almost exclusively on pollock. Greenland turbot, arrowtooth flounder, and Pacific halibut are large-mouthed flounders that make feeding attacks up into the water column. Less important predators in the outer shelf region include skates and bigmouth sculpin, *Hemitripterus bolini*.

Other cottids are additional predators of pollock in the middle shelf region, perhaps ambushing pollock from schools near the bottom. *Myoxocephalus* spp. are probably the most important of these because of their large mouth, body size, and high abundance.

Interspecific Competition

Whether or not competition occurs between pollock and other fish species is largely speculative. Although competitive interactions within and between species are generally thought to be as important as predation in population effects, competition has seldom been demonstrated in marine fish systems (Mercer 1982).

Because of their small mouth size, small pollock eat a relatively narrow size range of zooplankton. Co-occurring fishes that overlap in diet with small pollock include osmerids, clupeids, and juvenile salmonids. At present, it is not known whether zooplankton abundance ever becomes sufficiently limited for interspecific competition among these species to play an important role.

Other species may be important competitors of larger pollock. Pollock and Pacific cod overlap in diet and habitat during part of their life histories. When ecologically similar stages of both species occur together, food supplies are probably sufficiently plentiful such that competition may not be important. If food were limiting, however, the two species would probably shift their diets or habitats (e.g., Pacific cod shifting to a more demersal diet or pollock moving higher in the water column or offshore).

Pacific ocean perch, Sebastes alutus, is another potential competitor of pollock. In past years, it has shown high abundance, and may have dominated the fish fauna along the edge of the Bering Sea continental shelf. In general, however, Pacific ocean perch occurs deeper than pollock (at 200-500 m depth) and does not occur pelagically offshore.

ECONOMIC INTERACTIONS

Trawl fisheries in the eastern Bering Sea commonly take most, if not all, of the major species of the outer shelf fauna along with pollock. Alternative target species (or groups) that are important include Pacific cod, yellowfin sole, large-mouthed flatfishes (Greenland turbot and arrowtooth flounder), rockfish, Sebastes spp., and, sometimes, squid (Bakkala et al. 1979). Pacific cod, Atka mackerel, and rockfish are important targets in the Aleutian Islands region.

Other species that are taken in the pollock trawl fishery include sablefish (also taken by foreign and domestic longline fisheries); Pacific herring (also an important resource for inshore domestic sac-roe, roe-on-kelp, and food and bait fisheries (Skrade 1980)); Pacific halibut; salmon; king crab, Paralithodes camtschatica and P. platypus; and snow (Tanner) crab, Chionoecetes bairdi and C. opilio. Because of their socioeconomic importance in domestic fisheries, catches of these last four groups (Pacific halibut, salmon, king crab, and snow crab) are regulated as "prohibited" species that must be returned to the sea.

Seasonal restrictions on trawl fishing in certain closed areas to conserve Pacific halibut, king crab, and snow crab also reduce the fishing mortality of pollock in these areas (Smith et al. 1981). These regulations were established to reduce incidental catches of prohibited species and to minimize gear conflicts.

SUMMARY OF EXISTING KNOWLEDGE

The pollock ecosystem includes a large number of fish and invertebrate species that are ecologically linked to pollock as community associates, prey, predators, or competitors, or economically linked to pollock through the multispecies trawl fisheries (Table 1). Many of these species interact with pollock in a variety of ways and hence may have beneficial or detrimental impacts on pollock at different stages of their life.

Various sources of information are available that provide descriptions of the major species and their biological characteristics. In addition to

Table 1.--Summary of interactions between walleye pollock, other fish, and important invertebrates in the eastern Bering Sea.[a]

Species or group	Biological interactions				
	Community associates	Pollock prey	Pollock predators	Potential competitors	Economic links
Pelagic fauna					
Squid	+	++	+	+	++
Fish larvae		+			
Mesopelagic fishes		+	+	+	
Clupeidae					
Pacific herring	+	++	+[b]	?	++
Salmonidae	+	+		+	++
Sockeye salmon			++		
Osmeridae		+	+[b]	+	
Capelin	+	++			
Eulachon	+	+			
Rainbow smelt	+	+			
Gadidae					
Juvenile gadids		+			
Arctic cod			+	+	
Scorpaenidae					
Juvenile rockfishes		+			
Hexagrammidae					
Atka mackerel			++		++
Benthopelagic fauna					
Gadidae					
Saffron cod			+	+	
Pacific cod	++	?	++	+	++
Scorpaenidae					
Pacific ocean perch			+	+	++
Other rockfishes				+	
Anoplopomatidae					
Sablefish	++		++	+	++

Table 1 (Continued)

Species or group	Biological interactions				Economic links
	Community associates	Pollock prey	Pollock predators	Potential competitors	
Trichodontidae					
Pacific sandfish			+	+	
Ammodytidae					
Pacific sandlance	+	++	+[b]	+	
Benthic fauna					
Crab					
Crab larvae		+			
King crab					++
Snow (Tanner) crab					++
Shrimp		+			
Rajidae (Skates)	++		++		
Zoarcidae	++	++			
Lycodes palearis	++				
Cottidae					
Larval cottids		++			
Dasycottus setiger			++		
Gymnocanthus spp.			+	+	
Hemilepidotus spp.	++		++	+	
Hemitripterus spp.			++	+	
Icelus spp.			++	+	
Myoxocephalus spp.	++		++	+	
Pleuronectidae					
Juvenile pleuronectids		+			
Arrowtooth flounder	++		++	+	++
Flathead sole	++		++		
Pacific halibut	++		++	+	++
Rock sole	++				
Yellowfin sole	++				++
Longhead dab	++				
Alaska plaice	++				
Greenland turbot	++		++	+	++

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[a] Symbols: ++ = observed relationship; + = inferred relationship; ? = possible relationship.

[b] Predator of pollock eggs and larvae.

the general biological literature on each species, descriptions of the major populations, their abundance, and population dynamics are available from the following sources: bottom trawl surveys (Bakkala et al. 1982; Smith and Walters 1982); analytic models (Wespestad 1982; Wespestad et al. 1982); status of stock evaluations (Bakkala and Low 1983); and ecosystem simulation models (Dunn 1979; Laevastu and Favorite 1981; Laevastu and Larkins 1981).

MODEL OF POLLOCK INTERACTIONS WITH OTHER FISHES AND SQUID

A conceptual model of the relationships between other fish and pollock must encompass the ecological groups discussed above. Three major functional groups, in addition to the pollock itself, that must be included in such a model are pollock prey, pollock predators, and potential pollock competitors (Fig. 6). Each of these functional groups includes species with sizes that may range over two orders of magnitude. Consequently, the relationships of each group with pollock must include consideration of the sizes of species within the group to the entire size range of pollock. Further, the component species must be considered in terms of their foraging behaviors and position in the water column. Several of the species play multiple roles as prey, predator, or potential competitor at different stages in their life history and therefore may be members of more than one functional group.

We have classified species that potentially interact with pollock into four general categories based on a combination of size, habitat, and behavior: small pelagics, large pelagics, benthopelagics, and benthic fishes. The small pelagics group includes species or life history stages that are generally less than 25 cm in length: osmerids, Pacific herring, Pacific sand lance, mesopelagic fishes (in the oceanic domain), and the juvenile stages of salmon, rockfishes, and sablefish. Small pelagic species can be prey, predators, or

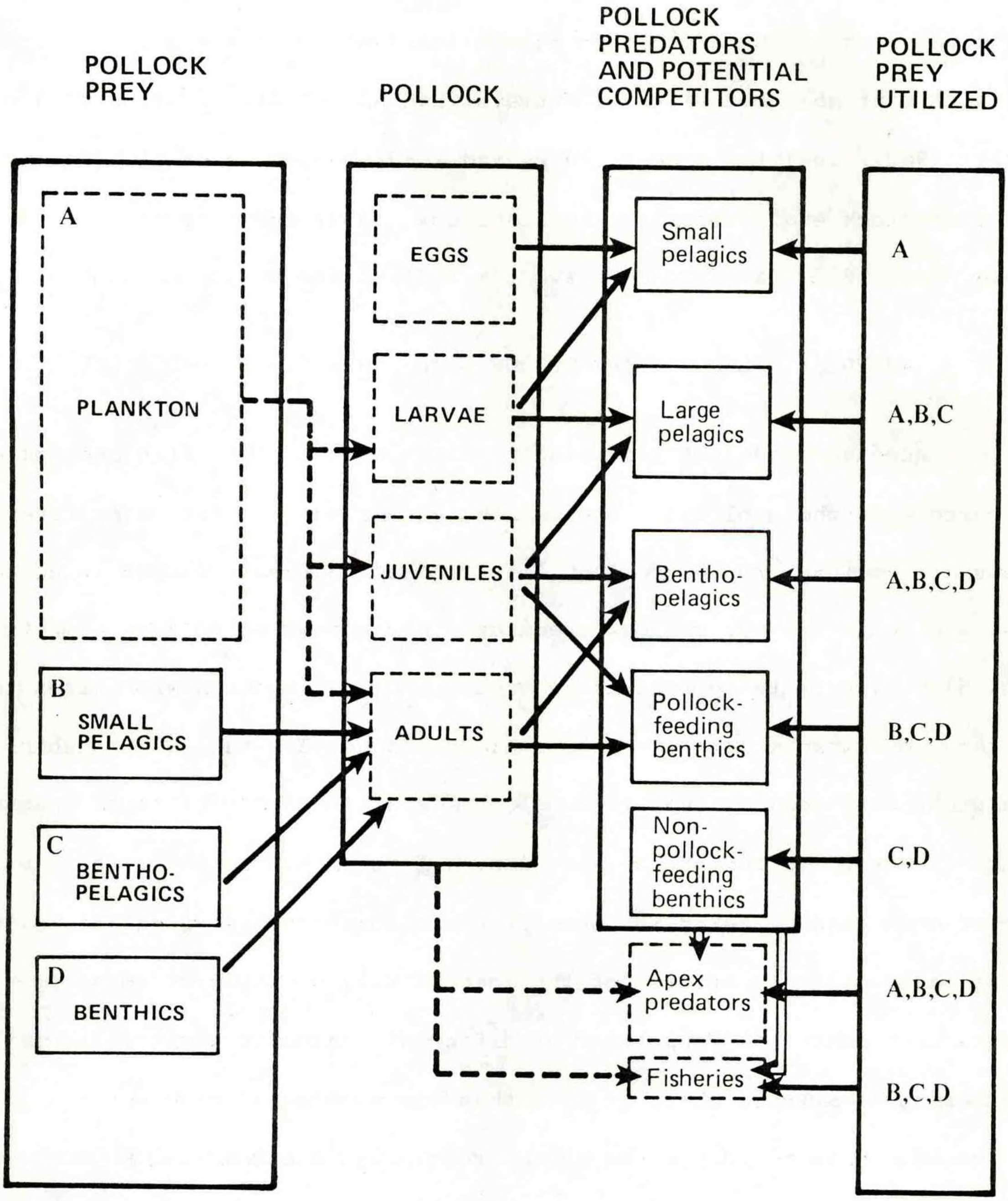

Figure 6.--Conceptual model of predator/prey relationships in the pollock ecosystem. Arrows show the direction of carbon flows. Boxes enclosed with dotted lines include components of the ecosystem that are not considered in this paper. Letters in the fourth column refer to box labels in the first column.

potential competitors. For example, small pelagic species that eat planktonic prey feed on the egg and larval stages of pollock. At the same time, they may be competing with pollock for planktonic prey and may serve as prey for adult pollock.

The large pelagics group, comprised of species generally larger than 25 cm, includes salmon, rockfishes, and squid. These species act as predators on larval and juvenile pollock and may be competitors for planktonic, small pelagic, and benthopelagic prey.

The benthopelagics group includes fishes such as Pacific cod and sablefish that are important in several different size classes. The smaller fish are available as prey for adult pollock and a number of the other fishes. They may also be competitors with juvenile pollock. The larger fish act as predators on juvenile and adult pollock as well as potential competitors.

The benthic fishes group includes many of the cottids and large-mouthed flounders which are also important over a large size range. The smaller sizes of these species may be prey for pollock, while the larger fish act as predators or potential competitors.

Although the primary concern here is with the fishes and squid that interact with pollock, other biological and fishery components are also intimately related to this system. For instance, the planktonic prey items provide organic matter and energy not only to pollock but to many potential competitors as well (Fig. 6). Apex predators and fisheries act as both predators and potential competitors. In terms of pollock prey utilized, the apex predators are similar to the benthopelagic fishes as potential competitors and the trawl fisheries are similar to the benthic fishes.

At this point, we are able to identify the major elements of the model and to describe the feeding relationships. Values of the material and energy fluxes, however, are largely unknown; hence, the extent to which other species compete with pollock is also unknown. The amounts of removals of pollock are certainly large, particularly by the apex predators and fisheries. Similarly, rates of food ingestion by pollock must necessarily be large due to the large population biomass. Before these fluxes can be quantified it is important to determine what gaps exist in the knowledge of the ecological interactions of pollock with other species.

INFORMATION GAPS

Information on species related ecologically to walleye pollock is often limited or lacking. For many of the species, little is known of their population sizes and distribution, reproduction, birth and death rates, feeding biology, energy partitioning and growth, competition, and their responses to oceanographic conditions.

Population Size and Distribution

A large data base exists on the distribution, abundance, and other biological attributes of many fish and invertebrate species in the Bering Sea (Mintel and Smith 1981); nevertheless, data gaps still exist. For instance, demersal fish populations in the Aleutian Islands region are not well known. Among pelagic fishes, information exists for only a few of the small-sized species in each region, but it exists for large-sized species in all regions except the middle shelf. Because most data are limited to summer (particularly in the Aleutians) and spring seasons, little is known about the seasonal migrations of many species. Estimates of population size for any species are limited by the sampling methods and data. Most of the biological data, such as size, age, and sex ratio, exist for commercial species only.

Age determination data vary in availability and quality for these species and are virtually nonexistent for other species.

Reproduction

Basic data on fecundity, spawning areas and times, and maturation, are generally lacking for most species (Hirschberger and Smith 1983). Among species for which such data exist, regional coverage is generally poor, particularly for small pelagic fishes (excluding Pacific herring), cottids, and small flounders.

Birth and Mortality Rates

For the purposes of a fishery, the birth rate of a species is equivalent to the number of fertilized eggs produced minus prerecruit mortality. In general, the biotic and abiotic causes of mortality on eggs, larvae, and juveniles are not known for most species and critical life history stages have not been identified. In particular, little is known about the importance of predation on planktonic life history stages. Because of this lack of information on prerecruit mortality, the relationship of recruitment to spawning stock size is poorly understood.

Knowledge of postrecruit mortality occurring within the other fish and squid system is also poor. Age- and sex-specific mortalities related to fishing, predation, disease, starvation, and abiotic influences are virtually unknown. The limitations of methods used to estimate population abundance also limit our abilities to make good mortality estimates.

Feeding Biology

Information on the feeding habits of most species is limited to diet composition and little is known about feeding rates and amounts of energy exchange. Although the feeding habits of some of the major demersal species have been described, the diets of coastal benthic species and all pelagic species are poorly understood. Seasonal coverage of feeding habits is generally poor because most sampling occurs during the spring and summer. Diel coverage is also limited due to the long day lengths in the Bering Sea during the spring and summer. Poor information on the factors affecting prey availability, food selection, and preference prevents the calculation of food selectivity coefficients. The functional relationships of the diet and feeding rates of the species to abiotic and biotic factors such as temperature, prey densities, and size are also poorly understood.

Energy Partitioning and Growth

Information on the assimilation and partitioning of energy found in food ingested by the fishes is generally limited or lacking. Little is known concerning assimilation efficiencies, respiration rates, the relationship between metabolic rates and ammonia excretion, evacuation rates, and the amounts of energy available for growth and reproduction.

Competition

Field and experimental studies on competition among the species have not been conducted; therefore, any limiting factors affecting competition are not known. Only limited comparisons of dietary similarity exist and competition coefficients have not been determined.

Responses to Oceanographic Conditions

The responses of many fishes to physical oceanographic conditions is poorly understood. For some species limited knowledge exists on the effects of climate on population distribution, migrations, recruitment, and mortalities. However, knowledge of the effects of environmental conditions on feeding and predator-prey relationships is generally lacking.

RECOMMENDATIONS

The conceptual model of the "other fish and squid" component of the pollock ecosystem provides a framework for identifying information gaps so that further studies can be directed toward reaching a better understanding of the relationships of these species to pollock in the Bering Sea. The first step in reaching this goal is to quantify the feeding relationships between the various functional groups and pollock (Fig. 6). First estimates of the rates of organic and energy transfers may be obtained by a detailed reexamination of existing data and literature. Unless these values are based on complete and high quality studies, further studies will be necessary to provide better estimates of the rates of interaction between each group. The exercise of assigning estimated values to each exchange will also identify which species are likely to be most important to pollock and hence the best choices for further research. We expect this exercise will indicate a need for more feeding studies to better describe the fundamental predator-prey relationships between pollock and the other species. In addition, it will probably be necessary to determine better estimates of population abundance, distribution, and dynamics for these species (particularly for species which are not economically important in a direct sense). Perhaps most obvious and critical is the need for more knowledge on how pollock and the other species respond to variations in oceanographic conditions and how these various responses interact.

CONCLUSIONS

1. The walleye pollock occupies a keystone position in the Bering Sea ecosystem because of its wide distribution and great abundance, and because of its role as prey, predator, and potential competitor to many other fish species.

2. Most fish species in the Bering Sea that are trophically related to pollock interact with pollock in different ways as they grow, often serving as prey when small, potential competitors when larger, and predators when fully grown.

3. The species that are most similar to pollock ecologically are pelagic and semipelagic species which grow to a relatively large size, such as salmonids, other gadids, and some rockfishes.

4. Due to the large number of potential interactions between pollock and the other fishes, many gaps exist in the knowledge of the ecological relationships between pollock and the other fish and squid in the Bering Sea environment.

5. Before the "other fish and squid" model can be fully incorporated into a larger model of the pollock ecosystem, these gaps should be ranked according to their importance and eliminated by conducting studies specifically designed to obtain the missing information.

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APEX PREDATORS IN THE WALLEYE POLLOCK ECOSYSTEM IN THE EASTERN BERING SEA AND THE ALEUTIAN ISLANDS REGIONS

by

Hiroshi Kajimura[1] and Charles W. Fowler[1]

ABSTRACT

The eastern Bering Sea is an area of high biological productivity as indicated by the abundant populations of invertebrates, fishes, marine avifauna, and marine mammals. Twenty-six species of marine mammals including the polar bear are known to seasonally inhabit the eastern Bering Sea-Aleutian Island area. Of these, 13 are known to feed on walleye pollock, Theragra chalcogramma. McAlister (1981) suggests that marine mammals consume approximately 6% per year of the standing stock of all finfish in this area.

The fish fauna of the Bering Sea includes approximately 300 species which feed primarily on invertebrates and other fish. Approximately 64 species of seabirds are present in the Bering Sea, of which the Procellariidae (fulmars and shearwaters), the Laridae (gulls, kittiwakes, and terns), and the Alcidae (murres, puffins, and auklets) are of ecological importance because of their large numbers and/or biomass. Most marine birds and baleen whales forage and depend on invertebrates; however, some marine birds and baleen whales are polyphagous, foraging on both invertebrates and fish. Conversely, most pinnipeds depend on pollock and other fishes and squids for their sustenance.

Walleye pollock in the eastern Bering Sea is the most important demersal fish in terms of biomass and commercial landings. This species apparently feeds on a broad variety of prey during its life and, in turn, is a major

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food resource for other fishes, marine birds, marine mammals, and man. With the exception of man's removal of pollock through the commercial fishery and the research conducted on the northern fur seal, Callorhinus ursinus, the interactions on predator-prey relationships among inhabitants of the Bering Sea ecosystem are poorly understood. In many cases only small numbers of marine mammals have been collected and extrapolations from these limited data form the basis for characterizing their trophic relationships. To better understand the trophic relationships within the Bering Sea ecosystem, in-depth studies on all marine resources, not just the commercially important species, need to be done.

BACKGROUND REVIEW

Direct Predation on Walleye Pollock

In this section we identify predators which feed directly on walleye pollock, *Theragra chalcogramma*, and give some indication as to the relative importance of pollock in their diets. Predation on pollock in the eastern Bering Sea involves man, marine mammals, seabirds, fishes, and probably squids (Fig. 1). During some part of their life cycle, all predatory species feed on alternative prey such as other nekton, plankton, benthos, and fishes. Marine mammals and seabirds generally feed on zooplankton, fishes, and squids. Adult pollock and other fish feed on immature pollock. The most important predators on pollock are probably man, through the commercial fishery, and the northern fur seal, *Callorhinus ursinus*.

Studies conducted in the Bering Sea during 1958-74 indicate that pollock is one of the principal prey species of fur seals while they are in the Bering Sea. Predation by most other marine mammals is not as well understood at present because there has been little research conducted regarding their trophic relationships. Much of the information available is based only on small samples from examination of stomach contents primarily from incidental take, subsistence harvest, strandings, and from meager research efforts. The trophic relationships and population trends of seabirds are beginning to be understood (Hunt et al. 1981a, b, c; Gould et al. 1982).

