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A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea

J. M. NAPP,[1,*] **A. W. KENDALL JR**[1] **AND J. D. SCHUMACHER**[2,3]

[1]*NOAA/Alaska Fisheries Science Center, Seattle, WA 98115, USA*
[2]*NOAA/Pacific Marine Environmental Laboratory, Seattle, WA 98115, USA*
[3]*Present Address: Two Crow Environmental Consultants, Silver City, NM 88062, USA*

ABSTRACT

Biological and physical phenomena that affect conditions for larval survival and eventual recruitment differ in the oceanic and shelf regions. In the oceanic region, 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 eddies are transported onto the shelf, thereby providing larvae to the Outer Shelf Domain. Advection, rather than local production, dominated the observed springtime increase in chlorophyll (often a correlate of larval food) in the oceanic region. Over two-thirds of the south-eastern shelf, eddies are absent and other phenomena are important. Sea ice is a feature of the shelf region: its interannual variability (time of arrival, persistence, and areal 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. In the oceanic region, interannual variation in food for first-feeding pollock larvae is determined by advection; in the shelf region, it is the coupled dynamics of the atmosphere–ice–ocean system.

Key words: Bering Sea, circulation, fisheries oceanography, larval feeding, larval fish survival

INTRODUCTION

The Bering Sea is the site of some of the most productive fisheries in the North Pacific Ocean. Besides the lucrative king crab, halibut, and salmon fisheries, 50% of the world 1998 catch of walleye pollock (*Theragra chalcogramma*) came from the Bering Sea (estimated total catch = 3.4 million tonnes; V. Wespestad, personal communication, Resource Analyst International). Pollock is the most abundant species harvested in the Bering Sea, accounting for >65% of the total groundfish biomass (Bakkala *et al.*, 1987). Pollock, of which the total biomass in the Bering Sea during the 1980s exceeded 20 million tonnes, is harvested in Bering Sea waters of the exclusive economic zones (EEZ) of Russia and the US (Wespestad, 1993). Formerly there was a large pollock fishery in international waters of the Bering Sea basin (known as the 'doughnut hole'), but it is now closed. The annual US catch of pollock in the Bering Sea in recent years has amounted to 1.3 million tonnes, with an ex-vessel value of $210 million (USD). Pollock are important to the Bering Sea ecosystem, providing most of the food for the extensive marine mammal and bird populations found there (Springer and Byrd, 1989; Lowry *et al.*, 1996; Sinclair *et al.*, 1996).

Pollock in the Bering Sea do not form one homogeneous population, but the actual number and distribution of distinct stocks are not known. For example, distributions of pollock eggs show a broad geographical range (Fig. 1). Research using spawning adult 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 indicate that there are differences between pollock from the eastern and western parts of the Bering Sea (Bailey *et al.*, 1999). Within the eastern Bering Sea, there are several spawning areas, and these may also be discrete stocks (Hinckley, 1987). Higher-resolution molecular techniques (more pollock-specific microsatellite primers) are needed to determine whether or not separate stocks exist in the eastern Bering Sea (Bailey *et al.*, 1999).

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*Correspondence. e-mail: jeff.napp@noaa.gov
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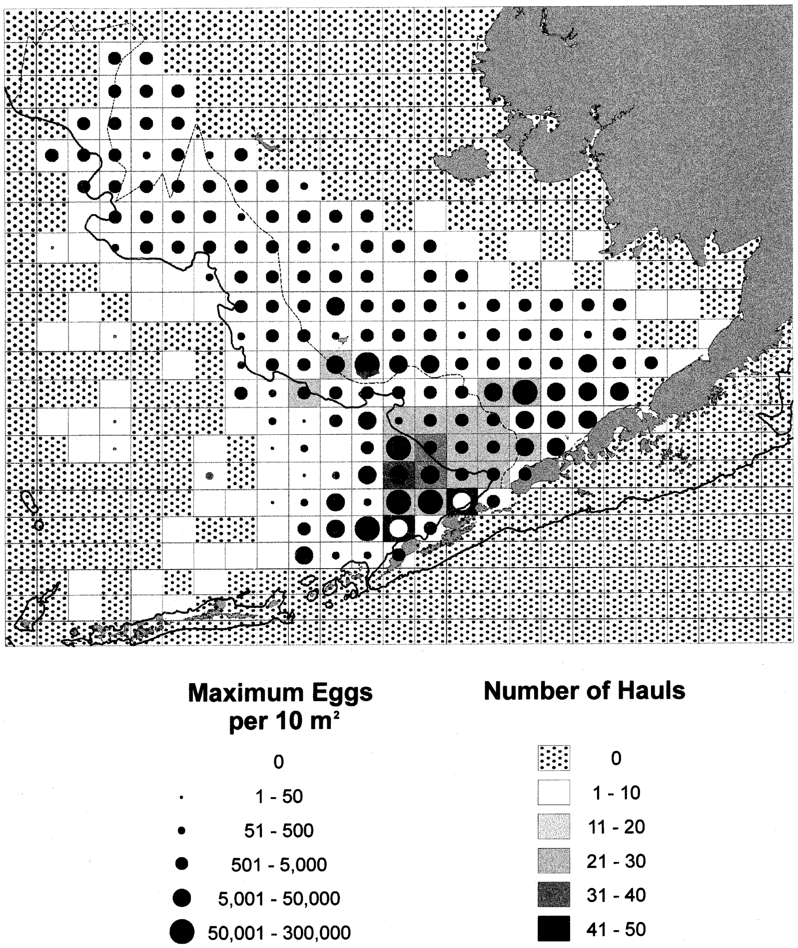


Figure 1. Maximum densities of walleye pollock eggs in the south-eastern Bering Sea, February to May 1971–1993 ($N = 15$ cruises; Dell Arciprete, personal communication). Sampling effort and maximum number of eggs found per quadrant are indicated by the key. The thick black line is the 200 m isobath; the dashed line is the 100 m isobath. Note the widespread distribution of eggs with centres of abundance in the oceanic (>200 m) and shelf (<200 m) regions.

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 fishery quotas and harvest levels. Knowledge of processes that strongly affect larval survival would provide early evidence for emerging year-class strength. To understand recruitment variations, we must understand the relations among various spawning populations, and the contribution of each to recruitment of the entire stock. Recruitment in Bering Sea pollock, as in most other marine fishes, is thought to be largely set during their first year (Rothschild, 1986; Kendall and Duker, 1998). On average, 66–84% of Gulf of Alaska walleye pollock generational mortality occurred in the first 5 months of life (Bailey *et al.*, 1996). Studies on causes of mortality of these early life history stages of pollock are needed to understand recruitment variation (Kendall *et al.*, 1996).

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 interdisciplinary 5-year (1992–1996) study – Bering Sea Fisheries Oceanography Coordinated Investigations (BS FOCI; Schumacher and Kendall, 1995). The programme's goals were: (1) to determine stock structure in the Bering Sea and its potential relationship to physical oceanography; and (2) to examine recruitment processes in the eastern Bering Sea. The major emphasis of the recruitment studies was to determine the dominant physical oceanographic features (e.g. turbulence, temperature, sea ice and transport) that could influence survival of pollock larvae, either directly or indirectly, through modulation of food production for larvae. Other regional studies (not reported here) examined the direct affect of transport on survival (Wespestad *et al.*, in press).

