Effect of ocean conditions on the cross-shelf distribution of walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*)

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ABSTRACT

Acoustic trawl surveys were conducted in 2000 and 2001 in two troughs located off the eastern coast of Kodiak Island in the Gulf of Alaska as part of a multiyear, multidisciplinary experiment to examine the influence of environmental conditions on the spatial distribution of adult and juvenile walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*). Continuous underway sea surface temperature samples and water column profiles collected in 2000 and 2001 showed the presence of a sharp shelf-break front in Chiniak Trough and a mid-trough front in Barnabas Trough. At distances <22 km from shore, the water column was well mixed, whereas a well-defined mixed layer was present beyond approximately 22 km from shore. Satellite drifter tracks in Barnabas Trough entered along the upstream edge of the trough and appeared to follow the frontal boundary across the middle portion of the trough. A storm in 2001 weakened stratification and cooled surface water temperature by 1.6–2.1°C. Wind mixing associated with the storm event mixed subsurface chlorophyll *a* to the surface and enhanced nutrients in the surface waters. The storm event revealed spatial partitioning of summer production in Barnabas Trough, with production concentrated in regions inside the mid-trough front. In contrast, post-storm summer production was distributed throughout Chiniak Trough. The spatial distribution of walleye pollock and capelin differed and appeared to be related to differences in habitat characteristics. Acoustic survey data identified four acoustic sign types: age-1 pollock, adult pollock, capelin, capelin–age-0 pollock mix. The spatial distribution of these four sign types appears to be influenced by the oceanographic and topographic features of the two troughs. Adult pollock were broadly distributed throughout Chiniak Trough, whereas adult pollock were aggregated on the coastal side of the frontal system in Barnabas Trough. In 2000, capelin occurred with age-0 pollock. In Chiniak Trough, capelin were most abundant along steep topographic gradients at the edges of the trough and in a deep region near Cape Chiniak, whereas the capelin–age-0 mix (2000) or capelin (2001) concentrations were observed in slope water intrusions over the outer shelf in Barnabas Trough. Results suggest that habitat selection of walleye pollock and capelin are controlled by different processes. Capelin distributions appear to be limited by oceanographic conditions while other factors appear to be more important for pollock.

Key words: Barnabas Trough, capelin, Chiniak Trough, Kiliuda Trough, oceanography, temperature, trough, walleye pollock, wind mixing

INTRODUCTION

Attributing the response of marine populations to factors influencing prey distribution, abundance, diversity, or quality is a complex problem that requires knowledge of the spatial distribution and abundance of predators and their prey, the utilization of prey by each predator, and the degree of flexibility in consumer choice for alternative prey (Rose and Leggett, 1990; Logerwell *et al.*, 1998; Abrams, 1999). Designing experiments to measure these relationships is difficult in the marine environment where measurements of prey and predator distributions require considerable investments in ship time. Efforts are further impeded by environmental disturbances that may mediate the impact of competition for limited resources (see Rice, 2001 for review).

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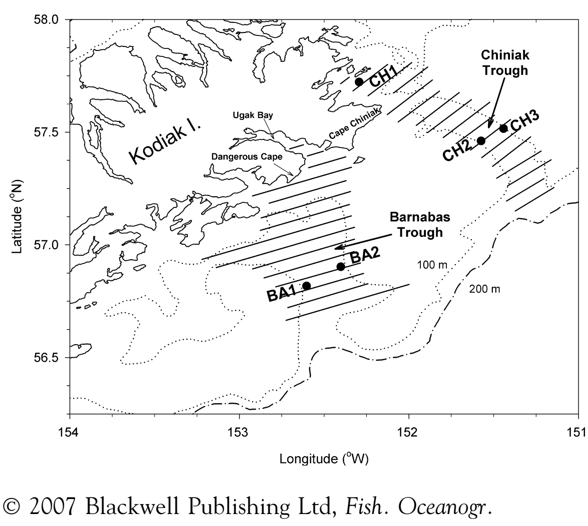
In August 2000, scientists from the National Oceanic and Atmospheric Administration (NOAA), Alaska Fisheries Science Center (AFSC), Resource Assessment and Conservation Engineering (RACE), and Resource Ecology and Fisheries Management (REFM) Divisions initiated a 4-yr investigation on the effects of fishing on sea lion prey abundance and distribution in a commercial fishing ground located on the east side of Kodiak Island (Fig. 1). In 2001, investigators from the NOAA's Pacific Marine Environmental Laboratory (PMEL) joined the project to provide enhanced biophysical sampling to characterize the marine habitat. Investigators posed the following hypotheses:

1 the local distribution and abundance of Steller sea lion prey in an unfished condition is equal to the distribution of prey in a fished condition; and
2 walleye pollock and capelin respond similarly to habitat characteristics of the study region.

Analysis of the 2001 survey data showed commercial fishing did not produce a significant effect on fish distribution and abundance (Wilson *et al.*, 2003). This finding suggested that hypotheses that linked environmental factors to the distribution of sea lion forage should also be examined. Wilson *et al.* (2003) describe the effect of commercial fishing on prey distributions and abundance. This report describes the potential role of biophysical factors in regulation of the spatial distribution and abundance of walleye pollock and capelin.

The Kodiak Island region was of particular interest because sea lion populations in this region have exhibited marked declines since the 1970s and populations continue to exhibit a low level of decline (Sinclair and Zeppelin, 2002). Steller sea lion diet studies reveal that in the summer, walleye pollock (*Theragra chalcogramma*) represented 64% and smelt, including capelin (*Mallotus villosus*), represented 7% of the diet (Sinclair and Zeppelin, 2002). These fish species represented the principal pelagic fish biomass in the region in 2000 and 2001.

Figure 1. Study region east of Kodiak Island, Alaska. Transect lines and locations of oceanographic moorings (circles) are indicated.



MATERIALS AND METHODS

Study area

The region selected for this study was located on the east side of Kodiak Island. This region features a wide shelf punctuated by several troughs (Fig. 1). The region supports a high level of primary production from April to November with seasonal blooms in May and October (Stabeno *et al.*, 2004). Two current systems dominate the region: the Alaska Coastal Current (ACC) and the Alaska Stream. The ACC flows westward along the coast of Alaska. While most of the flow along the Kenai Peninsula passes between Kodiak Island and the Alaskan coast, and continues down Shelikof Strait, a significant portion (approximately 25%) flows along the south side of Kodiak Island (Stabeno *et al.*, 1995). The average current speed in this system is approximately 25 cm s^{-1}, but can exceed 100 cm s^{-1} during periods of strong winter storms (Musgrave *et al.*, 1992; Stabeno *et al.*, 2004). The Alaskan Stream is the western boundary current of the subarctic gyre and dominates the flow at the shelf-break and in the basin. Mean flow in this system is approximately 50 cm s^{-1}, but flow can exceed 100 cm s^{-1} (Reed and Schumacher, 1986).

Sampling design

The sampling design consisted of two or more survey passes in each of two troughs located along the east side of Kodiak Island. Conducting two or more passes over a 20-day study period allowed for measurements of natural variability in the study region. Selecting two sites that exhibited similar topography and contained fish of similar size allowed for an evaluation of biophysical factors underlying local differences in fish distribution and abundance.

Barnabas (also known as Kiliuda Trough) and Chiniak Troughs were selected as the study sites for our experiment. These troughs share many biological and physical characteristics. The troughs have similar average depths (approximately 115 m). Examination of survey and commercial fishery data collected during the 1990s revealed that the species composition of the

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catch from both troughs was similar during summer months. The size distribution and size at age of adult pollock from each trough was similar. Feasibility studies conducted in the absence of commercial fishing revealed that the distribution of fish in each trough was stable during the 20-day study period (Wilson *et al.*, 2003).

In 2001, the survey design was expanded to include periods before and during a commercial fishing season to evaluate hypothesis 1. Regulations were established to close Chiniak Trough to fishing. All transects within a trough ('a pass') were surveyed twice before the start of the fishing season, and one full pass of each trough was made after fishing commenced.