Twenty-six species of marine mammals including the polar bear, *Ursus maritimus*, are known to seasonally inhabit the eastern Bering Sea-Aleutian Island area (Table 1). Of these only 13 species of marine mammals, 7 pinnipeds, and 6 cetaceans, are known to feed on pollock. Beside the northern fur seal, other pinnipeds known to feed on pollock include the northern sea

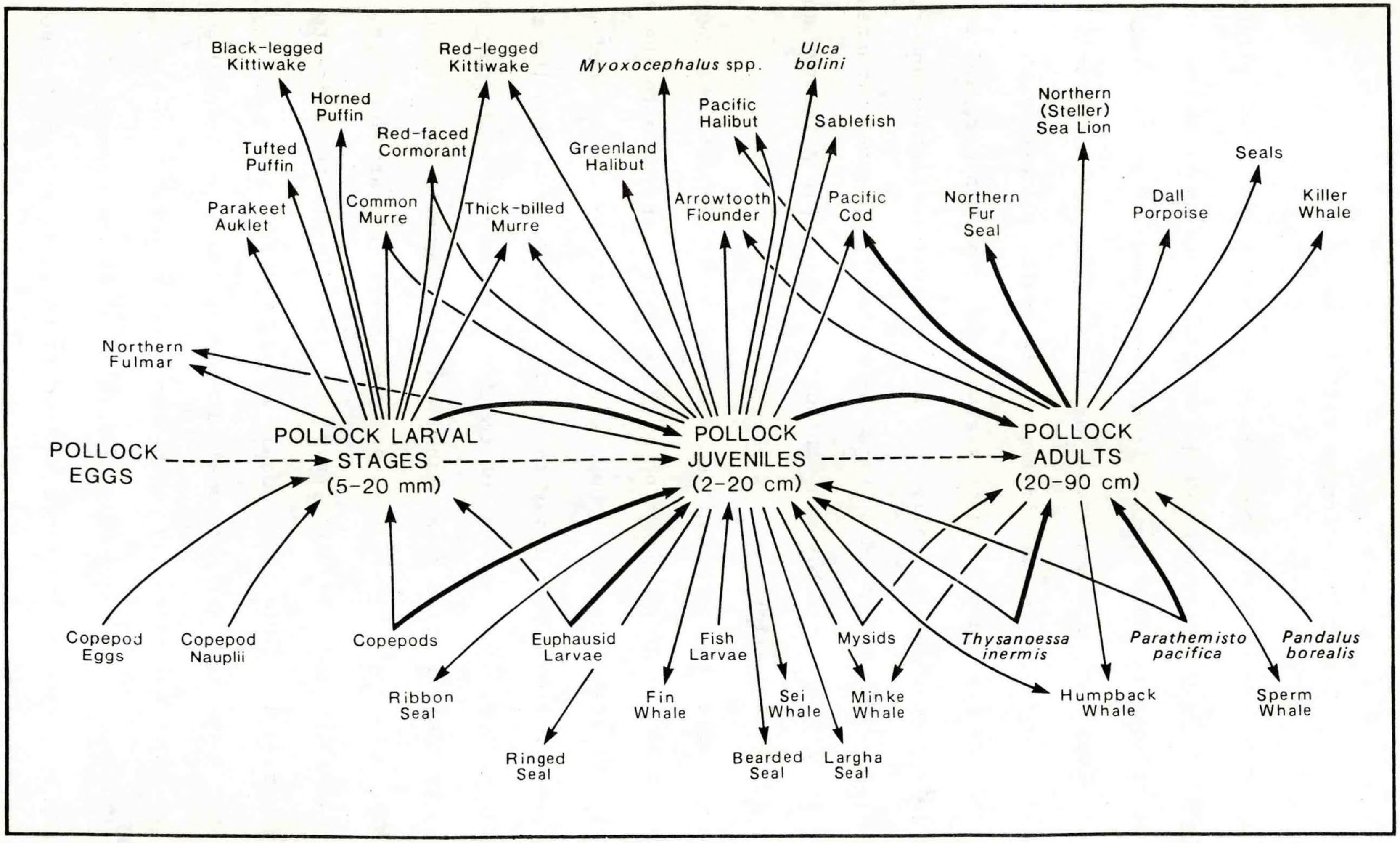

Figure 1.--Apparent food web based on walleye pollock in the eastern Bering Sea (modified from Smith 1981).

Table 1.--Marine mammal population estimates and consumption of walleye pollock in the eastern Bering Sea-Aleutian Islands area (from McAlister 1981).

Common name	Scientific name	Population estimates		Food consumption (10^3 m ton)	Fish consumption (10^3 m ton)	Pollock consumption (percent)
		Summer	Winter			
Northern sea lion	*Eumetopias jubatus*	95,000	57,000	470	456	60
Northern fur seal	*Callorhinus ursinus*	556,000	56,000	615	476	35
Pacific walrus	*Odobenus rosmarus*	10,000	200,000	2044	0	-
Spotted or largha seal	*Phoca largha*	15,000	150,000	288	259	5
Harbor seal	*Phoca vitulina richardsi*	55,000	55,000	130	88	25
Ringed seal	*Phoca hispida*	small	600,000	686	569	-
Ribbon seal	*Phoca fasciata*	50,000	50,000	131	103	24
Bearded seal	*Erignathus barbatus*	small	180,000	666	113	-
Polar bear	*Ursus maritimus*	-	small[a]	-	-	-
Sea otter	*Enhydra lutris*	(55,100 to 73,700)[a]		-	-	-
Gray whale	*Eschrichtius robustus*	8,000	-	315	-	-
Minke whale	*Balaenoptera acutorostrata*	3,000	-	58	39	-
Sei whale	*Balaenoptera borealis*	(8,600 to 21,000)[a]		-	-	-
Fin whale	*Balaenoptera physalus*	1,000	-	83	8	-
Blue whale	*Balaenoptera musculus*	(1,400 to 1,900)[a]		-	-	-
Humpback whale	*Megaptera novaeangliae*	200	-	12	3	-
Right whale	*Balaena glacialis*	(100 to 200)[a]		-	-	-
Bowhead whale	*Balaena mysticetus*	100	1,000	53	-	-
Killer whale	*Orcinus orca*	1,000	500	21	6	-
Harbor porpoise	*Phocoena phocoena*	1,000	500	2	2	-
Dall's porpoise	*Phocoenoides dallii*	25,000	10,000	87	8	-
Beluga or white whale	*Delphinapterus leucas*	5,000	16,000	150	74	-
Sperm whale	*Physeter macrocephalus*	10,000	-	795	80	-
Baird's beaked whale	*Berardius bairdii*	1,000	-	37	3	-
Cuvier's beaked whale	*Ziphius cavirostris*	(unknown)		-	-	-
Bering Sea beaked whale	*Mesoplodon stejnegeri*	(unknown)		-	-	-

[a] From Lowry et al. (1982).

lion, Eumetopias jubatus; harbor seal, Phoca vitulina richardsi; ribbon seal, P. fasciata; and to a minor extent the largha (spotted) seal, P. largha, ringed seal, P. hispida, and bearded seal, Erignathus barbatos (Table 2).

Among cetaceans, the fin whale, Balaenoptera physalus, a baleen whale, may consume the largest amount of pollock in the eastern Bering Sea. Other cetaceans that are known to feed to some extent on pollock include minke whale, Balaenoptera acutorostrata; sei whale, B. borealis; humpback whale, Megaptera novaeangliae; and Dall's porpoise, Phocoenoides dalli (Table 2). There are no records of sperm whale, Physeter macrocephalus, and the killer whale, Orcinus orca, feeding on pollock but these two species are capable of consuming all sizes of pollock.

Approximately nine species of seabirds are known to feed on pollock and of these, seven species rely extensively on pollock as one of the principal foods for their subsistence. These are the northern fulmar, Fulmarus glacialis; black-legged kittiwake, Rissa tridactyla; red-legged kittiwake, R. brevirostris; common murre, Uria aalge; thick-billed murre, U. lomvia; horned puffin, Fratercula corniculata; and the tufted puffin, Lunda cirrhata (Table 3).

Commercial Fisheries

Walleye pollock is the most important demersal fish population in the eastern Bering Sea in terms of biomass and landings. Its biomass from a 1975 survey was estimated at 2.4 million metric tons (t) or 41% of the total fauna available to the trawl gear (Pereyra et al. 1976). Information concerning man as predator is given in Table 4 to show removal of walleye pollock by the commercial fishery. The estimated population biomass of pollock is shown in Table 5.

Table 2.--Relative importance of walleye pollock in the diet of pinnipeds and cetaceans in the eastern Bering Sea.

Predators	Walleye pollock	Fish and/or squid	Remarks
Pinnipeds			
Northern sea lion	major	major	Capable of consuming all sizes
Northern fur seal	major	major	Capable of consuming all sizes
Largha seal	minor	major	Consume principally juveniles, <20 cm length
Harbor seal	major	major	Capable of consuming all sizes
Ribbon seal	major	major	Consume principally juveniles, <20 cm length
Ringed seal	minor	major	Consume principally juveniles, <20 cm length
Bearded seal	minor	major	Consume principally juveniles, <20 cm length
Cetaceans			
Minke whale	minor	major	Probably <30 cm length
Sei whale	minor	major	Probably <30 cm length
Fin whale	major	major	<30 cm length
Humpback whale	minor	major	30 to 40 cm length
Dall's porpoise	minor	major	Probably <40 cm length

Table 3.--Relative importance of walleye pollock in the diet of seabirds in the eastern Bering Sea, 1975-78 (from Hunt et al. 1981a).

Common name	Scientific name	Percent occurrence	Percent volume	Percent number	N
Northern Fulmar	*Fulmarus glacialis*	10.0	60.6	11.8	10
Red-faced Cormorant	*Phalacrocorax urile*	6.5	3.2	2.2	169
Black-legged Kittiwake	*Rissa tridactyla*	38.2	45.5	10.2	605
Red-legged Kittiwake	*Rissa brevirostris*	18.6	23.8	15.4	376
Common Murre	*Uria aalge*	39.3	56.2	21.2	117
Thick-billed Murre	*Uria lomvia*	40.3	39.6	18.4	233
Parakeet Auklet	*Cyclorrhynchus psittacula*	9.1	4.5	3.6	55
Least Auklet	*Aethia cristatella*	0.4	0.3	0.0	258
Horned Puffin	*Fratercula corniculata*	30.8	8.5	25.9	39
Tufted Puffin	*Lunda cirrhata*	60.9	40.7	45.9	23

Table 4.--Summary of annual catch (metric tons) of walleye pollock from the eastern Bering Sea by trawl by trawl fisheries, 1964 to 1979[a] (from Smith 1981).

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

[a] Bakkala, R., L. Low, and V. Wespestad. 1979. Condition of groundfish resources in the Bering Sea and Aleutian area. Unpubl. manuscr., 107 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[b] Preliminary estimates.

[c] Foreign fishing allocations (Pileggi and Thompson 1979).

Table 5.--Summary of estimates of absolute population size for eastern Bering Sea walleye pollock (from Smith 1981).

Source	Region and time period[a]	Method[b]	Estimated population (X 10^6 t)
Based upon research survey data			
Pereyra et al. 1976[c]	Eastern Bering Sea shelf, Unimak Pass to 61°N (August-October 1975)	1	2.426
Bakkala and Smith 1978[d]	Eastern Bering Sea shelf, Unimak Pass to 59°N (April-June 1976)	1	0.679
Okada 1978[e]; Nunnallee 1978[f]	Aleutian Basin (June-July 1978)	1	0.840
Based upon commercial fisheries data			
Chang 1974	Eastern Bering Sea shelf, INPFC areas 1 and 2 (1969-70)	1	2.3-2.6
Chang 1974	Eastern Bering Sea shelf, INPFC areas 1 and 2 (1970)	2	2.3-2.4
Low 1974	Eastern Bering Sea, primarily INPFC areas 1 and 2 (1964-71)	1	3.45-5.83
Based upon model estimates			
Laevastu and Favorite 1977[g]	Eastern Bering Sea shelf	3	8.235

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

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

[c] Pereyra, W. T., J. E. Reeves, and R. G. Bakkala.
1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Processed Rep., 619 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[d] Bakkala, R. G., and G. B. Smith.
1978. Demersal fish resources of the eastern Bering Sea; spring 1976. Processed Rep., 234 p. plus 534 p. append. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[e] Okada, K.
1978. Preliminary report of acoustic survey and mid-water trawl on pollock stock of the Aleutian Basin and adjacent waters in summer of 1978. Unpubl. manuscr., 13 p. In Japanese with English summary. Jpn. Fish. Agency., 2-1, Kasumigaseki, Chiyoda-Ku, Tokyo, Jpn.

[f] Nunnallee, E. P.
1978. Report on observations aboard the Japanese research vessel Tomi Maru 52 during a Bering Sea (Aleutian Basin) pollock survey conducted in June-July 1978. Unpubl. manuscr., 31 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[g] Laevastu, T., and F. Favorite.
1977. Preliminary report on dynamical numerical marine ecosystem model (DYNUMES II) for eastern Bering Sea. Processed Rep., 81 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd E., Seattle, WA 98112.

Relative Importance of Walleye Pollock in the Diet of Marine Mammals

Northern fur seal -- The most extensive information available concerning marine mammal feeding on pollock is that of the northern fur seal. Even in one of the earliest studies of feeding habits conducted on the northern fur seal, it was found that pollock was one of the principal forage species (Alexander 1896). Recent studies (Kajimura in press; Perez and Bigg in press) conducted on fur seals show that these animals feed on a variety of prey and that smaller schooling fishes are usually the principal forage species over the continental shelf region and oceanic squids are important seaward of the continental slope and in deep water areas. Evidence suggests that fur seals are opportunistic feeders preying on the most available species throughout their range (Kajimura in press). One must keep in mind that the location of fur seal collection generally influences the importance of different prey species as their principal forage food. For example, when the area of operation during ocean research was limited to 100 miles (1973) and 35 miles (1974) around the Pribilof Islands, pollock (and unidentified gadids which were most likely pollock) was the principal forage species of fur seals contributing 82 and 86% of the total stomach content volume for these 2 yr. In comparison, capelin, Mallotus villosus, was the principal forage species when samples were primarily taken near the Aleutian Islands in 1962 and 1963 (Fiscus et al. 1964, 1965).

The size of pollock consumed by fur seals in the Bering Sea varied according to depth of water in which seals were collected. For example, a fur seal collected between St. Paul Island and St. George Island (depth 40 fathoms) in 1973 had eaten 46 pollock of 12-17 cm length; another seal taken southeast of St. George Island (depth 100 fathoms) had foraged on 11 walleye pollock, two of which were whole specimens of 37 and 39 cm length while the remaining 9 pollock appeared to be slightly smaller in size judging from the bodies (headless). Another seal taken relatively close to the shelf edge southwest of St. George Island had consumed a pollock in excess of 40 cm based on the 36 cm length of the vertebral column (less head).

The relative importance of pollock to the fur seal diet during the breeding season is approximately 40% (Perez and Bigg 1983). Perez and Mooney (1983) estimated that pollock contributes nearly one-half of the total energy intake of adult female fur seals during July-September. They also estimated that lactating females' consumption rate is nearly Twice that of nonlactating animals to satisfy requirements for milk production. The monthly occurrence of pollock in fur seal stomachs is shown in Figures 2, 3 and 4 and for months combined in Figure 5.

Northern sea lion -- Information on the feeding habits of northern sea lions in the Bering Sea-Aleutian Islands area is minimal. In 12 sea lion stomachs examined by Wilke and Kenyon (1952) and Fiscus and Baines (1966), pollock was not among the principal prey eaten. Lowry et al. (1982) reported that based on stomachs of four sea lions collected near the Pribilof Islands in March 1976 all had fed principally on pollock (97% stomach content volume). The mean size of pollock was 46.9 cm (range 18.4-61.4 cm) in length based on otolith sizes (Frost and Lowry, Alaska Department of Fish and Game, Fairbanks, AK 99701. Unpubl. data). Loughlin (National Marine Mammal Laboratory (NMML), Seattle, WA 98115. Pers. commun.) indicated that 6 of 10 sea lions collected near the Aleutian Islands during 1981-82 had fed on juvenile and adult pollock. Until more samples are collected from the Bering Sea-Aleutian Islands area, the feeding habits of this animal are, at best, speculative. McAlister (1981) estimated that 60% of the forage food of the northern sea lion consists of pollock (Table 1).

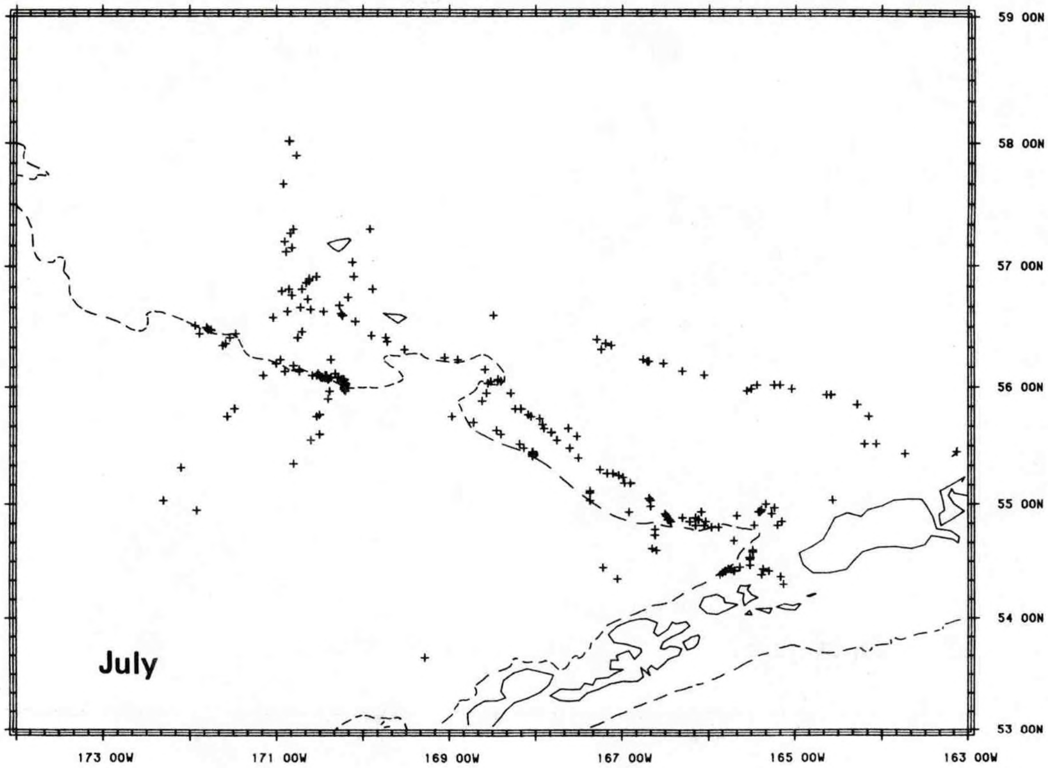

Figure 2.--The occurrence of walleye pollock in stomachs of fur seals during July, 1958-74. The 200 m depth contour is shown.

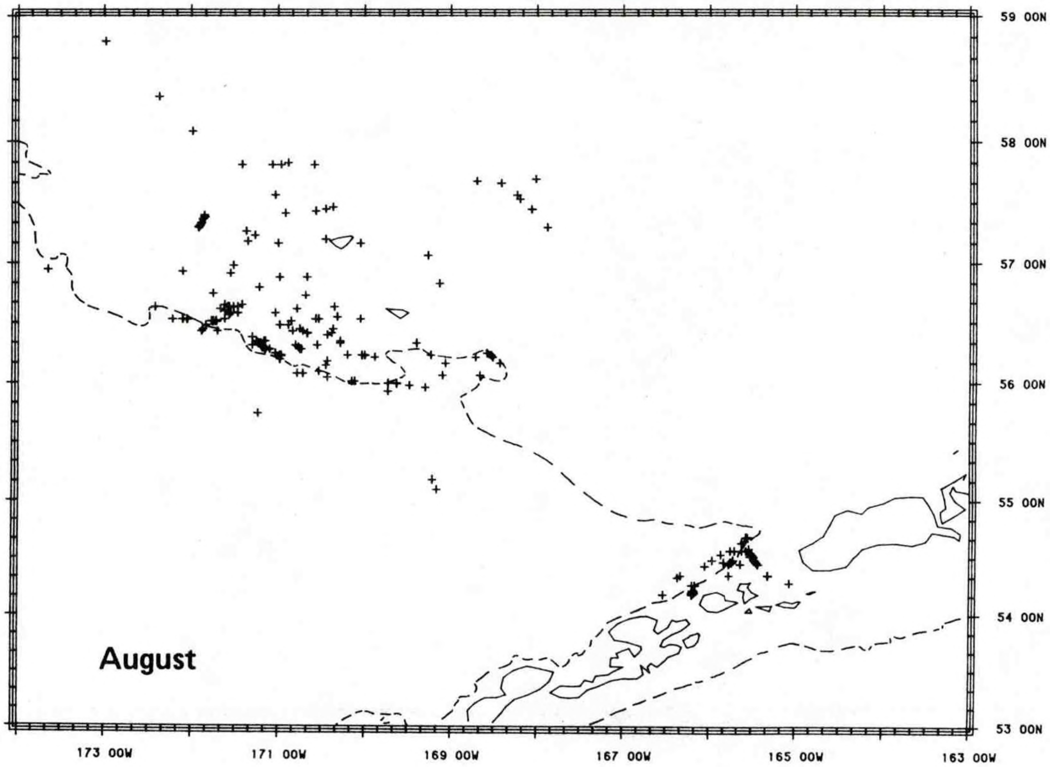

Figure 3.--The occurrence of walleye pollock in stomachs of fur seals during August, 1958-74. The 200 m depth contour is shown.