A switch model (cf. Megrey *et al.*, 1996) was developed as the conceptual framework guiding the recruitment research (Fig. 2). The model represents successive environmental conditions that must occur for walleye pollock larvae to survive. The switches are

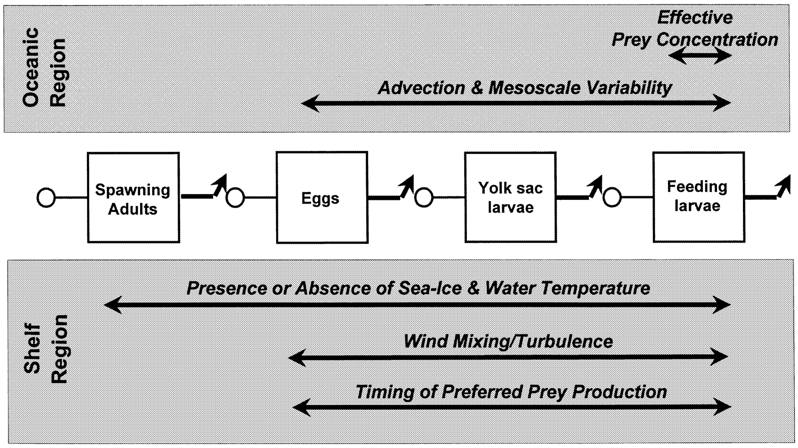


Figure 2. Switch model of walleye pollock early larval dynamics in the south-eastern Bering Sea. Each box represents a life history stage through which survivors must pass. Biophysical processes thought to be important regulators of survival variability are shown separately for the oceanic and shelf regions.

relevant to individuals, cohorts, and populations. Field studies of recruitment processes included 20 cruises to the area, deployment of four, long-term biophysical moorings, and use of over 40 satellite-tracked drifters. Our research focused on modulation of food supply as affected by physical processes. We assumed that interannual variability of larval survival resulted, in part, from variability in food resources. In this article, results of research by Bering Sea FOCI on recruitment processes are synthesized to address two working hypotheses: (1) local processes dominate prey production over the shelf, and regional processes dominate prey production in the oceanic region; and (2) larval prey concentrations are higher over the shelf than the oceanic region.

PHYSICAL OCEANOGRAPHIC SETTING

The Bering Sea (Fig. 3a), a semi-enclosed portion of the North Pacific Ocean, is divided almost equally between a deep basin (maximum depth 3500 m) and a continental shelf (<200 m) which are separated by a convoluted continental slope. 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 Bering Sea occurs mainly through the deeper western passes, although transport through the eastern passes is important to regional circulation and water properties. This net northward transport of shelf water requires an onshelf flux of nutrient-rich water for mass balance because other sources (river discharge, flow through Unimak Pass) account for only 50% of the total. Several processes have been observed that bring oceanic water on to the shelf (Stabeno *et al.*, 1999a).

Within the broad (>500 km) shelf region of the south-eastern Bering Sea, three distinct Domains (Fig. 3b) exist spring through fall that are characterized by contrasts in the vertical structure of the water column, currents and biota (Iverson *et al.*, 1979a; Coachman, 1986). 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 a layer of slowly increasing density). The Domains provide habitats with different physical properties for the biota. The zooplankton community in the two shallower domains is composed primarily of the small copepods and euphausiids, whereas in the Outer Shelf Domain and oceanic region large copepods dominate (Cooney and Coyle, 1982; Vidal and Smith, 1986).

General circulation

A cyclonic gyre dominates circulation with a western boundary current (Kamchatka Current) along the Asian side of the basin (Fig. 3a; 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.*, 1999a). This gyre is mainly an extension of the Alaskan Stream with the majority of volume transport ($6–12 \times 10^6$ m^3 s^{-1}) entering through the western 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 wind forcing shows that eastward and northward-propagating storm systems dominate the surface stress at short periods (<1 month), which

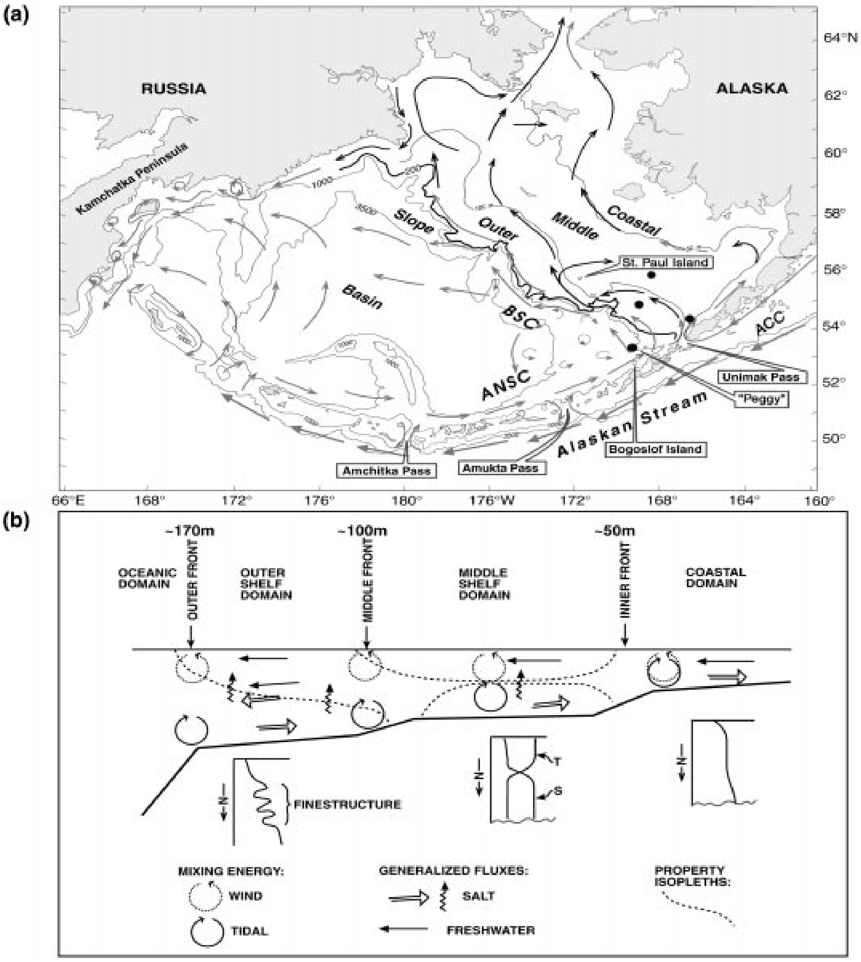


Figure 3. Bering Sea physical regime. (a) Major currents, upper ocean circulation (0–50 m) of the Bering Sea, and biophysical domains of the south-eastern Bering Sea shelf. The ● indicate locations of BS FOCI instrumented moorings. ANSC, Aleutian North Slope Current; BSC, Bering Slope Current; ACC, Alaska Coastal Current. (b) Water column structure and nominal depths separating the three shelf domains.

principally serve to mix the upper ocean (Bond *et al.*, 1994). At longer periods (>1 month), the wind-driven transport estimated by the Sverdrup method accounts for roughly one-half of the observed transport within the Kamchatka Current. Interannual variations in the Sverdrup transports are ≈25% of the mean. Thus, while wind-driven transport contributes to circulation, geostrophy in the form of the Alaskan Stream is the dominant forcing mechanism for general circulation in the Bering Sea.