Survey methodology

Fish distributions in each trough were assessed using Echo Integration Trawl (EIT) survey techniques during daylight hours on the National Oceanic and Atmospheric Administration Research Vessel *Miller Freeman* (Wilson *et al.*, 2003). Multiple passes were conducted in each trough to measure variability in abundance and distribution during the survey (Table 1). Each pass consisted of parallel transects uniformly spaced at 5.6 km apart (Fig. 1). A complete pass of the study region took approximately 5 days. The survey methods are similar to those used during other routine EIT surveys (Williamson and Traynor, 1984; Traynor *et al.*, 1990). Abundance of adult pollock, juvenile pollock, capelin, and capelin age-0–pollock mix was measured from estimates of acoustic backscattering (S_A; defined in MacLennan *et al.*, 2002). Variance estimates were calculated using the geostatistical approach and are reported in Wilson *et al.* (2003). Trawl hauls were conducted when significant acoustic sign was encountered to determine the length and species composition of the acoustic layer. The trawls used to sample mid-water acoustic sign types included a large, mid-water Aleutian Wing Trawl (AWT), and occasionally, a smaller mid-water Marinovich trawl. A poly Nor'eastern (PNE) bottom trawl was used to sample acoustic sign near the bottom. A 1.25 in codend liner was used in 2000. In 2001, a smaller mesh liner (0.875 in) was used to improve sampling of small fish.

Table 1. Dates of acoustic mid-water trawl surveys in Barnabas and in Chiniak Troughs in 2000 and 2001.

Chiniak	Barnabas
2000	
Pass 1 (August 9–10)	Pass 1 (August 11–12)
Pass 2 (August 14–16)	Pass 2 (August 17–18)
2001	
Pass 1 (August 9–11)	Pass 1 (August 11–14)
Pass 2 (August 14–16)	Pass 2 (August 16–19)
Pass 3 (August 23–26)	Pass 3 (August 26–29)
	Pass 4* (August 29–30)

*Pass 4 did not include the six southernmost transects.

Biophysical measurements

Near-surface temperature and salinity measurements were collected while the ship was underway and along vertical water column profiles performed at selected sites. A flow-through ship-intake sampling system allowed continuous measurement of sea surface temperature and conductivity. In 2000, 45 profiles were taken with a conductivity temperature depth (CTD) profiler, expendable bathythermographs (XBT), or a trawl-mounted temperature probe. In 2001, 57 profiles were taken. Mixed layer depth was estimated by the depth where the temperature difference between 1-m records was greatest.

Other oceanographic data were collected to describe the influence of biophysical factors on the distribution and abundance of sea lion prey. Five moorings were deployed in May 2001 (Fig. 1). Three moorings (BA1, CH2, and CH3) were designed to measure temperature, conductivity, and near-bottom currents. They were deployed at the west side of both troughs and at the head of Chiniak Trough. The other two moorings (BA2 and CH1) were deployed on the east side of both troughs. These moorings were taut-wire moorings instrumented to measure currents, temperature, salinity, and fluorescence. A bottom-moored Acoustic Doppler current profiler (ADCP) measured currents in 4-m depth intervals to within approximately 15 m of the surface. Conductivity was measured at three depth intervals. Temperature sensors were located at nominal depths of 15, 25, 35, 45, 55, 65, 75, 85, 95 and 120 m. Fluorescence was measured at 15 m below the surface. Data from all sensors was recorded internally every hour. The moorings in Chiniak Trough were recovered in September 2001, and those in Barnabas Trough were retrieved in February 2002.

Satellite-tracked drifters were deployed in 2001 to measure the spatial characteristics of the ACC. Several of these drifters were deployed near Prince William Sound as part of the U.S. GLOBEC Northeast Pacific research program (Stabeno *et al.*, 2004). All drifters were drouged at 40 m to reduce direct effects of wind and wind-wave generated currents. Positions were reported via the Argos satellite-based system 15–20 times per day. Stabeno and Reed (1991) provide a detailed description of the data control and accuracy of these instruments.

