NOAA ERL Special Report

Bering Sea FOCI Final Report

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Part 1

Introduction

To develop an understanding of stock structure and recruitment variation in Bering Sea pollock, the Coastal Ocean Program of the National Oceanic and Atmospheric Administration (NOAA) funded an 7-year (1991–1997), interdisciplinary project named Bering Sea Fisheries-Oceanography Coordinated Investigations (BS FOCI; Schumacher and Kendall, 1995) for which NOAA and academic researchers were selected through a competitive process (Macklin, this report). The project goals, based on recommendations from an international symposium on pollock (Aron and Balsiger, 1989) were to (1) determine stock structure in the Bering Sea and its potential relationship to physical oceanography, and (2) examine recruitment processes in the eastern Bering Sea. Both of these have direct implication to management. An integrated set of field, laboratory, and modeling studies were established to accomplish these goals. To address the first goal, project objectives were to establish details of oceanic circulation relevant to larval dispersal and separation of stocks, and determine if unique chemical or genetic indicators existed for different stocks. The recruitment component of BS FOCI, addressing the second goal, focused on understanding causes of variable mortality of pollock larvae in the different habitats of the eastern Bering Sea. The emphasis of recruitment studies was to determine the dominant physical oceanographic features (turbulence, temperature, and transport) that could influence survival of pollock larvae, and investigate factors controlling food production for the larvae. A later component contrasted juvenile habitat in three hydrographic regimes around the Pribilof Islands (Brodeur, this report).

BS FOCI field studies included 20 cruises to the area, deployment of four long-term biophysical moorings (some of which supported meteorological sensors), use of over 40 satellite-tracked drifters, and a series of aircraft overflights (NOAA P3) using meteorological and ocean surface color and temperature sensors (Macklin, this report). Laboratory studies examined genetic relationships, chemical composition of otoliths, assays of pollock larval condition, and pollock larval feeding mechanisms and patterns. Modeling activities included basin circulation, one-dimensional nutrient-phytoplankton-zooplankton-fish relationships, and ecosystem aggregations.

This report comprises six parts. Part 1 is this Introduction. Part 2 discusses BS FOCI's first goal, stock structure, and part 3 addresses BS FOCI's second goal, recruitment studies. Parts 4 and 5 present administration and management of the project, and technical achievements, respectively. A list of BS FOCI publications, numbering about 70 at the time this report was written, is part 6 of this report.

Part 2

Population ecology and structural dynamics of walleye pollock, *Theragra chalcogramma* (Kevin M. Bailey[1])

Executive Summary

New paradigms for managing fisheries in a sustainable manner are under development; these renovated concepts will include better definitions of stock distributions, interrelationships, and conservation. Management of many marine fisheries has been based on the assumption of shallow (little) population structure with considerable gene flow. However, recent studies of several species (previously assumed to be panmictic) using high resolution techniques indicate more genetic structure than was found previously. These results have implications for effective management, as overfishing of local stocks can deplete the productivity of the larger (meta) population. A summary view of genetic structure in walleye pollock suggests a pattern of considerable geographic stock structure. Phenotypic differences between stocks, elemental composition of otoliths, and parasite studies indicate restricted mixing of juveniles and adults. Genetic differences appear between broad regions, but resolution between adjacent stocks, especially within the eastern Bering Sea, is currently lacking. Genetic studies to date indicate a varying degree of genetic differentiation between pollock in the Gulf of Alaska and Bering Sea. The potential for gene flow during larval drift is high between adjacent stocks, but since there appears to be an unresolved degree of structuring within the Bering Sea, reduced gene flow due to larval retention mechanisms or strong natal homing and philopatry is possible. Significant progress has been made in understanding the genetic structure of pollock.

2.1 Introduction

Walleye pollock is among the world's largest commercial fisheries with annual harvests ranging from 4 to 7 million tons in the North Pacific Ocean over the past decade. In U.S. waters catches are on the order of 1.5 million metric tons with a dollar value exceeding hundreds of millions. A large portion of the resource is bound for the export market, contributing to reduction of the U.S. trade deficit. Without question, this natural resource is of critical importance to the health of domestic fisheries. Pollock is the dominant groundfish species in many of the regional ecosystems across the North Pacific Ocean, including the eastern Bering Sea, and has been implicated in the dynamics of higher trophic levels (see National Research Council, 1996). As a key element in the North Pacific ecosystem, pollock is the target species for numerous research programs, past and present, in the eastern Bering Sea as well as in other seas. The stock structure of pollock is important knowledge

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for management of this resource because of the potential for overfishing of local stocks when it is assumed that large basin populations are panmictic.

The stock structure of pollock across the North Pacific Ocean, and especially in the Bering Sea, has been a topic of investigation for many years. Many early studies were based on pollock's phenotypic characteristics, such as meristics and morphometrics, and other studies have been based on genotypic characters, such as DNA analyses. In general, biochemical genetic studies have weakly distinguished eastern Pacific populations from western Pacific populations, but phenotypic characters suggest a more detailed stock structure. Only recently, using high resolution molecular techniques (Powers, unpublished data: reported here) has there been good resolution between populations on either side of the Bering Sea and between Gulf of Alaska populations and eastern Bering Sea populations.

Fisheries resource management is based on the concept of renewable stocks. For walleye pollock the regional stocks are managed separately; for example, the Gulf of Alaska population is managed separately from the Bering Sea, and the eastern and western Bering Sea and Aleutian Basin populations are managed separately. However, there may be isolated populations on even finer scales; within the Gulf of Alaska there may be separate spawning populations in Shelikof Strait, Prince William Sound, and the Shumagin Islands region. Furthermore, the degree of intermingling of stocks, recolonization of depleted areas from healthy stocks, and other ecological questions about resource mixing within the greater population framework are almost completely unknown.

Although the overall catch of pollock on the U.S. side of the North Pacific Ocean is relatively stable, some populations have experienced declines and fisheries closures in recent years, including stocks in Puget Sound, Shelikof Strait, Donut Hole, and Bogoslof Island. More recently, there are reports that the western Pacific stocks are in a state of decline. Although eastern Bering Sea shelf populations have been at healthy levels in the past, there is concern about the sustainability of present harvest levels.

Pollock harvests were especially high from the mid-1980's through about 1992 resulting from relatively strong recruitment, high abundance levels, and unrestricted high seas fisheries. Wespestad (1996) lists 12 geographically distinct stock (although not necessarily genetically distinct) groupings and their catch trends (Table 2.1). Biomass and catch trends for the major stock groupings indicate generally declining levels since the late-1980s in the major fishing grounds (Figs. 2.1a, b). The greatest declines in biomass and catches for pollock have been away from the center of pollock's biomass. For example, in the Gulf of Alaska, catches peaked at 307,000 tons in 1984 and have declined to 55,000 tons in 1996. At the extreme southern end of its range in the eastern North Pacific, pollock in southern Puget Sound may almost be extinct (Palsson *et al.,* 1996). Likewise for the southern end of its range in the western North Pacific around northern Japan, catches are reduced by 3 to 4 times from their maximal values in the 1970's (H. Yoshida, Hokkaido Central Fisheries Experimental Station, Hamanaka 238, Yoichi-cho, Hokkaido 046, Japan, personal communication, February 1994).

There are many complex and unresolved issues involving the structure of

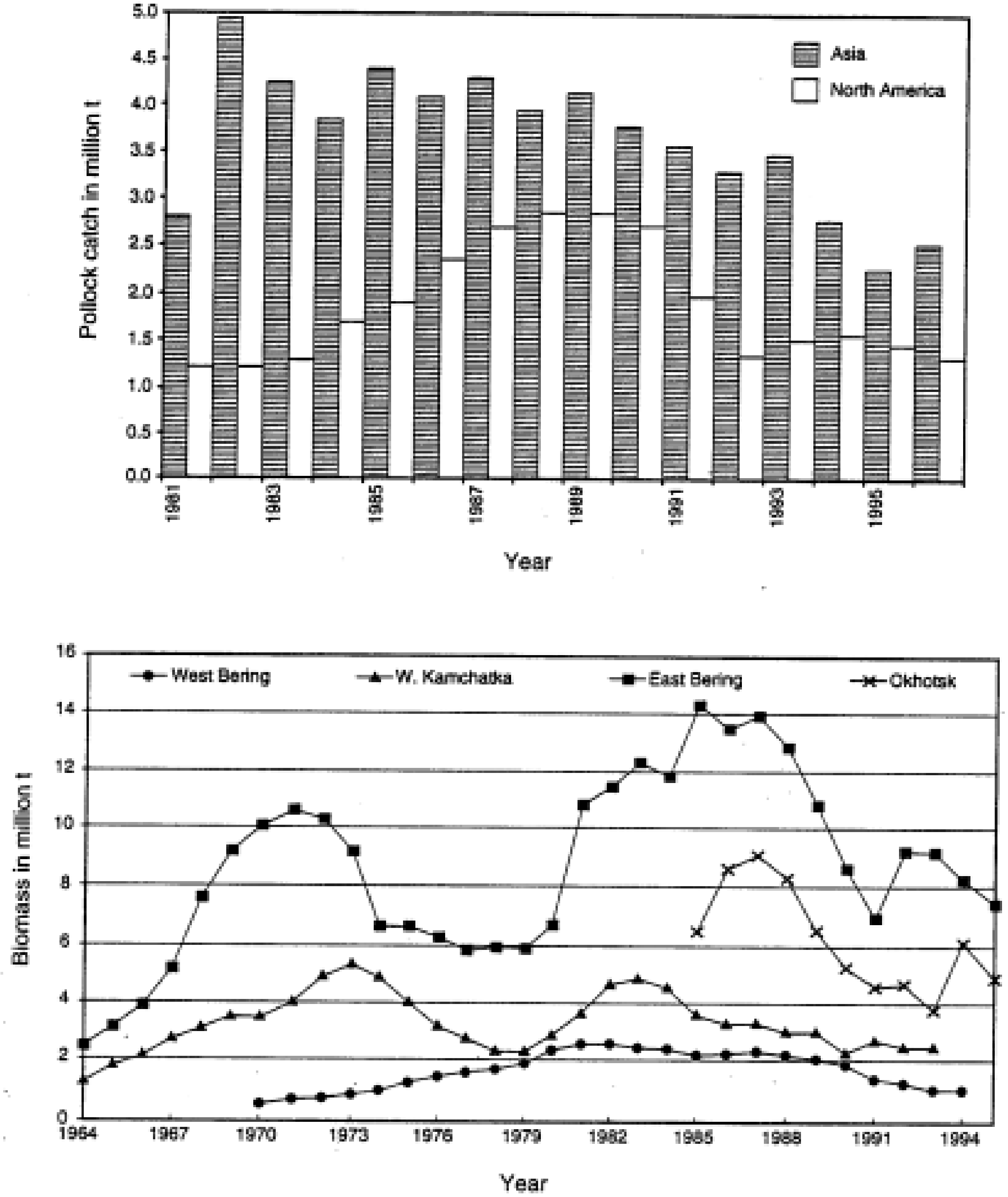


Figure 2.1: Trends in major stock grouping of walleye pollock: (a) Abundance trends for major stocks, (b) catch trends for Asian and North American stocks (from Wespestad, 1996).

Table 2.1: Geographical distribution of walleye pollock stocks according to Wespestad (1996).

Stock	**Stock characteristics**
	North American
Southeast Alaska-Canada	Small stock—minor fisheries
Western-Central Gulf of Alaska	Variable stock, 50,000–200,000 t catch
Eastern Bering Sea	Large stock, 1–2 million t catch
	Asian
Northwest Bering Sea	Mix of U.S. and Russian fish, 0.5–1 million t catch
Western Bering Sea	Moderate stock, 0.5–1 million t catch
East Kamchatka	Small-medium stock, 100,000–300,000 t catch
West Kamchatka	Large stock, near 1 million t catch
North Sea of Okhotsk	Moderate stock, 0.5–1 million t catch
Sakhalin	Small stock, 65,000 t average catch
Kuril Islands	Small-moderate stock
Japan Sea	Heavily fished
Japan Pacific	Moderate catch to 0.5 million t

the pollock population, including recent stock declines, discoveries of heretofore unknown stocks, potential consequences of fishing on certain elements of the population, possible relationships between subunits, and potential fishing pressure on the same subpopulation at different times from different geographic and quota regions. What is needed, but currently lacking, is an understanding of the macroscale population ecology of pollock that incorporates the relationship among different subpopulations of the greater metapopulation, the rate of gene flow between these subpopulations, the relationship between juvenile and adult distributions as linked together by ontogenetic migrations, and the magnitude of colonization processes. A theoretical framework about the geographical structure and population ecology of pollock needs to include recently developed ecological concepts that can help us better understand the dynamics of this species and consider new approaches to management. One such concept is macroecology, the study of patterns of distribution of organisms in relation to their environment (Brown, 1995). Many of the macroecological questions regarding pollock are unanswered, such as the relationship between range size and population abundance, and the effect of environmental factors on distribution of pollock. Another recent concept is that of metapopulation dynamics, the study of conditions by which the processes of population turnover and establishment of new populations are maintained in balance (Hanski and Gilpin, 1991). Viewing pollock in the context of a metapopulation is a framework to study the linkage of stock structure, dispersal, and colonization events.

In this report, the concepts of macroecology, metapopulations, and stock structure are reviewed and areas where they intersect are indicated. Historical and current information on pollock, including mechanisms that may isolate and maintain stock structure, are summarized and a "strawman" conceptual model of the population macroecology of walleye pollock is proposed.

2.2 Theoretical Framework: Structural Dynamics

The size of fish populations is determined by three major elements: (1) available habitat determines the potential size, (2) dynamics within local populations as influenced by the environment, competition, and predation determine the specific size of a subpopulation, and (3) movement and colonization determine the spread of a population and modify local dynamics. In this model, distribution, dispersal, and population structure are closely linked, interwoven characteristics of metapopulations.

A population is a group of individuals of the same species living within a sufficiently restricted area such that any member can mate with any other; in large widespread populations it is recognized that individuals in the same locality are more likely to mate and share common ancestry. Thus local subpopulations can be made of largely intrabreeding units of geographically structured populations. Geographical structure in populations is the non-random pattern of spatial distribution that may be related to historical or current barriers between local populations, environmental patchiness, and/or environmental gradients. The term structural dynamics integrates change in population structure, and aspects thereof, such as range, genetics, and dispersal patterns.

2.2.1 Distribution and Macroecology

Geographic range considerations are an important characteristic of populations. Species with broad niches become both widespread and locally abundant (Brown, 1984), and large ranges, abundance, and invasion ability are linked characteristics within a species (Lawton *et al.,* 1994). Species with extraordinary invasion abilities are generally those best adapted for marginal habitats (MacArthur and Wilson, 1967). As described below, these concepts are especially relevant to pollock population biology. On the other hand, specialized feeders, such as benthic feeding flatfishes, would appear to be tied to specific habitat requirements; thus they cannot move and colonize new habitats freely as adults or settled juveniles compared with species that have more generalized requirements. Furthermore, where the range of a species with specialized requirements is made of a mosaic of habitat patches, colonization by demersal stages may be impeded by regions of unfavorable habitat.

Some populations may expand their range as they become more abundant, although others do not show this trend but show increases in local density. As noted above, species with highly specialized niches may not expand readily, and indeed no range/abundance relationships have been found for some specialized flatfish species such as rock sole, Alaska plaice (McConnaughey, 1995), and American plaice (Swain and Morin, 1996). Thus for these species, the range size/population size relationship due to density-dependent dispersal may not occur. More generalized species such as Atlantic cod (Swain and Wade, 1993) and arrowtooth flounder (McConnaughey, 1995) expand their range as abundance increases.

Range expansions may be limited by physical impediments, such as temperature, salinity, and substrate availability, and by biological factors, including the presence of competitors and predators. There is also historical structure in the environment, such as changes in the occupation of niches due to disease and environmental events. Often when competition or predation pressure is removed there is an "ecological release" (MacArthur and Wilson, 1967), resulting in an invasion event.

2.2.2 Metapopulations and Geographical Structure

Within the distributional range of animals, there may be considerable structure. The realization that animal populations are composed of local populations has a rich history going back to Andrewartha and Birch (1954). In fisheries, knowledge of local populations goes back to the developments and ideas of Schmidt, Heincke, and Hjort in the early 1900s (Sinclair, 1988). The concept of population structure was formalized as that of metapopulations by Levins (1970). In the metapopulation view, a local population is the spatial unit within which most interaction such as breeding occurs, and a metapopulation is an ensemble of local populations (Taylor, 1991a) with some potential of interaction.

Harrison (1991) showed five potential types of metapopulations with examples of their degree of dependency and interaction (Fig. 2.2). These include: (a) the Levins metapopulation, where population sizes are nearly equal and all populations interact and habitats are patchy within the range area; (b) the core-satellite (Boorman and Levitt, 1973) metapopulation where habitats are patchy within the range, but one major population is the source of fringe populations; (c) the patchy population, where habitats are continuous throughout the species range, but local populations are aggregated; (d) non-equilibrium population, which is like the Levins model except that there is no movement between local populations; and (e) an intermediate model between (b) and (c). According to Harrison (1991) the dominant metapopulation structure is that of a large local population in a large favorable habitat patch, surrounded by relatively unstable populations in smaller habitat patches. This is similar to the mainland/island population structure of MacArthur and Wilson's (1967) theory of island biogeography.

In the metapopulation view, local subpopulations are connected by dispersal, which include larval dispersal and colonizing movements of adults. Migrations, which are movements of individuals coordinated in space and time (Quinn and Brodeur, 1991), can be ontogenetic, seasonal, or daily. These migrations are distinguished from dispersal or nomadic behavior, which is undirected and out of the natal or home range. Dispersal can occur due to environmental factors, such as El Niño events, and also due to density-dependent effects. As demonstrated for some fishes, fidelity to home range depends on habitat quality (Matthews, 1990), which can depend on density. The advantages of dispersal are colonization of new habitats and avoidance of unfavorable local conditions (Quinn, 1993). The effectiveness

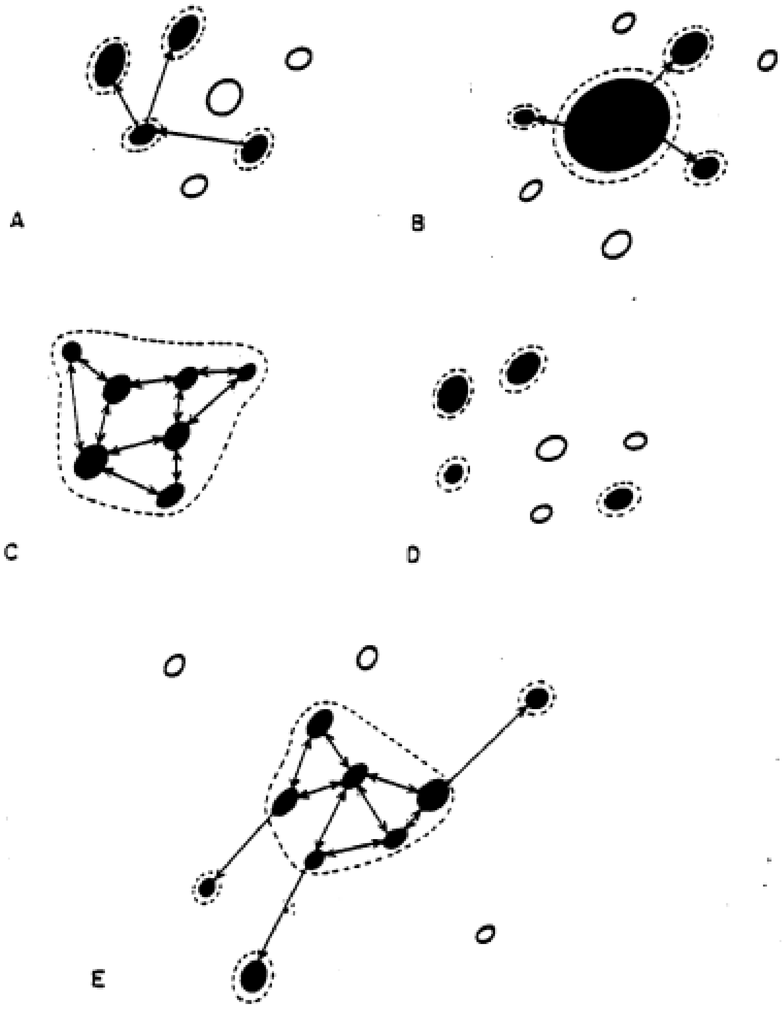


Figure 2.2: Different kinds of metapopulations. Closed circles represent habitat patches; filled = occupied, unfilled = vacant. Dashed lines indicate the boundaries of populations. Arrows indicate dispersion or migration (colonization). (a) Levins metapopulation. (b) Core-satellite metapopulation. (c) Patchy population. (d) Non-equilibrium metapopulation. (e) An intermediate case that combines (b) and (c) (from Harrison, 1991).

of movement between populations depends on the extent of the movement and the mortality of the dispersing individuals.

One of the major issues of the subpopulation concept is the fidelity to a home range or natal site (natal philopatry). Through natal homing, animals that stray away from their natal site may return for reproduction. In many fishes where juveniles and adults make seasonal and ontogenetic migrations related to feeding or reproduction, they may utilize either of three mechanisms, or a combination thereof, to return to their natal site and maintain philopatry including: (1) imprinting on environmental cues, (2) learning from other fishes (social tradition), or (3) genetically based homing. The nature of the homing mechanism, when it occurs, has some interesting implications for management issues, as discussed below.

2.2.3 Genetic Structure

How populations are organized as metapopulations and their genetic structure are closely linked; genetic structure being determined by the amount of gene flow between local populations. There are widely differing opinions on the degree of structure in marine fish populations, ranging from a lot of subpopulation structure to almost none. At one end is Sinclair's (1988) member/vagrant hypothesis, whereby there are many discrete populations, genetically distinct through larval retention and mortality of vagrants. This concept was founded on observations of specific spawning locations that seem to favor retention of larvae. At the other end of the spectrum is Smith *et al.* (1990) whose dynamic population concept has stocks with no discrete genetic status as homogeneous isolates, but as dynamic heterogeneous components of the species; some genetic differences may occur from isolation by geographical distance and gene selection. This concept arises from observations of high genetic variability within an area and low genetic differentiation between areas.

Genetic divergence among subpopulations is promoted by mutation, genetic drift, and natural selection favoring adaptation to local environments and hindered by the homogenizing process of gene flow from movements of gametes, individuals, or populations (Slatkin, 1987). Phenotypic and genotypic characteristics have been used to distinguish fish subpopulations. The use of phenotypic characters is still widely practiced, but when used alone is generally received with some skepticism because phenotypes are influenced by environmental conditions as well as genetic makeup. Biochemical and molecular genetic techniques are powerful tools for fisheries; there have been many studies of protein polymorphisms and more recently molecular genetics, looking for differences between nearby geographical populations, with the goal of finding genetically isolated management units. Many studies of marine fishes fail to distinguish populations (Pawson and Jennings, 1996), either due to the state of technology as applied to population genetics, high levels of gene flow, either historical or ongoing, or poor resolution power due to small sample sizes (Taylor, 1991b). However, there have also been some great successes, e.g., distinguishing smelt populations on opposite sides of the St. Lawrence River (Bernatchez and Martin, 1996), mosquito fish populations within several hundred meters of shoreline (Kennedy *et al.,* 1986), and *Fundulus* populations along coastal transects (Gonzalez-Villasenor and Powers, 1990).

In marine fishes, the importance of larval dispersal on gene flow and population structure has been shown by several studies (Waples, 1987; also see Avise, 1994). For example, Doherty *et al.* (1995) used isozymes to show that a reef species *Acanthochromis polycanthus*, whose offspring are reared in the parental territory and lacks larval dispersal, demonstrates negligible gene flow over ca. 1000 km. Doherty showed that other species with larval dispersal had genetically homogeneous subpopulations resulting from gene flow. However, high dispersal potential may not always translate into high gene flow and genetic homogeneity. There may be physical impediments to dispersal, such as retention mechanisms, early life stages may not be passive drifters, and later stages may have natal homing mechanisms.

There are several points of controversy about genetic differentiation, the most critical and pervasive being the selective neutrality of genes, about which there is still a lot of controversy (Gauldie, 1991; Avise, 1994; Rand, 1996). Hedgecock (1994) has noted a high degree of heterogeneity on a microgeographic scale for some marine fish and invertebrate species and has proposed that a linkage between oceanographic conditions and variance in reproductive success of marine animals is related to genetic heterogeneity. Thus microgeographic heterogeneity results from temporal variation in the genetic composition of recruits due to selection on larval populations matching survival windows of favorable oceanographic conditions, or to geographic heterogeneity in the environment.

The level of genetic diversity in the population is also important for successful population differentiation. For some species, both allozymes or mtDNA may have a low degree of allelic variation (Bentzen *et al.,* 1997). For example, in western Atlantic cod Carr *et al.* (1995) found that 80% of samples for cyt-b gene in mtDNA were of one haplotype, with the remaining 20% split between 16 other haplotypes. Differences between populations are determined by the statistical differentiation of the frequency distribution of a few rare haplotypes. Low levels of diversity in marine fish populations have been attributed to historical bottlenecks or recent founding of the population relative to the rate of mutation and genetic drift detectable in the particular genetic structure (mtDNA, microsatellite, etc.) analyzed.

New techniques look promising for distinguishing subpopulations. Bentzen *et al.* (1997) have applied nuclear DNA microsatellite analysis to examine stock structure of western Atlantic cod. Previous studies using allozymes and mtDNA had limited success in differentiating cod stocks, but Bentzen *et al.* (1997) found multiple stocks using their technique. Microsatellite DNA sequences appear to have high resolution for stock structure analysis due to the high rate of change in these regions of the DNA molecules, the degree of allelic variation, and the likelihood that selection may be a minor factor in determining microsatellite allele frequencies (Wright and Bentzen, 1994). Selection may promote or discourage population differentiation, and since microsatellites are noncoding regions of the genome, polymorphisms may be bound by structural contraints since there isn't a protein product.

2.3 Characterization of Pollock

2.3.1 Distribution and Population Ecology

The walleye pollock is a species with a very broad niche. Although commonly associated with the outer shelf and slope regions of oceanic waters, as a species it is capable of utilizing a wide variety of habitats including nearshore eelgrass beds (J. Norris, School of Fisheries, University of Washington, Seattle, WA 98195, personal communication), large estuaries like Puget Sound, coastal embayments, and open ocean basins such as the Aleutian Basin of the Bering Sea. Although adults of the species are often described as semidemersal, in some areas they are strictly pelagic (Bakkala, 1993). Pollock commonly feed on a wide assortment of prey from pelagic copepods to epibenthic organisms, and pelagic and demersal fishes.

Pollock has an extremely broad range from Puget Sound to the northern Bering Sea and on across the North Pacific Ocean (Fig. 2.3); it is most abundant in the eastern Bering Sea and the Sea of Okhotsk. In addition to an extensive range, the local abundance of pollock is usually high, often dominating regional groundfish communities. Given its ecological plasticity, broad range, and high levels of abundance, pollock appear to be a classical generalist species capable of invading and adapting to marginal habitats.

The distribution of pollock is closely linked to temperature. The vertical distribution of juvenile pollock, and schools of adults and juveniles are influenced by fronts, temperature, and depth (Bailey, 1989; Swartzman *et al.* 1994). Interaction of temperature with behavior of pollock has been well-studied (Olla *et al.* 1996; Sograd and Olla, 1996). The horizontal distribution of pollock is limited by cold temperatures, from 0° to 2°, as shown by distribution of commercial catches, and catches of juveniles and adults in research surveys (Francis and Bailey, 1983). Detailed studies have not been conducted at high temperatures, but the range of pollock appears to be limited by temperatures of 10° to 12°C.

We tracked the distribution pattern of several year classes in the eastern Bering Sea to examine ontogenetic dynamics in distribution of different year classes. The 1982 year class was found predominantly in the outer shelf region of the southeast Bering Sea as larvae (Fig. 2.4a); as age-0 juveniles they had moved northward and inshore (Fig. 2.4b). As age-1 fish, they had distributed themselves farther northward, and also a large portion of the population was found shoreward (Fig. 2.4c). As age-3 fish in summer, a portion of the 1982 year class returned to the southern outer shelf region, but a large number of fish remained in the northeast outer shelf (Fig. 2.4d). The 1989 year class was not sampled as larvae, but as age-0 juveniles in summer it was broadly distributed across the middle shelf in the south and along the outer shelf region in the northwest (Fig. 2.5a). This pattern persisted for age-1, age-2, and age-3 fish (Figs. 2.5b–d). Portions of the year class distributed inshore tended to persist there through age-3. The 1993 year class was sampled as larvae along the outer shelf region of the south (Fig. 2.6a). It was not sampled as age-0 juveniles, but as age-1's was found far northward in a band extending along the northern outer shelf (Fig. 2.6b, c). The

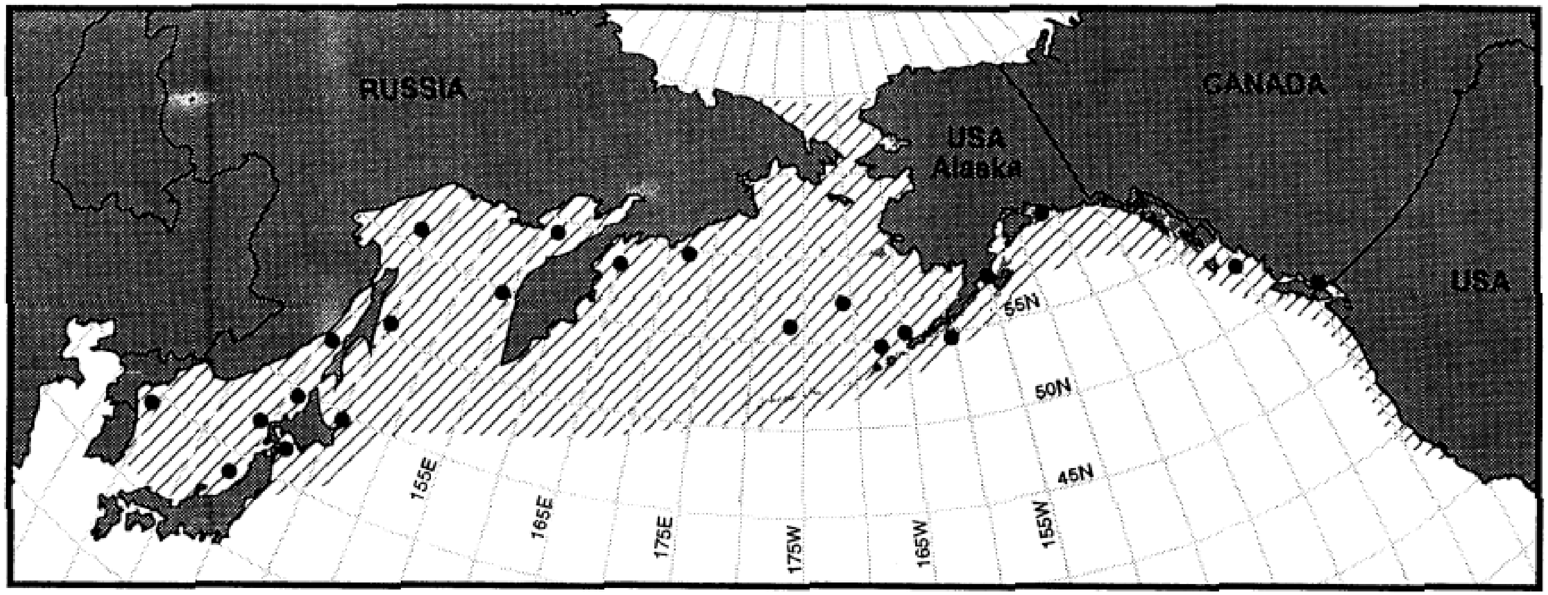


Figure 2.3: The distribution range of walleye pollock shown with cross-hatching. Major spawning locations are shown with closed circles.

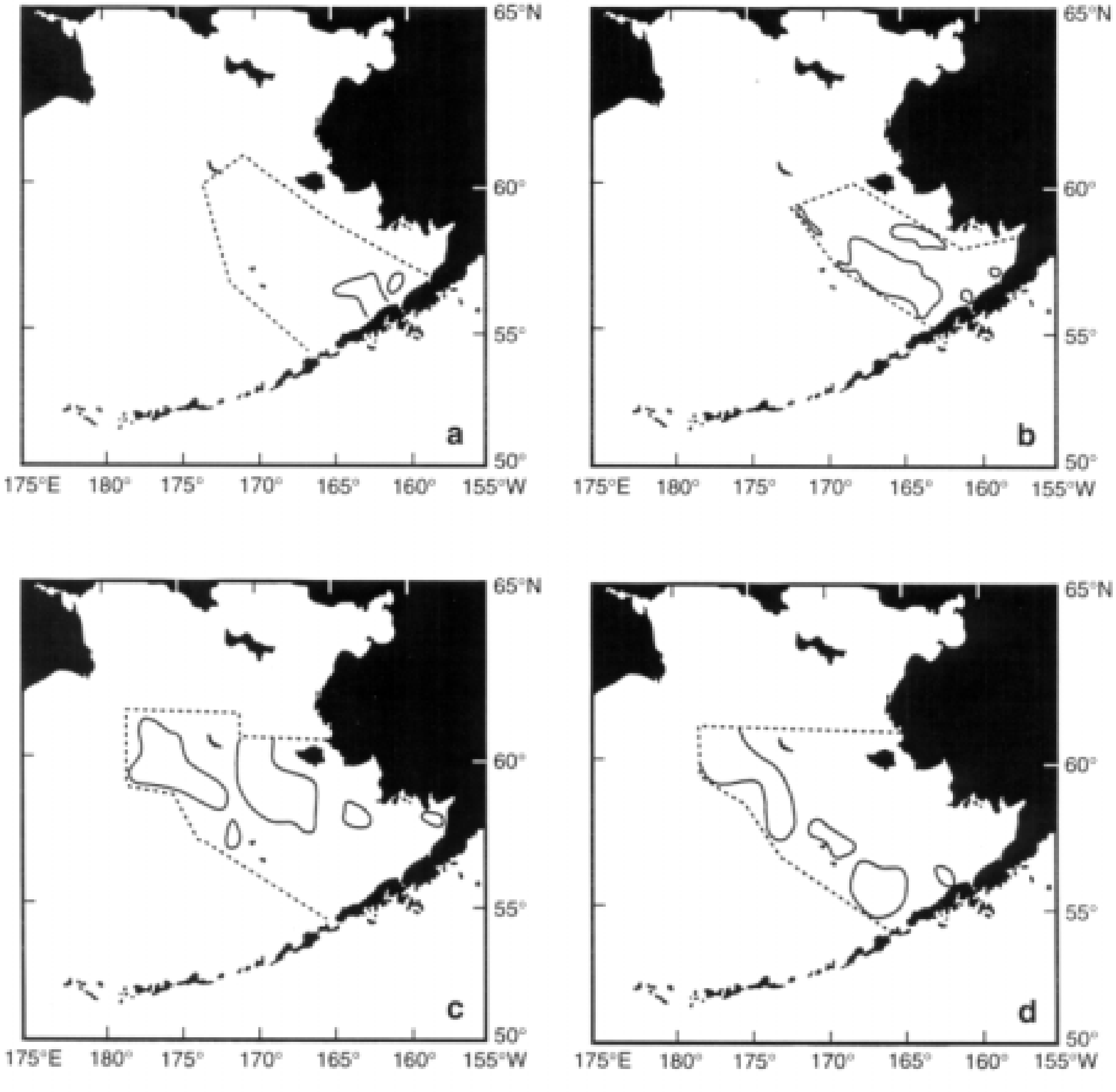


Figure 2.4: Relative distribution patterns of the 1982 year class of walleye pollock in the eastern Bering Sea: (a) larvae in June from ichthyoplankton surveys, (b) age-0 juveniles in autumn from midwater trawl surveys, (c) age-1 in summer from bottom trawl surveys, (d) age-3 in summer from bottom trawl surveys. Contour shows area of highest abundance. Dashed line shows approximate region surveyed.

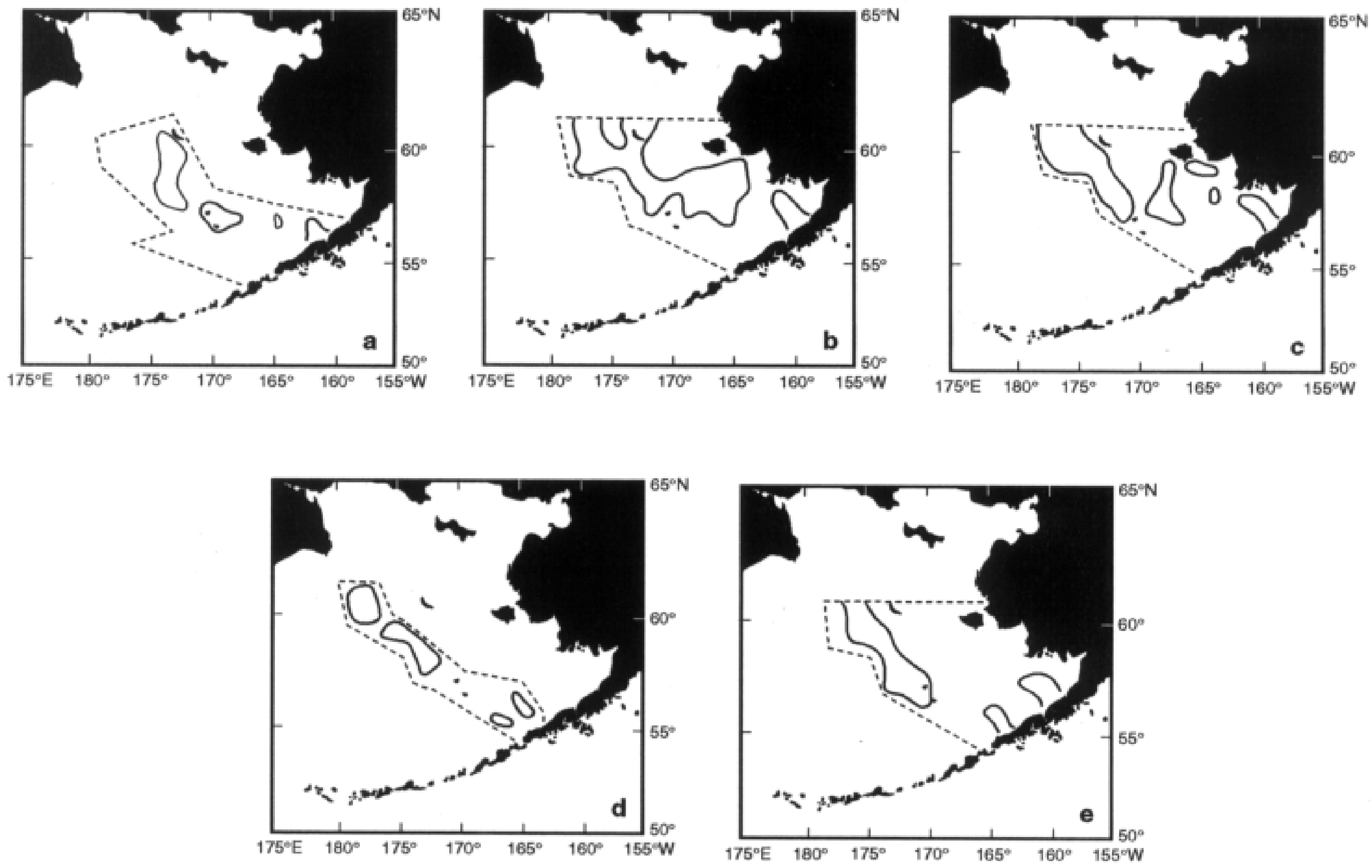


Figure 2.5: Relative distribution patterns of the 1989 year class of walleye pollock in the eastern Bering Sea: (a) age-0 juveniles in summer from midwater trawl surveys, (b) age-1 in summer from bottom trawl surveys, (c) age-2 in summer from bottom trawl surveys, (d) age-2 in summer from midwater trawl surveys, (e) age-3 in summer from bottom trawl surveys. Contour shows area of highest abundance. Dashed line shows approximate region surveyed.

distribution of age-3 fish appears similar to that of age-2, perhaps with a slight shift southward (Fig. 2.6d). Overall, these patterns indicate generally northward movements of age-0 and age-1 fish. However, there appears to be considerable interannual variability in distribution patterns; sometimes these age groups move shoreward also. By age-3 it appears that pre-spawning fish shift their distribution southward again.

Characterization of pollock as a colonizing species lends some support to historical suggestions that the rapid increase in pollock populations occurring in the late 1960s was due to an “ecological release” caused by harvesting off the competitive pressure of Pacific Ocean perch (Somerton, 1978) and decreases in abundance of Pacific herring. Under this scenario, pollock are a classic r-selected species with opportunistic rapid growth, early maturity, and high fecundity that were capable of rapidly taking over a niche opening; most likely, juvenile pollock were the stage capable of exploiting prey resources made available. The expanding population of juveniles could have made them the most available prey for pollock adults resulting in cannibal-

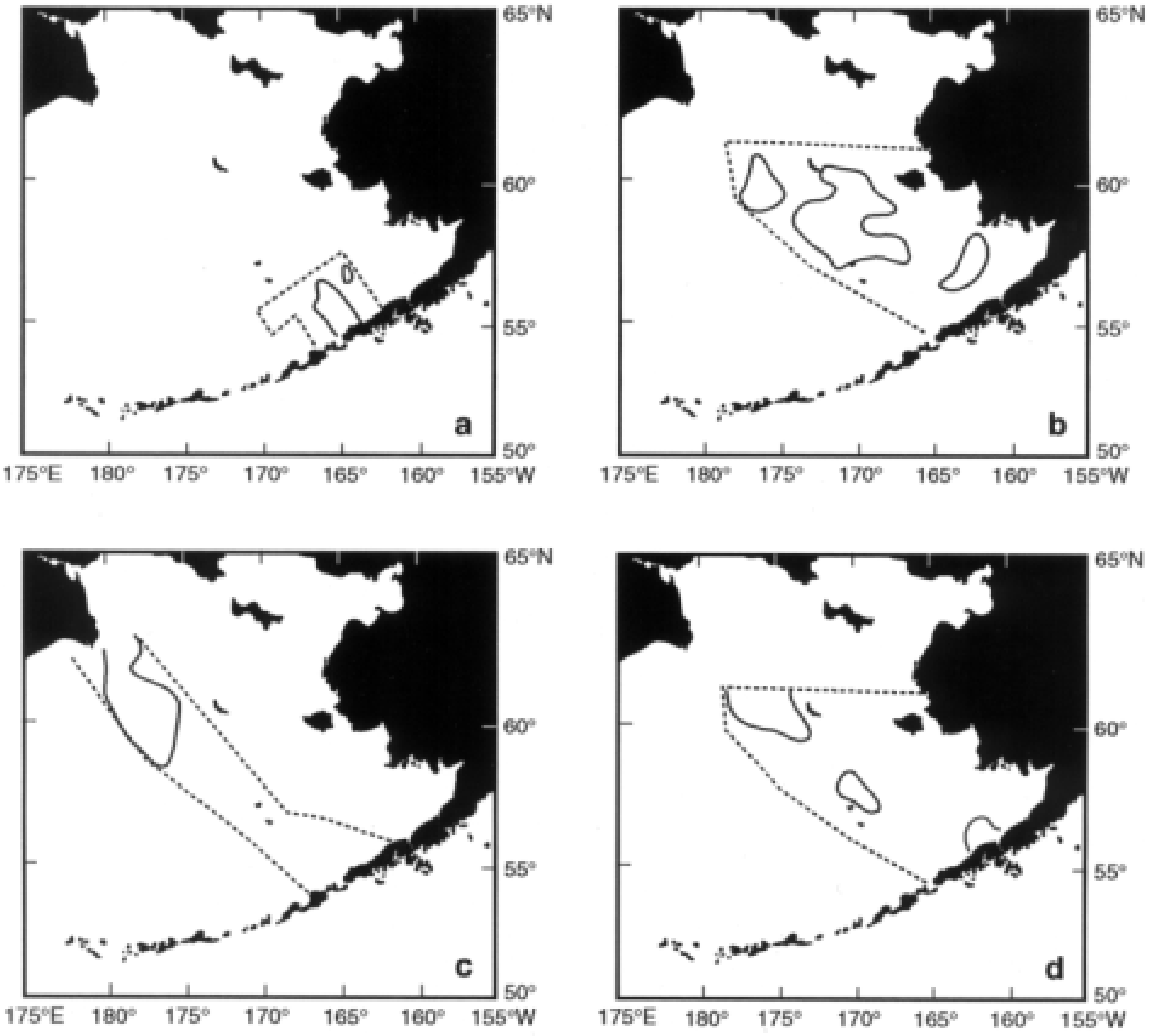


Figure 2.6: Relative distribution patterns of the 1993 year class of walleye pollock in the eastern Bering Sea: (a) larvae in May from ichthyoplankton surveys, (b) age-1 in summer from bottom trawl surveys, (c) age-1 in summer from midwater trawl surveys, (d) age-3 in summer from bottom trawl surveys (age estimated from length class). Contour shows area of highest abundance. Dashed line shows approximate region surveyed.

ism in the eastern Bering Sea. In the Gulf of Alaska, an increase of pollock in the mid-1980s coincided roughly with a regime shift occurring in 1977–1978 by Tsuji's (1989) assertion that during times of increasing commercial catch levels (and therefore abundance) pollock expand into adjacent waters. Likewise, Stepanenko (1997) reports range expansions of pollock in the Bering Sea related to increasing abundance and warming temperatures.

Comparing the mean and variance of subpopulation abundances over time can characterize how populations are controlled in different areas of the species range. In the case of pollock, a plot of mean subpopulation abundance versus variability shows a slope less than unity, indicating that peripheral, less abundant pollock stocks vary more than central, more abundant stocks (Fig. 2.7). These results could either indicate more density dependence in the central stocks, including density-dependent colonization of peripheral populations, or that environmental conditions are more variable and have a greater effect on peripheral populations.

2.3.2 Year Class Dynamics

For all of the major pollock groupings stock fluctuations are strongly influenced by intermittent recruitment of strong year classes. For example, Fig. 2.8 shows the impact of a series of strong year classes on stock abundance in the Gulf of Alaska, as well as the drop in abundance related to subsequent recruitment of relatively poor year classes. In the eastern Bering Sea the 1978 year class comprised 67% of the pollock population in 1981 and 53% of the population in 1982. Many regions share the same strong year classes; for example, 1978 was a strong year class in the Gulf of Alaska, Aleutian Basin, eastern Bering Sea, western Bering Sea, and Sea of Okhotsk. Likewise 1982, 1984, and 1989 were strong across the Bering Sea, although not in the Gulf of Alaska. Strong year classes in the Gulf of Alaska including 1976, 1977, 1979, and 1988 did not appear strong in the Bering Sea. Therefore, although some strong year classes are shared, there is not a consistent association of strong year classes among the Bering Sea and Gulf of Alaska populations that would clearly indicate density dependent dispersal between these geographic regions. However, within the Bering Sea there appears to be an association of strong year classes among the different regions. The occurrence of similar strong year classes in different regions of the Bering Sea has been cited as evidence of panmixia within the Bering Basin (Dawson, 1994). At the extreme ends of the range of pollock, e.g., Puget Sound, the strong year classes (1972–1975) were quite different from those in the major centers of abundance.

2.4 Population Structuring Mechanisms in Pollock

In fish populations, gene flow can occur as a result of movements of adult, juvenile, or larval stages. Species with a high degree of adult vagility living in fine-grained habitats often have little genetic structure in their populations (Avise, 1994). As well, species like salmon, whose larvae have little opportunity to mix, attain whatever gene flow between major drainages by straying

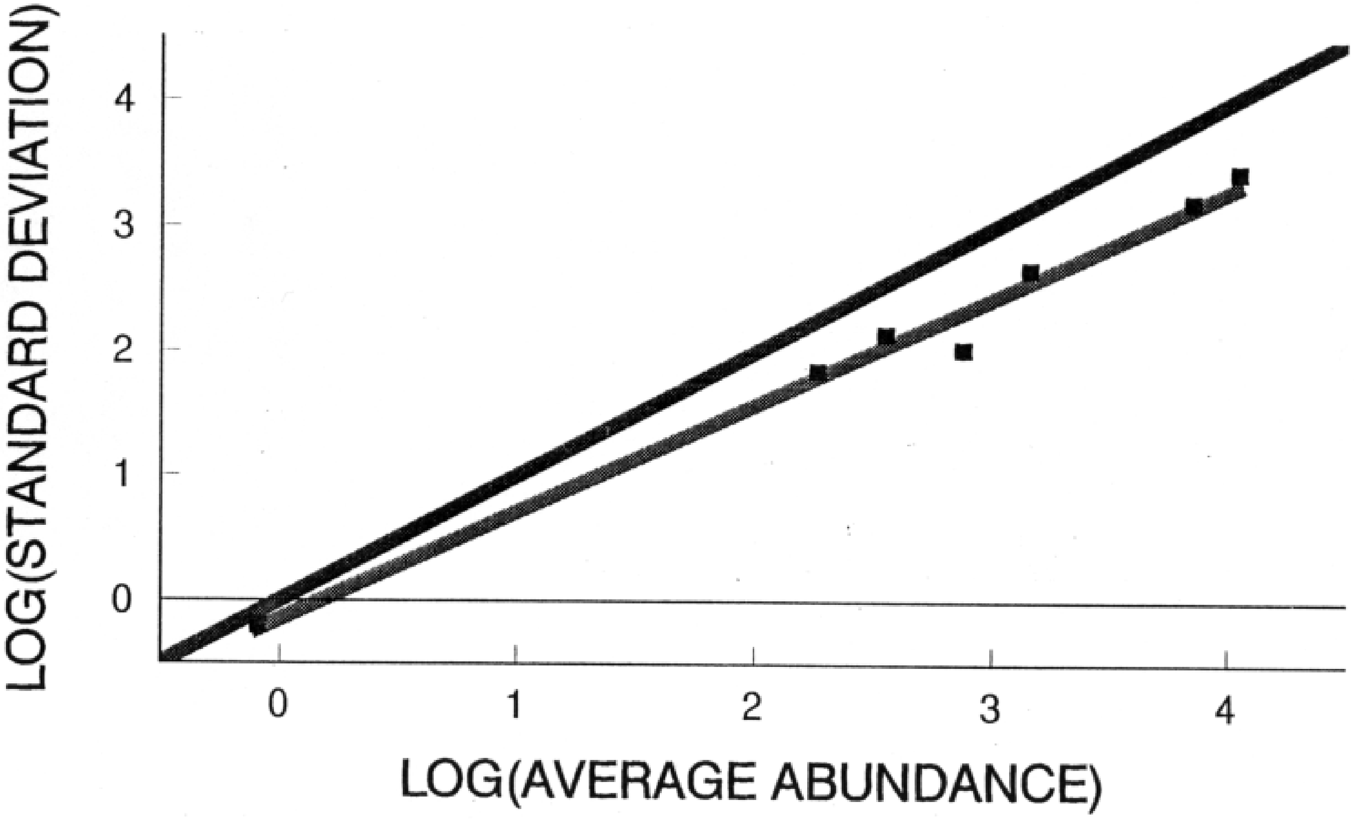


Figure 2.7: The standard deviation of pollock abundance against average abundance for seven stocks of walleye pollock, 1979–1991, showing that peripheral, less abundant stocks vary more than central, more abundant stocks. Upper line has a slope of unity, bottom line is regression line of stock data (slope = 0.864).