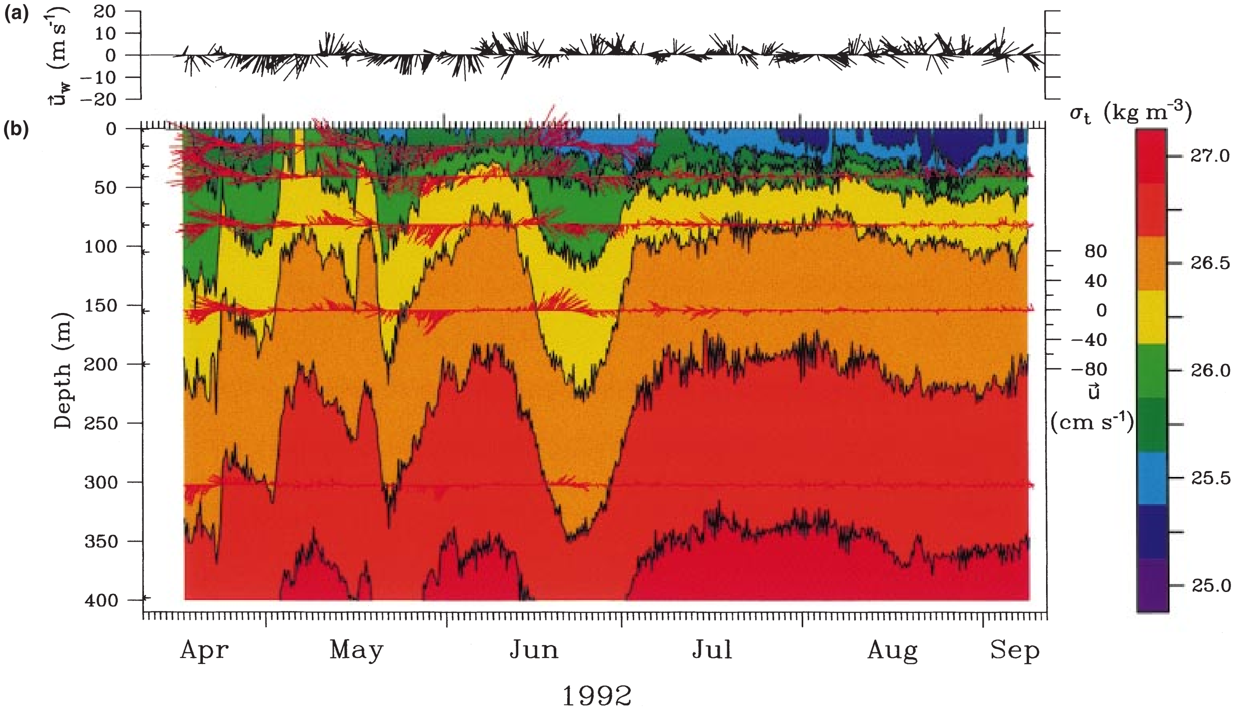
Northward inflows of the Alaskan Stream through Amchitka Pass and Amukta Pass (Fig. 3a) produce the eastward Aleutian North Slope Current (ANSC; Reed and Stabeno, 1999). The ANSC is often fairly narrow (<50 km) and shallow (upper 500 m), with peak speeds >40 cm s^{-1}. Eddy-like features occur in this current and some are formed by flow through Amukta Pass (Schumacher and Stabeno, 1994). The ANSC typically transports $2–4 \times 10^{6}$ m^{-3} s^{-1}, providing the main source of the north-westerly Bering Slope Current (BSC), while having a profound impact on the subsurface thermal environment (Reed, 1996) and circulation (Schumacher and Stabeno, 1994; Reed and Stabeno, 1999). The BSC exists in two modes: an ill-defined, highly variable flow interspersed with eddies, meanders and instabilities or a more regular north-westward-flowing current (Stabeno *et al.*, 1999a). It is likely that shelf–slope exchange mechanisms differ 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 region (including the spawning region near Bogoslof Island; Fig. 3a) to the Outer Shelf Domain, and we speculate that their inherent eddies provide habitat that may favour larval survival.

Mesoscale features and processes

Eddies are a ubiquitous feature of the south-eastern Bering Sea (Schumacher and Stabeno, 1994; Stabeno *et al.*, 1999a). Data from a moored instrument platform located over the south-eastern oceanic region (Peggy; Fig. 3a) provided the most complete time-series of water properties and currents over the south-eastern basin, to date. Results showed the influence of eddies on water properties, current velocity and chlorophyll concentration, and permitted a characterization of eddies as often being anticyclonic, 20–100 km in diameter, and extending to a depth of 400–1000 m with rotational speeds >20 cm s^{-1} (Fig. 4; Cokelet and Stabeno, 1997). Between 1986 and 1994, 45 satellite-tracked buoys were deployed in the oceanic region (Schumacher and Stabeno, 1994; Stabeno *et al.*, 1999a). In three of these years, buoys were deployed where larval pollock were abundant, and in all four cases, trajectories of the buoys defined eddies. Conversely, buoys ($N = 33$) that were not deployed in a larval patch did not indicate eddies. This association of pollock larvae and eddies may have a significant impact on larval survival (Schumacher and Stabeno, 1994). Eddies are also common in waters just seaward of the eastern shelf break (Schumacher and Reed, 1992). Until recently, eddies were not considered to play an important role in Outer Shelf Domain dynamics. A recent interpretation of hydrographic observations (Reed, 1998), however, suggests anticyclonic eddies sometimes exist even where water column depth is between 100 and 122 m. Shoaler than 100 m, eddies are uncommon.

Shelf–slope exchange can occur virtually anywhere along the shelf break north of Unimak Pass, but preferential transport onto the shelf has been observed in two regions: Bering Canyon (along the Aleutian Islands near Unimak Pass) and in the vicinity of the Pribilof Islands. An enhancement of nutrient concentrations has been observed near Unimak Pass and likely originates from ANSC waters interacting with canyon topography, i.e. up-canyon transport (Schumacher and Stabeno, 1998). South of the Pribilof Islands, the outer shelf narrows, and flow accelerates along the 100 m isobath which then turns northward (Stabeno *et al.*, 1999b). This phenomenon likely results in slope water being entrained onto the shelf from Pribilof Canyon (Schumacher and Stabeno, 1998) 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 onshelf trajectories of satellite-tracked drifters released over the canyon, and the presence of Outer Shelf Domain zooplankton taxa on the eastern side of the islands in the Middle Shelf Domain (Napp, unpublished; Stabeno *et al.*, 1999b). Shelf–slope exchange also occurs elsewhere along the shelf break. Episodic events of onshelf flow can result from both eddy–topography interactions and as a result of instabilities

Figure 4. Mesoscale eddies detected in the Bering Slope Current during spring and summer 1992 using moored instruments (Cokelet and Stabeno, 1997). (a) Wind speed, and direction measured at the mooring. (b) Sigma-T (colour contours) and current speed and direction. Isopycnal depression indicates the passage of eddies.



in the BSC, as revealed by drifter trajectories (Stabeno and van Meurs, 1999). Such trajectories also have shown movement of an eddy with high concentrations of pollock larvae onto the shelf (Schumacher and Stabeno, 1994). Moored current records at ≈56.7°N revealed that eddies were common over the slope and significantly contributed to onshore fluxes of salt and temperature (Schumacher and Reed, 1992). Regardless of the mechanisms, such episodic events of onshelf flow transport nutrients and, depending on time of year, pollock larvae onto the shelf.