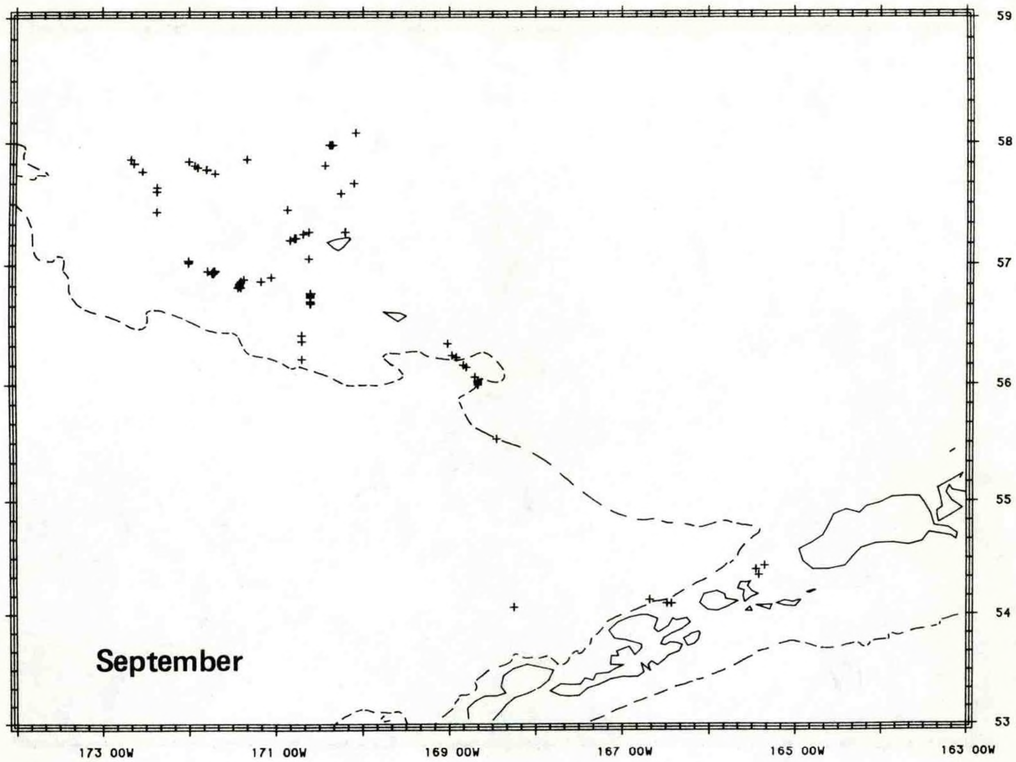

Figure 4.--The occurrence of walleye pollock in stomachs of fur seals during September, 1958-74. The 200 m depth contour is shown.

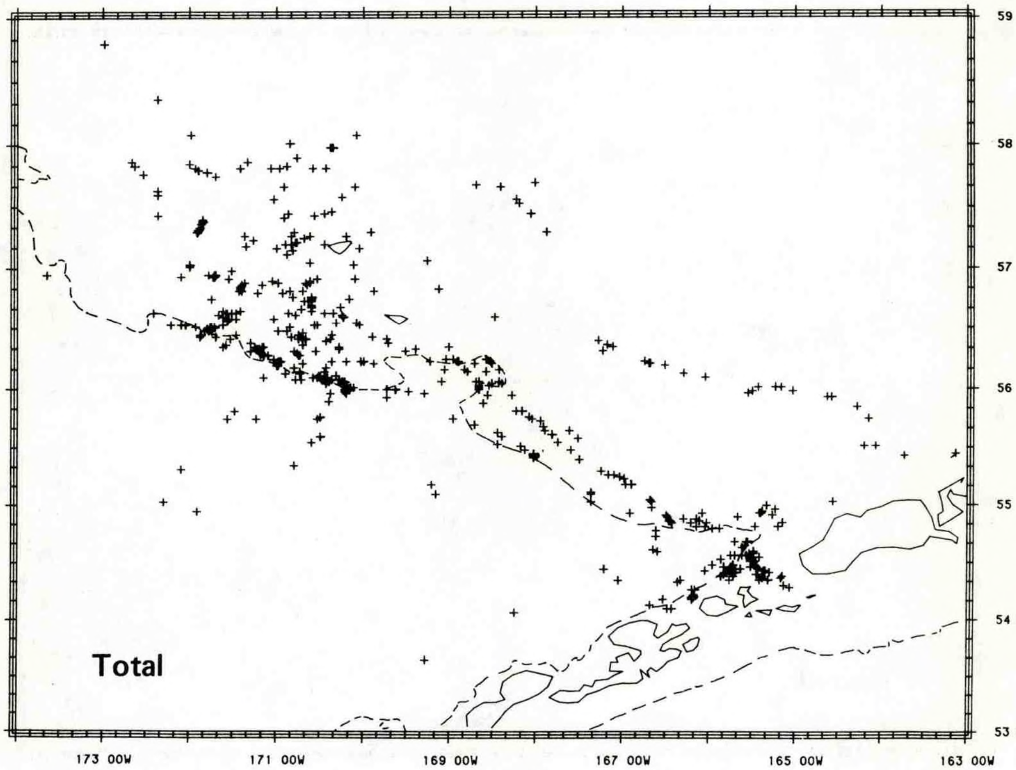

Figure 5.--The occurrence of walleye pollock in stomachs of fur seals during July, August, and September, 1958-74. The 200 m depth contour is shown.

Harbor seal -- Very little information is available on the food of harbor seals in the Bering Sea-Aleutian Island area. Wilke (1957) reported on seven harbor seals taken from Amchitka Island with only one occurrence of pollock in the stomach. Pollock was not found in the stomachs of seven harbor seals taken in the Bering Sea during pelagic fur seal research (four seals from Amak Island; two seals from Unalaska Island; and one seal from the Pribilof Islands) (unpubl. data from NMML files). Lowry et al. (1979) reported pollock in stomachs of three harbor seals taken from Unalaska Island. Lowry and Frost (1981) reported the stomach contents of 15 harbor seals collected in 1979 at Otter Island (Pribilof Islands). Pollock comprised 44% by number of the fishes in eight stomachs containing food. Lowry et al. (1982) reported on the stomach contents of 30 harbor seals taken October 1981 from five different areas of southeastern Bering Sea. Pollock ranked second, third, and fourth among the fishes consumed. Based on otolith sizes, pollock consumed by harbor seals in the Bering Sea averaged 24.5 cm long (range 8.2-56.3 cm: Frost and Lowry, unpubl. data). McAlister (1981) estimated that 25% of the forage food of harbor seals consists of pollock (Table 1).

Largha seal -- Information available on feeding habits of largha seals in the Bering Sea is from seals collected in spring. These seals are present in numbers only from about November to May in the Bering Sea. Lowry and Frost (1981) reported that fish were the major food of largha seals in the eastern Bering Sea. Capelin was the most important and pollock was the third leading prey in the southeastern Bering Sea. Pollock was the major food in the south central and central Bering Sea. Pollock eaten averaged 10.9 cm (range 8.0-15.0 cm) in length (Frost and Lowry unpubl. data). In the northern Bering Sea, pollock was a minor food species. McAlister (1981) estimated that 5% of the forage food of largha seals consists of pollock (Table 1).

Ribbon seal -- All studies on prey of ribbon seals are based on animals collected during the spring period of reduced feeding. Frost and Lowry (1980) reported on the feeding of ribbon seals in the Bering Sea in spring. Although the sample sizes were small, pollock was the principal food of ribbon seals in the south-central Bering Sea (N=9, March-April, 1976-77) and in the central Bering Sea (N=12, April-May 1978-79). Pollock eaten averaged 11.2 cm long (range 6.5-34.4 cm)(Frost and Lowry unpubl. data). Arctic cod, Boreogadus saida, was the principal forage species in the northern Bering Sea. Burns (1981) examined the stomach contents of two ribbon seals during the period of active feeding. One seal fed exclusively on pollock while the other fed on arctic cod. McAlister (1981) estimated that 24% of the forage food of ribbon seals consists of pollock (Table 1).

Bearded seal -- Lowry and Frost (1981) reported that bearded seals feed primarily on benthic organisms. Antonelis (NMML pers. commun.) reported that bearded seals collected (during the 1981 U.S.-U.S.S.R. cooperative research) in the vicinity of St. Matthew Island had consumed juvenile pollock. The length of the pollock were estimated at 8.2 cm. This is the first indication that bearded seals in the eastern Bering Sea forage on pollock.

Fin whale -- Fin whales are polyphagous feeders and are capable of feeding on both plankton and fishes. Baleen whales are grouped into two types: those that feed by swallowing or gulping and those that feed through a skimming activity. Gulping type whales include fin, minke, and humpback whales which have thick coarse baleen fringes and take macroplankton and fish. The sei whale is a skimming type feeder. It has fine baleen fringes, generally takes microplankton, and probably does not feed on pollock. The surface feeding sei whale is often associated with the occurrence of the copepod Calanus plumchrus and Pacific saury, Cololabis saira. The migration and movement of baleen whales is apparently influenced by the annual changes in abundance and distribution of plankton (Nemoto 1957). Most baleen whales feed primarily on plankton but also feed on pollock and other fishes when both are foraging on the same plankton. Based on stomach content examinations, some of the baleen whales (fin, minke, and humpback whales) feed on pollock to a certain extent. Plankton which they feed on consist of euphausiids, Euphausia pacifica, Thysanoessa inermis, T. longipes, T. spinifera and T. raschii; and copepods Calanus cristatus, C. plumchrus, and Metridia lucens. Fishes which they feed on include pollock; Pacific herring, Clupea harengus pallasi; capelin, Pacific saury, Pacific sand lance, Ammodytes hexapterus; and Atka mackerel, Pleurogrammus monopterygius.

Pollock was the dominant fish consumed by fin whales along the continental shelf edge between latitude 58°N and 61°N (Fig. 6). The pollock consumed by fin whales were small and did not exceed 30 cm in length (Nemoto 1957).

Minke whale -- Minke whales are one of the most frequently observed cetaceans in the Bering Sea (Braham et al. 1982). Frost and Lowry (1981) reported that pollock was the only food found in the stomach of a stranded minke whale on Unalaska Island in the Aleutians. The pollock eaten averaged 14.5 cm (range 11.8-17.5) in length (Frost and Lowry unpubl. data).

Humpback whale -- Humpback whales are known to feed on pollock but Atka mackerel appears to be the most abundant fish in the stomachs of this species taken in the Bering Sea-Aleutian Islands region (Nemoto 1957). Humpback whales also feed on euphausiids.

Dall's porpoise -- Very little is known about the feeding habits of Dall's porpoise in the eastern Bering Sea and Aleutians. Pollock occurred

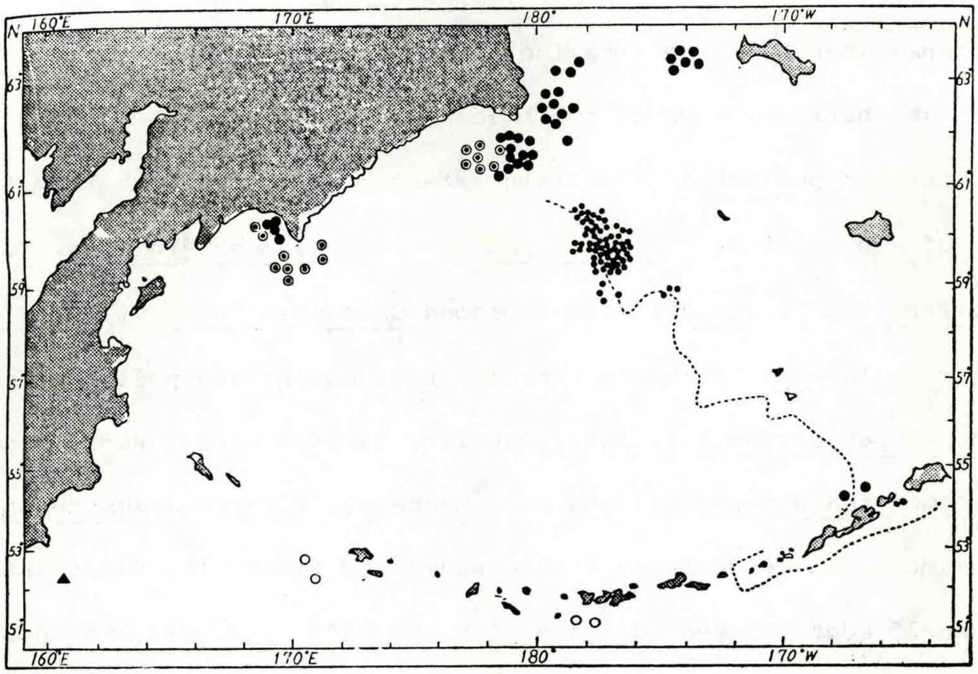

Figure 6.--Occurrences and distributions of fish in the stomachs of fin whales caught from 1952 to 1958 in the northern part of the North Pacific (from Nemoto 1959). ● --Capelin, ⊙ --Herring, • --Alaska pollock, ○ --Atka mackerel, ▲ --Saury.

as one of the prey items eaten by a Dall's porpoise taken in the eastern Bering Sea in 1968 (Kajimura et al. 1980). Crawford (1981) reported that Dall's porpoise taken in conjunction with the high seas salmon fishery were feeding primarily on myctophids. Pollock identified from otoliths was a minor prey item and occurred in only eight stomachs.

Killer whale -- Killer whales are known to prey on a variety of marine life including sharks, fishes, squids, and marine mammals (Rice 1968). There are no known records of predation on pollock by the killer whale in the Bering Sea-Aleutian Islands area. Because of the abundance of pollock in the area, it is probable that killer whales do forage on pollock to some extent. One killer whale taken during a pelagic fur seal research cruise near the Aleutian Islands in 1968 contained the remains of a salmonid, arrowtooth flounder, *Atheresthes stomias*, and squid beaks of the family Gonatidae (unpubl. data from NMML files). Nishiwaki and Handa (1958) reported that Pacific cod, *Gadus macrocephalus*, was the dominant fish found in the stomachs of killer whales taken in coastal waters off Japan.

Sperm whale -- Sperm whales are known to feed primarily on oceanic squids but are capable of foraging on demersal fishes. There is no known record of sperm whale feeding on pollock in the eastern Bering Sea (Okutani and Nemoto 1964). McAlister (1981) indicates that sperm whales are probably the highest consumers of fish, followed by beluga, *Delphinapterus leucas*, and the minke whale.

Relative Importance of Walleye Pollock in the Diet of Seabirds

In recent years, information has become available regarding the diet of seabirds in the eastern Bering Sea. The highest densities of seabirds in the eastern Bering Sea are closely associated with the location of their breeding colonies and the availability of food (Gould et al. 1982). This work also showed that more species of seabirds were located over the continental shelf than in any other habitat, and fewer species were found in oceanic areas. Ecologically, three families, the Procellariidae (fulmars and shearwaters), the Laridae (gulls, kittiwakes and terns), and the Alcidae (murres, puffins, and auklets), are of overwhelming importance in the pelagic areas of the Bering Sea because of their large numbers and/or biomass. Ainley and Sanger (1979) summarized studies of seabird diets available in the literature prior to OCSEAP (Outer Continental Shelf Environmental Assessment Program). Hunt et al. (1981a) reported on the trophic relationships of seabirds of the eastern Bering Sea shelf and estimated the annual consumption of pollock by seabirds at 3.0×10^5 t which is equal to about 50% of the commercial catch. This estimate was based on samples collected during the OCSEAP studies (Pribilof Islands) during the summer months of 1975-78. During this study, it was noted by Hunt et al. (1981a) that in the Bering Sea the major portion of the diets of marine birds consists of only a few kinds of food and that most of these birds appear to be opportunistic feeders. For example, in the Pribilof Islands the stomachs of all species of birds examined (except auklets) contained at least 70% fish with some containing up to 99% fish. Pollock was unquestionably the most important prey item for most fish-eating species (the exceptions being the red-legged kittiwake and the inshore feeding red-faced cormorant). Along the Bering Sea ice front in March and April, Divoky (1981) reported that pollock and capelin were the primary prey items of black-legged kittiwake, common murre, thick-billed murre, and the ivory gull, *Pagophilia eburnea*.

Northern Fulmar -- Northern fulmars obtain their food at or near the surface (Ashmole 1971; Ainley and Sanger 1979). Fulmars are widely distributed in the southeastern Bering Sea coinciding with areas of large numbers of pollock (Gould et al. 1982). Fulmars make heavy use of pollock and squids since they usually feed along the shelf break (Hunt et al. 1981c). The annual consumption of pollock by northern fulmars was estimated to be 2.6 X 10^4 t (Table 6).

Red-faced Cormorant -- Red-faced cormorants forage by diving and capturing fish and crustaceans under water (Ashmole 1971; Ainley and Sanger 1979). Although their primary source of food is fish, pollock is only a minor item in the diet of this seabird primarily because red-faced cormororants forage near the bottom close to land (Hunt et al. 1981a).

Kittiwakes -- Black-legged kittiwakes forage by dipping and are unable to obtain food from more than 0.5 m below the surface (Ashmole 1971, Ainley and Sanger 1979, Hunt et al. 1981a). Pollock were clearly the most important food taken by the black-legged kittiwakes but there was a marked seasonal variation in the use of food compared to other seabirds. The size of pollock taken by this seabird also appears to change during the breeding season (Hunt et al. 1981a). The annual consumption of pollock by blacklegged kittiwake was estimated to be 1.2 X 10^4 t (Table 6).

The feeding methods and diet of red-legged kittiwake are similar to that of the black-legged kittiwake (Ashmole 1971; Ainley and Sanger 1979, Hunt et al. 1981a), although red-legged kittiwakes utilize myctophids heavily. The red-legged kittiwakes' pelagic distribution is near the shelf break and the fact that all of the species' colonies are close to the shelf edge is the reason given for the heavy use of myctophids by these seabirds (Hunt et al. 1981a). As a result, pollock is not as important in their diet as it is in the case of the black-legged kittiwake.

Murres -- Common murres forage by diving (Ashmole 1971; Ainley and Sanger 1979). Pollock is the most important prey of this species in the

Table 6.--Estimated annual consumption of pollock by selected seabirds of the eastern Bering Sea shelf (from Hunt et al. 1981a).

Species	Wt	Estimated Bering Sea population[b]	Residence in days[b]	mt[c] of food/yr[a]	mt[d] of food/yr[a]	Percent by weight[a]	Yearly consumption in mt x 10^{4}[a]
						Pollock	Pollock
Northern Fulmar	620[e]	2.1 X 10^6	180	4.6 X 10^4	3.4 X 10^4	55	2.6
Short-tailed Shearwater	790[f]	13.5 X 10^6	120	22.6 X 10^4	45.0 X 10^4	-	-
Sooty Shearwater	790[g]	1.5 X 10^6	120	2.8 X 10^4	5.6 X 10^4	-	-
Fork-tailed Storm Petrel	50[h]	4.0 X 10^6	270	1.0 X 10^4	2.0 X 10^4	-	0.2
Red-faced Cormorant	1900[i]	1.3 X 10^5	360	1.8 X 10^4	3.6 X 10^4	5	-
Black-legged Kittiwake	450[i]	2.5 X 10^6	210	4.6 X 10^4	9.4 X 10^4	25	1.2
Red-legged Kittiwake	375[i]	2.5 X 10^5	240	0.2 X 10^4	0.4 X 10^4	20	0.0
Common Murre	980[i]	4.2 X 10^6	300	24.6 X 10^4	49.4 X 10^4	35	8.6
Thick-billed Murre	1080[i]	4.9 X 10^6	330	35.0 X 10^4	69.8 X 10^4	35	12.2
Parakeet Auklet	290[i]	5.3 X 10^5	300	1.0 X 10^4	1.8 X 10^4	5	0.0
Crested Auklet	275[i]	1.2 X 10^6	300	2.0 X 10^4	4.0 X 10^4	-	-
Least Auklet	100[i]	4.5 X 10^6	300	2.6 X 10^4	5.4 X 10^4	-	-
Horned Puffin	560[i]	3.5 X 10^5	210	0.8 X 10^4	1.6 X 10^4	10	0.2
Tufted Puffin	780[i]	1.7 X 10^6	210	5.6 X 10^4	11.2 X 10^4	40	2.2
Total		52.7 X 10^6		109.2 X 10^4	218.8 X 10^4		

[a] Reported values were for 10 and 20% of body weight consumed. These values represent 20 and 40% (Hunt pers. commun. 1983). Values adjusted for best-guess estimate of yearly diet for whole eastern shelf region.

