

## SOME INTERACTIONS BETWEEN YOUNG WALLEYE POLLOCK AND THEIR ENVIRONMENT IN THE WESTERN GULF OF ALASKA

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### ABSTRACT

Surveys in Shelikof Strait, Alaska, show that large concentrations of walleye pollock (*Theragra chalcogramma*) enter the sea valley each March and spawn early in April. Surveys for eggs and larvae have disclosed dense regions of eggs that become patches of larvae. Processes that transport larvae to nursery grounds or to the open ocean seem important to recruitment. Early results suggested that larvae could be rapidly removed (in 14 days) from the shelf by the vigorous, varying flow of the Alaska Coastal Current (ACC). In the upper 100 m, however, most of the volume transport remains on the shelf. Baroclinic instability between the ACC and coastal waters can create eddies (first observed in infrared satellite images) at the exit of Shelikof Strait. Eddies frequently contain the highest concentrations of larvae. The phasing and location of eddies, the ACC, and hatching determine how a given mechanism will affect retention of larvae on the shelf. Year-class size seems largely determined by the end of the larval period, although events during the following summer may also reduce the year class. Storms during the early larval period may be particularly detrimental to survival, although the mechanism is not yet clear. An index of storminess in the Gulf of Alaska may provide a way of predicting year-class size. Studies of physical and biological conditions in larval patches and adjacent shelf waters are being made to determine whether growth and mortality rates differ in these areas.

### RESUMEN

Estudios en el Estrecho de Shelikof, Alaska, muestra que grandes concentraciones de *Theragra chalcogramma* entran el valle marino en marzo y desovan a principios de abril. Estudios sobre la distribución de huevos y larvas han indicado la existencia de densas regiones de huevos que se convierten en manchas de larvas luego de la eclosión. Los procesos que transportan las larvas a las zonas de cría o al mar abierto dominan el reclutamiento. Resultados anteriores sugieren que las larvas pueden desaparecer rápidamente de la plataforma continental (en 14 días) de-

bido al flujo rápido y variable de la Corriente Costera de Alaska (CCA). Sin embargo, la mayor parte del volumen transportado en los 100 m superficiales se queda en la plataforma. Inestabilidades baroclínicas entre la CCA y aguas costeras pueden crear remolinos (observados por imágenes de satélite infrarrojas) en la boca del Estrecho de Shelikof. Estos remolinos contienen, con frecuencia, las concentraciones más altas de larvas. La fase y ubicación de los remolinos, la CCA, y la eclosión determinan la manera que un cierto mecanismo influye en la retención de larvas sobre la plataforma. El tamaño de las clases de edad parecen enteramente determinadas hacia el final del período larval, aunque sucesos que ocurren durante el verano subsiguiente pueden reducir también la clase de edad. Tormentas durante el principio del período larval pueden afectar negativamente la supervivencia, aunque el mecanismo no está todavía claro. Un índice relacionado a las tormentas del Golfo de Alaska podría proveer una forma de predicción de la clase de edad anual. Se están haciendo estudios sobre las condiciones físicas y biológicas en las manchas de larvas y en aguas vecinas de la plataforma para determinar si las tasas de crecimiento y de mortalidad entre estas áreas son distintas.

### INTRODUCTION

An important scientific challenge during the remainder of this and the beginning of the next century is to understand natural fluctuations in fish populations. This is especially true for fishes that constitute a major portion of the total annual catch and are thus commercially valuable. Knowledge of recruitment dynamics will improve management of exploited marine fish populations. Traditional approaches have to be changed. "A better understanding of the population dynamics process requires more interdisciplinary research among fisheries scientists and oceanographers" (Beamish et al. 1989), and this will occur only through dedicated, long-term research efforts. The Fisheries Oceanography Coordinated Investigations (FOCI) program is a long-term, cooperative effort between scientists at

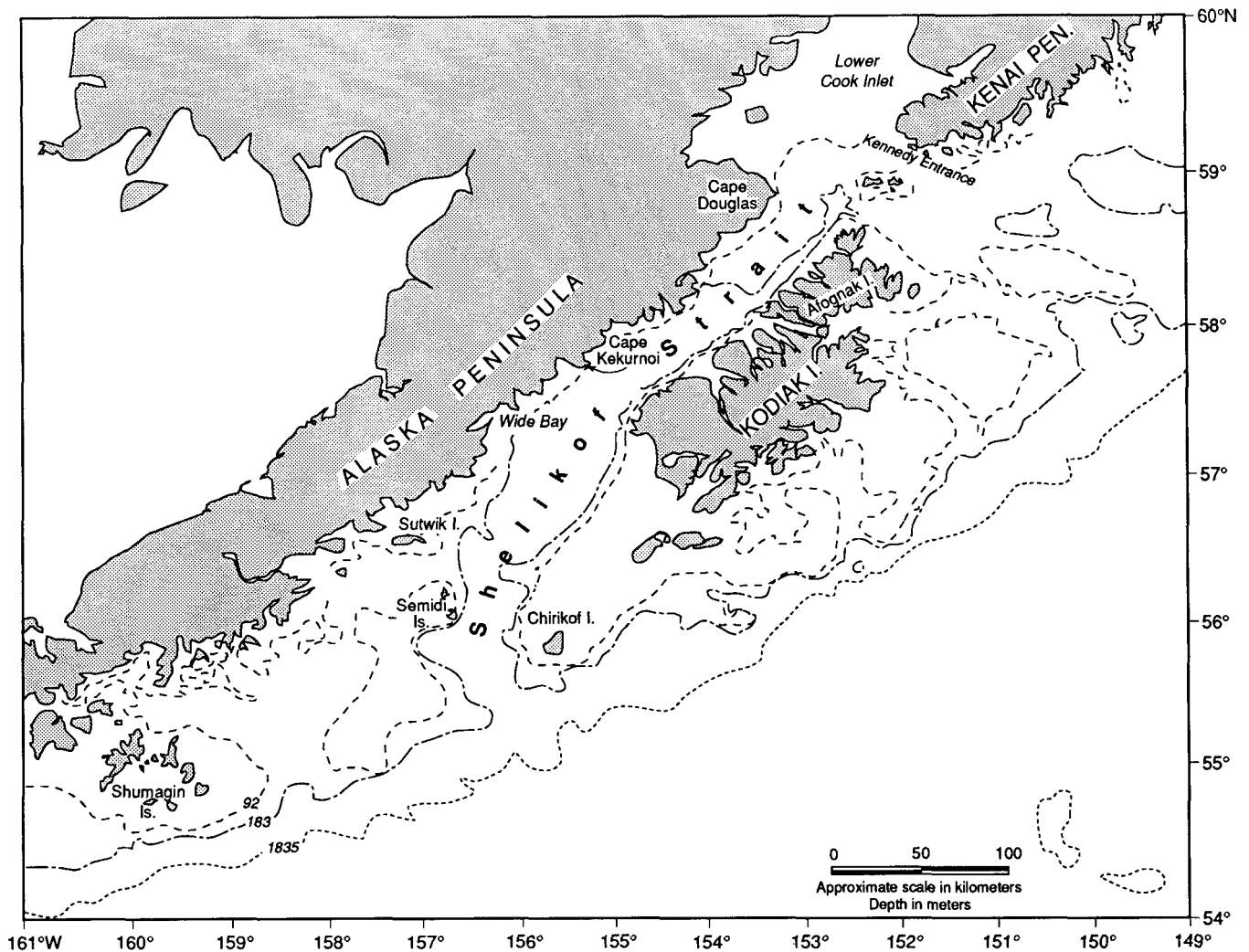


Figure 1. Map of the FOCI study region in the Gulf of Alaska. Depth contours are in meters.

the Pacific Marine Environmental Laboratory of the Oceanic and Atmospheric Research component of the National Oceanic and Atmospheric Administration (NOAA) and the Alaska Fisheries Science Center of the National Marine Fisheries Service. The goal of FOCI is to understand how the environment affects recruitment to commercially valuable fish and shellfish stocks in Alaskan waters.

Some of the largest fisheries in the world exist in the North Pacific Ocean and the Bering Sea. Walleye pollock (*Theragra chalcogramma*) is an important commercial species along both the Asian and North American coasts. Although exploited since the turn of the century, walleye pollock became a target species in 1964 when the Japanese developed shipboard methods for producing surimi. Between 1970 and the mid 1980s, world catches varied between 5 and 6 million metric tons (Fishing News International 1985). In the 1980s, walleye pollock was the single

most important species in the world fish catch by weight (Bakkala et al. 1987). Since the mid 1980s pollock catches have increased dramatically and averaged between 6 and 7 million MT annually (FAO 1990).

FOCI research was initiated in 1984 to understand processes determining recruitment of walleye pollock in Shelikof Strait, Alaska (figure 1). Large concentrations of the fish aggregate each March in a limited area of the strait. The fish spawn in early April, producing dense patches of eggs. By late April, the eggs hatch, and patches of yolk-sac larvae form. Currents transport the larvae to their nursery grounds along the Alaska Peninsula (Kim 1989). The early life history of walleye pollock in Shelikof Strait provides a tractable problem for a commercially important species (Kim and Gunderson 1989). We originally believed that larvae and juveniles that remain along the Alaska Peninsula are more likely to survive than those that leave the continental shelf.

Our field studies have demonstrated that in most years larvae are found mainly in patches on the shelf. We have not been able to test our original transport hypothesis directly, because it would require sampling over a large area where we expect larval abundance to be very low. Numerous studies have shown that other fishes whose early life pattern is closely tied to an advective system suffer increased mortality when transport is abnormal (Norcross and Shaw 1984). Also, fewer copepods, which serve as larval prey, are found in oceanic waters of the Gulf of Alaska than in coastal areas (Cooney 1987). We have focused our research on the physical and biological environment, especially on processes within the larval patch.

## BACKGROUND

### *Physical Setting and Features of the Physical Environment*

The study area is dominated by a high, nearly continuous mountain chain along the Alaska Peninsula, and a deep (>250 m) sea valley between Kodiak Island and the peninsula (figure 1). The mountains perturb geostrophic winds (geostrophic winds adjusted in speed and direction to account for friction). Ageostrophic winds are typical in Shelikof Strait (Schumacher et al. 1989). Numerous gaps in the mountains cause spatial variability on the scale of tens of kilometers. The sea valley forms a natural guide for shelf circulation, a conduit connecting the continental slope to the inner shelf. Immediately east of Sutwik Island and the Semidi Islands, the sea valley becomes more orthogonal to the continental slope. The sill between the valley and continental slope has a minimum depth of approximately 225 m. The shelf between the Semidi and Shumagin islands is generally deeper than 150 m, but there is a shoal region (< 100 m) southwest of the Semidi Islands. The many embayments along the Alaska Peninsula provide a nursery ground for young walleye pollock.

Much of the variability in the Gulf of Alaska is due to large-scale atmospheric phenomena. An annual cycle in the number of low-pressure centers crossing the region results from global patterns in upper-level atmospheric pressure (Niebauer 1988). The consistent passage of storms along the Aleutian Island chain, a feature known as the Aleutian Low, dominates atmospheric circulation over the Gulf of Alaska in winter and plays a crucial role in the hydrological cycle. To provide a time series representation of atmospheric circulation, Emery and Hamilton (1985) defined the Northeast Pacific Pres-

sure Index (NEPPI: the difference between surface pressure at Reno, Nevada, and 50°N, 170°W). This index is a measure of the strength, frequency, and location of storm passage (a measure of the Aleutian Low). There is correlation between NEPPI and sea-level temperature and height observed along the coast of British Columbia. Because gradients in coastal sea level generate currents, coastal circulation should also be related to NEPPI. Analysis of NEPPI and nearly 5 years' worth of current data from the Shelikof Strait region indicate a statistically significant relation between fluctuations in NEPPI and in the current (Roach and Schumacher 1991). Frequent storms along the mountainous coastline of Alaska produce much precipitation (>330 cm yr<sup>-1</sup>). The hydrological cycle has a maximum discharge rate in October and a minimum in August, reflecting seasonal variations in air temperature, precipitation, runoff, and freshwater storage from the previous winter (Royer 1981).