SeaWiFS satellite images taken on August 13, August 21, and August 22, 2001 were used to describe the cholorophyll-a distribution in the study areas. The images were obtained from level 2A data files from the SeaWiFS web site. Images were processed using the SEADAS analysis package. Chlorophyll concentration was calculated using the OC4 algorithm.

RESULTS

Major oceanographic findings

Underway temperature measurements collected in 2000 and 2001 show differences between years, between troughs, and between passes. With the exception of pass 3 in 2001, the mean sea surface temperatures in Chiniak and in Barnabas Troughs were cooler in 2000 than in 2001 (Table 2). In both years, sea surface temperatures were cooler in Chiniak Trough than in Barnabas Trough (Table 2; Figs 2 and 3). These sea surface temperature records revealed a shelf-break front in Chiniak Trough and a mid-trough front in Barnabas Trough in both years (Figs 2 and 3).

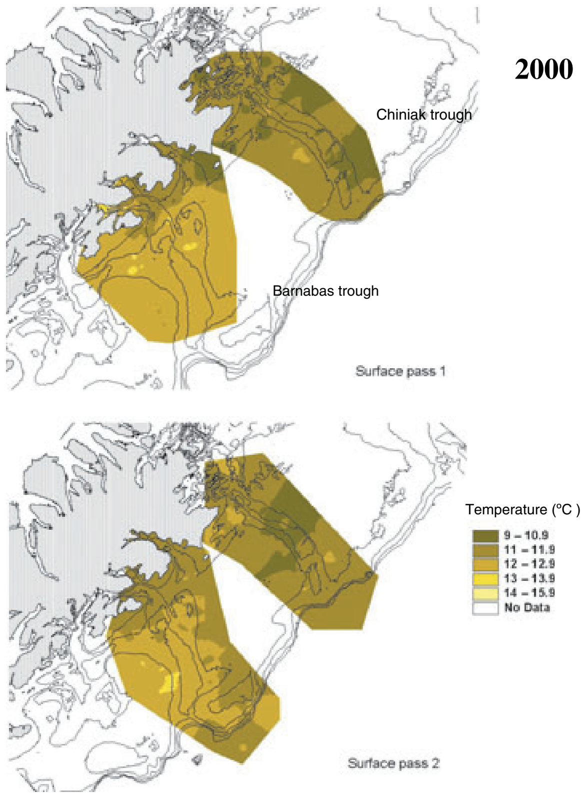
A storm occurred on August 19–20, 2001 between passes 2 and 3. This storm resulted in surface wind mixing as indicated by cooler surface ocean conditions in both troughs during pass 3 (Fig. 3). Post-storm sea surface temperatures were cooler than previous passes, and Barnabas Trough average temperature (11.7°C) was similar to Chiniak Trough (11.5°C).

Temperature profiles from the 2000 and 2001 surveys revealed that at distances <22 km from shore the water column (hereafter 'inshore area') was mixed, whereas a distinct thermocline was detected in the region beyond 22 km (hereafter 'offshore area'; Figs 4 and 5). The storm-related wind mixing in 2001 had a marked impact on the vertical structure in each trough at stations in the offshore area. In the offshore area of

Table 2. Average sea surface temperature (°C) of all transects in Chiniak and in Barnabas Troughs.

		2000		2001	
Trough	Pass	Temperature	SD	Temperature	SD
Barnabas	1	12.08	0.67	13.88	0.95
	2	11.92	0.52	13.23	1.21
	3			11.74	0.46
Chiniak	1	11.12	0.51	12.20	0.95
	2	11.52	0.59	12.87	0.73
	3			11.49	0.71

Figure 2. Contours of sea surface temperature for passes 1 and 2 during August 2000.