Although most of the physical oceanographic research effort during BS FOCI was concentrated in the oceanic region, some studies and coordinated experiments were conducted on the shelf. For the first time, current and temperature measurements were collected from moored instruments around St Paul Island. The results showed that interaction of tidal currents with island topography resulted in a mean flow around the island (Stabeno *et al.*, 1999b). This result, together with those from prior satellite-tracked drifter trajectories, suggests that plankton (including pollock eggs and larvae) transported along the outer shelf can become incorporated in a trapped circulation around St Paul Island.

Three studies were conducted primarily over the middle shelf: a retrospective analysis of all available hydrographic data; a satellite-tracked drifter study of kinematics and diffusivity; and the first deployment over the Bering Sea shelf of moorings with instruments that measure both biological and physical properties. The hydrographic observations revealed an eastward flow from the vicinity of the Pribilof Islands across the middle shelf (Reed and Stabeno, 1996). Analysis of the drifter data revealed that the implied eddy diffusion coefficient was less than one-tenth of that required to satisfy salt and heat balances (P.J. Stabeno, personal communication). Current and temperature measurements from the moored array during ice cover revealed that advection played a critical role in bottom-layer temperature changes (Stabeno *et al.*, 1998). Previous dynamic models of the shelf used tidal diffusion to describe nutrient, heat, and salt transport (Coachman, 1986). These models must now be modified to include advection. At times advection is significant, and at different latitudes on this vast shelf different mechanisms may play the dominant role in cross-shelf fluxes. Future research is needed to describe how these mechanisms affect biota.

Sea ice and the cold pool

Seasonal sea ice extent fluctuates over 1000 km between the Bering Strait in summer and south to the Alaska Peninsula and shelf break in winter. Interannual variations occur in ice coverage (Fig. 5), time of advection over the open shelf and subsequent melt-back. The amount of production and advection of ice depends upon storm tracks, with greatest ice production occurring in years when the Aleutian Low is weaker than normal and northerly winds occur. Formation of sea ice generally begins in November, with maximum ice extent occurring in late March. Ice-free conditions typically exist from June to October (Niebauer 1988; Niebauer *et al.*, 1999). Other characteristics of sea ice cover that exhibit interannual variability over the south-eastern shelf 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, 1995a). Ice advection and eventual melting play a critical role in fluxes of heat and salt and in the

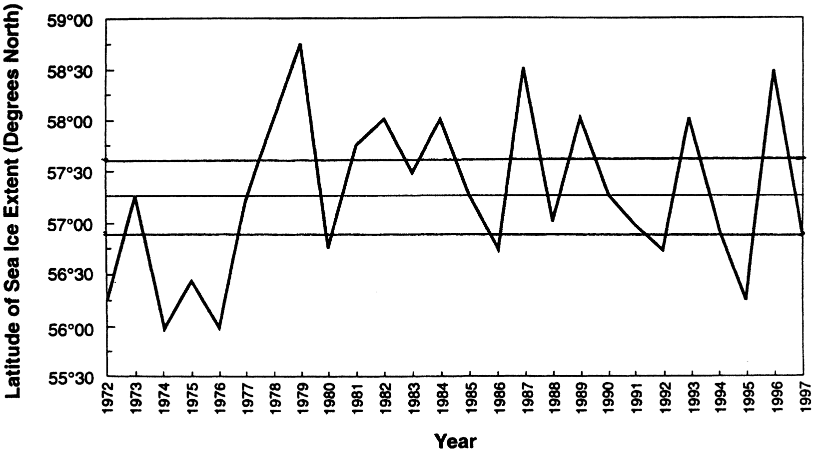


Figure 5. Time series of annual maximum sea ice extent 1972–1997 (redrawn from Wyllie-Echeverria and Wooster, 1998). The index is the southernmost latitude of seasonal sea ice extent along longitude 169°W in the Bering Sea. The 26-year mean (57°15′N) and standard deviation (±22′) are shown as solid horizontal lines.

generation of both baroclinic flow and the cold pool located over the Middle Shelf Domain (Wyllie-Echeverria, 1995a; Schumacher and Stabeno, 1998). The positive buoyancy from melting ice initiates both baroclinic transport along the marginal ice zone and stratification. Cooling and mixing associated with ice advance help to condition the entire water column over the Middle Shelf Domain (Stabeno *et al.*, 1998). Following ice cover, seasonal surface heating occurs; the lower layer becomes insulated and bottom temperatures often remain below 2.0°C (Reed, 1995). It is these waters that are commonly called the 'cold pool', the area of which varies by $\approx 2.0 \times 10^5$ km^2 between maximum and minimum extent. Also associated with the presence of sea ice is a bloom of phytoplankton (Stabeno *et al.*, 1998), which accounts for 10–65% of the total annual primary production (Niebauer *et al.*, 1990). Ice cover and the cold pool also influence distributions of higher trophic level biota (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995b).

PRODUCTION OF PREY FOR LARVAL POLLOCK – VARIABILITY IN THE TIMING AND MAGNITUDE OF THE SPRING PHYTOPLANKTON BLOOM

The Program's working hypotheses were: (1) interannual variability of larval survival results, in part, from variability in food resources; and (2) prey densities in the oceanic region are generally less than those encountered in the shelf region. We assumed that springtime production of most larval prey was initiated by the phytoplankton bloom. Thus, BS FOCI's research on lower trophic levels had two main objectives: to describe interannual variability in the timing of spring phytoplankton blooms, and to compare variability in springtime standing stocks of larval pollock prey between the oceanic and shelf regions. Variability in the timing and magnitude of the spring bloom is reported in this section, and variations in prey concentration are presented in the larval feeding section.

Prior to our studies, knowledge of spring phytoplankton bloom dynamics and the zooplankton community that produces prey for larval pollock was greatest for the shelf region (Iverson *et al.*, 1979a; Dagg *et al.*, 1984; Sambrotto *et al.*, 1986; Vidal and Smith, 1986). Little was known of the phytoplankton dynamics and pollock prey densities of the oceanic region, although the zooplankton community, in general, was well known (Motoda and Minoda, 1974; Iverson *et al.*, 1979b, Coyle *et al.*, 1996).