The dominant circulation feature over the continental shelf is the Alaska Coastal Current (ACC). The ACC extends more than 1,500 km along the south coast of Alaska (Reed and Schumacher 1987). It is identifiable by its low salinity, which results from the large freshwater input (Royer 1981, 1982). This is one of the most vigorous coastal currents in the world, with surface speeds of 25 to 175 cm s<sup>-1</sup>. Volume transport results from the addition of fresh water along the entire coastline and is perturbed by the alongshore wind through both confinement of the fresh water and alteration of coastal sea level (Schumacher and Reed 1980; Royer 1981; Reed and Schumacher 1981). Between Kodiak Island and the peninsula, differential Ekman pumping also appears to generate fluctuations in transport (Reed and Schumacher 1989a). Estimates of volume transport computed from observations of water property along the Kenai Peninsula exceed 10<sup>6</sup> m<sup>3</sup> s<sup>-1</sup>; maximum values occur in fall, when freshwater flux is greatest (Schumacher and Reed 1980; Royer 1981).

Circulation in Shelikof Strait and the western Gulf of Alaska is complex. Baroclinic instability is evident in satellite images and in analysis of current energy (Mysak et al. 1981). Satellite imagery (Reed et al. 1988; Schumacher et al., in press) and tracked buoys (Incze et al. 1990) show eddies. The observed mean transport in the sea valley is 0.85 × 10<sup>6</sup> m<sup>3</sup> s<sup>-1</sup>; wind-forced pulses exceed 3.0 × 10<sup>6</sup> m<sup>3</sup> s<sup>-1</sup> (Schumacher et al. 1989). The ACC bifurcates east of Sutwik Island; one branch flows along the Alaska Peninsula, and the other transports about 75% of the total volume seaward through the valley (Schumacher et al. 1989). Few observations have been col-

TABLE 1  
 Annual Abundance Estimates of Several Life Stages of Walleye Pollock from Shelikof Strait, Gulf of Alaska

Source	Numbers of fish			Cohort abundance from spawning year						
	Blend	Hydro	Blend	Blend	Plankton	Plankton	Plankton	Trawl	Trawl	VPA
Stage	3-10 adults	All adults	3-10 spawners	Spawned eggs	Eggs	Early larvae	Late larvae	Age-0 juveniles	Age-1 juveniles	3-yr-old juveniles
Date	1 Apr	1 Apr	1 Apr	10 Apr	7 Apr	22 May	10 Jun	15 Sep	15 Sep + 1	1 Apr + 3
Age of cohort	1	1	1	10	7	52	71	168	533	1095
Log age	0.00	0.00	0.00	1.00	0.85	1.72	1.85	2.23	2.73	3.04
Authors*	H&M	W	H&M	H&M	R&P	R&P	B&S	B&S	B&S	H&M
Exponent	9	9	9	14	†	†	†	†	†	9
Year										
1972	—	—	—	—	—	—	—	—	—	1.6505
1973	—	—	—	—	—	—	—	—	—	0.3765
1974	—	—	—	—	—	—	—	—	—	0.2665
1975	2.393	—	0.367	0.828	—	—	—	9.76	—	1.4895
1976	1.889	—	0.417	1.091	—	—	—	18.19	—	2.3790
1977	1.405	—	0.394	1.230	—	—	—	19.44	—	1.8855
1978	2.302	—	0.447	1.309	—	—	—	11.96	—	3.2715
1979	3.796	—	0.634	1.594	—	114.7	298.9	—	10.74	1.6800
1980	4.298	—	0.824	2.181	—	—	—	2.90	3.74	0.5645
1981	6.016	7.881	1.130	2.896	52.82	458.1	2064.6	10.90	3.18	0.5025
1982	5.467	—	1.265	3.491	9.32	3.8	29.9	3.83	—	0.2460
1983	4.056	4.593	1.180	3.657	—	20.8	849.4	—	2.65	0.4550
1984	2.954	2.987	0.966	3.255	16.00	—	83.5	11.92	1.25	0.8570
1985	1.872	1.015	0.658	2.373	10.73	2.9	986.0	22.08	3.84	0.8120
1986	1.393	0.782	0.423	1.534	5.69	—	82.2	6.21	0.29	0.1355
1987	1.702	—	0.394	1.286	2.44	38.5	56.7	9.76	0.48	—
1988	1.880	1.231	0.412	1.221	0.93	—	307.2	14.91	—	—
1989	1.322	1.018	0.377	1.189	—	—	—	—	—	—
Sum	42.745	19.507	9.8892	29.135	97.93	638.8	4758.4	141.86	26.17	16.5715
Minimum	1.322	0.782	0.367	0.828	0.93	2.9	29.9	2.9	0.29	0.1355
Maximum	6.016	7.881	1.265	3.657	52.82	458.1	2064.6	22.08	10.74	3.2715
Max/min	4.551	10.078	3.447	4.417	56.796	157.966	69.050	7.614	37.034	24.144
n	15	7	15	15	7	6	9	12	8	15
Mean	2.850	2.787	0.659	1.942	13.990	106.467	528.711	11.822	3.271	1.105

\*H&M = Hollowed and Megrey, NMFS, Seattle, pers. comm.; B&S = Bailey and Spring, in press; W = Williamson, NMFS, Seattle, pers. comm.; R&P = Rugen and Picquelle, NMFS, Seattle, pers. comm.  
 †Indices of abundance

lected between the Semidi and Shumagin islands, but it appears that some of the water flowing seaward in the valley returns to the shelf (Schumacher and Reed 1986).

**Early Life History of Walleye Pollock**

Before 1981 little was known of the early life history of walleye pollock in the Gulf of Alaska; until then it was not even possible to separate their larvae from those of other gadids in field samples (Dunn and Matarese 1987). Annual hydroacoustic/mid-water trawl surveys through the 1980s showed that large concentrations of prespawning walleye pollock migrate from the southwest end of Shelikof Strait to the area near Cape Kekurnoi. The fish spawn mainly in the deep sea valley, between late March and mid-April (Kim and Nunnallee 1990). The spawning population has varied between 1.3 and 6.0 billion fish during the 1980s (A. B. Hollowed and B. A. Megrey, NMFS, Seattle, pers. comm.: see table 1). Each female produces hundreds of thousands of

free-floating planktonic eggs in a series of about ten batches over 2-3 weeks. Laboratory observations have shown that the fish spawn primarily in pairs and mainly in the evening (Baird and Olla 1991). Egg diameter (ca. 1.3 mm) decreases with time but is not related to female size (Hinckley 1990).

The eggs are found deep in the water column (nearly all below 150 m, and many within 25 m of the bottom) and hatch in about 2 weeks, depending on temperature (Matarese et al., in press). Because of the large spawning population, the localized spawning area, the short season, and generally the lack of strong spatial differences in the deep currents, a large "patch" of eggs is produced that can be recognized through plankton surveys of the region (Kendall and Picquelle 1990).

The larvae are about 3-4 mm standard length (SL) at hatching and are relatively undeveloped, without functioning mouths or eyes. They quickly rise from their deep hatching depth to the upper 50 m of the water column, where they drift in the prevailing

currents from late April into June. They generally remain as a large identifiable patch, and grow about  $0.2 \text{ mm d}^{-1}$  during this time. Their diet consists mainly of copepod nauplii, and the size range of prey increases as the larvae grow. They are visual feeders, and eat mostly during the day (Kendall et al. 1987).

By the end of May the patch of larvae is usually near the Semidi Islands, and the larvae have reached 8–11 mm SL (Kendall and Picquelle 1990). The biology of young-of-the-year walleye pollock after May is poorly known. During June and July they have reached about 20–30 mm and remain as a patch that drifts to the area of the Shumigan Islands (Hinckley et al. 1991). They remain planktonic during this period, and do not seem to form schools. By the end of their first summer, at least some of them are found in bays along the Alaska Peninsula (Bailey and Spring, in press).

## APPROACH

It is generally accepted that physical oceanic processes influence and may even primarily determine the eventual recruitment of fish. Predation on eggs and larvae and the condition of larvae during transport to nursery grounds are believed to be the most important factors in determining recruitment (Rothschild 1986). Survival is affected by two broad categories of physical mechanisms: turbulence of the water column, which influences food availability, and fluctuations in the currents that transport eggs and larvae to nursery areas. How physical conditions affect predation is less well known. Water properties, particularly temperature, affect growth rate, thus affecting phasing between stage of development (through late larvae) and transport. By the time fish become juveniles, they are no longer planktonic and thus are less affected by transport. Where they spend their first summer, however, results from their transport since spawning (Norcross and Shaw 1984).

A research plan developed at the Alaska Fisheries Science Center and the Pacific Marine Environmental Laboratory is reviewed and updated annually. Four program advisors act as independent reviewers. The primary forum for evaluating the quality of the research is scientific publications (presently there are 147 publications, nearly half in refereed journals) and presentations. Initially, research focused on field observations to determine transport, water properties, and egg and larval distributions. Laboratory work centered on immunoassays and growth studies of larvae. As the program matured, it became apparent that two additional types of research were

needed: process-oriented studies of mortality within and outside the larval patch, and examination of various indices of climate and abundance of animals versus estimates of three-year-olds. Many of the physical and biological data are being put into a model of dispersion of larvae (Stabeno et al. 1990). This model includes advective, diffusive, and biological source/sink terms and has been used to simulate larval distributions.

The success of FOCI results from effective interdisciplinary research. The program melds theoretical and observational scientists with backgrounds in meteorology, physical and biological oceanography, and fishery biology from government, private laboratories, and universities. Developing and maintaining communication and cooperation among researchers with varying backgrounds has been a necessary condition for success. A report presenting our managerial and administrative techniques is available on request.

## RECENT RESULTS

### *Egg and Larval Distributions*

Kendall and Picquelle (1990) analyzed the seasonal and geographic distribution of walleye pollock eggs and larvae (1,929 samples collected during 32 ichthyoplankton cruises in the Gulf of Alaska from 1972 to 1986). They found eggs primarily in April, and larvae in late April and May. Most eggs are found in Shelikof Strait, in a small area off Cape Kekurnoi (figure 1). In most years larvae drift southwestward in a large patch (Kim and Kendall 1989). The number of larvae decreases, and their size increases during this drift. Significant interannual differences in location of the patch and size of the larvae become apparent by late May.

To determine the vertical distribution of the eggs, we studied incubated eggs in a density gradient water column and analyzed vertically discrete plankton tows (Kendall and Kim 1989). During the 2-week incubation period, a complex pattern of interaction between stage of egg development and local water density determines depth; many of the eggs are located below 200 m. As the eggs begin to develop, they rise in the water column until they reach a level of neutral buoyancy at about 150 m. Later in development the eggs sink, then rise again just before hatching. Recent studies (Kendall et al., in press) have confirmed this pattern with more extensive sampling in different areas and years. Sampling with an epibenthic sled has revealed that some eggs are even found within 1 m of the bottom (A. C.

Matarese, NMFS, Seattle, pers. comm.). Interannual differences in water density in the spawning area may affect the vertical distribution of the eggs, which may in turn affect their hatching location because of vertical shear of the currents. Below about 150 m, currents are fairly weak, and on the south side of the sea valley they flow toward the northeast; above 150 m, currents are generally stronger and flow to the southwest (Schumacher et al. 1989).

By late May the larvae have reached a mean length of 11 mm SL and live between about 15 and 50 m. They follow a diel pattern of limited vertical migration (Kendall et al. 1987). Current shear decreases exponentially from approximately  $0.005 \text{ s}^{-1}$  at 15 m to a nearly constant value of only  $0.002 \text{ s}^{-1}$  between 20 and 50 m (figure 2). Given the observed mean shear, the daily difference between transport of plankton at 15-m and 45-m depths is  $<1 \text{ km}$ . The larvae follow a crepuscular pattern of activity, and are concentrated between 14 and 28 m during twilight. At night they are more dispersed, and during the daytime they are concentrated in the lower portion of their depth range.