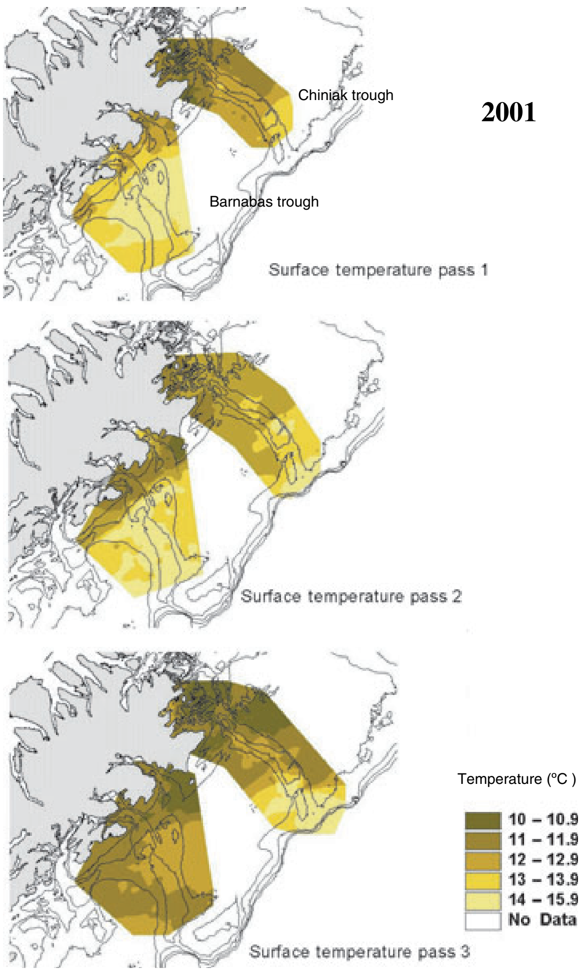


Chiniak Trough, the upper mixed layer ranged between 14 and 22 m before the storm, and between 35 and 64 m after the storm. In the offshore area of Barnabas Trough, the mixed layer depth ranged between 12 and 22 m before the storm, and between 24 and 29 m after the storm (Fig. 5). The storm event cooled the upper 15 m of the surface waters of the offshore area by approximately 1.7 and 2.1°C in Chiniak and in Barnabas troughs respectively (Table 3).

Subsurface waters at 75 m were cooler in Barnabas Trough than in Chiniak Trough (Figs 4–7). Barnabas Trough is broader than Chiniak Trough, which allows slope water to intrude further into the trough (Figs 4–7). In Chiniak Trough, cool waters <8°C extended farther into the trough in 2000 than in 2001 (Figs 6 and 7). In 2001, comparison of the spatial distribution of subsurface temperatures in passes 1, 2, and 3 revealed that the storm event had no impact on the spatial distribution of temperature at 75 m.

Comparison of SeaWiFS chlorophyll *a* composites from 2000 to 2001 shows influence of storm events on the local production in the study region. In 2000, chlorophyll *a* was concentrated in regions north and south of the study region (Fig. 8). With the exception

Figure 3. Contours of sea surface temperature for passes 1–3 during August 2001.



of near-shore regions, chlorophyll *a* concentrations were low throughout Barnabas Trough and most regions of Chiniak Trough. Similar conditions were observed in 2001 prior to the storm event (Fig. 9). The storm event in 2001 had a marked influence on chlorophyll *a* concentrations in the Kodiak region. Chlorophyll *a* composites from satellite images taken before the storm event revealed surface concentrations were low (Fig. 9). Chlorophyll *a* concentrations were substantially higher one day after the storm (August 21, Fig. 9). These increased concentrations were probably linked to mixing subsurface chlorophyll and other organic matter to the surface because the short time interval between the storm and surface production was less than the doubling time for phytoplankton in that season. Subsequent increases observed on August 22 could be attributed to nutrient replenishment in the surface waters (Fig. 9). In Barnabas Trough, the post-storm chlorophyll *a* concentrations were restricted to the region landward of the mid-trough temperature front (Fig. 9). Within this region, increased chlorophyll *a* concentration was observed along the eastern (upstream) side of the trough.