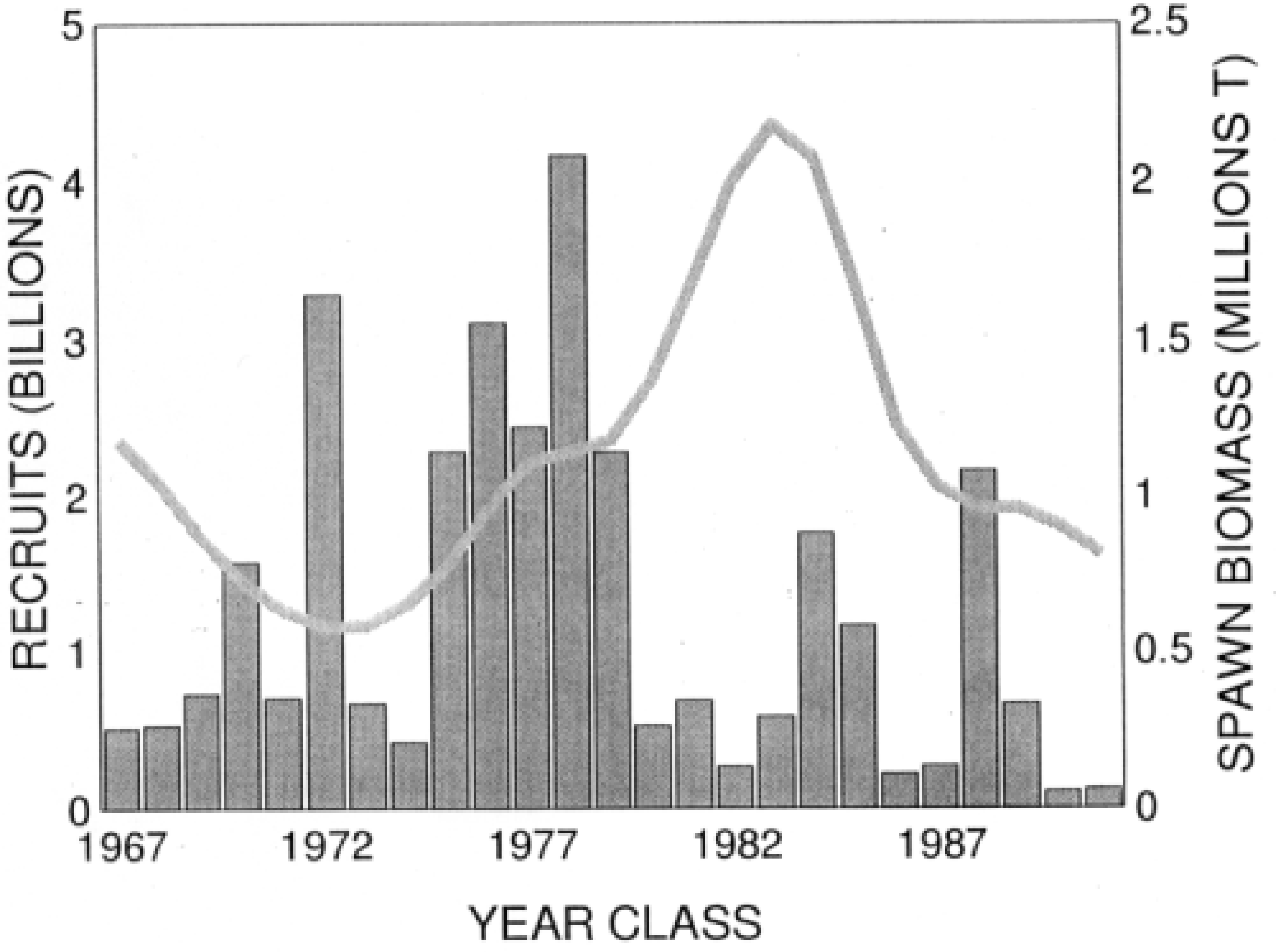


Figure 2.8: Year class abundance as age-2 recruits (bars) compared to spawning biomass of walleye pollock in the western Gulf of Alaska (line), showing the dramatic effects of year class strength on population biomass.

and mixing of adult gene pools. In species whose adults and juveniles migrate widely, genetic structure may be maintained by natal homing, as is well recognized in Pacific salmon. For other species as well, such as rainbow smelt, natal homing ability seems quite remarkable (Bernatchez and Martin, 1996).

Walleye pollock provide an excellent opportunity to study different population structuring mechanims. Pollock appear to have immigrated to the North Pacific within a period between the submergence of the Bering Sea land bridge and the coming of the ice age, about 3–5 million years ago (Svetovidov, 1948). In fact, the earliest records of gadids in the North Pacific are found in Pliocene sediments off the California coast. Pollock spawning populations are now found across the rim of the North Pacific Ocean from central Japan to Puget Sound. Larger populations are contained in the major basins of the Bering Sea and Sea of Okhotsk, but smaller populations are found in many bays, fjords, and sea valleys along the continental shelf. During the last period of major glaciation about 10,000–18,000 years ago, when sea levels could have been as much as 150 m lower than present day levels, the major basins were substantially more isolated with strong geographical barriers between populations. Many of the fjords presently inhabited by pollock would have been in the process of being scoured by glaciers. Consequently, pollock stock differentiation could have occurred by several mechanisms, including founder effects and genetic drift of small re-colonizing populations in the fjords, loss of genetic diversity by population bottlenecks, isolation by barriers and by distance combined with selection, and genetic drift.

Pollock have been the subject of studies of larval transport in relation to oceanographic conditions in the Gulf of Alaska since 1981 (Kim and Kendall, 1989). Pollock eggs and larvae are found in large aggregations that can be tracked and monitored (Bailey *et al.,* 1996b) and their distribution can be predicted reasonably well from ocean currents. Pollock larvae are also associated with oceanographic features such as eddies (Vastano *et al.,* 1992; Schumacher *et al.,* 1993). Larval abundance levels are correlated with environmental conditions related to transport (Bailey and Macklin, 1994) and recruitment levels of the population have been linked to events during early life history (Bailey *et al.,* 1996a). In the following section, I discuss the role of variability in larval transport and retention by features, such as eddies, in mortality and genetic structuring of the walleye pollock population, and explore the possible linkages between them. These linkages are made using both published and original sources of data. Other mechanisms of population structuring in pollock are discussed, with the main emphasis on populations in the Bering Sea and Gulf of Alaska.

2.4.1 Regional Oceanography and Transport

In the Gulf of Alaska, the major spawning of pollock is in Shelikof Strait, a deep sea valley (>250 m) penetrating the continental shelf between the Alaska Peninsula and Kodiak Island. Flow in this region is dominated by the Alaska Coastal Current, which is one of the most vigorous coastal currents in the world with speeds of 25–100 cm s^{-1} (Stabeno *et al.,* 1995). The

Alaska Coastal Current bifurcates east of Sutwik Island, with one branch continuing along the shallow continental shelf (∼100 m) along the Alaska Peninsula. This branch has relatively weak flow, with speeds of about 10 cm s^{-1}. The other branch flows seaward through the sea valley with a portion that joins the Alaska Stream (with speeds of 50–100 cm s^{-1}) and the remainder recirculating onto the shallow shelf.

Frontal features, meanders, and eddies are prominent in the Shelikof sea valley (Vastano *et al.,* 1992; Napp *et al.,* 1996). Horizontal density gradients and vertical shear in the flow result in baroclinic instabilities, which generate eddies in the region. The location of eddy formation coincides with the area of pollock spawning (Schumacher and Kendall, 1995), and in the springtime spawning period three to four eddies form per month (Bograd *et al.,* 1994), some of which may remain stationary for weeks (Schumacher *et al.,* 1993).

In the Bering Sea a cyclonic gyre dominates circulation, with the Kamchatka Current flowing southward along the western side and the Bering Slope Current northward along the eastern side of the central Aleutian Basin. Alaska Stream water can enter the Aleutian Basin through any of the deep Aleutian passes, but predominately through Amchitka, Amutka, and Buldiur Passes, and Near Strait. The transport through the passes varies on time scales of months. Over the main area of our interest, the southeast basin and the shelves, the flows of interest are the Bering Slope Current (BSC) and Aleutian North Slope Flow (ANSF). The ANSF flows eastward along the north slope of the Aleutian Islands and connects flow through the passes with the BSC. Instabilities in the BSC can result in onshelf flow from the basin onto the shelf.

The shelf is divided into three regions, the inner shelf (depth <50 m), the middle shelf (50–90 m), and the outer shelf (100–170 m). Flow on the middle shelf is very weak (mean flow <1 cm s^{-1}). Stronger flows occur at the transition zones between the inner middle shelf and the middle outer shelf. Flow along the 100-m isobath is generally northwestward at ∼5–10 cm s^{-1}, while the northeastward flow along the 50-m isobath is weaker at ∼2–3 cm s^{-1} (Schumacher and Stabeno, 1997). Flow along the 100-m isobath originates from onshelf flow from the basin and from flow through Unimak Pass. The flow along the 50-m isobath originates from the flow through Unimak Pass.

Eddies in the eastern Bering Sea are relatively common (Schumacher and Stabeno, 1994), and are formed in regions of high current shear, or by the interaction of inflowing Alaskan Stream water with topography. Eddies that may transgress the continental shelf break up in shallow water over a period of days. Eddies may circulate vigorously (25 cm s^{-1}), but their net movement is generally slow (1–5 cm s^{-1}). Diameters of eddies may vary from 5–80 km.

2.4.2 Larval Transport, Eddy Retention, and Mortality

Pollock spawn at predictable times and locations, generally in sea valleys, canyons, or indentations in the outer margin of the continental shelf; but they are also known to spawn in very deep water over the Aleutian Basin and in fjords (Fig. 2.3). These locations are known to be repeat spawning areas, year after year. In Shelikof Strait, Alaska spawning occurs during the last week of March and the first week of April. In the Bogoslof Island region in the Aleutian Basin, pollock spawn in late February to early March, and over the southeastern Bering Sea shelf most fish spawn from mid-April to May. Depending on the region, eggs are spawned deep in the water column (100–400 m) and after hatching the larvae are located in the upper portion of the water column (generally from 20–60 m depth).

In Shelikof Strait, pollock show a mean downstream progression of their center of abundance over time (Fig. 2.9). However, there is a great deal of interannual variability within these mean patterns. Larval transport patterns show good correspondence with satellite-tracked drifter patterns. In years when larvae are transported onto the shallow shelf west of the sea valley, larvae drift downstream at speeds of 4 to 6 cm s^{-1} (Hinckley *et al.,* 1991).

About 70 satellite-tracked drifters drogued at 40 m to simulate larval drift have been released in the Shelikof sea valley. The drifters show the pattern of bifurcation of the ACC and the variability in fate of larvae during the 50 d or so when they are planktonic (Fig. 2.10). Residence time of the drifters on the shelf ranges from 35–122 d, with a mean of 55 d. Drifters can exit the sea valley in about 15 d and enter the Alaska Stream where they are quickly transported westward.

Eddies in the Shelikof Sea Valley can retain larvae for several weeks in the region. In 1990 an eddy was found with an aggregation of larvae (Fig. 2.11). Satellite-tracked drifters remained in the eddy for ~22 d, until the eddy moved westward, and interacted with shallow topography of the shelf and disintegrated.

The role of eddies in larval mortality is not completely understood. Eddies early in the spawning season before peak larval abundance have been associated with enhanced phytoplankton and zooplankton concentrations, and enhanced larval feeding and nutritional condition (Canino *et al.,* 1991; Napp *et al.,* 1996). However, the eddy in 1990 had similar microzooplankton concentrations, larval feeding, and condition compared to regions sampled outside the eddy, and mortality rates in the eddy were not significantly different from mortality rates calculated for the whole sea valley region (0.05–0.07 d^{-1} in eddy based on birthdate cohorts: Bailey, unpublished data; 0.04–0.11 d^{-1} for whole region: Bailey *et al.,* 1995). How larvae are entrained in eddies is not well understood. Birthdate distributions of larvae within the 1990 eddy sampled about 20 d apart indicate that larvae continue to be recruited into the eddy well after it is formed, which complicates mortality calculations based on the conservation of properties within the eddy (Fig. 2.12).

In some years with strong and frequent storm activity, wind-driven transport increases and flushes most larvae from the sea valley into the Alaskan Stream. An excellent example of this is 1991; winds were extremely high, with three storm events during the late April early May period, and drifter trajectories indicated that most water vigorously flowed out the sea valley (Fig. 2.13). Under these conditions, primary production and microzooplankton levels were depressed, larval feeding and nutritional conditions were poor,

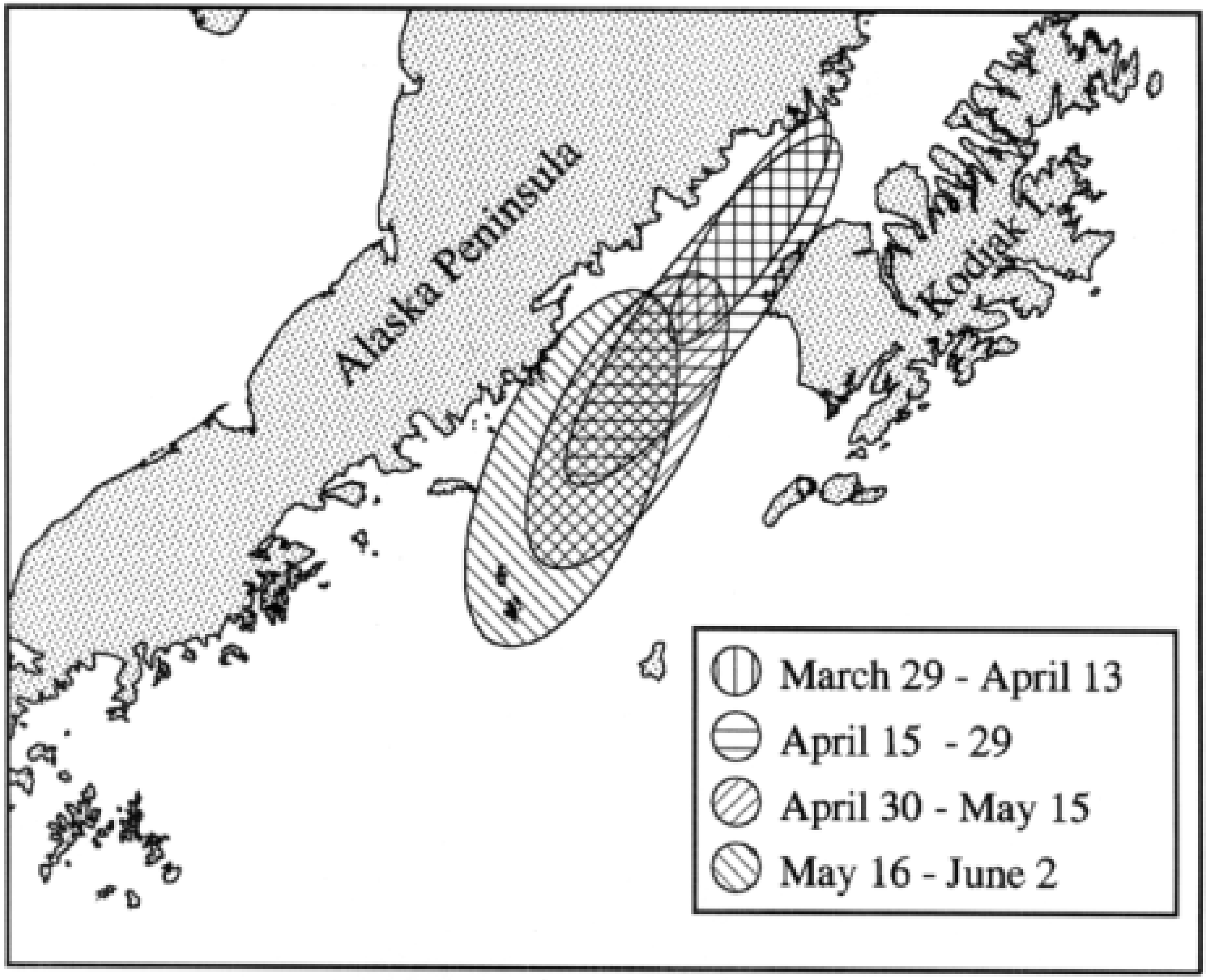


Figure 2.9: Centroids of larval pollock distribution tracked by month, averaged over 1987–1992.

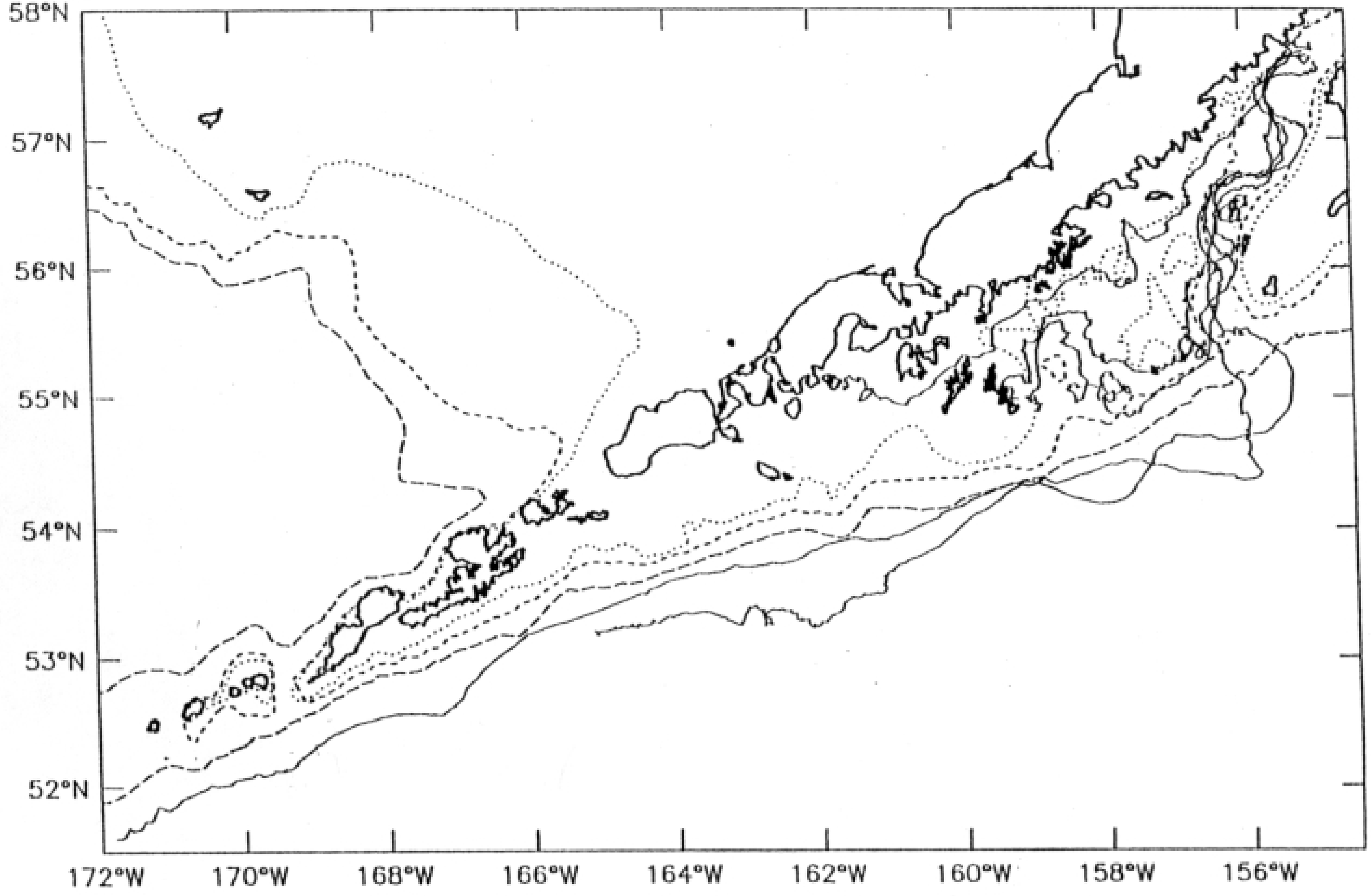


Figure 2.10: Composite of representative satellite-tracked drifter trajectories in the Gulf of Alaska. Drifters were drogued at 40 m, released near larval pollock aggregations and pathways tracked for 50 d, approximating the duration of larval drift.

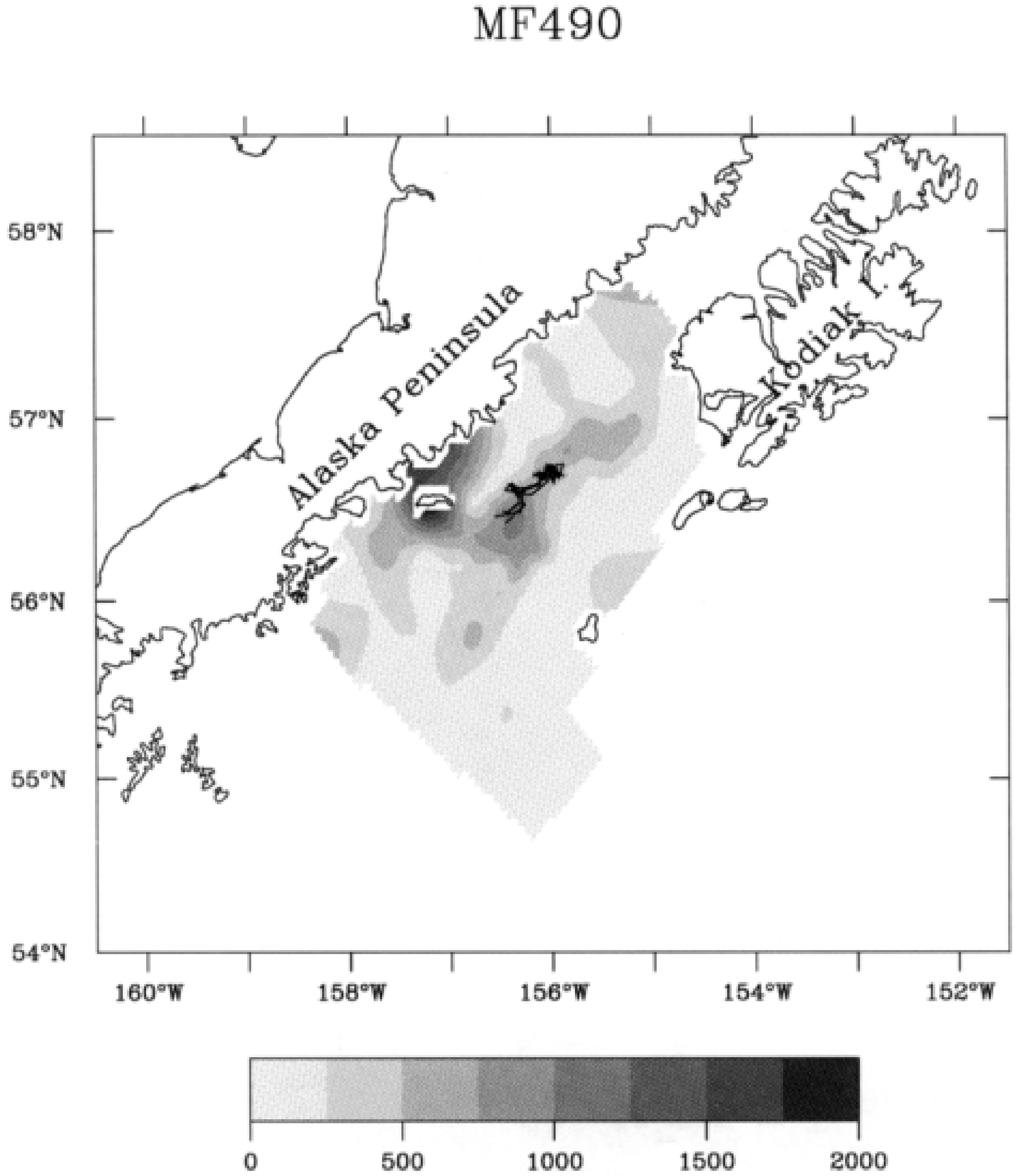
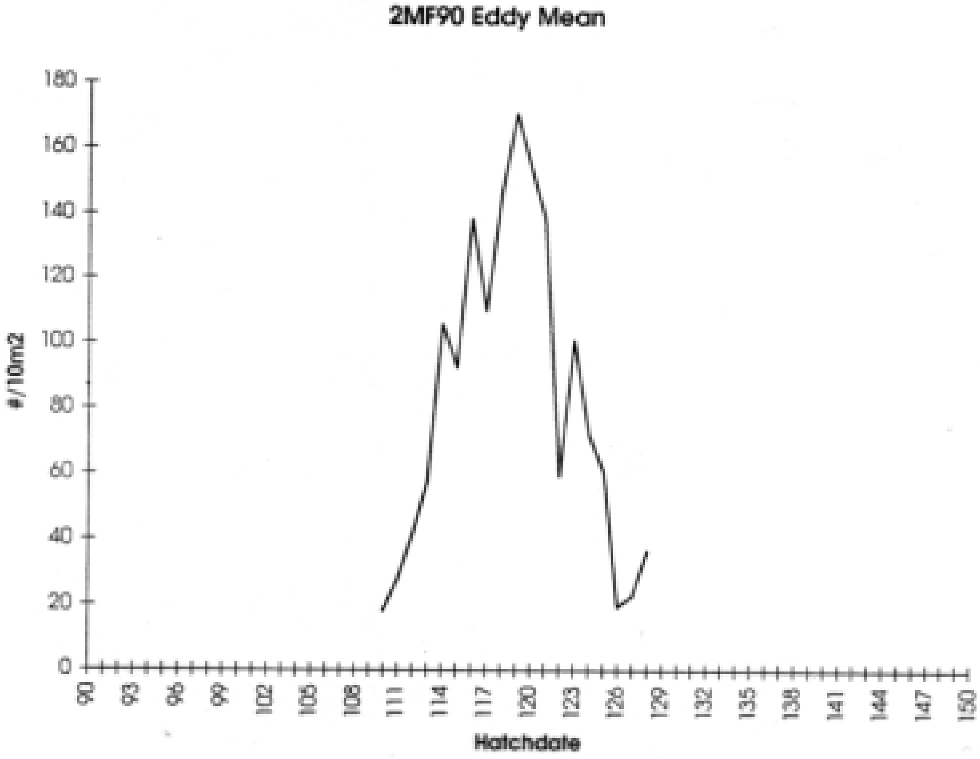


Figure 2.11: Distribution of walleye pollock larvae during late May 1990. Lines are satellite-tracked drifter trajectories from releases on the larval patch in early May. Units in catch 10 m^{-2}.



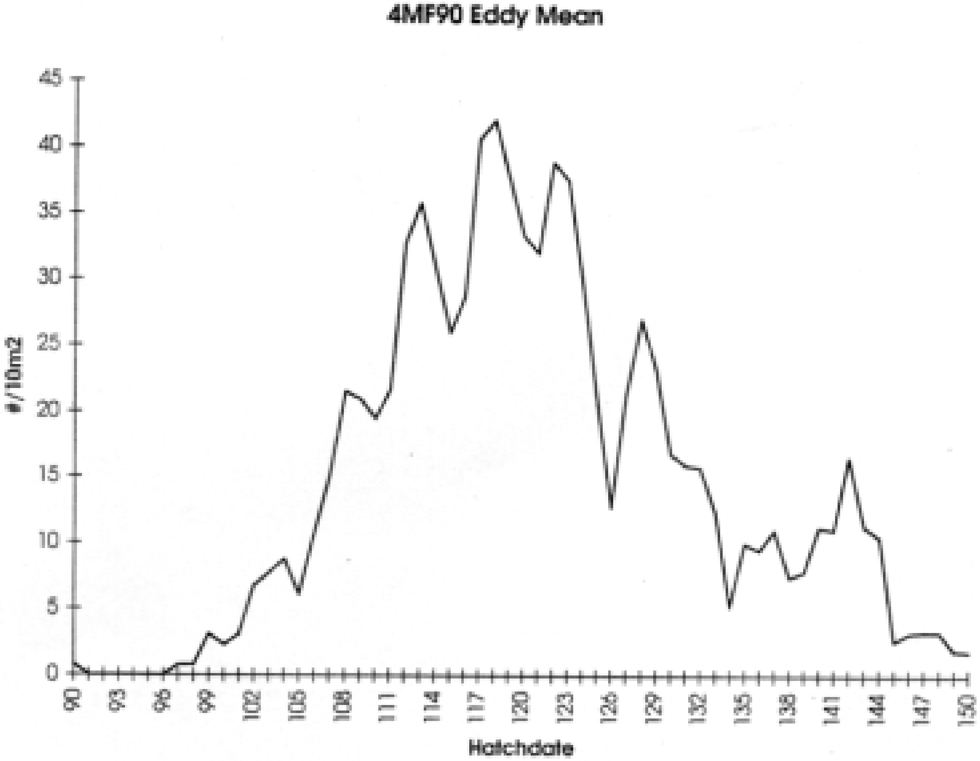


Figure 2.12: Hatchdate distributions determined from otolith increment counts and day of capture for (a) larvae sampled at stations within the eddy in early May 1990, and (b) larvae sampled at stations within the eddy in late May 1990.

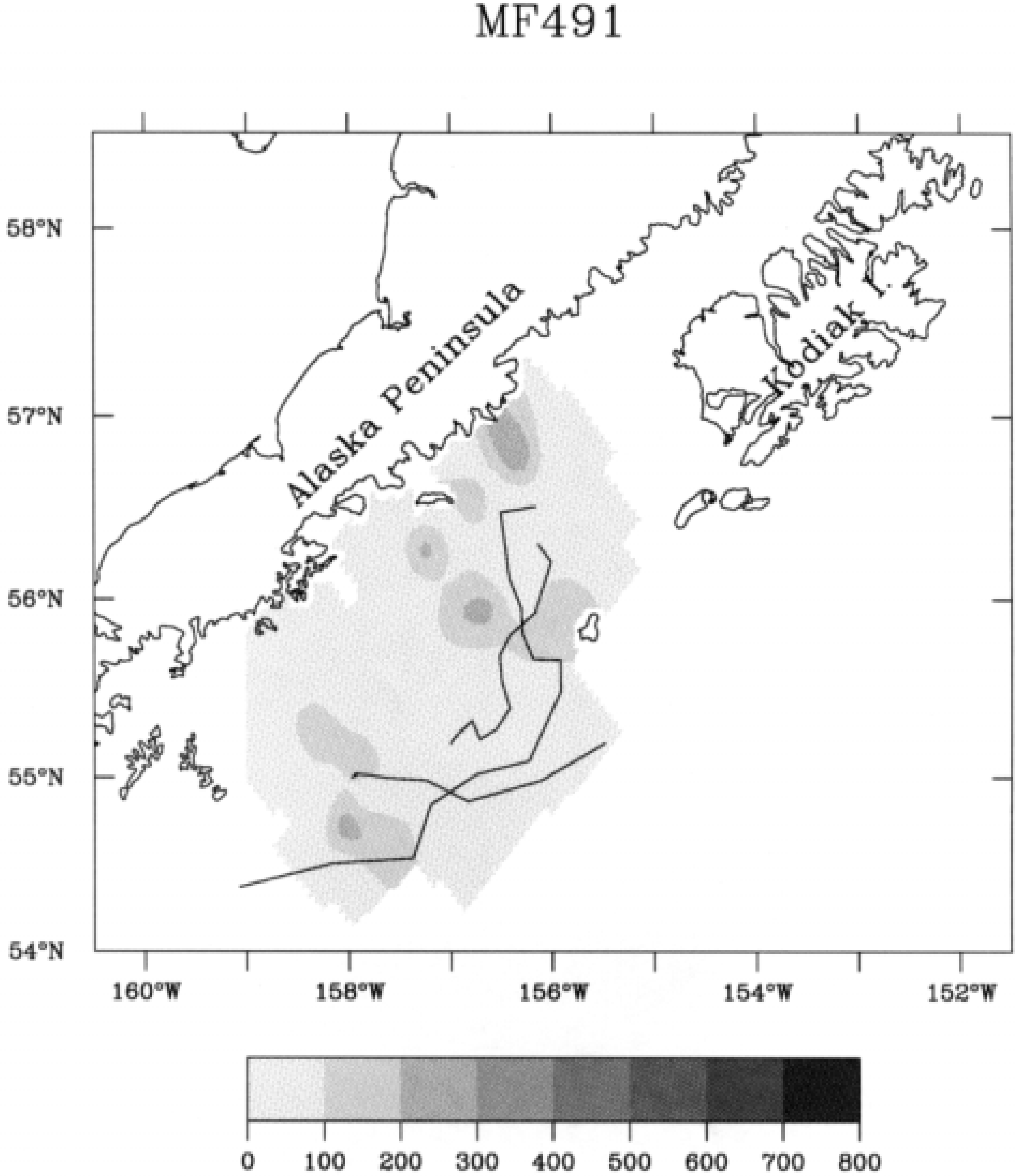


Figure 2.13: Distribution of walleye pollock larvae during late May 1991. Lines are satellite-tracked drifter trajectories from releases on the larval patch in early May. Units in catch 10 m^{-2}.

and larval mortality was high (Bailey *et al.,* 1995). In general, larvae experiencing conditions associated with high transport will have low survival.

There are limited data to compare larval condition in the Alaskan Stream water compared to other areas. However, microzooplankton levels are relatively low compared to nearshore stations (Bailey *et al.,* 1995) and larval growth rates are significantly lower than for larvae found over the shelf region. In 1991, the few surviving larvae that were caught at offshore stations had significantly lower growth rates than larvae caught in the sea valley (0.14 mm d^{-1} compared to 0.20 mm d^{-1}; $P < 0.05$).

In the eastern Bering Sea, larval pollock concentrations have not been tracked as effectively as in the Shelikof region. There are several areas where repeated spawning is known to occur (Fig. 2.14) and where larvae are frequently concentrated. From drifter studies it appears that larvae from different areas can readily mix during the larval drift period. About 80 satellite tracked drifters have been released in the Bering Sea to study potential larval drift patterns (typical patterns are shown in Fig. 2.15). On the middle shelf area (50–100 m depth) the flow is weak and all drifters remained resident there for more than 60 d. Drifters released in the Unimak Pass spawning region are either transported along the 100-m isobath until reaching the Pribilof Islands, at which time they may circle the islands, flow eastward across the shelf along the 50-m isobath, or continue northward to St. Matthew Island. Residence time in the slope region is 30–90 d, with a mean northward velocity of 5 cm s^{-1}. Drifters released near Bogoslof Island usually follow the ANSF into the BSC. Although about 15% of drifters go onto the shelf, drifters in this area may re-circulate in a small sub-gyre in the southeast corner of the Aleutian Basin.

There are eddies in the Bering Sea similar to those in Shelikof Strait that may act as larval retention mechanisms (Fig. 2.16). An eddy found in 1993 over the southeastern corner of the Aleutian Basin was associated with very high numbers of larvae; however, it later entered the outer shelf and disintegrated, providing a vehicle for mixing of larvae between spawning regions.

The Aleutian Basin region may act as a geographical barrier to gene flow across the Bering Sea. Microzooplankton concentrations are low and larval feeding levels are also low compared with other regions (Hillgruber *et al.,* 1995; Theilacker *et al.,* 1996). Furthermore, studies of larval mortality done in the basin region indicate relatively low larval growth rates and potential for high levels of mortality (Dell'Arciprete, 1992).

2.4.3 Migration Patterns and Philopatry

Other mechanisms of maintaining population structure include philopatry and natal homing. Pollock show repeated and predictable spawning at specific sites and times, which is one piece of evidence for natal philopatry. Some of these persistent spawning sites are shown in Fig. 2.3. Among the best studied spawning aggregations is that in Shelikof Strait which has been monitored since 1981; the Shelikof Strait spawning aggregation is the largest spawning biomass in the Gulf of Alaska, and mostly spawns within a lim-

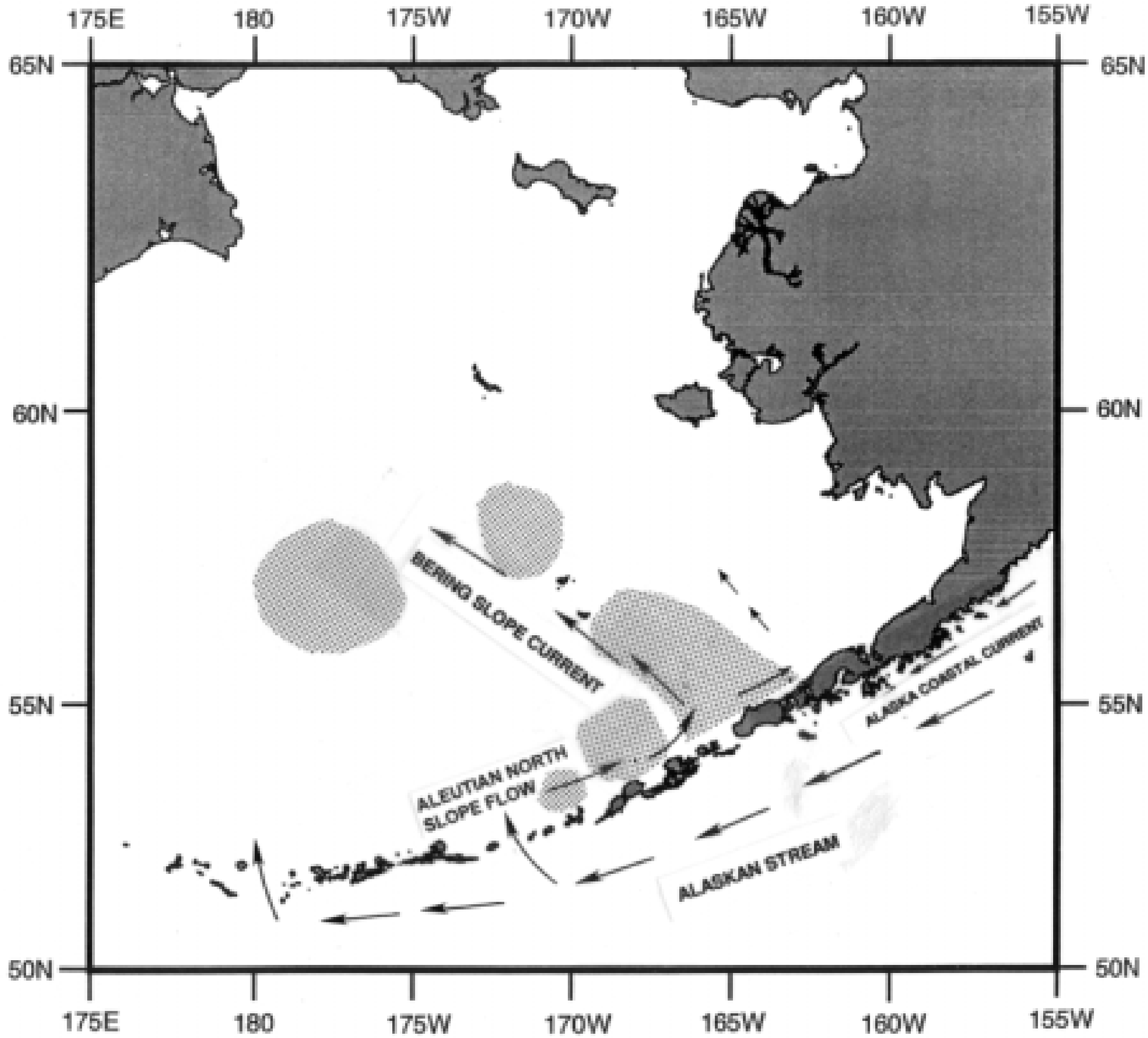


Figure 2.14: Major areas of spawning and larval concentrations in the eastern Bering Sea (shaded area).

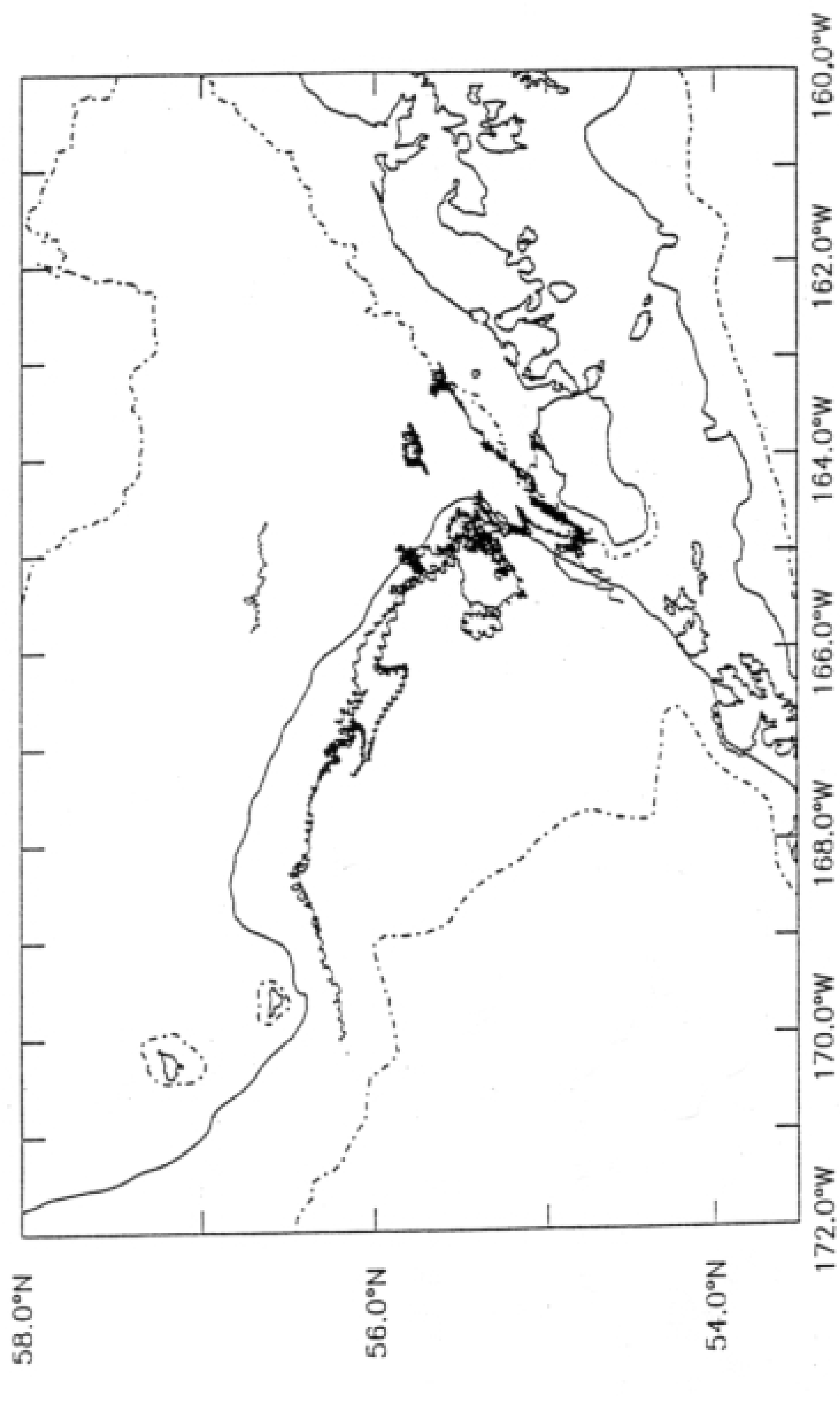


Figure 2.15: Composite of representative satellite-tracked drifter trajectories in the Bering Sea. Drifters were drogued at 40 m, released near larval pollock aggregations or on spawning grounds and pathways tracked for 50 d, approximating the duration of larval drift.

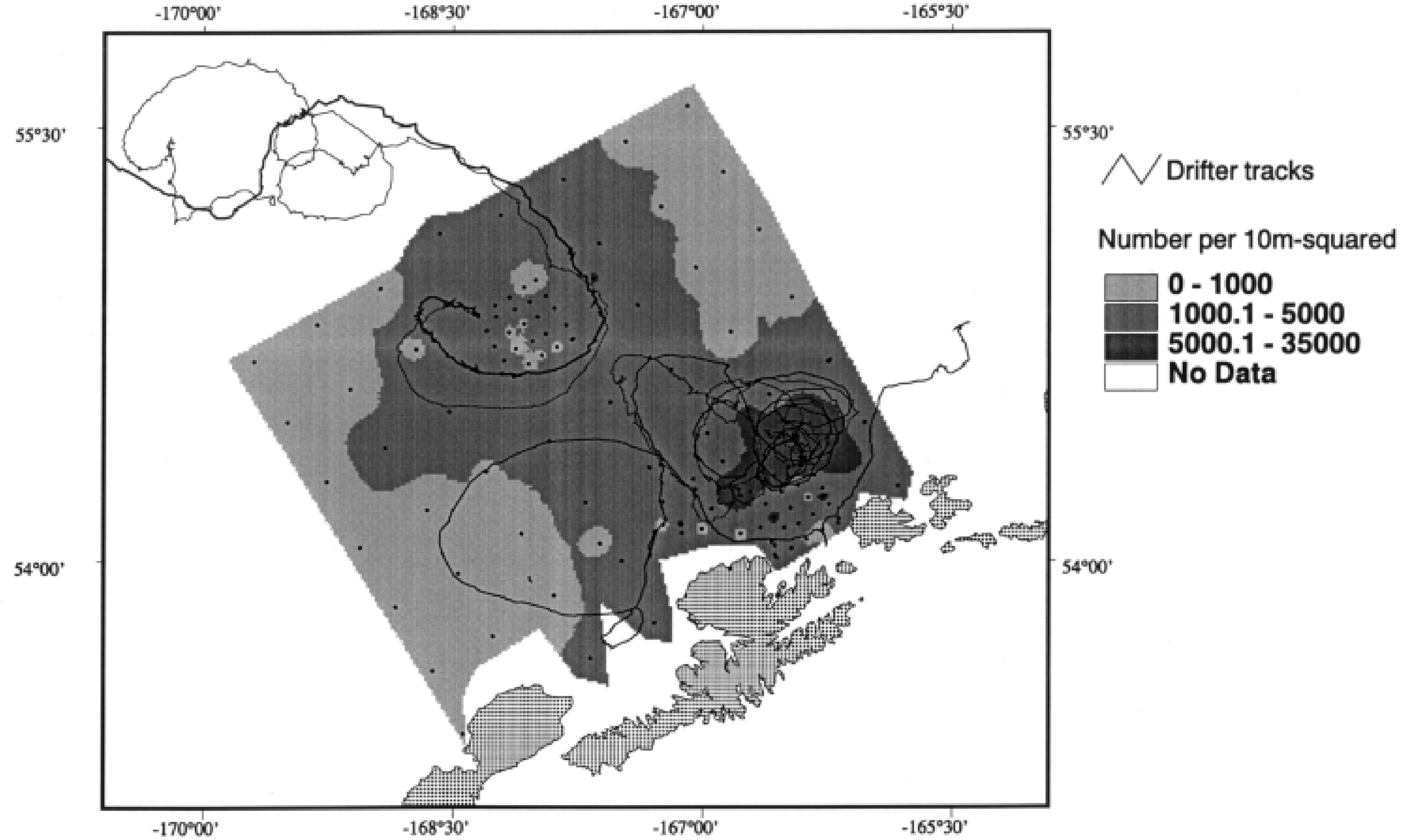


Figure 2.16: Distribution of walleye pollock larvae in April 1993 in the eastern Bering Sea. Also shown are satellite-tracked drifter trajectories showing location of eddy in the region.

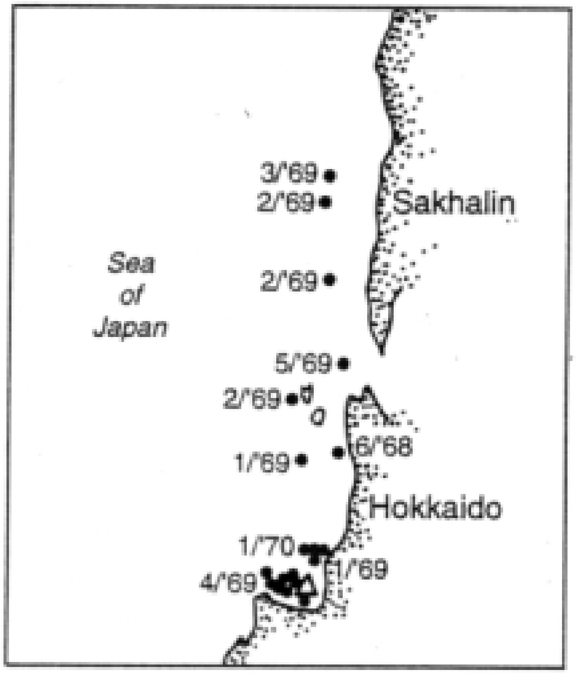


Figure 2.17: Recapture distribution for experiment in which 666 pollock were tagged and released (triangle) in the northern Sea of Japan on April 17, 1968. Locations and dates of recaptures are shown by closed cirlces. H: Hokkaido Island, S: Sakhalin Island (from Tsuji, 1989).

ited area (40 km × 80 km) during the first week in April (Kendall *et al.,* 1996). The geographic and temporal consistency of spawning for this and other spawning aggregations argues against the notion that the timing and position of spawning is random, depending on suitable conditions.

Mark-recapture studies around Japan where pollock were tagged during the spawning season (April) showed dispersed feeding migrations but return homing to specific previous spawning locations (Tsuji, 1989; Fig. 2.17). In other studies, pollock tagged during the summer feeding periods were later recaptured across a wide geographical expanse (Fig. 2.18). Those recaptured around the time of the spawning season were located near well-established spawning grounds. Pollock appear to widely disperse after spawning, and the location of summer feeding grounds may vary. The fact that fish tagged in summer in the western Bering Sea were recaptured in the eastern Bering Sea, along with the significant population differentiation between eastern and western Bering Sea spawning pollock discussed below, indicates isolation of spawning groups even though they may mix during the summer feeding period. While not unequivocally proving natal spawning, the persistence of spawning locations over time (Fig. 2.3) and repeat spawning are two elements of natal philopatry.

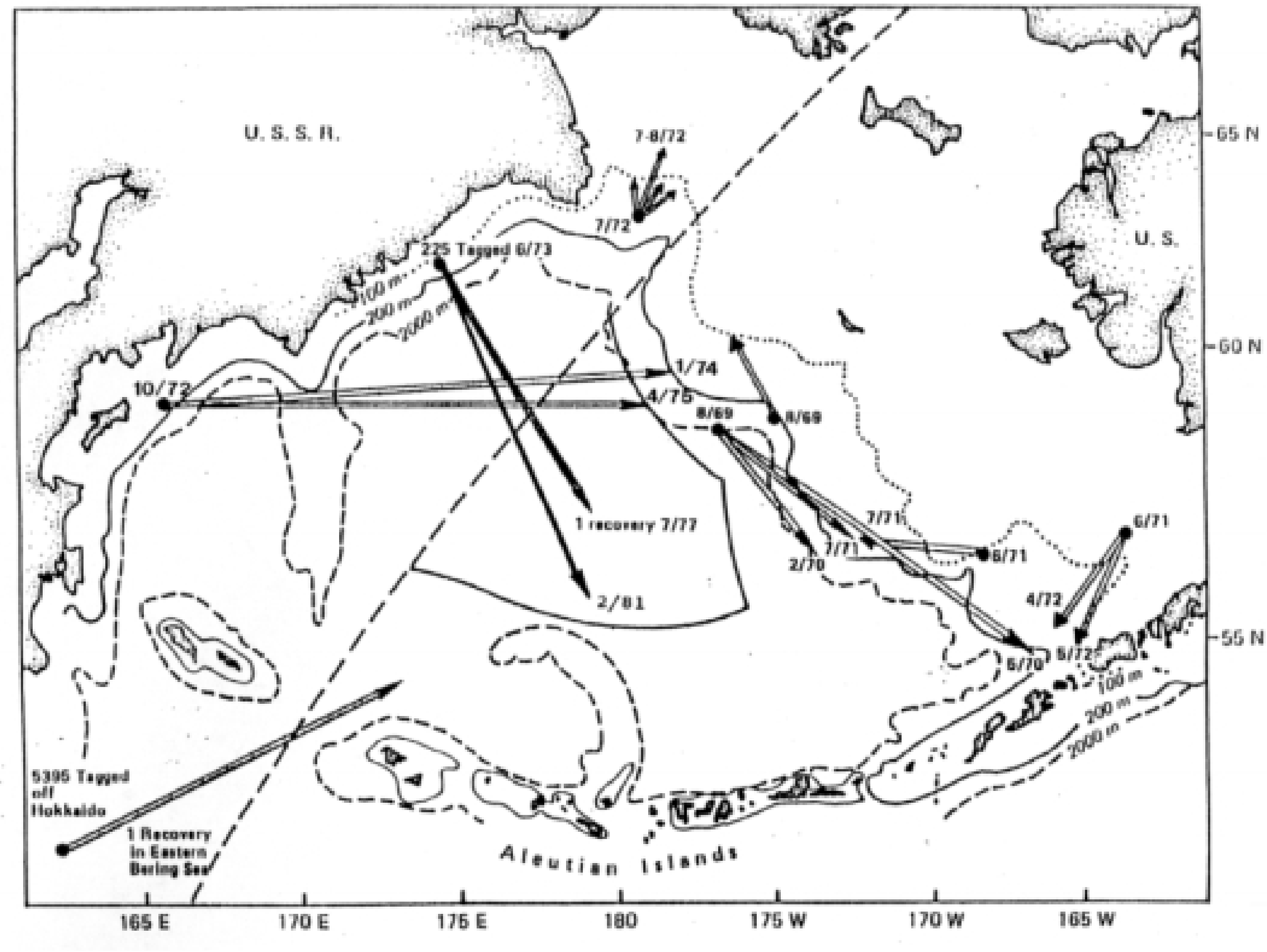


Figure 2.18: Movement of walleye pollock tagged by Japanese scientists in the Bering Sea (from Dawson, 1994). Note: most tagging and recoveries occurred during the summer/autumn feeding season. Note cluster of April recoveries near Unimak Pass in the spawning season.

Table 2.2: Summary studies of pollock stock structure using phenotypic characteristics.