[b] Residence times and numbers of Fulmars, Short-tailed and Sooty Shearwaters, Fork-tailed Storm-Petrels, and Black-legged Kittiwakes based on Hunt et al. (1981b); numbers of other species based on Sowls et al. (1978).

[c] Calculated on the basis of a consumption of 20% of the body weight daily X the number of bird-days in the Bering Sea. This is a conservative estimate since no allowance is made for reproductive effort.

[d] Calculated on the basis of a consumption of 40% of the body weight daily X the number of bird-days in the Bering Sea.

[e] Hatch 1979.

[f] Sanger and Baird 1977.

[g] Palmer 1962.

[h] Best-guess estimate.

[i] Hunt et al. in prep.

vicinity of the Pribilof Islands. It is estimated that this species consumes enough pollock to rank second among the species of seabirds in the study area. Hunt et al. (1981a) estimated the annual consumption of pollock by common murres in the eastern Bering Sea shelf to be 8.6 X 10^4 t (Table 6).

Thick-billed murres forage by diving (Ashmole 1971; Ainley and Sanger 1979). Pollock was found to be the principal forage food during July and August but was not important in the diet in June or September (Hunt et al. 1981a). The annual consumption of pollock by thick-billed murres was estimated to be the highest among seabirds at 12.2 X 10^4 t (Table 6).

Parakeet Auklet -- The parakeet auklet is common in the eastern Bering Sea from the Aleutian Islands to the Bering Strait and feeds by diving (Ashmole 1971; Ainley and Sanger 1979). The parakeet auklet's diet is the most varied among the auklets in that it takes plankton and epibenthic invertebrates and fish, while the other auklets forage primarily on mid-water zooplankton. Pollock is only a minor food item among the species of fish consumed.

Puffins -- Horned puffins forage by diving and their foraging efforts during the breeding season are restricted to the vicinity of the islands where they nest (Hunt et al. 1981b). Pollock is not as important to the horned puffin as it is to the tufted puffin.

The tufted puffin feeds by diving to obtain its food and its pelagic distribution indicates that it is primarily an offshore feeder (Hunt et al. 1981b). Fish is the principal prey of tufted puffins and pollock contributes nearly one-half of the fish diet. The annual consumption of pollock by tufted puffin was estimated to be 2.2 X 10^4 t (Table 6).

The importance of pollock in the diet of fishes may be found in the article by Smith et al. in this Technical Memorandum.

Indirect Effects of Apex Predators

In this section we examine the relationships of apex predators with pollock through indirect interactions. Indirect interactions are divided into three major components. These are the effects of apex predators upon competitors with pollock, the indirect interaction of apex predators through their consumption of prey that are also consumed by pollock, and predation upon species which also serve as predators upon pollock.

Predation on Species Which Compete with Walleye Pollock

Marine mammals -- Most marine mammals influence the pollock ecosystem through their consumption of species which prey upon fauna that feed at the same trophic level as pollock. This is primarily due to the widely varied diets of most marine mammals. Northern sea lions, fur seals, spotted seals, ribbon seals, some harbor seals, minke, fin, humpback, and killer whales, Dall's and harbor porpoise, and beluga whales consume to a varying degree species which are known to compete with pollock. Available information indicates that salmon, *Oncorhynchus* spp., Pacific herring, various osmerids, Pacific cod, and Pacific ocean perch, *Sebastes alutus* are probably the principal competitors with pollock and are species fed upon by such higher level predators. The reader should consult the article by Smith et al. in this Technical Memorandum to obtain further details on the nature of competition between fishes and pollock.

Marine birds -- The species which serve as competitors with adult pollock, as listed above, are generally not viewed as principal components in the diets of most marine birds.

Predation on Species Preyed Upon By Walleye Pollock

Marine mammals -- In addition to their role in the pollock ecosystem as direct consumers of pollock, marine mammals also function as competitors with pollock for the same food. Dividing the prey of pollock into two major groups, we see that there are actually two corresponding groups of marine mammals that compete for the same food. Baleen whales that eat zooplankton are the first major source of competition. These include minke, sei, fin, bowhead, blue, humpback, and right whales. The fin whale is the principal competitor species at present.

The second group of species serving as common prey for pollock and apex predators includes fishes and squids. Higher level predators feeding on such species include the northern fur seal, northern sea lion, spotted seal, harbor seal, and ribbon seal. Several baleen whales (especially fin, minke, and humpback) and three toothed whales (Dall's porpoise, harbor porpoise, and beluga) also feed on the various species of fish and squid which serve as prey for pollock.

Marine birds -- Several species of birds compete with pollock for zooplankton. These include the short-tailed shearwater, thick-billed murres, black-legged kittiwakes, and crested and least auklets, and to a lesser extent, parakeet auklets. Short-tailed shearwaters take the greatest portion of their euphausiid diet from coastal waters of 50 m or less in depth.

Smaller fishes and squid are also consumed by northern fulmar, short-tailed shearwaters, common and thick-billed murres, and tufted puffins. These species, therefore, compete with pollock through their consumption of fishes and squid.

Predation On Species Which Are Predators On Walleye Pollock

Marine mammals -- There is an important set of interactions among higher level predators insofar as they prey on each other and the fish predators which also prey on pollock. The killer whale and northern sea lion, for example, are known to prey on other marine mammals which prey on pollock. Both of these species, along with fur seals, harbor seals, and of course man, serve as predators on many of the fish species which consume pollock.

Marine birds -- Available information concerning the diets of marine birds in the Bering Sea ecosystem indicate that marine birds eat few animals that feed on pollock. However, northern fulmars take a number of large jellyfish, *Cryphora* spp., which may prey on young pollock and also squids which are potential pollock predators (Hunt pers. commun. 1983).

RESULTS OF POLLOCK ECOSYSTEM WORKSHOP MEETING

Participants who met at the Pollock Ecosystem Workshop to discuss the role of apex predators considered the background material above and attempted to identify the main components (or groups of components) and processes involved in the Bering Sea ecosystem. The need to know more about both the system and species involved became apparent. The informational gaps were identified by direct questions. Having noted the kinds of information found to be of use and importance in other systems, the apex predator working group developed a list of information that will be of importance in future consideration of the roles of apex predators in this ecosystem. The following summary identifies major groups in the Bering Sea ecosystem, and presents what are thought to be the principal items of missing information that can be used to help guide future research.

Major Ecosystem Components

Marine Mammals

On the basis of available information concerning the feeding of marine mammals in the eastern Bering Sea, it appears that there are three major species at the apex predator level among marine mammals. These are the northern fur seal, northern sea lion (with potential for being described in a way which would include some of the phocid seals in this ecosystem), and fin whales (also with the potential of being described in a way which would incorporate the dynamics and influences of major baleen whales as a group).

Fur seals -- As described, the diet of fur seals contains a number of different species. Pollock are estimated to make up approximately 40% of the fur seal diet. The majority of pollock consumed range from 4-40 cm in length (Perez and Bigg 1983). Squids of 5-25 cm make up another 30% of the fur seal diet. Capelin of 7-15 cm in length constitute about 20% of the fur seal diet. Herring of 10-25 cm constitute approximately 10% of the fur seal diet. Fur seals eat other fishes, of course, and it is recognized that the diet described here is a generalization from which specific cases vary both according to location and date. Areas in which fur seals are known to exhibit a predatory influence include Area 2, 3, and the edge of Area 7 (see figure 7 in the article by Schumacher in this Technical Memorandum).

Northern sea lion -- Pollock constitute approximately 60% of the diet of northern sea lions in the eastern Bering Sea in summer and autumn. The majority of the pollock consumed have been found to be between 18 and 61 cm in length (although the sample sizes upon which these numbers are based are relatively small). Approximately 20% of the prey of northern sea lions is herring. Capelin make up about 7%, salmon about 5%, squids 4%, and Pacific cod and sculpin make up another 2%. This information is based on data extrapolated from investigations in the Gulf of Alaska (Calkins and Pitcher 1982). The stomachs of sea lions taken from the Aleutian Islands area of Alaska contained 53% pollock, 20% Atka mackerel, 15% flatfish, 7% squid, and 6% Pacific cod. Based on known distribution at sea and rookery and haul site locations, most of the influence of sea lions on pollock is expected to be exerted in the southern and southeastern part of the Bering Sea.

Fin whales -- The planktonic diet of the baleen whales includes euphausiids and copepods. Small pollock and other fishes such as herring and capelin are also known to occur in the diet of these whales. Generally speaking, fishes found in the stomachs of baleen whales are less than 30 cm in length. The major influence of baleen whales in the Bering Sea ecosystem will be felt in the months of July and August.

Marine Birds

The working group identified three major categories of birds: shearwaters, kittiwakes, and murres. The differences among these categories are primarily based on diet and location of feeding.

Shearwaters -- This category of birds consumes primarily euphausiids and to a much lesser extent small fish such as pollock, sand lance and capelin, and squids. Generally speaking, these birds are absent from the Bering Sea during the winter, but their numbers are relatively high during the summer and fall (Gould et al. 1982). Data from the Gulf of Alaska indicate that fish of 3-15 cm are preferred. Feeding is restricted to the upper 5-10 m of water. Most foraging is thought to be concentrated over the shelf and shelf break during the summer, but occurs particularly in shallow coastal waters.

Kittiwakes -- These birds eat approximately 50% pollock and 30% euphausiids; other fishes and squids comprise about 20% of the diet. Most foraging by this group occurs during spring and summer; most individuals of these species are absent during winter. Feeding is restricted to the upper 0.5 m of the water column. The overall impact of this group in terms of the volume of the food consumed is thought to be only about 5% of that of the shearwaters. Prey items are usually in the size range of 2-20 cm, and are taken in Areas 3, 6 (with some feeding in Areas 2, 5, and the edge of 7) (see figure 7 in the article by Schumacher in this Technical Memorandum).

Murres -- The generalized diet of this group is thought to consist of about 30% pollock, 25% euphausids, and about 15% hyperiid amphipods. The remainder of their diet consists of other crustaceans, fish, and squid. This group tends to feed at the edge of ice during the winter in moderate numbers. During the spring, feeding extends out over the shelf and continues in this region into the summer. Foraging is accomplished throughout the water column down to at least 125 m (Forsell and Gould 1981). As a very rough approximation the size of prey taken by this group range up to 20 cm in length.

Key Ecosystems Processes

Some of the obvious and apparent processes that are important in the Bering Sea ecosystem include consumption (or predation, as it relates to the determination of the dynamics of other components within the ecosystem), mortality, reproduction, and competition. Conceptually, competition involves the process of consumption of common prey. There are aspects of the competitive process, however, which may involve processes other than the simple ingestion of prey items. One processes thought to be of importance involves habitat selection by the major species.

Diseases, parasites, and other microscopic organisms undoubtedly play a role due to their effects on apex predators and the relationships with these components of the ecosystem. The behavioral traits of complex organisms such as the mammals and birds are also thought to play a key role in determining the various functions of this ecosystem. Humans influence the ecosystem through social/legal processes involved in decision making. Man's influence on populations of birds and mammals is also felt through things such as entanglement and incidental take in commercial fisheries.

Predation is a major process influenced by a host of microprocesses. The process of prey selection is dependent on species, size, quality, and type; location, depth, and distribution are very important. Selectivity can also be based on size, age, health condition, and energy content of the prey items. Consumption rates of prey by predators are known to be influenced by the relative abundance of prey. However, actual consumption rate may, in some cases, also depend on other factors which make the abundance of a particular prey item relatively unimportant. The predatory habits, mode of searching, anatomical adaptations, and required energy for predation are influential factors in determining rates of consumption. Availability is a factor in determining whether or not an abundant prey item is consumed and is dependent on such things as depth and microscale distribution or patchiness. The effect of the presence or absence of apex predators could be quite important. It is possible that the presence of one predator may trigger the attraction of a number of other species of predators. The reverse could also be true.

Mortality, of course, is one of the main pathways through which individuals of the populations of an ecosystem are reduced. Mortality can be caused by factors involving the physical environment (e.g., weather, currents, and salinity). Other forms of natural mortality are brought about by aging, starvation, diseases, predation, and parasites. The influence of man as a predator is through the taking of animals either in a directed harvest or indirectly through unintentional mortality caused by entanglement or incidental take.

From the point of view of the pollock ecosystem, as geographically defined in this effort, there is a source of loss to populations due to mortality which occurs in geographic areas outside of the system. Many of the birds, mammals, and fish migrate out of this system for significant portions of the year. During these times, of course, mortality which is undefined within the system occurs. Stresses brought on by man-induced changes in the environment (such as the presence of aircraft and oil rigs) can occur in a way that brings about additional mortality. Habitat degradation can cause mortality through similar processes. This can involve the presence of toxins and contaminants, oil spills, and the use of habitat for man's purposes (such as the occupation of breeding areas or the use of ocean habitat for drilling and production of oil).

The issue of incidental take and entanglement are of particular interest. Incidental take is defined here as the process of killing or capturing animals in actively fished gear. Entanglement involves the process of animals becoming ensnared in debris (very commonly fishing gear which has been lost or discarded). Mortality brought about by these factors depends on the location of the fisheries and the size of the fishery (presumably through the quantity of materials involved in either the discarding of debris or the fishing of gear). The presence of previously entangled animals is thought to be of importance in determining the probability of an animal becoming entangled.

Reproduction is influenced by a number of factors. Nutrition, intake of necessary nutrients, and energy requirements are of obvious and well-documented importance. The composition of the diet as related to caloric value is of particular note. Reproduction is also influenced by the age structure of each population involved, the presence or absence of diseases and disease levels, behavioral factors, and the composition of the population by sex.

The role of nutrition in influencing the rates of reproduction is influenced through density dependent processes. This often occurs as a result of intra- as well as interspecific competition. Density dependence can also express itself through behavioral and social mechanisms, and the functional aspect of the predatory process. Reproduction is also influenced by harvesting or harassment due to the presence of man. The abiotic environment as expressed in the weather, currents, and conditions of the oceanic environment such as the distribution of ocean fronts can also be of importance in the reproductive process.

As mentioned above, many of the animals being considered as apex predators migrate extensively. As such, the levels of these populations in the eastern Bering Sea ecosystem are heavily influenced by seasonal migration. The distribution of the various populations of apex predators is also determined to a large extent by yearly environmental conditions. Environmental determinants of distribution include the locations of the ice edge, breeding colonies, ocean currents and fronts, temperature, and water depth. The natural reproductive cycle of most of the higher trophic level species dictates the time of year during which they are present or absent (for example, fur seals breed on the Pribilof Islands during late spring, summer, and early fall). Distribution often varies by age and sex. Although there are seasonal patterns, there is limited flexibility in the timing of migration and breeding period. The flexibility of these processes may be tied to variation in the abiotic environment.

INFORMATION GAPS

Understanding the roles played by apex predators in the eastern Bering Sea ecosystem requires more precise information concerning the abundance and seasonal distribution of the species involved. A limited amount of information is available for some species. This is particularly true for fur seals during the spring, summer, and fall months. Some information is also available for sea lions, harbor seals, and several species of birds. Again, most of this information relates to the summer season. Information for the remaining species is limited, especially for the cetaceans. Information for most species is nearly nonexistent for the winter months. This information is needed to be able to describe the temporal and spatial changes which occur in the normal life cycles of the species involved. It is also important to be able to describe trends which may be occurring as a result either of the influence of man in the eastern Bering Sea or as a result of long-term abiotic changes in the environment. There is a general need for quantitative information of this type for all species.

Related information is needed concerning the co-occurrence of prey species populations and the populations of apex predators. There is only a limited understanding of the distribution of prey species as it relates to the distribution of predatory species and of how the co-occurrence of the two species influences their interactions.

The general feeding ecology of most species of apex predators is poorly understood. Questions still exist concerning the factors involved in determining foraging activity of apex predators. It is not known to what extent the species involved are generalists or to what extent they are selective in their choice of prey. It is thought that the species, size, caloric value, and similar qualitative values of prey are important in determining the degree to which selectivity is important. The nature of these dynamics is unclear for the Bering Sea ecosystem. The physiological aspect of food utilization is poorly understood for most species. Information concerning seasonal variability in amounts of food consumed and dietary composition is almost nonexistent. Questions remain concerning the degree to which variability in the diet occurs by sex and age within species. Very little is known about the winter feeding ecology of apex predators in the Bering Sea. It would be useful to have information concerning the nutritional and caloric value of prey consumed on a seasonal basis. Studies should be conducted to determine the nutrient concentration and caloric value of various species by age and sex, and how these change seasonally. Specific feeding patterns as they vary diurnally have not been described. This may be particularly significant for marine birds but is also thought to be of importance for marine mammals as well.

The relative contribution of limiting factors and ways in which they are influential in the dynamics of apex predators have not been described. More information is needed concerning the role of weather, food, diseases, predatory interactions, behavioral mechanisms, and social interactions that influence the dynamics of the populations of apex predators in this ecosystem.

Although it is known that there are interactions between apex predators and commercial fisheries, the nature of many of these interactions remains to be described in detail. It is particularly urgent that the reasons behind animals becoming entangled be discovered and work should be undertaken to determine under what conditions animals become involved in an incidental take.

Since the baleen whales are mainly plankton feeders and capable of consuming particles of relatively small size, work should be conducted to determine to what degree they consume the eggs and larvae of important fishes in the pollock ecosystem.

The environmental cues which are important in determining the timing of various components of life cycles of the apex predators need elucidation.

A better understanding of the future of management objectives and a better definition of current management objectives are needed. These are specifically important in relationship to the conflict of management as it involves the protection of apex predator species in an ecosystem versus the harvest of other resources. There is often a conflict between these management objectives which needs to be resolved.

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FISHERIES AND ECONOMICS

by

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ABSTRACT

Although the walleye pollock, Theragra chalcogramma, resource in the eastern Bering Sea supports the most productive single-species fishery in the U. S. fishery conservation zone, the economics of this fishery and related fisheries have only recently been studied. The pollock ecosystem workshop provided an opportunity to use economic research conducted in other fisheries and economic theory to develop a preliminary, conceptual multispecies fishery economics submodel. The background paper prepared for the workshop consisted of three sections: 1) a brief overview of the historical and seasonal harvest of the commercial fisheries in the eastern Bering Sea, 2) a discussion of economic issues that need to be addressed in modeling the fisheries of the eastern Bering Sea, and 3) a brief discussion of how scientific information is used in the management of the eastern Bering Sea groundfish fisheries. An annotated bibliography of the economics of multispecies fisheries was prepared after the workshop. The objective of the fisheries and economics subgroup was to develop a conceptual model of 1) how those who harvest, process, and market fishery products respond to changes in the regulatory, market, oceanographic, and biological environments in which they operate; and 2) how

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these responses will affect economic indicators and area, age, and species specific fishing mortalities. The subgroup's efforts were concentrated on modeling the harvesting sector of the fishing industry. The basis of the model is necessarily a behavioral assumption. After discussing alternative objectives, it was decided to proceed as though the objective of each fleet was profit maximization constrained by resource availability, fishery regulations, market conditions, and oceanographic factors.

The conceptual model presented in this paper may provide a useful point of departure in the development of a model which could be used to evaluate alternative management options or to estimate the effects of past fishery management policies. The development of such a model will require that issues concerning market analysis, the estimation of production functions, and fleet behavior be resolved.

INTRODUCTION

Walleye pollock, Theragra chalcogramma, is the most productive single species fishery resource in the eastern Bering Sea. The economics of the pollock fishery and related fisheries, however, have only recently been studied. Only a limited amount of economic information specific to these fisheries is available. The walleye pollock ecosystem workshop held at the Northwest and Alaska Fisheries Center in Seattle, 2-4 May 1983, provided an opportunity to develop a preliminary, conceptual multispecies fisheries economics submodel. This development process identified areas for future economic research and generated increased awareness for such studies. The conceptual model and the background information that aided in its development are the subjects of this paper.

BACKGROUND

The background paper prepared for the workshop consisted of three sections: 1) a brief overview of the historical harvest of the commercial fisheries in the eastern Bering Sea, 2) a discussion of economic issues that need to be addressed in modeling commercial fisheries in this region, and 3) a brief discussion of how scientific information is used in the management of the eastern Bering Sea walleye pollock fishery. These sections, as rewritten after the workshop, are presented below. An annotated bibliography of the economics of multispecies fisheries prepared after the workshop appears in the Appendix.

Historical Harvest

The eastern Bering Sea supports very productive finfish and shellfish fisheries. Between 1972 and 1982, the annual foreign and domestic harvest in this region ranged from 1.4 to 2.0 million metric tons (t) with an average of 1.6 million t. Groundfish accounted for over 90% of the total finfish-shellfish harvest during this period and walleye pollock accounted for approximately 80% of total groundfish removals. Annual pollock harvests ranged from 0.9 to 1.7 million t between 1972 and 1982. In 1982, the pollock harvest of 1.0 million t was 76% of the commercial groundfish harvest and 71% of the total finfish-shellfish harvest. Historical catches are presented in Figures 1-5.

The groundfish resources of the eastern Bering Sea have been primarily exploited by foreign fleets. Despite large increases in the combined domestic and joint-venture harvests in recent years, the foreign fleets still took over 90% of the total groundfish harvest in 1982.