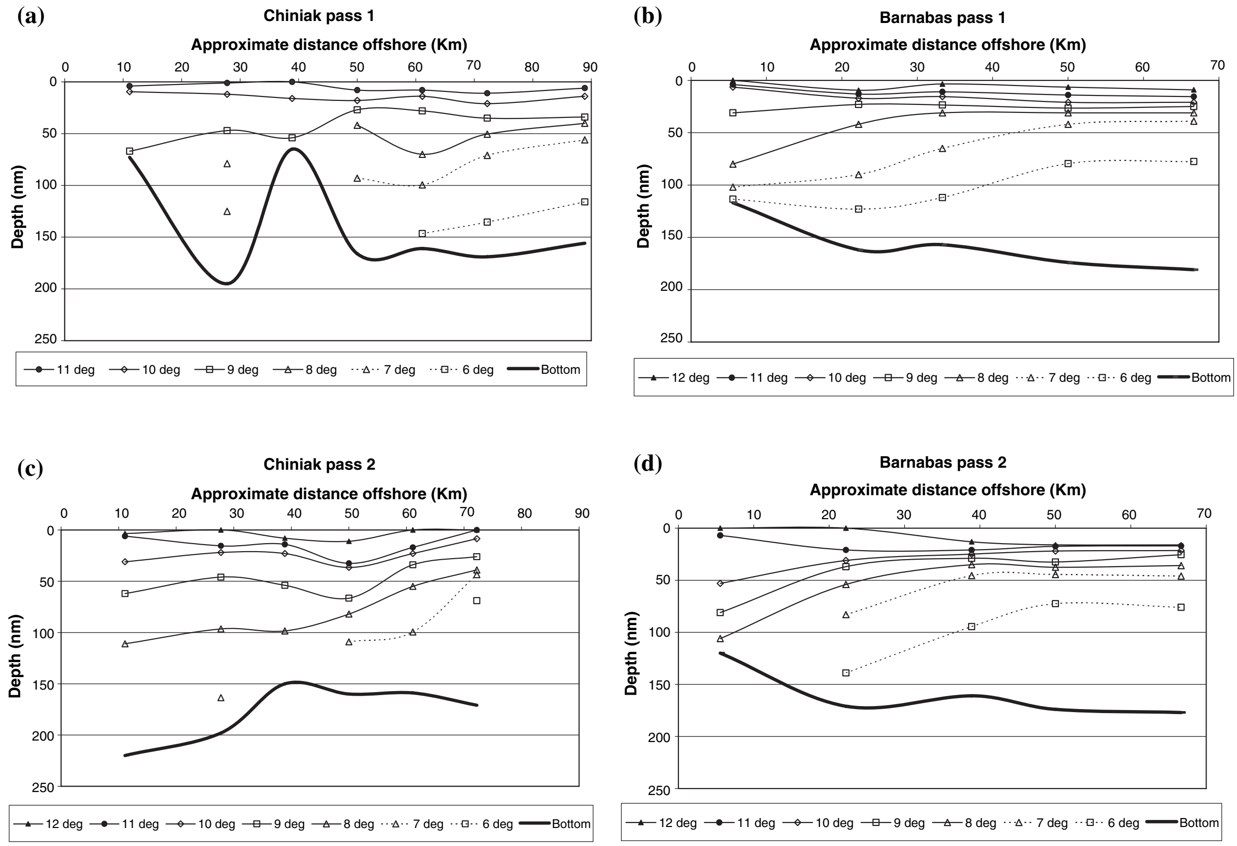
Comparison of satellite images taken before and after the storm and fluorescence taken from moorings revealed the importance of spatial location for the moorings. The post-storm increase in chlorophyll *a* occurred throughout Chiniak Trough, whereas, the post-storm increase in chlorophyll *a* was restricted to the ‘nearshore area’ of Barnabas Trough (Fig. 9). The spatial partitioning of production in Barnabas Trough is evident in the satellite images (Fig. 9). While the satellite image shows a marked increase in chlorophyll *a* after the storm, this may have been organic material mixed from deeper regions of the water column.