Recent studies (Kendall et al., in press) have shown that larvae over a considerable size range (4–11 mm SL), and throughout the season in Shelikof Strait have a similar pattern of vertical distribution. In the laboratory, walleye pollock larvae swim upward in low light and darkness, and downward at high light intensities, when they are also more active (Olla and Davis 1990). These changes in activity are not endogenous, but rather are responses to the daily light cycle. The larvae also change their vertical distribution to avoid low temperature and turbulence. Only a few larvae, mainly smaller than 4 mm SL, are found deep in the water column, as would be expected from the vertical location of late-stage eggs (Kendall et al., in press). Apparently the eggs hatch deep, but the larvae quickly swim to the upper layers ( $<50 \text{ m}$ ) and remain there during development. Under laboratory conditions walleye pollock larvae react positively to light within 24 hours of hatching (Olla and Davis 1990).

**Water Properties**

Three classes of water exist in the study area: Lower Cook Inlet, Alaska Coastal Current, and bottom water. From April to June, water in lower Cook Inlet is generally colder and less saline than water in the ACC; the differences are about  $0.5^\circ\text{C}$  and  $0.5 \text{ psu}$ . The interannual variation of bottom-water properties is striking: off Cape Kekurnoi salinity has varied from  $<32.5$  to  $>33.5 \text{ psu}$  while tem-

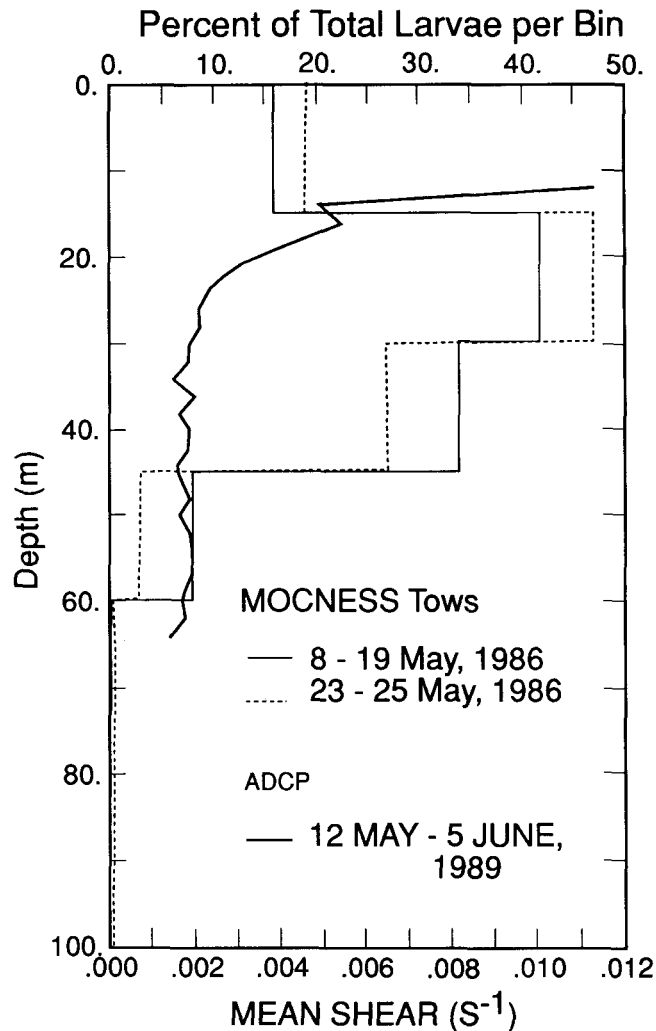


Figure 2. Observed vertical mean velocity shear ( $\text{s}^{-1}$ ) and percent of larvae caught per 15-m bin.

perature varied between  $<3.8^\circ$  and  $>5.8^\circ\text{C}$  (Reed and Schumacher 1989a). During spring, however, the bottom waters are always warmer and more saline than ACC water above them. The bottom waters also provide nutrients for primary production (Reed et al. 1987). The juxtaposition of ACC and Lower Cook Inlet water accounts for baroclinic instability (Mysak et al. 1981), which leads to formation of eddies.

Water temperatures in the upper 150 m follow a clear seasonal pattern: the warmest values occur in August–September and the coldest values in March–April (Reed and Schumacher 1989a; Roach and Schumacher, in press). The largest standard deviations occur in May when walleye pollock eggs hatch and develop into first-feeding larvae. There

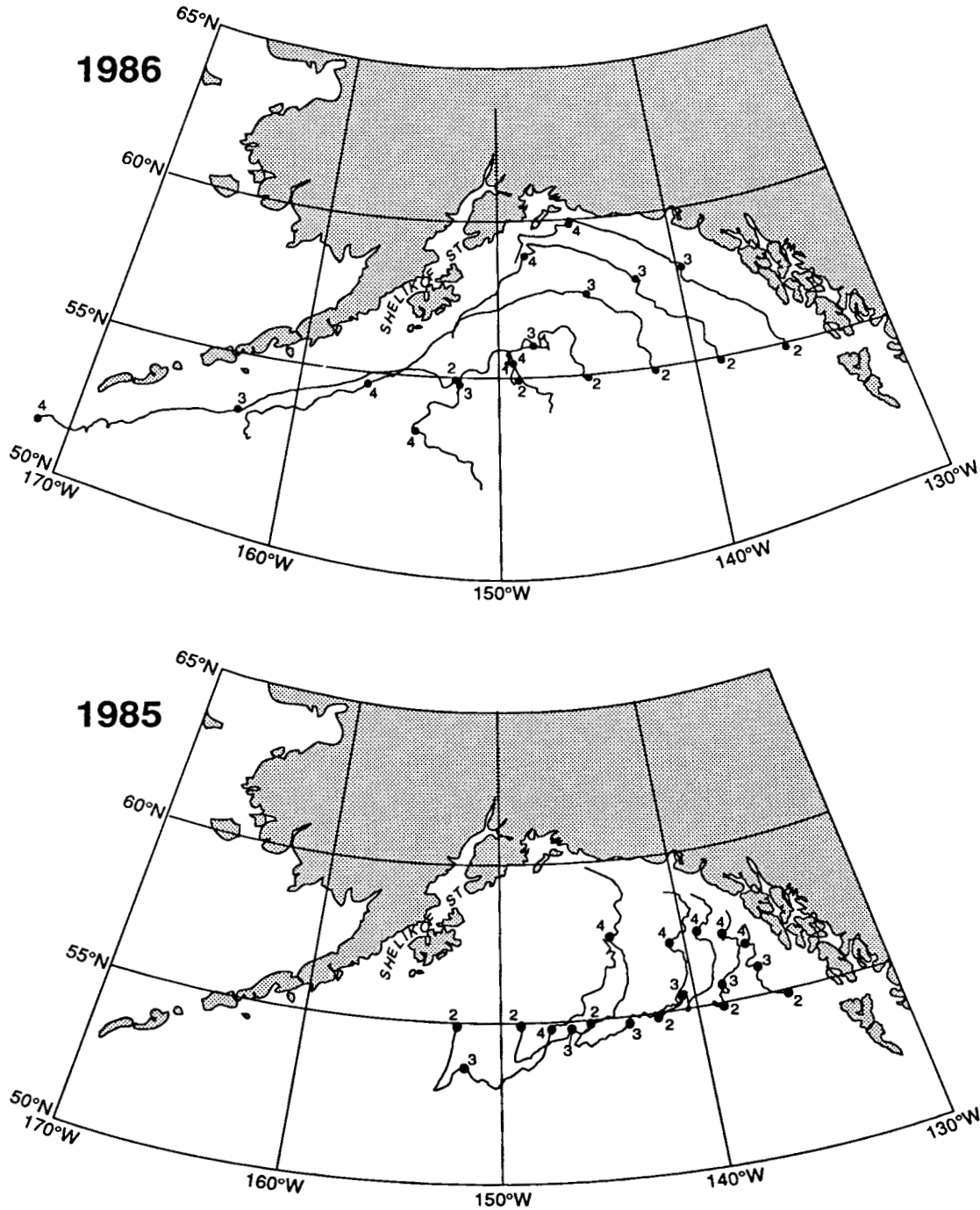


Figure 3. Trajectories from a wind-driven circulation model with a steady baroclinic field: upper panel, conditions during a typical year (1986); lower panel, anomalous trajectories (1985).

are also interannual variations in the bottom-water temperature: during spring 1986, bottom waters were more than 0.5°C colder than in other years.

A wind-driven model with a density field that varies in space but is constant with time has been used to examine interannual variations of water-parcel trajectories in the North Pacific Ocean (Ingraham and Miyahara 1989). In some years the typical

flow into the head of the Gulf of Alaska is weakened (1979, 1982, 1985), and the westward intensification of the Alaska Stream is minimal (figure 3). The anomalies in flow trajectories coincide with anomalies in the NEPPI index. During these years, more saline water is found at depth in the sea valley (Ingraham et al. 1991). This information links local water properties to large-scale processes, and strengthens the

MEAN ALONGSHORE CURRENT ( $\text{cm s}^{-1}$ )

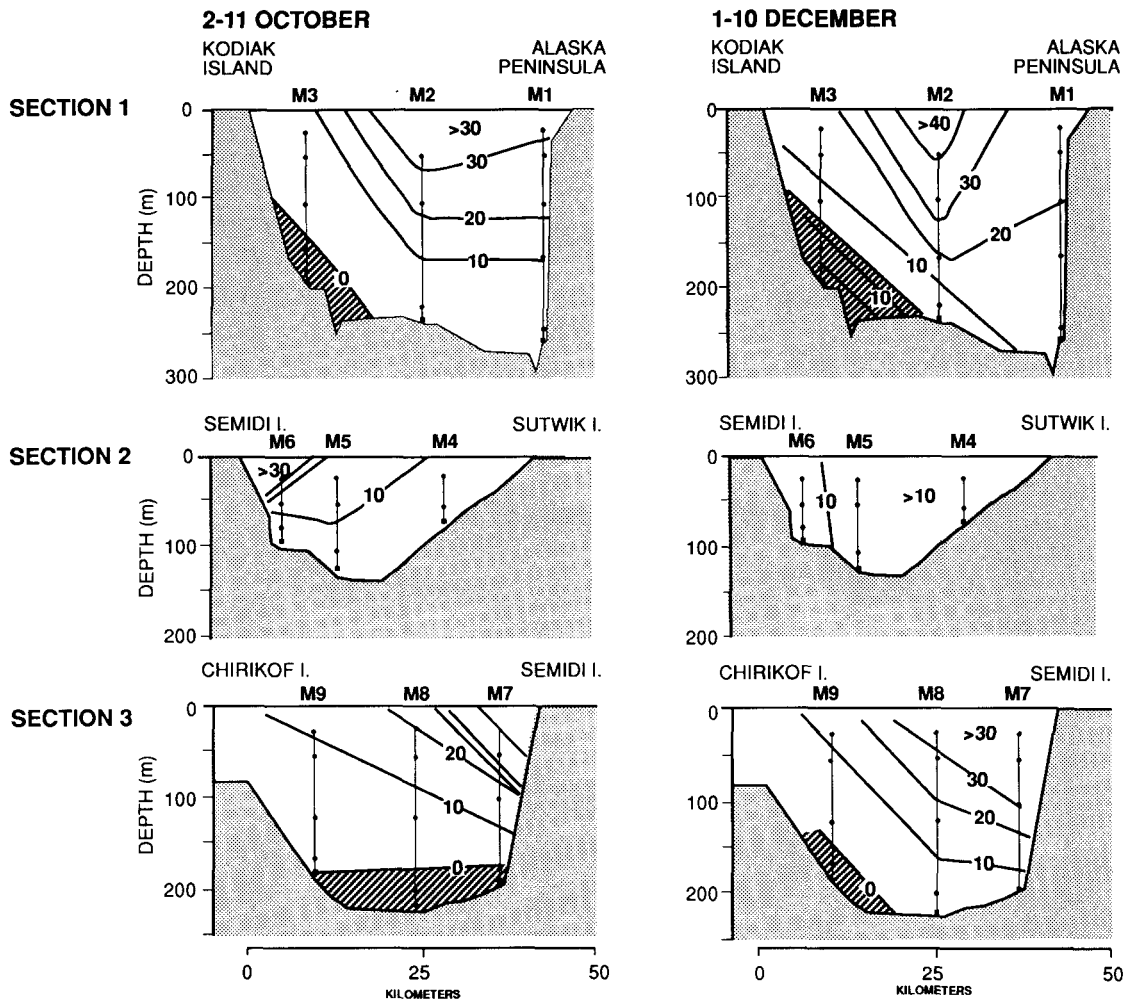


Figure 4. Structure of mean current speed ( $\text{cm s}^{-1}$ ) from measurements (current meters are shown as dots on moorings) over the sea valley (sections 1 and 2) and over the shallower shelf (section 3) during two 10-day events (after Schumacher et al. 1989). These are examples of the estuarine-like flow over the sea valley; the region with flow into the valley is shaded.

use of NEPPI as an index of conditions in the study area. The occurrence of different water in the sea valley may indicate that the composition of the zooplankton community varies interannually.