Due to the relatively low ex-vessel price (the price per unit received by fishermen) of groundfish and the relatively low levels of domestic participation in the groundfish fisheries, a comparison of the groundfish, salmon, and crab fisheries in terms of harvest weight greatly overstates the current relative value of groundfish to the domestic fishing industry. For example, although groundfish comprised 94% of the total finfish-shellfish harvest in 1982, groundfish accounted for less than 55% of the ex-vessel value of the 1982 harvest, less than 10% of the groundfish harvest was taken by domestic vessels. An average groundfish ex-vessel price of $0.06 per pound was used in this comparison.

The level of activity in the groundfish fisheries varies greatly from quarter to quarter. The third quarter, July-September, is the peak quarter in the walleye pollock fishery with the harvest often approaching 50% of the annual harvest (Fig. 6). The dominance of a single quarter is less pronounced in other groundfish fisheries (Fig. 7).

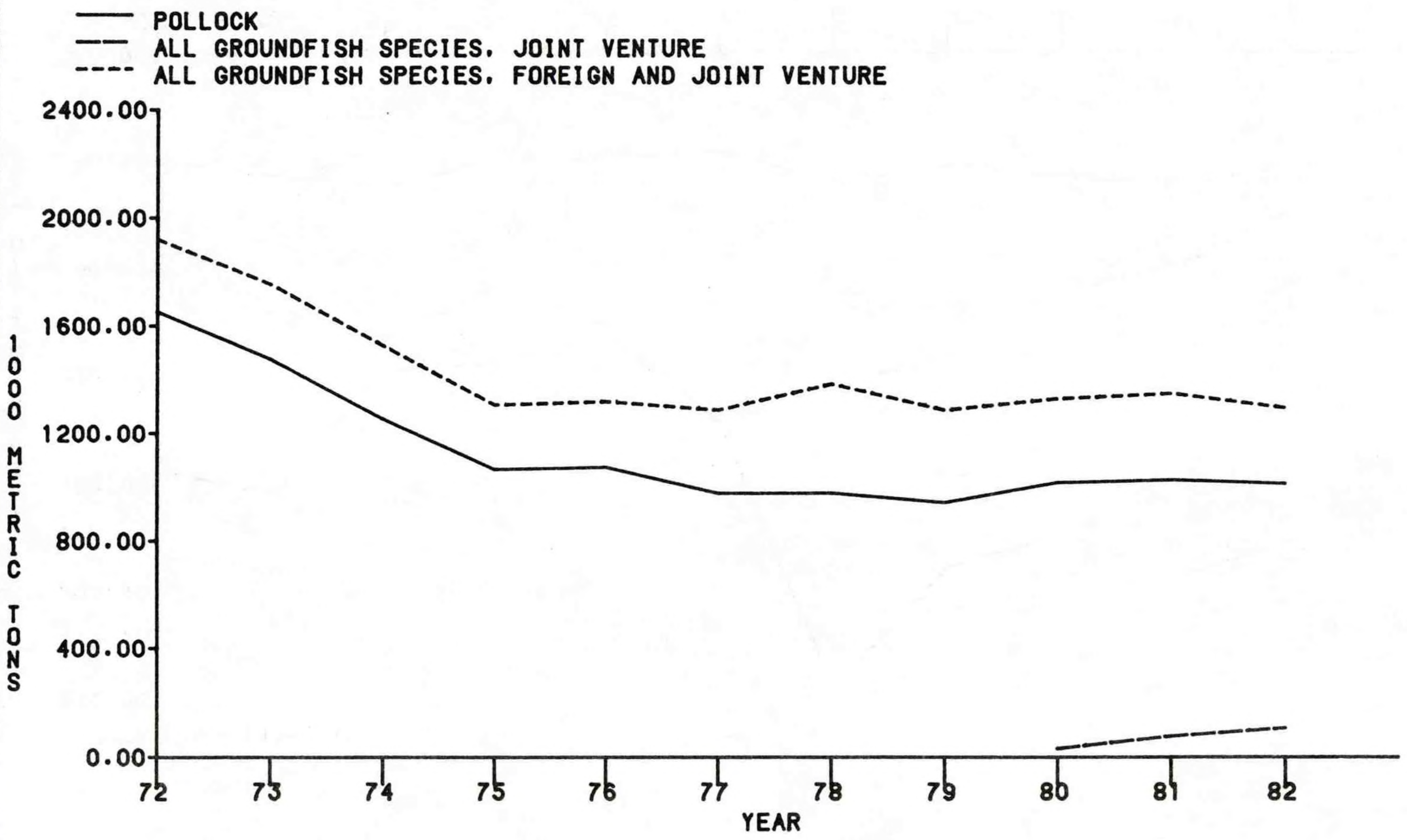

Figure 1.-- Catch of walleye pollock and all groundfish species by foreign and joint venture fisheries in the eastern Bering Sea, 1972-82.

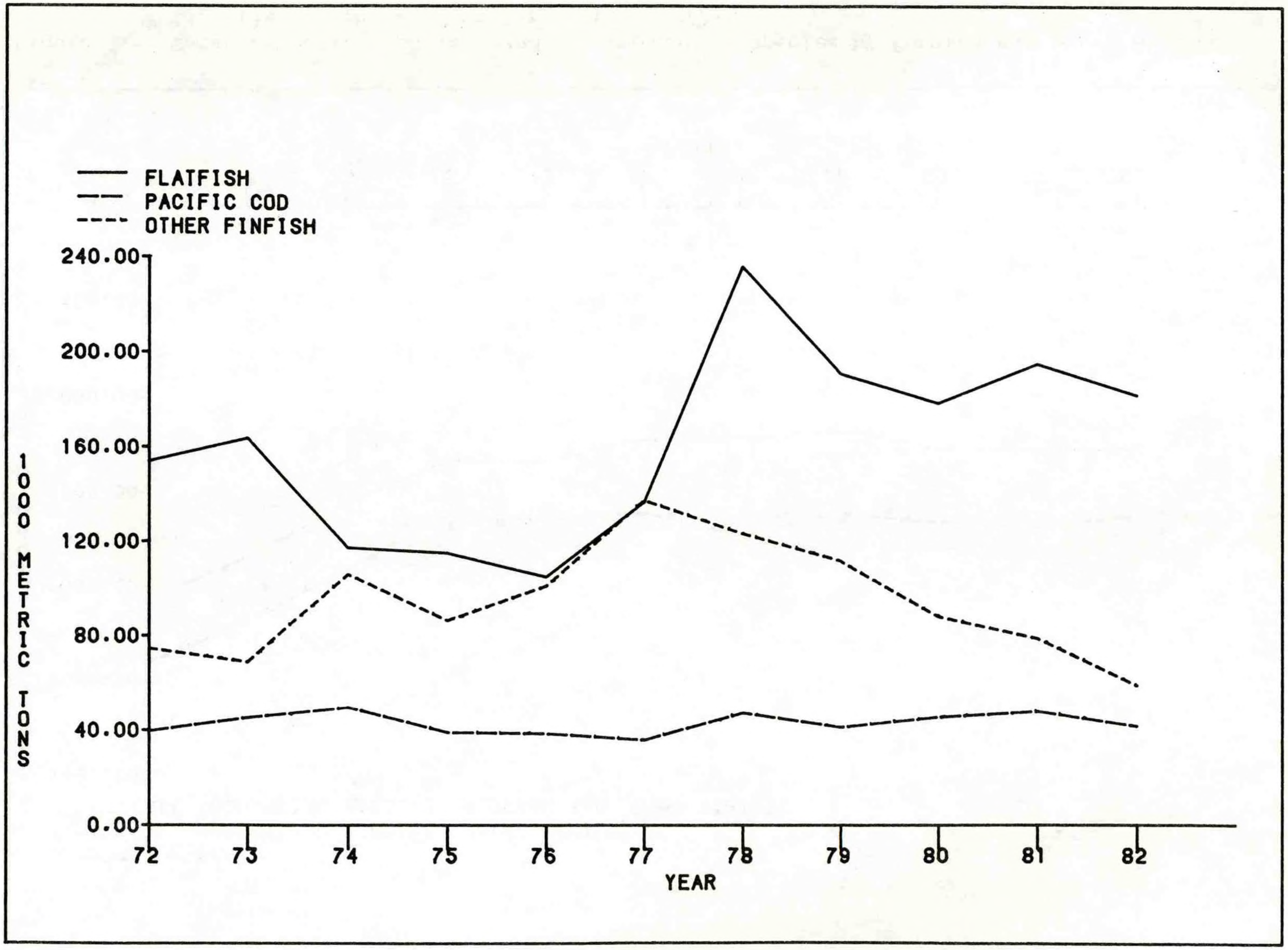

Figure 2.--Commercial harvests of flatfish, Pacific cod, and other finfish from the eastern Bering Sea, 1972-82.

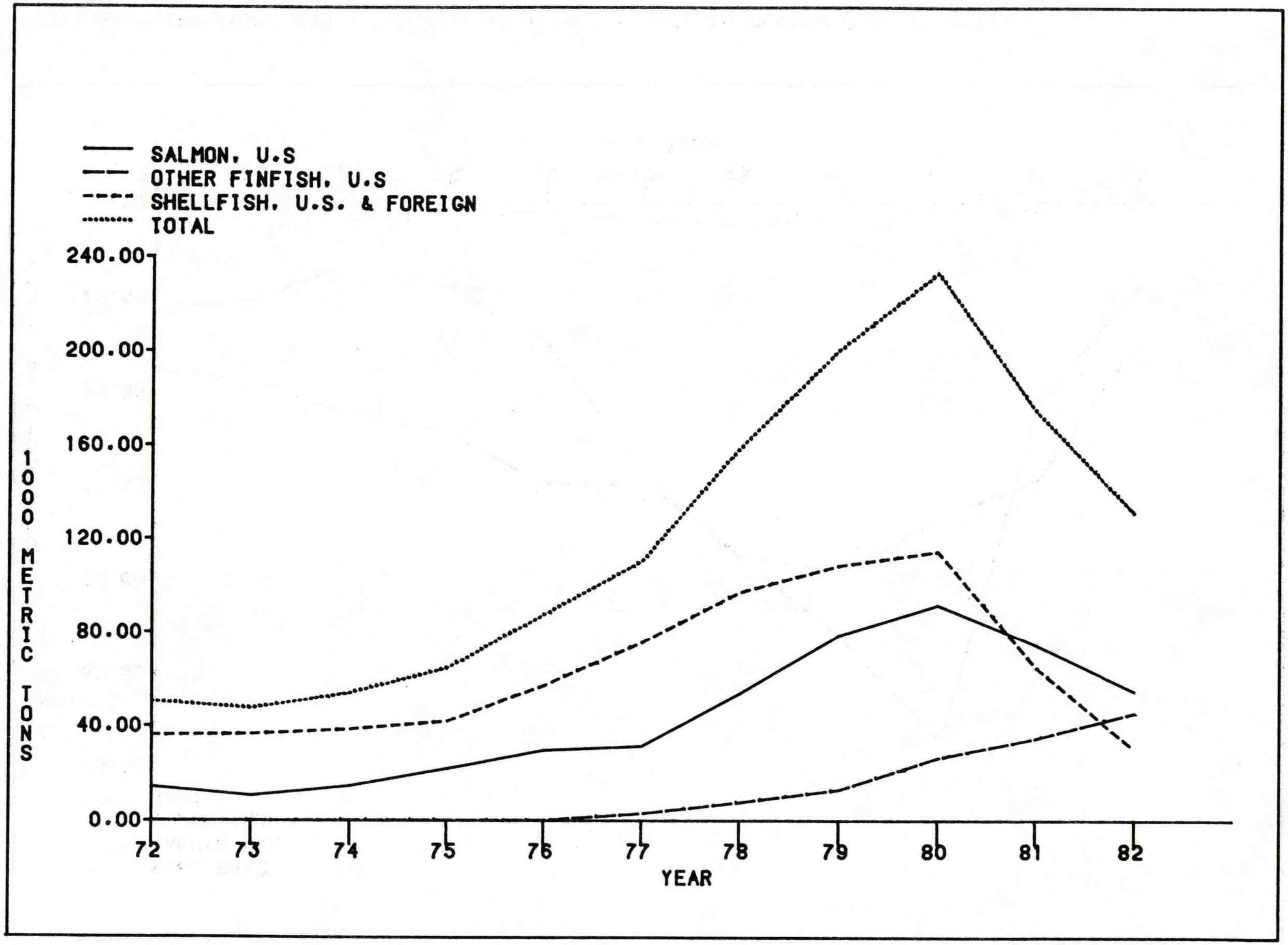

Figure 3.--The U.S. harvest of salmon and other finfish and combined U.S.-foreign harvest of shellfish from the eastern Bering Sea, 1972-82.

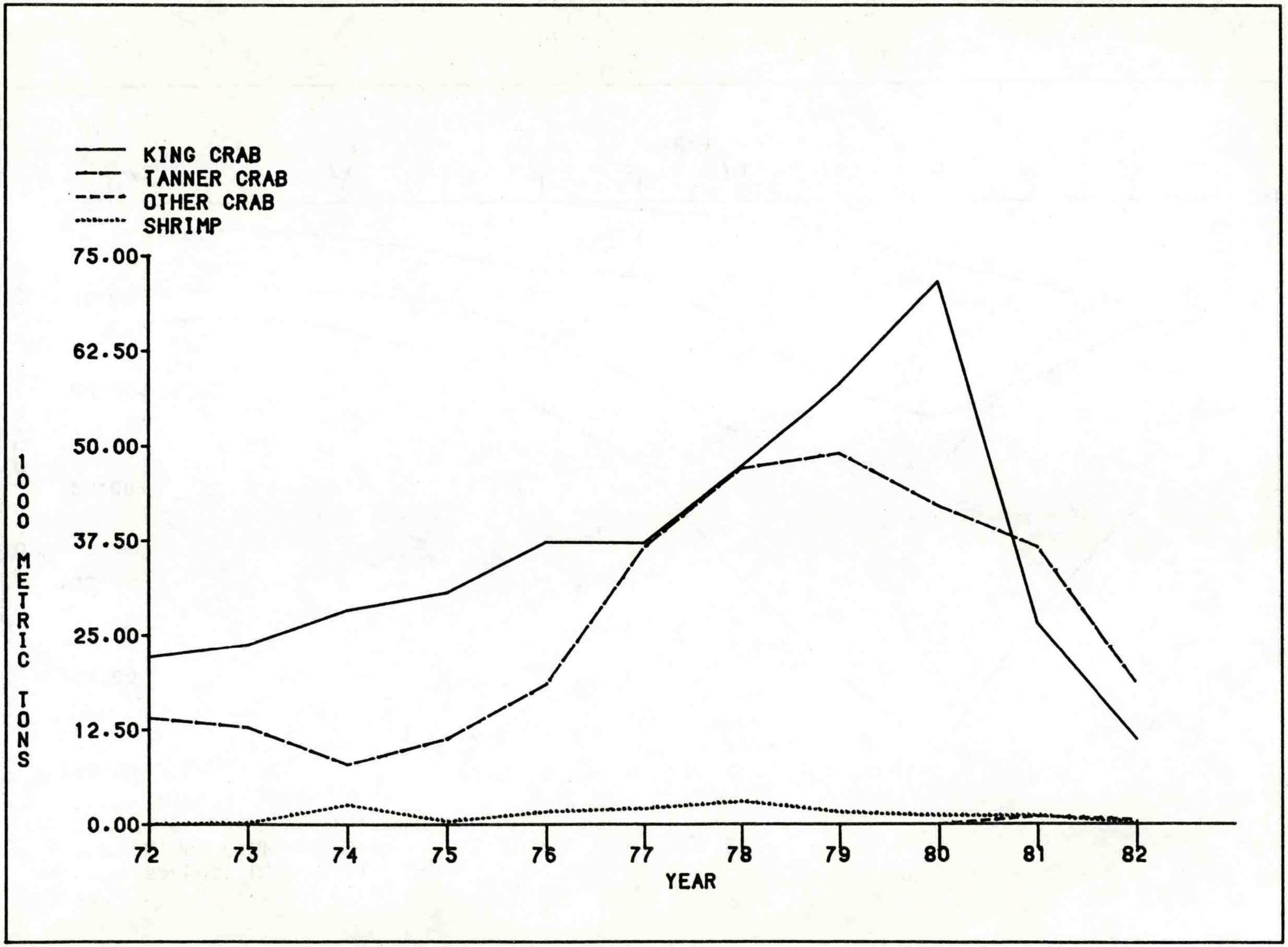

Figure 4.--Commercial shellfish harvest from the eastern Bering Sea, 1972-82.

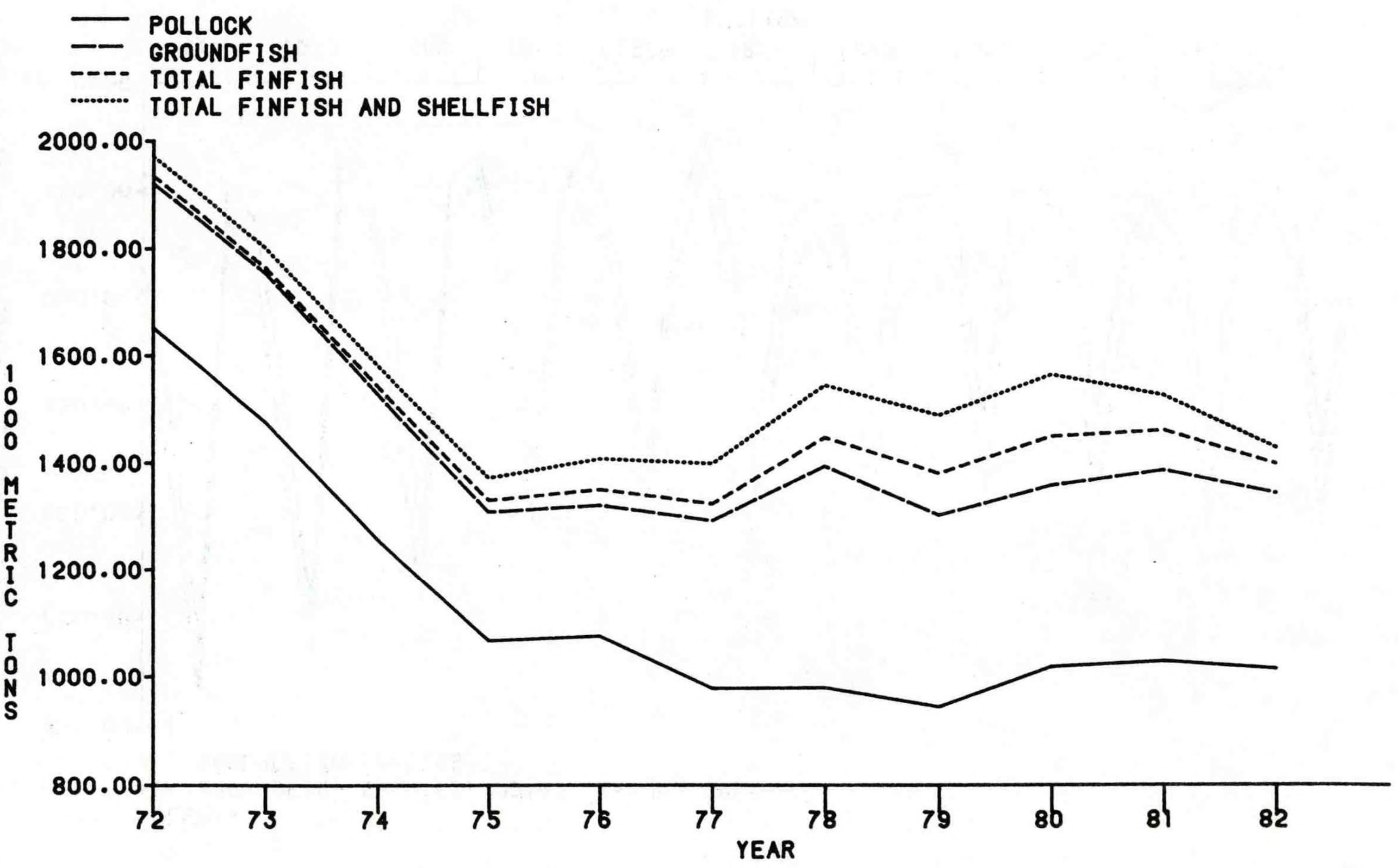

Figure 5.--Commercial harvest of walleye pollock, groundfish, total finfish, and total finfish and shellfish (combined) from the eastern Bering Sea, 1972-82.