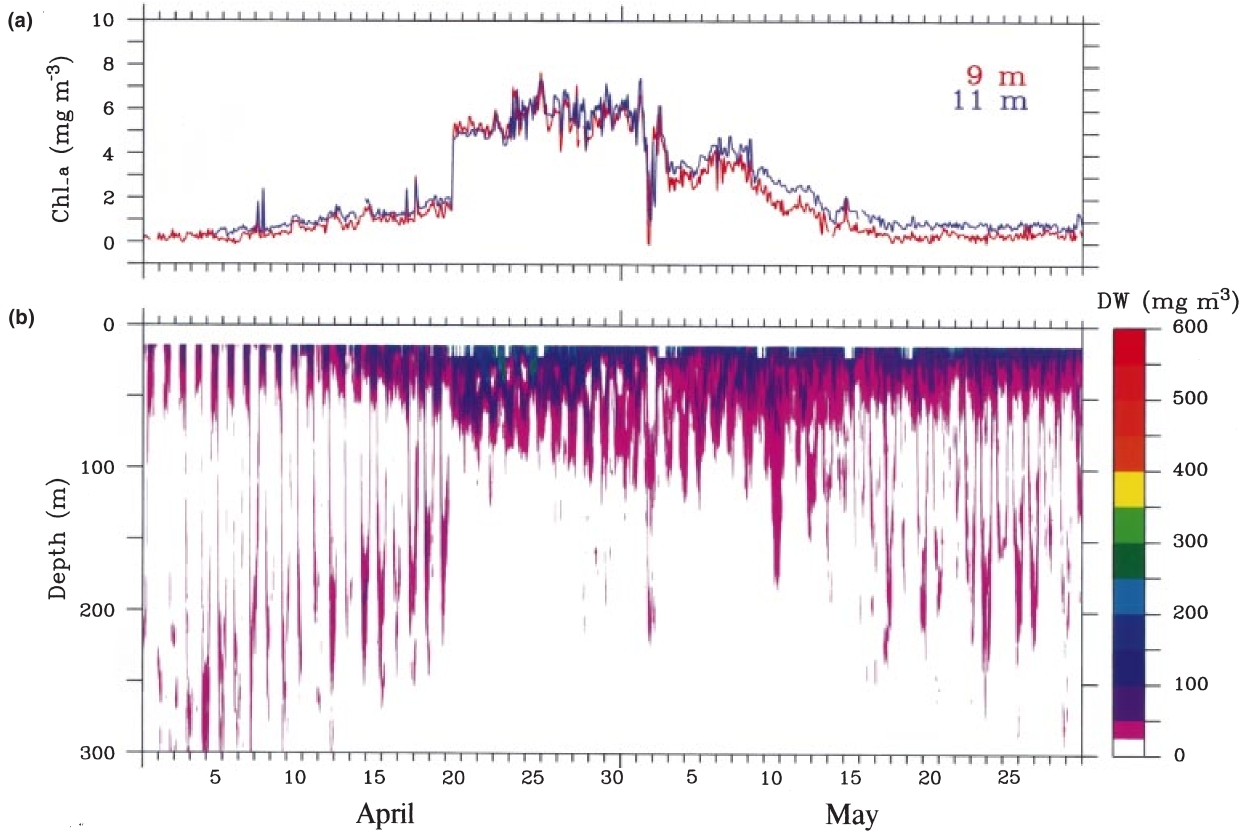
Oceanic region

Continuous time-series of phytoplankton biomass (chlorophyll absorbance; Davis *et al.*, 1997), wind speed, and incident radiation were obtained during multiple-month deployments (February to April and April to September) of moorings containing biological and physical sensors. In the spring of 1993, a gradual increase in chlorophyll concentration was interrupted by a sharp (fourfold), rapid (<1 day) increase (Fig. 6a). Elevated concentrations at the mooring persisted for ≈20 days before gradually returning to lower, pre-event levels. A simultaneous increase in the mixed layer depth (from 65 to 78 m) and appearance of warmer surface water (Cokelet and Stabeno, 1997, Plate 2e) suggest that the large increase in phytoplankton biomass arose through advection rather than *in situ* growth. Currents were weak (≈ 10 cm s^{-1}), however, during the transition period, but rotated from south-westward to eastward (Cokelet and Stabeno, 1997, Plate 2b). The same pattern was observed in the spring of 1994, although the sharp increase in chlorophyll occurred over a slightly longer time period. Note that during the 1993 event, the diel vertical migration pattern of sound scatterers (RDI 150 kHz Acoustic Doppler Current Profiler, ADCP) radically changed (Fig. 6b). These measurements support the previous point that mesoscale physical variability over the continental slope is important, and demonstrate that at times biological and physical variability are strongly linked in this system. In some years the Bering Slope Current is eddy-rich; pollock larvae are found in association with spring Slope Current eddies (Schumacher and Stabeno, 1994). To the extent that phytoplankton biomass is a proxy for larval prey concentrations, larvae that find themselves in these dynamic features may have a lower probability of starvation than those outside such features.

Shelf region

Moored biological and physical instruments enabled us to observe previously unreported dynamics of an under-ice spring phytoplankton bloom. In 1995, when sea ice extent was much further south than usual and persisted longer than average, we measured a single, large, early phytoplankton bloom over the Middle Shelf Domain (≈72 m of water). It began in mid-March; the chlorophyll concentration at 7 m steadily increased until late April despite an unstable water column in late March (Fig. 7; Stabeno *et al.*, 1998). Before these observations, ice-associated spring blooms were described as ice-edge phenomena where initiation of positive net growth followed water column

Figure 6. A rapid change in springtime oceanic chlorophyll concentration and zooplankton biomass. The change in conditions occurred on 21 April 1993, indicating an advective event (E.D. Cokelet, unpublished). (a) Chlorophyll concentration (mg m^{-3}) from two depths. (b) ADCP-derived zooplankton biomass (mg dry weight m^{-3}) as a function of depth. Observations were recorded using Greenwich Mean Time (GMT): subtract 8 h for local time.