No direct impact of the temperature and salinity variations has been observed on early stages of walleye pollock. Secondary effects, however, may be important in the chain of events that dictates year-class success. For example, when bottom temperatures are significantly lower, incubation time is increased. Similarly, differences in salinity (at the ambient temperatures, salinity dominates the equation of state of seawater and hence dictates density) would affect the depth of eggs in the water column, altering when and where the eggs hatch. The importance of hatching location to eventual transport

and retention on the shelf is a function of phasing between biological and physical processes.

**Transport and Mesoscale Features of Circulation**

The FOCI hypothesis is focused on transport of planktonic life stages to nursery grounds; before FOCI, however, little was known about volume transport in the study area. An experiment was conducted between 1984 and 1985 to measure volume transport and to examine its temporal variability (Schumacher et al. 1989). Estuarine-like flow (flow is seaward in the upper 150 m and reverses below this depth [Reed and Schumacher 1989a]) was found in the sea valley, with warmer, more saline water from the continental slope entering on the southeastern side of the valley (figure 4). Mean volume



transport of the Alaska Coastal Current was measured at  $0.85 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ . This is in good agreement with estimates of transport from CTD data, provided that the level of no motion is carefully selected to approximate the two-layered velocity field over the sea valley (Reed and Schumacher 1989a). Approximately 75% of the mean transport was through the sea valley, with the remaining flux along the Alaska Peninsula. Wind-related changes in volume transport can be as large as four times the mean value. During such extreme events, transport of eggs could alter the usual pattern of hatching location and eventual transport of larvae to coastal nursery grounds.

The ACC does not span the sea valley, and estimates from current records of coherence become insignificant for separations  $>10 \text{ km}$  (Reed and Schumacher 1989b). Thus where walleye pollock eggs hatch relative to the ACC is important. Larvae hatched shoreward of the ACC remain in coastal waters and drift toward the southwest. Larvae that are advected with the portion of volume transport that flows along the peninsula also remain on the shelf. Larvae transported in the ACC can be removed from the sea valley within a few weeks (Incze et al. 1989). The fate of animals transported out of the sea valley is uncertain, because dynamics and patterns of shelf-slope exchange are not well known. It has been suggested that some of the flow out of the sea valley enters the next valley to the southwest (Schumacher and Reed 1986), giving larvae a pathway back onto the shelf. Estimates of how flow affects larval distribution suggest that horizontal advection, divergence, and turbulent diffusion are all important (Reed et al. 1989). To further address questions of larval dispersion, a slab model of the change in concentration with time of larvae has been used to simulate observed data (Stabeno et al. 1990). Although preliminary results from this model are encouraging, our ability to input advection at the necessarily small length scales is limited.

Since 1986, twenty-five satellite-tracked buoys (drogued at 40 m) were deployed in the study area. Most of the deployments have been in spring, near Cape Kekurnoi. The circulation inferred by averaging all independent buoy trajectories in a spatial grid ( $8 \times 8 \text{ km}$ ) provides the most comprehensive description of circulation available (figure 5). There is good agreement between velocities as measured by buoys and moored instruments (comparisons were made at 20 locations). To date, 25% of the buoys have continued along the peninsula. The rest flowed seaward past the Semidi Islands, but most turned southwest immediately past the islands or returned

to the shelf downstream, eventually becoming part of the flow along the peninsula. Only 25% of the buoys left the shelf permanently and became incorporated in the Alaskan Stream (Stabeno and Reed, in press).

Satellite imagery (Reed et al. 1988; Schumacher et al., in press) has greatly enhanced knowledge of variability and spatial scales of the velocity field. Estimates of sea-surface flow are made from measurements of sea-surface temperature pattern displacements between sequential images by means of an interactive visualization algorithm (Vastano and Borders 1984). Whenever possible, surface flow vectors have been compared to Eulerian measurements and flow estimates from a drift-current model; there is good agreement throughout the upper 60 m of the water column (A. C. Vastano, Texas A&M Univ., College Station, TX, pers. comm.).

Eddies and patches of walleye pollock larvae are sometimes congruent (figure 6). Eddies have been identified in both Advanced Very High Resolution Radiometer (AVHRR) and synthetic-aperture radar (SAR) images, as well as in data about water properties (figure 7). Most eddies observed so far have been at the exit of the strait proper and off Wide Bay (Incze et al. 1990) and may result from baroclinic instability. All of these features appear to translate toward the southwest with the dominant current. A sequence of images from May 1987 shows that an eddy remained quasi-stationary off Wide Bay for at least two weeks. In May 1990, three satellite-tracked buoys were deployed in a region where high concentrations of larvae were observed. These buoys define an eddy that remained nearly stationary for approximately two weeks (figure 8). The eddy had a radius  $\sim 10 \text{ km}$ , and the mean current speed increased from  $\sim 20 \text{ cm s}^{-1}$  near the center to  $>30 \text{ cm s}^{-1}$  at a radius of 10 km. The measured speeds were greater than baroclinic speeds calculated from water properties, suggesting a significant barotropic component of velocity. After two weeks, the eddy moved southwest.

A second mechanism has been identified that affects transport and can cause formation of larval patches. In the vicinity of Kodiak Island, complex wind patterns develop as storms interact with mountains. As low-pressure systems approach Shelikof Strait from the southwest, the surface atmospheric pressure field is perturbed. Wind data collected from a research aircraft show convergence of geotriptic and ageostrophic winds in the region off Wide Bay (Macklin et al. 1984). The potential effect of this wind pattern on surface flow has been modelled (figure 9). Based on direct wind measure-

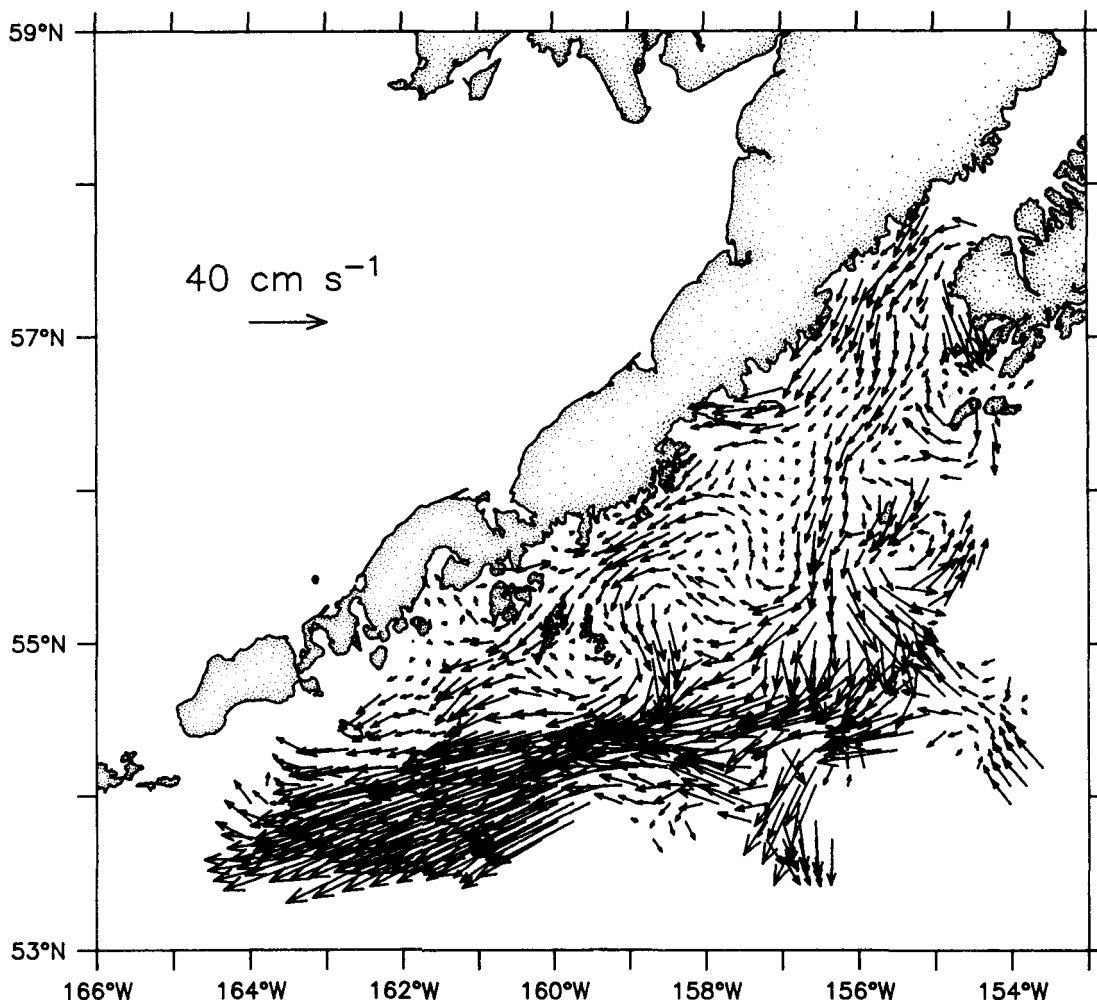


Figure 5. Mean circulation vectors based on satellite-tracked buoys.

ments made at five locations around the open-shelf region southwest of Kodiak Island (Lawrence et al. 1991) and on surface pressure charts, a "standard" wind pattern was developed. This wind field was used with a simple algorithm to generate surface current vectors that indicate a region of convergence off Wide Bay. High atmospheric pressure southwest of Shelikof Strait generates offshore winds over the open shelf and northeastward winds in Shelikof Strait (Schumacher et al. 1989). This wind pattern causes divergent and offshore currents. Under these conditions, plumes of cold coastal water have been observed leaving Wide Bay and extending across the shelf. As the plumes interact with bathymetry and currents in the sea valley, they may form eddies. Both eddies and wind-driven convergence zones can contribute to the observed patterns of larval distribution.

#### ***Growth and Condition of Larvae***

Much of our work has been devoted to measuring growth rates and condition of larvae. Daily increment deposition on the otoliths was verified by laboratory experiments (Bailey and Stehr 1988), and techniques to determine the age of juveniles were developed (Brown and Bailey, in press). Several techniques to measure larval condition were investigated, and use of RNA/DNA was found most satisfactory. Bioenergetic requirements of the larvae were established through laboratory experiments (Bailey and Stehr 1986; Yamashita and Bailey 1990). These studies were related to environmental conditions through studies of the prey field (primarily copepod nauplii).

Growth rates (determined from otolith analysis) of young larvae showed no year-to-year differences. But there were geographic variations: growth rate

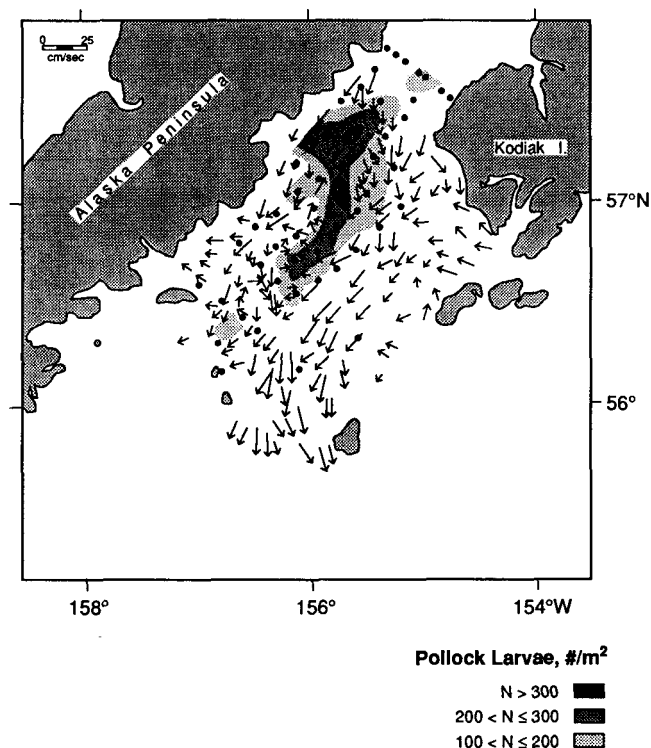


Figure 6. Surface velocity field inferred from AVHRR images of sea-surface temperature and contours of larval abundance. The contours are in units of  $m^{-2}$ . The pattern of surface currents was developed by tracking features on images between 28 and 29 April 1986.

increased from southwest to northeast along the Alaska Peninsula (Yoklavich and Bailey 1990). Time of maximum larval occurrence varied among the years, possibly because of changes in time of spawning, differential mortality, or drift out of the area. Decreases in numbers of larvae (from each day of spawning) between May and June–July 1987 surveys were used to determine daily mortality rates of 0.10–0.14 for young larvae and 0.01–0.02 for older larvae (integrated over a month between surveys).