Author	Method	Area	Results
Ogata (1959)	meristic—vertebrae counts	Sea of Japan and Pacific Ocean side of Japan	Sea of Japan has 3 different stocks. Sea of Japan differs from the Pacific Ocean side.
Iwata and Hamai (1972)	meristic—vertebrae counts	Sea of Japan, Okhotsk Sea, and Pacific Ocean near Hokkaido	8 "local forms"— 2 groups in the Sea of Japan 3 groups in the Okhotsk Sea 3 groups in the Pacific Ocean
Hashimoto and Koyachi (1969)	morphometrics—body length and other morphological features	northern Japan	3 groups discriminated
Janusz (1994)	meristics and morphometric	Sea of Okhotsk	3 stocks distinguished
Temnykh (1991)	morphometrics	Sea of Okhotsk	S. Kurils population distinguished from N. Sea of Okhotsk
Temnykh (1994)	morphometrics	W. Bering Sea and E. Kamchatka	W. Bering and E. Kamchatka stocks distinguished
Ishida (1954)	morphometrics—otoliths	northern Sea of Japan, Okhotsk Sea, and northern Pacific Ocean coast of Japan	Otolith size is larger in Sea of Japan pollock than Okhotsk Sea. Otoliths are similar between Sea of Japan and Pacific Ocean pollock.
Shaw and McFarlane (1986)	morphometrics—length-at-age	British Columbia—Dixon Entrance, Strait of Georgia	2 stocks discriminated—Strait of Georgia pollock are smaller. Little interaction between pollock north and south of Queen Charlotte Sound.
Thompson (1981)	morphometrics—length-at-age	British Columbia—Dixon Entrance, Strait of Georgia, Queen Charlotte Sound	3 separate stocks—each area contains its own distinct stock. Little mixing occurred between them.
Saunders *et al.* (1989)	morphometrics, life history	British Columbia	Separate stocks in Strait of Georgia, Hecate Strait/Dixon Entrance, Queen Charlotte Sound and W. Vancouver I.
Lynde *et al.* (1986)	morphometrics—length-at-age	eastern Bering Sea and Bering Sea basin	northeastern shelf and slope and Aleutian Basin represent one stock distinct from other regions of the eastern Bering Sea
Hinckley (1987)	spawning time and location; morphometrics—length-at-age; fecundity	Aleutian Basin and eastern Bering Sea shelf and slope	3 spawning stocks in the eastern Bering Sea—basin, northeastern slope and eastern shelf and slope

Table 2.2: (continued).

Author	Method	Area	Results
Mulligan *et al.* (1989)	spawning time and location	eastern Bering Sea and Aleutian Basin	three spawning areas separated in space and time: EBS SE Shelf, EBS NW shelf, Aleutian Basin
Serobaba (1977)	morphometrics and meristics	northern, western, eastern and southern Bering Sea	different stocks occupy each region
Dawson (1994)	morphometrics	Bering Sea	Three stocks—eastern Bering Sea shelf, Aleutian Basin, and Aleutian Islands
Janusz *et al.* (1989)	meristics and morphometrics	Donut hole and eastern Bering sea shelf	2 stocks distinguished in Donut Hole and eastern Bering Sea
Nitta and Sasaki (1990)	morphometrics	Donut hole, eastern Bering Sea, near Japan	Characteristics distinguish 3 stocks, with about 90% classification accuracy
Gong *et al.* (1990)	meristics	Asian and Bering Sea	Asian and Bering Sea stocks distinguished but stocks within these regions not distinguished
Wilimovsky *et al.* (1967)	meristic (fin ray and vertebral counts) and morphometric	entire Pacific Ocean	morphometric—no strong evidence for discrete stocks. meristic—no differences between Bering Sea and Puget Sound pollock. No differences between Gulf of Alaska and Northern B.C. pollock.
Koyachi and Hasimoto (1977)	meristic—fin ray, gill raker, and vertebrae counts	entire Pacific Ocean	12 subpopulations, including the Bering Sea and Gulf of Alaska

2.4.4 Genetic and Metapopulation Structure

We have summarized studies on stock structure of pollock according to their phenotypic, acquired, or genetically based nature. Briefly, phenotypic characteristics of pollock, such as meristic or morphometric measurements, both within small geographic regions and across much broader areas, have indicated considerable population structure (Table 2.2). For example, Koyachi and Hashimoto (1977) used differences in vertebral, gill raker, and fin ray counts to distinguish 12 groups of pollock across its range. Within much smaller geographic regions there are also distinct groups. For example, around the islands of Japan and Sea of Okhotsk, Iwata and Hamai (1972) identified eight groups, and in the Sea of Okhotsk three stocks were distinguished (Janusz, 1994). Within the eastern Bering Sea, including the eastern Aleutian basin, three to five stocks have been distinguished using morphometrics and life history characters (Lynde *et al.,* 1986; Hinckley, 1987; Dawson, 1994). Gulf of Alaska and Bering Sea populations appear to be phenotypically differentiated (Koyachi and Hashimoto, 1977). For example, Koyachi and Hashimoto (1977) and Hashimoto and Koyachi (1977) used differences in vertebral counts and in growth rates to distinguish 11 groups of pollock across its range. Within a small area, for example around the islands of Japan, there are also distinct groups (Iwata and Hamai, 1972).

Naturally acquired tags, such as elemental composition of otoliths and parasite characteristics, indicate restricted mixing among pollock juveniles and adults of different subpopulations (Table 2.3). For example, the chemical "fingerprint" of otoliths near the nucleus (deposited during early larval life) could be utilized to assign fish to their capture location as juveniles with 70–85% accuracy over broad regions of the eastern Bering Sea (Mulligan *et al.,* 1989), indicating limited movement and mixing of fish from different geographic regions. Using parasite frequencies, adult pollock caught on the south side of Vancouver Island can be distinguished from those on the west side with about 75% accuracy (Arthur, 1983). In the Sea of Okhotsk, several different populations of pollock were distinguished based on parasite frequencies (Avdeev and Avdeev, 1989). By contrast, mark-recapture studies where pollock were tagged in summer indicate broad movement of individuals across areas of the Bering Sea (Fig. 2.18). However, critical studies of marking spawning pollock have not been conducted. Tagging results thus far indicate potential for dispersal during the summer feeding period. Historical tagging studies do not provide information indicating whether individuals are moving with large schools as migrating populations, whether individuals are vagrants and mixing with local populations, or if dispersal patterns in the Bering Sea are part of ordered seasonal migrations. Tagging studies around Japan do support dispersed feeding migrations and homing migrations to specific spawning areas (Tsuji, 1989).

Studies using biochemical and molecular methods on pollock show mixed results for distinguishing stock structure of pollock, varying somewhat by technique (Table 2.4). Using allozymes, Grant and Utter (1980) detected minor differences between the Gulf of Alaska and Bering Sea, but no differences within either region. Using mtDNA sequence data from a 276 bp spacer sequence near the cytochrome b gene, and the left side of the control region, Shields and Gust (1995) reported slight genetic differences between eastern and western Bering Sea pollock. However, the season samples were acquired was not reported; if samples were collected in the summer feeding season when stocks may be mixed, genetical resolution can be blurred. The relatively small size of the control region of pollock mtDNA, lack of length mutations within the control regions sequenced to date, and the very low transition to transversion ratios of the control and spacer regions (1.2:1.0 and 1.29:1.0, respectively) suggest that these regions may not be variable enough to provide greater genetic discrimination among populations. Mulligan *et al.* (1992) employed mtDNA RFLP on fish collected during the spawning season and distinguished among stocks in the Gulf of Alaska, Donut Hole/Bogoslof Island, and Aleutian Island. Profiles from nine restriction enzyme digests yielded 65 composite genotypes. Pairwise comparisons of Gulf of Alaska ver-

Table 2.3: Summary studies of pollock stock structure using acquired characteristics.

Author	Method	Area	Results
Nakano *et al.* (1991)	otolith chemistry: adults, whole otolith homogenates	eastern Bering Sea, western Bering Sea, Donut hole	differences in 3 areas, little mixing
Mulligan *et al.* (1989)	otolith chemistry: juveniles, inner early life otolith increments	eastern Bering Sea, (SE Shelf, NW Shelf, Aleutian Basin)	differences in 3 areas, some mixing
Severin *et al.* (1995)	otolith chemistry: juveniles, outer otolith increments	eastern Bering Sea (Bristol Bay), Gulf of Alaska	distinguish 5 areas, some mixing
Arthur (1983)	parasites	British Columbia—Strait of Georgia, West side of Vancouver Island, Queen Charlotte Sound, and Dixon Entrance	3 stocks in this area; Strait of Georgia, Vancouver Island and Queen Charlotte Sound/ Dixon Entrance
Avdeev and Avdeev (1989)	parasites	Sea of Okhotsk, Kommader Is., Kamachatka Penin.	Seven distinct groups within the NE Sea of Okhotsk, distinct groups in Kommander I., E. Kamchatka, and Shirshov Ridge
Misc. Authors, see Figs. 2.17, 2.18.	Tagging studies	western and eastern Bering Sea, Japan	Broad movements, homing migrations to spawning site

sus the Bering Sea showed significant genetic differentiation between these populations (Fig. 2.19).

More recently, using sequences of mtDNA cytochrome-b and ATPase-8, Powers (1996) and his colleagues (J. Quattro and D. Powers, unpublished data, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950; see Appendix 2a) identified haplotype differences between Asian and North American pollock. The unique DNA sequences allowed them to develop an enzyme method to rapidly identify individuals by RFLP. An analysis of molecular variance on the combined data identified sharp distinctions between Asian and North American fish and considerable substructure within the American and Asian clusters (Fig. 2.20).

A promising technique for examining genetic variance among fish populations is the study of genomic DNA microsatellites. Microsatellites are nuclear DNA sequences comprising tandem arrays of di-, tri-, or tetranucleotide repeats such as (GT)n or (CAC)n that usually extend over less than 300 base pairs (bp) (Wright and Bentzen, 1994). Microsatellites are dispersed at intervals of 10–30 kilobase (kb) intervals throughout eukaryotic genomes, and alleles exhibit high levels of size variation associated with variation in the number of repeating units. Hence, microsatellites constitute an extremely abundant class of highly polymorphic genetic markers. Allelic variation in

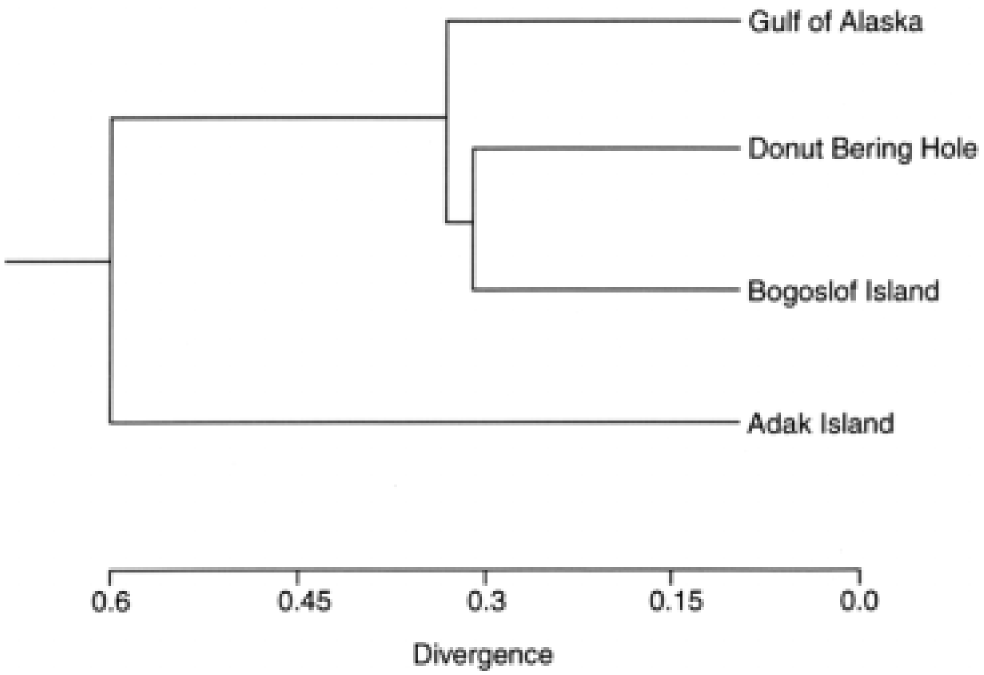


Figure 2.19: UPGMA clustering of genetic distances among walleye pollock stocks in the eastern Bering Sea and Shelikof Strait (from Mulligan *et al.,* 1992).

microsatellites can be detected by using oligonucleotide primers specific to DNA sequences flanking the satellite and amplifying between the primers using the polymerase chain reaction. Alleles are discriminated by using electrophoresis to separate the PCR products according to size in polyacrylamide gels. Studies of microsatellite markers in Atlantic cod populations (Bentzen *et al.,* 1996) have yielded finer genetic discrimination of geographic subpopulations than had been possible previously. Powers and his colleague Gary Villa (unpublished data, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950; see Appendix 2a) screened populations for DNA microsatellite loci that allowed the discrimination between pollock populations on a finer scale than was possible by mtDNA analysis. Using PCR primers that allow amplification of microsatellites in Atlantic cod (Bentzen *et al.,* 1996), pairwise comparisons from the first two microsatellite loci examined, Gmo145 and Gmo2, confirmed differences between Asian and American pollock stocks, and further resolved differences between Gulf of Alaska and Bering Sea stocks (Fig. 2.21). However, in the case of Gmo145 there was a null allele scored for this primer that was responsible for the major east-west differences. The presence of a null allele indicates that nucleotide sequences in the flanking regions of microsatellite markers are not homologous between these populations, resulting in no scorable PCR product.

Microsatellite alleles may be “the most powerful Mendelian markers ever found” (Jarne and Logoda, 1996). Microsatellites have a number of valuable

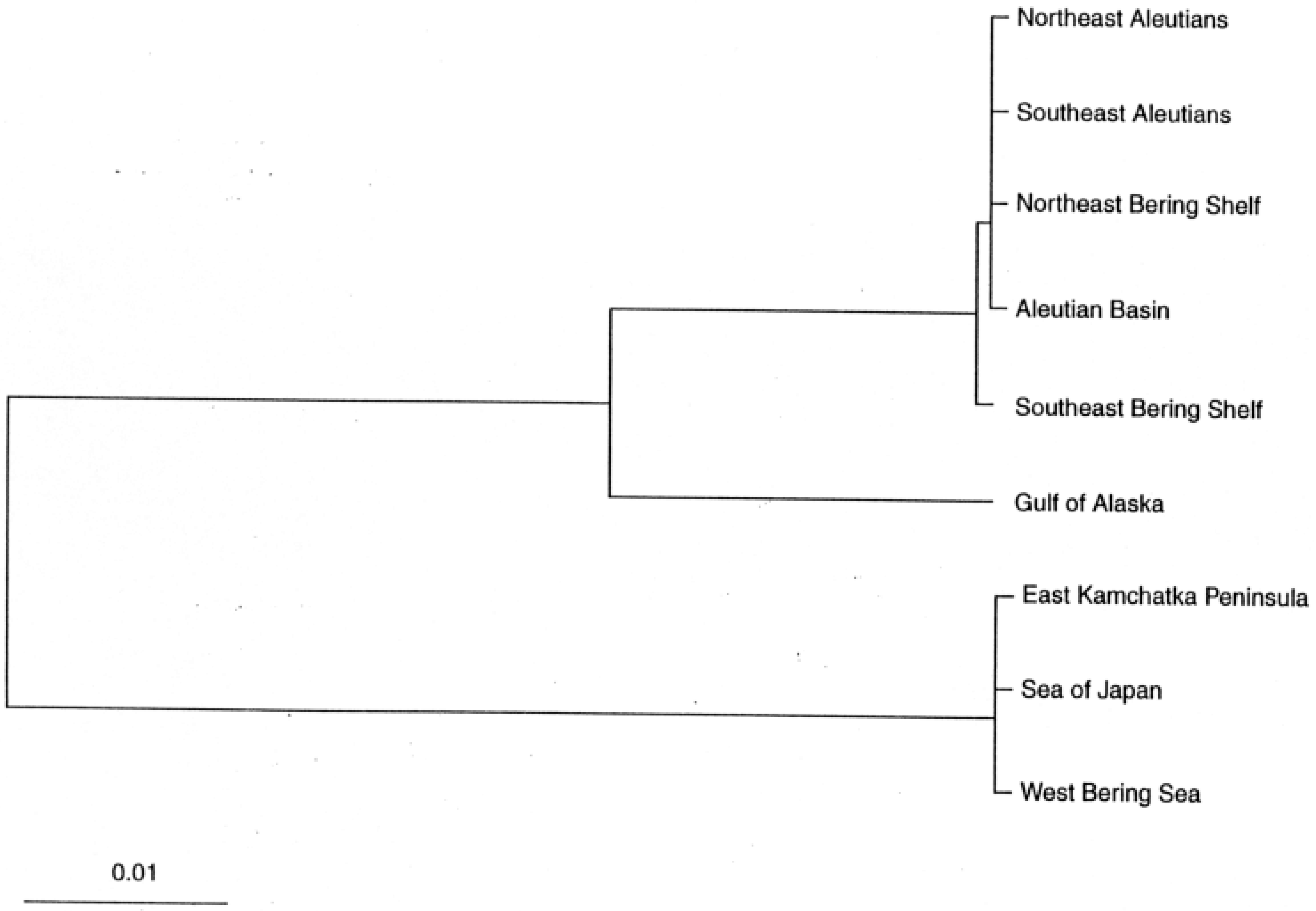


Figure 2.20: UPGMA dendogram of walleye pollock stocks from mt-DNA RFLP data utilizing the DA-Genetic Distance Method of analysis (from Powers).

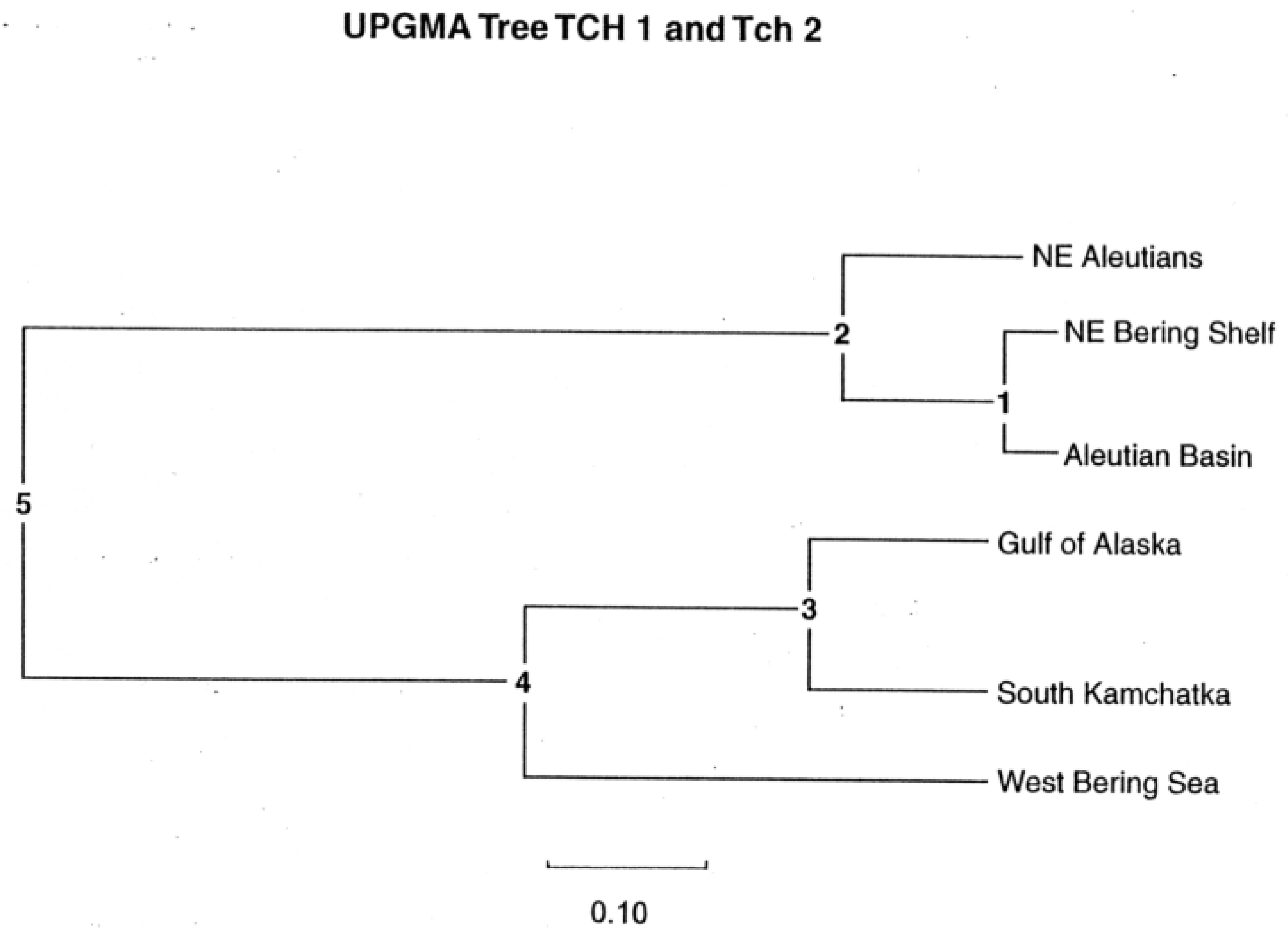


Figure 2.21: UPGMA dendogram of walleye pollock stocks from microsatellite polymorphism frequencies from primers Gmo2 and Gmo145 (from Powers).

Table 2.4: Summary studies of pollock stock structure using acquired characteristics.

Author	Method	Area	Results
Mulligan *et al.* (1992)	mtDNA RFLP	eastern Bering Sea basin, Aleutian Is. and Gulf of Alaska	2 distinct stocks in Aleutian Is. and Donut Hole/Bogoslof, Gulf and Donut Hole/Bogoslof have informative differences
Shields and Gust (1995)	mtDNA sequencing	across Bering Sea and Gulf of Alaska	significant differences between eastern and western Bering Sea
Grant and Utter (1980)	allozyme	southeastern Bering Sea and Gulf of Alaska	minor genetic differences between the two areas. No differences within the areas.
Johnson (1977)	allozyme	eastern Bering Sea and Gulf of Alaska	No significant differences found
Iwata (1973)	allozyme	northern Sea of Japan and north Pacific coast of Japan	No differences found
Iwata (1975a, b)	allozyme	northern Sea of Japan and eastern Bering Sea	Highly significant differences found between the two areas
Efremov *et al.* (1989)	allozyme	northern Sea of Okhotsk	Allozyme variability suggesting that aconitase could be genetic marker
Powers (1996)	mtDNA RFLP and DNA microsatellite	Bering Sea and Gulf of Alaska	eastern and western Bering Sea distinguished using mtDNA, Gulf of Alaska and eastern Bering Sea stocks have informative differences using microsatellite DNA

attributes as tools in stock discrimination. First, they typically exhibit much higher levels of variability than other conventional genetic markers, such as allozymes or mitochondrial DNA. In marine fishes and invertebrates they typically have 10 or more alleles, and heterozygosities of 50–95% (Wright and Bentzen, 1994; Bentzen *et al.,* 1996; García de León *et al.,* 1997). This higher level of polymorphism may confer greater resolution in surveys of population structure than that obtained with either allozymes or mtDNA, a generalization supported both by theoretical analyses and several empirical studies in which microsatellite surveys have revealed population structure not evident with either allozymes or mtDNA (Bentzen *et al.,* 1996; Ruzzante *et al.,* 1996a, b). As well, rates of change of microsatellites appear to be on the order of 10^4 greater than those for coding DNA. These rates of change are due to replication errors causing size polymorphisms rather than mutation rates resulting in base pair changes. Second, microsatellites are more likely to be selectively neutral than either allozymes or mtDNA, which increases their value for estimating gene flow (migration) rates. Third, the DNA basis of microsatellites, their small size and the use of PCR in their assay present logistical advantages in sample acquisition (minimal tissue requirements and no need for frozen storage) and makes possible the use of archival materials such as scales and otoliths as tissue sources, hence making retrospective studies a possibility.

An emerging view of genetic structure in walleye pollock suggests a more complex pattern of stock structure than recognized previously. Studies to date indicate varying degrees of genetic differentiation between pollock in the Gulf of Alaska and Bering Sea. Phenotypic differences between stocks, elemental composition of otoliths, and parasite studies are consistent with this interpretation. Distinction between adjacent putative stocks at the sub-basin scale, for example in the eastern Bering Sea, is currently lacking but is more likely to be observed when higher-resolution molecular techniques are used. Therefore, more pollock-specific microsatellite primers need to be developed and tested to survey a greater number of microsatellite loci. Although the microsatellite analyses presented here are tentative, they are generally supportive of data from life history characteristics and phenotypic patterns that indicate considerable population heterogeneity.

2.4.5 Discussion of Gene Flow and Larval Transport

Among the major basin regions of the Sea of Japan, Sea of Okhotsk, Bering Sea, and Gulf of Alaska there is good evidence of genetic structure in pollock that is supported by genetic, phenotypic, and life history data. Probably these major basin regions were largely isolated from each other during the last major glaciation, as well as at other times during pollock's ancient history in the North Pacific. Considering the colonizing ability of pollock the potential limited degree of genetic mixing between populations is somewhat surprising, but perhaps can be attributed to larval retention mechanisms, differences in reproductive characteristics (timing and temperature adaptations), natal homing, or outbreeding depression of vagrants that reproduce with historical local populations.

In spite of substantial opportunities for gene flow through larval transport and dispersal of juveniles and adults within a major region like the Bering Sea, there appears to be genetic differentiation of populations across a wide distance, such as the eastern versus western Bering Sea. The inhospitable nature of the Aleutian Basin as a nursery for larvae and juveniles may act as a barrier to population mixing. Among adjacent spawning regions in the eastern Bering Sea, the potential for gene flow during larval drift is high. However, since there appears to be an unresolved degree of structuring within the Bering Sea, reduced gene flow due to larval retention mechanisms or strong natal homing and philopatry may be indicated.

Genetic differentiation between the Gulf of Alaska and Bering Stocks presents an interesting scenario. The Alaska Peninsula presents an obvious land barrier to mixing. Larvae spawned in Shelikof Strait are frequently retained in the sea valley region by fronts and eddies, and larvae transported onto the shallow continental shelf between the Shumagin Islands and the

Shelikof sea valley have a long residence time there due to slow and meandering currents. Years with conditions that favor transport into the Alaska Stream are also years of high larval mortality. When larvae do enter the Alaskan Stream, where they could be transported into the Bering Sea, they encounter conditions that are poor for survival. Furthermore, the transit time is usually greater than the 50 d planktonic life of larvae. If larvae did survive the journey in the Alaskan Stream, they would enter the Bering Sea through the relatively deep western island passes. To mix with the gene pool on the eastern Bering Sea shelf, they would have to cross the Aleutian Basin region, where feeding conditions are poor and mortality is high. Unimak Pass is the only conduit between the shelf of the North Pacific and eastern Bering Sea. While several drifters deployed in Shelikof Strait have entered the Bering Sea through Unimak Pass, the transit time exceeded 60 d in each case. Consequently, it appears that vagrants from the Shelikof Strait spawning have a high mortality, limiting gene flow and population homogenization between the Gulf and Bering populations. These populations could have become differentiated during isolation by glaciation and founder effects, or alternatively, during recent periods of bottlenecks and genetic drift. Whereas the Bering Sea pollock population is extremely large and unlikely to experience genetic drift, the Gulf of Alaska population is smaller and is known to fluctuate widely, perhaps experiencing periods of enhanced genetic drift.

2.4.6 Metapopulation Summary

A summary view of genetic structure in walleye pollock suggests a pattern of considerable geographic stock structure in walleye pollock. Phenotypic differences between stocks, elemental composition of otoliths, and parasite studies indicate restricted mixing of juveniles and adults. Genetic differences appear between broad regions, but resolution between adjacent stocks, especially within the eastern Bering sea, is currently lacking. All of the genetic studies to date indicate a varying degree of genetic differentiation between pollock in the Gulf of Alaska and Bering Sea. The potential for gene flow during larval drift is high between adjacent stocks. However, since there appears to be an unresolved degree of structuring within the Bering Sea, reduced gene flow due to larval retention mechanisms or strong natal homing and philopatry is indicated.

The standard metapopulation models of Harrison (1991; Fig. 2.2) do not fit the apparent population structure of pollock as known to date. A strawman metapopulation structure can be proposed that represents an intermediate model. This metapopulation model of pollock is made of several large populations separated by long distances and geographical barriers (such as the eastern Bering Sea and Sea of Okhotsk populations) with little gene flow between them, and numerous smaller populations with potential linkages among each other and the larger populations (Fig. 2.22). Some populations may show local adaptations to their specific habitat, minimizing gene flow through reliance on larval retention features and natal homing.

In spite of the importance of this resource, and the importance of stock structure to its management, we don't have a comprehensive genetic sur-

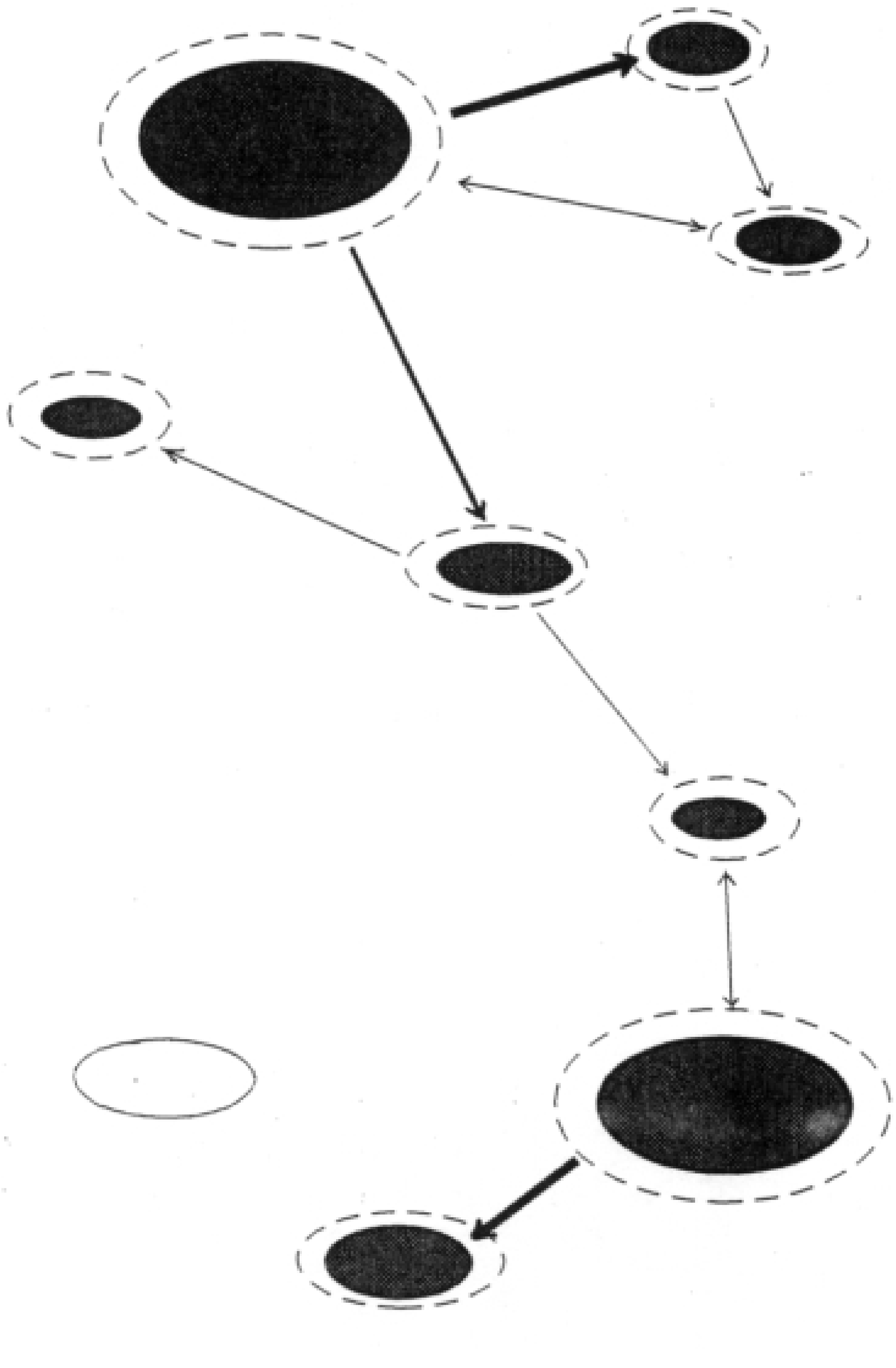


Figure 2.22: Hypothetical nondimensional pictogram representing the population structure of walleye pollock. Closed ellipses represent habitat patches; filled = occupied, unfilled = vacant. Dashed lines indicate boundaries of populations. Arrows indicate relative gene flow through migration or larval transport. Probable main populations for pollock are Sea of Okhotsk and eastern Bering Sea shelf.

vey across the whole range using modern genetic techniques. Nor is there a finescale genetic survey, within a region where different stocks have been identified. Such a survey would need to be adequate to determine if there are clines that represent differences by distance, or a sudden transition representing a barrier. Many of the smaller fjord populations represent an opportunity to examine founder effects on genetic differentiation within the pollock metapopulation. However, these populations have not been included in past genetic surveys. Future work should concentrate on genetic structures with high mutation rates, such as microsatellites, capable of resolving genetic structure that may have evolved recently. Stock mixing problems can be better addressed using these techniques in conjunction with applied tags and natural environmental tags, such as elemental composition of otoliths.

2.5 Management Implications

The question of whether fisheries fluctuations result from local populations waxing and waning independently or movements among populations has been a central issue in fisheries since the time of Hjort (1914). Since that time, most fisheries research has assumed that local populations are closed and homogeneous systems. However, many scientists are currently suggesting that we re-examine the large-scale patterns underlying the dynamics of fish populations (Frank, 1992). For example, prior to the collapse of the northern cod population in the Northwest Atlantic Ocean it was believed that there was no genetically based population structure due to extensive egg and larval drift, followed by opportunistic and nonphilopatric recruitment of juveniles to adult assemblages (deYoung and Rose, 1993). Studies of allozymes and mtDNA studies had little success in discriminating among Northwest Atlantic cod stocks. However, Bentzen *et al.* (1996) examined nuclear DNA microsatellite distributions and found that the northern cod population does not represent a single panmictic assemblage, but is comprised of genetically distinguishable subunits, each of which is affiliated with a distinct spawning area. It is of great interest that considerable finestructure has been found in Atlantic cod populations, because cod and pollock have taxonomic as well as life history similarities.

There are several issues especially relevant to pollock stocks when genetically or geographically discrete subpopulations are lumped as single management units. Daan (1991) indicates that if catch-at-age analysis is applied to a heterogeneous unit stock (a metapopulation), then fishing effort is underestimated and fishing mortality deviates from the recent true trend, leading to the possibility of overfishing. Pawson and Jennings (1996) indicated that lumping of stocks may lead to reductions in short-term yields. The depletion of unidentified local subpopulations and their possible extinction is another issue (Ovenden, 1990). The rate of recovery of geographically but not genetically discrete populations will depend on the level of gene flow between subpopulations. Genetically distinct subpopulations, by definition, have low levels of gene flow among them, and specific stock adaptations to local habitat conditions can impede recovery from extrinsic source populations.

There are some other key areas where high-resolution stock identification would be extremely useful in management of pollock harvests. A central issue in the case of pollock management is whether broad-scale migrations occur that result in seasonal mixing of subpopulations. For example, if eastern or western Bering Sea fish migrate across or around the Basin (as believed by Dawson, 1994), they may be harvested on both sides of the Bering Sea basin. Therefore, a migratory population would experience two independent sources of fishing mortality in two management regions.

Recently, new local populations of pollock have been discovered. Whether they will be maintained as self-sustaining populations or whether they are ephemeral stocks is a question that depends upon the mechanism of natal spawning and local adaptation for reproductive success. For example, in recent years a spawning population of 300,000 tons has been found around the Shumagin Islands in the western Gulf of Alaska (C. Wilson, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, personal communication, October 1996). This population is largely composed of the 1989 year class, which was strong in the Bering Sea, but weak in the rest of the Gulf of Alaska. It is unknown whether this population originated from density-dependent dispersal from the Bering Sea, or whether it represents an increase in a previously unknown local subpopulation. Another explanation may be that vagrants from the Bering Sea could have joined a small local spawning population.

Research on spawner-recruitment relationships is also dependent on the definition of stock structure among populations. For example, consider the following hypothetical but realistic example: if two genetically distinct and asynchronously fluctuating populations, A and B, are lumped together in a VPA analysis, dominance shifts could result in a spawner-recruit relationship where recruits from population A are compared to egg production from population B. Shifts in dominance between putative stocks appears to be a situation particularly applicable to pollock in the Bering Sea (Francis and Bailey, 1983). In this case, knowledge of the underlying population structure would vastly improve the understanding of spawner-recruit relationships. Alternatively, different spatial scales can be a problem when early life dynamics in the juvenile nursery of population A are compared to recruits derived from VPA analysis of lumped populations; this type of comparison is common in fisheries research. Other confounding cases may occur where there is vagrancy of recruits or an exogenous source of recruits, such as might occur with pollock in the Gulf of Alaska. All of these circumstances can result in misinterpretations of the factors underlying the dynamics of these populations.

The mechanism of natal-site fidelity has broad implications to fisheries management and sustainable harvesting of these populations. For example, if fish learn their migration routes from older fish, currently thought to be important for cod (Rose, 1993) and herring (Corten, 1993), then removing older fish from the population can lead to increased straying of younger fish due to loss of social tradition. Furthermore, this mechanism implies that larvae dispersed from the range of adults can adopt new local populations. The mechanism of “innate” or “genetic memory” implies that removal of any fish is of equal importance to the population, but it is essential not to drive a population into extinction, because recolonization will depend on the process of natural selection and adaptation to local conditions. Vagrants from other populations are unlikely to spawn with local populations in the same region. Imprinting implies that harvesting will not have an impact on migratory routes, and heavily depleted populations can be re-seeded. In fact, marine fish species probably use a combination of all of these mechanisms for natal fidelity, and the response to any one stimulus is graded against others. It is not known which homing mechanisms are utilized by pollock during spawning migrations; however, the existence of genetic structure in the population, which is maintained in spite of larval drift and highly dispersed feeding migrations, tends to indicate a genetic-based mechanism. Based on the complex range of behaviors pollock are capable of exhibiting (Olla *et al.,* 1996) it should not be surprising that they show considerable flexibility in their homing behavior.

New paradigms for managing fisheries in a sustainable manner are urgently needed, and these concepts are largely dependent upon better definition of stock distributions and interrelationships. In a review of stock structure methods, Pawson and Jennings (1996) suggest that despite widespread application of genetic techniques, there are only a few cases where these studies have provided information to managers that could have been adopted, except for salmon. Certainly, information indicating multiple genetic-based stocks adds another element of concern to fisheries managers and makes their task more complex (Lincoln, 1994). As noted by Carvalho and Hauser (1994) good communication between fisheries managers and geneticists is needed for effective implementation of stock structure information, including clear objectives for proposed work and utilization of appropriate techniques. Future work on stock structure of walleye pollock should be closely coordinated with scientists responsible for establishing pollock harvest policies.

Given the high potential for gene flow in marine species including pollock, genetic approaches alone may not completely resolve stock structure issues at the level of harvest stocks or ecological populations; tagging studies offer another way to study linkages between fish populations. Gauldie (1991) suggests that tagging studies and monitoring catch statistics are methods to assess how much fishing in one place/time affects groups of fishes in other places (harvest stocks). Pawson and Jennings (1996) are also proponents of tagging studies for providing evidence of stock separation and migration, and indicate that carefully planned tagging experiments, or experiments utilizing naturally acquired tags, are needed to establish a relationship between fishes in different regions. Although not necessarily showing levels of gene flow between areas, well thought out and executed tagging and/or transplant experiments would offer a powerful approach to studying migration mechanisms. Tagging pollock has been problematic in the past due to issues of barotrauma, tag recovery bias, and distribution of effort, and the large number of tags necessary to characterize such large populations. New technologies should be developed to minimize these problems, including environmental tags, such as otolith chemical fingerprints, and in situ tagging. Studies of fish dispersal that are coordinated with modern genetic studies should contribute significantly to understanding linkages between population dynamics and structure of marine fish populations.

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Part 2A

The use of molecular techniques to dissect the genetic architecture of pollock populations

(Dennis A. Powers[1])

One of the main goals of fisheries biologists is to understand the mechanisms that regulate the distribution and abundance of marine fish. Elucidation of these mechanisms requires an understanding of the genetic architecture of the fish species, including the ability to discriminate between stocks and determine the relative contributions of these stocks to the fishery. During the initial phase of our project, we developed pollock-specific polymerase chain reaction (PCR) methods to test the hypothesis that "there are distinct Pollock stocks in the Bering Sea." After these methods were developed, we analyzed 164 individual pollock samples that represented populations sampled from the Gulf of Alaska, Bering Sea, and Sea of Japan. Using 47 individuals as population representatives, we initially sequenced 300 base pairs of DNA for each of two mitochondrial genes (i.e., cytochrome-b and ATPase) for each individual fish. Our sequencing results identified 14 mtDNA haplotypes, three of which were in high enough frequency to be informative for tests of population subdivision. These three haplotypes were defined by base substitutions at two different DNA sequence sites: Haplotype 3 – AA; Haplotype 7 – GA, and Haplotype 13 – GG.

Forty-seven individuals were sequenced for approximately 600 base pairs; 300 base pairs each for cytochrome-b and ATPase. Individuals represented all populations sampled from the Gulf of Alaska, Bering Sea, and Sea of Japan. Fourteen mtDNA haplotypes were found, three of which were in high enough frequency to be informative for tests of population subdivision. These three haplotypes were defined by base substitutions at two sites.

Haplotype 3 – AA
Haplotype 7 – GA
Haplotype 13 – GG

where the first position is found in cytochrome-b, and the second in ATPase-8. Substitutions at both sites were silent, the first a third-position substitution in a threonine codon, the second a third-position substitution in a glutamic acid codon. A restriction enzyme assay was developed to score 117 additional individuals for these three haplotypes (a total of 164 individuals) (Table 2A.1).

An analysis of molecular variance (AMOVA) was performed on the aggregate data (164 individuals) representing nine populations. Most of the variation was found to be within populations (85.5%), although a small but significant proportion was among populations (14.5%). A UPGMA den-

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Table 2A.1: Cytochrome-b and ATPase-8 haplotypes from different areas of the Bering Sea.

	Haplotype Pairs		
	AA	GO	GA
America			
Northeastern Shelf	4	12	4
Aleutian Basin	6	7	3
Southeastern Aleutian	6	11	2
Northeastern Aleutian	3	9	2
Gulf of Alaska	3	20	5
Southeastern Shelf	8	11	1
Asia			
East Kamchatka	3	6	12
West Bering Sea	4	9	10
Sea of Japan	0	1	2

Table 2A.2: Tests for temporal variation.

Locality	Years Compared	Probability	Significance
Gulf of Alaska	1988 vs 1994	0.3866	ns
Southeast Shelf	1988 vs 1991	0.1648	ns
Northeast Aleutians	1988 vs 1991	0.9021	ns

drogram (Fig. 2A.1) using among-population genetic distances revealed evidence for a distinct split between American (Gulf of Alaska and Eastern Bering Sea) and Asian (Sea of Japan and Western Bering Sea) populations, primarily in the distribution of the GG and GA haplotypes. An AMOVA revealed that haplotype frequencies within each group differed significantly ($P < 0.0002$). An analysis of these data using the Neighbor Joining Method was consistent with the distinct division between American and Asian populations. As was the case for the dendogram derived by the DA genetic distance analysis (Fig. 2A.2), the Neighbor Joining Method also revealed considerable substructure within the larger American and Asian clusters. Some of the smaller clusters were consistent with the substructure derived by the UPGM genetic distance dendogram illustrated in Fig. 2A.2, while others were slightly different. If we could significantly expand the sample size for each of the nine populations involved in this study and provide data for these populations between year classes, there is a very high likelyhood that we could discriminate between all nine populations on the basis of RFLP analysis of mtDNA haplotypes.

Based on the DNA sequence data of these 47 individuals, we developed a restriction enzyme assay that allowed the rapid identification of mtDNA haplotypes based on restriction fragment length polymorphisms (RFLP) using gel electrophoresis. Employing this RFLP analysis, 117 additional individual pollock were analyzed for the three mtDNA haplotypes identified by DNA sequence analyses. After the methods were developed, we analyzed 164 pollock DNA samples representing nine populations from the Gulf of Alaska, Bering

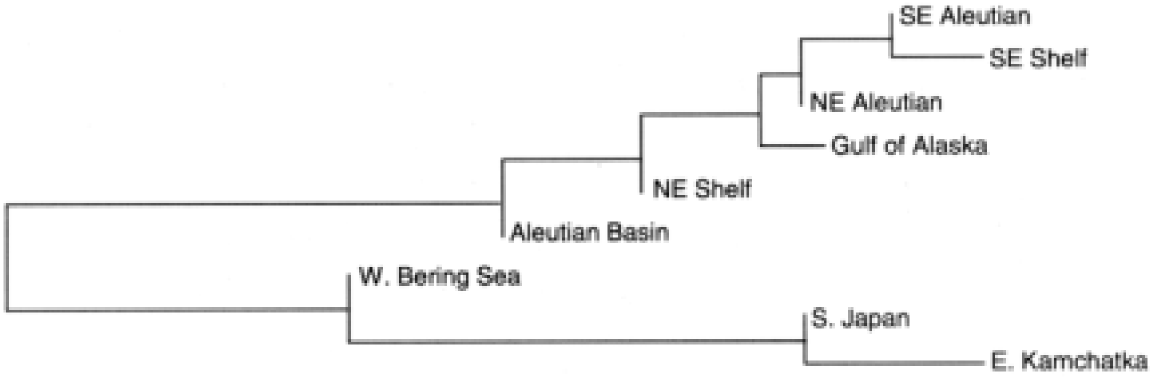

Figure 2A.1: UPGG Dendogram utilizing the Standard Genetic Distance Method of analysis.

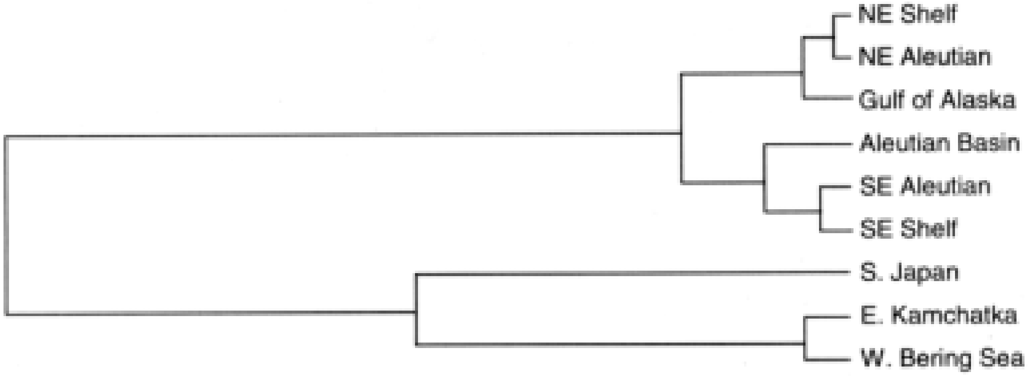

Figure 2A.2: UPGM Dendogram utilizing the DA-Genetic Distance Method of analysis.

Sea, and Sea of Japan. An analysis of molecular variance (AMOVA) was performed on the aggregate data of 164 individuals representing nine populations. Most of the variation was found to be within populations (85.5%), although a small but significant proportion was among populations (14.5%). In order to better define those populations, we expanded the sample size and analyzed samples from an earlier year to determine if the greater variation within populations was the result of pooling samples collected from different year classes. We developed the following specific goals for October 1995 through September 30, 1996 in order to attack this problem:

(i) analyze samples collected from populations in 1988,

(ii) analyze new samples collected from nine populations in 1994,

(iii) compare the results of the 1988 and 1994 samples with those collected and analyzed early,

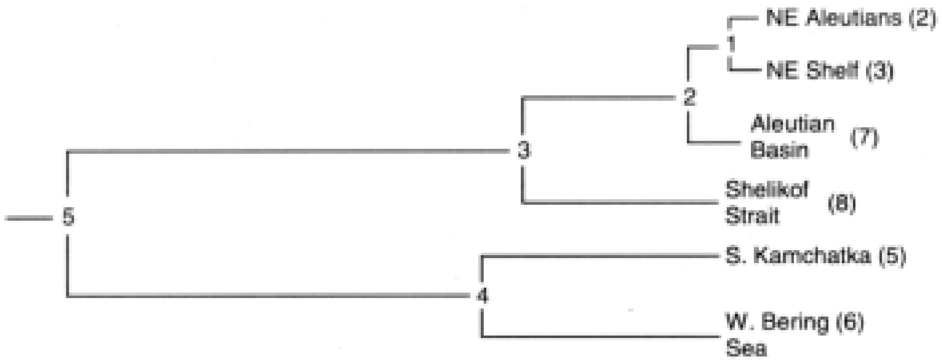

Figure 2A.3: UPGMA dendrogram of Bering Sea and Gulf of Alaska walleye pollock, based on genetic distances at the microsatellite locus Gmo-2. Number in parentheses correspond to the population numbers on the map (Figure 4).

(iv) do an analysis of variance of the temporal and spatial data sets.

By the end of 1995 we had already made substantial progress toward achieving these specific goals. For example, we had expanded the sample size from 164 individuals to 262 samples. In an attempt to determine if there was a temporal component of the data that could help explain the larger variation within populations than between populations that we reported last year, we analyzed samples collected in 1988 from the Gulf of Alaska, the Northeast Aleutians, and the Southeast Shelf and compared them with samples collected in 1994 and 1991 from those sites. However, tests for temporal variation between 1988 samples and samples collected later did not identify significant differences between year classes (Table 2A.2). Consequently, we reject the hypothesis that the larger variation that we observed within populations was derived from temporal variation between year classes.

Since our previous report, we have identified a small proportion (i.e., four) of the AG haplotype. This haplotype is probably a rare convergent change. The distribution of the haplotypes between geographical regions for 1988, 1991, and 1994 are shown in Table 2A.3.

Even though there was still greater variation within than between populations, the additional data maintained the same small but significant difference between populations that we previously reported. There remained a sharp discrimination between Asian and American groups. However, expanding the sample size did not provide better discrimination between populations.

Since expanding the sample size of the populations did not dramatically improve our ability to discriminate between populations, we undertook an analysis of minisatellite elements (i.e., "DNA Fingerprinting") of pollock populations. However, none of the minisatellite loci screened yielded useful information. We surveyed some of the pollock nuclear genome for variation in the number of tandemly repeated microsatellite elements. We screened seven

Table 2A.3: Distribution of haplotypes between geographical regions for 1988, 1997, and 1994.

	Haplotype			
	AA	GG	GA	AG
America				
Northeastern Shelf 1991	4	12	4	0
Aleutian Basin 1991	6	7	3	0
Southeastern Aleutian 1991	6	11	2	1
Northeastern Aleutian 1988	10	23	6	1
Northeastern Aleutian 1991	3	9	2	0
Gulf of Alaska 1988	3	20	6	1
Gulf of Alaska 1994	3	20	5	0
Southeastern Shelf 1988	6	21	5	0
Southeastern Shelf 1991	4	9	10	0
Asia				
East Kamchatka 1991	4	8	9	0
West Bering Sea 1991	4	9	10	0
Sea of Japan 1994	0	1	2	0

microsatellite primers for the polymerase chain reaction (PCR) that have been previously shown to amplify regions in several gadid species (Brooker *et al.*, 1994). These primers were used to analyze 221 individual pollock representing seven pollock populations. Of those primers, three pairs (Gmo2, Gmo9, Gmo145) gave detectable product, and two (Gmo2 and Gmol45) showed genetic variation. Using the Gmo145 primer, we identified 19 detectable alleles and one allele that appeared that did not yield a PCR product (Table 2A.4).

Since there was a lack of detectable PCR product, conditions of the template DNA were tested with two universal PCR primers (ACT1 and ACT4). Because all the individuals that did not yield a PCR product with Gmo145 primers gave detectable PCR products when amplified with the ACTI and ACT4 primers, these data suggest that the absence of product for Gmo145 may be due to a "null allele" at this locus resulting from one or more sequence differences in the priming region of Gmo145. When the putative "null allele" is scored as a separate allele, it is clear that the vast majority of the Asian populations have much higher frequencies than American populations.

The microsatellite data in Table 2A.5 appears to give the same general discrimination between Asian and American populations as was obtained by the haplotypes described earlier in this report. Moreover, there is a suggestion for further subdivisions in Table 2A.5 but a proper statistical analysis must be done before we can be sure if the apparent trend is significant.

The statistical analysis of haplotype and microsatellite data is one of our major goals for the remainder of our funding period after which we will publish the results in internationally refereed journals. For the haplotype data, an analysis of molecular variance (AMOVA) like that performed last year on the aggregate data (164 individuals) representing nine populations will be done on the expanded data set. Dendograms utilizing DA genetic

Table 2A.4: Alleles for Gmo 145 microsatellite locus.