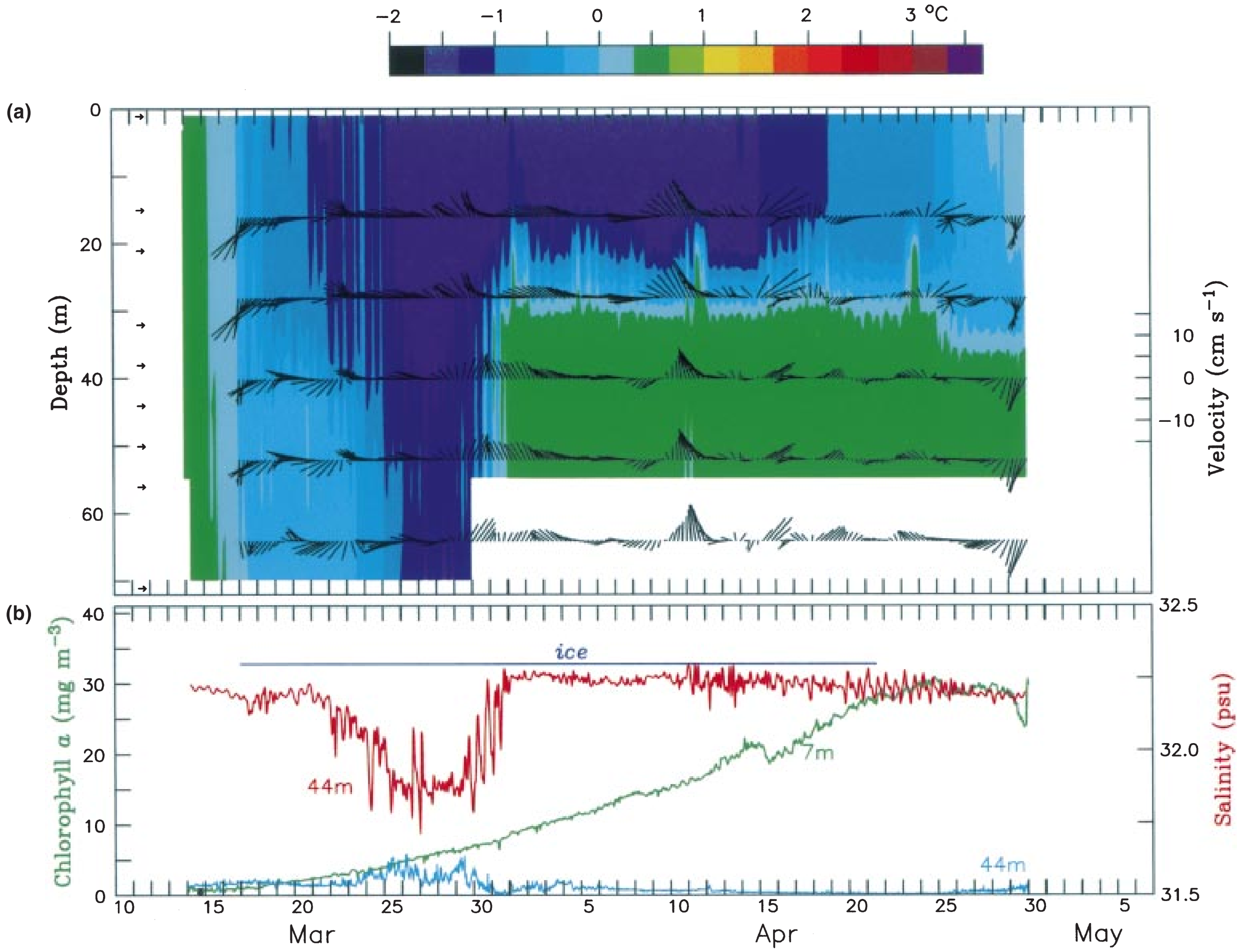
stabilization via ice melt. After the ice-edge bloom, a main spring bloom was described that required wind mixing to erode the thin fresh surface layer and restore depleted nutrients (e.g. McRoy and Goering, 1974; Niebauer *et al*., 1990). In 1995, however, the under-ice bloom persisted despite an unstable water column. A subsequent main bloom was not detected by optical sensors on Lagrangian drifters launched within two weeks of the receding ice. Spring winds that year were not strong enough to erode the pycnocline and replenish surface nutrients.

During the early 1980s, when the south-eastern shelf of the Bering Sea was ice-free, the spring bloom was described as a feature that began in the Outer Shelf Domain, working its way shoreward as the stability of the water column increased. Cessation of strong winter wind mixing of the water column was the trigger. The bloom usually commenced in late April or early May (Sambrotto *et al*., 1986). Thus, the presence or absence of sea ice and springtime winds influence the timing, location, and number of spring blooms. To the extent that the bloom is responsible for the major production of pollock prey, variability between these two physical factors (ice and wind) may have a strong impact on larval fish survival during spring.

LARVAL POLLOCK FEEDING AND CONDITION

Much of the information on larval walleye pollock feeding and condition is based on studies done in Shelikof Strait, Gulf of Alaska (Theilacker *et al*., 1996). Information on larval diet and prey availability also exists for Funka Bay, Japan and the south-eastern Bering Sea (Kamba, 1977; Clarke, 1984). In Shelikof Strait, starvation can be a significant source of mortality (up to 32% per day; Theilacker *et al*., 1996) for first-feeding larvae (≤6.5 mm in length). Larval condition is closely related to the amount of food in the

Figure 7. Dynamics of a spring phytoplankton bloom under sea ice on the south-eastern Bering Sea Middle Shelf Domain during a heavy ice year, 1995 (Stabeno *et al.*, 1998). Shown are temperature and currents as a function of depth and time (a), and chlorophyll concentration at 7 m (mg m^{-3}), and chlorophyll fluorescence and salinity (PSU) at 44 m (b). Arrows in the left-hand margin of (a) indicate discrete depths of temperature measurements. The presence of sea ice is indicated by the labelled horizontal line in (b). Note the well-mixed water column (indicated by isothermal conditions and a decrease in salinity at 44 m) during the initial stages of the phytoplankton bloom.



water; at prey concentrations of fewer than 20 L^{-1}, condition indices were low and mortality elevated. The number of prey per larval pollock gut in Shelikof Strait was positively correlated with the number of prey in the water (Theilacker *et al.*, 1996). 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 constant (Nakatani, 1988). Our dietary studies were limited to prey items that leave some sort of hard body part in the digestive tract. Pollock larvae ingest items of known nutritional value (e.g. copepod nauplii, rotifers) and items of unknown value where inefficient or ineffectual digestion is suspected (e.g. copepod eggs and phytoplankton). Laboratory studies have shown that pollock larvae modify their swimming behaviour in the presence of food, turning more frequently, swimming slower and spending more time in a horizontal rather than vertical orientation (Spring, 1996). Vertical movements in the absence of food may help to locate concentrations of prey in a stratified water column or in thin layers of food (Iverson *et al.*, 1979b; Owen, 1981).

Oceanic region

Copepod nauplii were the most common food item in the guts of first-feeding pollock larvae in the oceanic region in April 1992 (Hillgruber *et al.*, 1995). Naupliar concentrations ranged from <5 to >40 L^{-1} (Paul *et al.*, 1996). Cyclopoid nauplii (*Oithona* spp.) tended to dominate the assemblage at most depths. Larval pollock, however, preferred late-stage calanoid nauplii (NIII – NVI: *Eucalanus*, *Metridia*, *Pseudocalanus*, *Microcalanus*) over the more abundant cyclopoid nauplii (*Oithona*) and earlier stages of calanoid nauplii (Hillgruber *et al.*, 1995). Late-stage *Oithona* and *Microcalanus* nauplii are about the same size, therefore this demonstrates prey selection on a basis other than size. Infrequent motion by *Oithona* nauplii relative to other copepod genera may explain their disproportionately low occurrence in larval fish guts (Paffenhöfer, 1993). Copepod eggs were prevalent in larval pollock guts, but it is not known if pollock are able to obtain nutrition from them. Flinkman *et al.* (1994) found that eggs from one particular copepod species (*Eurytemora herdmanni*) were of little nutritional value to herring larvae.