Analysis of RNA/DNA from field samples shows that early in the season larvae are not in as good condition as later in the season. This may indicate that first-feeding larvae from early in the spawning season may sometimes be present before the spring bloom has brought copepod naupliar abundance to levels sufficient for larval growth. Also, larval condition varies spatially, and we are examining how this relates to hydrographic conditions and zooplankton distributions (M. F. Canino, NMFS, Seattle, pers. comm.). Laboratory experiments have shown that first-feeding larvae require 76 copepod nauplii per day for metabolism and growth, indicating that lack of food may sometimes limit growth (Yamashita and Bailey 1990).

### Determinants of Year-Class Strength

Although most of our studies have focused on the early stages of walleye pollock, we have also investigated factors, including environmental indices, that may correlate with year-class strength. One of the first questions is, When is year-class strength first established? We have concentrated on the egg and larval stages, following the traditional paradigm that this is when year class is determined. As an attempt to validate this, we compared indices of abundance of late larvae, and age-0 and age-1 juveniles with level of recruitment (age 3) determined by cohort analysis (Bailey and Spring, in press). Age-0 and age-1 abundance was correlated with age-3 recruitment. It appears from the limited time series available that high larval abundance is a prerequisite for strong year classes, and low numbers of larvae always result in low numbers of recruits. Low recruitment, however, also results in some years when late larvae and age-0 juveniles are abundant. It seems that sometimes events after the larval period adversely affect juvenile survival.

Abundance estimates of the walleye pollock that spawn in Shelikof Strait have been made over the last several years at various life stages (table 1). Although data are not available for all stages in all years, and some are indices rather than absolute population estimates, these data do help establish ranges of variation and suggest relationships between inter-annual trends in abundance at various stages. Estimates of the adult population are available from 1975 through 1989. The estimates used here are based on a blend of hydroacoustic and bottom trawl surveys and commercial catches (A. B. Hollowed and B. A. Megrey, NMFS, Seattle, pers. comm.). The number of spawned eggs has been derived from the annual estimates of adult abundance and age structure and an age/fecundity relationship (B. A. Megrey, NMFS, Seattle, pers. comm.). Indices of abundance of eggs and early larvae are based on analysis of plankton collections in Shelikof Strait over several years (W. C. Rugen and S. J. Picquelle, NMFS, Seattle, pers. comm.). Numbers of late larvae are estimated from larval surveys conducted in late May. Because these surveys have been made at slightly different times over the years, the numbers here are estimated numbers of larvae of the year class reaching 15 mm SL, given a certain mortality and growth rate (Bailey and Spring, in press). Such estimates are available for every year from 1979 through 1988, except 1980. The numbers of age-0 and age-1 juveniles are indices based on late-summer trawl surveys, which did not always encompass the entire area occupied by the year classes (Bailey and Spring,

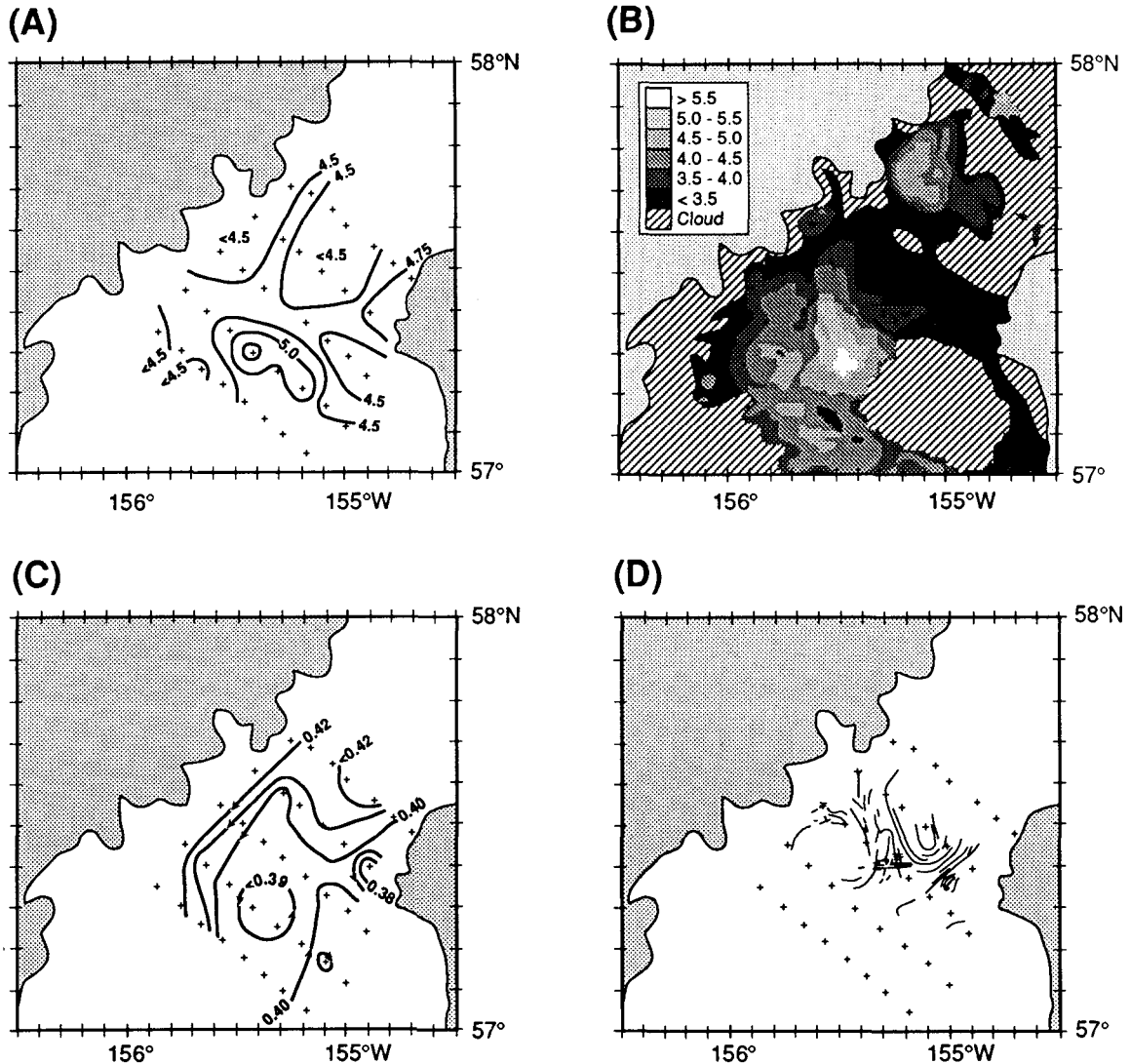


Figure 7. (A) Sea-surface temperature contoured from a 38-station CTD survey occupied between 27 and 29 April 1988; (B) AVHRR image of Shelikof Strait obtained on 29 April 1988; (C) geopotential topography; (D) sketch map of detectable current features seen in an SAR image from July 1978.

in press). Age-0 indices are available for all but two years from 1975 through 1988, and age-1 indices are available from 1979 through 1987, except 1982. Recruitment to the fishery is at age 3, and this is the basis for the cohort analysis of year-class size, results of which are given here for 1972 through 1986 (A. B. Hollowed and B. A. Megrey, NMFS, Seattle, pers. comm.).

From 1975 through 1989 the adult population had a 4.6-fold range of variation. Abundance of adjacent years is highly correlated. The population had a single peak abundance in 1981, with lesser and approximately equal numbers of fish at the beginning and

end of the series. This distribution was due primarily to the passage of several adjacent moderate-to-very-strong year classes through the population (1975-79).

Because the age structure of the population changed markedly during this period, the number of eggs produced lagged behind the trend in population abundance. Numbers of eggs produced had a 4.2-fold range of variation. Over  $2 \times 10^{14}$  eggs were produced every year from 1980 through 1985; the most eggs were produced in 1983 (figure 10). The indices for eggs in the plankton between 1981 and 1988 showed a 57-fold variation. The early larvae

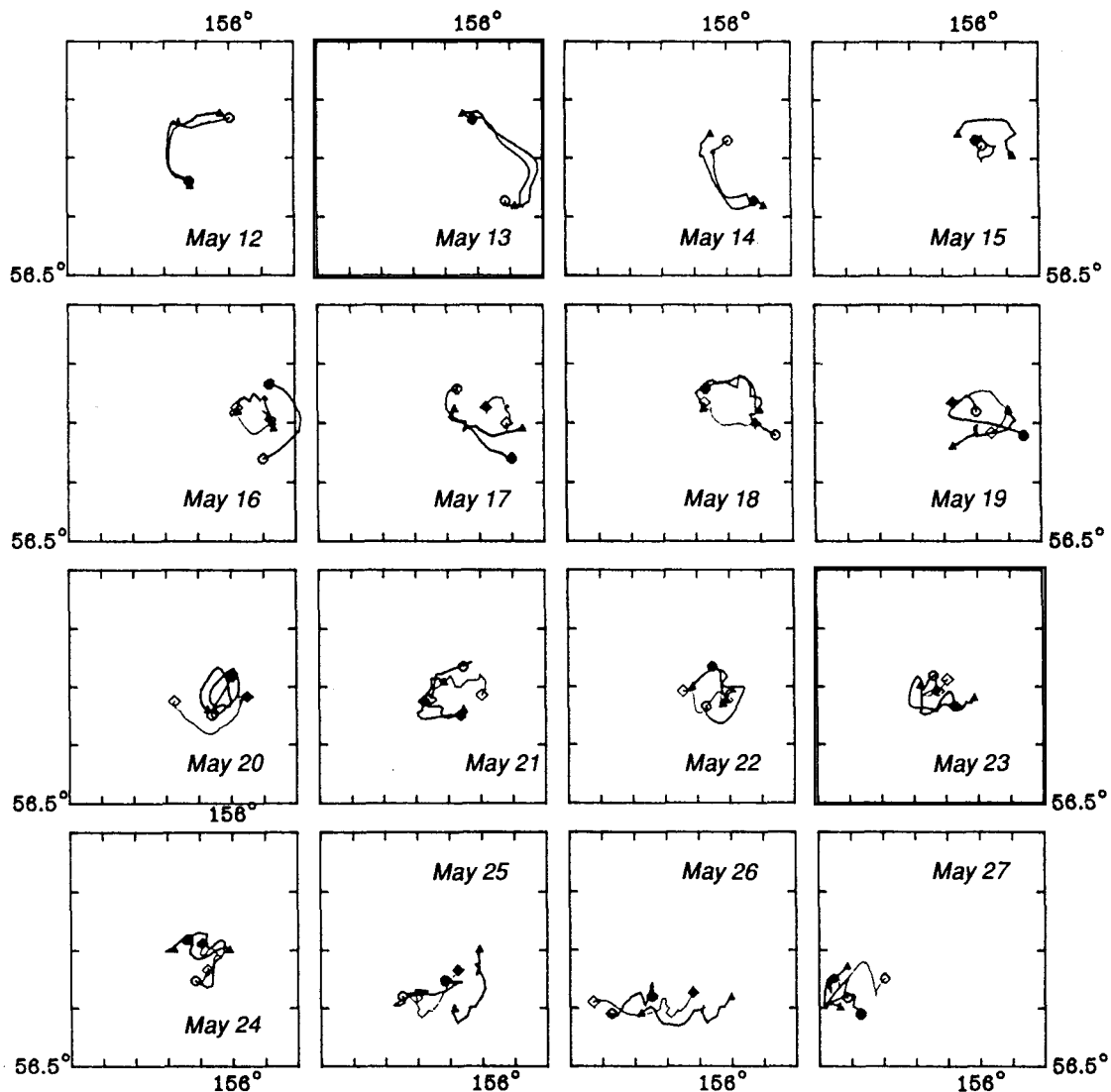


Figure 8. Satellite-tracked buoys in an eddy during May 1990.

varied more than any of the other stages, 158-fold, from 1979 through 1987.