Alleles	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	18	Null	Total
NE Aleutians	1	0	3	2	5	7	0	23	6	1	0	0	0	0	0	0	0	0	0	0	48
NE Shelf	0	0	0	1	3	2	1	8	3	1	0	0	0	1	0	0	0	0	0	0	20
Aleutian Basin	0	0	1	1	6	6	0	29	4	2	1	0	0	0	0	0	0	0	0	0	50
S. Kamchatka	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	68	68
W. Bering Sea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	34
Shelikof Strait	1	1	6	3	19	12	0	48	42	9	3	1	2	2	4	1	2	1	1	0	158

Table 2A.5: Frequencies of microsatellite alleles of pollock populations.

Alleles	1	2	3	4	5	6	7	8	9	10	11	13	14	15	16	17	18	18	Null
NE Aleutians	.020	.000	.063	.042	.104	.146	.000	.479	.125	.020	.000	.000	.000	.000	.000	.000	.000	.000	.000
NE Shelf	.000	.000	.000	.050	.150	.100	.050	.400	.150	.050	.000	.000	.050	.000	.000	.000	.000	.000	.000
Aleutian Basin	.000	.000	.020	.020	.120	.120	.000	.580	.080	.040	.020	.000	.000	.000	.000	.000	.000	.000	.000
S. Kamchatka	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.00
W. Bering Sea	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.00
Shelikof Strait	.006	.006	.038	.019	.120	.076	.000	.304	.266	.057	.019	.006	.013	.013	.006	.013	.006	.006	.000

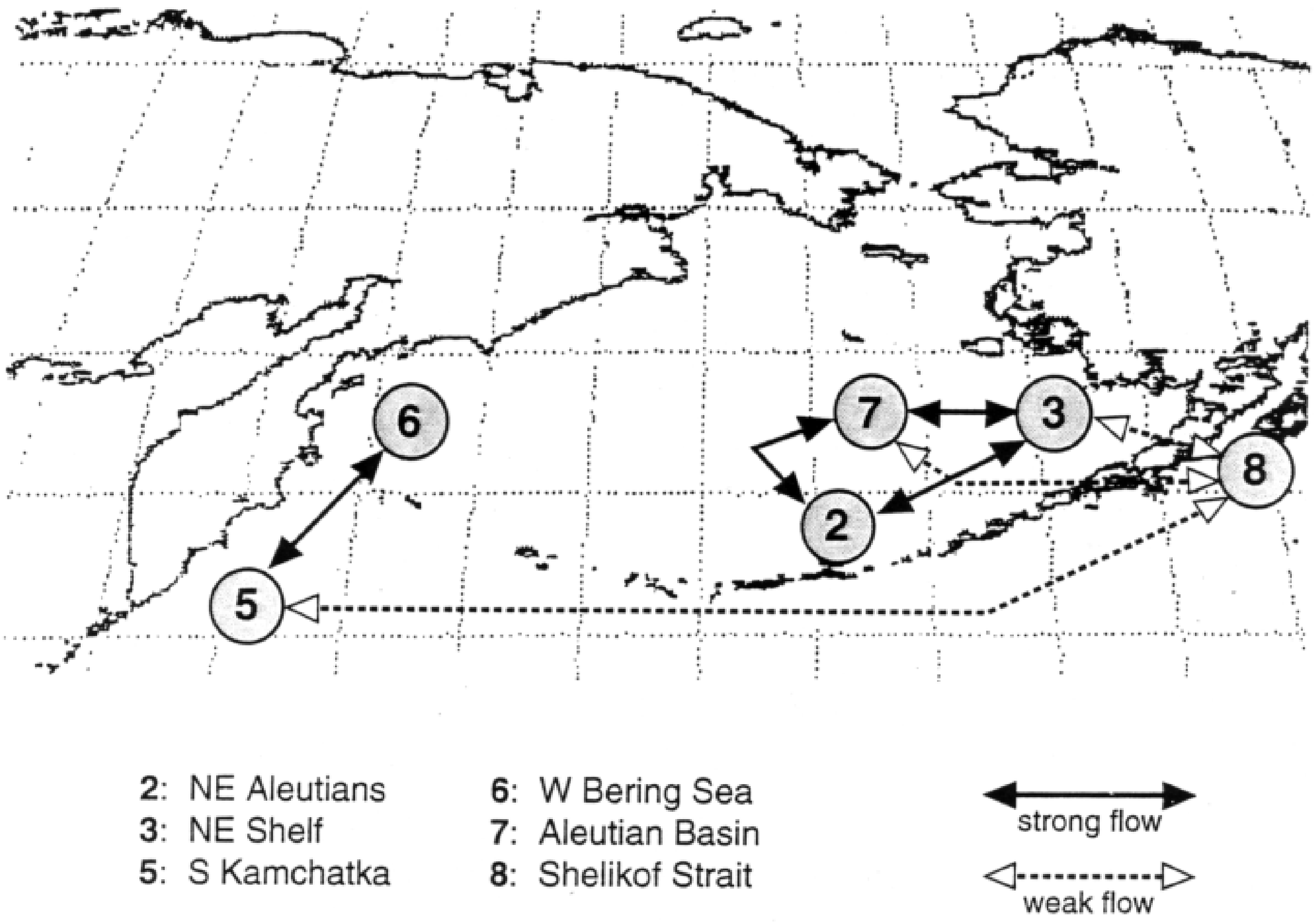

Figure 2A.4: Map of sampling sites and hypothetical schematic showing routes of gene flow between pollock populations. The genetic relationships are summarized from studies of differences in microsatellite allele distributions and from differences in mtDNA sequences. These studies indicate strong separation and little gene flow across the Pacific Ocean, and differences between the Gulf of Alaska and Bering Sea.

distances, standard genetic distance, and the Neighbor Joining Method will be used. The DNA sequences from individuals will be aligned and compared with software written to handle large numbers of sequences, and analyzed using parsimony (PAUP), maximum likelihood (PHYLIP), and neighbor-joining methods to construct phenograms as we have in our earlier analyses. Gene flow will be estimated using the phylogenetic approach of Slatkin and Madison (1989). Population structure will be measured using the G_{st} statistic (Takahata and Palumbi, 1985) which has been modified for DNA sequence analysis and tested against a random null model using bootstrapping (Palumbi and Wilson, 1990). In the event that recombination within alleles is detected, allele phylogenies will be constructed with genetic distance techniques (Slatkin and Madison, 1989). Coding regions will be examined for patterns of amino acid versus silent nucleotide changes among individuals (Hughes and Nei, 1988).

Although the mtDNA data was sufficient to differentiate between Asian populations and American populations, it did not adequately detect more finescale structure within these groups. As stated above, we therefore began using DNA microsatellites to study this smaller scale population structure of pollock.

Microsatellites are segments of DNA that consist of a small (2–5 bases) motif repeated in tandem several times, such as GTGTGTGT. They have been found to be useful for population studies in many organisms. Microsatellites often give a finer scale of resolution than other molecular genetic markers.

Several microsatellite loci have already been found in pollock and other related fishes. While we are still screening pollock populations for these loci to determine which of them will be useful in this study, one microsatellite locus, Gmo2, has been optimized for pollock, and yielded useful data. We have studied 315 individual pollock from six localities at this locus. Our results so far have identified 11 alleles ranging in length from 1 to 13 units.

Information derived from this one microsatellite locus revealed the same detectable difference between Asian and American areas of the Bering Sea that was detected by using the combined data from the sequences of the two mitochondial loci, i.e., cytochrome-b, and ATPase-8. Moreover, this single microsatellite locus also revealed a difference between the Gulf of Alaska and Eastern Bering Sea populations that was not detectable using the two mtDNA loci sequence data. Pairwise ANOVA comparisons (Table 2A.6) suggest that the Aleutian Islands block some gene flow between the Pacific and the Bering Sea. The consequence of this is that Gulf of Alaska fishes appear to be mixing with western Pacific fishes nearly as much as with Eastern Bering Sea fishes. A UPGMA dendrogram (Fig. 2A.3) shows the relationship of the six localities according to genetic distance at the Gmo2 locus.

We have identified 13 more microsatellite loci that could provide the discrimination between populations within each region that we have tried to find for the past 3 years. We have already found that at least four of these (pTCR-1, Gmo-1, Gmo-9, and Gmo-145) appear to be detectable in pollock and highly variable.

Table 2A.6: Pairwise ANOVA comparisons of Bering Sea and Gulf of Alaska pollock populations based on polymorphism at the Gmo-2 microsatellite locus. Three distinct groups emerge: Eastern Bering Sea, Western Bering Sea, and Gulf of Alaska.

	NE Shelf	S. Kamchatka	W. Bering Sea	Aleutian Basin	Shelikof Strait
NE Aleutians	P=0.847	P=0.029	P=0.0002	P=0,700	P=0.0195
NE Shelf		P=0.031	P=9.8E-5	P=0.831	P=0.030
S. Kamchatka			P=0.308	P=0.025	P=0.056
W. Bering Sea				P=0.0002	P=0.0001
Aleutian Basin					P=0.036

If we can obtain additional funding, we would construct primers for PCR (polymerase chain reaction) that are optimized to amplify these loci in pollock. Also, we would continue screening the other nine loci in order to increase the number of usable markers for this study which could not only provide finescale discrimination between pollock from each of the three geographical regions we have already identified, but these additional markers would also allow us to calculate gene flow between populations.

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Part 2B

Trends in north Pacific pollock and 1998 harvest prognosis (Vidar G. Wespestad[1])

Pollock

Walleye, or Alaska pollock, has been the basis of the largest groundfish harvests since the early 1980s. The majority of the harvest is taken in the U.S. and Russian EEZs, and relatively small amounts are harvested off Canada, Japan, and Korea. However, in recent years there has been a downward trend in harvest, primarily in the Russian EEZ. Pollock harvests peaked in 1986 at 6.8 million t, declined until 1994, and in recent years has been stable near 4 million t (Table 2B.1). One reason for the high harvest levels in the 1980s was the advent of high seas fisheries in the Bering Sea Donut Hole and in the Okhotsk Sea Peanut Hole (Fig. 2B.1). These fisheries have been halted by international agreements, and are not expected to resume operation in the near future.

North American catch has been stable, varying annually only slightly from the 1981–1997 average of 1.3 million t. In Asia, on the other hand, catch decreased significantly over the same time period, decreasing from a peak of 5 million t in 1981 to 2.2 million t in 1994. Part of the decline was due to overfishing, principally in Japan and Korea, and some in Russia, including the Peanut Hole Fishery. A partial reason for the very low catches observed in 1994 was the collapse of the Russian fishing industry, and their inability to fully exploit pollock and other fish in the Russian EEZ. However, harvesting capacity has increased in Russia and catch has been increasing in recent years. In other areas of Asia, catches appear to remain at relatively low levels, and where data are available, there do not appear to be any prospects for near-term increases in stocks or harvest.

North American Pollock

The principal fisheries in North America are off Alaska, in the eastern Bering Sea, and in the western Gulf of Alaska (Table 2B.1). Minor fisheries occur in the eastern Gulf of Alaska and off Canada (Table 2B.1).

The eastern Bering Sea pollock fishery is the largest fishery in North America, and has averaged a harvest of 1.2 million t since the early 1980s (Fig. 2B.2, Table 2B.1). While catch has been stable, biomass has fluctuated greatly in response to strong variation in recruitment. In the late 1970s and early 1980s three strong year classes occurred which increased the population to very high levels in the mid-1980s (Fig. 2B.3). In the late 1980s to early 1990s only one strong year-class occurred, 1989, and the population declined to lower levels of abundance. This year, 1997, trawl surveys and hydroacoustic-midwater trawl surveys of the eastern Bering Sea found that the overall biomass of eastern Bering Sea pollock decreased slightly from

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Table 2B.1: Alaska pollock catch by area, 1981–1986, 1997 preliminary catch estimates, and 1998 preliminary catch recommendations.

					Russia: *Russian Catch Only to 1993*												
		Gulf of	Eastern	Donut	Western	Kamchatka		North	East	South	W. Sakhalin	Peanut		Korea			
	Canada	Alaska	Bering Sea[a]	Hole[b]	Bering Sea	East	West	Okhotsk	Sakhalin	Kuril I.	Japan Sea	Hole	Japan[c]	South	North	Total	FAO
1981	5	148	1029	0	1133	329	482	102	82	260	67	0	665	166	1644	6112	4177
1982	5	169	1014	0	976	260	572	139	85	94	58	0	559	138	1365	5433	4478
1983	6	216	1040	0	1006	187	704	107	72	128	36	0	655	86	852	5095	4858
1984	6	307	1174	181	755	165	935	456	89	132	24	0	653	107	1058	6041	5986
1985	7	285	1198	363	662	121	975	540	82	97	27	0	632	85	838	5912	6132
1986	6	84	1189	1040	838	86	719	746	154	387	25	0	405	79	787	6545	6759
1987	7	62	888	1704	688	192	786	729	58	221	29	0	475	34	334	6206	6724
1988	6	56	1272	1484	1253	114	713	655	83	314	29	0	472	16	161	6628	6659
1989	6	73	1246	1484	961	123	791	687	47	316	53	0	477	24	0[d]	6287	6321
1990	5	78	1534	1069	573	186	537	946	40	375	42	0	454	27	0[d]	5866	5736
1991	5	83	1296	558	467	221	688	792	70	203	38	297	397	20	0[d]	5135	4893
1992	4	58	1218	10	596	253	760	509	14	161	43	698	358	15	0[d]	4698	4987
1993	4	106	1352	3	677	205	827	408	17	69	58	264	264	17	0[d]	4270	4617
1994	4	109	1422	0.6	382	104	733	608	25	17	36	124	258	11	0[d]	3833	4299
1995	4	77	1321	0.3	399	60	1074	915	1	5	29	NA	NA	7	NA	3893	
1996	4	53	1128	0.4	489	96	1250	756	49	19	18	Closed	NA	NA	NA	3863	
1997	4	74	1100	trace	757	55	1180	650	NA	NA	NA	Closed	258	NA	NA	4078	
1998		**98**	**1000**	**0.1**	**750**	**45**	**800**	**460**				**300**				**3453**	
Mean		120	1201	494	742	162	807	573	61	175	38	99	466	55	880	5288	5473

[a] Includes Aleutian Islands

[b] Includes Bogoslof Island catch in U.S. EEZ

[c] Japan catch: Fisheries Agency of Japan catch statistics: Local catch to 1986, 1987–1994 includes catch from Russian EEZ

[d] Pollock fishing prohibited since 1989 due to low stock abundance

Gulf of Alaska and Bering Sea catches include discards in 1990–1996

Russian data from Fedeev, N.S. and V. Wespestad (in press), Harvest history of pollock (in Russian), and TINRO, Vladivostok, and KoTINRO, Petropavlovsk, Russia

S. Korea catch: Jank Uk Lee, Natl. Fish. Res. Dev. Ag. (personal communication)

N. Korea catch: C. Zhang Kunsan, Natl. U. (personal communication), estimated from ratio of north-south catch 1926–1940

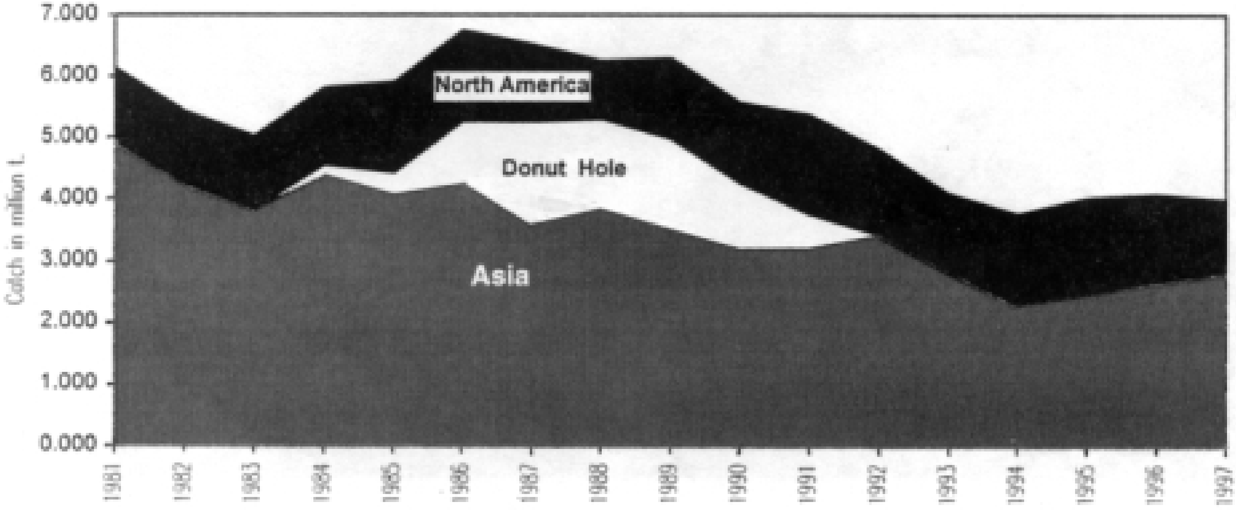

Figure 2B.1: Catch of pollock in Asia, North America, and the Donut Hole, 1981–1997.

1996, as expected, with a preliminary estimate of about 5.5 million t. However, the survey confirmed the presence of a very large 1996 year-class, which was first noted by fishers during the 1997 pollock A season. The analysis is not complete, but it appears that this year-class may be of similar size to the 1978 year-class which initiated the high abundance of the 1980s. The 1997 survey also found the 1985 year-class to be much bigger than previously estimated. In 1996 Russian surveys reported 1995 to be a strong year-class based on results from the northwest Bering Sea, but the same year-class was not found to be abundant in U.S. waters. The large numbers of juvenile fish suggest that the exploitable pollock stock will begin to increase in 1999–2000. It should be noted that although eastern Bering Sea pollock are at a relatively low level, the level of exploitation is currently less than 20%, much below that of other major gadid stocks.

The western Gulf of Alaska is also increasing in abundance due to a strong 1994 year-class. This year-class is entering the fishable population, and the recommended allowable catch has been raised for 1998 to 98,000 t, up from 76,000 in 1997.

Aleutian Islands pollock, which appear to be a geographic extension of eastern Bering Sea pollock, are stable or increasing. A 1997 survey indicates that biomass has increased from a 1994 survey. The pollock size frequency obtained in the survey indicates that the 1989 year-class is the dominant age group. Aleutian Islands pollock quotas were halved in 1996 to 28,000 t. Based on survey abundance estimates, the catch may remain at the current level of 28,000 t. The Aleutian Islands pollock biomass may be an underestimate of actual abundance due to the lack of an estimate of the pelagic portion of the population.

Adjacent to the Aleutian Islands is the Bogoslof Island area, which is the

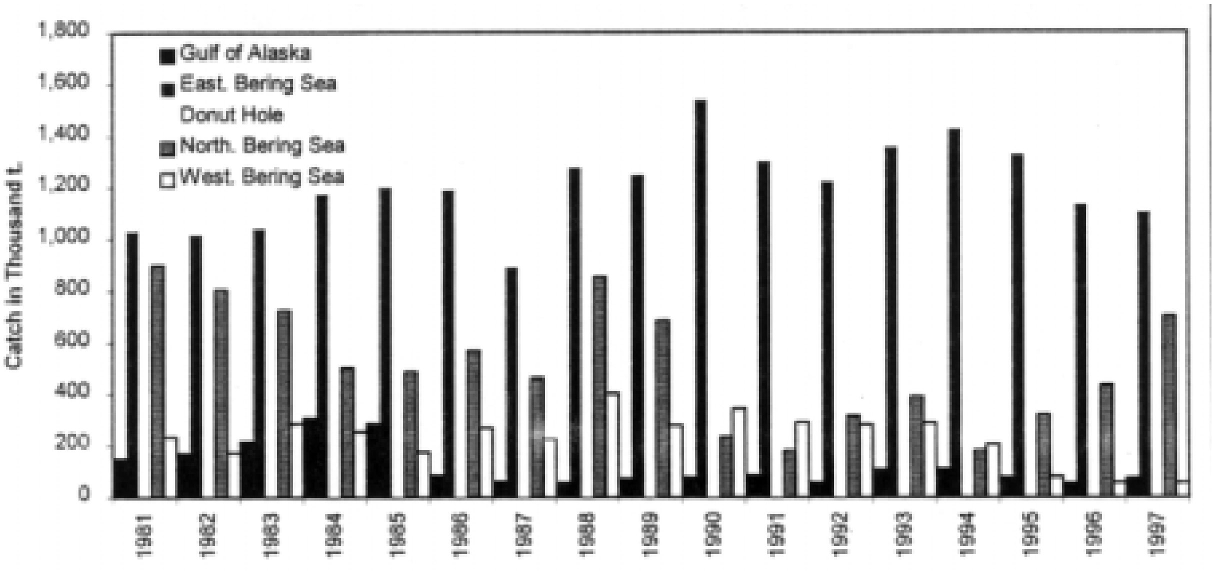

Figure 2B.2: Pollock catch in the Gulf of Alaska and regions of the Bering Sea, 1981–1997.

primary spawning area of the Aleutian Basin/Donut Hole "stock." These pollock also continue to decline. In the 1997 survey the biomass was estimated to be near 300,000 t, down from 2.4 million t in 1988. Until the "stock" increases to 1.1 million t no fishery will occur in the Bogoslof Island area or in the Donut Hole. This level of biomass is not expected to occur until 5–10 years from now, at the earliest, since it appears that Donut Hole pollock mainly accrue from strong year-classes from the eastern and western Bering Sea.

Asian Pollock

Pollock fisheries occur in the Japan Sea within the EEZs of Japan, Korea, and Russia, on the Pacific side of Hokkaido. Stocks in these waters are currently small, primarily due to overfishing. Recent official catch data is scant (Table 2B.1). The greatest amount of catch is by Japan where the catch quota was established as 258,000 t in 1997. South Korea has had very small harvests in its EEZ in recent years, and the catch from North Korea is unknown, although it is reported to have been closed since 1989 due to low abundance. Russia also harvests relatively small amounts of pollock from the Japan Sea and South Kurile Islands. The expected 1998 harvest from these and other minor stocks in Russian waters is estimated to be less than 300,000 t.

The primary harvest areas for pollock in Asia are in the Sea of Okhotsk and northwestern Bering Sea. The Okhotsk Sea is the primary Asian harvest area, and contains two main stocks, the northern Okhotsk, and west Kamchatka stocks. The preliminary estimate of the 1997 pollock catch in west Kamchatka is 1.18 million t, about equal to 1996. In the Northern Okhotsk

Figure 2B.3: Eastern Bering Sea pollock abundance trend, 1964–1996.

the catch decreased slightly between 1996 and 1997, dropping to 650,000 t from 756,000 t. For 1998, Russian biologists are recommending sharp reductions that would decrease the west Kamchatka catch to 800,000 t, and the northern Okhotsk to 460,000 t. The 1998 Russian pollock quotas are not yet finalized, and it is possible that the final quotas may be different from those recommended by scientists.

Scientists are concerned that the over-harvest in 1995–1996 reduced the amount of mature pollock available in 1997, leading the fishery to harvest small pollock. The problem of small fish also may have been caused by regulations that prohibit trawling in the coastal spawning areas where adult pollock congregate, forcing trawl vessels to fish immature pollock in offshore areas.

The 1997 fishery was also reported to be affected by large area fishery closures of areas with high bycatch of herring and undersized pollock. Adult pollock abundance in Okhotsk Sea is expected to continue to decline in 1998. Russian data indicates that the 1995 year-class is a large year-class, and 1992–1993 are near average. The oldest of these year-classes are just reaching maturity, and the 1995 year-class will not mature until 2000.

The western-northern Bering Sea is the second largest producer in the Russian EEZ. The catch of western Bering Sea stock used to average about 250,000 t, but in recent years has decreased to 50,000–70,000 t due to decrease in stock abundance and concentration of fishing effort in more productive areas such as the Okhotsk and northern Bering Sea. The recommended catch quota for the western Bering Sea in 1998 is up, increasing to 150,000 t.

The northern Bering Sea has the second largest quota in the Russian EEZ, with a recommended 1998 quota of 600,000 t. Pollock in this area originate from the western Bering Sea and eastern Bering Sea stocks, and

Table 2B2: Estimated 1998 harvest of walleye pollock by major areas of the north Pacific.

Gulf of Alaska	Bering Sea			Kamchatka		North Okhotsk	South Kurils	West Sakhalin	Japan	Korea	Total
	Eastern	Western	Northern	West	East						
98	1000	150	600	800	45	460		300			3453

little to no spawning is observed in the area. Russian vessels have fished the area since the early 1970s, and the catch has average near 500,000 t, with a peak of 900,000 t in 1981.

This fishery is problematic for several factors, which include that the fish are primarily of U.S. origin in recent years, the area (and the harvest) is dominated by juvenile pollock that will recruit to U.S. fisheries at maturity, there is little dialogue between the U.S. and Russia in developing a coherent management plan, and there are questions on the level of Russian fisheries monitoring in the area.

The magnitude of the harvest of small pollock in the Russian northern Bering Sea is not fully known, but from reports of masters of vessels fishing the area it may be significant. The effect on eastern Bering Sea stocks cannot be fully determined at the present. Simulation of the catch and population time series using likely scenarios of pollock movement suggests that the worst case effect of the current levels of Russian fishing in the northern Bering Sea is that harvest levels in the eastern Bering Sea may have to be reduced. This will not lead to stock collapse in the eastern Bering Sea.

Russian scientists had been concerned that the percentage of undersized pollock would increase in the 1998 west Kamchatka fishery. However, they believe new regulations may decrease the anticipated problems. In 1998, for the first time, trawlers will be able to fish in selected coastal spawning areas which will allow a harvest of large pollock. Secondarily, mesh size and minimum retention size increases have been proposed which should further reduce the harvest of juvenile fish. The mesh size and minimum retention size increases also apply to the Bering Sea, so that catch of juvenile pollock should also decrease in this area as well.

Prognosis Summary for 1998

The estimated projected harvest of pollock for 1998 is shown in Table 2B.2. The projected harvest is 3.4 million t. This is about 600,000 t less than in 1997. A large part of the projected decrease is in the Sea of Okhotsk. However, since quotas have not been finalized, it is not certain that these reductions will occur. At last year's Groundfish Forum, the 1997 pollock harvest was forecast to be 3.8 million t, slightly less than the actual harvest of 4 million plus t. It is equally likely that this year's pollock projection may be on the conservative side.

Part 3

Biophysical processes relevant to recruitment dynamics of walleye pollock (*Theragra chalcogramma*) in the Eastern Bering Sea (J.M. Napp,[1] A.W. Kendall, Jr.,[1] and J.D. Schumacher[2])

Abstract

Walleye pollock is a nodal species in the Bering Sea ecosystem (NRC Report 1996): juvenile pollock are the dominant prey of fishes, seabirds, and marine mammals in this productive ecosystem. The estimated adult pollock biomass in the eastern Bering Sea and central basin exceeds 9 MMT, and is the target of an ∼$1 billion fishery.

We constructed a conceptual model for larval pollock dynamics using factors we found to influence their distribution and feeding success in the southeastern Bering Sea. These factors may have a strong influence on recruitment success by modifying larval survival. The model is based on relevant biophysical variables and pollock early life history traits. Pollock spawning occurs in discrete concentrations during winter and spring in a variety of habitats which include oceanic (basin and slope) and shelf waters. Biophysical phenomena that affect conditions for larval survival and eventual recruitment exhibit marked differences between the Oceanic and Shelf Regimes. In the Oceanic Regime eddies are a common feature. While their genesis is not well known, eddies have unique biophysical characteristics and occur with such regularity that they likely affect larval survival. High concentrations of larval pollock often are associated with eddies. Some of these eddies are transported onto the shelf, thereby providing larvae to the Outer Shelf Domain. Observations from biophysical instrument platforms moored over the basin demonstrated that advection rather than local production dominated the observed springtime increase in chlorophyll (often a correlate of larval food). Over most of the southeastern shelf eddies are absent and other phenomena are important. Seasonal sea-ice and the associated cold pool of bottom layer water are striking features of the Middle Shelf Domain. Interannual variability in sea-ice and cold-pool extent affects developmental rate of larvae, timing of the phytoplankton bloom (and potentially the match/mismatch of larvae and prey), and abundance and distribution of juvenile pollock.

3.1 Introduction

3.1.1 Description of the Area

The Bering Sea (Fig. 3.1) is a semi-enclosed portion of the North Pacific Ocean that lies between the northernmost land masses of the North Amer-

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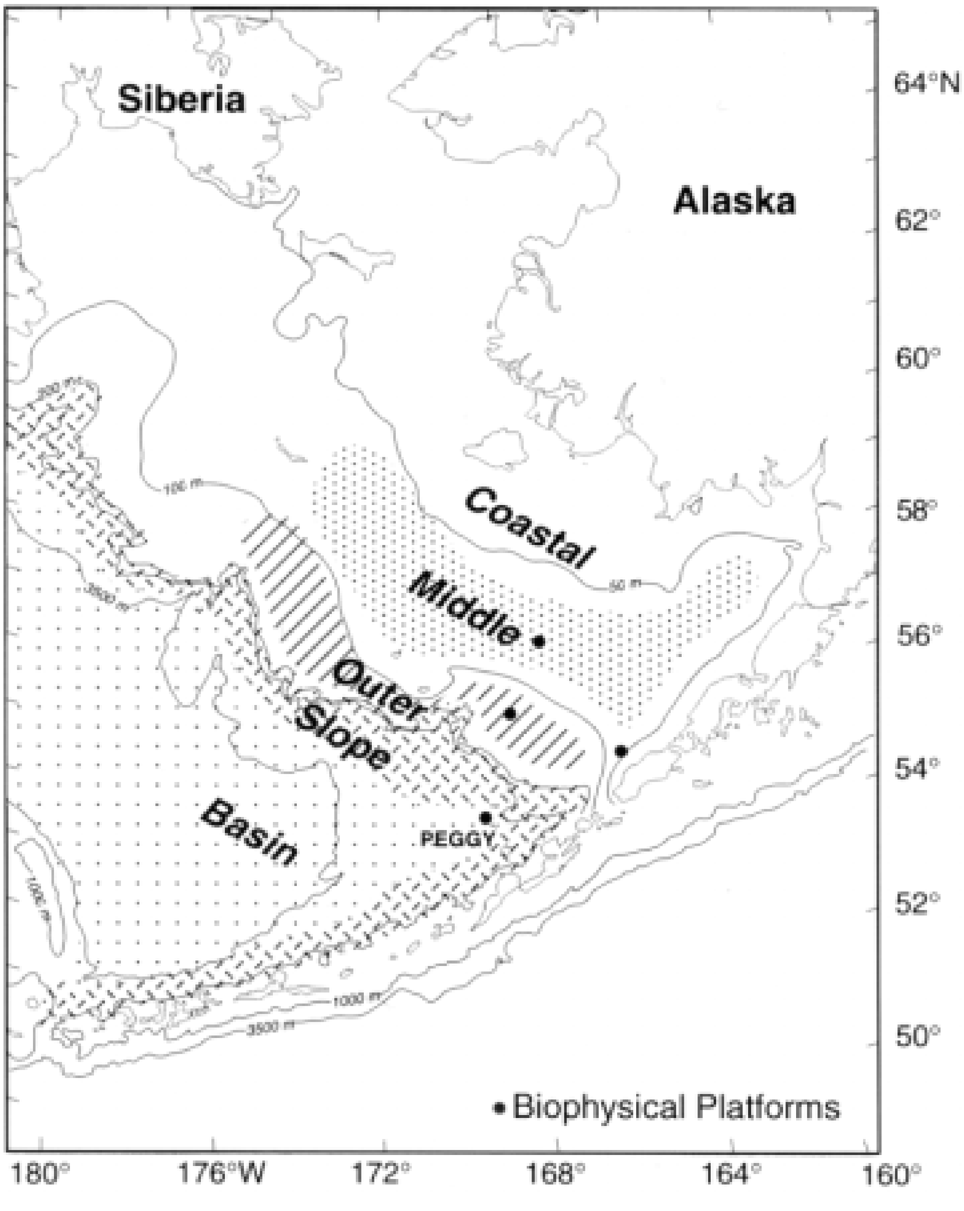


Figure 3.1: Southeast Bering Sea and associated biophysical domains. The solid circle indicate locations of the BS FOCI biophysical platforms.

ican and Asian continents. It is divided almost equally between a deep basin (maximum depth 3,500 m) and a continental shelf (<200 m) which are separated by a steep convoluted continental slope (Hood, 1981; Macklin, in press). The Bering Sea is bounded to the south by the Aleutian Island chain with its many passes and to the north by the shallow (<60 m) Bering Strait, providing the only connection from the Pacific to the Arctic Ocean. Water exchange between the North Pacific Ocean and the Bering Sea occurs mainly through the deeper western passes, although transport through the eastern passes is important to regional circulation and water properties. The broad (>500 km) eastern shelf is the second broadest continental shelf in the world. The southeastern Bering Sea consists of an Oceanic and Shelf Regime (Fig. 3.1). Within the Shelf Regime, three distinct Domains exist which are characterized by contrasts in water column structure, currents, and biota (Iverson *et al.,* 1979a; Coachman, 1986; Schumacher and Stabeno, in press). These Domains include the Coastal (<50 m deep with weak stratification), Middle Shelf (50–100 m deep with strong stratification), and Outer Shelf (100–200 m deep with mixed upper and lower layers separated by slowly increasing density). The zooplankton community in the two shallower Domains is comprised primarily of the small copepods and euphausiids whereas in the Outer Shelf Domain and in the Oceanic Regime large open-ocean copepods are numerically dominant (Cooney and Coyle, 1982; Vidal and Smith, 1986).

Being a high-latitude sea, seasonal extremes occur in solar radiation (length of daylight), meteorological forcing, and ice cover (Niebauer, 1981; Overland, 1981). Interannual variations in ice extent (Mysak and Manak, 1989; Wyllie-Echeverria, 1995a) and its associated phenomenon, the cold pool, are marked and interdecadal changes (sometimes called regime shifts or Decadal Climate Oscillations: DCO) in the atmosphere above the North Pacific Ocean affect the surface wind stress, Sverdrup transport, surface ocean heat flux (Trenberth and Hurrell, 1995), and likely have significant implications for the biota (Mantua *et al.,* 1997).

3.1.2 Description of the Problem

The Bering Sea is the site of some of the most productive fisheries on Earth. Besides the lucrative king crab, halibut, and salmon fisheries, most of the world catch of walleye pollock comes from the Bering Sea. Pollock is the most abundant species harvested in the Bering Sea, accounting for 80% of the total weight of the harvest. Pollock, with a total biomass in the Bering Sea approaching 20 MMT, is harvested in Bering Sea waters of the exclusive economic zones (EEZ) of Russia and the U.S. Formerly there was a large pollock fishery in international waters of the Bering Sea basin (known as the “donut hole”), but it is now closed by international agreement. The annual U.S. catch of pollock in the Bering Sea in recent years has amounted to 1.3 MMT, with an ex-vessel value of $210 million. Pollock also dominate the ecosystem of the Bering Sea, providing most of the food for the extensive marine mammal and bird populations found there (e.g., Springer and Byrd, 1989; Lowry *et al.,* 1996; Sinclair *et al.,* 1996).

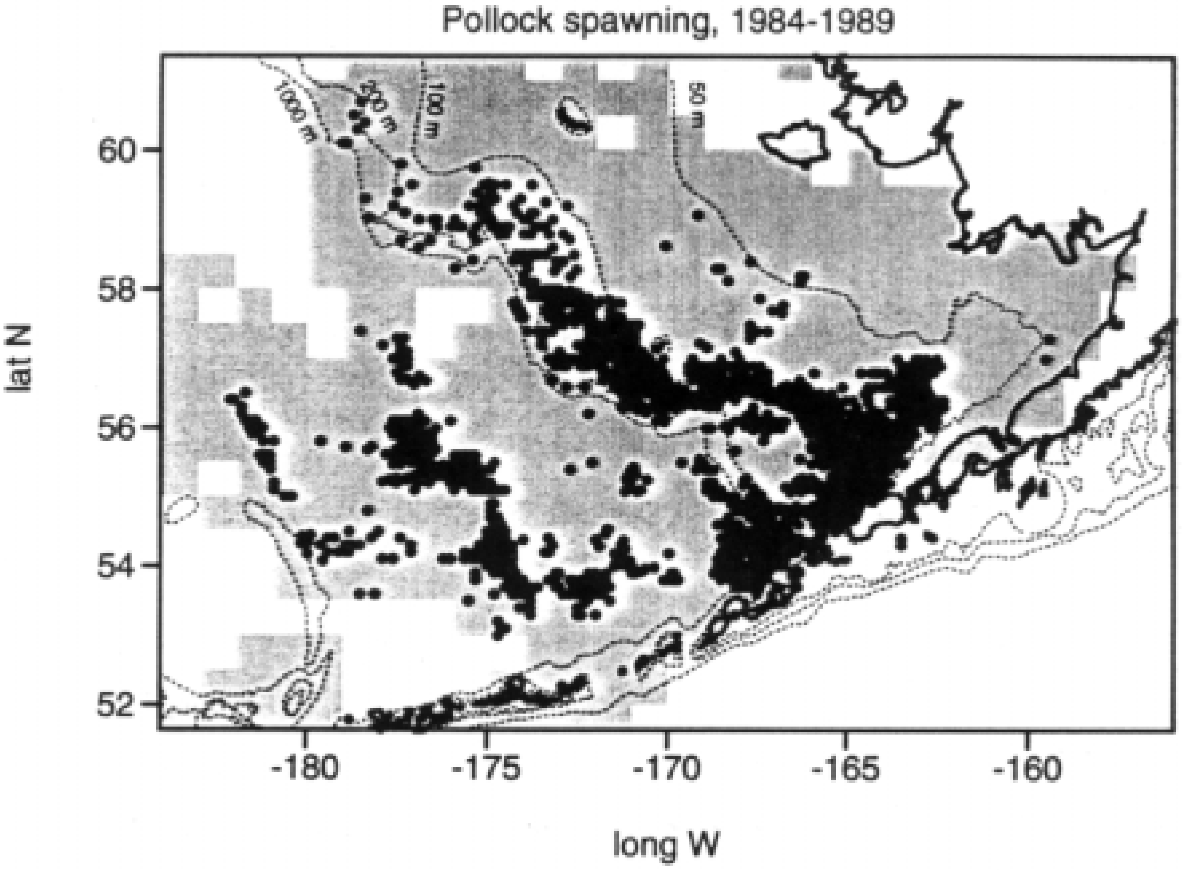


Figure 3.2a: Distribution of selected walleye pollock life history stages in the southeastern Bering Sea. (a) pollock spawning areas, 1984-1989 as defined by the fishery; fishing areas are the dark squares and the black dots are where spawning fish were found (from Dell'Arciprete, personal communication).

Pollock in the Bering Sea do not form one homogeneous population, but the actual stock structure is not well known. For example, distributions of spawning adults, eggs, and larvae show a broad geographic range (Dell' Arciprete, in preparation; Fig. 3.2). Research using spawning and juvenile distributions and elemental composition of otoliths suggested that four populations were identifiable in the eastern Bering Sea (Mulligan *et al.,* 1989). More recent genetic studies, conducted as part of Bering Sea FOCI, indicate that there are differences between pollock from the eastern and western parts of the Bering Sea (Bailey, this report). Within the eastern Bering Sea, there are several spawning areas, and these may also be discrete stocks. However, presently used genetic techniques are unable to detect significant differences between spawning areas—genetic variability within subjectively defined spawning areas is large relative to that between areas.

In the eastern Bering Sea there are large interannual variations in recruitment of pollock (more than one order of magnitude), and these drive population size and thus harvest levels. Without reliable forecasts of recruit-

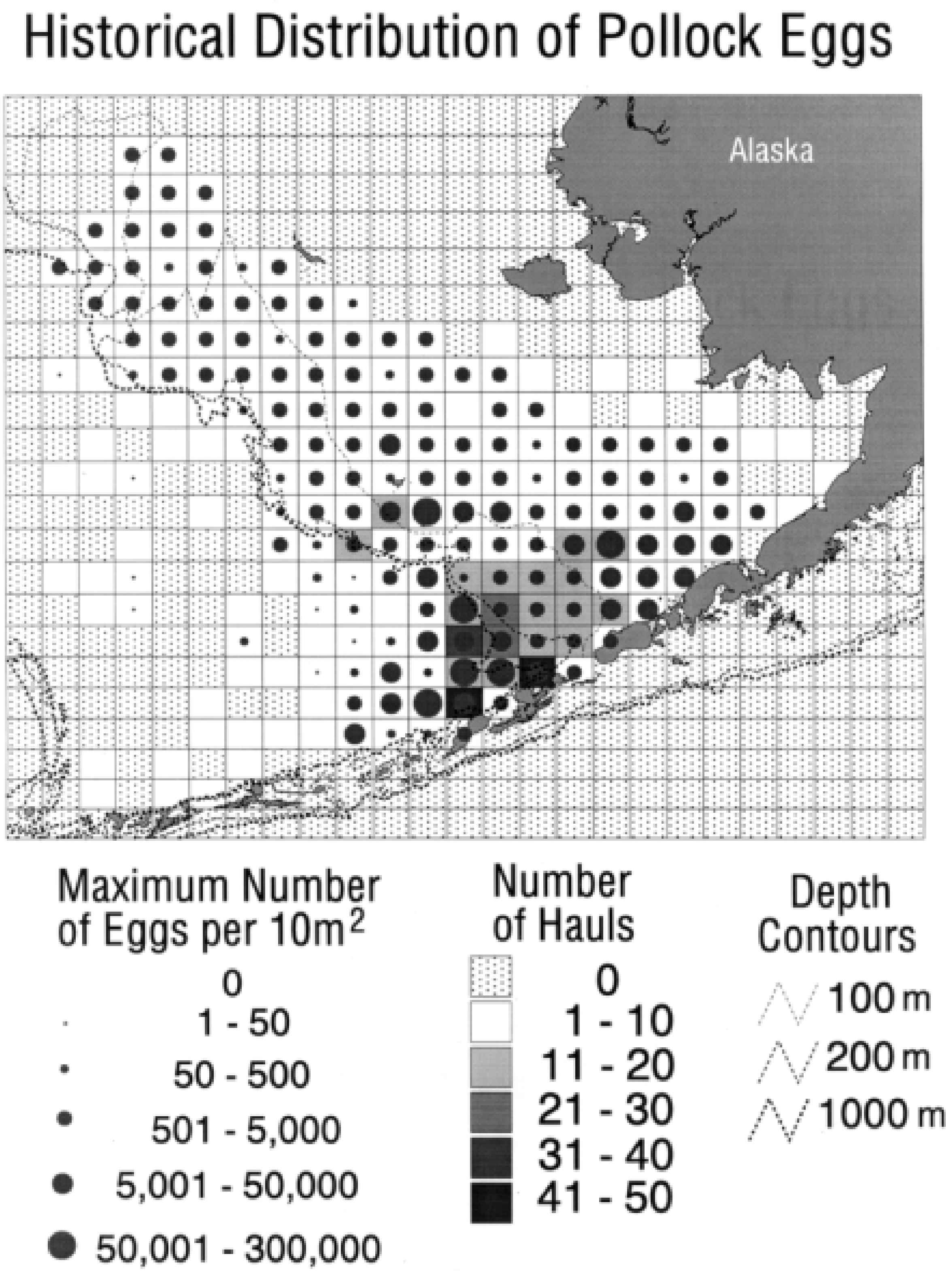


Figure 3.2b: Distribution of selected walleye pollock life history stages in the southeastern Bering Sea. (b) pollock eggs; fishing areas are the dark squares and the black dots are where spawning fish were found (from Dell'Arciprete, personal communication).

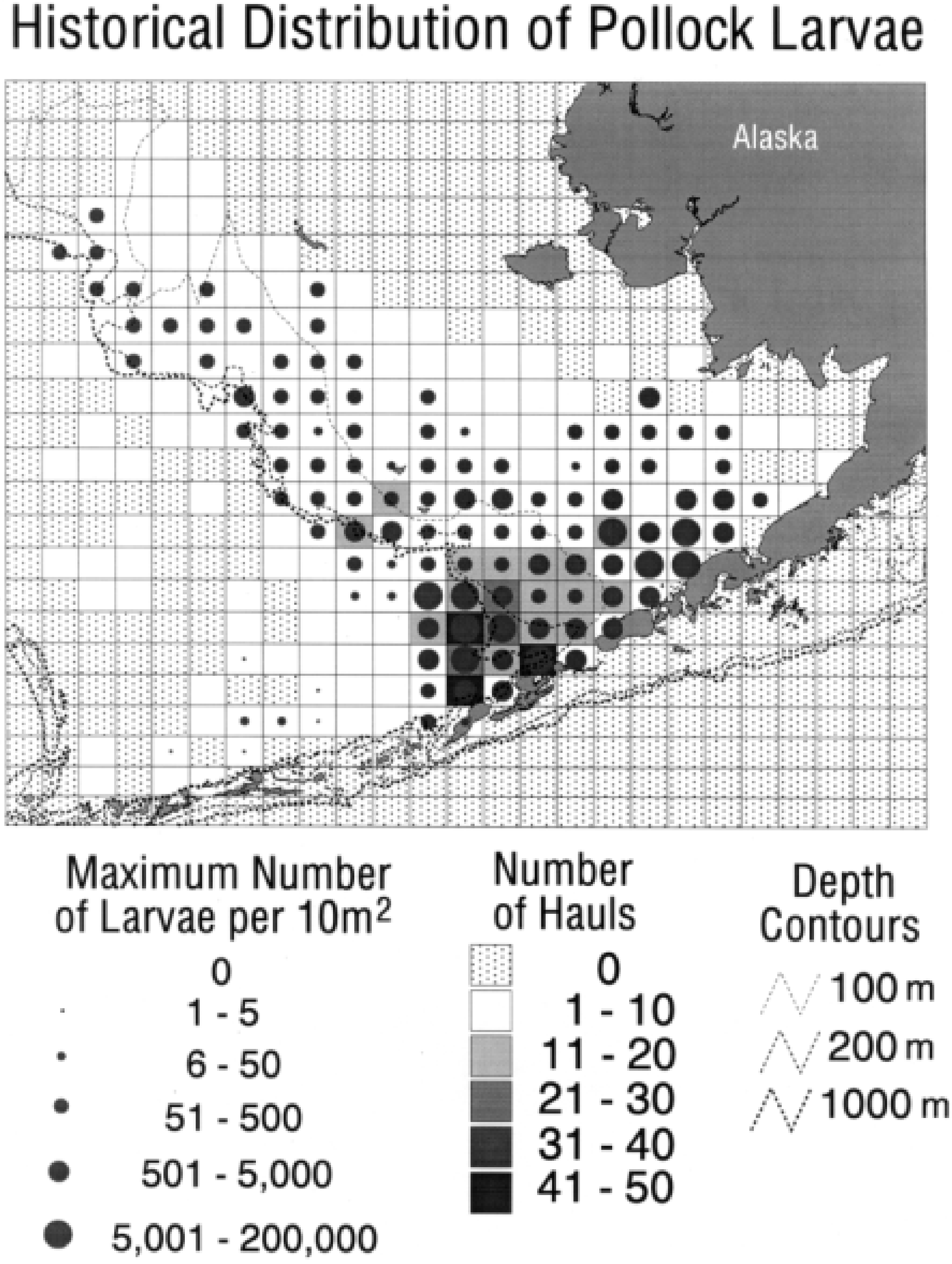


Figure 3.2c: Distribution of selected walleye pollock life history stages in the southeastern Bering Sea. (c) pollock larvae; fishing areas are the dark squares and the black dots are where spawning fish were found (from Dell'Arciprete, personal communication).

ment, based on an understanding of the processes that determine recruitment variability, harvest levels must be set very conservatively. In order to understand recruitment variations, we must understand the relationships among the various spawning populations, and the contribution of each to recruitment to the total stock. Recruitment in Bering Sea pollock, as in most other marine fish, is thought to be largely set during their egg and larval stages. Studies on causes of mortality of these early life history stages of pollock are needed to understand recruitment variation.

3.2 Physical Oceanographic Setting

3.2.1 Marine Climatology and Sea Ice

Complex interactions among ocean, ice, and atmosphere dominate the physics of the Bering Sea. The migration of storms results in a statistical feature known as the Aleutian Low, one of the two main low pressure systems in the high latitude northern hemisphere. During summer with its long periods of daylight and high insolation, the Aleutian Low is typically weak and the weather is benign. During the darkness of winter, a marked change occurs in atmospheric pressure fields. The Asian continent is dominated by high sea level pressure (Siberian High) while the Aleutian Low intensifies and dominates weather over the North Pacific and Bering Sea. The juxtaposition of these features results in strong, frigid winds from the northeast. The frequency and intensity of storms in the southern Bering Sea decreases from winter to summer and frequency also decreases with increasing latitude (Overland and Pease, 1982). In the winter, an average of three to five storms per month move eastward along the Aleutian Island Chain forming the primary storm track, while less than two storms per month cross the northern Bering Sea. A secondary storm track curves northward along the Asian coast. A difference in the number of storms also occurs across the broad eastern shelf, with more activity occurring over the Outer Shelf than the Coastal Domain (Schumacher and Kinder, 1983).

Seasonal sea ice extent in the eastern Bering Sea fluctuates over 1000 km between the Bering Strait in summer and south to the Alaska Peninsula and shelf break in winter. The actual mechanism of ice formation for the eastern shelf has been described by a “conveyor belt” analogy (Overland and Pease, 1982). Ice is produced along leeward (south-facing) coasts primarily located in the northern region of the shelf, and driven by wind to its thermodynamic limit where it melts. Brine rejection occurs as water freezes and regions of open water, or polynyas, are created by downwind advection of ice. The sea ice limit advances southward as ice-melt cools and freshens the upper ocean. The amount of production and advection of ice depends upon which storm track dominates in a given winter, with greatest ice production occurring in years when the Aleutian Low is well developed and storms migrate along the primary storm track.

Variations in overall ice coverage (Fig. 3.3), time of advection over the open shelf, and subsequent melt-back are striking features of the physical environment. Formation of sea ice generally begins in November, with max-

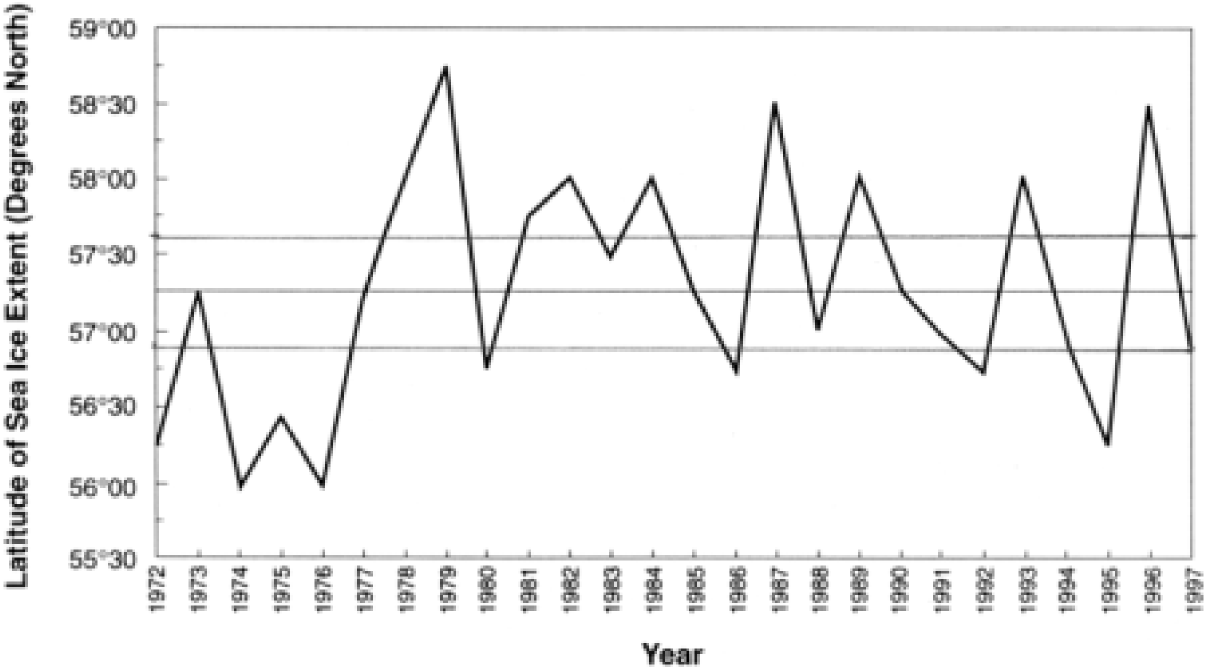


Figure 3.3: Time series of annual maximum sea ice extent, 1972 to 1997 (Wyllie-Echeverria and Wooster, submitted). The index is the southernmost latitude of seasonal sea ice extent along longitude 169°W in the Bering Sea. The 26-year mean (57°15′N) and standard deviation (±22′) are shown as solid horizontal lines.

imum ice extent occurring in late March. Ice-free conditions typically exist from June through October. Observations of ice cover over the eastern Bering Sea shelf show a nearly 40% interannual variation about the mean (Niebauer, 1988). Other characteristics of ice cover that exhibit great variability include duration of ice at its southern extent (3–15 weeks), time of retreat from the southernmost extent (between mid-March and June), and number of weeks that ice remains over the Middle Shelf Domain (3–28 weeks with a mean of 20 weeks; Wyllie-Echeverria, 1995b).