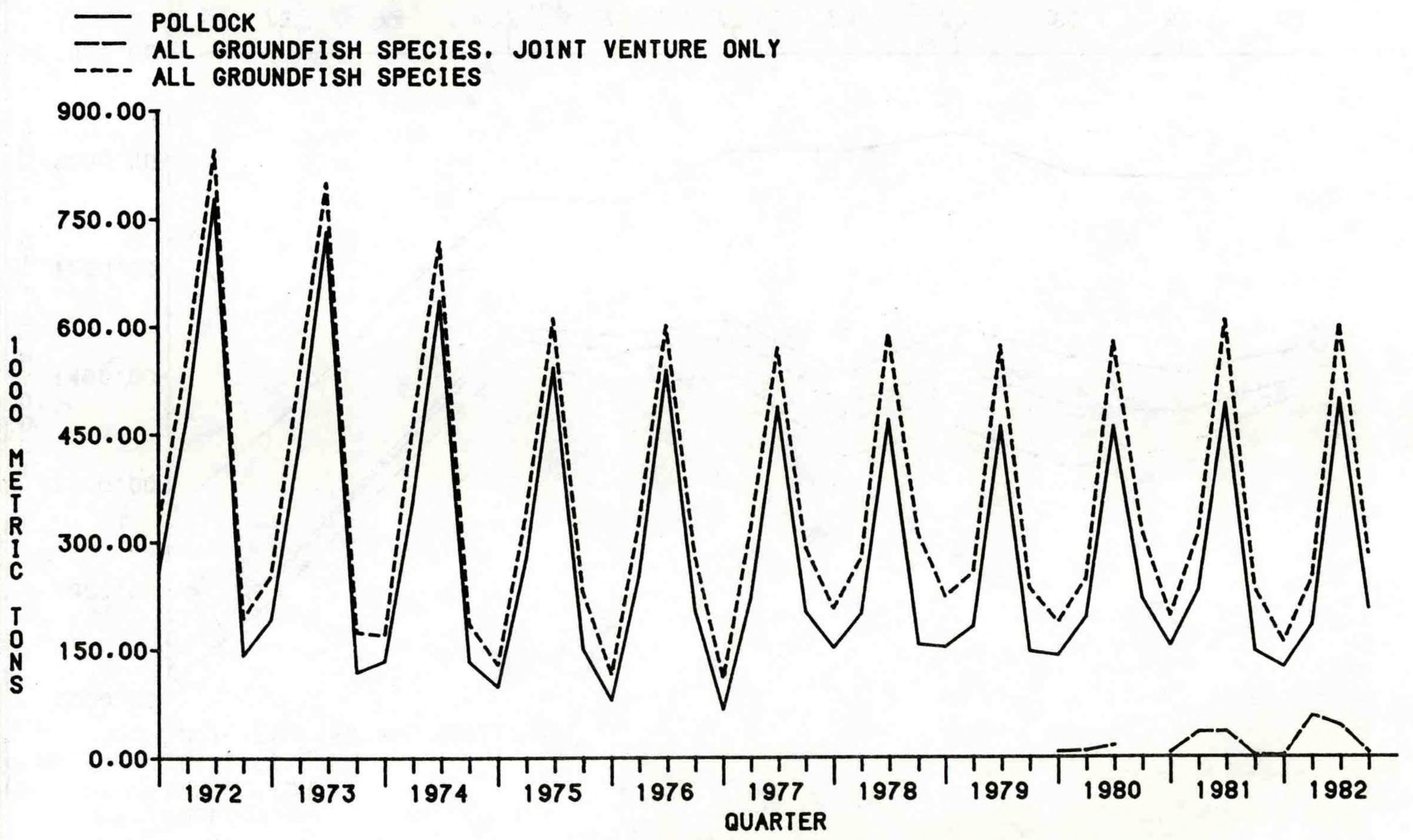

Figure 6.--Catch of walleye pollock and all groundfish species by foreign and joint venture fisheries by quarter in the eastern Bering Sea, 1972-82.

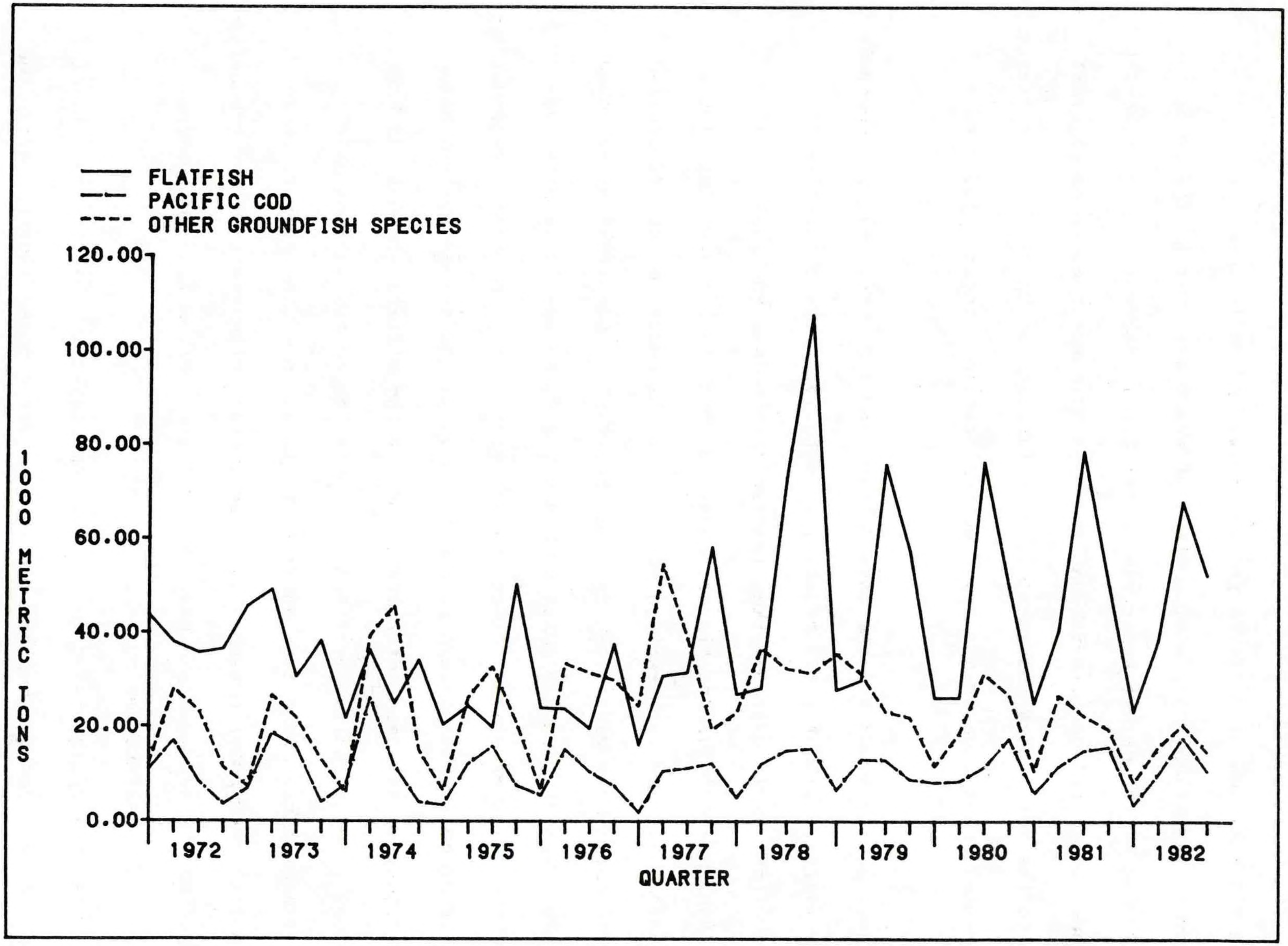

Figure 7.--Catch of flatfish, Pacific cod, and other groundfish species by quarter in the eastern Bering Sea, 1972-82.

Economic Issues Related to Walleye Pollock in the Eastern Bering Sea

Economic analyses of multispecies fisheries generally focus on one or more economic variables. The most obvious of these are prices of fish at various levels of the market and costs of catching, processing, and marketing fish. These price and cost variables, together with the associated physical outputs, define total cost and total revenue functions. These functions are of fundamental importance in anticipating the level of effort applied to a fishery.

Perhaps less obvious are the more complex and less well-measured economic variables, such as latent fleet capacity, fleet diversity, thresholds of change in effort application, market interrelationships, and risk attitudes of fishermen, scientists, and fishery managers (Bockstael and Opaluch 1981; Carter 1981). All are important in determining the amount of effort applied to fish stocks. These variables are also important in identifying the types of economic interactions that exist within markets, between risk attitudes and targeting strategies, and between target species and incidental catches.

With respect to the eastern Bering Sea walleye pollock ecosystem, major economic concerns include: determinants of fishing effort; economic linkages among latent fleet capacity, domestic processing capacity, current joint-venture arrangements, and fuller domestic utilization of the eastern Bering Sea groundfish resources; potential for fleet overcapitalization; and mechanisms for increasing the net economic benefits that are derived from the marine resources of the eastern Bering Sea.

When the fishery is viewed as a bioeconomic system, the simultaneity of biological, oceanographic, and economic forces becomes readily apparent. The biology underlying the production of pollock populations is complemented by the economic decisions to apply fishing effort to that fishery. Convenient disciplinary bounds serve only to define components that interact with other components of the larger system. These components include management objectives and regulations, the fishing fleet, stocks of living marine resources both exploited and unexploited, and oceanographic conditions.

In this section, several areas of economic analysis relevant to the walleye pollock fishery are outlined, and some biological and economic linkages are discussed. Areas of mutual concern and particular biological data needed for economic analyses are identified as a basis for discussion.

Economic analysis of fisheries can be categorized into four general areas: market analysis, production function estimation, fleet behavior analysis, and optimal use.

Market Analysis

The current market structure for walleye pollock is characterized by a dominance of foreign participation in harvesting, processing, and marketing with U.S. participation, primarily joint-venture contracts between foreign processors and U.S. catcher boats. With few exceptions, pollock is currently marketed by the United States only at the ex-vessel level through these arrangements. Several market issues emerge centering on the potential for a completely domestic fishery.

1) The initiation of domestic processing facilities--either shore based or on factory ships--may be associated with substantial setup costs (Martin 1979). If these costs are high, processors will need to have an expectation of continuous availability of fish from fishermen in order to spread the costs out over time. Biological questions of seasonality enter here: are pollock available steadily throughout a long season, or in short-run gluts? What is known about the potential for long-run stock availability?

2) Also important to the processor, in terms of limits on processing capacity, is the overlapping availability of pollock with other species to be processed.

3) Would processor capacity limits impose market limits on fishermen?

4) The possiblity of matching biological availability with market demand (location of markets, acceptable product form) is another unaddressed economic issue.

5) What is the economic structure of the processing sector? (Clark and Munro 1980).

6) Current market demand for pollock and roe may result in wholesale prices low enough to limit processing possibilities to factory ships, particularly if the costs of travel between fishing ground and shore-based processors is substantial.

7) Institutional arrangements restricting international trade may exist; for example, import restrictions on pollock to the Republic of Korea and Japan may hinder expansion of the domestic walleye pollock fishery.

8) Data on market availability should be considered simultaneously with biological availability. In a multispecies fishery, economic groupings of species in the market (in terms of relative prices) become as important as biological groupings on fishing grounds. Both disciplines may benefit by sharing information on respective stock distinctions.

9) For jointly fished stocks, estimation of a joint maximum sustained yield is important in establishing biological limits of availability. Catch quotas may serve indirectly as limits to resource availability. Estimation of joint revenues from those stocks is also important because of price relations in the market and yield variability.

10) The importance of relative price relationships of different stocks of fish as well as price differences for different sizes of pollock requires good biological information related to pollock growth processes. Estimates of available species mixes can be used to estimate the expected revenues from the catch of those mixes (Hannesson 1983a).

Production Function Estimation

Estimation of fishing mortality serves as a basic tool of biological production function analysis. The question is, how do combined fishing mortality and natural mortality affect the size of the stocks and hence yields of fish? Economic analysis of production seeks to define the relationship between fishing effort and fishing mortality. Economic production involves the use of a given technology to transform a set of inputs into single or multiple outputs (e.g., fishing effort into yield). Underlying this relationship is a more basic linkage between the prices of fish and other economic factors and the application of effort in the fishery.

When the ability to target on selected stocks is limited or when targeting occurs on stocks that are mixed over time or space, catch mixes are joint products to the fishing firm which may or may not correspond exactly to available species mixes. Well-estimated joint product yield-effort relationships would be extremely useful for predicting fleet responses to changes in relative prices of species within the mix and to changes in management policies (Huppert 1979).

Several problems in the estimation of multispecies (joint product) production functions currently exist (Conrad et al. 1982). These include the definition of basic production units (inputs, outputs, transformation technology, and the fishing firm) and problems of availability of both biological and economic data.

Production functions of fishing firms may be estimated using biological production functions or by modifying economic production functions to include biological factors (Agnello and Anderson 1977, 1981; Hoppensteadt and Sohn 1981). If cost and price data are more available than production data, duality methods of estimation may be used (Conrad et al. 1982). Duality methods take advantage of known symmetries between complementary functions (e.g., cost and production functions) to estimate the parameters of one function indirectly through the estimation of the second function. This is useful when enough data are not available for direct estimation. Maximum likelihood techniques have been used to estimate population parameters when biological population data are unavailable, but this requires assumptions about the statistical properties of biological and oceanographic parameters.

Problems of variable definition have presented substantial obstacles to production function estimation. A more detailed taxonomy of inputs, costs, and outputs is essential to economic estimation. The composite "effort" variable is a good example of a single variable embedding a complex array of substitution possibilities. Actual units of effort may be masked by differences in gear, in skill levels, and in time and geographic location. The inability to differentiate between direct and incidental effort hinders yield-effort estimation.

Multioutput fisheries, fisheries in which landings consist of species mixes rather than single species, present problems of appropriate aggregation levels for production function estimation (Hoppensteadt and Sohn 1981). Can inputs and outputs be indexed and measured in the aggregate? What individual skill differences are masked by the estimation of industry (aggregated) production functions?

Other production parameters of interest are nonlinear cost effects, including area related fishing costs, and economies of scale for different vessel types and fishing grounds. Economies of scale are the changes in outputs resulting from proportional changes in inputs. The concept of "elasticity" is also important in economic analysis. Elasticity refers to the percentage change in a given variable caused by a one percent change in another variable. Examples of elasticity estimation for fisheries include the elasticity of substitution between inputs, the total elasticity of transformation between inputs and outputs, and the price elasticity of demand for single or multiple species (Conrad et al. 1982). Possible stability ranges of elasticity estimates should be identified as well as the separability of target catch and incidental catch.

Lack of biological data is a problem in production function estimation for the fishery, particularly in terms of the biological and technological (gear) interdependencies between sizes of fish (Anderson et al. 1981; May et al. 1979; Rothschild 1967). Direct and indirect biological interrelationships affect future availability of inputs to production. Because critical threshold of change in pollock stocks (ranges of compensatory or depensatory growth rates) affect resource availability to the fishery, they represent basic information for good production work in economics. Particularly important is information on the properties of biological estimates, e.g., growth rates, including the sensitivity of those estimates to changes in other parameters when used in production function estimation.

Another problem in production analysis is that changes in the selectivity of gear or other aspects of vessel performances require reestimation of production relationships.

Fleet Behavior Analysis

Behavioral analysis of fishermen is important for an increased understanding of supply response functions, strategy choices, real effort on fish stocks, and the objectives of fishermen. The study of these areas is necessary at both the individual level and at the fleet level. Effort has been traditionally considered a single variable composed of several elements: gear, fishing time, vessel size, skill. Once fishing gear is applied to more than a single stock of fish, effort units affect multiple stocks through direct exploitation and indirect effects on other stocks; in these cases the meaning of catch per unit unit of effort (CPUE) indicators becomes unclear. More informative CPUE measures will result from effort analysis that examines fisherman behavior at the individual and fleet level directed at single and multiple stocks of fish.

Individual skill and strategy differences as well as categories of fishing objectives need to be identified for analysis of production relations. The relation between strategy choices and different levels of system variability has biological and economic application to the development of a fishery. Emergent properties of the total effort system are expected to be qualitatively different from the sum of individual objectives and effort choices. Behavioral analysis in the fishery is an underdeveloped area of research but one that is crucial to better modeling and prediction of response functions. Structural differences between foreign and domestic fleets as well as a lack of appropriate data on decision making in foreign fleets will limit this type of analysis to domestic fisheries.

The disaggregation of effort measures will provide a more sensitive system performance index. Effort may be partitioned into relevant divisions by examining differences in gear types, vessel classifications, areas fished, and risk attitudes of eastern Bering Sea fishermen. Effort analysis is data intensive. For both spatial and temporal aspects of effort application, biological data are needed on the catch mixes, the physical bounds of those mixes, discards, and the location of catch. Data management on the basis of species mixes, if appropriate, rather than single species would facilitate economic analysis.

Changes in the effort efficiencies of vessels due to the increased sophistication of gear need to be tracked to account for changes in catchability coefficients and hence real effort. The interaction of effort on multiple stocks with different growth rates and varying prices complicates the derivation of an effort index and requires simultaneous biological and economic estimation of fishing mortality rates and the economic basis for the mortality mix.

Another potentially productive area of bioeconomic analysis concerns the general question of diversity. Included in this question is the degree of importance of preservation of diversity among mixed stocks and the structure and functions of economic diversity among fishermen, both in gear choices and catch mixes (McKelvey 1982b). Biological information is needed on the geographical bounding of diverse groups of species.

Further empirical analyses to build a foundation for the understanding of the relation between economic diversity and stability could center on switching behavior of operators in the pollock fishery, including switching costs, opportunity costs of not switching, and switching thresholds (Holt 1981; McKelvey 1982a). A solid biological definition and bounding of the geographical aspects of a fishery is required for this type of work (Tyler et al. 1981).

The role of expectations in effort decisions is another area of behavioral investigation. A fisherman's expectations apply to the potential actions of other fishery participants as well as to resource stock estimates

(Wilen 1979; Wilson 1982). Time series of stock size estimates with particular emphasis on the variance of those estimates would allow information comparisons to fishermen's subjective estimates of the same variable.

Types of biological and economic uncertainty that exist in the pollock fishery are important for research in both disciplines. Identification of the variability inherent in biological parameters would provide economists with the basis for the analysis of incentive structures for different types of competitive behavior among fishermen. A question currently being examined is whether the degree of variability in the decision environment of fishermen, i.e., in the fishery, is related to fishing patterns. It would be helpful to know what kind of yield variation to expect as a result of short- and long-run variations in production cycles.

Potential fleet capacity as a determinant of fishing effort is of interest to both biologists and economists. Results of individual risk and diversification analysis would apply directly to this question (McKelvey 1983). Another immediate area of investigation would be potential net revenues from a completely domestic pollock fishery. The calculation of potential net revenues requires data on expected biomass availability as well as expected prices and costs. A related question is under what set of expectations about future net revenues are trawl conversions financed (Bockstael and Opaluch 1981)?

Optimal Use

No clear rules for optimum multispecies management exist. Optimal bioeconomic use of a multispecies fishery involves an objective function which incorporates both biological and economic goals. The problem becomes one of finding the appropriate management structure to achieve the optimal level of yields and economic rent from the fishery. Establishing a bioeconomic optimum for a multispecies fishery requires reliable data on costs, prices, and rates of discount, as well as fisheries growth and mortality functions. Conflicts may exist in objectives for different fisheries.

The pollock fishery may have varying effects on populations of other fish. Smaller populations may be depletable even though the fishery targets on larger populations. Interdependencies that exist between stocks, including the indirect effects of one species on another, become important biological information to the economist.

Optimal resource use involves an intertemporal allocation. The optimal rate of exploitation will depend on the rate at which expected future returns from the fishery are discounted in the present (Hanna 1983; Silvert and Smith 1977). Important related economic questions are intergenerational use of the fishery and the effects of open, unconstrained competition on discount rates (time preference rates) used by competitors for the resource (Hannesson 1983b). Data on pollock population processes are important, because the relative sizes of the discount rates and the growth rates of the stocks determine the resulting equilibrium population size. For example, it has been demonstrated (Clark 1973) that extinction of a population may result from the combination of a low reproductive rate and a market-based discount rate. The combination of the discount rate and the growth rate for pollock may also affect the survivability of smaller populations. Economists should provide other fishery scientists more specific information on the variation in the discount rates used by fishermen of different income groups and in different fisheries.

Optimal use problems are often specified within a framework of maximizing the welfare to be gained from the fishery over time. The "welfare function" to be maximized may be specified to include whatever indicators of benefits are deemed desirable and solved as an optimal control problem to determine the appropriate rate of use. To solve an intertemporal welfare maximization problem for the pollock fishery, biomass growth functions of pollock need to incorporate age structure because age structure differences will interact with the targeting behavior of the fishery to affect population fluctuations. Optimal use determinations may involve choices between the size and variability of yields (May et al. 1978).

Maximum sustainable yield (MSY) as an equilibrium relation gives only long-run equilibrium solutions. The degree of natural variability in the pollock fishery affects optimal rates of use: is the variability sufficient to require periodic fishing (Beddington and May 1977)? A related economic question concerns the availability of alternative fisheries for displaced effort. What would be the economic dislocation problems from yearly adjustments of yield and effort figures? What problems would stem from capital fixity in trawlers (McKelvey 1983)?

An interesting joint research problem is the hypothetical relationship between different levels of biological depletion of the pollock fishery and economic depletion (the inability to support a commercial fishery).

Of interest to economists would be the identification by biologists of the normative aspects of biological analysis; i.e., states that are considered desirable to maintain. For example, when the term depletion is used, does this refer to population levels that are less than the maximum possible, population levels that are less than virgin levels, or population levels low enough to threaten survival? Another consideration is the kind of resilience and diversity that should be maintained in a biological system (May et al. 1978). Is there value in maintaining "environmental capital," an array of resource use options, as a safety factor when parameter uncertainty exists?