The numbers of late larvae had a 69-fold range of variation among the 9 years for which there are data. The indices of abundance of age-0 juveniles showed a 7.6-fold range of variation among the 12 years for which there are data. Eight years of data for the age-1 juveniles produced indices of abundance with a 37-fold range of variation. The time series for 3-year-old recruits is 15 years long and has a range of variation of 24.1. The recruitment time series is dominated by five successive strong year classes (1975-79). When the adult population was at its height (1980-83), weak year classes were produced (figure 10).

We compared annual abundance estimates between stages by ranking the abundance of each stage through the time series for that stage. For each pair of stages, we used only those years when estimates of both stages were available. We did not consider the indices for planktonic eggs and early larvae because the time series were so short. When the ranked abundances of two stages are plotted against each other, an indication of their relationship can be seen, and this is probably the limit to which these data can be analyzed (figure 11). The number of adults is related to the number of eggs produced, but there is considerable scatter in the data because of changes in the age composition, and thus the egg-producing capacity of the adults (figure 11A). Numbers of eggs

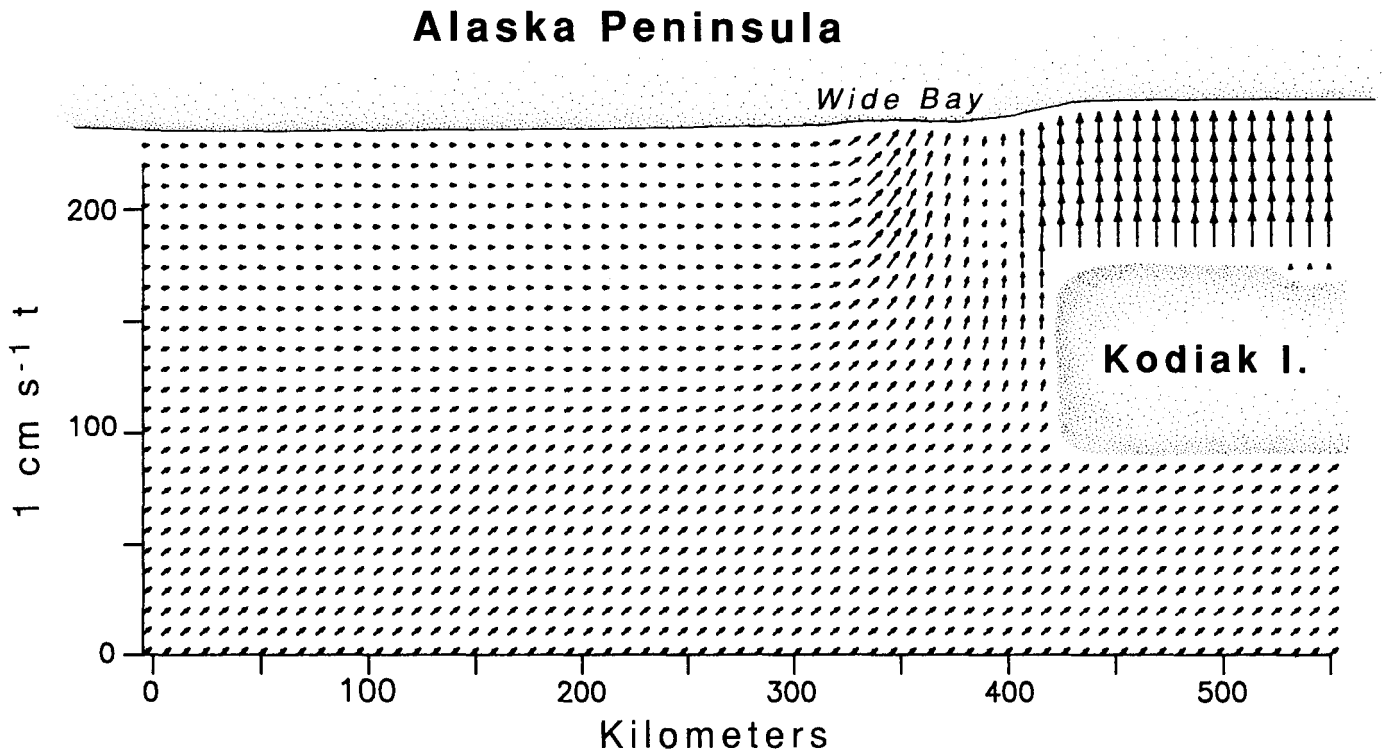


Figure 9. Surface velocity field as generated by a wind-driven model. Note the region of convergence off Wide Bay.

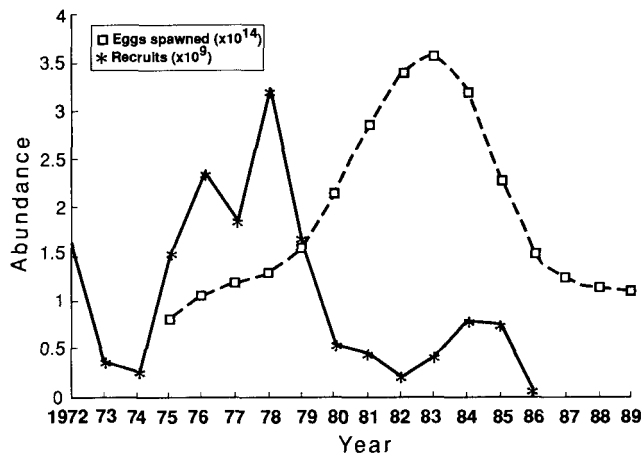


Figure 10. Numbers of eggs produced and number of recruits for the Shelikof Strait, Gulf of Alaska, walleye pollock population.

produced are considered in subsequent diagrams as a measure of the relationship between spawning stock size and year-class abundance. When the numbers of eggs produced are plotted against the numbers of late larvae, no pattern of relationship can be seen (figure 11B). High numbers of eggs resulted in low and high numbers of late larvae, and low numbers of eggs also resulted in low and high numbers of late larvae. A positive relationship is indicated between the numbers of late larvae and the numbers

of age-0 juveniles, for the 7 years with the data (figure 11C). The numbers of age-0 and age-1 juveniles also seem to be positively related, but there are only 6 years of data. An exception was the 1980 year class, which seemed very low as age-0 juveniles, but high as age-1 juveniles (figure 11D).

Combined with the above, plots of year-class size at various life stages against ranks of 3-year-old recruits can indicate when year class is established (figure 12). When numbers of late larvae are plotted against 3-year-old recruits, little indication of relationship is seen (figure 12B). Very high numbers of recruits resulted when there were moderate and low numbers of late larvae. In the two years when there were few larvae, few recruits were produced. It appears that in years when few larvae survive to reach 15 mm, the numbers of recruits will be low; however, high numbers of late larvae do not always produce high numbers of recruits. Therefore, inter-annual variation in survival sometimes occurs after the late larval stage. Age-0 and age-1 juvenile abundance both showed a positive relationship to numbers of recruits (figures 12C and 12D). Except for 1984, the numbers of age-1 juveniles gave a very good indication of how many recruits there would be.

We calculated daily rates of change between successive stages (late larvae to age-0 juveniles, age-0

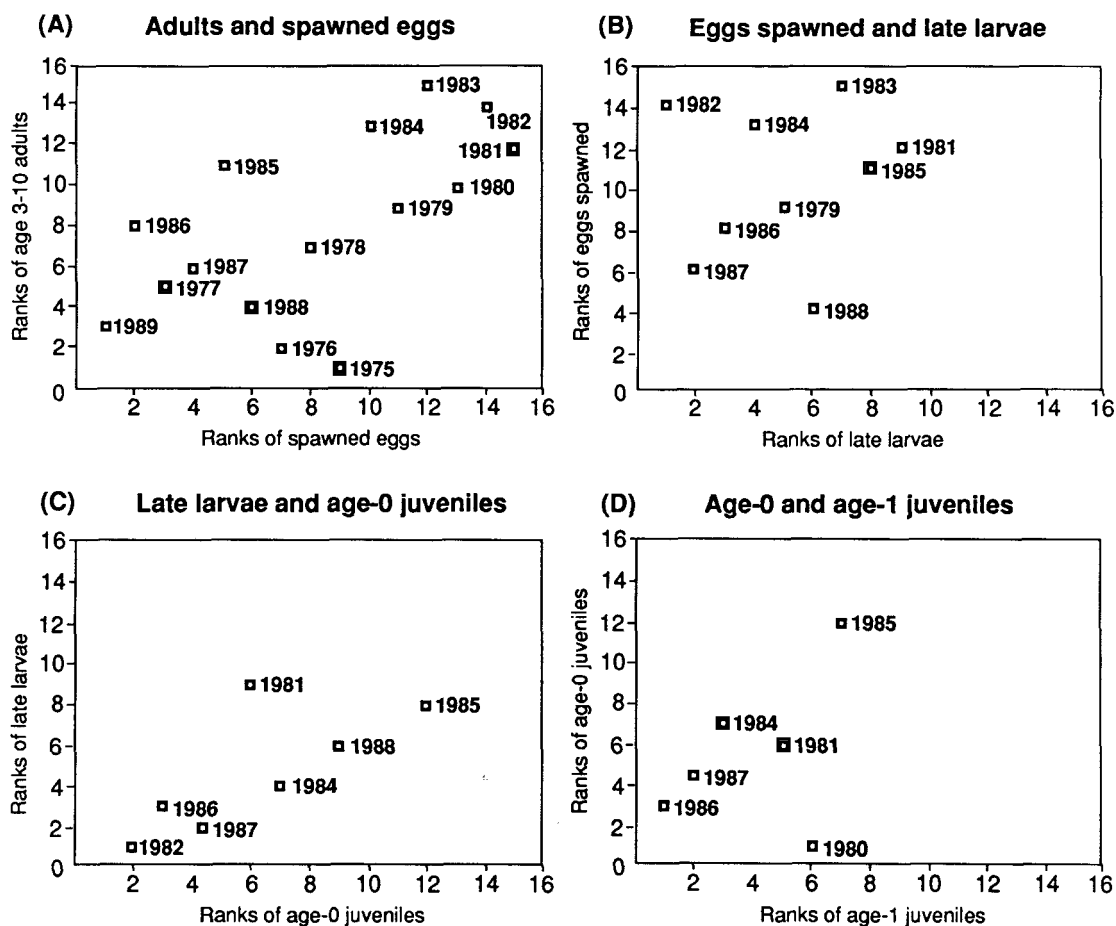


Figure 11. Comparisons of ranks of annual abundance estimates of walleye pollock from Shelikof Strait, Gulf of Alaska, at various stages. Positive relationships are indicated by values on a diagonal from the lower left to the upper right; negative relationships are indicated by values on the diagonal from upper left to lower right. Random scatter of values throughout a diagram indicates no relationship between abundance of the two stages.

to age-1 juveniles, and age-1 juveniles to age-3 recruits) for years when abundance estimates of both stages were available (figure 13). Because only indices of abundance of age-0 and age-1 juveniles were available, the "mortality" rates cannot be considered absolute, but rather a means of comparison among years. These rates were plotted against the abundance of the year class at the beginning of the time interval from which the rate was derived. A positive relationship on these plots would indicate that higher mortality occurs in years when abundance is high (density-dependent mortality). The plots of age-0 and age-1 juveniles showed no pattern, but the plot of the late larvae indicated that density-dependent mortality may occur between the late larval and age-0 stages. Sources of such mortality should be investigated but may include increased predation on young walleye pollock when they are exceptionally abundant, or reduced food levels because the feeding

requirements of the walleye pollock exceed the production capacity of their prey.