Ice formation, brine rejection, advection, and eventual melting play a critical role in fluxes of heat and salt and generation of both baroclinic flow and the cold pool located over the Middle Shelf Domain (Schumacher and Stabeno, in press; Wyllie-Echeverria, 1995b). The positive buoyancy from melting ice initiates both baroclinic transport along the marginal ice zone ($\sim 0.3 \times 10^6$ m^3 s^{-1}) and stratification. Cooling and mixing associated with ice advance help to condition the entire water column over the Middle Shelf Domain and as seasonal heating occurs, the lower layer becomes insulated, often with temperatures remaining below 2.0°C (Reed, 1995). It is these waters that are commonly called the "cold pool" and whose area varies by $\sim 20 \times 10^4$ km^2 between maximum and minimum extent. Also associated with ice-melt is a bloom of phytoplankton that accounts for 10–65% of the total annual primary production over the eastern shelf (Niebauer *et al.,* 1990).

Ice production and the cold pool also influence distributions of higher trophic level biota (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995a).

3.2.2 *Oceanic Circulation*

The major objectives for BS FOCI research on circulation over the basin were to identify potential pathways which could connect the various pollock stocks in the Bering Sea and to identify features and mechanisms which could provide habitats that favor survival of larval fish and/or transport onto the shelf. Prior to BS FOCI research many schematics existed of circulation in the Bering Sea. In these, wind stress was considered to provide the primary forcing (Hughes *et al.,* 1974). Using observations (Stabeno and Reed, 1994; Leben, personal communication; Stabeno *et al.,* in press a) and model studies (Bond *et al.,* 1994; Overland *et al.,* 1994) conducted during BS FOCI, we have greatly enhanced knowledge of currents and meteorological forcing. A cyclonic gyre dominates circulation with a western boundary current (Kamchatka Current) along the Asian side of the basin (Fig. 3.4; Reed *et al.,* 1993; Cokelet *et al.,* 1996) and the Bering Slope Current (BSC) forming the eastern boundary (Stabeno and Reed, 1994; Stabeno *et al.,* in press a). This gyre is mainly an extension of the Alaskan Stream with the majority of volume transport (6–12 × 10^6 m^3 s^{-1}) entering through the eastern passes and exiting via the Kamchatka Current (Stabeno and Reed, 1994). When instabilities in the Alaskan Stream inhibit flow into the Bering Sea through Near Strait (Stabeno and Reed, 1992), transport in the Kamchatka Current can be reduced by ~50% and the alteration of flow can persist for months to years (Reed and Stabeno, 1993). A climatology of the wind forcing shows that eastward- and northward-propagating storm systems dominate the surface stress at short periods (<1 month), which serves principally to mix the upper ocean (Bond *et al.,* 1994). At longer periods (>1 month), the wind-driven transports estimated by the Sverdrup method account for roughly one-half of the observed transport within the Kamchatka Current. The interannual variations in the Sverdrup transports are ~25% of the mean. Thus, while wind driven transport contributes significantly to circulation, the Alaskan Stream is the dominant circulation feature in the Bering Sea.

Results from BS FOCI studies described the previously unknown Aleutian North Slope Current (ANSC: Reed and Stabeno, in press) and a refined view of the Bering Slope Current (BSC: Leben, personal communication; Stabeno *et al.,* in press a). Northward inflows of the Alaskan Stream through Near Strait, Amchitka Pass, and Amukta Pass produce the ANSC, which is an eastward flow along the north side of the Aleutian Islands. The ANSC is often fairly narrow (<50 km) and shallow (upper 500 m) with peak speeds >40 cm s^{-1}. Eddy-like features occur in this region and some are formed by flow through Amukta Pass (Schumacher and Stabeno, 1994). The ANSC typically transports 2–4 × 10^6 m^3 s^{-1}, providing the main source of the BSC and having a profound impact on regional water properties and circulation (Schumacher and Stabeno, 1994; Reed and Stabeno, in press; Reed and Stabeno, submitted). BS FOCI research also synthesized satellite altimetry, hydrographic, and satellite-tracked drifter data to elucidate features

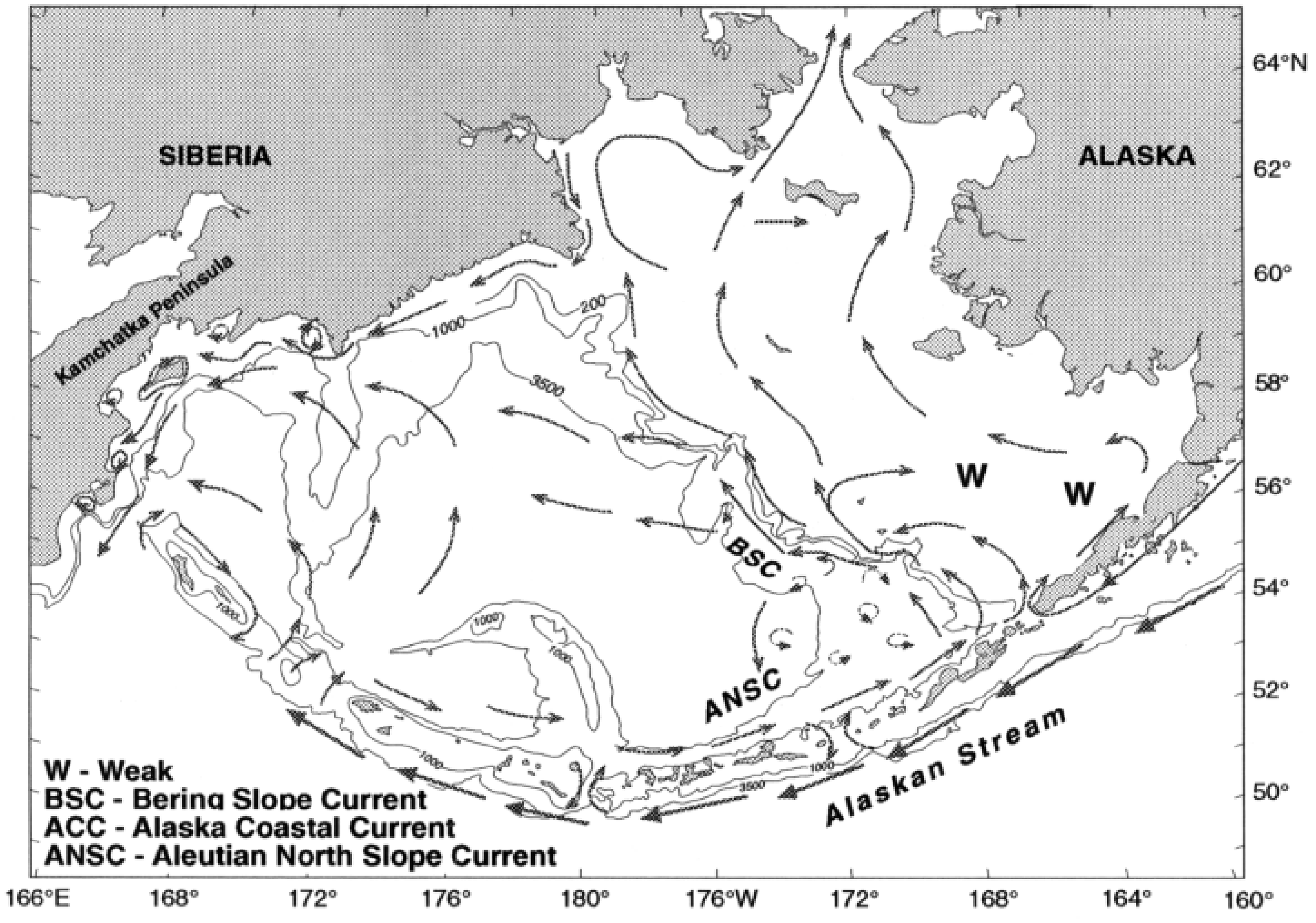


Figure 3.4: Major current features and general circulation of the upper 50 m of the Southeast Bering Sea.

of the BSC. The BSC exists in two modes: an ill-defined, highly variable flow interspersed with eddies, meanders, and instabilities, or a more regular northwestward flowing current. It is likely that shelf/slope exchange differs significantly depending upon which mode dominates in the BSC. The potential importance of both the ANSC and BSC to pollock larvae is twofold: they can provide transport from the Oceanic Regime (including the important spawning region near Bogoslof Island) to the Outer Shelf Domain, and their inherent eddies may provide a habitat that favors survival.

3.2.3 Eddies

Eddies are a ubiquitous feature of the southeastern Bering Sea (Schumacher and Stabeno, 1994; Stabeno *et al.,* in press a). During 3 years of BS FOCI (1992, 1993, 1994) a moored instrument platform, named Peggy, was located in 2200 m of water over the southeastern Oceanic Regime (54°48′N, 168°34′W; Fig. 3.1). Data from this biophysical platform provided the most complete time series of water properties and currents over the southeastern basin available to date. The results showed the marked influence of eddies on water properties, current velocity, and chlorophyll concentration and permitted a characterization of the eddies as often being anti-cyclonic, 20–100 km in diameter, and extending to a depth of 400–1000 m with rotational speeds >20 cm s^{-1} (Fig. 3.5 and 3.6; Cokelet and Stabeno, 1997). Eddies are also common at the eastern shelf break (Schumacher and Reed, 1992) and shoreward to depths of ∼150 m. A recent interpretation of hydrographic observations (Reed, submitted) suggests anticyclonic eddies exist in the region between 100 and 122 m <20% of the time. Shoaler than 100 m, eddies are uncommon. Until recently, eddies were not considered to play a role in Outer Shelf Domain dynamics. Between 1986 and 1994, 45 satellite-tracked buoys were deployed in support of studies of pollock and their environment. In three of these years, satellite-tracked buoys were deployed in areas where larval pollock were abundant. In all four cases trajectories of the buoys defined eddies (Fig. 3.6). Conversely, the buoys (33) which were not deployed in a larval patch did not indicate eddies. This association of pollock larvae and eddies may have significant impact on larval survival (Schumacher and Stabeno, 1994).

3.2.4 Exchange Between the Oceanic and Shelf Regimes

Shelf-slope exchange can occur virtually anywhere along >1200 km of shelf break north of Unimak Pass; however, preferential transport onto the shelf has been observed in two regions: Bering Canyon (along the Aleutian Islands near Unimak Pass) and west of the Pribilof Islands. The enhanced concentration of nutrients observed near Unimak Pass likely originates from ANSC waters interacting with canyon topography and coming onto the shelf (Schumacher and Stabeno, in press). South of the Pribilof Islands the outer shelf narrows and accelerates the flow along the 100 m isobath which then turns northward (Stabeno *et al.,* in press). This phenomenon likely results in slope water being entrained onto the shelf from Pribilof Canyon (Schumacher and Stabeno, in press) and thereby provides a somewhat continuous source of nutrients to the vicinity of the Pribilof Islands. Evidence for this flow near the Pribilof Canyon is the on-shelf trajectories of satellite-tracked drifters released over the canyon and the presence of Outer Shelf Domain mesozooplankton taxa on the eastern side of the islands in the Middle Shelf Domain (Stabeno *et al.,* in press b; Napp *et al.,* submitted).

Episodic events of onshelf flow have been observed resulting from both eddy-topography interactions and instabilities in the BSC (VanMeurs and Stabeno, in press). Along the slope of the central shelf (∼56.7°N), current records reveal that eddies are common and estimates of salt and temperature fluxes indicate that significant onshore fluxes exist (Schumacher and Reed, 1992). In 1992 an excellent set of data was collected when an eddy translated onto the shelf (Schumacher and Stabeno, 1994). Three satellite-tracked drifters had been deployed in the center of an eddy. The drifters remained in the eddy for weeks until the eddy translated onto the shelf. The drifters were deposited onto the shelf as the eddy disintegrated. Both of these episodic events of onshelf flow were related to the stability of the BSC

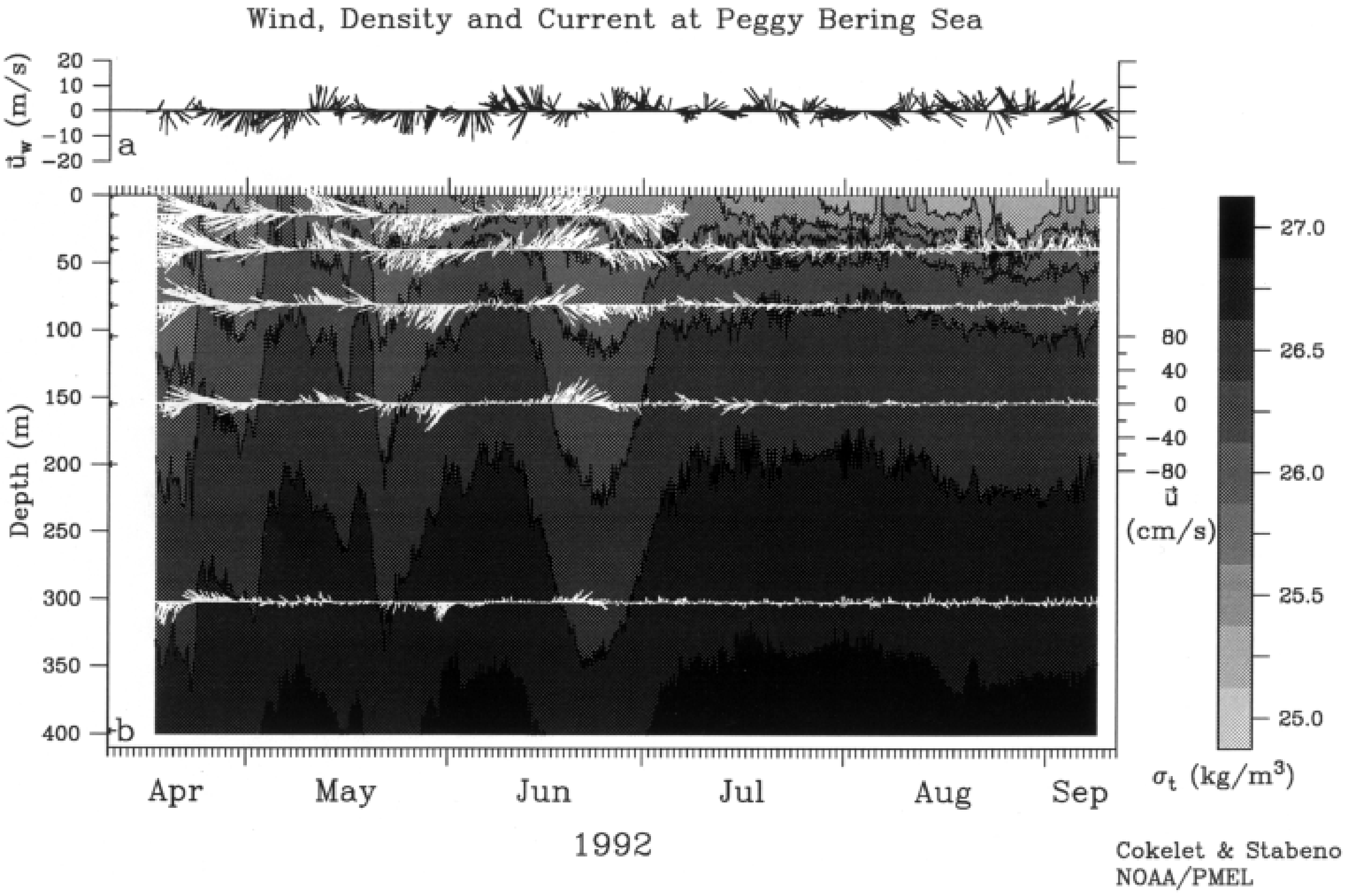
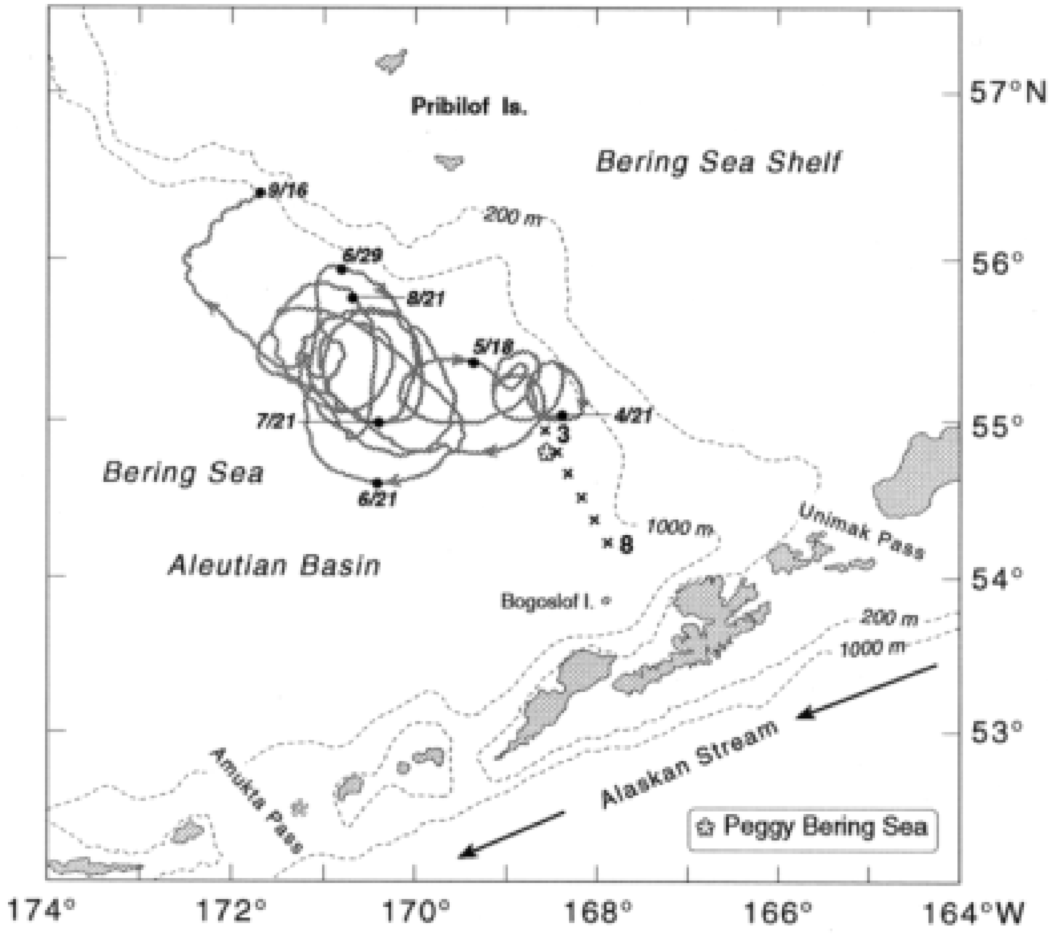


Figure 3.5: Mesoscale eddies detected in the Bering Slope Current using moored instruments (Cokelet and Stabeno, 1997). Wind, density, and current at Peggy Bering Sea, spring 1992, showing the passage of eddies.



Satellite-tracked drifter trajectory of an eddy near Peggy Bering Sea in 1992

Cokelet and Stabeno (1997)
NOAA/PMEL

Figure 3.6: A mesoscale eddy detected in the Bering Slope Current using Lagrangian drifters (Cokelet and Stabeno, 1997). The satellite-tracked drifter was released in the vicinity of Peggy Bering Sea, spring 1992.

and are mechanisms that could transport both nutrients and pollock larvae onto the shelf.

3.3 Production of Prey for Larval Pollock—Variability in the Timing and Magnitude of the Spring Phytoplankton Bloom

Two of the Program's hypotheses were (1) interannual variability in the timing of prey production limits larval survival, and (2) prey densities in the Oceanic Regime are generally less than those encountered in the Shelf Regime. We assumed that production of most larval prey was initiated by the spring phytoplankton bloom. Thus, the lower trophic level research component of BS FOCI had two main objectives: describe interannual variability in the timing of spring phytoplankton blooms, and compare variability in springtime standing stocks of larval pollock prey between the Oceanic and Shelf Regimes. Variability in the timing and magnitude of the spring bloom are reported in this section and variations in prey density are presented in the larval feeding section.

Knowledge of spring phytoplankton bloom dynamics and the mesozooplankton community that produces prey for larval pollock is greatest for the Shelf Regime (e.g., Iverson *et al.,* 1979a; Dagg *et al.,* 1984; Sambrotto *et al.,* 1986; Vidal and Smith, 1986). Knowledge of the phytoplankton dynamics and pollock prey densities in the Oceanic Regime are less well known, although the mesozooplankton community, in general, is well known (e.g., Motoda and Minoda, 1974; Iverson *et al.,* 1979b; Coyle *et al.,* 1996). The waters in the vicinity of the shelf break, between the two regimes, are thought to be a region of sustained productivity during the spring and summer (a "green belt") due to continuous flux of nutrients into the euphotic zone (Springer *et al.,* 1996).

3.3.1 Oceanic Regime

Bering Sea FOCI's major contribution to the study of plankton dynamics and interannual variability in the Oceanic Regime resulted from the use of moored biophysical platforms to obtain continuous time-series of phytoplankton biomass, measurements of associated physical forcing functions (e.g., winds for mixing and incident radiation), and acoustically derived zooplankton biomass. Time-series of phytoplankton biomass were obtained using chlorophyll absorbance meters (ChlAM) attached at discrete depths in the euphotic zone. During our long-term deployments contamination of the signal due to instrument biofouling was minimized using new technology—less hazardous chemical biocides and subtraction of absorbance in several wavebands outside the peak absorbance of chlorophyll (Davis *et al.,* 1997). Seasonal changes in zooplankton biomass and vertical distribution were estimated from continuous records of 150 kHz ADCP backscatter (Cokelet *et al.,* in preparation).

In the spring of 1993 a slow and gradual increase in chlorophyll was interrupted by a sharp (four-fold), rapid (<1 day) increase (Fig. 3.7a; Cokelet

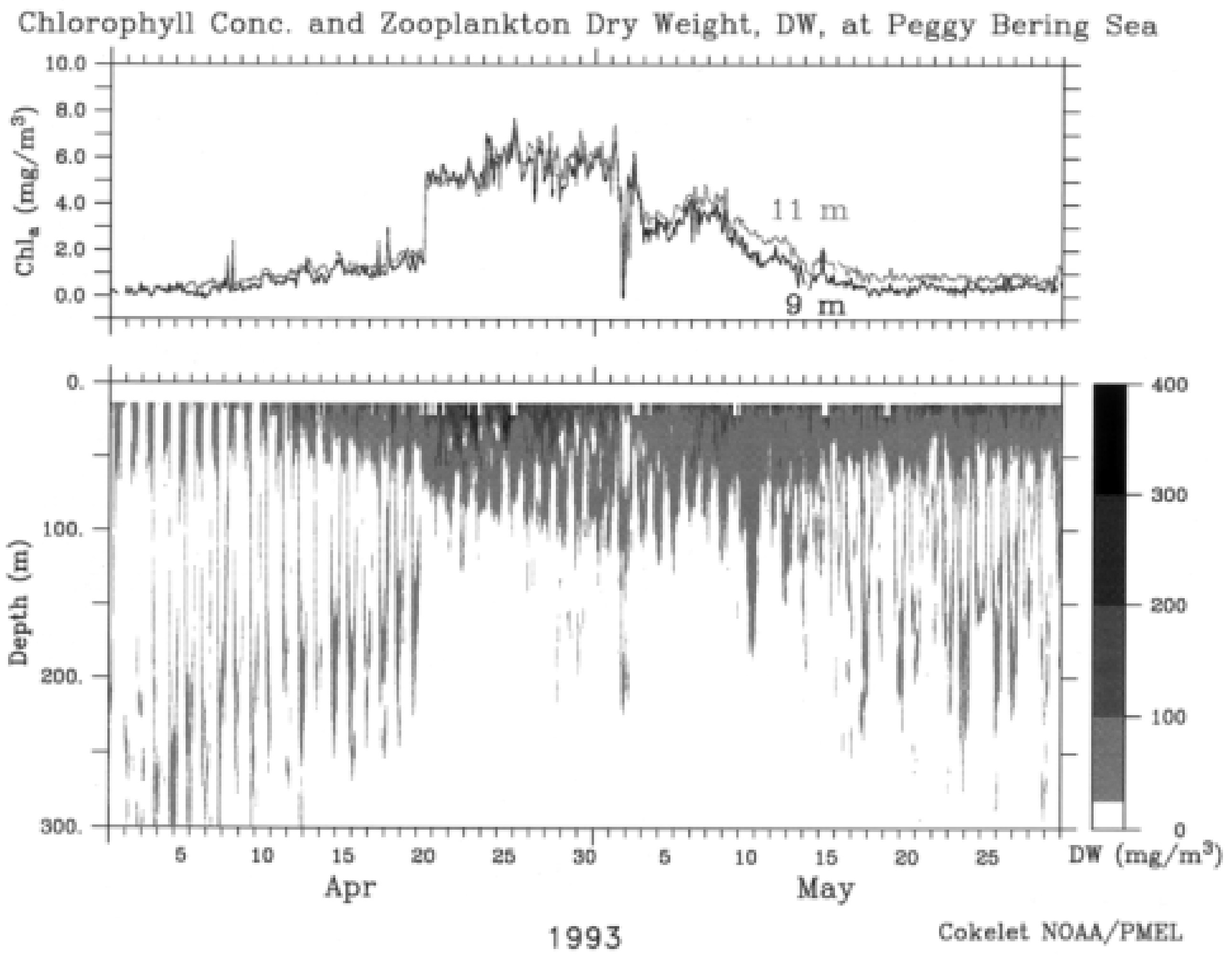


Figure 3.7: Springtime (1993) Peggy Bering Sea observations of chlorophyll and zooplankton biomass showing a rapid change in conditions on 21 April indicating an advective event (Cokelet *et al.*, in preparation). (a) Chlorophyll concentration (mg m^{-3}) from two depths as a function of time; (b) ADCP-derived zooplankton biomass (mg DW m^{-3}) as a function of depth and time.

et al., in preparation). A simultaneous increase in the mixed layer depth and appearance of warmer surface water (3.75°C) suggest that the large increase in phytoplankton biomass was due to advection rather than in situ growth. Currents were weak (~10 cm s^{-1}) during this period, but rotated from southwestward to eastward. Elevated concentrations at the mooring persisted for ~20 days before gradually returning to lower pre-event levels. The same pattern was observed in the spring of 1994, although the rapid increase in chlorophyll was somewhat slower. Note that during the 1993 event, diel vertical migration of the zooplankton community radically changed (Fig. 3.7b). Without net samples we are unable to say whether this was due to a change in behavior by the pre-event assemblage or whether a new assemblage of zooplankton with different behavior arrived with the high chlorophyll waters. These Eulerian biological measurements support the previous point that mesoscale physical variability over the continental slope is important, and demonstrates that at times biological and physical variability are strongly linked in this system. The Bering Slope Current is eddy-rich and pollock larvae are sometimes found in association with these eddies (Schumacher and Stabeno, 1994). To the extent that phytoplankton biomass is a surrogate for increased production and standing stock of larval prey, larvae that find themselves in these dynamic features may have a lower probability of starvation than those outside such features.

3.3.2 Shelf Regime

BS FOCI's major contributions to our knowledge of spring bloom dynamics in the Shelf Regime resulted from our combined use of moored biophysical platforms and Lagrangian drifters equipped with optical sensors. The platforms enabled us to observe previously unreported under-ice spring phytoplankton bloom dynamics. In 1995, when sea ice extent was much further south than usual, we measured a single, large, early phytoplankton bloom over the Middle Shelf Domain (~72 m of water) that continued to develop despite an unstable water column (Fig. 3.8; Stabeno *et al.,* in press c). Note the low water temperatures (–0.5°C). Previous researchers have described an initial ice-edge bloom stimulated by increased water column stability (ice melt) followed by a main spring bloom that occurs when wind mixing from storms erode the thin fresh surface layer and restore nutrients (e.g., McRoy and Goering, 1974; Niebauer *et al.,* 1990). In 1995, however, the bloom occurred despite an unstable water column and Lagrangian drifters equipped with optical sensors did not detect a subsequent "main" bloom. Springtime winds were not strong enough to erode the pycnocline that year and surface nutrients were never replenished after the under-ice bloom.

In 1996, a year with minimal ice extent, the spring bloom was first detected by aircraft in the Outer, rather than Middle Shelf Domain as in the previous year, but not until the first week of May (Cullen, personal communication). Thus, the presence or absence of sea ice and springtime winds influence the timing, location, and number of spring blooms.

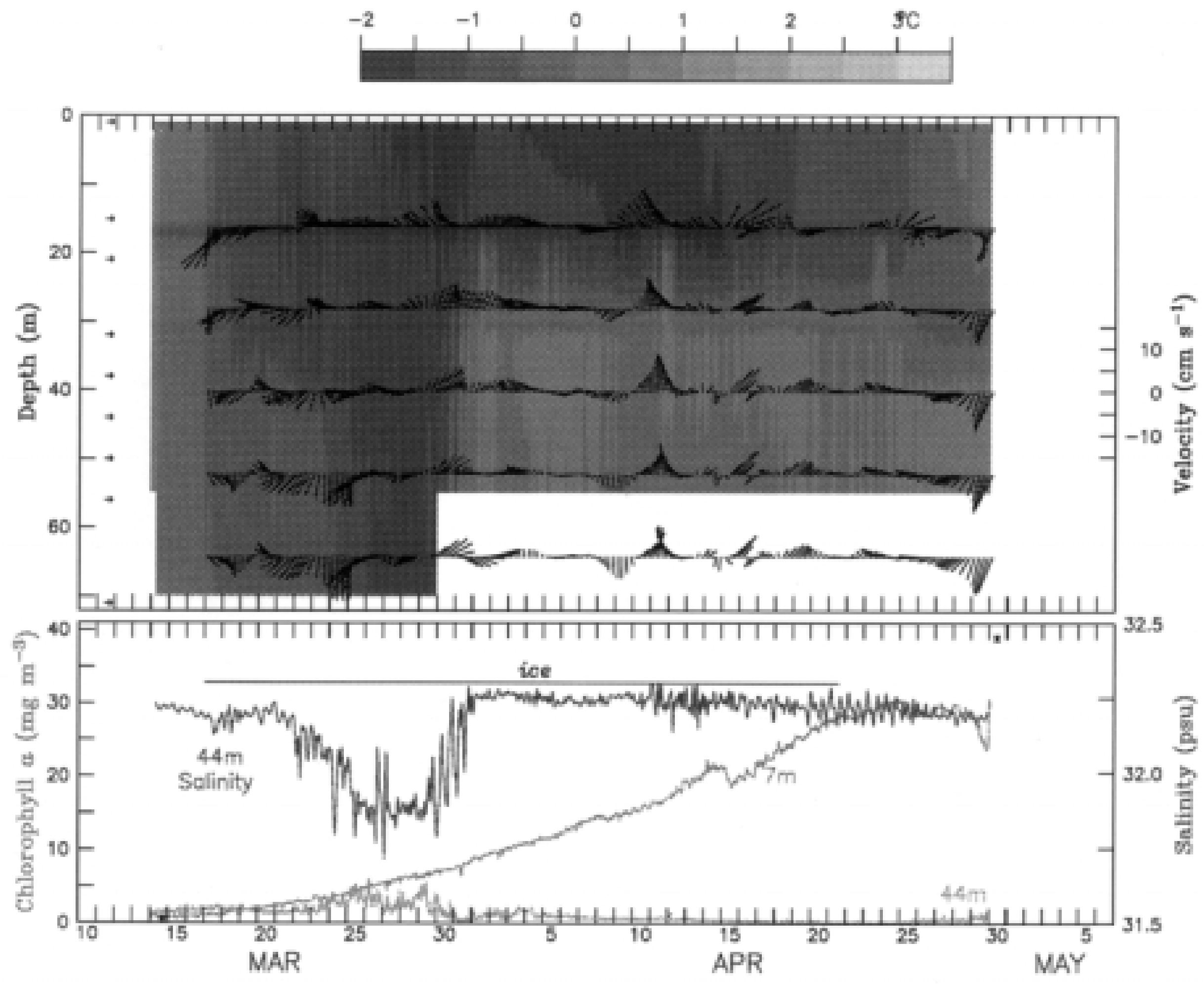


Figure 3.8a: Dynamics of a spring phytoplankton bloom under sea ice on the southeastern Bering Sea shelf during an extremely heavy ice year, 1995 (Stabeno *et al.,* in press). Both panels show temperature and currents as a function of depth and time (upper panel) and chlorophyll concentration (mg m^{-3}) or fluorescence, salinity (PSU), and sea-ice presence as a function of time. (a) Middle Shelf Domain.

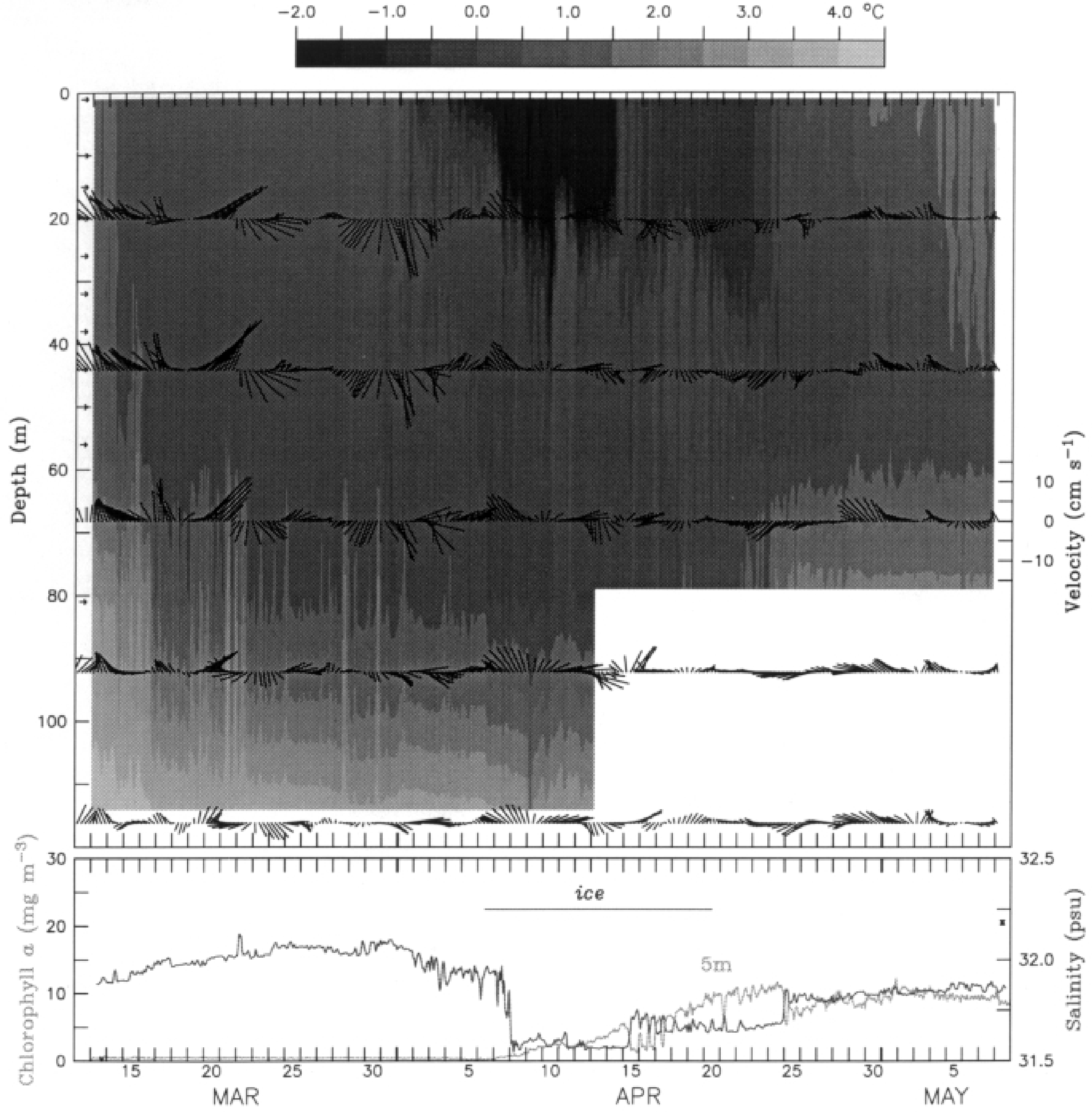


Figure 3.8b: Dynamics of a spring phytoplankton bloom under sea ice on the southeastern Bering Sea shelf during an extremely heavy ice year, 1995 (Stabeno *et al.,* in press). Both panels show temperature and currents as a function of depth and time (upper panel) and chlorophyll concentration (mg m^{-3}) or fluorescence, salinity (PSU), and sea-ice presence as a function of time. (b) Outer Shelf Domain.

3.4 Larval Pollock Feeding

Much of the information on walleye pollock larval feeding is based on studies done in Shelikof Strait, Gulf of Alaska (Theilacker *et al.,* 1996). There they found that starvation can be a significant source of mortality (up to 32% per day) for first-feeding larvae, up to about 6.5 mm in length. Larval condition is closely related to the amount of food in the water; at prey concentrations of less than 20 l^{-1}, condition indices are low and mortality elevated. Numbers of prey per gut is positively correlated with numbers of prey in the water at prey densities of less than about 20 l^{-1} (Canino, personal communication). First-feeding pollock larvae ingest particles of maximum dimension 100–400 μm. Maximum prey size increases with the size of fish, while the minimum prey size remains more or less constant (Nakatani, 1988). Our dietary studies are presently limited to prey items that leave some sort of hard body part in the digestive tract. Pollock larvae ingest items of known (e.g., copepod nauplii, rotifers) and unknown nutritional value where inefficient or ineffectual digestion is suspected (e.g., copepod eggs and phytoplankton). Laboratory studies have shown that pollock larvae modify their swimming behavior in the presence of food: in prey they turn more frequently, swim slower, and spend more time in a horizontal rather than vertical orientation (Spring, 1996). Vertical movements in the absence of food may facilitate locating concentrations of prey in a highly stratified water column or in thin microlayers of food (Iverson *et al.,* 1979b; Owen, 1981).

3.4.1 Oceanic Regime

As in other areas, copepod nauplii were the most common food item in the guts of first-feeding pollock larvae in the Oceanic Regime (bottom depth 1900 m) in April 1992 (Hillgruber *et al.,* 1995). A suite of ca. 5 genera of copepod nauplii (*Eucalanus*, *Metridia*, *Pseudocalanus*, *Microcalanus*, and *Oithona*) were available in the water, 1992–1995. Concentrations ranged from <5 to >40 liter^{-1} (Paul *et al.,* 1996; Napp *et al.,* in preparation). Cyclopoid nauplii (*Oithona* spp.) tended to dominate the assemblage in all years and most depths. Larval pollock, however, preferred the later stages (NIII–NV) of calanoid nauplii over the more abundant cyclopoid nauplii and earlier stages of calanoid nauplii (Hillgruber *et al.,* 1995). In particular, they selected for the older stages of the genera *Metridia* and *Microcalanus*, but against *Oithona*. Late stage *Oithona* and *Microcalanus* nauplii are approximately the same size; therefore, this demonstrates prey selection on a basis other than size. Copepod eggs were also prevalent in the guts, but they are probably of little nutritional value, may have inordinately long gut residence times, and may indicate a generally poor feeding environment (Flinkman *et al.,* 1994).

In 1992, larvae and their prey were most abundant at 30 m, where light was sufficient for feeding (Fig. 3.9). At that depth, 97.5% of the larvae were feeding, and they contained an average of 4.6 prey per larva. Densities of copepod nauplii were 26.3 l^{-1} at 30 m; however, >80% of the available

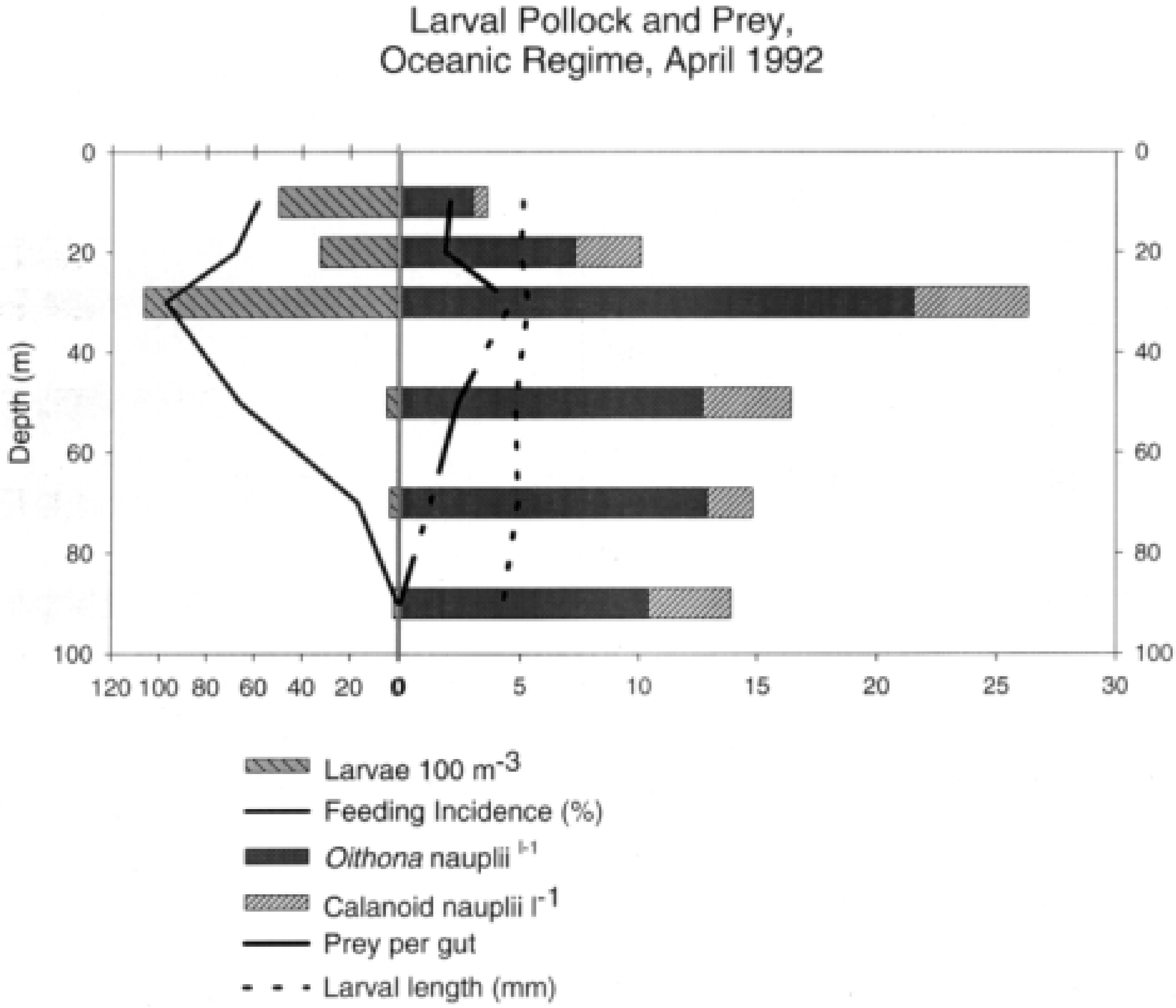


Figure 3.9: Vertical distributions of larval pollock, larval length, prey concentration, feeding incidence, and prey per larval gut for larvae collected in the Oceanic Regime, April 1992 (Hillgruber *et al.*, 1995).

nauplii were *Oithona* spp. (Hillgruber *et al.,* 1995). Naupliar densities and feeding incidence were much lower at other depths, leading to the conclusion that overall, prey were below saturation densities at that station. This, along with modeling results (Bollens *et al.,* in preparation) leads us to explore the possibility that protozoans could be an additional source of nutrition for pollock larvae. Microzooplankton abundance (protozoans >20 μm) in the Oceanic Regime in April 1992 ranged from 300–6233 organisms l^{-1} (0.58–9.7 μg C l^{-1}; Howell-Kübler *et al.,* 1996). Thus, in some situations, first feeding pollock larvae could potentially meet their maintenance ration by grazing on both protozoa and nauplii. Whether or not significant ingestion of protozoa occurs in the field is not yet known, but a new technique for live staining protists was developed and used to show that pollock larvae ingest protozoa in the laboratory (Lessard *et al.,* 1996; cf. Last, 1978).

3.4.2 Shelf Regime

The feeding environment of larval pollock in the Shelf Regime was investigated using samples collected at 2-week intervals in an area of high concentration of pollock larvae in late April and mid and late May 1995 (Brase, 1996). The highest densities of pollock larvae were found in mid May (Fig. 3.10). Mean standard lengths of larvae were 6.13 mm in late April, 6.40 mm in mid May, and 7.37 mm in late May. The temperatures at the depths of maximal larval abundance were 2.5°C in late April, 3.5°C in early May, and 3.75°C in late May (Fig. 3.10). Total copepod naupliar densities were always less than 8 l^{-1}; maximum water column integrated abundance was in late May. In most samples, 100% of the larvae were feeding. Copepod eggs were usually the most numerous prey item, with *Pseudocalanus* spp. nauplii being the second most abundant item (Fig. 3.11). In late April 41% of the diet by numbers, excluding copepod eggs, was rotifers, in mid May euphausiid nauplii made up a significant fraction of the diet (24% by number, 64% by volume), and in late May copepod nauplii (*Pseudocalanus* spp. and *Acartia* spp.) were abundant in the larval diets (25% by number, 35% by volume). First-feeding larvae (5.0–6.9 mm), however, had very few prey items in their guts when copepod eggs were excluded from the analysis (April, 1 larva^{-1}; mid May 0.5–1 larva^{-1}; late May, 3–5 larva^{-1}).

In conclusion, it seems that in 1995 there was a mismatch between the period of maximal first feeding larval abundance (the period of greatest vulnerability to starvation) and the maximum standing stock of copepod nauplii. During the period of maximal abundance of first feeding larvae prey densities were much less than 20 l^{-1}, the critical value determined from research in Shelikof Strait. Evidence for a deleterious effect of low prey concentrations on larvae was contrary to expectations. We lack specific estimates of larval mortality; however only 1% of the larvae sampled during mid May 1995 were starving (Porter and Theilacker, in preparation). In Shelikof Strait, at comparable prey densities (but slightly higher water temperatures) ca. 34% of the first feeding larvae were starving. A late larval/early juvenile survey of the Shelf Regime during the summer of 1995 revealed much lower

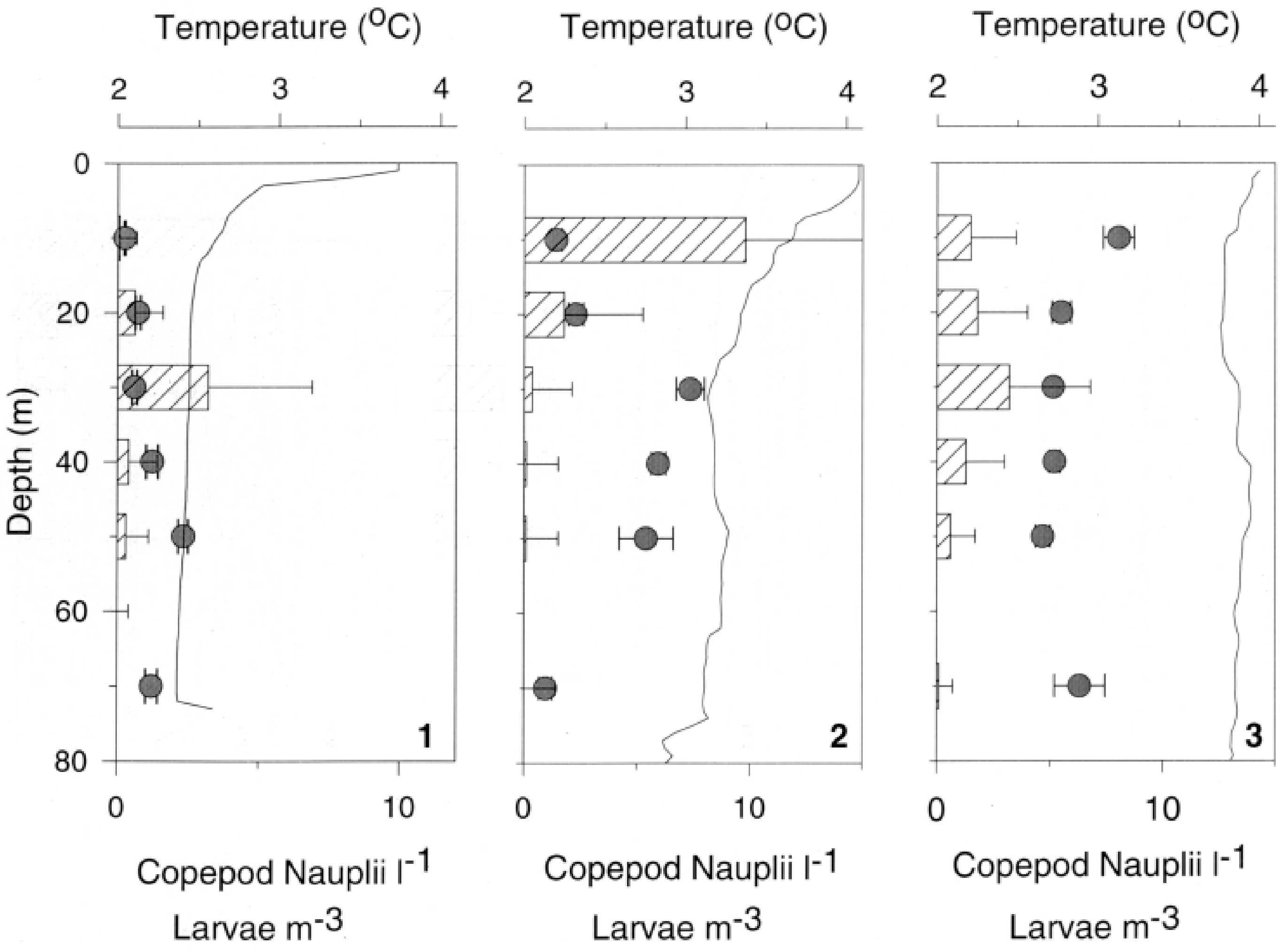


Figure 3.10: Springtime vertical distributions of larval pollock (horizontal bars), copepod nauplii (filled circles), and water temperature (solid line; °C) at three stations over the southeastern shelf during a year of maximal ice extent (1995). Shown are the mean concentrations ± SE (pollock; Brase, 1996) and ±95% confidence interval (nauplii; Napp *et al.*, in preparation). Station 1, late April; Station 2, early May; Station 3, late May.

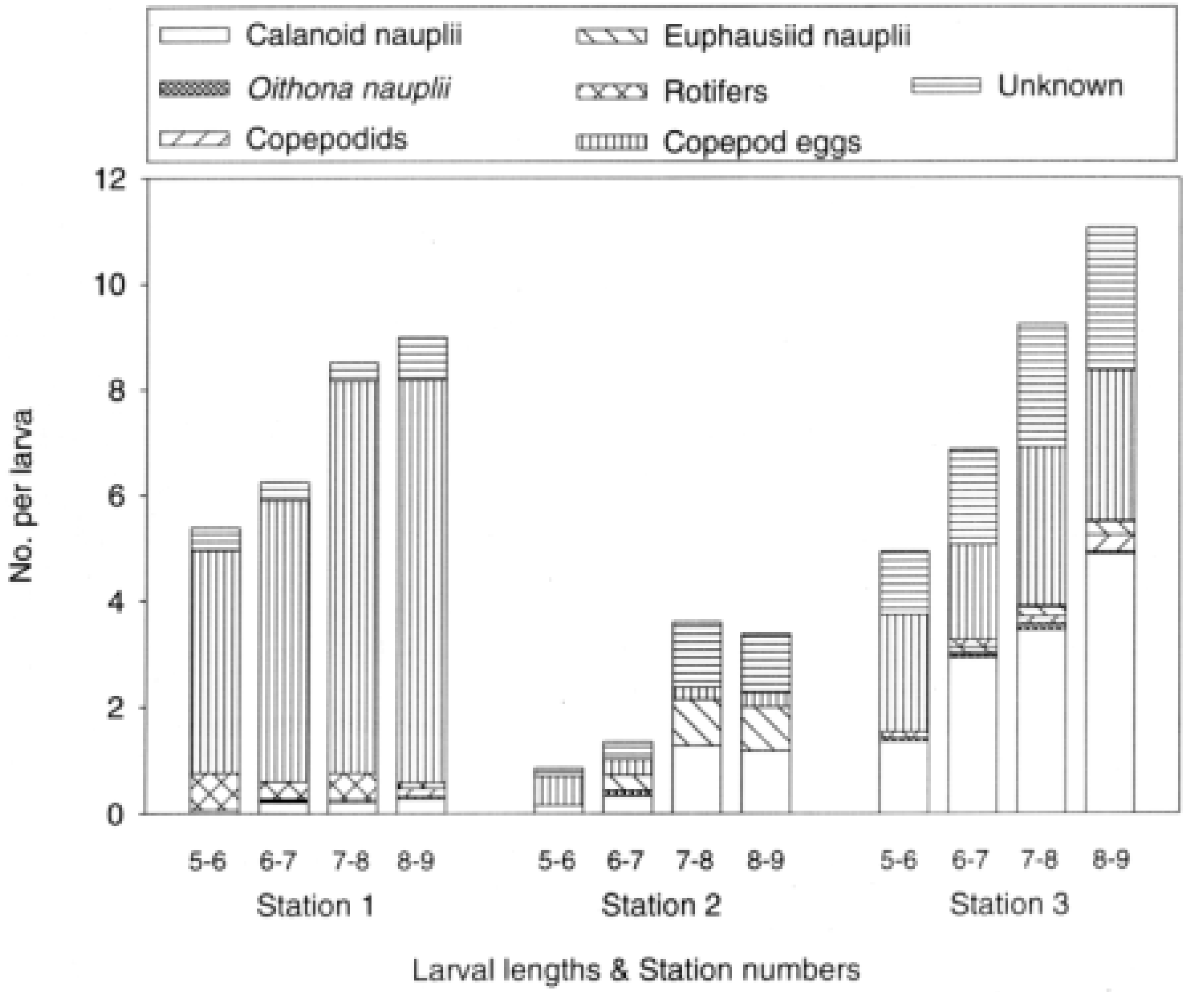


Figure 3.11: Larval gut contents by station and larval length during late April (Station 1) and early and late May (Stations 2 and 3, respectively), 1995 (Brase, 1996).

late larval/age-0 juvenile abundances than found in 1996, a minimal ice year (Brodeur, this volume).