Economists can offer other fishery scientists analyses of the economic consequences of alternative biological goals. If a welfare function incorporating both biological and economnic goals can be jointly defined, some approximation of value measures of alternative actions in the pollock fishery are possible.

Summary

Various areas of economic analysis appropriate to the walleye pollock fishery have been discussed. In most cases, analysis would benefit from biological information on both general tendencies in the fishery and interactions specific to the pollock fishery in the eastern Bering Sea.

Economic data required to conduct analyses of the eastern Bering Sea walleye pollock fishery include:

1) Ex-vessel pollock prices.

2) Wholesale pollock prices.

3) Information on domestic and foreign market channels.

4) Pollock landings, domestic and foreign.

5) Cost structures for different vessel types.

6) Costs of fishing under different levels of resource availability.

7) Economic status of fisheries that compete for domestic fleet's effort, i.e., the domestic opportunity cost of fishing pollock rather than another species.

8) Distribution of vessel types over eastern Bering Sea fisheries; harvesting technology.

9) Spatial and temporal fishing patterns.

10) Tax structures affecting fishing firms.

11) Institutional structure of international trade in pollock.

12) Joint-venture contract stipulations.

13) Historical foreign/domestic percent shares of the fleet.

Biological data for immediate analysis are needed by economists in the following areas:

1) Temporal patterns of pollock availability, seasonal geographic distributions and migration patterns.

2) Variability of pollock abundance, short-run effects and long-run trends.

3) Estimated tradeoffs between abundance variability and yields.

4) By-catch estimates, species mixes, and amounts.

5) Effects on yields of time-variant catch rates vs. steady-state policies.

6) Factors affecting the value of fish, i.e., flesh quality, parasitism.

7) Data base management flexibility to allow simultaneous investigation of more than one economically important species.

8) Definition of appropriate biological species groupings, geographic bounds of these groupings, direct and indirect linkages between species associated with pollock. Economic interest is in the way fishing patterns are affected by these areas of biological availability.

9) Reversibility of different biological processes affected by fishing.

How Scientific Information is Used in Managing the Walleye Pollock Fishery in the Eastern Bering Sea

The fishery management plan for groundfish in the Bering Sea/Aleutian Islands area has been modified by amendment to provide the North Pacific Fishery Management Council (NPFMC) with the best scientific information available for making annual management decisions. The walleye pollock resource is managed primarily by establishing and updating quotas. While there are other aspects of the management system which affect the harvest of pollock (time/area closures, incidental catch rate restrictions, gear restrictions) it is in the annual determination of the total allowable catch (TAC), or quota, that current fisheries research plays the most important role.

Procedures have been established which allow the most current scientific information on the status of the pollock resource to be presented to the NPFMC in advance of the decision to establish the TAC. At the July NPFMC meeting, the Plan Maintenance Team (PMT), made up of scientists from the principal fishery research and management agencies, presents to the NPFMC and its advisory bodies a resource assessment document (RAD). The RAD attempts to provide the biological information necessary to determine TAC, including:

1) historical catch trend;
2) estimates of maximum sustainable yield of the groundfish complex and its component species groups;
3) assessments of the multispecies and ecosystem impacts of harvesting the groundfish complex at current levels given the assessed condition of stocks, including considerations of rebuilding depressed stocks; and
4) alternative harvesting strategies and related effects on the component species groups.

The RAD is reviewed by the NPFMC, its advisory bodies and the public until September, at which time the NPFMC proposes TACs for the coming fishing year. The NPFMC makes a final decision on the TACs at the December meeting. Any new biological information which becomes available between July and December can be presented to the NPFMC for consideration. It is the responsibility of the PMT to be aware of any new information and to present it to the NPFMC.

The TACs are to be based on socioeconomic considerations, as well as biological assessments. Some of these considerations include:

1) the need to promote efficiency in the utilization of fishery resources, including minimizing costs;
2) the need to manage for the optimum marketable size of a species;
3) the impact of groundfish harvests on prohibited species and the domestic fisheries which utilize these species;
4) the desire to enhance depleted stocks;
5) the seasonal access to the groundfish fishery by domestic fishing vessels;
6) the commercial importance of a fishery to local communities;
7) the importance of a fishery to subsistence use; and
8) the need to promote utilization of certain species.

To date, relatively little socioeconomic information has been available to the NPFMC. Although the PMT is the main advisory body for generating biological and socioeconomic information, there has been less of a commitment on the part of the agencies represented on the PMT to provide the NPFMC with the latter.

In summary, scientific information is used to manage the eastern Bering Sea pollock fishery in a two-step process. Step one is establishing the biological information, with procedures designed to make the information available to the NPFMC and the public, and an opportunity to incorporate new information as it becomes available up to the time TACs are set. The second step is consideration of socioeconomic information. This part of the process suffers from a paucity of information and a lack of well-defined procedures for making such information available to the NPFMC.

FISHERIES AND ECONOMICS SUBGROUP

The first products of the pollock ecosystem workshop were a list of actions that might be taken to manage eastern Bering Sea fisheries and a list of indicators of the ecological and economic well-being of these fisheries. The economic indicators include 1) catch by species age, size, and gear type; 2) variability of catch; 3) profit by gear type and vessel class; and 4) price by species. The actions affect the constraints faced by those who harvest and process fishery resources and are, therefore, inputs of the fisheries economics submodel. The other inputs include outputs from the other submodels and what will collectively be referred to as market conditions. These include the demand for fishery products; the price and availability of inputs such as capital and labor; harvesting, processing, and marketing technologies, and their determinants which would include tax incentives, contractual arrangements, and other institutional factors.

The objectives of the fisheries and economics subgroup were to develop a conceptual model of 1) how those who harvest, process, and market fishery products respond to changes in the regulatory, market, oceanographic, and biological environments in which they operate; and 2) how these responses affect economic indicators and area, age, and species specific fishing mortalities. Such a conceptual model could guide the development of an analytical model. The analytical model could then be used to estimate the effects of alternative sets of fishery management actions on economic indicators and fishing mortalities.

The subgroup's efforts were concentrated on developing a conceptual model for the harvesting sector. This model, however, should be considered preliminary because issues concerning market analysis, the estimation of production functions, and fleet behavior are unresolved.

The basis of the model is necessarily a behavioral assumption. Such an assumption can be stated in terms of the objectives of individual decision makers. Possible objectives include the maximization of expected profit, catch, revenue, or utility; the minimization of the cost or effort associated with a given level of catch; or a combination of these. Although objectives are thought to vary by fleet and nation, it is not clear which objective or set of objectives is appropriate for a given fleet. After discussing alternative objectives, it was decided to proceed as though the objective of each fleet was profit maximization constrained by resource availability, fishery regulations, market conditions, and oceanographic factors. Two justifications for this are: 1) with sufficiently broad definitions of revenues and costs and with an appropriate combination of constraints, the profit maximization assumption can be very flexible; and 2) the information necessary to model the fishery under alternative assumptions tends to be a subset of that required under the assumption of profit maximization. The assumption that decisions are made at the fleet level is not restrictive because fleets can be defined as narrowly as is necessary.

Profit is the difference between total revenue and total cost. Total revenue, total cost, and therefore profit, are functions of effort, a variable individual fleets control, and other variables which individual fleets do not control. Therefore, a fleet is assumed to allocate its fishing effort temporally, spatially, and between gear in the manner that will maximize its annual profit subject to the constraints it faces.

The smallest unit of effort data available is typically a trawl hour; however, for many purposes, such as estimating variable costs, an aggregate unit of measure is more useful. For this reason, a standardized effort unit will be defined for each fleet, area, and quarter based on seasonal operating characteristics. The use of effort as a composite input consisting of a fixed combination of various categories of capital, labor, and other inputs is a simplification which may be acceptable in terms of the short-run decision making that occurs during a fishing year. However, it should be noted that the assumption of a fixed mix of inputs is not equivalent to the standard short-run assumption of at least one fixed input.

Microeconomic production theory can be used to both formulate and solve the profit maximization problem confronted by fleets. Each fleet must decide 1) how to allocate its total effort among areas, depths, months or quarters, and gear configurations; and 2) what its total effort will be. The allocation problem confronting a fleet can be more easily understood if we consider a two-dimensional example. Assume that effort is only allocated between two areas and that there are no depth, temporal, or gear allocation decisions to be made. The efficient allocations of effort between the two areas are those which minimize the input cost of alternative levels of output or equivalently those that maximize the output for alternative input costs. Such allocations are depicted in Figure 8 by the points of tangency between the isocost and isorevenue curves. Output is measured in monetary terms because the results of applying effort in different areas are expected to be different combinations of fish for which a physical measure of output is not meaningful unless ex-vessel prices are equal for all species.

The input costs and levels of output together with the levels of total effort associated with these efficient allocations define total cost and total revenue curves. These curves can be used to identify the profit maximizing level of effort of a fleet. The position and shapes of the isocost and isorevenue curves and therefore the efficient allocations of effort and the profit maximizing level of effort are functions of:

1) the cost of a unit of effort in each area, and

2) the productivity of a unit of effort in each area.

The cost of a unit of effort is a function of the following interdependent factors:

1) the combination of inputs that define a unit of effort,

2) the cost of individual inputs,

3) the number of units of effort being used, and

4) the harvesting technology.

Market prices for input such as fuel, food, and labor provide the basis for calculating most input costs. The cost of vessel time is probably best calculated in terms of opportunity cost, where opportunity cost is determined by the net return to vessel time in the best uses other than those being modeled. The tax structure, contractual arrangements, and other institutional factors can influence input costs.

The productivity of a unit of effort in each area is a function of:

1) physical productivity, and

2) net ex-vessel prices.

Physical productivity is a function of:

1) the harvesting technology,

2) resource availability,

3) the level of effort, and

4) oceanographic conditions

where resource availability is measured in terms of:

1) population by age or size,

2) localized densities, and

3) species assemblages.

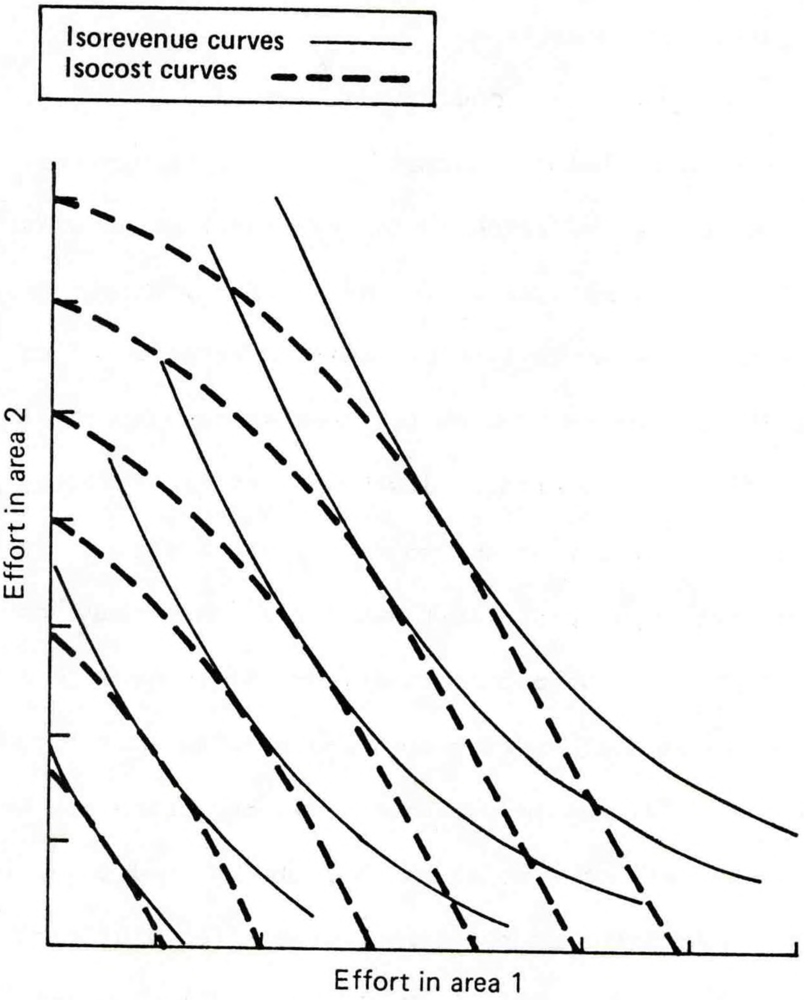

Figure 8.--Plot of isorevenue and isocost curves.

Net ex-vessel prices are functions of:

1) catch or expected catch,

2) roe content,

3) flesh quality,

4) level of parasitism,

5) exogenous market conditions, and

6) fee schedules for target and nontarget species.

The net ex-vessel price is the ex-vessel price minus the poundage fee imposed by fishery managers. In the case of prohibited species or marine mammals, the net ex-vessel price would be negative if there were poundage fees for these species because the species cannot be retained.

Each fleet is assumed to develop an effort strategy prior to the beginning of each fishing year and to reevaluate its strategy each quarter. The effort strategy selected by a fleet for a quarter and the market, regulatory, biological, and oceanographic conditions that occur that quarter jointly determine the economic performance and fishing mortality of the fleet.

The conceptual model outlined above may provide a useful point of departure in the development of a model which could be used to evaluate alternative management strategies or to estimate the effects of past fishery management policies. The development of such a model will require that the following conceptual gaps be eliminated.

1) The functional forms and parameters of the model have not been specified due to both unresolved issues and a lack of data.

2) The decision making processes of fishermen-vessel owners and fishery managers, including their attitudes toward risk, are not well understood.

3) Future market conditions are particularly difficult to predict in the case of a fishery that is just beginning to develop.

4) The allocation of fixed costs among fisheries has not been adequately addressed.

5) The appropriate definition of opportunity costs has not been determined.

6) The definitions of several variables in the model are not well specified; examples include resource availability, roe content, flesh quality, and oceanographic conditions.

ACKNOWLEDGMENTS

The conceptual model discussed above is the product of the diverse contributions of the individuals who participated as members of the Fisheries Economics subgroup. Besides the authors, members include: Eric Anderson, Philip Chitwood, Robert Everitt, Arthur Gallagher, Wayne Getz, Douglas Larson, Richard Marasco, and Lewis Queirolo. The preparation of this chapter has benefited from review comments made by these individuals and Gary B. Smith.

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APPENDIX

Annotated Bibiliography

Agnello, R., and L. Anderson. 1977. Production relationships among interrelated fisheries, In L. Anderson (editor), Economic impacts of extended jurisdiction., p. 157-193. Ann Arbor Science, Inc., Ann Arbor, Michigan.

The purpose of this chapter is to estimate yield or production functions from stocks of marine fish when it is believed that there is a biological or technological interrelationship between the different species. For a theoretical discussion of this problem, see Anderson (1975). Two different models are tested, each using two different measures of fishing effort. The chapter is divided into four sections, the first of which contains a derivation of the two models. The second describes the data used and shows how they are adapted to the model and how the various measures of fishing effort are derived. The third section presents the empirical findings, and the fourth section discusses the use of the results for fisheries management. (chapter introduction)

Agnello, R., and L. Anderson. 1981. Production responses for multispecies fisheries. Can. J. Fish. Aquat. Sci. 38:1393-1404.

Production equations are estimated for five major species of fish harvested in the Northwest Altantic including Atlantic cod (Gadus morhua), haddock (Melanogrammus aeglefinus), flounder (Pleuronectiformes), redfish (Sebastes marinus), and herring (Clupea harengus) using data collected by the International Commission for the Northeast Atlantic Fisheries from 1960 to 1974. A log-linear regression specification is used in which the relationship between catch of a vessel and several factors including days fished and vessel characteristics is estimated simultaneously. Vessel characteristics are represented as (0,1) categorical variables, and include a variable indicating the target species designated by the caption. Various settings for the target species variables allow the estimated equation to represent either a by-catch or target catch equation. The production parameters estimated by the regressions are used to analyze the effects of current quotas set by the New England Fisheries Management Council. For some fleets we find a likelihood of idle capacity given the current quotas. (journal abstract)

Anderson. L., A. Ben-Israel, G. Curtis, and C. Sarabun. 1981. Modeling and simulation of interdependent fisheries, and optimal effort allocation using mathematical programming. In K.B. Haley (editor), Applied operations research in fishing, Volume 10, p. 421-438. NATO Conference Series. Plenum Press, New York.

In this paper, both simulation and mathematical programming techniques are discussed as approaches to the analysis of fisheries management policies. Simulation modeling provides the best tool at present for evaluating alternative management policies in fisheries with complex interactions. Mathematical programming can be used under more simplified assumptions to determine optimal harvest levels and optimal effort allocations in fisheries, subject to relevant constraints.

Fishery interdependencies considered in this paper are both biological and technological. Biological interdependencies exist when fish stocks exist in either competitive or predator-prey relationships. Technological interdependencies exist when the harvest of one stock of fish leads to by-catch of another stock.

The simulation model incorporates both types of interdependencies. Biological and economic sectors of the model are linked by the amount of fishing days (effort) produced by the fleet, which effects the stocks of fish through fishing mortality. The authors have found appropriate parameter values of the model to be difficult to specify, particularly the catch coefficient and relative vessel power parameters. Each fishing vessel of a certain type is assigned the same relative fishing power coefficient. Each cohort of each species has the same relative catch coefficient. The model simulates profit levels, consumer surplus (given a specified demand curve), the effects of various management options such as quotas or taxes, and vessel entry-exit.

The mathematical programming model derives optimal allocations of effort according to a specified maximization criterion, subject to specified constraints. For example, maximizing the discounted present value of a fishery subject to contraints of biological (conservation), techological (capacity), and political (employment) type.

Further information and documentation of the programs used may be obtained for the authors at the University of Delaware.

Beddington, J., and R. May. 1977. Harvesting natural populations in a randomly fluctuating environment. Science (Wash., D.C.) 197:463-465.

As harvesting effort and yield are increased, animal populations that are being harvested for sustained yield will take longer to recover from environmentally imposed disturbances. One consequence is that the coefficient of variation (the relative variance) of the yield increases as the point of maximum sustained yield (MSY) is approached. When overexploitation has resulted in a population smaller than that for MSY, high effort produces a low average yield with high variance. These observations accord with observed trends in several fish and whaling industries. We expect these effects to be more pronounced for a harvesting strategy based on constant quotas than for one based on constant effort. Although developed in an MSY context, the conclusions also apply if the aim is to maximize the present value of (discounted) net economic revenue. (journal abstract)

Bockstael, N., and J. Opaluch. 1981. Discrete modeling of supply response under uncertainty: the case of the fishery. J. Environ. Econ. Manage. 10:125-137.

In the absence of complete control in a regulated industry, effective management requires prediction of firms' behavioral response to public policy. This paper develops a discrete choice model of supply response under uncertainty and applies it to fishery choice problems of New England fishing firms. While fishermen demonstrate a bias towards remaining within the same fishery, sufficient incentives, in terms of changes in expected returns and risk, are shown to elicit response. Due to extreme uncertainty concerning population dynamics of fish stocks, a satisfying approach to managememt, facilitated by this type of modeling, may be more appropriate than bioeconomic optimization. (journal abstract)

Carter, C. 1981. Multi-fishery activity in Oregon commercial fishing fleets: an economic analysis of short-run decision-making behavior. Ph.D. Thesis, Oregon State Univ., Corvallis, 200 p.

This thesis focuses on short-run decision-making behavior of Oregon trawl fishermen for the period 1974-79. Several models of the shortrun allocation of fishing time by a multi-purpose vessel operator are developed. Fishermen are hypothesized to react to expectation about economic returns in the fisheries which they can exploit. Simple Nerlovian agricultural supply response models are adapted for the statistical analysis of fishing time allocation. Fishermen's short-run behavior is hypothesized to depend on expectations of current rather than normal returns to fishing time. Four versions of a model which explain allocation of fishing time for a stable subfleet of trawl vessels are estimated using ordinary least squares regression.

Monthly days of fishing by fishery were significantly explained by variables representing expected gross revenues per unit of effort, weather conditions, and seasonal regulations. The analysis also indicates that fishermen are able to respond rapidly to perceived variations in gross returns.

Regulatory implications are that 1) fishery managers need to monitor the effects of regulation with little delay, and 2) the use of taxes and subsidies to shift significant amounts of effort among fisheries is not likely to be successful. (from author's abstract)

Clark, C. 1973. Profit maximization and the extinction of animal species. J. Polit. Econ. 81:950-961.

In this paper, I construct and analyze a simple mathematical model for the commercial exploitation of a natural animal population. The model takes into account the response of the population with decreasing population levels and the preference of the harvesters for present over future revenues. The principal conclusion of the analysis is that, depending on certain easily stated biological and economic conditions, extermination of the entire population may appear as the most attractive policy, even to an individual resource owner. (journal abstract)

Clark, C., and G. Munro. 1980. Fisheries and the processing sector: some simplications for management policy. Bell J. Econ. 11:603-616.

This paper discusses the economics of the commercial fishing industry under the hypothesis of independent harvesting and processing sectors (although the possibility of integration is also discussed briefly). The analysis is based on an explicitly dynamic fishery model. The competitive and monopsonistic cases are discussed in detail and compared with the social welfare optimum.