In 1992, larvae and their prey were most abundant at 30 m (Fig. 8), and light was sufficient for larval feeding (0.01–13 μmol m^{-2} s^{-1}; Olla and Davis, 1990; Kendall *et al.*, 1994). 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, but >80% of the available 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 modelling results (Francis *et al.*, 1999) led BS FOCI to explore the possibility that protozoans were an additional source of nutrition for larval pollock. Microzooplankton abundance (protozoans >20 μm) in the oceanic region ranged from 300 to 6233 organisms L^{-1} (0.58–9.7 μg C L^{-1}; Howell-Kübler *et al.*, 1996). In some situations, first-feeding pollock larvae could potentially meet their maintenance ration by grazing on both protozoans and nauplii. Whether or not significant ingestion of protozoans occurs in the field is not yet known, but a 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; Gallager, 1996).

Shelf region

The feeding environment of larval pollock in the shelf region was also investigated. Samples were collected at 2-week intervals in areas of high concentrations of pollock larvae in late April and mid- and late May 1995 (Brase, 1996). The highest concentrations of pollock larvae were found in mid-May (Fig. 9; average concentrations: late April, 0.75 m^{-3}; mid-May, 2.03 m^{-3}; late May, 1.35 m^{-3}; $P < 0.001$ that concentrations among dates were equal, ANOVA, Brase, 1996). 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. Temperatures at the depths of maximal larval abundance were cold: 2.5°C in late April, 3.5°C in early May, and 3.75°C in late May. Total copepod naupliar densities were always less than 8 L^{-1}; maximum water column integrated abundance was in late May after the peak concentrations of first-feeding larvae. In most samples (43 of 45 sampled depths with larvae), ≥90% of the larvae were feeding (Fig. 10). In late April, copepod eggs were the most numerous prey item. In early and late May, calanoid copepod nauplii increased in importance as prey items. 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

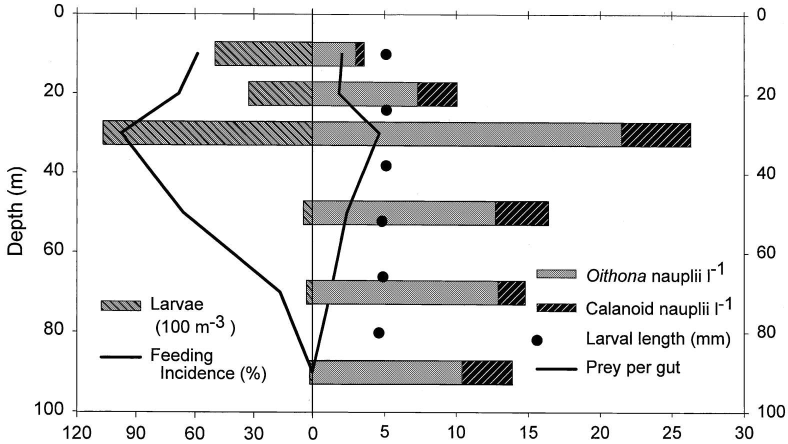
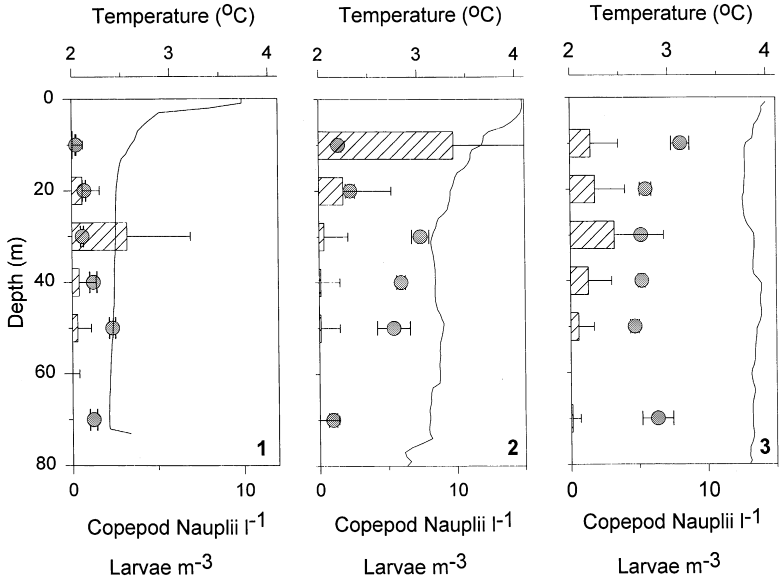


Figure 8. Vertical distributions of larval pollock, larval length, prey concentration, feeding incidence, and prey per larval gut for larvae collected in the oceanic region, April 1992 (Hillgruber *et al.*, 1995).

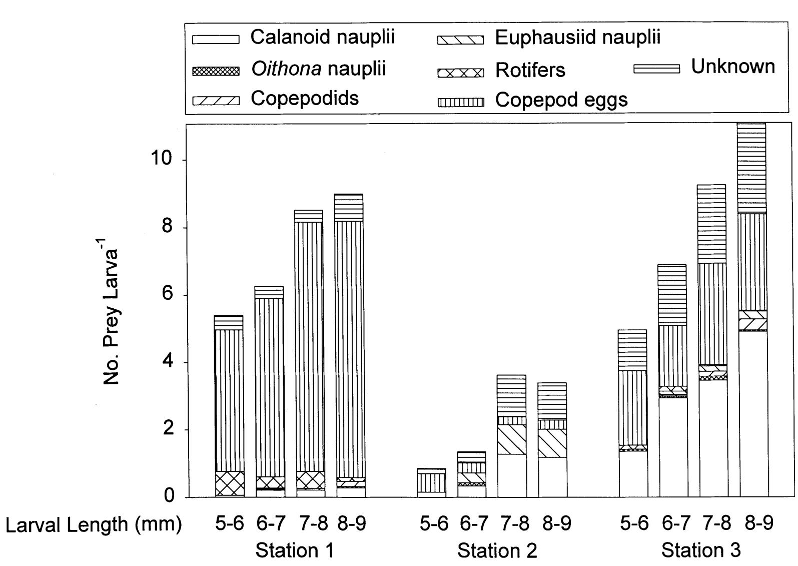
Figure 9. Vertical distributions of larval pollock (horizontal bars), copepod nauplii (filled circles), and water temperature (solid line) at three stations over the south-eastern shelf during a year of maximal ice extent (1995). Each station was located in an area of high larval pollock abundance and sampled once during the cruise: Station 1, late April; Station 2, mid-May; Station 3, late May. Three sequential samples were obtained from each depth during the cruise ($N = 3$). Shown are the mean concentrations ±SE of pollock larvae (Brase, 1996) and the mean ± 95% confidence interval for copepod nauplii (Napp, unpublished).



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}).