Overall, a weakly negative relationship is indicated between the numbers of eggs produced and the resulting numbers of recruits (figure 12A). Earlier studies have also revealed this relationship (Megrey 1989). This indicates that some density-dependent mechanism affected the prerecruits. With the intense nature of the spawning, egg cannibalism was a plausible mechanism. However, examination of stomach contents of adults in the spawning area during the time of spawning and egg presence over a three-year period revealed that no more than 10% of the eggs were eaten by adults (Brodeur et al. 1991). Another mechanism would be a decrease in egg size—and thus size of larvae at hatching—at large stock sizes. Indeed it was found that size at hatching was dependent on egg size, but also that interannual variations in egg size were not correlated

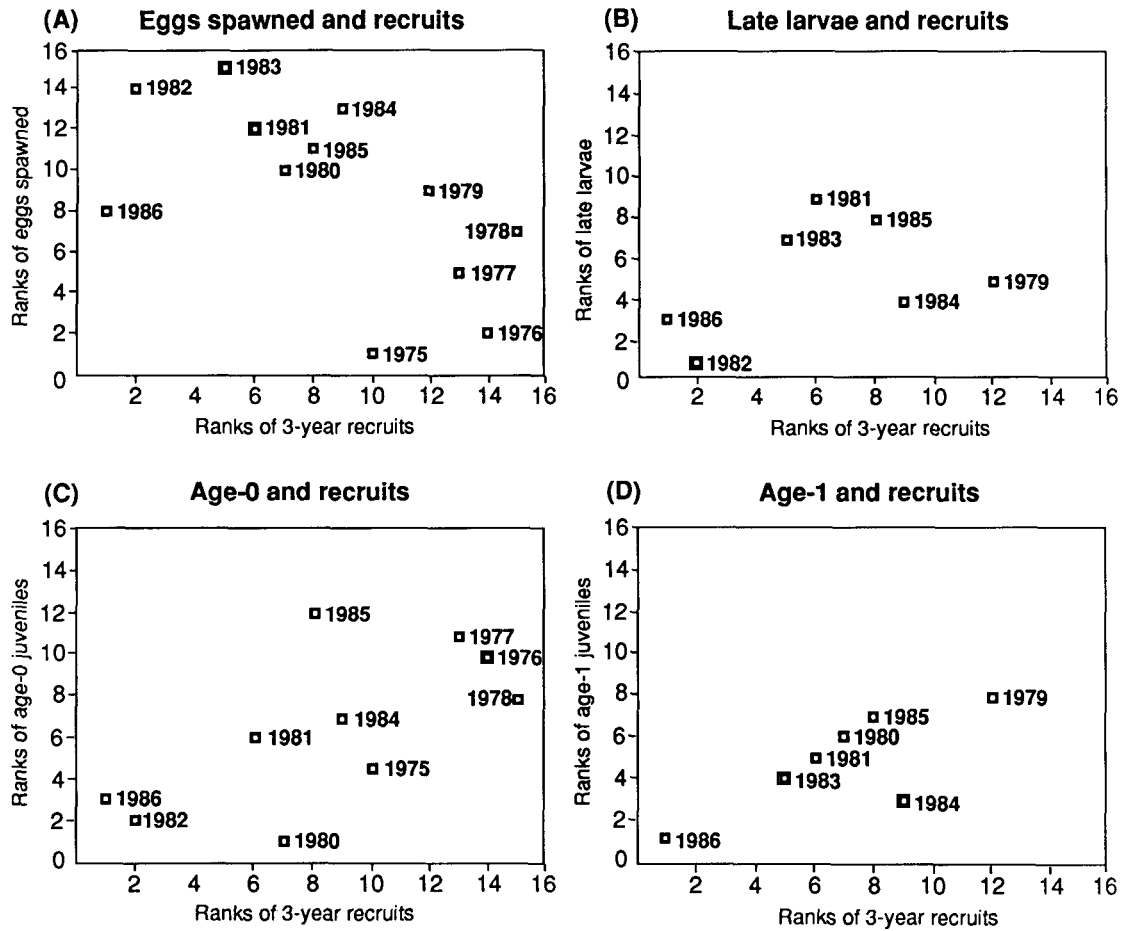


Figure 12. Comparisons of ranks of annual abundance estimates of 3-year-old recruits and various other stages of walleye pollock from Shelikof Strait, Gulf of Alaska. Positive relationships are indicated by values on a diagonal from the lower left to the upper right; negative relationships are indicated by values on the diagonal from upper left to lower right. Random scatter of values throughout a diagram indicates no relationship between abundance of the two stages.

with size of the spawning stock (Hinckley 1990). Given the short time series of data available, it is possible that the observed relationship of spawners and recruits is spurious. This is indicated by the fact that the numbers of late larvae bore no relationship to numbers of eggs produced.

Walleye pollock recruitment also seems to be negatively related to the large-scale climatic indicator NEPPI, which indicates storminess in the Gulf of Alaska. High NEPPI values are produced when the Aleutian Low is intense; low values indicate that the low is weak, absent, or displaced. Thus low recruitment seems to result from stormy years (Schumacher and Kendall 1989). On a smaller scale, birthdate distributions have shown increased mortality following April and May storms in the area of larval occurrence. Good larval survival occurs when there is calm weather during the week after hatching (K. M. Bailey, NMFS, Seattle, and S. A. Macklin, ERL, Seattle, pers. comm.). Olla and Davis (1990)

have shown in the laboratory that larvae avoid turbulence. Storms may increase mortality by decreasing food availability, destroying food patches, or decreasing insolation required for phytoplankton production. Incze et al. (1990) followed a patch of larvae marked by a drogue during the passage of a storm and investigated the storm's effects on microzooplankton's vertical distribution and abundance. Although the mixed layer and level of maximum microzooplankton deepened during the storm, quantities of prey remained >30 organisms per liter (well above a successful feeding threshold of 10 per liter) somewhere in the upper 45 m of the water column. Birthdate distributions of larvae collected later that year showed minimal survival of the first-feeding larvae that were present during the storm (K. M. Bailey, NMFS, Seattle, and S. A. Macklin, ERL, Seattle, pers. comm.), so some factor other than food availability may contribute to storm-related larval mortality.



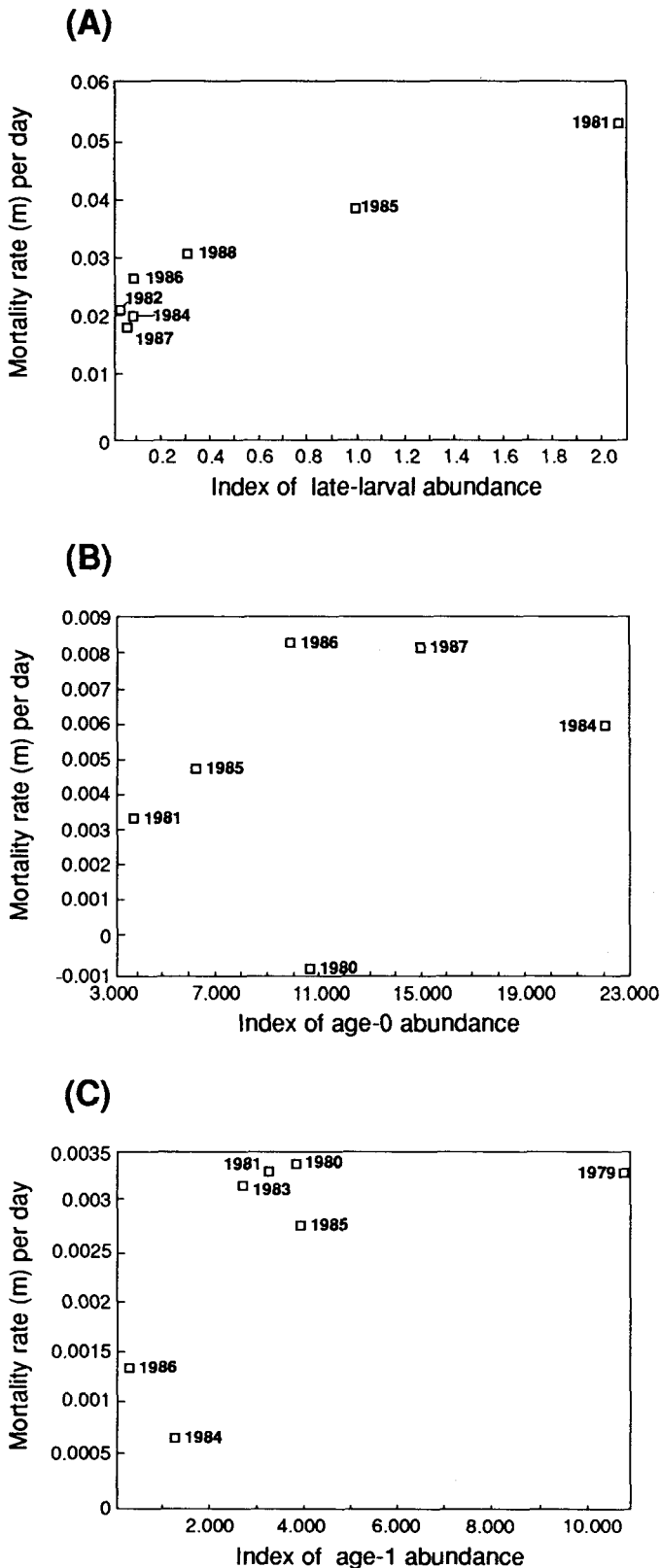


Figure 13. Estimates of daily mortality rates between successive stages and abundance estimates of the initial stage for walleye pollock from Shelikof Strait, Gulf of Alaska. (A) Late larvae to age-0 juveniles; (B) age-0 juveniles to age-1 juveniles; (C) age-1 juveniles to age-3 recruits.

## SUMMARY

Since 1984, the FOCI program has been conducting fisheries oceanographic research in order to understand how the environment affects recruitment to the walleye pollock stock in Shelikof Strait, Alaska. This research was based on fundamental knowledge of the physical environment and, to a lesser degree, knowledge of fisheries biology. We have focused on transport of the planktonic stages toward nursery grounds, and processes affecting mortality as the animals are transported. We consider the following observations to be of major importance in understanding how the environment is related to recruitment of walleye pollock.

1. Circulation is dominated by the Alaska Coastal Current, which is one of the strongest and most persistent currents along the coasts of North America. Although most volume transport throughout the water column is directed seaward through the Shelikof sea valley, approximately 75% of the water in the upper 50 m appears to stay on the continental shelf.

2. A persistent, relatively weak flow of slope water into the sea valley provides a nutrient source under and (at the near surface) to the south of the ACC. Interannual variations in bottom-water properties have been related to circulation anomalies in the Gulf of Alaska.

3. Baroclinic instability and wind-driven flow out of Wide Bay form features that tend to concentrate and retain larvae on the shelf. The role of these features in larval retention, and the potential impact on secondary production and larval mortality are ongoing topics of research.

4. Strong spatial variations in the wind field can cause an area of convergence of the surface-layer currents. The scale of this feature is consistent with the observed size of the patch of walleye pollock larvae.

5. During the 1980s, several adjacent strong year classes (1975-79) moved through the Shelikof Strait population of walleye pollock, causing a variation in numbers of adults from 6.0 to 1.3 billion. Only weak or moderate year classes have occurred since 1979. Thus during our studies we have not had the opportunity to observe conditions leading to a strong year class: interannual variations in the physical environment, and in the early life history of walleye pollock have resulted in only minor changes in year-class size.

6. There is little interannual variation in the timing and location of walleye pollock spawning and egg and larval development within the Shelikof Strait system. The fish spawn primarily in early April over the deep trench near Cape Kekurnoi. The

eggs stay mainly below 150 m in the water column and are advected little during their two-week incubation period. The larvae develop in the upper 50 m of the water column and are advected to the southwest as they grow at about 2 mm d<sup>-1</sup> during late April and May. During this time the larvae are often in large patches and have been found entrained in eddies, which increase their residence time in the area and lessen their chances of being advected offshore.