The implications for governmental regulation are also investigated. (journal abstract)

Conrad, J., J. Kirkley, and D. Squires. 1982. Lectures on the economics of fisheries production. Papers presented at the National Marine Fisheries Service Workshop on Fisheries Economics, Orlando, Florida, November 3-5, 1982, 67 p.

These lectures are an attempt to review the relatively recent advances in dynamic modeling and production theory as they relate to the economic management of single- and multiple-species fisheries. They will also assess the impediments to applying modern production theory when estimating bioeconomic parameters.

In the first lecture, Jon Conrad reviews the relationship between (a) the production function, (b) the growth function, and (c) the yield-effort function for the single-species fishery and extends these concepts to the multiple-species fishery using the multiple-output production function. The promise and problems inherent with duality-based approaches to estimating biosocioeconomic parameters are briefly discussed.

In the second lecture, Dale Squires reviews the early literature on fisheries production and examines in greater detail the assmptions underlying duality-based estimation techniques as they relate to multispecies production.

In the third lecture, Jim Kirkley discusses his recent empirical work on the New England trawler fleet. While the landings of individual species are aggregated into a single output index, two measures of effort are employed, and factor shares from the econometric analysis are compared with the results obtained from a cost simulator.

A common theme running through all three lectures is the need for better data, particularly input and cost data, if duality-based theory is to be successfully applied to multispecies fisheries. With a better understanding of models and methods, it is hoped that economists within the National Marine Fisheries Service and academia might be more effective in working together to establish the data base necessary for modern production analysis. Such analysis would seem necessary, though not sufficient, for rational fisheries management. (authors' preface)

Hanna, S. 1983. The economics of uncertainty: a survey of the literature on uncertainty with particular reference to the fishery. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-47, 193 p.

The literature on the economics of uncertainty covers a diverse range of topics. The scope of this review is restricted to a representative number of papers in those areas of the literature rather than an exhaustive bibliograhy. Papers are selected whose theoretical focus helps clarify and define particular problems of uncertainty that affect the fishery.

The literature reviewed covers nine general subject areas. Commonly used measures of levels of uncertainty, probabilities, and their interpretation are discussed in reference to their applicability to fisheries problems. The concept of probability helps clarify the role of information as a resolver of uncertainty. The use of information in individual and group decision making is examined along with the various risk indicators used by analysts to evaluate decision making.

Uncertainty affects the efficiency of resource allocation over time. Concepts of equilibrium are also modified under conditions of uncertainty, requiring the specification of explicit disequilibrium models in some circumstances. As a response to disequilibrium, economic adaptation includes the processes of learning, expectation formation, search, strategy development, and selection. The final topic covered by the review is the impact of uncertainty on the strength of property rights, with particular emphasis on problems in the management of open access fisheries.

Hannesson, R. 1983a. Optimal exploitation of cod and capelin in the Barents Sea: a study of species interdependence. Unpubl. manuscr., Inst. Econ., Univ. Bergen, Norway.

This paper deals with the relation between cod and capelin in the Barents Sea. On the basis of an apparent relation between the growth of cod and the abundance of capelin, a simple model of the two species is formulated. At the prices and fishing costs presently prevailing in Norway the Arcto-Norwegian cod seems likely to lead to a decline of the capelin fishery by a half or more. Such extreme solutions as depletion of the cod stock in order to increase the abundance of capelin, or entirely indirect utilization of the capelin as a source of food for the cod, do not seem likely as optimal solutions at the present level of prices and costs. The optimum fishing mortality of cod is shown to be appreciably higher in this two-species model than in single species models currently used by management authorities. (abstract from Fisheries Economics Newsletter)

Hannesson, R. 1983b. Optimal harvesting of ecologically interdependent fish species. Unpubl. manuscr., Inst. Econ., Univ. Bergen, Norway.

The optimal exploitation of a two species predator-prey system is considered, using Lotka-Volterra type equations. Due to the density dependence of ecological efficiency, both species should be harvested simultaneously over a range of relative prices. Beyond the limits of this price range, either the prey species should be utilized indirectly by harvesting the predator, or the predator should be eliminated in order to maximize the prey yield. Neglecting harvesting costs, the simultaneous harvest of prey and predators requires that a unit of prey biomass increase in value by being "processed" by predators.

Certain results from single species fishery models are shown not to apply to multispecies models. These are as follows:

1. Optimal regulation of a free access fishery may call for subsidizing instead of taxing the harvest of predator species;

2. Increasing the discount rate may, at "moderate" levels, imply that the optimal standing stock of biomass increases instead of decreases;

3. A rising price or falling cost per unit fishing effort of a species may raise and not lower the optimal standing stock of that species. (abstract from Fisheries Economics Newsletter)

Hilborn, R. 1976. Optimal exploitation of multiple stocks by a common fishery: a new methodology. J. Fish. Res. Board Can. 33:1-5.

Optimal harvest rates for mixed stocks of fish are calculated using stochastic dynamic programming. This technique is shown to be superior to the best methods currently described in the literature. The Ricker stock recruitment curve is assumed for two stocks harvested by the same fishery. The optimal harvest rates are calculated as a function of the size of each stock for a series of possible parameter values. The dynamic programming solution is similar to the fixed escapement policy only when the two stocks have similar Ricker parameters, or when the two stocks are of equal size. Normally, one should harvest harder than calculated from fixed escapement analysis. (journal abstract)

Holt, S. 1981. Multipurpose fishing behavior under open access and license limitation. Unpubl. manuscr., 24 p.

This paper develops a general theory of multipurpose fishing, where vessels target two different stocks available sequentially over a fishing year. It examines the behavior of unregulated multipurpose vessels and determines the extent to which simple license limitation improves resource allocation. The model assumes homogenous vessels, constraints on the physical length of fishing seasons, and declining daily stock abundance. The analysis shows (1) the open access fleet is characterized by excessive size, effort, and harvest, (2) vessel effort on the more profitable stock is generally insufficient, (3) vessel effort on the less profitable stock may be excessive (due to excessive fleet size), (4) license limitation is generally ineffective at improving resource allocation unless the fleet is reduced sufficiently to constrain the fishing season on the more profitable stock, and (5) increased capacity utilization as a signal of Pareto-improving change in a single-stock fishery may be entirely inappropriate in a multipurpose fishery. Suggestions for appropriate management policy are made. (author's abstract)

Hoppensteadt, F., and I. Sohn. 1981. A multiple species fishery model: an input-output approach. _In_ K. B. Haley (editor), Applied operations research in fishing, Volume 10, p. 115-124. Nato Conference Series. Plenum Press, New York.

Fisheries have been transformed from renewable to nonrenewable resources through overuse during a 35-yr post-war period characterized by an absence of conflict among developed nations. The status of fisheries makes it imperative to design workable policy measures. However, practical policy measures are difficult to formulate because an appropriate modeling framework is lacking.

Interdependencies in the fishery--both direct and indirect--suggest a Leontief input-output approach based on a structural description of system components. The model in process discussed by the authors includes both biological and economic components, but only biological components are discussed in this paper. The model consists of an ecology matrix, a renewal matrix, and an exogenous demand vector for several groundfish species. The four biological parameters of the model are the food intake coefficient, mortality rates, stock recruitment rates, and fish landings.

The input-output framework allows one to look at different management strategies based on different sets of assumptions regarding changes in parameters. The particular parameter values chosen determine the quantitative estimate of fish stocks required to sustain the system. The modeling methodology used by the authors is to describe the structural relations of the system to encourage the collection of relevant data, rather than to build the model around existing data. The authors propose to refine and modify the input-output framework to incorporate nonlinearities, by-catch, time lags, and economic components.

Huppert, D. 1979. Implications of multipurpose fleets and mixed stocks for control policies. J. Fish. Res. Board Can. 36: 845-854.

Management of harvests from mixed stocks and multipurpose fleets requires the use of concepts not discussed in single species fishery models. Optimum harvest of a group of mixed stocks implies that an aggregate objective pertaining to the multispecies catch is maximized. This usually prohibits the attainment of the maximum economic yield for each individual stock. Operation of a multipurpose fleet is economically justifiable when there are significant annual or seasonal fluctuations in fish stock abundance. A simple linear model is developed in this paper to demonstrate how the multipurpose fleet can be a necessary part of rational management. (journal abstract)

McKelvey, R. 1982a. Economic regulation of targeting behavior in a geographically extensive multispecies fishery. Univ. Mont., Missoula, Math. Dep., Interdisciplinary Ser. No. 19A, 28 p.

This paper presents a model of a multispecies, geographically extended fishery in which fishermen target on particular aggregations of fish, for the purpose of evaluating short-run regulatory controls. With multiple species and geographically dispersed pools of fish, shadow charges to achieve efficient regulation must vary over species and over space, as well as over time. Computation of shadow charges requires knowledge of costs and operating efficiencies of all vessels. Taxes and quota markets are found to be equivalent management schemes under complete information, but each impose different information requirements on fishermen. In an uncertain environment, a tax scheme allocates risk between fishermen and management agency; a quota market shifts the burden of risk to the fisherman.

McKelvey, R. 1982b. The fishery in a fluctuating environment: coexistence of specialist and generalist fishing vessels in a multipurpose fleet. Univ. Mont., Missoula, Math. Dep., Interdisciplinary Ser. No. 20, 55 p.

An important feature of many commercial marine fisheries is variability in both fish populations and in market conditions. Multipurpose vessels operating in a variety of fisheries may represent an adaptation to a fluctuating environment: that of the efficiency of specialization being replaced by flexibility to changing conditions. A simple analytical model is presented here to illustrate the behavior of generalist and specialist vessels fishing on a single stock of fish in both the short and long run.

The optimal run capital investment strategy for the socially managed fleet may be seen as the solution of a Markovian optimal control problem using a stochastic maximum principle. Coexistence of specialist and generalist vessel types will be optimal only in a fluctuating world. When rapid capital investment or disinvestment is not possible, optimal policy must show foresight; periods of noninvestment must be accepted, foregoing short-run profit in the interest of long-run welfare. By contrast, in a common property fishery, the expectation is to find excessive total effort and an inappropriate mix of vessel types, with too heavy a reliance on the less efficient multipurpose trawlers. Only direct regulatory intervention such as license limitation may be capable of preventing such entirely myopic investment patterns.

McKelvey, R. 1983. The dynamics of open-access exploitation of a renewable resource: the case of irreversible investment. Univ. Mont., Missoula, Math. Dep., Interdisciplinary Ser. No. 21, 43 p.

In section 1, we model the short-run exploitation of a renewable resource, where all private inputs are flows and no capital adjustments occur. Under these conditions, open access exploitation leads to an efficient time profile of harvest, which may in fact be corrected by a tax on output. Factor proportions then adjust automatically to achieve efficiency.

In section 2, we turn to the long-term processes of capital adjustment. The model includes two stock variables, the resource stock and a stock of productive capital. The flow of harvest output is determined by the resource stock level and the degree of utilization of capital (used in efficient combination with other flow factors). Capital accumulates from investment, which is irreversible, and is eroded by depreciation. One may determine, for free access conditions, the controlling flows of harvest and investment.

In section 3, this open access model is analyzed mathematically, most completely in the special linear costs case for which Clark, Clarke, and Monroe have analyzed optimal management. In section 4, we develop and analyze a normative optimal control model under the more general nonlinear conditions of section 2. Then in section 5, we are able to approach the issues of economic rationalization of the free-access system. (from the author's introduction)

Martin, J. 1979. An evaluation of the economic feasibility of pollock processing in southeast Alaska. Univ. Alaska, Fairbanks, Alaska Sea Grant Rep. 78-16, 123 p.

An economic feasibility analysis of processing walleye pollock, Theragra chalcogramma, was conducted, and the results reported as the wholesale pollock block prices at which the present value of the investment in pollock processing facilities equals zero. These break-even block prices were compared with current market prices of pollock blocks, and it was found that pollock processing is economically feasible under all sets of assumptions evaluated.

A case-study of the Icicle Seafoods, Inc. (ISI) plant at Petersburg, Alaska was undertaken in this work. ISI was the only domestic seafood processor handling pollock at the initiation of the research.

Economic feasibility research in three subject areas is reviewed: 1) food processing, 2) aquaculture, and 3) seafood processing. The aspects of each study relevant to pollock processing feasibility are emphasized.

Some of the more critical sources of uncertainty with which a pollock processor must deal are explained. Supply variability is found to be the most significant source of uncertainty, although pollock markets, new technology, and the institutional environment are also important sources of uncertainty for the processor.

Various measures of investment worth are evaluated. The Net Present Value (NPV) technique is chosen as an economically valid investment criterion and used in this research. Due to the supply variability problem, future volumes of production cannot be accurately predicted. The triangular distribution function and Monte Carlo simulation methods are used to generate probability distributions of volumes over the 10 yr investment horizon. Wholesale pollock block price projections over the next 10 yr were not available. Therefore, the NPV equation was solved for the pollock block price at which the NPV of the investment equals zero, for a given set of assumptions.

Results include distributions of the break-even pollock block prices under various production, cost, and discount rate assumptions. The break-even block prices are very sensitive to changes in ex-vessel prices, but quite insensitive to changes in the discount rate. It is found that the current market price exceeds the break-even block prices under all sets of assumptions, and concluded that pollock processing appears to be economically feasible.

Finally, it is noted that the results of the analysis depend on the production cost estimates provided by the personnel of ISI. It is recognized that relying on information from a single firm will produce results which are to some extent unique to that firm. The assumption was made that these results can be used as order-of-magnitude estimates of the expected costs and returns to other seafood processors in southeast Alaska entering pollock production.

May, R., J. Beddington, C. Clark, S. Holt, and R. Laws. 1979. Management of multispecies fisheries. Science (Wash., D.C.) 205:267-277.

Setting maximum sustained yield (MSY) figures for individual species is an inadequate management strategy for multispecies systems. Models of krill-baleen whale interaction are used to illustrate the way multispecies fisheries respond to harvesting at various trophic levels. Economic aspects of harvesting multispecies fisheries are considered primarily for the purpose of improving acceptability and predictability of management regimes. Overexploitation of fisheries arises from the lack of strong property rights among fishermen to current and future fish. Uncertainty in biological systems also has important economic implications and creates conflicting responses by biologists and fishermen. Under uncertainty, biologists will promote conservative management strategies but fishermen will discount future returns heavily and thus show an opposite response. Contingency plans to deal with unexpected changes are especially important for multispecies systems, although proper target levels for various species are difficult to determine. Multispecies systems often exhibit complex discontinuities in response to fishing or environmental change.

The authors reach several tentative conclusions about the management of multispecies systems: 1) for populations not subject to significant predation, MSY may be useful, 2) ecosystem preservation requires that stocks of prey species not be reduced to levels affecting its own or other species' productivity, 3) time scales affecting population processes must be kept in mind, 4) environmental stochasticity will cause population parameter estimates to fluctuate, and 5) multispecies systems have complex biological-economic-political interactions not found in single species systems.

May, R., J. Beddington, J. Horwood, and J. Shepherd. 1978. Exploiting natural populations in an uncertain world. Math. Biosci. 42:219-252.

We consider some aspects of the way random environmental variability can affect fish and other natural populations that are being harvested for sustained yield. A spectrum of 8 stock-recruitment curves, culled from the fisheries literature, is used to study the probability distribution of yield (Y) as a function of the level of exploitation or "effort" (E). If the environmental noise enters via the intrinsic growth rates ("density-independent noise"), the 8 curves are qualitatively in accord in predicting that absolute levels of fluctuation in Y increase as E increases; these trends become strongly marked once exploitation is significantly in excess of the maximum sustained yield (MSY) level. The quantitative details, however, depend on the specifics of the stock-recruitment curve (the CV or relative function of Y can increase or decrease as E increases toward the neighborhood of the MSY level, and the CV can increase relatively dramatically or relatively gradually as E increases beyond this level). The effects of density dependent noise, and of time delays in population regulatory processes, are also briefly discussed. Broadly, the analysis suggests that environmental unpredictability can pose "portfolio theory" trade-offs between desired levels of average yield and of fluctuations or risk. What seems really needed is not further mathematical refinement, but rather robust, self-correcting strategies that can operate with fuzzy knowledge about stock levels and recruitment curves. (journal abstract)

Rothschild, B. 1967. Competition for gear in a multiple-species fishery. J. Cons., Cons. Perm. Int. Explor. Mer. 31:102-110.

The catch-per-unit-of-effort (CPUE) for one species may affect the CPUE of another species in a multiple-species fishery. This effect is studied by means of a simple stochastic model. The model provides a "competition free" CPUE which is never less than the CPUE obtained under competition, is strongly dependent on the empty space on or in the gear, and varies as a function of the proportion of each species. The multinomial structure of the model enabled the derivation of maximum-likelihood estimators of its parameters. Estimates of the large sample sampling variances and covariance of the parameters are also provided. Application of concepts of the model to other fishery problems is discussed, and it is noted that the model also provides a maximum-likelihood estimate for the well-known yield equation. (journal abstract)

Silvert, W., and W. Smith. 1977. Optimal exploitation of a multi-species community. Math. Biosci. 33:121-134.

We consider the problem of exploiting a multi-species ecological community in such a way as to maximize the discounted present value,

$$\int_0^\infty e^{-pt}R(x,h)dt,$$

where R(x,h) is the net revenue obtained by harvesting stocks represented by the population vector x at rates given by the harvest vector h. When the system obeys $x=f(x)-h$ and two mild conditions hold on f and R, we reduce the determination of the optimal equilibrium state and exploitation strategy to the determination of the maximum of a simple scalar function of x. As an example, the method is applied to a generalized multispecies logistic model of a community. (journal abstract)

Tyler, A., W. Gabriel, and W. Overholtz. 1981. Adaptive management based on structure of fish assemblages of northern continental shelves. <u>In</u> M. Mercer (editor), Multi-species approaches to fisheries management advice, p. 149-156. Can. Spec. Publ. Fish. Aquat. Sci. 58.

Difficulties of managing ocean fisheries on a species by species basis arise due to catches of mixed species, data requirements for yield models for the large numbers of species within a region, and problems in accounting for species interactions in yield estimates. Furthermore, models have shown that the goal of yield maximization from an assemblage of species with a range of productivity capabilities leads to a reduction in the number of species that supply the yield. Sustained high productivity of those remaining species may not be possible in the simplified system. There is also the risk that return to the original species composition will not result from subsequent reduction of fishing effort. An operational characterization for management purposes is given for an assemblage production unit of fishes. This unit is a group of trophically coupled, resident species. Temporal and geographical characteristics of component species are selected to make it possible to manage the unit as an entity. Two approaches to adaptive management are proposed. In the adaptive procedure, yield or effort is judged by trial and error, and is also for systems in continuous fluctuation, producing highly variable yields. (journal abstract)

Wilen, J. 1979. Fisherman behavior and the design of efficient fisheries regulation programs. J. Fish. Res. Board Can. 36:855-858.

This paper examines the importance of hypotheses about fisherman behavior for predicting, understanding, and designing efficient fisheries regulation programs. Particular attention is paid to flexible technology fisheries where individuals are free to alter several dimensions of effort. It is suggested that the appropriate hypothesis of share-focused behavior ensures that there will always be an incentive to combine inputs inefficiently, although technical conditions may limit or block the actual ability to do so. Some observations on the success of existing programs are also offered. (journal abstract)

Wilson, J. 1982. The economical management of multispecies fisheries. Land Econ. 58:417-434.

This paper is concerned with developing an economic analysis appropriate to the biological and social characteristics of variable multispecies systems. The argument is based on three fundamental ideas: 1) limitations of knowledge and uncontrolled variation in fisheries constrain the range of economically feasible management options, 2) social costs of rule making and enforcement are high in highly variable environments, and 3) efficiency in variable environments is more closely related to adaptive individual learning behavior than to input cost minimization. These ideas are developed in the context of an institutional theory about the growth of collective mechanisms for the solution of potentially degenerative social situations.

The accepted economic theory of fisheries is misleading in that it tends to direct analysis away from a consideration of many reasonable and economical nonproperty rights policy alternatives. Consideration of "complicating factors"--multiple species, variability, patchiness, search and information costs--tends to lead to the conclusion that the social costs of unregulated fishing are less than traditional economic theory would suggest. These complicating factors indicate higher social costs associated with attempts to regulate. These two effects tend to limit the range of economically feasible management options and appear to create a strong preference for very simple systems of management rules.

APPENDIX 1

PARTICIPANTS OF THE WORKSHOP ON WALLEYE POLLOCK AND ITS ECOSYSTEM IN THE EASTERN BERING SEA

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Acronyms:

CD = Office of the Center Director
CQS = Center for Quantitative Science
CZES = Coastal Zone and Estuarine Studies Division
EC = Environmental Conservation Division
ESSA = Environmental and Social Systems Analysts Ltd.
NMFS = National Marine Fisheries Service
NMML = National Marine Mammal Laboratory
NOAA = National Oceanic and Atmospheric Administration
NWAFC = Northwest and Alaska Fisheries Center
OFIS = Office of Fisheries Information Systems Division
PMEL = Pacific Marine Environmental Laboratory
RACE = Resource Assessment and Conservation Engineering Division
REFM = Resource Ecology and Fisheries Management Division