3.5 Implications: Shelf and Oceanic Regimes as Feeding Environments for Pollock Larvae

Now that we know what pollock larvae eat and which prey they prefer, we can compare the two Regimes (Shelf and Oceanic) and examine interannual differences in the timing of the spring phytoplankton bloom and prey standing stocks. Note that our investigations of prey density and spring bloom dynamics were geographically and temporally limited. Prey density and larval feeding measurements were limited to places and times where pollock larvae were very abundant and feeding studies were conducted. Spring phytoplankton bloom dynamics data were limited to the locations of the biophysical platforms which were initially chosen to be representative of particular regions. In addition, our ability to resolve sources of interannual variability is tempered by the short duration of the Program and the emphasis on two large oceanographic regimes. We spent only two full field seasons in each region with a transition year between. Thus our intra-Regime interannual comparisons are limited to two adjacent years.

3.5.1 Timing of Prey Production

Egg production of many calanoid copepods is generally thought to be initiated by increased food availability (i.e., coincident with the spring phytoplankton bloom; e.g., Hirche, 1996). Our time-series observations of chlorophyll concentration (1993–1996) at the biophysical platforms suggest that the onset of larval prey production was less variable over the basin than over the shelf, despite the importance of mesoscale variability over the slope. The presence or absence of sea-ice was the physical factor most responsible for variability in timing over the shelf; variability in wind mixing may be important, but only when ice is absent (cf. Sambrotto *et al.,* 1986).

The assumption that production of prey is initiated by the spring bloom remains to be tested for the Bering Sea. Recent examination of one species of shelf prey producer (*Calanus marshallae*) revealed no correspondence between gonadal maturity (a proxy for egg production) and sea surface chlorophyll in April of 1995 (Baier and Napp, in preparation). In this species, most of the sampled population was sexually mature females with well developed eggs in their oviducts ready for release, despite very low sea surface chlorophyll values (0.5–1 μg l^{-1}).

The timing of egg production relative to the appearance of first-feeding larvae is also important. At 3°C, a typical springtime temperature for the Outer Shelf and Slope Domains, *Metridia pacifica* needs ca. 12 days to develop from egg to the fourth naupliar stage (NIV; Pinchuk and Paul, 1998) and *Pseudocalanus* spp. require ca. 15 days to do the same (Corkett and McLaren, 1978). The "critical period" of first feeding larvae is ca. 7–14 days at 5°C; therefore prey production must be initiated several weeks before first feeding larvae appear.

3.5.2 Amount of Prey Produced

Production of preferred prey involves two steps: egg production and development to the preferred developmental stage. Both are affected by variability in the physical environment. Total production of prey items may be decoupled from the absolute level of primary production depending on the amount of food required for maximal reproduction by the dominant calanoid copepods in the system (Runge, 1988). Egg production rates by one of the copepod genera responsible for prey production (*Pseudocalanus* spp.) would not be food-limited in either region (slope or shelf) during periods of maximal phytoplankton standing stock. This may not be true for the larger prey-producing copepods *Metridia*, *Calanus*, and *Eucalanus*.

Variability in prey densities within the Oceanic Regime and between the Oceanic and Shelf Regimes was found to be much larger than initially thought. We did find low densities over the Oceanic Regime of <10 nauplii l^{-1} in April of all years (Paul *et al.,* 1996; Napp *et al.,* in preparation), but also found several incidences where densities were >20 l^{-1}, the critical value determined for larvae from Shelikof Strait. Naupliar abundances over the shelf in April 1994 and 1995 and May 1995 were ≤ 10 l^{-1} at almost all sampled depths. Our Oceanic Regime prey densities are comparable to the slope values from PROBES with the exception of low values found in their cold year, 1980 (Dagg *et al.,* 1984; Walsh and McRoy, 1986). Shelf Regime naupliar densities sampled during cold years are comparable between the two programs, but BS FOCI did not sample the Shelf Regime in May and June of "warm" years. One important distinction between the results of the two programs is that BS FOCI has direct measurements of larval condition. Even at low prey densities found during cold years by both programs, larvae did not appear to be starving (Porter and Theilacker, in preparation).

Determination of prey density during the critical first feeding period is only one part of the recruitment story. Exposure to high prey concentrations is advantageous for rapid growth and potentially lower predation risk during the larval and early juvenile stages. Over the Middle Shelf Domain, in the absence of wind mixing, a rapid increase, then decline of phytoplankton and nutrients is observed. Springtime water column stratification separates the phytoplankton from their nutrient source. When nutrients become depleted the bloom sinks and continued prey production by copepods must rely on lower levels of phytoplankton standing stock sustained by regenerated nutrients. Thus, variability in insolation (heat flux) and wind mixing determines the absolute or annual level of larval prey production over parts of the shelf.

3.5.3 Taxonomic Composition of Prey

Since we know that pollock larvae are selective feeders, we must take into account the type of prey as well as the concentration of all available prey. A major difference between the Oceanic Regime and Shelf Regime is the ratio of calanoid to cyclopoid nauplii. At most depths sampled over the Oceanic Regime in April of 1994, 20–30% of the copepod nauplii were calanoids, while at the Outer Shelf Domain station on the same cruise, 50–60% were calanoid nauplii. The exception to this generalization for the slope region was at the depths where large concentrations of nauplii were found; they were 70% calanoid, i.e., more similar to the Shelf Regime, than the Oceanic Regime prey assemblage. Thus, when we take preferential feeding into account, starvation was not apparent even at very low effective prey concentrations.

3.5.4 Larval Condition

In the above discussion we noted that we have little or no evidence to support the hypothesis that starvation was an important source of mortality for larval pollock in the Bering Sea (one might argue that these data refute the hypothesis). Our limited measurements of larval condition were made in patches of water where larvae were abundant. Few larvae showed symptoms of recent food deprivation in these patches. However, these same larvae were feeding under prey-poor conditions and had few prey items in their guts. This contradiction, low prey levels, yet low incidence of starvation, is one of the more significant findings of BS FOCI. Investigations are underway to determine the affect of temperature on both prey production and larval feeding and metabolism.

3.6 Conclusions

Pollock spawn in two distinct Regimes in the Southeast Bering Sea: the Oceanic Regime and the Shelf Regime. At present, molecular genetic techniques are unable to distinguish between spawning fish in either regime or among the fish regularly found spawning at different times and locations on the southeastern shelf. Conditions for the emerging larvae can be very different for the two regimes as are the factors that affect variability in survival of early larvae between regimes (Fig. 3.12). In the Oceanic Regime advection is strong, but variable, and mesoscale features (eddies) are common. Conditions outside mesoscale features show very low interannual variability. Over the shelf advection is generally low, but there are large fluctuations in the environment due to interannual variability in the presence or absence of sea ice. This affects the stability and temperature of the water column. Spring phytoplankton bloom dynamics vary between the two regimes as a result of the differences in their physical characteristics. Variability in observed plankton standing stocks may be largely due to advective rather than local processes in the Oceanic Regime. In the Shelf Regime interannual variability in a complex set of forcing functions (sea ice, wind mixing, temperature, and insolation) result in phytoplankton blooms with different timing, magnitude, and transfer efficiencies to the zooplankton and nekton (or benthos). The two Regimes provide different feeding environments for larval pollock. In the Oceanic Regime prey concentrations are generally low and are dominated by less preferable prey items. This may necessitate the larvae supplementing their diet with protists. Mesoscale features of unknown origin, when present, may contain much higher prey densities with a larger proportion of the prey being the type preferred by first-feeding larvae. In the Shelf Regime, preferred prey constituted a larger fraction of the available prey, but copepod

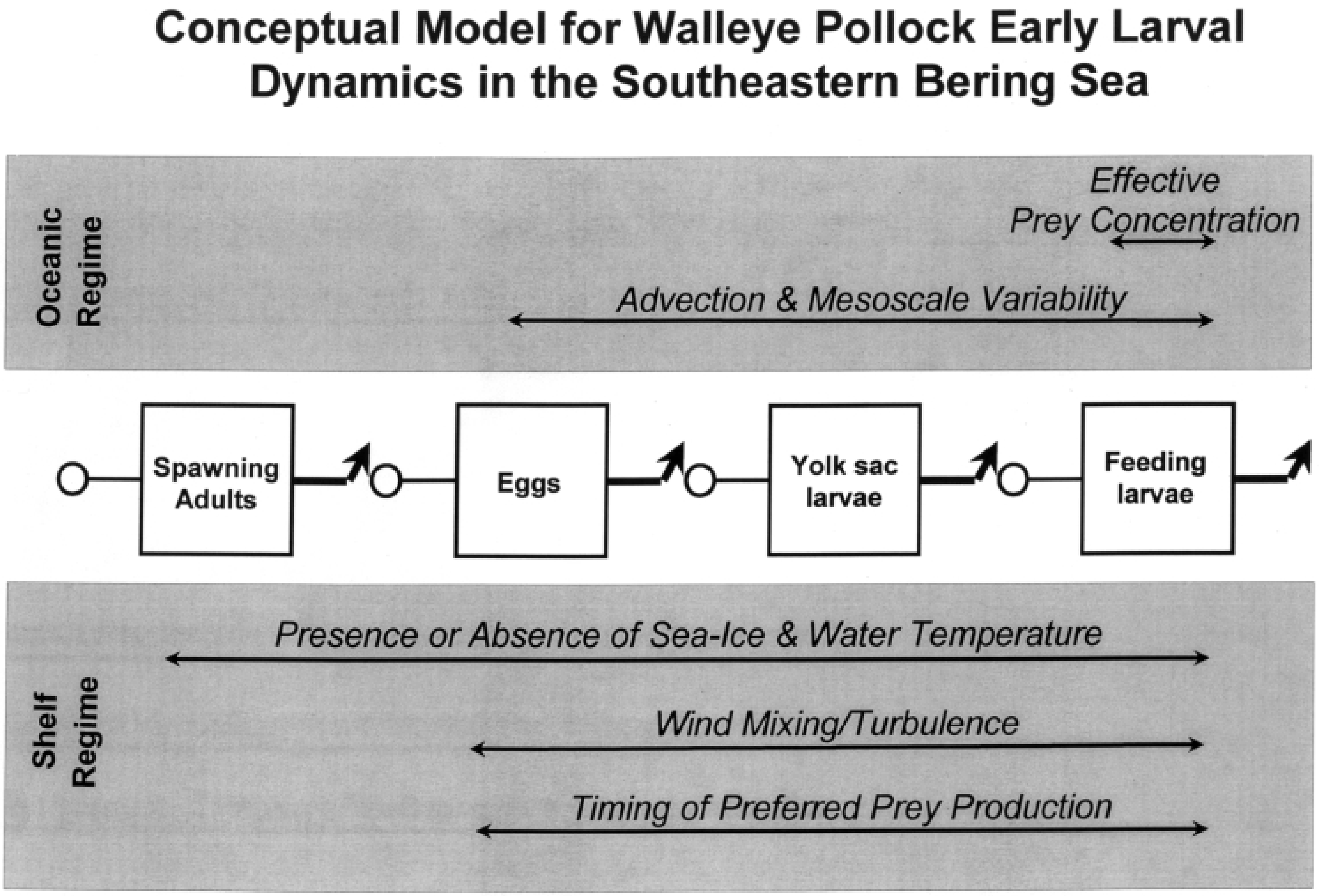


Figure 3.12: Switch model of walleye pollock early larval dynamics in the southeastern Bering Sea. Each box represents a life history stage through which survivors must pass. Biophysical processes thought to be important regulators of survival variability as a result of BS FOCI research are shown separately for the Oceanic and Shelf Regimes.

nauplii were still at minimal levels for growth and survival. There was no evidence to suggest, however, that these larvae were starving. Low temperatures associated with early sea-ice-associated spring phytoplankton blooms resulted in a mismatch between the maximal concentrations of first feeding larvae and their prey (cf. Walsh and McRoy, 1986; Townsend *et al.,* 1994). Thus the key to interannual variation in food for first feeding pollock larvae in the Oceanic Regime is advection, and in the Shelf Regime it is the coupled dynamics of the atmosphere-ice-ocean system.

3.7 Acknowledgments

We thank the Principal Investigators of BS FOCI for allowing us use of their published and unpublished results, and the FOCI Coordinator, S.A. Macklin, for facilitating the Program's research. We also express our thanks to the officers and crew of the NOAA Ships *Miller Freeman* and *Surveyor* for their field support during the Program.

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Part 3A

Juvenile pollock studies (R.D. Brodeur[1])

Summary

Analysis of summer survey data from several years indicate that age-0 pollock are more likely to be found in the waters surrounding the Pribilof Islands than the Bering Sea shelf in general and this area may represent an important nursery ground for juvenile pollock. The frontal zones that surround each island exhibit elevated levels of phytoplankton and small zooplankton compared to those found on either side of the front. Acoustic and trawl catch data show that age-0 pollock are concentrated at these fronts, as are many piscivorous fishes, seabirds, and marine mammals. Age-0 pollock and large jellyfish dominate by number and biomass, respectively, the catches of midwater trawls in the Pribilof Island area. In situ videos have demonstrated that these age-0 pollock are found in the same layer as the jellyfish during the day and are found to actually associate with these medusae, perhaps to gain protection from visual predators during the day. Age-0 pollock were larger offshore of the fronts, but an analysis of otoliths of these fish indicates that the offshore fish are older, suggesting an ontogenetic offshore movement. Analysis of hatch-date distributions suggests that the Pribilof fish were spawned on the southeastern Bering Sea shelf and slope. No indication was found of any size-selective predation on age-0 pollock by older age classes of pollock or other fish predators in any region, although fish predation overall was much greater offshore of the front due to high abundances of adult pollock in this region.

Summer Distribution of Age-0 Pollock on the Eastern Bering Sea Shelf

Pelagic trawling was done in 1995 and 1996 aboard a Japanese research vessel to study the mid-summer distribution of age-0 pollock and associated taxa. A similar set of grid stations was sampled both years using a rectangular fine-mesh beam trawl. Bottom temperatures in the Pribilof Island area were mostly between 3° and 4°C in 1995 and between 4° and 5°C in 1996. Thermocline depth was centered near 30 m depth in 1995 and around 40 m in 1996. In both years, standardized catches of age-0 walleye pollock, based on rough counts at sea, were the highest in the northwest part of the grid and in the area closest to the Pribilof Islands (Fig. 3A.1). The catch of juvenile walleye pollock in 1996 was over five times greater than in 1995. Relatively fewer fish were caught in the southern and eastern portions of the grid. Noticeably larger age-0 walleye pollock tended to occur in the eastern part of the survey area, although the actual length measurements will not be available until the 1996 samples are processed. Larvae of Greenland turbot

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[1] Alaska Fisheries Science Center, NOAA, Seattle, WA 98115, U.S.A.

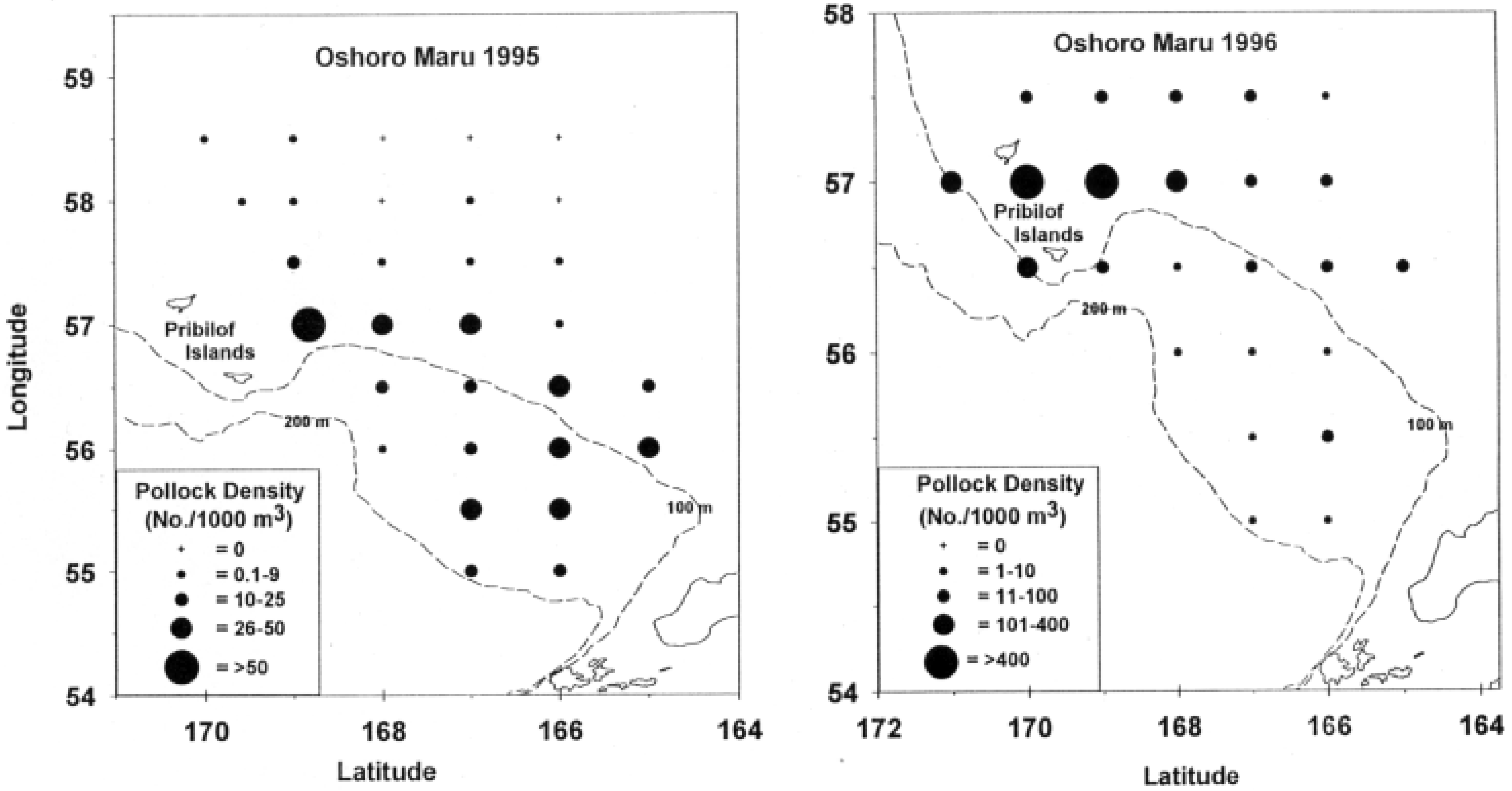


Figure 3A.1: Location of stations sampled in 1995 and 1996 by the *Oshoro Maru* for age-0 walleye pollock. The relative size of the dots correspond to the density of age-0 pollock according to the legend.

(*Reinhardtius hippoglossoides*), a common circum-arctic flatfish species, were frequently collected in 1995 beam trawl samples but were absent from 1996 samples.

There were also some interannual differences in the zooplankton collected during the 2 years. Both densities and biomass were much higher in 1996 than in 1995. Gelatinous zooplankton (chaetognaths and cnidarians) were predominant during 1995 whereas euphausiids dominated the 1996 invertebrate catches. In fact, five of the top seven most abundant species collected in 1996 were euphausiids. There were day/night differences in the catches of most crustaceans but not of the gelatinous zooplankton.

Distribution and Species Associations of Juvenile Pollock and Forage Fishes

This project analyzed archival data on abundance and distribution of juvenile pollock and other important forage fishes in the Bering Sea. Forage fish are currently a topic of active research due to recent declines of marine mammal and seabird populations which have historically depended upon them. At the "International Symposium of the Role of Forage Fish in Marine Ecosystems" held in 1996, many of our findings of this project were presented. This project allowed collaborative research with the Russian fisheries laboratory (TINRO) in Vladivostok whereby a Russian scientist was able to bring data from the western Bering Sea to Seattle and analyze it using similar analytical methods for both the eastern and western data sets.

Our study is the first to examine the large-scale distribution patterns of juvenile pollock and several dominant forage fish species throughout the Bering Sea. We analyzed new data on the association of these forage fishes with other taxa that may compete with these forage fishes and, in some cases, prey upon them. In this study, we examined survey data on some dominant pelagic forage fishes (herring *Clupea pallasi* and capelin *Mallotus villosus*) and the juvenile stages of major commercial groundfish species (walleye pollock and Pacific cod *Gadus macrocephalus*). Age-0 pollock had the highest biomass and were the most widely distributed forage fish on the eastern Bering Sea shelf (Fig. 3A.2), although jellyfish and age-2+ pollock dominated the biomass overall. Several geographically distinct assemblages were recognized in both the eastern and western Bering Sea. Age-0 pollock were associated with warmer bottom temperatures and capelin with colder bottom temperatures compared with other species.

Habitat Characteristics of Juvenile Pollock in the Eastern Bering Sea

Data from a midwater trawl survey of the eastern Bering Sea shelf and southern Bering Sea basin conducted in 1987 aboard the Russian research vessel *Darwin* was analyzed in detail to study the spatial relationships of juvenile pollock to other pelagic species and to begin to address how these

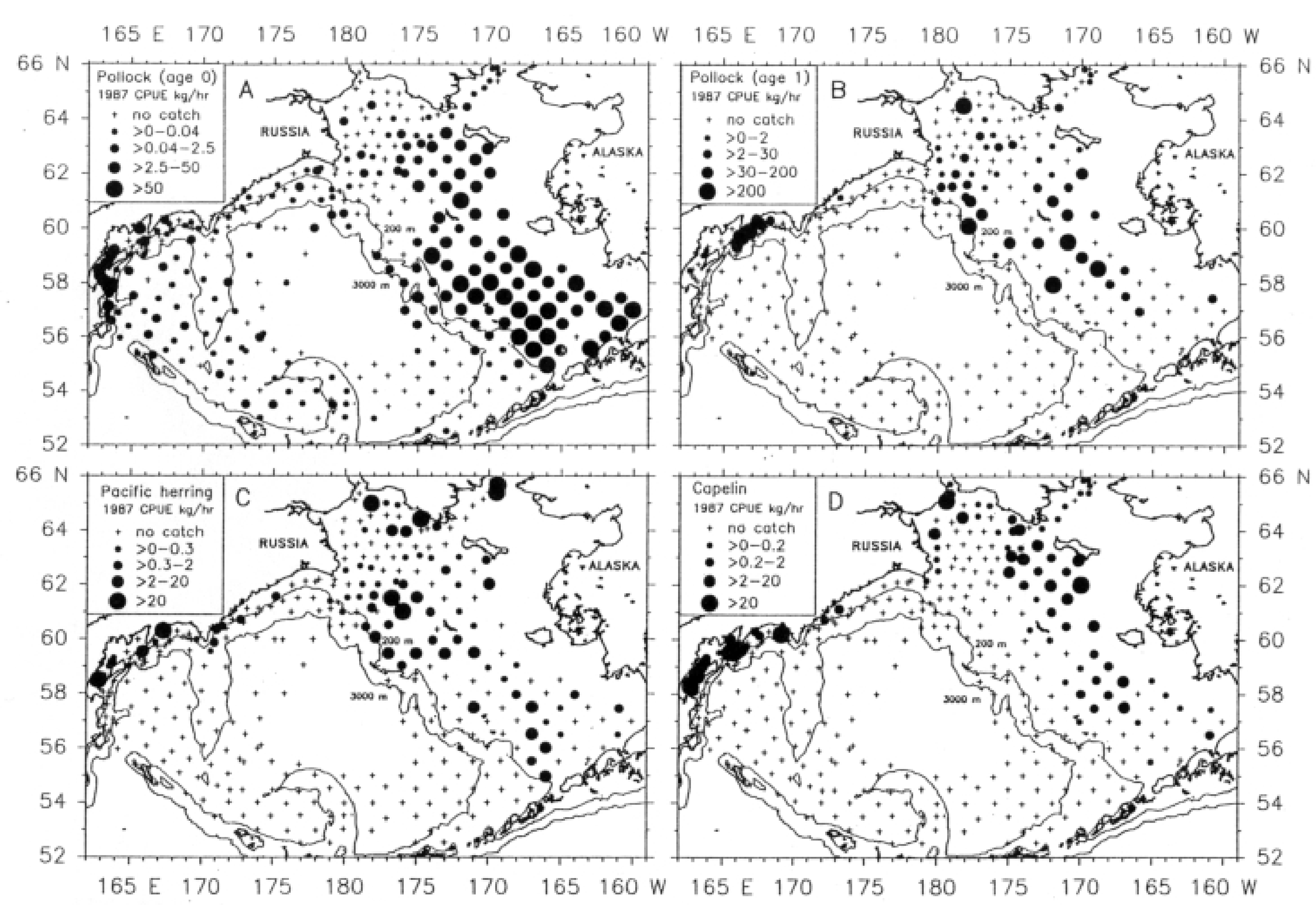


Figure 3A.2: Distributions of (a) age-0 and (b) age-1 walleye pollock, (c) Pacific herring, and (d) capelin, in the Bering Sea, based on 1987 surveys by Russian research vessels.

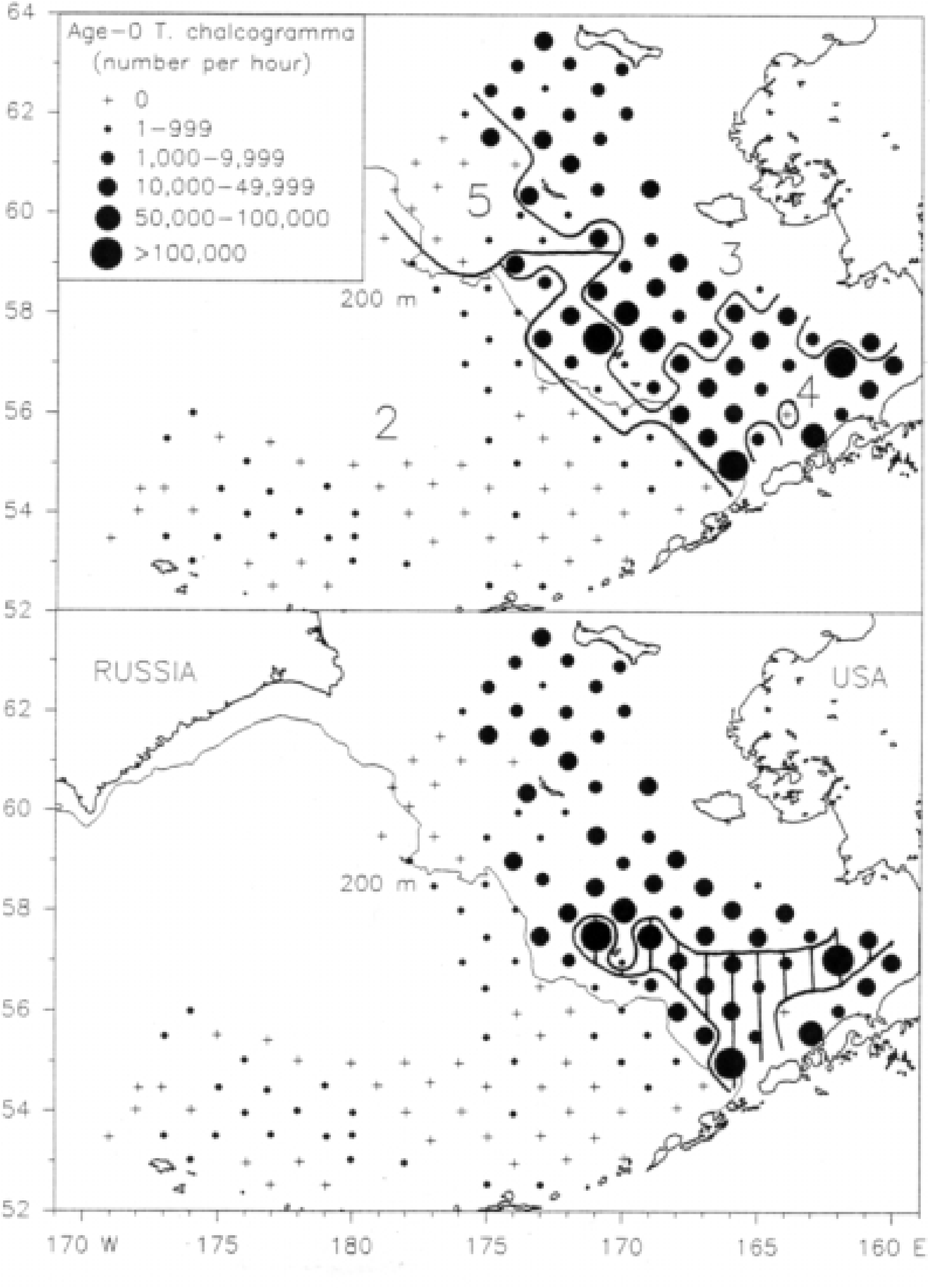


Figure 3A.3: Age-0 walleye pollock densities and the locations of four different taxonomic groups based on (top) catch composition and (bottom) optimal habitat of age-0 pollock based on optimal bottom depth, temperature, and dissolved oxygen, and salinity at 45 m depth. It was found that these were the combination of variables that were significantly associated with age-0 pollock distribution.

fish may respond to environmental variability. The availability of pollock length data made it possible to study the juveniles separately from the adults. Catch composition and hydrographic data (temperature, salinity, and dissolved oxygen) were collected during this survey making both a community and a single species approach possible. A synecological approach was first used assuming that an ordination of the ecological amplitudes of the various taxa collected may more effectively reflect influential environmental gradients than considering taxa singly. Cluster and ordination techniques, incorporating environmental constraints, revealed four bio-types and several prominent environmental gradients. A basin group and three major shelf groups were identified as having distinct catch compositions, environmental attributes, and geographic locations (Fig. 3A.3). Juvenile pollock were mostly found on the shelf. The principle environmental gradients were salinity and dissolved oxygen; temperature was less important. Juvenile pollock were intermediate in position along these gradients but differences between age-0 and age-1 cohorts were apparent.

Distribution of Juvenile Pollock and Other Biota in Relation to Fronts

Using midwater trawl observations from September 1994 and 1995, the abundance, distribution, and size composition of age-0 walleye pollock were examined in relation to the physical oceanography and biology of the structural front along a transect north of St. Paul Island (Fig. 3A.4). The frontal region occurred 12–20 km offshore in both years, but the thermocline was much shallower in 1995 (25 m) than in 1994 (45 m). The isothermal (<8°C) inner domain had low chlorophyll, and relatively low small (>153 μm) and large (>505 μm) fraction zooplankton concentrations. The highest chlorophyll and small zooplankton concentrations occurred at the front and were lower both inshore and farther offshore of the front. Large zooplankton (mainly euphausiids and cnidarians) were most abundant in the stratified offshore waters. By number, age-0 walleye pollock dominated the catches of midwater trawls (>99% and >95% in 1994 and 1995, respectively). Overall, however, large medusae dominated the total biomass. Age-0 walleye pollock densities were the highest at the front or inshore of the front. Age-0 pollock densities averaged about three times higher in 1994 than in 1995. Age-0 pollock were significantly smaller in 1994 inshore and at the front (mean = 43.4 and 44.6 mm, respectively) than in 1995 (52.2 and 51.7 mm; Fig. 3A.5).

Commensal Associations of Juvenile Pollock with Schyphomedusae

In September 1995, dense aggregations of large scyphomedusae (mainly *Chrysaora melanaster* and *Cyanea capillata*) were observed in 27 midwater deployments of a remotely operated vehicle (ROV) near the Pribilof Islands in the Bering Sea. Age-0 walleye pollock appeared to be frequently associ-

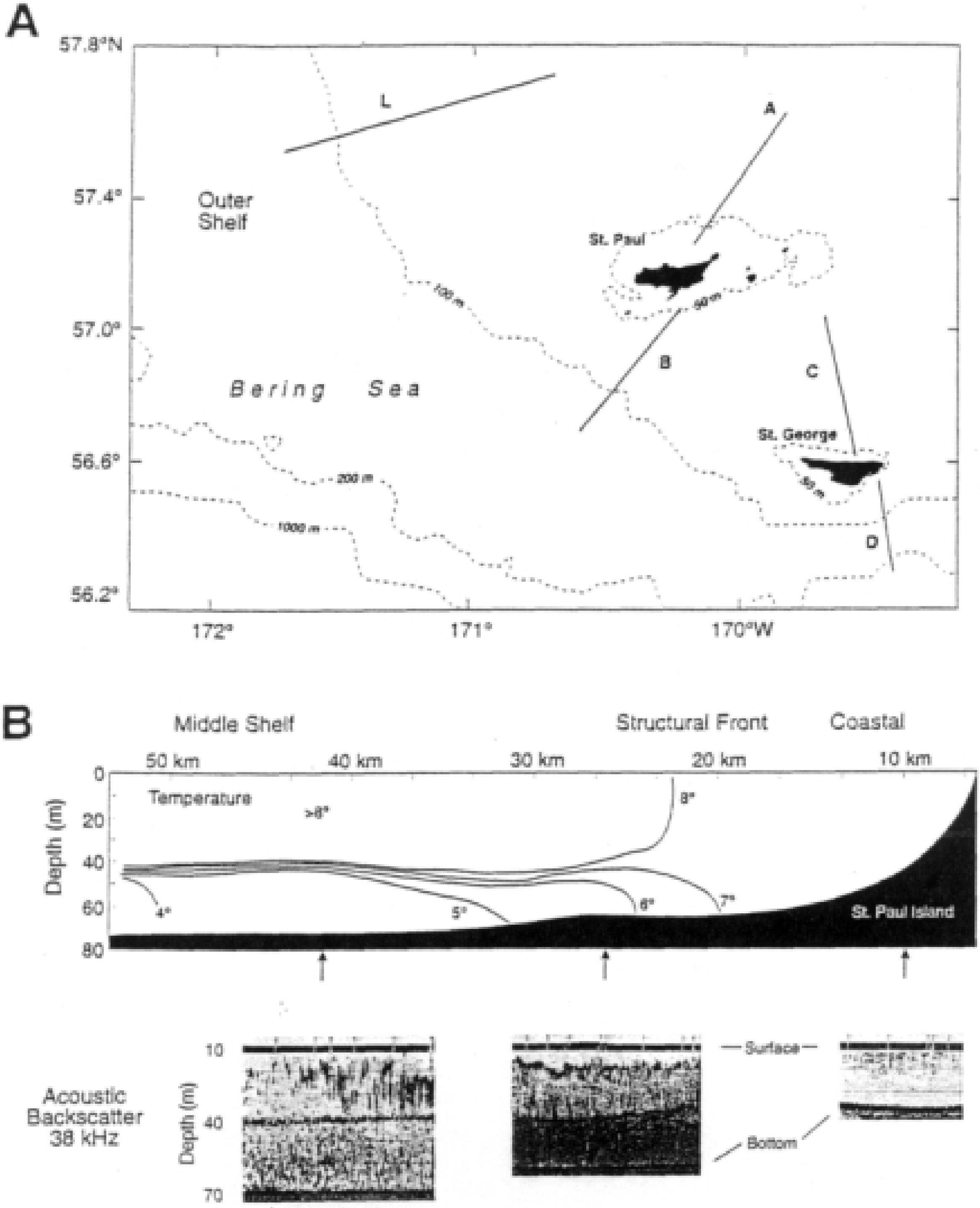


Figure 3A.4: (top) Location of sampling transects around the Pribilof Islands, (middle) cross-shelf section of temperature and identification of different habitats, and (bottom) acoustic backscatter, in the three different habitats along Transect A in 1994.

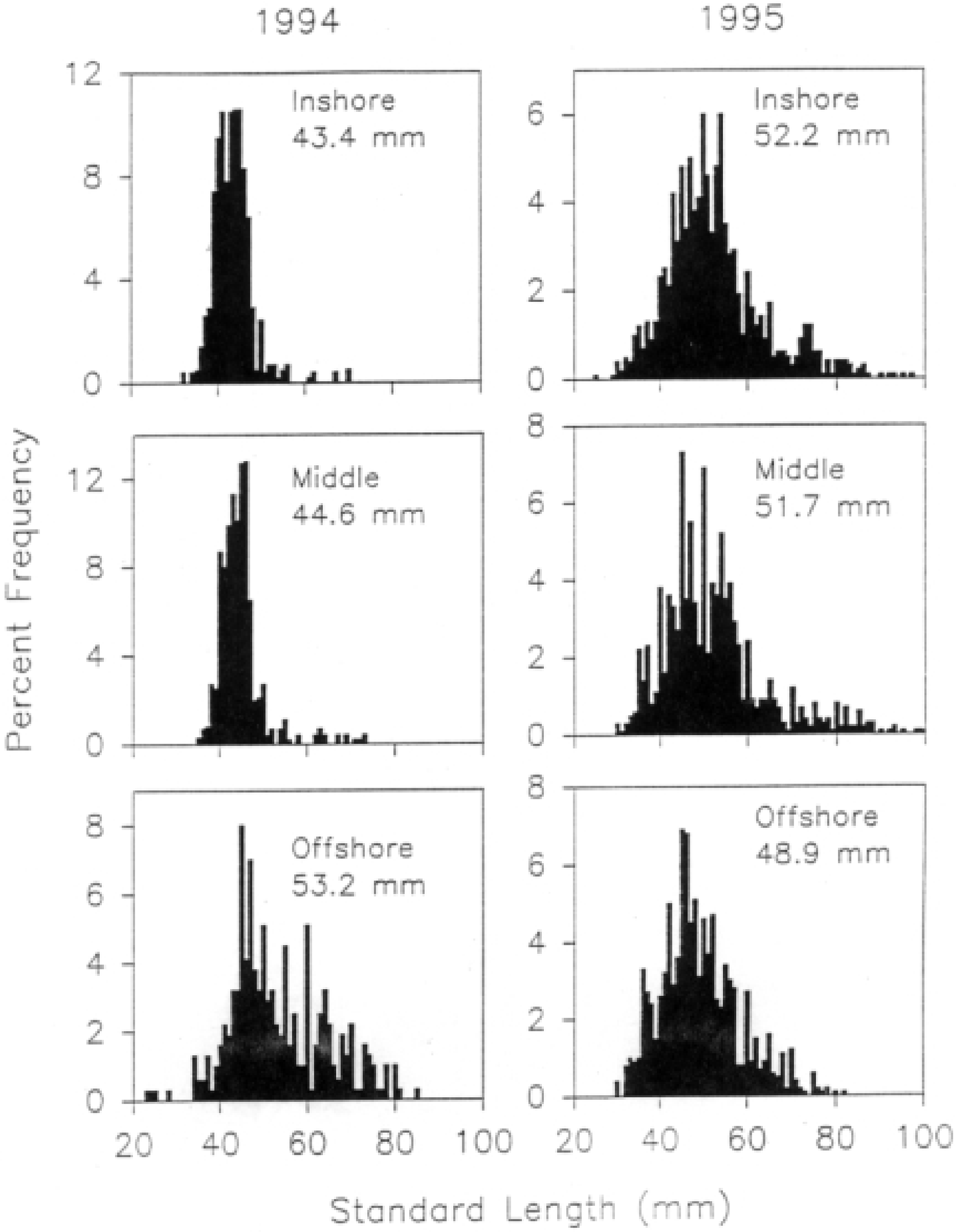


Figure 3A.5: Size distributions of age-0 pollock in the three habitats during 1994 and 1995.

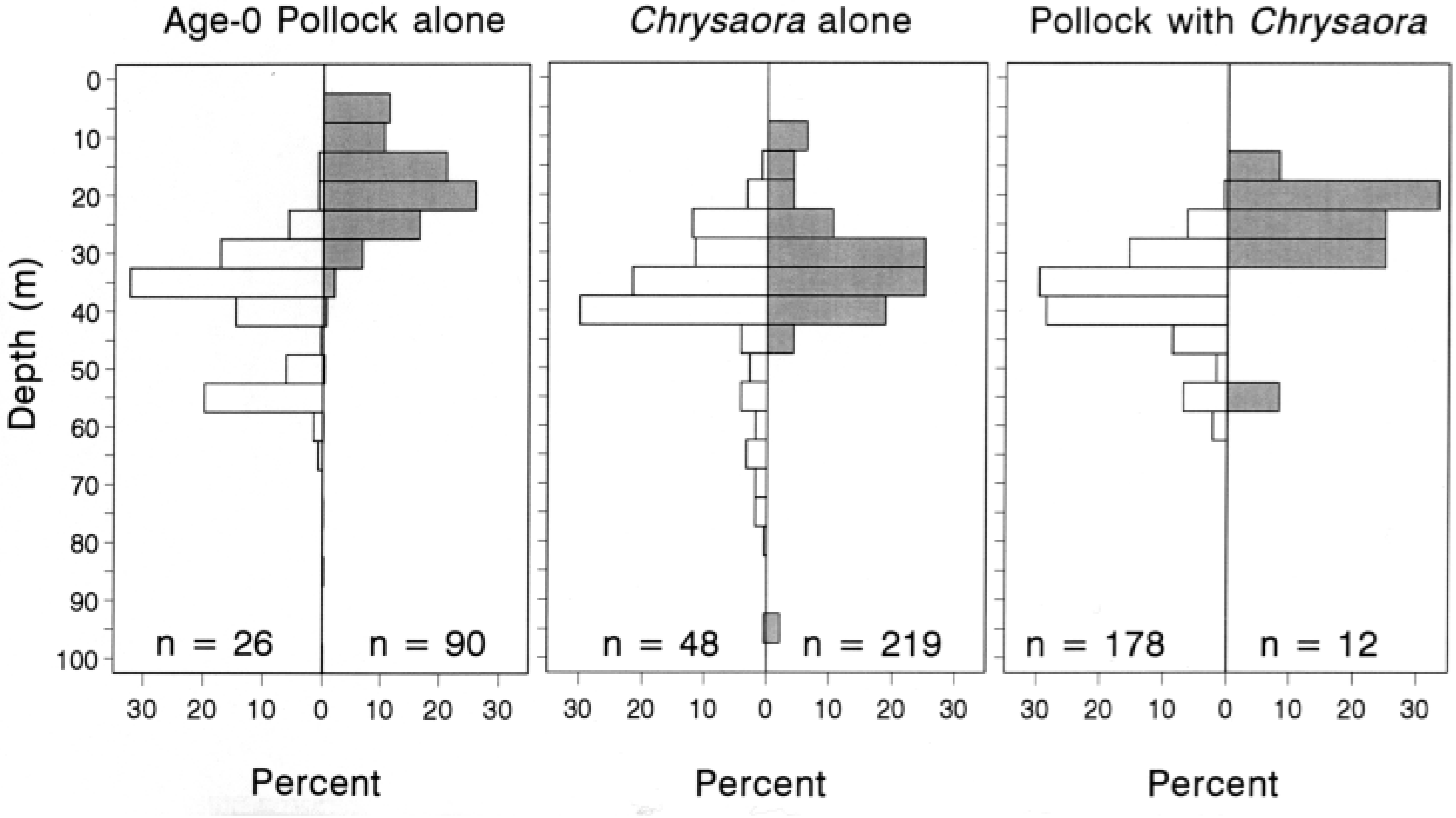


Figure 3A.6: (Open boxes) day and (shaded boxes) night differences in the vertical distribution of age-0 pollock and the dominant jellyfish (*Chrysaora* spp.) alone and found together based on in situ ROV observations made during 1995 around the Pribilof Islands. The number of observations of each occurrence are listed at the bottom of the figure.

ated with these gelatinous zooplankton. During daytime, up to 30 pollock were observed swimming within the tentacles of these medusae, but when approached by the ROV, the pollock generally left the vicinity of the jellyfish. At night, few such associations were observed and juvenile pollock moved closer to the surface (Fig. 3A.6), apparently feeding in loose aggregations, while the medusae remained close to the thermocline (35–40 m). Trawl collections during the day showed a strong association between age-0 pollock and medusae density, whereas at night no such association was observed. The lack of gelatinous material in the stomachs of the pollock suggests that juvenile pollock associate to gain shelter from predation. This commensal behavior with gelatinous zooplankton may have important implications relevant to pollock recruitment dynamics in the Eastern Bering Sea if these juvenile pollock substantially decrease their vulnerability to predation by seeking shelter within jellyfish tentacles.

Variability in Feeding and Condition of Age-0 Pollock in Relation to Fronts

Dietary composition, feeding intensity, and condition index of age-0 walleye pollock were examined for variations related to time of day, location, size of predator, and year. Stomach contents of pollock collected at a hydrographic front near the Pribilof Islands during September 1994 through 1996 were compared with those from pollock collected on either side of the front. Diets were dominated in all three regions by small zooplankton, mainly copepods, pteropods, euphausiids, and chaetognaths, but fish and some epibenthic crustaceans were also consumed. Copepods and pteropods dominated the diet in all years and areas by number but the diet was more mixed by weight with chaetognaths, euphausiids, and fish (smaller pollock) also being important (Fig. 3A.7). Copepods were more abundant in the diet during the day. No significant day/night differences in weight composition were noted. Stomach fullness was highly variable by year and habitat and no significant differences were observed. Stomach fullness peaked at around sunset for fish <50 mm and at night for the larger fish, implying that feeding chronology changed with ontogeny. Age-0 pollock condition factor (Fulton's K) varied from 0.45 to 1.20 (mean = 0.767 ± 0.09 (SD)). Year was not found to be an important factor in determining condition although location with respect to the front was important.

Age and Growth of Juvenile Pollock in Relation to the Fronts

The hatch-date distributions for the fish taken at ten stations in the 1994 sampling area showed that hatching occurred from mid April through early July with a peak occurring in June. Allowing approximately 1 month from spawning to hatching, at water temperatures of 1–3°C, it can be presumed that these fish were spawned from late March through early June with a

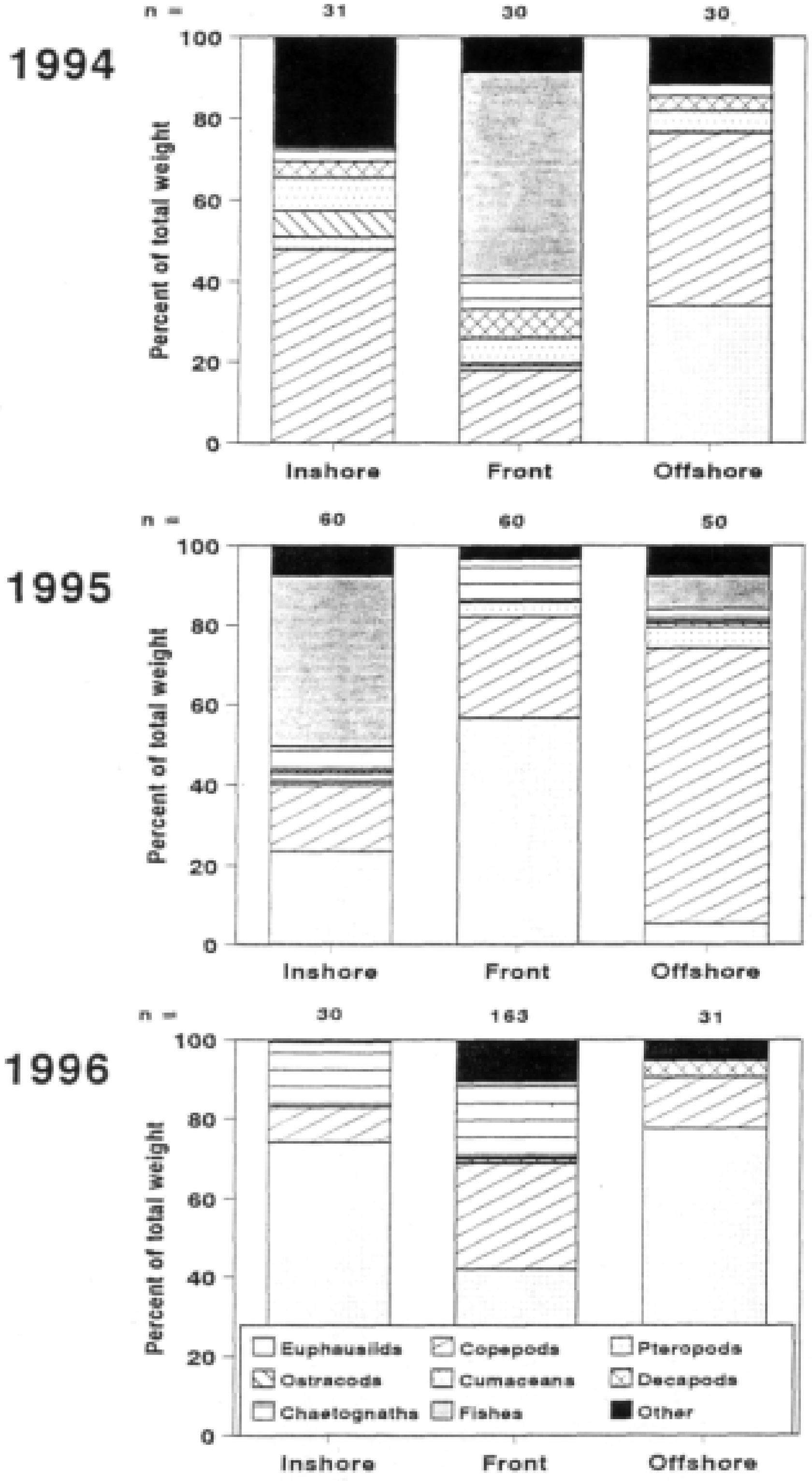


Figure 3A.7: Interannual and habitat differences in the percentage weight composition of the diet of age-0 pollock on Transect A north of St. Paul Island. Stomach contents are grouped into major prey categories. The number of stomachs examined in each category is given at the top of each figure.