7. Observable growth of surviving larvae varies little. Condition of larvae varies with season and location. Insufficient food may be available early in the spawning season. Larvae in eddies seem to be in better feeding condition than those outside eddies.

8. Events during the egg and early larval stages are important in establishing year-class size, which is unrelated to the number of eggs spawned. Year-class size seems largely determined by the end of the larval period, although events during the following summer may also reduce the year class. Storms during the early larval period may be particularly detrimental to survival, but the mechanism is not yet clear. An index of storminess in the Gulf of Alaska may provide a way of predicting year-class size.

Although much has been discovered about pollock, their environment, and processes that link the fish to their environment, there are many gaps in our observations and understanding of recruitment. Some important questions that FOCI research will attempt to address include: How beneficial is it for larvae to be within an eddy; is it a relatively food-rich safe haven or does it provide a concentrated source of food for predators? What mechanisms generate eddies; how often are they formed; what is their time history and relation to the general circulation? What processes are involved in the relation between wind mixing and survival of early larvae? What are the important survival processes during late larval and early juvenile life, and are these density dependent? How well are local wind, current, and mixing related to NEPPI? The answers to these questions will greatly enhance our understanding of environmental influences on the early stages of walleye pollock in the western Gulf of Alaska.

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#### LITERATURE CITED

- Bailey, K. M., and S. Spring. In press. Comparisons of larval, age-0 juvenile and age-3 recruit abundance indices of walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska. J. Conseil.
- Bailey, K. M., and C. L. Stehr. 1986. Laboratory studies on the early life history of the walleye pollock, *Theragra chalcogramma* (Pallas). J. Exp. Mar. Biol. Ecol. 99:233-246.
- . 1988. The effects of feeding periodicity and ration on the rate of increment formation in otoliths of larval walleye pollock *Theragra chalcogramma* (Pallas). J. Exp. Mar. Biol. Ecol. 122:147-161.
- Baird, T. A., and B. L. Olla. 1991. Social and reproductive behavior of walleye pollock, *Theragra chalcogramma*, in a captive group. Environ. Biol. Fish. 30:295-301.
- Bakkala, R. G., V. G. Weststad, and L.-L. Low. 1987. Historical trends in abundance and current condition of walleye pollock in the eastern Bering Sea. Fish. Res. 5:199-216.
- Beamish, R. J., G. A. McFarlane, and W. S. Wooster. 1989. The need for interdisciplinary research in fisheries and ocean sciences. In Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, R. J. Beamish and G. A. McFarlane, eds. Canadian special pub. of Fisheries and Aquatic Sciences 108:1-3.
- Brodeur, R. D., K. M. Bailey, and S. Kim. 1991. Cannibalism on eggs by walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 71:203-218.
- Brown, A. L., and K. M. Bailey. In press. Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska. Mar. Biol.
- Cooney, R. T. 1987. Zooplankton. In The Gulf of Alaska, physical environment and biological resources, D. W. Hood and S. T. Zimmerman, eds. U.S. Gov. Printing Office (NTIS#PB87-103230), pp. 285-303.
- Dunn, J. R., and A. C. Matarese. 1987. A review of the early life history of northeast Pacific gadoid fishes. Fish. Res. 5:163-184.
- Emery, W. J., and K. Hamilton. 1985. Atmospheric forcing of interannual variability in the northeast Pacific Ocean: connections with El Niño. J. Geophys. Res. 90:857-868.
- FAO. 1990. Yearbook of fishery statistics. Food and Agriculture Organization of the United Nations, Rome, p. 15.
- Fishing News International. 1985. World catch: total remains below 77 million tons. Fish. News Int. 25:50-51.
- Hinckley, S. 1990. Variation in egg size of walleye pollock (*Theragra chalcogramma*) with a preliminary examination of the effect of egg size on larval size. Fish. Bull., U.S. 88:471-483.
- Hinckley, S., K. M. Bailey, S. J. Picquelle, J. D. Schumacher, and P. J. Stabeno. 1991. Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska in 1987. Can. J. Fish. Aquat. Sci. 48:91-98.
- Incze, L. S., A. W. Kendall, Jr., J. D. Schumacher, and R. K. Reed. 1989. Interactions of a mesoscale patch of larval fish (*Theragra chalcogramma*) with the Alaska Coastal Current. Cont. Shelf Res. 9:269-284.
- Incze, L. S., P. B. Ortner, and J. D. Schumacher. 1990. Microzooplankton, vertical mixing and advection in a larval fish patch. J. Plankton Res. 12:365-379.

- Ingraham, W. J., Jr., and R. K. Miyahara. 1989. Tuning of the OSCURS numerical model to ocean surface current measurements in the Gulf of Alaska. NOAA Tech. Memo. NMFS F/NWC-168, 67 pp.
- Ingraham, W. J., Jr., R. K. Reed, J. D. Schumacher, and S. A. Macklin. 1991. Interannual variability of circulation in the Gulf of Alaska in relation to water properties and fisheries resources. EOS, Trans. Am. Geophys. Union, 72, p. 257.
- Kendall, A. W., Jr., and S. Kim. 1989. Buoyancy of walleye pollock (*Theragra chalcogramma*) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska. In Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, R. J. Beamish and G. A. McFarlane, eds. Canadian special pub. of Fisheries and Aquatic Sciences 108:69-180.
- Kendall, A. W., Jr., and S. J. Picquelle. 1990. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Fish. Bull., U.S. 88:133-154.
- Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert. 1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull., U.S. 85:499-521.
- Kendall, A. W., Jr., L. S. Incze, P. B. Ortner, and S. Cummings. In press. Vertical distribution of walleye pollock *Theragra chalcogramma* eggs and larvae. Fish. Bull., U.S.
- Kim, S. 1989. Early life history of walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska. In Proceedings of the International Symposium on the Biology and Management of Walleye Pollock, November 14-16, 1988, Fairbanks, AK. Alaska Sea Grant Rep. 89-1, Univ. Alaska, Fairbanks, pp. 117-139.
- Kim, S., and D. R. Gunderson. 1989. Cohort dynamics of walleye pollock in Shelikof Strait, Gulf of Alaska, during the egg and larval periods. Trans. Am. Fish. Soc. 118:264-273.
- Kim, S., and A. W. Kendall, Jr. 1989. Distribution and transport of larval walleye pollock (*Theragra chalcogramma*) in Shelikof Strait, Gulf of Alaska, in relation to water movement. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 191:127-136.
- Kim, S., and E. P. Nunnallee. 1990. Distribution of walleye pollock, *Theragra chalcogramma*, spawning in Shelikof Strait, Gulf of Alaska, based on acoustic and ichthyoplankton surveys 1981, 1984 and 1985. Bull. Korean Fish. Soc. 23:425-438.
- Lawrence, L. A., J. Gray, and D. M. Blood. 1991. Fisheries-Oceanography Coordinated Investigations (FOCI) field operations—1987. NOAA Data Report ERL PMEL-28, 61 pp.
- Macklin, S. A., J. E. Overland, and J. P. Walker. 1984. Low-level gap winds in Shelikof Strait. Third Conference on Meteorology of the Coastal Zone, January 9-13, 1984, Miami, FL. Am. Meteorol. Soc. pp. 97-102.
- Matarese, A. C., D. B. Blood, and M. M. Yoklavich. In press. Embryonic development of walleye pollock *Theragra chalcogramma* from Shelikof Strait, Gulf of Alaska. Fish. Bull., U.S.
- Megrey, B. A. 1989. Population dynamics of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. Ph.D. dissertation, University of Washington, Seattle, 385 pp.
- Mysak L., R. D. Muench, and J. D. Schumacher. 1981. Baroclinic instability in a downstream varying channel: Shelikof Strait, Alaska, J. Phys. Oceanogr. 11(7):950-969.
- Niebauer, H. J. 1988. Effects of El Niño-Southern Oscillation and North Pacific weather patterns on interannual variability in the subarctic Bering Sea. J. Geophys. Res. 93:5051-5068.
- Norcross, B. L., and R. F. Shaw. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Trans. Am. Fish. Soc. 113:153-165.
- Olla, B. L., and M. W. Davis. 1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63:105-112.
- Reed, R. K., and J. D. Schumacher. 1981. Sea level variations in relation to coastal flow around the Gulf of Alaska. J. Geophys. Res. 86(C):6543-6546.
- . 1987. Physical oceanography. In The Gulf of Alaska, physical environment and biological resources, D. W. Hood and S. T. Zimmerman, eds. U.S. Gov. Printing Office (NTIS# PB87-103230), pp. 57-75.
- . 1989a. Transport and physical properties in central Shelikof Strait, Alaska. Cont. Shelf Res. 9:261-268.
- . 1989b. Some mesoscale features of flow in Shelikof Strait, Alaska. J. Geophys. Res. 94:12,603-12,606.
- Reed, R. K., J. D. Schumacher, and L. S. Incze. 1987. Circulation in Shelikof Strait, Alaska. J. Phys. Oceanogr. 17:1546-1554.
- Reed, R. K., J. D. Schumacher, and A. W. Kendall, Jr. 1988. NOAA's Fisheries Oceanography Coordinated Investigations in the western Gulf of Alaska. EOS, Trans. Am. Geophys. Union 69:890-894.
- Reed, R. K., L. S. Incze, and J. D. Schumacher. 1989. Estimation of the effects of flow on dispersion of larval pollock (*Theragra chalcogramma*) in Shelikof Strait, Alaska. In Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, R. J. Beamish and G. A. McFarlane, eds. Canadian special pub. of Fisheries and Aquatic Sciences 108:239-246.
- Roach, A. T., and J. D. Schumacher. 1991. Observations of seasonal and interseasonal variability in Shelikof Strait, Alaska. Proc. 7th Symp. on Coastal and Ocean Mgt., Coastal Zone 91:3304-3317.
- Rothschild, B. J. 1986. Dynamics of marine fish populations. Cambridge: Harvard University Press, 277 pp.
- Royer, T. C. 1981. Baroclinic transport in the Gulf of Alaska. Part II. Freshwater driven coastal current. J. Mar. Res. 39:251-266.
- . 1982. Coastal fresh water discharge in the northeast Pacific. J. Geophys. Res. 87:2017-2021.
- Schumacher, J. D., and A. W. Kendall, Jr. 1989. Fisheries Oceanography Coordinated Investigations (FOCI): walleye pollock recruitment in the western Gulf of Alaska. In Proceedings of the Gulf of Alaska, Cook Inlet, and North Aleutian Basin Information Update Meeting, OCSEAP/MMS (OCS Study, MMS 89-0041), Anchorage, AK, pp. 39-47.
- Schumacher, J. D., and R. K. Reed. 1980. Coastal flow in the northwest Gulf of Alaska: the Kenai Current. J. Geophys. Res. 85:6680-6688.
- . 1986. On the Alaska Coastal Current in the western Gulf of Alaska. J. Geophys. Oceanogr. 91:9655-9661.
- Schumacher, J. D., P. J. Stabeno, and A. T. Roach. 1989. Volume transport in the Alaska Coastal Current. Cont. Shelf Res. 9:1071-1089.
- Schumacher, J. D., W. E. Barber, B. Holt, and A. K. Liu. In press. Satellite observations of mesoscale features in Lower Cook Inlet and Shelikof Strait, Alaska. NOAA-ERL Tech. Rep.
- Stabeno, P. J., and R. K. Reed. In press. Recent Lagrangian measurements along the Alaskan Stream. Deep Sea Res.
- Stabeno, P. J., J. D. Schumacher, L. S. Incze, and S. J. Picquelle. 1990. Modelling the diffusion and advection of pollock larvae in the Gulf of Alaska. EOS, Trans. Am. Geophys. Union. 71:93.
- Vastano, A. C., and S. E. Borders. 1984. Sea surface motion over an anticyclonic eddy on the Oyashio front. Remote Sens. Environ. 16:87-90.
- Yamashita, Y., and K. M. Bailey. 1990. A laboratory study of the bioenergetics of larval walleye pollock *Theragra chalcogramma*. Fish. Bull., U.S. 87:525-536.
- Yoklavich, M. M., and K. M. Bailey. 1990. Hatching period, growth and survival of young walleye pollock *Theragra chalcogramma* as determined from otolith analysis. Mar. Ecol. Prog. Ser. 64:13-2.