The maximum number of larvae occurred in mid-May, a time when prey concentrations were lowest. We conclude that in 1995 there was a temporal 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. Contrary to expectations, there was little evidence for a deleterious effect of low prey concentrations on larvae. We lack specific estimates of larval mortality, but 6–7 mm (post first feeding) larvae sampled in late April and early May exhibited low incidence of starvation as inferred from the mid-gut cell height condition index (Theilacker and Porter, 1995). In late April, 4 of 65 larvae (5 stations sampled) were starving and in late May, 1 of 116 larvae (11 stations) was starving. In Shelikof Strait, at comparable prey densities (but slightly higher water temperatures) ≈34% of first-feeding larvae were starving at comparable prey concentrations.

Figure 10. Prey taxonomic composition from larval pollock guts (mean number larva^{-1}) by station and larval length (TL, mm) during late April (Station 1) and early and late May (Stations 2 and 3, respectively), 1995 (redrawn from Brase, 1996).



IMPLICATIONS – LARVAL POLLOCK FEEDING ENVIRONMENTS IN THE SOUTH-EASTERN BERING SHELF AND OCEANIC REGIONS

Now that we know the prey preferences of larval pollock, we can compare the two regions (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. Data on dynamics of the spring phytoplankton bloom were limited to the locations of the biophysical platforms that 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 geographical regions. We spent only two full field seasons in each region, with a transition year in between. Thus, our intra-region interannual comparisons are limited to two adjacent years.

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 moorings suggest 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 Middle Shelf Domain; 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. One species of shelf prey producer (*Calanus marshallae*) begins egg production well before the spring bloom, but continues egg production through the period of peak phytoplankton biomass. (Naumenko, 1979; Baier and Napp, 1998).

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 Domain and continental slope, *Metridia pacifica* needs ≈12 days to develop from egg to the fourth naupliar stage (Pinchuk and Paul, 1998) and *Pseudocalanus* spp. require ≈15 days to do the same (Corkett and McLaren, 1978). *Calanus marshallae* over the Middle Shelf Domain would need ≈19 days to reach NIV at the same temperature. The 'critical period' of first-feeding larvae is ≈7–14 days at 5°C in Shelikof Strait and longer at colder spring temperatures observed on the south-eastern Bering Sea shelf. Therefore, prey production must be initiated several weeks before first-feeding larvae appear.

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 is a function of the standing stock of prey producers, and 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). Naupliar production rates by *Pseudocalanus* spp., a numerically abundant copepod over the south-eastern Bering Sea shelf, were implied to be temperature-limited, rather than food-limited, during the spring (Dagg *et al.*, 1984). This may not be true for the larger prey-producing copepods *Metridia*, *Calanus*, and *Eucalanus*.

Variability in prey densities within the oceanic region and between the oceanic and shelf regions was found to be much greater than initially thought. We did find low densities over the oceanic region of <10 nauplii L^{-1} in April (Paul *et al.*, 1996), but also found several instances over the slope where densities were >20 L^{-1} (Table 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 most sampled depths. Thus our second hypothesis can be rejected: prey concentration over the slope was not measurably less than over the shelf.

Prey densities in the oceanic region were comparable to the slope values from previous research in the Bering Sea (PROBES; Processes and Resources of the Bering Sea Shelf) with the exception of low values found in their cold year 1980 (Dagg *et al.*, 1984; Walsh and McRoy, 1986). Naupliar densities sampled in the shelf region during cold years are comparable between BS FOCI and PROBES, but BS FOCI did not sample the shelf in May and June of 'warm' years. A distinction between the results of the two programmes is that BS FOCI has some direct measurements of larval condition. Even at low prey densities found during cold years by both programmes, larvae did not appear to be starving in 1995.

Table 1. Availability of larval pollock prey by year, month and region. Each bin contains the number of sampled depths where the mean concentration of copepod nauplii was <10, 10–20, or >20 L^{-1}. Triplicate samples from each of six depths were used to construct a profile. –, Times and regions not sampled by the Program. Data sources are Brase (1996), Paul *et al.* (1996), and Napp (unpublished).

		Slope				Outer Shelf Domain				Middle Shelf Domain			
Year	Month	Profiles	<10	10–20	>20	Profiles	<10	10–20	>20	Profiles	<10	10–20	>20
1992	April	2	5	5	2	–	–	–	–	–	–	–	–
1993	April	2	4	5	3	–	–	–	–	–	–	–	–
1994	April	2	3	8	1	1	6	0	0	–	–	–	–
1995	April	1	3	3	0	1	6	0	0	–	–	–	–
	May	–	–	–	–	1	6	0	0	1	5	1	0
	June	–	–	–	–	1	6	0	0	–	–	–	–

Taxonomic composition of prey

Pollock larvae are selective feeders; prey type and prey concentration are both important determinants of *in situ* prey availability. A major difference between the oceanic and shelf regions was the ratio of calanoid to cyclopoid nauplii. At most depths sampled over the oceanic region 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 oceanic region was at the depths where large concentrations of nauplii were found; they were 70% calanoid, i.e. more similar to the shelf region prey assemblage than to that of the oceanic region. Thus, when we take preferential feeding into account, *effective* prey concentrations were much lower than starvation values determined from Shelikof Strait.

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 and included both first-feeding and post-first-feeding larvae. Few larvae showed symptoms of recent food deprivation in these patches. These same larvae were feeding, however, under prey-poor conditions and had few prey items in their guts. This contradiction – low prey levels, yet low incidence of starvation – could be explained either by high mortality of starving larvae prior to our sampling or by lower prey requirements at colder water temperatures. The critical number of prey to meet basic metabolic demands on the Bering Sea shelf at 3°C may be much lower than at 5–6°C as determined in Shelikof Strait. In the laboratory, mean respiration of post-first-feeding larvae at 3°C was 66% of that at 6°C (2.64 vs 3.99 μL O_2 mg^{-1} (dry weight) h^{-1}; Porter, 1999). Additional investigations are necessary to determine the effect of temperature on larval feeding and metabolism and prey production.

CONCLUSIONS

Pollock spawn in two distinct regions in the south-eastern Bering Sea: the oceanic and shelf regions. 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 south-eastern shelf. Conditions for the emerging larvae can be very different for the two regions, as are the factors that affect variability in survival of early larvae between regions (Fig. 2). In the oceanic region, 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 differ between the two regions as a result of the differences in their physical characteristics. Variability in observed plankton standing stocks may result largely through advective rather than local processes in the oceanic region. In the shelf region, interannual variability from a complex set of forcing functions (sea ice, wind mixing, temperature, and insolation) results in phytoplankton blooms with different timing, magnitude, and transfer efficiencies to the zooplankton and nekton (or benthos). The two regions provide different feeding environments for larval pollock. In the oceanic region, 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 types preferred by first-feeding larvae. In the shelf region, preferred prey constituted a larger fraction of the available prey, but copepod nauplii were still at minimal levels for growth and survival. There was no evidence to suggest, however, that these larvae were starving. Low water temperatures and an early spring phytoplankton bloom associated with sea ice resulted in a mismatch between the maximal concentrations of first-feeding larvae and their prey (Walsh and McRoy, 1986; Townsend *et al*., 1994). Thus the key to interannual variation in food for first-feeding pollock larvae in the oceanic region is advection; in the shelf region it is the coupled dynamics of the atmosphere–ice–ocean system.

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