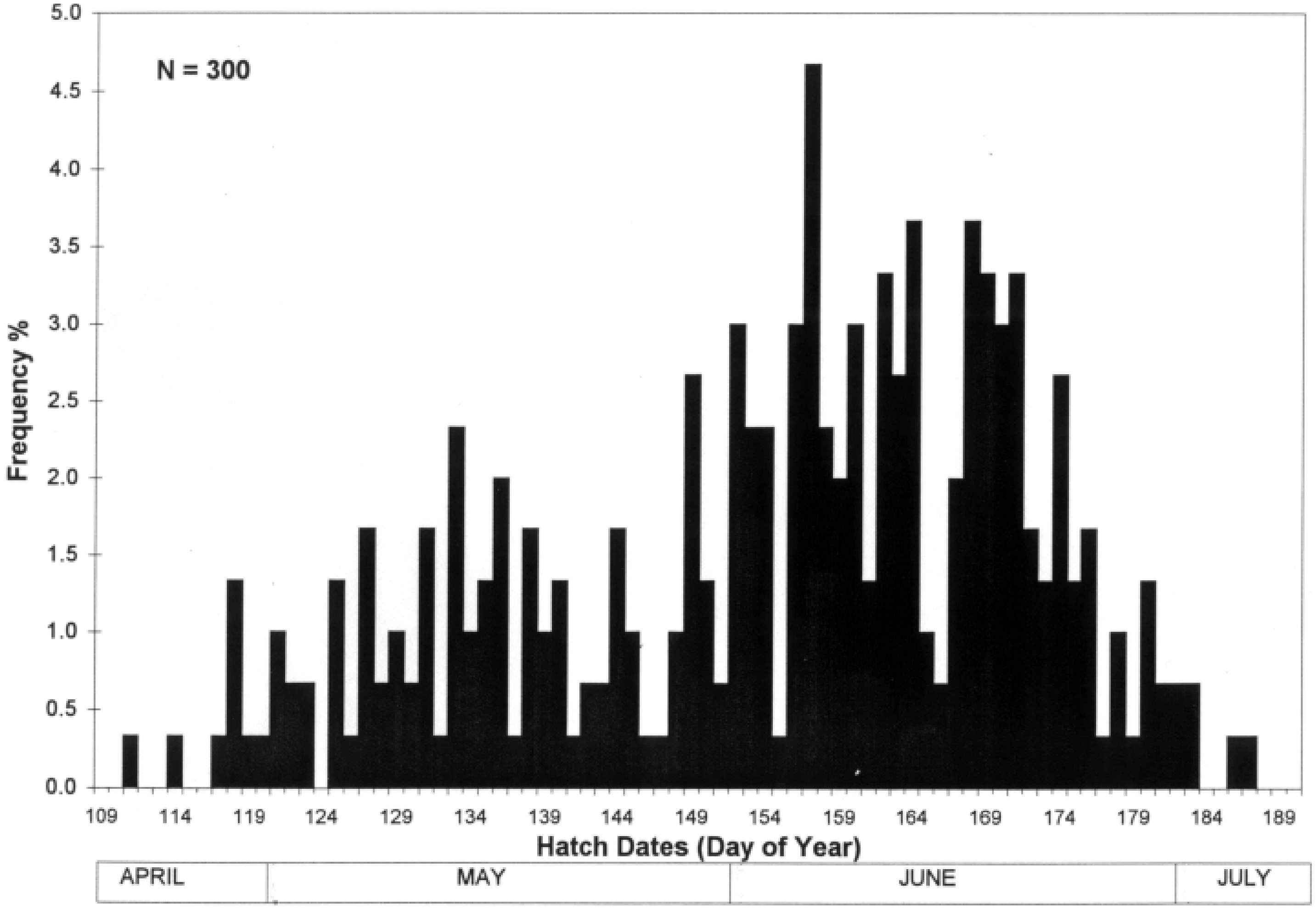


Figure 3A.8: Hatch-date distributions of age-0 walleye pollock collected around the Pribilof Islands during September 1994.

peak in spawning during May. This spawning period coincides with the spawning period for pollock on the southeastern continental shelf and slope of the Bering Sea. Age in days after hatching ranged from 76 to 152 and was predominantly less than 120 days (Fig. 3A.8). Some geographical distinction is noticeable in the age-length relationship, particularly among the larger fish. The possibility of variability in growth rates was investigated using growth among individual fish backcalculated using otolith microincrement measurements. Even though sampling was limited at and inshore of the tidal fronts around the Pribilof Islands, it seems from the data that fish were smaller and younger at these locations than those sampled offshore of the fronts.

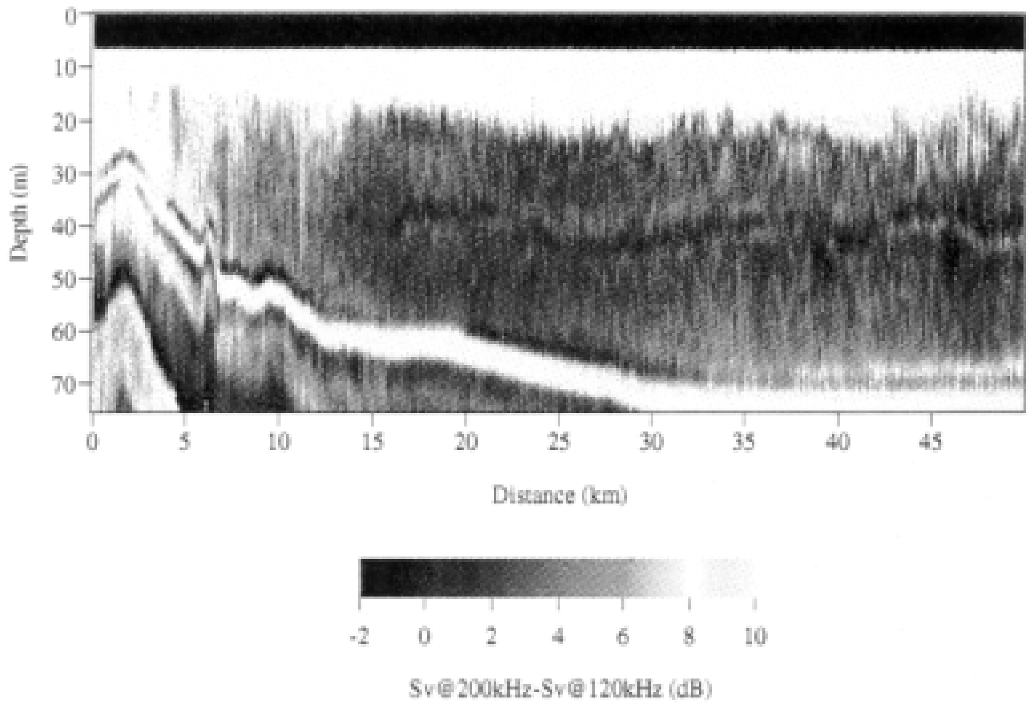
Covariation of Plankton, Juvenile Fish, and Seabirds at Tidal Fronts

Tidally generated shelf frontal systems around the Pribilof Islands offer a unique setting where the effects of ocean dynamics on the production and distribution of plankton, nekton, and seabirds can be observed. During a pilot study in late summer 1994, the frontal zone between inshore and offshore regimes northeast of St. Paul Island was sampled by continuous underway transects of hydroacoustics (38, 120, and 200 kHz) and seabird counts to determine the distributions of juvenile fish and their predators. Net sampling of juvenile fish and their planktonic prey followed. Echograms of volume backscatter (S_v) at all frequencies showed a correspondence between scatterer density and hydrography. By rendering differences in volume backscatter (Fig. 3A.9) at two frequencies as echograms (S_{v200}–S_{v120}), we were able to discriminate between layers of fish (with or without zooplankton) and layers of zooplankton (without fish). Juvenile walleye pollock comprised >90% of fish biomass captured with a pelagic trawl. The dominant zooplankton scatterers had different vertical distribution patterns in different hydrographic regimes (inshore, frontal, and offshore). In the offshore regime, fish were aggregated around the thermocline (ca. 40 m) during the day, and migrated to the surface at night. Biomass of large zooplankton was highest in this regime (250 ml m^{-3}), and some of the potential prey populations remained below the thermocline at night after the distribution of fish shoaled. Juvenile walleye pollock were more abundant in the front (>200–1000 m^{-3}) than either of the other regimes. Biomass of small zooplankton was highest in the frontal zone (>700 ml m^{-3}). Seabirds (murres, *Uria* spp.), whose diet is strongly dependent on the availability of juvenile fish, were most abundant just offshore of, rather than in, the front.

Predation on Juvenile Pollock by Major Teleost Predators

Spatial and temporal variation in the consumption of age-0 walleye pollock by arrowtooth flounder (*Atherethes stomias*) and older age classes of pollock

FOCI 1994 Transect A, Daytime, Sv Difference Smoothed



FOCI 1994 Transect A, Nighttime, Sv Difference Smoothed

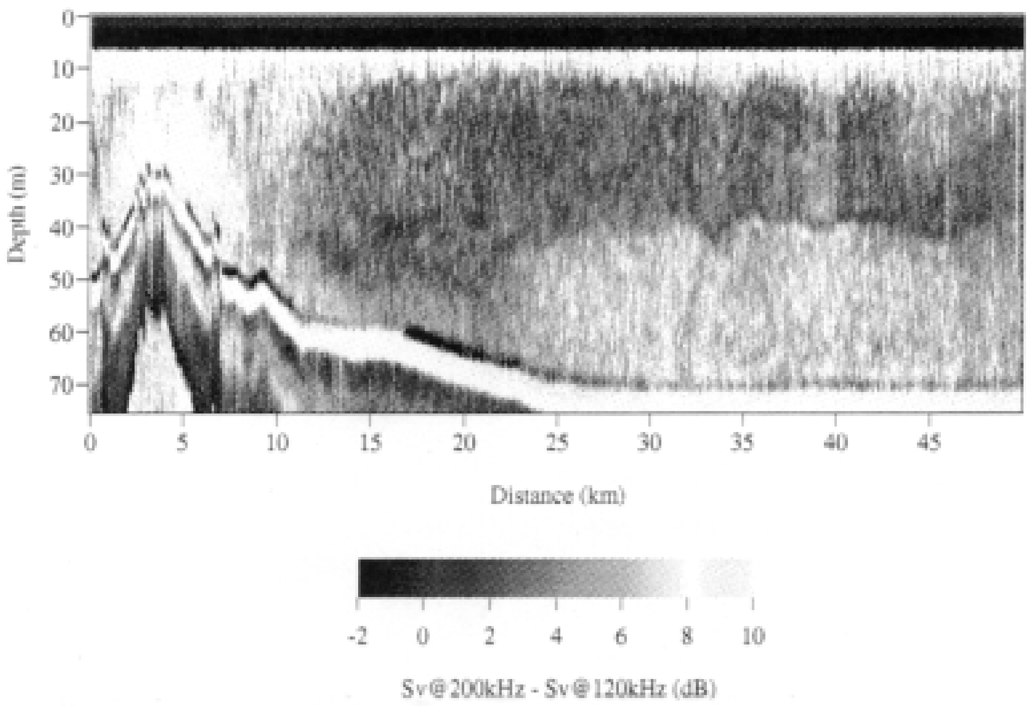


Figure 3A.9: Acoustic backscatter difference between 120 kHz and 200 kHz during the (top) day and (bottom) night along Transect A in 1994. Note the layering of what is apparently zooplankton at the thermocline around 40 m.

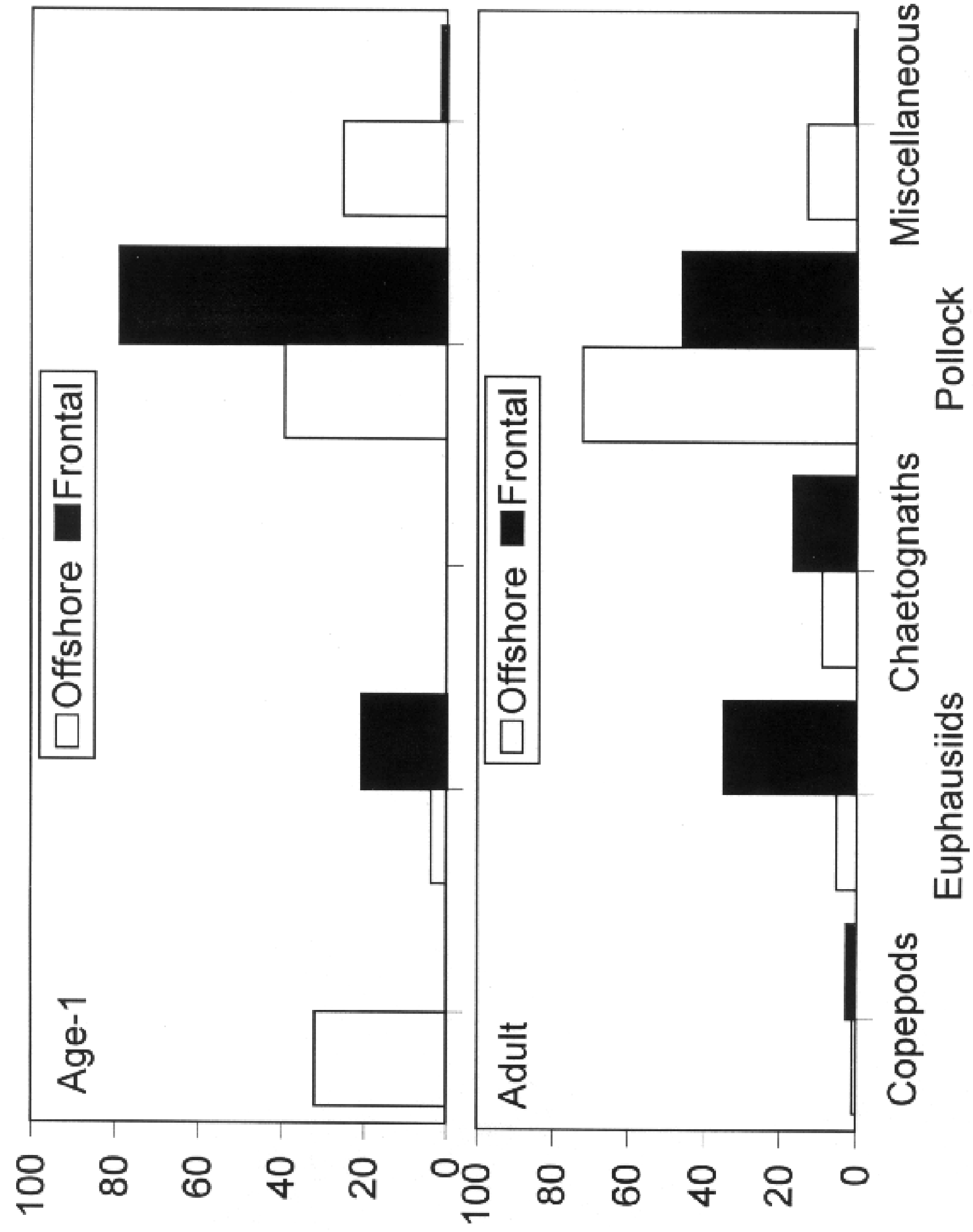


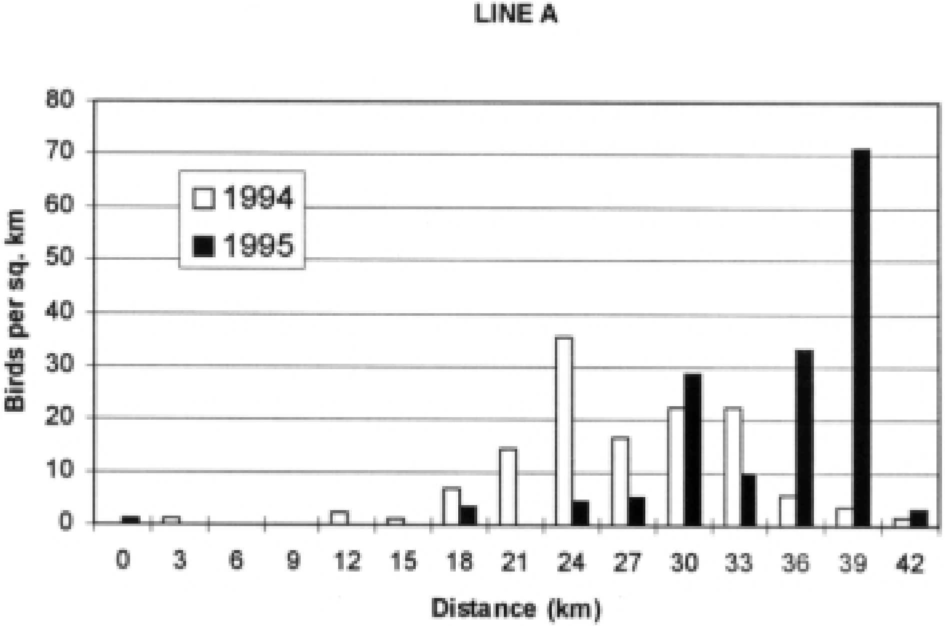
Figure 3A.10: Diet composition of age-1 and adult pollock at the front and offshore by major prey.

was examined at the tidal front located north of St. Paul Island, Alaska. Age-0 walleye pollock were the primary prey of arrowtooth flounder throughout the day, but were least digested in the late day, indicating a diurnal feeding pattern. A similar diurnal pattern was not seen in the vertical distribution of age-0 walleye pollock, suggesting that the feeding pattern exhibited by arrowtooth flounder was based upon their migratory behavior. Lengths of age-0 walleye pollock consumed by arrowtooth flounder were similar to those sampled from mid-water trawls. Walleye pollock cannibalism was examined along a transect that included samples collected at the front and offshore of the front. Age-0 walleye pollock were the primary prey (by weight) of walleye pollock at all locations (Fig. 3A.10). Adjacent cohort cannibalism was prevalent (age-0 walleye pollock were 79% of the diet by weight) at the frontal region. Age-0 walleye pollock cannibalism removal estimates were highest at the front for age-1 walleye pollock and offshore for the adults. The much higher removal rate of age-0 by age-1 walleye pollock at the front compared to the offshore region is due to an order of magnitude larger predator biomass at the front and nearly double the percent by weight of age-0 walleye pollock in the diet. Adults cannibalizing age-0 walleye pollock at a much higher rate offshore than at the front is also a result of higher adult walleye pollock biomass offshore than at the front. Prey selectivity analysis indicated that age-0 walleye pollock were more highly selected offshore than at the front.

Seabird Distributions Relative to Frontal Regions

Data on the distribution and abundance of seabirds were collected in 1994 aboard the R/V *Surveyor* (950 nautical miles surveyed), in 1995 aboard the *Surveyor* (250 nm) and R/V *Miller Freeman* (230 nm), and in 1996 aboard *Miller Freeman* (135 nm). Continuous counts of birds were made from the flying bridge while the ship was underway and all birds within an arc from 300 m ahead of ship to 90° off the port side were recorded using a standard strip transect method.

Murres (*Uria lomvia* and *U. aalge*) and puffins (*Fratercula cirrhata* and *F. corniculata*), whose diets consist of primarily juvenile pollock, breed in large numbers on the Pribilof Islands. High concentrations of murres foraged on the seaward edge of the front north of St. Paul Island. Murres were observed in these stratified waters in 1994 and 1995. In particular, the abundance of feeding murres was greatest in 1995 over stratified water 30 to 42 km north of St. Paul Island where acoustic sign was dense and close to the surface. South of St. Paul Island, relatively large numbers of feeding murres were found in the transition zone between stratified and mixed water. In addition to the area north of St. Paul Island, consistent aggregations of foraging piscivores were also observed along the first 12–15 km south of St. George Island. Murres and puffins were relatively abundant in the inshore, vertically mixed waters south of St. George in the fall of 1995, as was the case for murres in 1996 (Fig. 3A.11). North of St. George, murres and puffins were relatively abundant nearshore over a shallow (∼25 m) pycnocline in



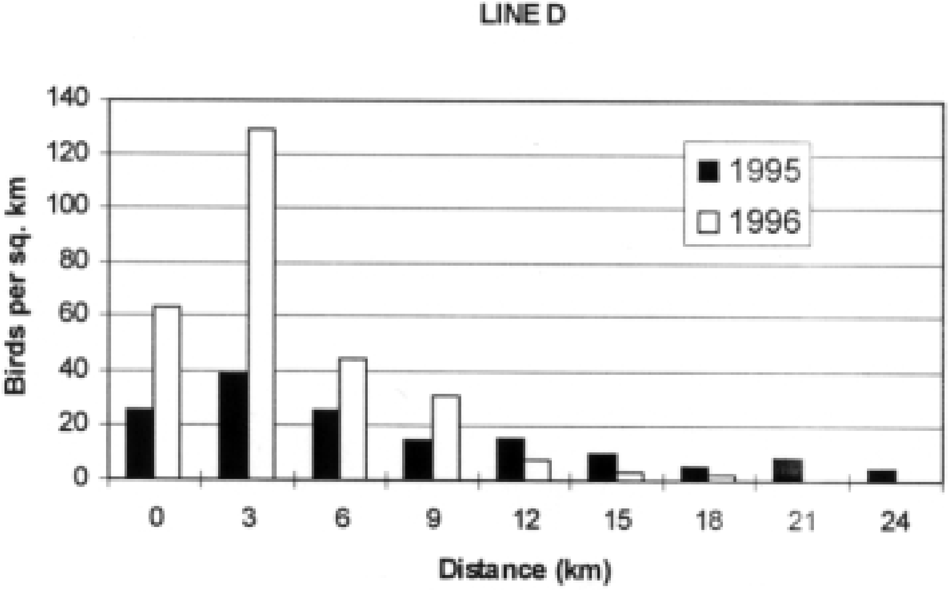


Figure 3A.11: The density of foraging murres observed on Line A (top) north of St. Paul Island. No more than 2.2 murres km^{-2} were observed on Line A in 1996; therefore, these observations were omitted. The density of foraging murres observed on Line D (bottom), south of St. George Island. Comparable area not sampled in 1994.

1996. Perhaps vertical mixing enhances production here and thus foraging birds are attracted to this location. Farther offshore during this same cruise, the depth of the pycnocline increased to 50 m and the pycnocline was no longer apparent at the northern end of the line. Despite the presence of dense acoustic sign near the Pribilof Canyon, we observed very few murres and puffins feeding in this location.

Fur Seal Distributions Relative to Frontal Regions

Marine mammal observations were conducted in 1994–96 from the flying bridge during daylight hours when the vessel was underway. Transects and ship movements were designed for oceanographic and trawling effort, so marine mammal observations were opportunistic and not conducted for abundance estimates. In 1995 and 1996, shipboard survey efforts were coordinated with concurrent studies on female fur seal movements using satellite telemetry. The vessel detoured for special prey trawling effort in areas of high fur seal density, as indicated by shipboard observations and satellite records.

The overall number of marine mammal sightings was quite low (n = 273). However, a preliminary analysis indicates that the highest density of fur seals sighted from the ship corroborate satellite records of female movement patterns during feeding bouts, and generalized areas of high pollock density. The greatest number of on-effort hours and the greatest number of sightings per unit effort were in 1995. In October of 1995, satellite tracked female fur seals from St. Paul Island concentrated their foraging efforts to the north and northwest of St. Paul Island. Fur seal females tracked from St. George Island foraged south of St. George Island exclusively. These patterns are very similar to the distribution of fur seals observed from the ship in September 1995, with the exception that relatively high densities of seals were also observed along the transect southeast of St. Paul Island (running between St. Paul and St. George). Correlation between observed and recorded movements of fur seals in 1996 are currently being analyzed as well as the larger question of the relationship between fur seal movements and the concentration of their prey along frontal boundaries.

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Part 3B

Modeling the upper ocean production dynamics of plankton and larval pollock in the Bering Sea (Stephen M. Bollens[1] and Bruce W. Frost[2])

Introduction

We constructed and applied a coupled multi-species biological-physical model to investigate the production dynamics of the pelagic ecosystem in the Bering Sea, especially in regards to the early life history stages of pollock. In addition, our work focused on assimilating into our model newly generated physical (e.g., PEGGY) and, to a lesser degree, biological (e.g., zooplankton) field observations. We then used this model and data to address several key questions regarding how and why different processes—namely, protozoan dynamics, short-term mixed layer depth variability, and species-specific copepod dynamics—affect growth of larval pollock on the shelf of the southeastern Bering Sea. This work will continue to aid the BS FOCI and the SEBSCC programs in identifying specific hypotheses to be tested in the field and laboratory, as well as generally lead to a better understanding of how and why variable physical and biological processes regulate dynamics of biological production in upper ocean ecosystems. This latter point has obvious implications for management of the pollock fishery in the Bering Sea, as discussed below.

Background

The eastern Bering Sea can be divided into four distinct oceanographic domains (Coachman, 1986). For the purposes of the current discussion, we focus on the deep (>3500 m) open basin and the mid-continental shelf. These two domains differ dramatically in both physical (e.g., Coachman, 1986) and biological (e.g., Smith and Vidal, 1986) oceanographic dynamics. In a general sense, different planktonic production dynamics in each domain would be expected to result in different levels of production of larval fish, with copepods and other zooplankton acting as "filters" of primary production (Runge, 1988). However, while such a linkage between larval fish production and lower-level planktonic production in the Bering Sea has obvious intuitive appeal, the exact nature of this linkage, and the role played by site-specific physical processes in regulating it, have yet to be determined. This was the fundamental problem we wished to address with the proposed research.

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Results

Model Construction and Elaboration

We have adapted the nutrient-phytoplankton-zooplankton model of Frost (1987) to include stage-structured dynamics of copepod populations and growth of larval pollock as a function of abundance of appropriately sized prey. Input data were taken from the Bering Sea (e.g., the PROBES study and other historical data) whenever possible, but were at other times taken from Ocean Station Papa in the North Pacific, as described below. Model output consists of daily concentrations of nutrient, phytoplankton, and all developmental stages of copepods, as well as growth rate of larval pollock. Protozoan microplankton and dynamically modeled mixed-layer depths were also added to the model as described below.

The dynamics of phytoplankton (P) in the mixed layer is modeled using the equation of Frost (1987) modified to include two types of grazers, a population of protistan herbivorous microzooplankton (M) and a stage-structured population of suspension feeding copepods (C_j):

$$\begin{aligned}\frac{dP}{dt} &= \frac{1}{z_m}\left\{\int_0^{z_m} P(PMAX)\tanh\left[\frac{\alpha PAR_z}{\psi PMAX}\right] - r_p(PMAX)P\right\}\frac{N}{d+N}\\ &\quad -\frac{e_M(P-P_0)M}{f_M+P-P_0} - \sum\frac{e_c(P+M-P_0)}{f_c+P+M-P_0}C_jW_j^{0.75} + v\left(P_{z_m+1}-P\right)\end{aligned}$$

where

$$PMAX = \left(e^{D\ln 2} - 1.0\right)DL/24,$$

with

$$D = \text{doublings } d^{-1} = 0.851\left(10^{0.02750}\right) \text{ and } DL = \text{day length},$$

and

$$PAR_z = 0.5I_z = I_0e^{-kz},$$

where I_0 is daily incident solar radiation, z is depth, and k is the attenuation coefficient for irradiance. It is assumed that irradiance is absorbed by both the water and phytoplankton; thus $k = aPy^{-1} + b\{a = 0.02\ \mathrm{m}^2\ (\mathrm{mg\ Chl}a)^{-1}$ and $b = 0.1\ \mathrm{m}^{-1}\}$. All other variables and parameters are defined in Table 3B.1. Phytoplankton production is integrated over the mixed layer (z_m), and then homogenized to calculate the change in phytoplankton stock due to production, grazing, and mixing. A constant phytoplankton carbon-to-chlorophyll a ratio (y) was assumed. Grazing mortality of the phytoplankton is due to both microzooplankton and copepods.

The dynamics of herbivorous protistan microzooplankton is described as:

$$\frac{dM}{dt} = M\frac{(a_M - r_M)\,e_M\,(P-P_0)}{f_M+P-P_0} - \frac{g_M\,(M-M_0)}{h_M+M-M_0}M + v\left(M_{z_m+1}-M\right)$$

It is assumed that the source(s) of predation mortality is not exclusively due to copepod ingestion, and thus mortality is parameterized with a Michaelis-Menten function. Also, microzooplankton behave as passively mixed particles (the third term).

Table 3B.1: Multi-species model variables and standard values.

Parameter description [units]				
Physical Environment				
maximum mixed-layer depth (MLD) [m]	75			
time of initial MLD shoaling [julian day]	90			
minimum MLD [m]	30			
time of initial minimum MLD [julian day]	135			
minimum temperature [°C]	0			
maximum temperature [°C]	8			
mixing rate (ν) [d^{-1}]	.01			
Phytoplankton	**Diatoms**	**Dinoflagellates**		
initial nitrate concentration N(t=0) [mM m^{-3}]	10.8	10.8		
intial chlorophyll concentration P(t=0)ψ^{-1} [mg chl$a$ m^{-3}]	.15	.15		
carbon:chlorophyll (ψ) [mgC (mg chl$a$)$^{-1}$]	30	30		
half-saturation of N uptake (d) [mM m^{-3}]	1.0	1.0		
photosynthetic efficiency (α) [mgC (mg chl$a$)$^{-1}$ ly^{-1}]	1.0	1.0		
maximum doublings per day (@10°C) [D]	1.6	1.6		
respiration as % phytosynthesis [r_P]	.10	.10		
Protozoa				
initial biomass M(t=0) [mgC m^{-3}]	2.45			
maximum ingestion rate (e_M) [d^{-1}]	.728			
half-saturation ingestion (f_M) [mgC m^{-3}]	20			
feeding threshhold (p_0) [mgC m^{-3}]	10			
respiration as % of grazing (r_M)	.40			
assimilation efficiency (a_M)	0.8			
maximum mortality rate (g_M) [d^{-1}]	.80			
half-saturation of mortality (h_M) [mgC m^{-3}]	50			
Copepods	**Calanus**	**Neocalanus**	**Pseudocalanus**	**Metridia**
initial biomass C(t=0) [mgC m^{-3}]	.0238	.26	.0238	.26
time of initial biomass [julian day]	90	30	30	30
period of introduction to the surface [days]	1	60	1	1
maximum ingestion rate (e_C) [d^{-1}]	1.25	.55	.75	1.5
half-saturation of ingestion (f_C) [mgC m^{-3}]	50	50	25	50
feeding threshhold (P_0) [mgC m^{-3}]	10	10	5	10
respiration as % of grazing (r_C)	.40	.40	.40	.40
assimilation efficiency (a_C)	0.8	0.8	0.8	0.8
maximum mortality rate (g_C) [d^{-1}]	.10	.10	.10	.10
half-saturation of mortality (h_C) [mgC m^{-3}]	1000	1000	1000	1000
minimum egg development time [days]	4	4	4	4
female:male to recruits	0.8	0.8	0.8	0.8
power dependence of weight on growth	0.75	0.75	0.75	0.75
egg weight [μgC]	0.25	1.0	.08	0.1
adult weight [μgC]	100	416	8	55
Larval Pollock				
maximum ingestion rate (e_F) [d^{-1}]	1.35			
half-saturation of ingestion (f_F) [mgC m^{-3}]	19			
intial larval weight [μgC]	140			
maximum size of food as % of larval weight	4			
power dependence of weight on growth	0.75			

The dynamics of copepod populations are simulated as the production of daily cohorts of eggs, and the subsequent changes in numbers and masses of individuals in those daily cohorts (e.g., Steele and Frost, 1977). The production of cohorts of eggs on day j was determined by the growth rate of adult female copepods:

$$C_j(t=0) = \left\{ \sum C_{ad} \frac{(a_C - r_c)\, e_c\, (P + M - P_0)}{f_c + P + M - P_0} W_{ad}^{0.75} \right\} / W(t=0)$$

where the summation is over 1 day for the broadcast spawner. The initial individual mass on day j $[W(t=0)]$ is the mass of the egg. It is assumed that copepods feed indiscriminately on phytoplankton and protistan microzooplankton. The subsequent change in individual mass (W_j) and numbers (C_j) in cohort j are described as:

$$\begin{aligned} \frac{dW_j}{dt} &= \frac{(a_C - r_c)\, e_c\, (P + M - P_0)}{f_c + P + M - P_0} W_j^{0.75} \\ \frac{dC_j}{dt} &= \frac{g_c C_j}{h_c + C_j} C_j \end{aligned}$$

Predation closure of the model is parameterized as a Michaelis-Menten function without a threshold abundance since it is assumed that larval fish do not significantly impact their prey populations. It was assumed that the copepods maintain their abundances in the mixed layer through vertical migration. That is, as the mixed-layer shoals, the concentration of copepods in the mixed-layer increases, and similarly decreases with mixed-layer deepening, thus conserving the actual number of animals in the mixed-layer.

Dissolved nitrogenous nutrient is described as:

$$\frac{dN}{dt} = \frac{-\xi}{z_m} \left\{ \int_0^{z_m} P(PMAX) \tanh\left[\frac{\alpha PAR_z}{cPMAX}\right] - r_p(PMAX)P \right\} \frac{N}{d+N}$$

$$+ \xi \frac{r_M e_M (P - P_0) M}{f_M + P - P_0} + \xi \sum \frac{r_z e_c (P + M - P_0)}{f_c + P + M - P_0} C_j W_j + v\,(N_{z_m+1} - N)$$

Where the first term represents the photosynthetic utilization of nitrate. A constant nitrogen-to-carbon ratio (x) is used to convert phytoplankton carbon uptake rate to an equivalent rate of nitrogen utilization. The second and third terms describe the nitrogen reintroduced into the system due to microzooplankton and copepod respiration. Finally, sub-mixed-layer nitrate (N_{z_m+1}) mixed (diffused) into the mixed layer.

Growth rate of larval pollock was modeled as a function of availability of copepod prey biomass ($C_j W_j$), including eggs, in the appropriate size range (j,k) and protozoan biomass (M):

$$\frac{dF}{dt} = \frac{0.3 e_F \left[\sum_j^k C_j W_j + M \right]}{f_F + \left[\sum_j^k C_j W_j + M \right]}$$

Each model is initialized with a standing stock concentration of phytoplankton (P) and protozoa (M). An initial biomass of adult female *Calanus* appear in the surface water in early spring over a period of 1 day. *Neocalanus,* on the other hand, is initialized as C1 copepodites appearing in the surface waters over a period of 2 months starting in mid-winter. Note the food web structure was simplified by initializing protozoa abundance to zero.

The physical characteristics of the basin and midshelf environment were simulated using idealized mean seasonal mixed-layer depths (Z_m), temperatures (T), and solar insolation (I_o). Wintertime conditions in the Bering Sea result in deep mixed-layer depths (150 m) in the basin (Dodimead, 1963); whereas Z_m of the shelf is limited by the depth of the bottom (75 m). Due to solar heating and decreasing winds, mixed-layer depths in both regions shoal in (the late) spring.

To evaluate the effect of daily mixed-layer depth variability on the food web dynamics, daily mixed-layer depth was simulated using the Price *et al.* (1986) mixed-layer model (PWP). The model has been successfully used to model daily mixed-layer variability in a variety of regions (e.g., Davis and Steele, 1994). Given the limited pertinent observations in the Bering Sea, the physical model was forced using representative meteorological data (i.e., 1977) from Ocean Station Papa in the north Pacific (50°N, 145°W). The initial subsurface density structure was prescribed to simulate mixed-layer depth and temperature in the Bering Sea (Dodimead *et al.*, 1963; Favorite *et al.*, 1976). The resulting daily mixed-layer depths were then used to force the biological model described above. Since this version of the biological model is limited to two layers, and thus the subsurface structure is poorly resolved, we have constrained the model not to dilute the passive constituents (e.g., phytoplankton and protozoa) with rapid deepening of the mixed layer (otherwise extreme and unrealistic dilution occurs).

We recently extended this model to include stage-structured dynamics of four copepod populations *(Calanus, Pseudocalanus, Metridia,* and *Neocalanus),* two functional groups of phytoplankton (diatoms and dinoflagellates), and larval pollock feeding and growth. Model variables and standard values for the multi-species model are given in Table 3B.1. This extended model was for the most part driven by extremely simplified physical oceanographic dynamics, with the water column consisting of two layers (mixed layer and deep layer), and exchange between layers occurring as a result of mixed layer shoaling/deepening (detrainment/entrainment) and turbulent vertical mixing. Model output consists of simulated daily abundances of nitrogenous nutrients, diatoms, dinoflagellates, protistan microzooplankton, copepod developmental stages of each of four species, sizes (weight) of larval pollock, and instantaneous growth rates of larval pollock.

Model Results-Generic Seasonal Cycles

Early model results highlight several important phenomena. (Note that these results have appeared elsewhere, i.e., numerous presentations at scientific meetings and previous annual reports, as well as manuscripts soon to be published (e.g., Francis *et al.*, in press; Bollens *et al.*, in preparation). What follows is only a very brief summary of these results). First is the species composition and dynamics of meso/macrozooplankton: larval pollock dependent on *Calanus* (e.g., on the shelf) should experience much better growth conditions later in the spring, whereas those dependent on *Neocalanus* (e.g., in the deep basin) are likely to grow more slowly, generally, although somewhat better earlier in the year when young *Neocalanus* are first recruited to the surface layer. Second is the role of protozoans: larval pollock in this model are highly dependent on these organisms for sustaining high growth rates, especially during times of year when young copepods are not abundant (i.e., early spring on the shelf and late spring/summer in the basin). A third process, short-term mixed-layer depth variability, has significant impacts on lower trophic levels (phytoplankton and protozoans) but less effect on copepods and larval pollock growth rate. We are in the process of examining this last point in much greater detail by fully coupling our biological model to the Price-Weller-Pinkel mixed-layer physical model (Price *et al.*, 1986).

These modeling results point to several data gaps and processes/phenomena that need to be addressed through further modeling, field, and laboratory studies. The first is the functional response of larval pollock (ingestion vs. prey concentration), the parameterization of which could only be crudely approximated in this study, but to which the model is very sensitive. Second is the distribution and abundance of protozoans (of which we know virtually nothing in the Bering Sea) and the degree to which these organisms provide nutrition for larval pollock. Third is the field collection of time series data on basic biological, physical, and meteorological variables, especially early in the year (winter/early-spring).

Multi-Species Model and Assimilation of 1992–1994 Physical Oceanographic Data

Results of the multi-species model—including the dynamics of *Calanus, Pseudocalanus, Metridia,* and *Neocalanus,* as well as two functional groups of phytoplankton (diatoms and dinoflagellates), and larval pollock feeding and growth rates—need to be evaluated in light of recent field data on zooplankton abundance and composition. (Note: these field data, from the 1992–1994 field seasons, were only made available to us in September 1997). Nevertheless, preliminary model results (Fig. 3B.1) indicate that there are significant differences in the dynamics of the main mesozooplankton taxa, and that *Metridia* may in particular be a key link between primary producers and larval pollock growth rate. More work is needed in this area, however.

We have also run the multi-species model using the physical oceanographic data collected by the PEGGY mooring during 1992–1994 (Figs. 3B.2–4). Clear differences are evident between years. For instance, larval pollock growth rate is very low in late June of 1993 (0.03–0.06 per day) compared with rates predicted for either 1992 or 1994 (0.12–0.15 per day). This low rate of growth seems to be due to the rapid deepening of the mixed layer in 1993, and would be expected to have the effect of diluting concentrations of

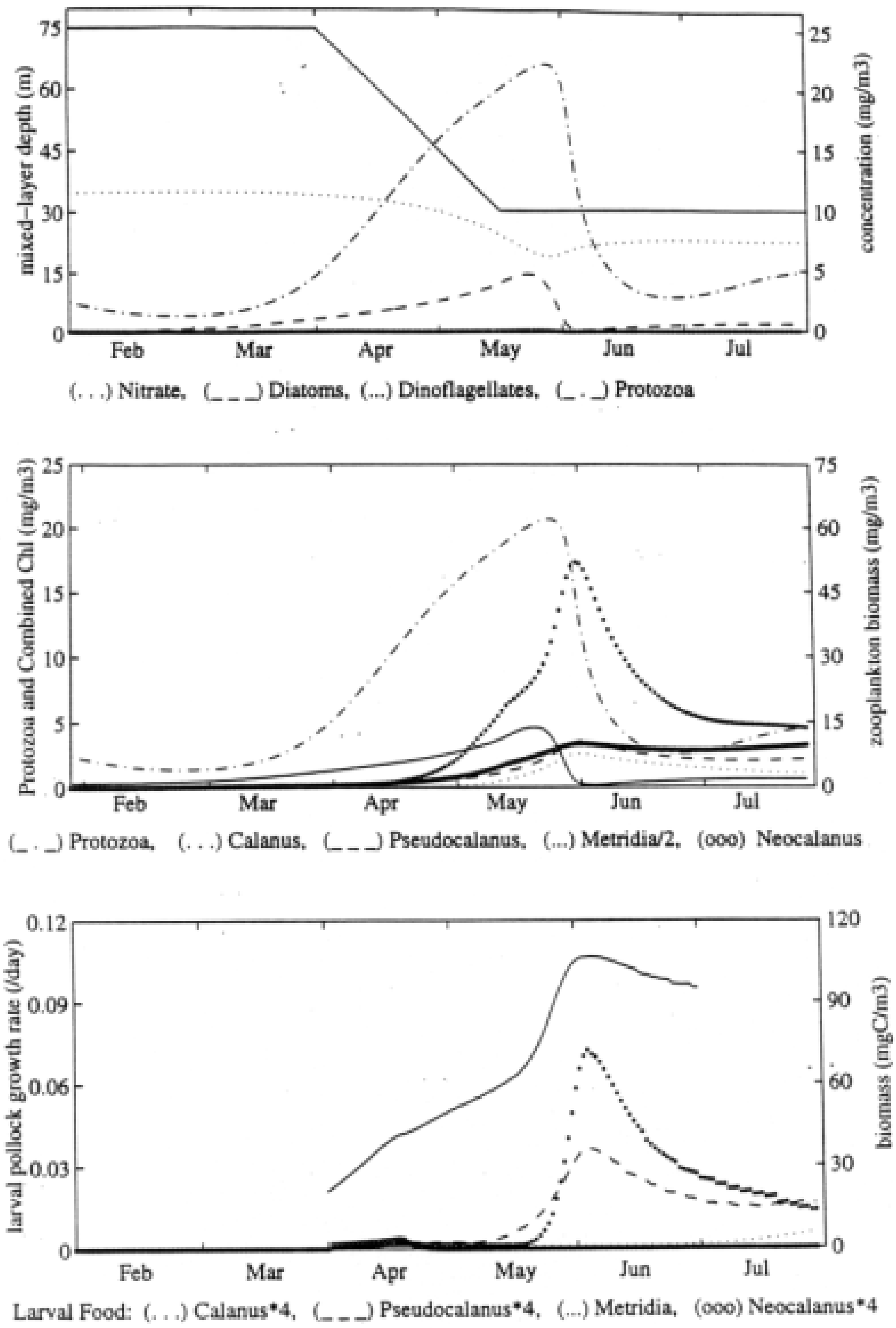

Figure 3B.1: Multi-species plankton—larval fish model on the shelf.

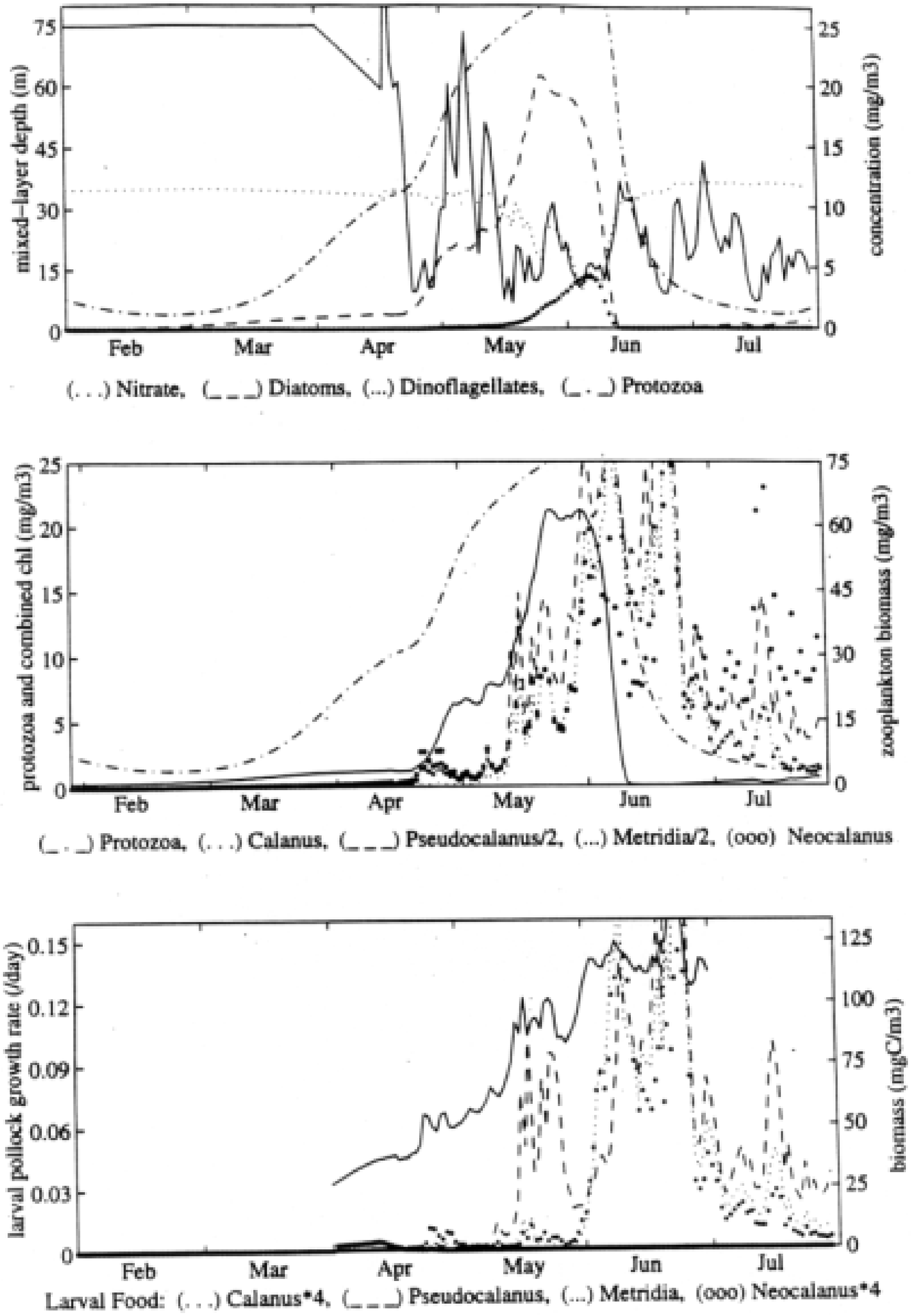

Figure 3B.2: Multi-species plankton—larval fish model on the shelf, 1992.

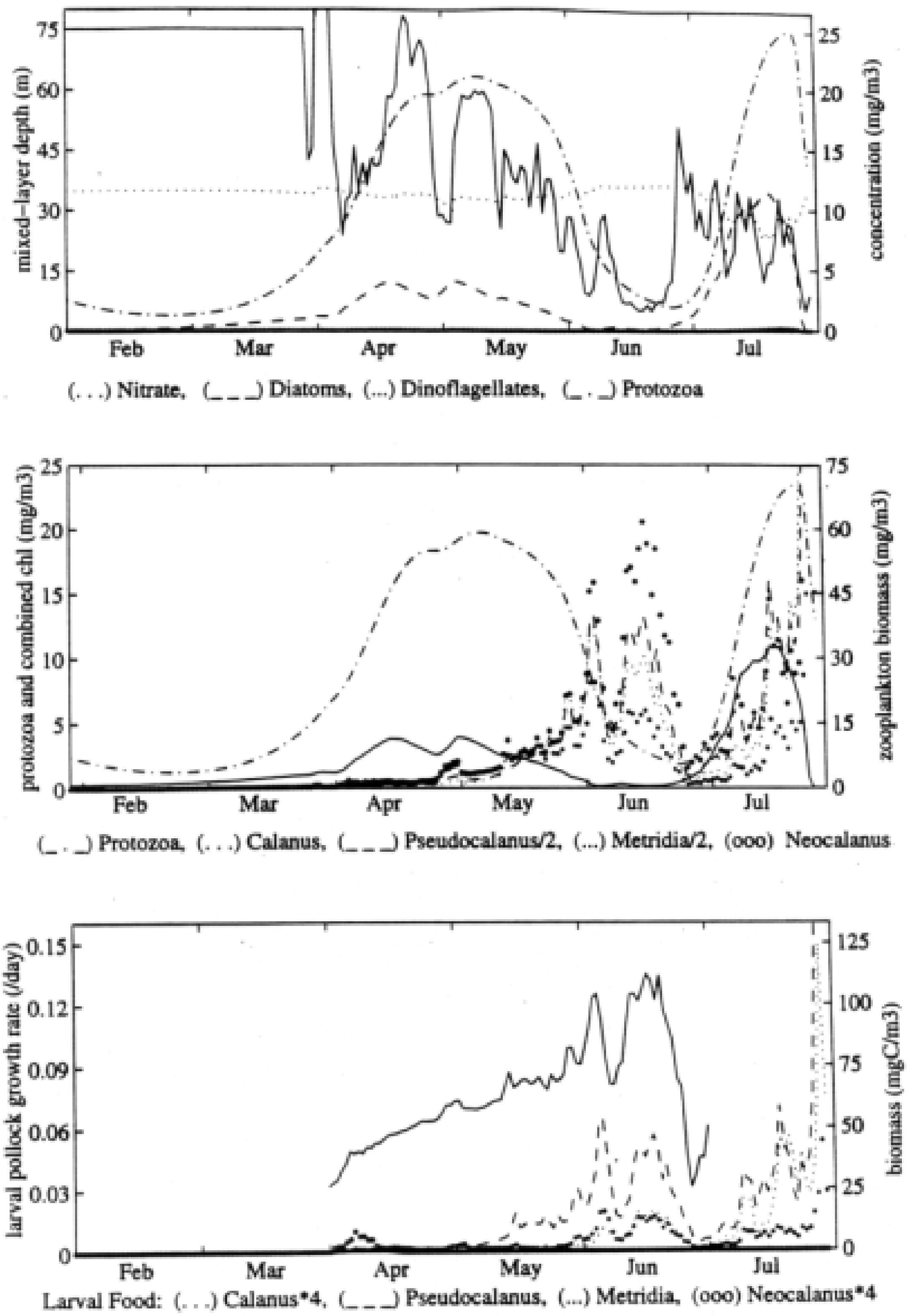

Figure 3B.3: Multi-species plankton—larval fish model on the shelf, 1993.

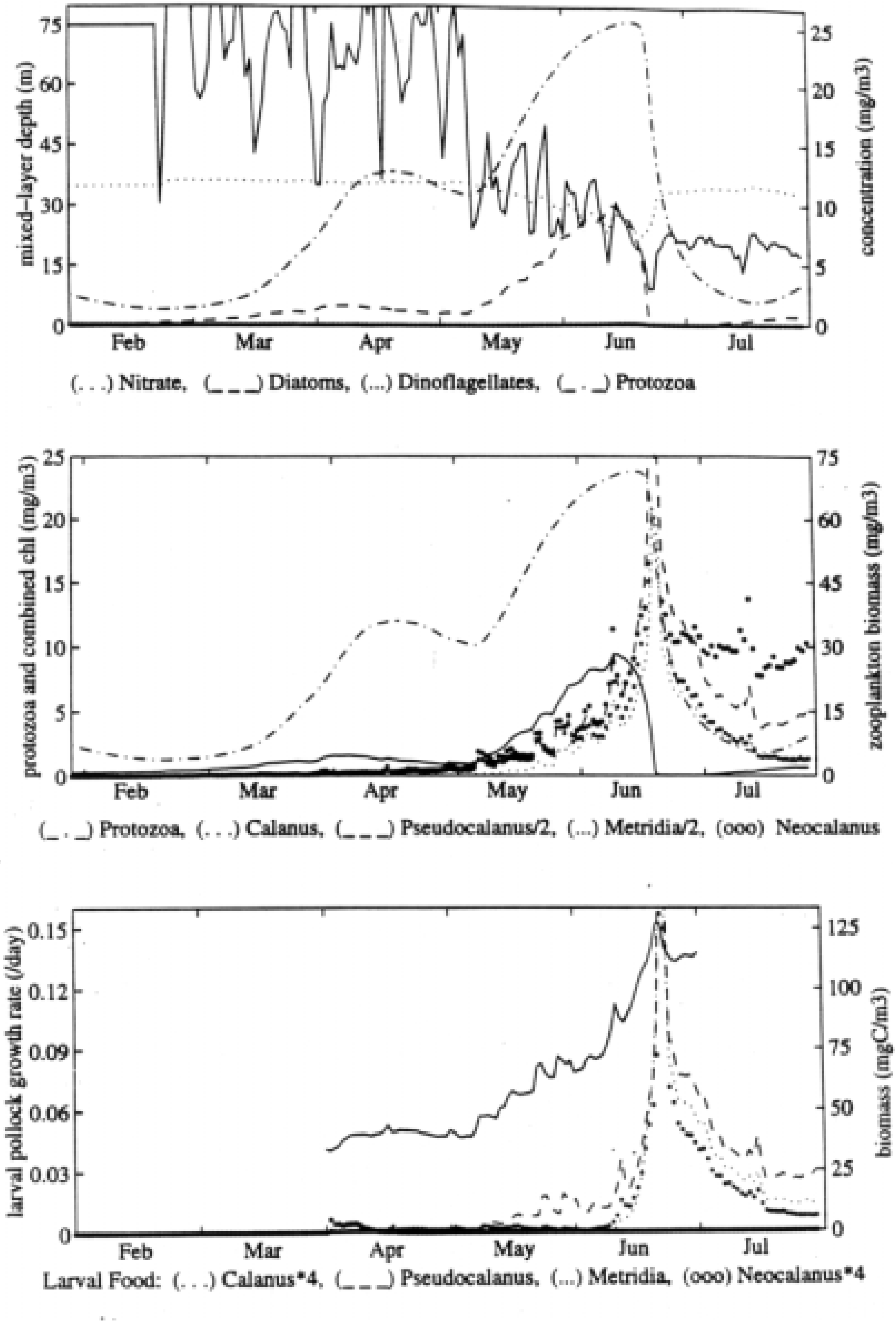

Figure 3B.4: Multi-species plankton—larval fish model on the shelf, 1994.

larval pollock prey (nauplii and protozoans). Here too more work is needed to fully assimilate the field data and otherwise validate the model.

Future Activities and Anticipated Milestones

We plan to continue our modeling work with emphasis on data assimilation from the 1992, 1993, and 1994 field studies (particularly zooplankton data and physical and meteorological data from the PEGGY moorings). We anticipate producing one or more manuscripts detailing the results of our multi-species model and data assimilation for publication in *Marine Ecology Progress Series, Fisheries Oceanography, Journal of Marine Science,* or related peer-reviewed journal; submission of such manuscript(s) would be expected in late 1997 or early 1998.

Management Implications

As noted above, this work will continue to aid current (e.g., SEBSCC) and future scientific programs in identifying specific hypotheses to be tested in the field and laboratory. Moreover, our modeling work has led to a better understanding of how and why variable physical and biological processes regulate dynamics of biological production in upper ocean ecosystems generally, and the Bering Sea in particular.

This has obvious implications for management of the pollock fishery in the Bering Sea. For instance, if appropriate physical oceanographic data could be collected in "real time," via moorings (e.g., PEGGY) or satellites, a model such as described above could be implemented and predictions generated of larval pollock growth rate. When coupled with other models concerned with larval mortality and/or juvenile growth and mortality, such a model could generate predictions of pollock recruitment strength. While such a series of coupled models may not yet be in hand, it is a very reasonable short-term to medium-term (2–5 yrs.) goal, and would provide managers another tool with which to manage the Bering Sea pollock fishery.

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Part 3C

Seasonal sea ice in the Eastern Bering Sea (James D. Schumacher[1] and Tina Wyllie-Echeverria[2])

A striking feature of the physical environment of the eastern Bering Sea is the occurrence of seasonal sea ice. The extent fluctuates over 1000 km between waters north of the Bering Strait in the summer south to the Alaska Peninsula and southeastern shelf break in winter. The actual mechanism of ice formation for the eastern shelf has been described by a "conveyor belt" analogy (Pease, 1980; Overland and Pease, 1982). Ice is produced along leeward (south-facing) coasts primarily located in the northern region of the shelf, and driven by wind to its thermodynamic limit where it melts. As water freezes brine rejection occurs and the salinity of the ice varies between 5–12 psu. Regions of open water, or polynyas, are created by downwind advection of ice. The sea ice limit advances southward as ice-melt cools and freshens the upper ocean. During winter, a climatological average of 3 to 5 storms per month move eastward along the Aleutian Chain forming the primary storm track, while less than two storms per month cross the northern Bering Sea. The amount of sea ice production and advection depends upon which atmospheric conditions dominate in a given winter. The greatest ice production occurs in years when the Aleutian Low is well developed and storms migrate along the primary storm track.

For the Bering Sea, variations in overall ice cover (Fig. 3C.1), time of advection over the open shelf, and subsequent melt-back are important features of the physical environment. Formation of sea ice generally begins in November with maximum ice extent occurring in late March. Ice-free conditions typically exist from June through October. Observations of ice cover over the eastern Bering Sea shelf show a nearly 40% variation about the mean (Niebauer, 1988). Other characteristics of ice cover that show great variability include duration of ice at its southern extent (3–15 weeks), time of retreat from the southernmost extent (between mid-March and June), and number of weeks that ice remained over the middle shelf domain (3–28 weeks with a mean of 20 weeks) (Wyllie-Echeverria, 1995b). The differences in these characteristics vary greatly between years with maximum and minimum ice extent (Fig. 3C.2).

Ice formation, brine rejection, advection and eventual melting play a critical role in fluxes of heat and salt (Aagaard *et al.,* 1985; Hendricks *et al.*, 1985; Coachman, 1986) and in generation of baroclinic flow (Schumacher *et al.*, 1983; Muench and Schumacher, 1985). The production of dense (cold saline) water has a marked impact on the halocline of the Arctic Ocean with water from the Anadyr and Anadyr Strait polynyas providing a substantial fraction of the total (Cavalieri and Martin, 1994). From 9–25 m of ice formation occurs over the winter season depending on location and meteorological

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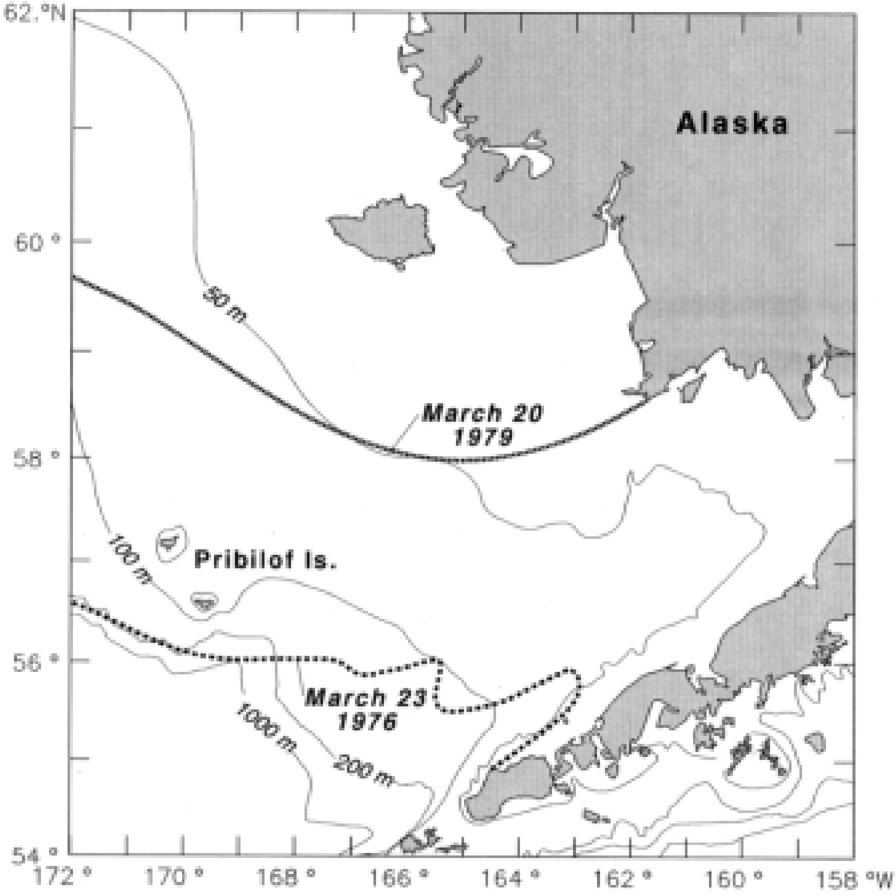

Figure 3C.1: Approximate location of the maximum sea ice extent in a year with extreme ice cover (1976) and in a year with minimal ice cover (1979).

conditions (Cavalieri and Martin, 1994). A growth rate of ∼6 cm d^{-1} was estimated from changes in salinity (Schumacher *et al.*, 1983; Roach *et al.*, 1995). The average thickness of ice at any given instant over most of the open southeastern shelf, however, is only ∼0.5 m (Coachman, 1986). The positive buoyancy flux from melting ice initiates both baroclinic transport along the marginal ice zone ($\sim 0.3 \times 10^6$ m^3 s^{-1}) and stratification of the water column.

Sea ice also exerts an important influence on the biota. Associated with ice-melt is a bloom of phytoplankton that accounts for 10–65% of the total annual primary production over the eastern shelf (Niebauer *et al.,* 1990, 1995). More recent observations (Stabeno *et al.,* 1998) demonstrate that chlorophyll concentrations begin to increase concomitant with the presence of sea ice even though the water column is not stratified. Sea ice plays a central role in the timing of primary secondary production cycles which can influence food availability for first feeding pollock larvae. Ice production

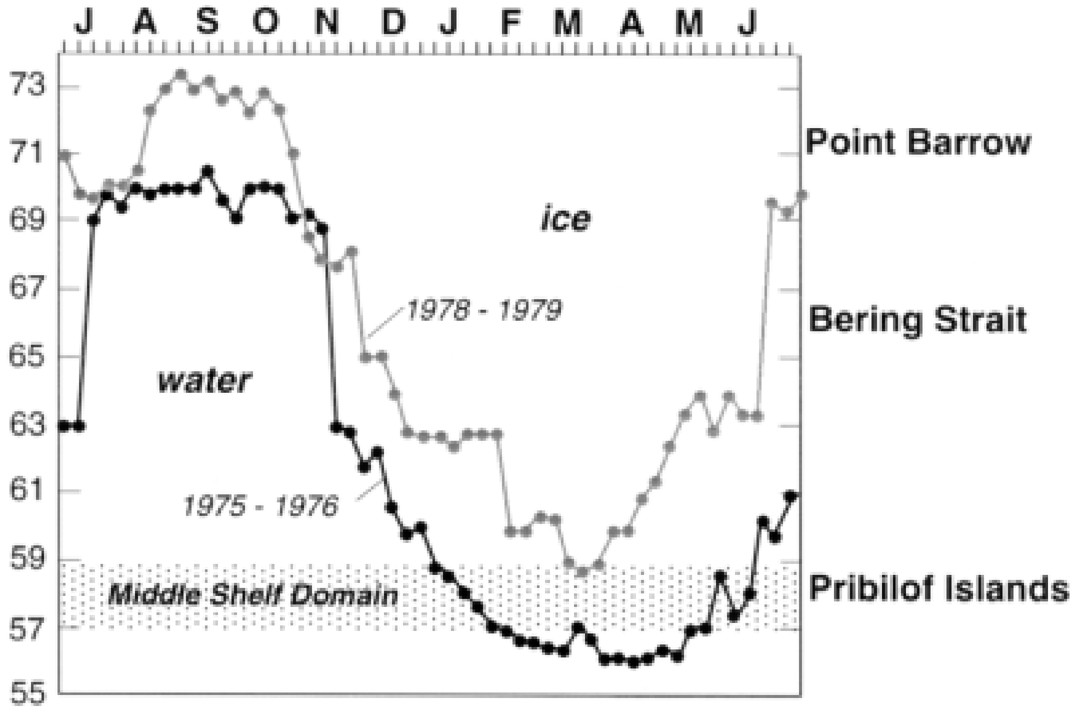

Figure 3C.2: Characteristics of sea ice extent measured along 169°W each week for atmospheric conditions during a cold year (1975–1976: shown as dark line and dots) and a warm year (1978–1979: shown as light line and dots). Note the differences in time of advance, southern limit, duration over the Middle shelf and time of retreat (after Wyllie-Echeverria, 1995b).

and formation of cold bottom water (the cold pool) also influences the distributions of higher trophic level biota over the eastern shelf (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995a, b). This latter effect may influence the overlap of young of the year pollock and older fish, thereby providing a physical determinant for the extent of cannibalism in a given year.

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Part 4

Administration and management of the Bering Sea FOCI Program (S. Allen Macklin)

4.1 Beginning of the Project

Bering Sea Fisheries-Oceanography Coordinated Investigations (BS FOCI) developed from the need to better understand environmental characteristics and processes affecting the rapidly developing walleye pollock fishing industry in the Bering Sea. NOAA previously had funded a study in the Gulf of Alaska, Shelikof Strait FOCI (Kendall *et al.,* 1996), that had established an understanding of processes affecting survival of young pollock. Although the Shelikof Strait pollock fishery was of commercial importance, it was dwarfed by the catch of pollock in the Bering Sea.

A chronology of BS FOCI is provided in Table 4.1. In May of 1990 BS FOCI published an implementation plan (BS FOCI, 1990) for a Fisheries-Oceanography Coordinated Investigation of Pollock in the Bering Sea. This plan was in response to the establishment of a coastal fisheries ecosystems (CFE) project by NOAA's Coastal Ocean Program (COP; Boyles and Scavia, 1993; Wenzel and Scavia, 1993). The goal of CFE was to reduce uncertainty in resource management decisions through ecological research.

The premise of BS FOCI was that the Bering Sea was among the most productive of northern high-latitude seas. The primary commercial resource was walleye pollock, prevalent on the continental shelves of the Bering Sea and in the basin. With the passage of the Magnuson Fisheries Conservation and Management Act of 1976, the coastal fishery came under management control of the United States. By the 1980s, a domestic fishery industry developed to replace foreign industry in the U.S. Exclusive Economic Zone (EEZ). However, over-exploitation in the international deep basin was an important issue in the management of the fishery, as basin pollock stocks were thought to be linked to stocks in the EEZ. Despite biological assessment of the southeast Bering Sea shelf through a number of research programs provided by the National Science Foundation and NOAA with the Bureau of Land Management, the information base for the region, especially the deep basin and its ties to the shelf, was almost nonexistent.

BS FOCI's implementation plan called for examination of the hypothesis that transport of larval pollock from the deep Aleutian basin to the continental shelf contributes to the viability of U.S. fisheries. Four objectives were established, based on research recommendations from an International Scientific Symposium on Bering Sea Fisheries held in Sitka, Alaska during July 1988 (Aron and Balsiger, 1989):

1. Determine the differences between pollock spawning aggregations through techniques of molecular biology.

2. Determine circulation of the Bering Sea, including the deep basin and the extensive eastern continental shelf.

Table 4.1: A chronology of significant Bering Sea FOCI events.

Year	Month	Event
1990	June	Implementation Plan with hypothesis that transport of larval pollock from the deep Aleutian Basin to the southeastern shelf contributes to the viability of U.S. fisheries
1991	March	Project Study Plan 1991–1996
	August	Cruise: large scale CTD and ADCP survey of the Bering Sea basin
	November	Principal investigators organizational meeting, Seattle, Washington
1992	April	Cruise: first deployment of *Peggy Bering Sea*, larval survey
	September	Cruise: recover *Peggy Bering Sea*
1993	March	Cruise: deploy *Peggy Bering Sea*
	April	Cruise: larval survey
	August	Principal investigators meeting in Portland, Oregon
	September	Cruise: recover *Peggy Bering Sea*, CTD survey
	October	Sponsored Juvenile Pollock Symposium, Seattle, Washington
	November	Reviewed by National Research Council, Washington, D.C.
1994	January	Reviewed by National Research Council with Technical Advisors present, Seattle, Washington
	February	Cruise: deploy *Peggy Bering Sea*
	April	Cruise: larval survey
	September	Cruises: CTD survey, acoustics; Pribilof juvenile pollock studies, mooring recoveries
	November	Principal investigators meeting, Seattle, Washington
1995	March	Cruise: deploy moorings
	April	Cruise: larval studies
	May	Cruise: larval studies
	August–September	Cruises: moorings, Pribilof juvenile pollock studies
1996	February	Cruise: deploy moorings
1996	April	Cruise: moorings, CTD and larval survey
	May	Joint cruise and aircraft flights: moorings, groundtruth, primary productivity survey
	September	Cruises: Pribilof juvenile pollock studies; mooring recoveries
	October	Juvenile studies principal investigators synthesis meeting, Seattle, Washington
	December	Biophysical interactions principal investigators synthesis meeting, Seattle, Washington
1997	January	Biophysical interactions principal investigators synthesis meeting, Seattle, Washington
	March	Juvenile studies principal investigators synthesis meeting, San Diego, California
	June	Publication of Bering Sea and North Pacific Ocean Theme Page on the Worldwide Web
	September	Larval ecology principal investigators synthesis meeting, Juneau, AK

3. Determine patterns and processes involved in vertically mixing the water column.

4. Study how different oceanographic domains in the Bering Sea contribute to larval growth and mortality.

After the implementation plan was reviewed by the CFE Advisory Committee in January 1991, BS FOCI was asked to submit a Project Study Plan (BS FOCI, 1991) to describe research from 1991 through 1996. The Project Study Plan, submitted in March 1991, identified two goals for the project. The first goal was to address the issues of pollock stocks in the Bering Sea based on objectives 1 and 2. The second goal dealt with the processes that affected the survival of basin pollock in their earliest life stages and their subsequent recruitment, and was based on objectives 3 and 4. During the last 2 years of BS FOCI, the arena for recruitment studies was shifted to the

Table 4.2: Bering Sea FOCI Executive Committee

William Aron (ex officio) NOAA/Alaska Fisheries Science Center	Allen Macklin (coordinator) NOAA/Pacific Marine Environmental Laboratory
Eddie Bernard (ex officio) NOAA/Pacific Marine Environmental Laboratory	Jeffrey M. Napp NOAA/Alaska Fisheries Science Center
Stephen Bollens San Francisco State University	James E. Overland NOAA/Pacific Marine Environmental Laboratory
Lewis Haldorson University of Alaska Fairbanks	James D. Schumacher NOAA/Pacific Marine Environmental Laboratory
Arthur Kendall Jr. NOAA/Alaska Fisheries Science Center	Gary L. Stauffer NOAA/Alaska Fisheries Science Center

southeastern shelf. A component examining juvenile pollock near the Pribilof Islands during the late summer and fall of their birth year was added in 1994.

4.2 Project Management

The Project Study Plan designated co-project managers from the Alaska Fisheries Science Center (AFSC; G. Stauffer) and the Pacific Marine Environmental Laboratory (PMEL; J. Overland). The co-managers, together with senior scientists from each laboratory and the laboratory directors, formed an Executive Committee (Table 4.2). This committee was responsible for directing BS FOCI consistent with COP's guidelines, coordination of BS FOCI with other NOAA base programs concerned with Bering Sea pollock, and evaluation of proposals from academic institutions. A project coordinator was added to the Executive Committee in August 1993, and two academic members were added in 1994 in response to a suggestion by the National Research Council (1994).

The plan further identified an intramural research team of scientists from the Alaska Fisheries Science Center and the Pacific Marine Environmental Laboratory. These scientists brought expertise on Bering Sea pollock stocks, circulation, and recruitment processes, including the collected wealth of Shelikof Strait FOCI established in 1985. To provide balance and expertise in needed areas, extramural contracts were established in September 1991 for genetic studies, satellite remote sensing of circulation, and studies on vertical distribution of zooplankton. A Principal Investigator group consisted of the two project managers and all the principal participating scientists. This group met at least quarterly, published a quasi-annual Progress and Plans document, coordinated all contracts with academic research institutions, and obtained peer review of scientific results at national meetings and in refereed journal publications.

At the end of the first year, COP conducted a review of the project. As a

Table 4.3: Bering Sea FOCI Technical Advisory Committee

Dr. Michael Dagg Louisiana University Marine Consortium Chauvin, LA 70344	Dr. Thomas Royer Old Dominion University Norfolk, VA 23505
Mr. Bart Eaton Trident Seafoods Corporation Seattle, WA 98107	Dr. Al Tyler University of Alaska Fairbanks Fairbanks, AK 99775-1080
Dr. Eileen Hofmann Old Dominion University Norfolk, VA 23505	Dr. Warren Wooster University of Washington Seattle, WA 98195-5685
Dr. William Leggett Queens University Kingston, Ontario Canada K7L 3N6	

result of this review, BS FOCI implemented a Technical Advisory Committee (Table 4.3) to help guide the project.

4.3 Budget

Funds for BS FOCI were allocated in the first year at just under a million dollars. The project was level funded through 1995, then funds tapered off during the final 2 years. The funding profile for BS FOCI was

FY 1991	$950K
FY 1992	$950K
FY 1993	$950K
FY 1994	$950K
FY 1995	$950K
FY 1996	$750K
FY 1997	$200K

4.4 Competitive Process and Research Cycles

For the first round of research (FY 1991 through FY 1993), AFSC and PMEL FOCI scientists submitted work statements addressing the objectives of Phase I and Phase II research. These were evaluated by the co-managers and a team of intramural scientists was established. To provide academic balance, proposals were solicited from the outside community in a competitive process for $260K. These were evaluated by the co-managers and Executive Committee. From the evaluations, extramural contracts were established in September 1991 for genetic studies, satellite remote sensing of circulation, and studies on vertical distribution of zooplankton to last through FY 1993. In FY 1993, proposals for FY 1994 and FY 1995 research were solicited from the scientific community at large. Proposals were evaluated by the Executive Committee and the Technical Advisory Committee. Finally, the Executive Committee solicited work statements from specific researchers for

FY 1996 to complete objectives of the project. Funds in FY 1997 were used to support publications, analysis of samples and data, synthesis meetings, and development of data access through the World Wide Web. Table 4.4 lists all BS FOCI research components.

BS FOCI developed collaborations with Russian, Korean, and Japanese scientists. These associations provided scientific leverage through the sharing of data and research vessels.

4.5 Meetings and Workshops

BS FOCI intramural researchers met monthly at a FOCI Principal Investigators meeting. An electronic bulletin board was established to share notice and agenda of these meetings, and to publish their minutes, so that extramural researches could be represented and informed.

The Executive Committee met several times a year to establish procedure, evaluate proposals, and provide guidance.

During October 1993, BS FOCI hosted a 3-day international workshop in conjunction with the second annual meeting of the North Pacific Marine Science Organization. The subject of the workshop was the importance of prerecruit walleye pollock to the Bering Sea and North Pacific ecosystems (Brodeur *et al.,* 1996).

The full suite of principal investigators met on several occasions to discuss research plans and progress and to implement field plans.

Small working groups of principal investigators associated with juvenile pollock ecology and biophysical processes held synthesis meetings in the fall and winter of 1996–1997.

4.6 Field Experiments

BS FOCI conducted more than 20 cruises and one aircraft expedition during its 7-year lifetime. Because the project was focused on the early life history of pollock and determining circulation and stock structure of pollock, the field season developed a recurring routine. In general, the earliest cruises of the year were conducted during February and March. Their purpose was to deploy moorings for the late winter, spring, summer, and early fall observation period, to ascertain ground truth for the moorings, and to sample water conditions prior to spawning of pollock in the spring. During spring, cruises worked to sample larval pollock distributions as well as their prey and predators, to monitor the progress of the nutrient-phytoplankton-zooplankton cycle, and to document biophysical processes important to survival of larval pollock. Fall cruises observed the ecosystem associated with juvenile pollock in the Pribilof Islands habitat and recovered moorings.

The project utilized a number of research vessels. The primary carrier was the NOAA Ship *Miller Freeman.* Other vessels supporting BS FOCI were the NOAA Ship *Surveyor* and the Japanese Fishery Research Vessel *Oshoro Maru.*

Table 4.4: Bering Sea FOCI research components and principal investigators.

Component	**Principal Investigator**
Larval feeding mechanisms of walleye pollock	Kevin M. Bailey NOAA/Alaska Fisheries Science Center
U.S./Japan cooperative studies	Kevin M. Bailey NOAA/Alaska Fisheries Science Center
Population ecology of walleye pollock	Kevin M. Bailey NOAA/Alaska Fisheries Science Center
	Dennis A. Powers Stanford University
Modeling the upper ocean production dynamics of plankton and larval pollock in the Bering Sea	Stephen Bollens San Francisco State University
Spatial and temporal characteristics of wind forcing of the Bering Sea	Nicholas A. Bond JISAO/University of Washington
Impact of invertebrate predators on walleye pollock larvae	Richard D. Brodeur NOAA/Alaska Fisheries Science Center
Juvenile pollock studies	Richard D. Brodeur NOAA/Alaska Fisheries Science Center
Larval pollock nutritional condition assay	Michael Canino NOAA/Alaska Fisheries Science Center
Basin vertical processes: mixed-layer dynamics from the Peggy Bering Sea mooring	Edward D. Cokelet NOAA/Pacific Marine Environmental Laboratory
Determining chlorophyll concentration from ocean color measurement in the Bering Sea	John Cullen and Richard Davis Dalhousie University
Bimodal distribution of juvenile pollock in the southeastern Bering Sea	Miriam Doyle JISAO/University of Washington
Growth, transport, and mortality studies of larval walleye pollock	Robert C. Francis University of Washington
Feeding ecology of larval walleye pollock in oceanic and neritic domains of the Bering Sea: effects of variation in prey	Lewis J. Haldorson University of Alaska Fairbanks
An aggregated ecosystems model for the southeastern Bering Sea	Albert J. Hermann JISAO/University of Washington
Ichthyoplankton collections in the eastern Bering Sea	Arthur W. Kendall, Jr. NOAA/Alaska Fisheries Science Center
A retrospective analysis of GEOSAT altimeter data in the Bering Sea	Robert Leben University of Colorado
Role of protozoa in the diet of larval pollock in the Bering Sea	Evelyn J. Lessard University of Washington

Table 4.4: (continued).

Component	Principal Investigator
Monitoring of mesoscale ocean processes by synthetic aperture radar (SAR)	Antony K. Liu NASA/Goddard
Food chain dynamics: spring bloom hypothesis and larval survival	Jeffrey M. Napp NOAA/Alaska Fisheries Science Center
Otolith technique for tracing geographic life history of pollock	Brenda L. Norcross University of Alaska Fairbanks
Modeling Bering Sea circulation	James E. Overland NOAA/Pacific Marine Environmental Laboratory
Microcrustacean production potential during the onset of feeding by walleye pollock larvae in the Aleutian Basin and Bering Sea shelf	A.J. Paul University of Alaska Fairbanks
The use of molecular techniques to dissect the genetic architecture of pollock populations: analysis of mitochondrial and nuclear genes by the polymerase chain reaction	Dennis A. Powers Stanford University
Circulation of the eastern Bering Sea: Aleutian North Slope Flow	Ronald K. Reed and Phyllis J. Stabeno NOAA/Pacific Marine Environmental Laboratory
Larval transport and mesoscale circulation	James D. Schumacher NOAA/Pacific Marine Environmental Laboratory
Shelf-slope exchange along the eastern Bering Sea shelf break	James D. Schumacher and Phyllis J. Stabeno NOAA/Pacific Marine Environmental Laboratory
Data integration system and theme page for the Bering Sea	Nancy Soreide NOAA/Pacific Marine Environmental Laboratory
Nutritional condition of larval walleye pollock	Gail H. Theilacker NOAA/Alaska Fisheries Science Center
Relationships between pollock distribution and extent of seasonal sea ice on the Bering Sea shelf	Tina Wyllie-Echeverria JISAO/University of Washington
Phytoplankton dynamics from moored optical instruments in the southeastern Bering Sea	J. Ronald V. Zaneveld Oregon State University

4.7 Data Dissemination

In order to facilitate data exchange between investigators and to make BS FOCI data available to the scientific community, the project underwrote creation of the Bering Sea and North Pacific Ocean Theme Page, a World Wide Web resource at `http://www.pmel.noaa.gov/bering`. The theme page provides pathways to much of the physical and biological data collected by BS FOCI, as well as other information grouped by scientific discipline. The Bering Sea Ecosystem Biophysical Metadatabase, an annotated index of data holdings, is available through the theme page.

4.8 Project Reviews

BS FOCI was reviewed formally on two occasions. The first was an internal review by COP in the spring of FY 1992. As a result of this review, the project convened its Technical Advisory Committee.

A more extensive review was conducted by the National Research Council (1994) during FY 1994. There were two phases of this review of accomplishments and plans of the NOAA Coastal Ocean Program. The first phase was a briefing of the panel by senior project scientists in Washington D.C. The second was held in Seattle with BS FOCI's technical advisors present. At this meeting, project principal investigators gave a series of presentations to the panel. Administrative changes suggested by the panel and adopted by BS FOCI were the expansion of the Executive Committee to include academic investigators, formalization of the competitive process, and formation of small working groups based on the scientific structure of the project.

The importance of the Bering Sea's commercial resources and the success of BS FOCI in addressing questions pertaining to walleye pollock in the Bering Sea have helped generate increased interest in the Bering Sea ecosystem. New programs such as COP's Southeast Bering Sea Carrying Capacity and NOAA's Arctic Research Initiative, as well as ongoing research by FOCI, build on these concepts developed by BS FOCI, and continue to advance our understanding of the complex, productive ecosystem of the Bering Sea.

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Part 5

Selected monitoring, modeling, and technical achievements (compiled by S. Allen Macklin)

The development and application of new technology allows the field of fisheries oceanography to move forward. During BS FOCI's $6\frac{1}{2}$-year lifetime, its scientists and technicians made numerous and significant technological contributions to the field. Some of these achievements were specific to the Bering Sea region, some were specific to walleye pollock, and some were more wide-ranging in their applications. In the following sections, selected achievements are discussed under the headings of monitoring, modeling, and technology.

5.1 Monitoring

BS FOCI used moorings, satellite-tracked drifters, and shipboard measurements to monitor physical and biological oceanographic conditions in the several distinct domains of the Bering Sea basin and the eastern Bering Sea.

a. refined understanding of circulation in the Bering Sea basin through observations with vessel-mounted acoustic Doppler current profiler (Cokelet *et al.,* 1996) and satellite-tracked drifters (Stabeno and Reed, 1994):

   A month-long circumnavigation of the Bering Sea basin in August 1991 was one of BS FOCI's first field operations. During the cruise, scientists made the first use of an acoustic Doppler current profiler in the Alaskan Stream and Bering Sea. Observations of three-dimensional current velocity led to an increased knowledge of circulation and transport in the Bering Sea basin and improved the ability to compute geostrophic circulation from hydrographic casts.

   From 1986 through 1996 (and continuing since then under sponsorship from other research funding), BS FOCI deployed more than 120 satellite-tracked drifters in the North Pacific Ocean and Bering Sea. Most drift buoys were drogued at 40 m. A composite current pattern was derived from data telemetered by these drifters. This pattern helped identify large- and mesoscale features of circulation and led to discovery of a new current, the Aleutian North Slope Current (Reed and Stabeno, 1998).

b. unique time series of water column temperature, salinity, estimated chlorophyll-a, and phytoplankton fluorescence during ice advance and retreat (Stabeno *et al.,* 1998):

   During 1995 three surface moorings were deployed over the southeast Bering Sea shelf. Each mooring had instruments that measured temperature, salinity and fluorescence. After the moorings were deployed in February, the most severe ice conditions in the last 20 years developed. Two of the moored platforms were struck by the sea ice but continued to function. They provided unique time series of water-column temperature, salinity, chlorophyll-*a* and fluorescence under an advancing and retreating ice field. One platform was located in the weakly advective middle shelf regime. Here, contrary to earlier findings, chlorophyll-*a* concentrations increased prior to the formation of a well-defined two-layer system. Events of strong advection, rather than vertical fluxes, dominated changes in water column structure and properties. These advective events provide a mechanism for nutrients (required to support the rich blooms that occur over the middle shelf during spring) to be transported onto the middle shelf. A second mooring was located in the more advective outer shelf. The ice also reached this site, and chlorophyll-*a* concentrations increased with the advent of ice. The final mooring was deployed to the east of Unimak Pass. Sea ice was not advected this far south, and the spring bloom did not occur until May.

c. upper ocean phytoplankton survey (Davis *et al.,* 1997a):

For its last field experiment, in spring 1996, BS FOCI conducted a survey of sea surface chlorophyll over the southeastern Bering Sea using a research aircraft and ship. The project documented the spatial and temporal evolution of chlorophyll concentration during the spring bloom in the Bering Sea and how this concentration related to the ocean's physical characteristics. Chlorophyll concentration was estimated from the aircraft using remote color-sensing instrumentation designed to detect upwelling radiance from the ocean. The ocean's physical characteristics were assessed using air-expendable bathythermographs deployed from the plane; instrumented, moored buoys; and by CTD casts and ADCP transects aboard ship. Preliminary results showed higher chlorophyll concentrations in the northern portion of the domain where sea ice was melting, and a prominent 100 × 200 km patch southeast of the Pribilof Islands with concentrations an order of magnitude greater than background levels. This patch was in a region of the shelf where pollock spawning occurs.

5.2 Modeling

BS FOCI used models to conceptualize program strategies, to expand the time-space domain of field observations, to guide program direction through hypothesis generation, and to understand features of biophysical processes.

a. numerical model of circulation of the Bering Sea basin and exchange with the North Pacific Ocean (Overland *et al.,* 1994):

At the beginning of the Bering Sea FOCI project, use was made of a high-resolution, 1/8°-grid, numerical model to investigate the circulation of the Bering Sea basin and the adjacent North Pacific Ocean.

The modeling was based on the Navy Layered Ocean Model, one of the highest-resolution ocean circulation models at the time, and run on the University of Alaska Fairbanks' supercomputer. There was a generally cyclonic, but spatially complex and non-stationary, circulation within the Bering basin, fed by flow through the Aleutian passes. The numerical study demonstrated that internal flow instabilities, and not just external forcing such as wind and inflow current, contribute to substantial interannual variability in the circulation of the Bering Sea and adjacent northwestern Pacific Ocean.

b. coupled, one-dimensional, biophysical model investigating production dynamics of the pelagic ecosystem with respect to growth of larval pollock (Francis *et al.,* 1998; Bollens *et al.,* in preparation):

   A coupled, one-dimensional, biophysical model investigated production dynamics of the pelagic ecosystem with respect to growth of larval pollock. The approach used field observations to determine rates and appropriate species composition for several of the distinct physical and biological domains in the eastern Bering Sea. The model included stage-structured dynamics of copepod populations (*Calanus* and *Neocalanus*) and larval pollock feeding and growth. The temporal behavior of the mixed layer was obtained from observations from *Peggy Bering Sea*, a moored biophysical platform. Model results showed that the species composition of zooplankton has a strong influence on growth of larval pollock, and the presence of protozoan prey becomes important when young copepods are scarce, i.e., during early spring over the slope. Results from the model also suggested that variability of the mixed-layer depth has significant impact on larval growth by affecting lower trophic level production. These results led to the addition of a field research component that developed a new method for live-staining protists and showed that microprotozoan biomass levels are sufficient to augment prey levels and support estimated metabolic needs of first-feeding larval pollock.

5.3 Technology

At the beginning of the project, there was scant knowledge of processes that affect recruitment of walleye pollock in the Bering Sea. Some findings from FOCI's Shelikof Strait project were applicable, but steps had to be taken to develop new methods to address specifics of the Bering Sea environment and ecosystem. BS FOCI made nearly 20 significant technological developments that furthered understanding of general and regional physical and biological oceanography.

a. a modified PROTEUS mooring that withstands the arctic marine climate of the Bering Sea and measures winds, insolation, air temperature, humidity, salinity, and temperature at ten depths, currents from acoustic Doppler current profiler and acoustic current meters, acoustic backscatter, and chlorophyll absorption (Cokelet and Stabeno, 1997):

Because there were no continuous time series of biophysical conditions from pre-spring bloom conditions through the summer, BS FOCI developed and deployed a surface mooring, *Peggy Bering Sea*, in the southeast basin at 2195 m depth in the spring and summer of 1992–1994 and the winter of 1994. It recorded the first long-term oceanographic time series in the basin. The winter observations are particularly valuable due to the lack of wintertime measurements in this region. The platform was a PROTEUS (PROfile TElemetry of Upper ocean currentS) similar to moorings deployed in the tropical Pacific Ocean, but modified to withstand the arctic marine climate of the Bering Sea. Included in its suite of measurements were winds, insolation, air temperature, humidity, salinity, and temperature at ten depths, currents from acoustic Doppler current profiler and acoustic current meters, acoustic backscatter, and chlorophyll absorption. Some of the observations were telemetered real time via satellite and System ARGOS. Useful information for understanding the Bering Sea ecosystem was deduced from *Peggy Bering Sea* measurements. At that part of the basin there is a weak background flow of a few cm s^{-1} and little density variation with internal tides superimposed. Anticyclonic (clockwise) eddies pass by sporadically, inducing currents up to ~80 cm s^{-1} and depressing isopycnals by as much as ~200 m. The thermal structure in the upper 400 m shows a deep temperature maximum from warm Alaskan Stream inflows and a minimum above due to winter cooling. A sea surface cooling event was observed in the late winter of 1994, with cold water penetrating to ~120 m depth. Spring warming begins in late April to early May of each year, marked by the arrival of the 3.75°C isotherm. The local wind plays little role in forcing ocean currents at the site except at the inertial frequency. Because some data were telemetered in real time, *Peggy Bering Sea* permitted direction of field sampling to provide in situ measurements by ship. The mooring design later was modified for shallow-water use, and two moorings were deployed during early March 1995—one over the outer and one over the middle southeastern Bering Sea shelf. They were inundated by sea ice, providing unique time series of water column temperature, salinity, estimated chlorophyll-*a*, and phytoplankton fluorescence during ice advance and retreat.

b. remote methods for determining mesoscale ocean circulation and features using high resolution synthetic aperture radar (Liu *et al.,* 1994) and radar altimetry (Stabeno *et al.,* in preparation) from satellites, and shipboard acoustics (Brodeur *et al.,* 1996):

Results from the slope waters of the eastern Bering Sea indicated that the highest abundances of pollock larvae often reside in eddies. To examine the nature of biophysical processes present in these features and determine their influence upon survival required in situ observations. Finding a reliable method to locate an eddy for field studies was a challenge. Although infrared imagery has proved useful, cloud cover and generally weak sea surface temperature gradients limit this approach for the Bering Sea. High-resolution synthetic aperture radar (SAR) eliminates both of these constraints. Mesoscale features are imaged by SAR through several possible mechanisms that are not well understood, including current-induced wave refraction. SAR images were examined for mesoscale features in Alaskan coastal waters, and BS FOCI maintained an image library. A new method for time-varying signal analysis, called the Wavelet Transform was developed (Liu *et al.,* 1997) and gives spectral decompositions via the scale concept. A two-dimensional wavelet transform is a highly efficient band-pass-filter that can be used to separate various scale processes and show their relative phase and location as a matched filter detector. A two-dimensional Gaussian wavelet transform of a SAR image can be used with threshold as an edge detector for small-scale features. The evolution of mesoscale features such as oil slicks, fronts, eddies, and internal waves can be tracked by wavelet analysis using satellite data from repeating paths. Real-time, remote tracking of eddies enabled BS FOCI to guide sampling by a Japanese research vessel working cooperatively with project scientists during summer 1993.

A new technology, near real-time altimetry, was employed in the Bering Sea to help locate an anticyclonic eddy for field surveys. Near real-time data from TOPEX/POSEIDON (T/P) and ERS-2 were processed at the University of Colorado's Center for Astrodynamics Research (CCAR) to map sea surface height anomalies in the southeast Bering Sea basin, and these maps were posted daily on the CCAR website (`http://www-ccar.colorado.edu/∼leben/bering/`). This method came to fruition for Bering Sea research in the year following BS FOCI's final field operations. In May 1997, the development of an 8-cm high at 55°N, 169°W was monitored by a BS FOCI scientist using maps posted on the CCAR website. Using the near real-time information supplied by the satellite altimetry, she was able to direct the NOAA ship *Miller Freeman* to the location of the eddy. Subsequent surveys and satellite tracked drifters confirmed eddy circulation.

Acoustic backscatter signals from hull-mounted echo sounders also were used to identify and characterize mesoscale biophysical features in the ocean. Higher frequency transponders are able to scatter their acoustic energy from zooplankton and other smaller marine life that are contained by eddy circulation.

c. method for measuring the growth and retreat of seasonal sea ice along a longitudinal meridian (Wyllie-Echeverria, 1996):

Data for the position of the ice edge along 169°W longitude were extracted from products of the Navy/NOAA Joint Ice Center's data base presenting weekly concentration and position of sea ice cover. This longitude was chosen because it lies over open water for the entire extent of the Bering and Chukchi shelves and intersects the shelf break at the shelf's southernmost reaches. Data were verified using weekly ice charts for the western Arctic provided by the Naval Polar Oceanography Center. Comparison with areal ice coverage between 160°W and 180°W (Chapman and Walsh, 1993) revealed that the southernmost latitude reached by ice along 169°W is significantly correlated with ice-covered shelf area ($r = 0.91$). This method developed by BS FOCI for measuring the growth and retreat of seasonal sea ice along a longitudinal meridian was also adopted for application by NMFS to evaluate sea ice conditions in the western Bering Sea.

d. development of digitally recording chlorophyll absorption meters and an anti-fouling system to enable their long-term deployment (Davis *et al.,* 1997b):

BS FOCI has played an instrumental role in the ongoing development and deployment of digitally recording chlorophyll absorption meters. These instruments enable accurate, long-term, in situ monitoring of phytoplankton standing stock, and are unique in the world. Absorption data from the meters are used to calculate accurate estimates of chlorophyll concentration by the simple subtraction of a baseline value for background absorption. Time series of phytoplankton biomass coupled with hydrographic properties can then be used to validate biophysical algal growth models and investigate ecological processes on several time scales. BS FOCI was one of the first programs to make use of these meters. *Peggy Bering Sea* served as a test platform for this developing technology. The development of a simple, low-cost, low-toxicity antifoulant system has made it possible to collect long-term, high-quality data on in situ light absorption, even in remote environments such as the Bering Sea. The ability to deploy optical instruments for extended periods of time produces considerable savings in resources since periodic servicing of instruments may be made at longer intervals. First-generation optical instrumentation for the detection of spectral absorption and attenuation of light was included as part of the 1993 *Peggy Bering Sea* mooring. For this deployment, a chemical method was developed to reduce the extent of the biofouling. To prevent biofouling in the sample chamber of the absorption meters, a novel system was implemented that utilized the enclosed flow tube of the instruments. A perforated inner canister was filled with solid bromine tablets and then placed into a vented outer canister. The holes in the inner canister allow the slow dissolution of the bromine tablets into the sea water within the outer canister, with the rate of bromine dissolution being determined by the size of the holes. A dissolution was chosen such that a concentration of ~30 parts per million (ppm) built up in the enclosed flow tube of the optical instrument within 15 min after a sampling period, a concentration about 10 times the minimum toxic level determined from tests on natural waters from

Newport, Oregon. The sample chamber was flushed for 5 s prior to data collection using a Sea-Bird pump model 5T, which provided more than three full volume exchanges in the flow tube. This flushing insured that the bromine did not compromise absorption measurements.

e. relationships between ADCP acoustic backscatter and zooplankton abundance (Cokelet *et al.,* in preparation):

The *Peggy Bering Sea* surface mooring contained, along with other meteorological and oceanographic instruments, a downward-looking 153-KHz acoustic Doppler current profiler (ADCP) to measure vertical profiles of ocean currents. The ADCP computes ocean currents by measuring the Doppler frequency shift of sound of a known transmitted frequency as it reflects off scatterers carried by the moving water. The scatterers themselves are usually zooplankton whose concentration and time-dependent behavior are valuable for biological studies. One BS FOCI research objective was to determine the zooplankton biomass from ADCP measurements. To do so involved a two-step process: determining the volume backscattering strength (Sv in dB) from ADCP-measured quantities and relating Sv to the zooplankton concentration.

The volume backscattering strength at a fixed acoustic frequency is a physical property of the scattering medium and represents its ability to reflect sound. It cannot be measured directly by the ADCP. As a byproduct of the current measurements, the ADCP records automatic gain control counts that can be related to Sv via factory-specified relationships utilizing the thermally induced circuit noise to which the signal is referenced. This circuit noise was determined by tank-testing the ADCPs. Tracking the noise calibrations over time gave an indication of calibration variability and has been used to determine the overall error in the zooplankton biomass via a new error analysis.

To relate the volume backscattering strength to the zooplankton biomass, BS FOCI collected zooplankton from 23 MOCNESS (Multiple Opening Closing Net Environmental Sampling System) hauls with up to nine nets each, giving a total of 111 samples. Computer software was developed to integrate the ADCP backscatter along the same time-depth trajectories as the net tows. Trajectory-averaged acoustic volume backscattering strength was then compared to zooplankton displacement volume which in turn was related to biomass via published relationships. Not all of the MOCNESS tows were near the mooring, but all tows were made from a ship with an ADCP of the same frequency as the mooring. Therefore, to provide the largest possible sample size, Sv-zooplankton comparisons were also made for the shipboard ADCP whose noise level was calibrated at sea.

Results show that the logarithm of the zooplankton dry weight concentration (DW mg m^{-3}) is linearly related to the volume backscattering strength ($r^2 = 0.61$). The error analysis shows that the inferred biomass is correct to within a factor of two. The variance is probably due to the size, orientation, and relative species composition of the scatterers which were dominated by copepods (*Neocalanus* spp., *Eucalanus bungii* and *Metridia pacifica*). Observations give zooplankton dry weight concentrations varying from vanishingly small at 300 m depth to 400 mg m^{-3} at 14 m during the spring bloom. Rapid behavioral changes have been observed in which the zooplankton cease their usual diel vertical migration from below 300 m to the surface and concentrate in the upper 100 m during a phytoplankton bloom. These quantitative, long-term time series of zooplankton biomass and behavior are useful for understanding the Bering Sea ecosystem.

f. a dual-frequency hydroacoustic analytical procedure that pioneered visualization of distributions of upper-trophic-level predators and their prey in marine ecosystems (Napp *et al.,* submitted):

   BS FOCI researchers collaborated with bio-acousticians from the Southwest Fisheries Science Center, La Jolla, California, to apply a dual frequency hydroacoustic analytical procedure to examine distribution patterns of predators (age-0 pollock) and prey (zooplankton) in structural fronts around the Pribilof Islands. The fronts are hypothesized to be important habitat for age-0 pollock in the eastern Bering Sea. The technique exploits the difference in volume backscattering measured at two acoustic frequencies, 200 and 120 kHz. A 50-km transect from a cruise during September 1994 near the Pribilof Islands was analyzed. The differencing technique (Greenlaw, 1977; Mitson *et al.,* 1996) assumes that only two different types and sizes of organisms dominate the acoustic backscatter at these frequencies. Low differences indicate that scattering is dominated by fish; high values are interpreted to be primarily invertebrate zooplankton such as copepods and euphausiids, the main prey of juvenile fish. During daytime conditions, the upper layer to about 20 m is dominated by zooplankton. Juvenile fish are distributed at mid depth and show a preference for the thermocline. This could be a strategy for avoiding predators during daylight. At night, there is a strong upward migration by fish over the inner front and middle shelf, presumably to feed on the zooplankton in the upper layer. After the fish migrate upwards, the bottom layer is dominated by invertebrates. Juvenile pollock in the Gulf of Alaska have been shown to be night feeders. This visualization of the diel pattern in and around the structural front suggests how physics affects the distribution and behavior of fish and their prey through the tidal mixing process. When coupled with net samples and physical measurements, this dual-frequency technique has the potential to reveal important information about the ecosystem.

g. a mitochondrial DNA probe to discern pollock population differences between the eastern and western Bering Sea (Bailey *et al.,* 1998):

The genetics component of BS FOCI surveyed mitochondrial DNA (mtDNA) sequence variation in pollock throughout a major portion of its range. A total of 512 nucleotides were examined in 45 individuals from populations representing the eastern and western portions of the Bering Sea. Fourteen haplotypes were uncovered, of which three were frequent enough to be of use in population differentiation. Testing of an additional 119 samples allowed determination of significant differences among populations within the eastern and western portions of the Bering Sea. A rapid restriction enzyme assay for mtDNA surveying of a large number of pollock from all populations allows near real-time analysis of genetic material from fish collected at sea, and also permits retrospective analysis of samples that have been preserved in alcohol.

h. a microsatellite primer technique for pollock DNA that can discriminate sub-populations (Villa and Powers, in press):

In order to detect distinct pollock stocks within the Bering Sea, primers were developed for the polymerase chain reaction that would amplify microsatellite loci in pollock. Working from primers developed for Atlantic cod (Brooker *et al.,* 1994), pollock-specific primers were developed for two microsatellites. Individual fish from six sites in the eastern and western Bering Sea were screened. The microsatellite loci showed a significant difference between eastern and western fish. Analysis of additional samples collected northwest of the Pribilof Islands indicate that there may also be a distinct stock structure between northern and southern Bering Sea pollock.

i. methods for analyzing chemical deposition in pollock otoliths as a record of the environment experienced by the larvae at various times during their development (Severin *et al.,* 1995):

The incorporation of dissolved oceanic constituents in the otoliths of pollock has potential as a chemical tracer for reconstructing their early life history. Wavelength dispersive spectrometers on an electron microscope were used to measure Na, Mg, P, S, Cl, K, Ca, and Sr concentrations on the outer margins of 57 juvenile walleye pollock otoliths from five locations in the Gulf of Alaska and Bering Sea. Discriminant analyses that used various combinations of Na, P, K, Sr, and fish standard length and/or age showed that 60–80% of the samples could be assigned to the correct capture locality. While the concentrations of some of the measured elements correlated with standard length of age of the fish, there are measurable differences among localities when concentrations are length of age corrected, mainly due to differences in Na and K concentrations. Elemental composition of otoliths potentially could be used to assign fish from a mixed stock fishery to original stocks, information that is greatly needed for the effective management of fish stocks.

j. sophisticated 3D video cinematography to examine how larvae find patches of prey and maintain themselves in these patches (Spring 1996):

   Two synchronized CCD cameras were used with time-lapse video recorders to film larvae under experimental laboratory conditions. A shadowgraph filming technique was used with light provided by infrared diodes. Direct Linear Translation was used to retrieve 3D coordinates from the video images. The techniques developed were successfully applied to examine larval swimming speed, path aspect and tortuosity in relation to the presence of food particles.

k. a new method for live-staining protists (Lessard *et al.,* 1996):

   A method was developed to live-stain protists with the fluorescent nuclear stain, DAPI, for use in tracing ingestion of protists by larval pollock. DAPI was shown to effectively live-stain eight species of protists and showed no toxic effects. The stain is simple to apply, easy to visualize in larval guts using epifluorescence microscopy, and does not appear to adversely affect the swimming behavior or growth rate of protists. With this stain, it was shown that larval walleye pollock are able to ingest a relatively small (60 μm) aloricate ciliate. This new method provides a means for visually following the ingestion of previously undetectable, but potentially important, prey in larval pollock. It provides a simple laboratory tool that can be used to determine larval pollock gut evacuation rates and functional feeding responses to different types and sizes of protists. Such laboratory measurements would help to provide the information needed to predict the importance of heterotrophic protists in the diets of pollock larvae.

l. an antibody to protist-specific protein for an immunoassay to detect ingestion by pollock larvae in the field (Howell-Kubler *et al.,* 1996):

   BS FOCI researchers used SDS-PAGE to survey the protein signatures of a large number of protists to identify a protein that would be protist-specific for use in the development of an immunoassay for ingestion of protists in pollock larvae. A 21-kD protein was found in all heterotrophic protists, but not photosynthetic protists, copepods, or pollock larvae. Antibodies to this protein have been developed and purified, and are now available for immunoassay development. When fully tested, the immunoassay will be used to detect the presence and quantity of protist proteins in the guts of field-caught pollock larvae. As protists generally do not leave visible remains after digestion, the immunoassay method will provide a means for detecting otherwise undetectable food items in the guts of pollock larvae and allow the determination of the prevalence of protist ingestion in wild pollock larvae.

m. a simple procedure for sampling and releasing a suspension of nuclei from larval pollock muscle cells and for storage of the nuclei for subsequent analyses of larval condition (Theilacker *et al.,* 1996):

   Muscle cell nuclei were examined by marking them with fluorescent dyes and submitting them to laser flow cytometry for cell cycle analysis. These methods were applied successfully to assess the nutritional condition of pollock larvae in field studies.

n. techniques for determining larval pollock health by cytological examination of brain cells (Theilacker and Shen, 1993a, b):

   This method includes marking RNA and DNA from a suspension of brain cells with a fluorescent dye and quantifying the amounts of each nucleic acid using laser flow cytometry.

o. techniques for distinguishing between Stage I and Stage II nauplii of the copepods *Metridia* and *Pseudocalanus* (Siefert, 1998):

   Food availability for pollock larvae is one of the key factors controlling larval growth and survival. To determine the role of the copepods *Metridia* and *Pseudocalanus* in the ecosystem and to learn specifically more about their role as prey of larval pollock, it is necessary to understand their life history and identify all their developmental stages. Because the developmental stage of the prey changes with the ontogeny of the fish, recent studies have stressed the importance of identifying copepod nauplii of *Metridia* and *Pseudocalanus* to the lowest possible taxon. Past attempts to distinguish between the younger stages of these dominant taxa have been unsuccessful. Recent work by BS FOCI has enabled identification of the developmental stages of *Metridia* and *Pseudocalanus* in field samples. Stage I nauplii of *Metridia pacifica*, Stage I and II nauplii of *Metridia lucens* and the equivalent stages of *Pseudocalanus minus* were reared from eggs to find morphological characters for separating the genera at these stages. Differences in naupliar body shape and caudal armature permit the differentiation of Stage I and II *Metridia* from *Pseudocalanus* in southeastern Bering Sea plankton. These characters are potentially useful for distinguishing *Metridia* and *Pseudocalanus* nauplii from other regions, contributing to the understanding of their role in various ecosystems.

p. Bering Sea and North Pacific Ocean Theme Page (`http://www.pmel.noaa.gov/bering`):

   Funding from BS FOCI was used to support the creation of a Bering Sea and North Pacific Ocean Theme Page. The theme page provides pointers to information and images generated by NOAA, universities, and other governmental sources and other information grouped by scientific discipline. This page includes links to up-to-date satellite imagery, new research, and educational material related to the Northern

Pacific Ocean and the Bering Sea. Efforts included the design of the pages, location of resources to be included in the pages, prototyping of the theme page family of pages, interaction with PMEL and AFSC researchers to refine the page, and production of a public version of the page that became available in June 1997. The primary page includes sub-pages covering physical and biological sciences in the North Pacific; research, monitoring, and assessment information; a subject index; and a What's New section providing direct access to both new links on the pages and information on technical changes in the pages. With completion of the public version of the page, efforts turned to development of data access routines and pages to bolster data access. Routines for the display of drifter data and for the overlaying of biological data on physical oceanographic properties have been developed. The drifter data page allows selection of a single drifter or a set of drifters, and plotting of either the current location or the history of the drifter. Development of data displays for biological data has included: design of EPIC data formats for biological bottle data; development of routines to take bottle data from original database format and transform it into EPIC format files; routines to locate concurrent bottle and CTD data files; and routines to plot biological data as an overlay on a plot of physical data. Information is also available on user access to the theme page; during winter 1998 there were about 20,000 hits each month on the site. An up-to-date summary of access statistics is available from `http://corona.pmel.noaa.gov/~rees/stats/bering/no_pmel`.

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Part 6

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