In 2001, satellite-tracked drifters and moorings revealed varying degrees of topographic steering of the circulation. In Chiniak Trough, some drifters moved shoreward along the eastern edge of the trough and offshore on the west side, whereas others continued along the shelf-break without entering the trough (Fig. 10). In Barnabas Trough, all drifters flowed shoreward into the trough along the east side and exited the trough through an adjacent trough in an alongshore direction to the southwest (Fig. 10).

In 2001, temperature records taken at five moorings revealed strong tidal mixing. Flow at all five locations was dominated by tides with currents exceeding 70 cm s^{-1}. The average velocity (May–September) at Mooring 3 in Chiniak Trough (CH3 located in 140 m of water) was >13 cm s^{-1} at 15 m depth and weakened to approximately 10 cm s^{-1} near the bottom. On the west side of the trough (CH2 located in 120 m of water) the flow was out of the trough at approximately 6 cm s^{-1}. Current speeds along the eastern mooring (BA2) in Barnabas Trough were slightly weaker than in Chiniak Trough. At the eastern mooring (BA2), average flow (May–January) was strongest in the upper water column (approximately 9 cm s^{-1}), and flow was weakest (approximately 6 cm s^{-1}) near the bottom. The western mooring (BA1) measured currents (approximately 10 cm s^{-1}) near the bottom flowing in the opposite direction to those at BA2.

Mooring temperature contours based on data collected at CH3 and BA2 reveal that near-surface temperatures in May (collected at 15 m) were approximately 5.5°C (Fig. 11). Temperatures increase to >11°C in August. There is a marked difference in temperature at the two sites at depth. Vertical mixing is much stronger at the Chiniak mooring site than at the Barnabas site. Explanations for this finding are being examined; however, it is likely that the Chiniak

Figure 4. Temperature profiles based on conductivity temperature depth (CTD) casts taken in Chiniak and in Barnabas Troughs for passes 1 and 2 (August 2000).



mooring is positioned deeper into the trough where tidal mixing is stronger. The striped effect is because of tidal currents. Temperatures decrease as the tides flow into the trough, and then increase when the tides reverse. Mooring CH3 appeared to be located near the shelf-break frontal zone, with temperatures varying by as much as 4–5°C on tidal cycles. The impact of the storm (August 19–20, 2001) is evident in the mixing of warmer water (>9°C) to a depth of 60 m. In contrast BA2 was located farther from the slope and the temperatures did not vary as strongly on tidal frequencies, although some variability is evident. The sharp mixing that occurred as a result of the August storm is evident in both time series, but mixing penetrated to a greater depth at Chiniak.

Relationship between frontal regions, topographic features, and distributions of fish

Acoustic backscatter was attributed to four groups of fishes in 2000 and 2001. In 2000, trawl samples confirmed that observed sign types were: a mixture of adult capelin and age-0 pollock, adult pollock, age-1 pollock. In 2001, three sign types were detected: capelin, adult pollock, and age-1 pollock. A complete description of the acoustic signature of these sign types including a discussion of the vertical distribution and abundance is included in Wilson *et al.* (2003).

In 2000, the adult pollock and capelin–age-0 pollock mix exhibited different spatial distributions that were related to environmental conditions within each trough. In Chiniak Trough, adult pollock were observed in scattered pockets throughout the trough (Fig. 12, top). Concentrations of capelin–age-0 pollock mix in Chiniak Trough were associated with regions of sharp topographic gradients including a deep region near Cape Chiniak and to a lesser degree along the edges of Chiniak Trough (Fig. 12, bottom). Age-1 pollock were only observed in Chiniak Trough (Fig. 12, middle). In Barnabas Trough, adult pollock were concentrated in the 'nearshore area' particularly along the northeastern side of the trough (Fig. 12 top). Capelin–age-0 pollock mix was observed in the 'offshore area' in Barnabas Trough (Fig. 12, bottom).

Figure 5. Temperature profiles based on conductivity temperature depth (CTD) casts taken in Chiniak and in Barnabas Troughs before (passes 1 and 2) and after (Pass 3) a storm event in August 2001.

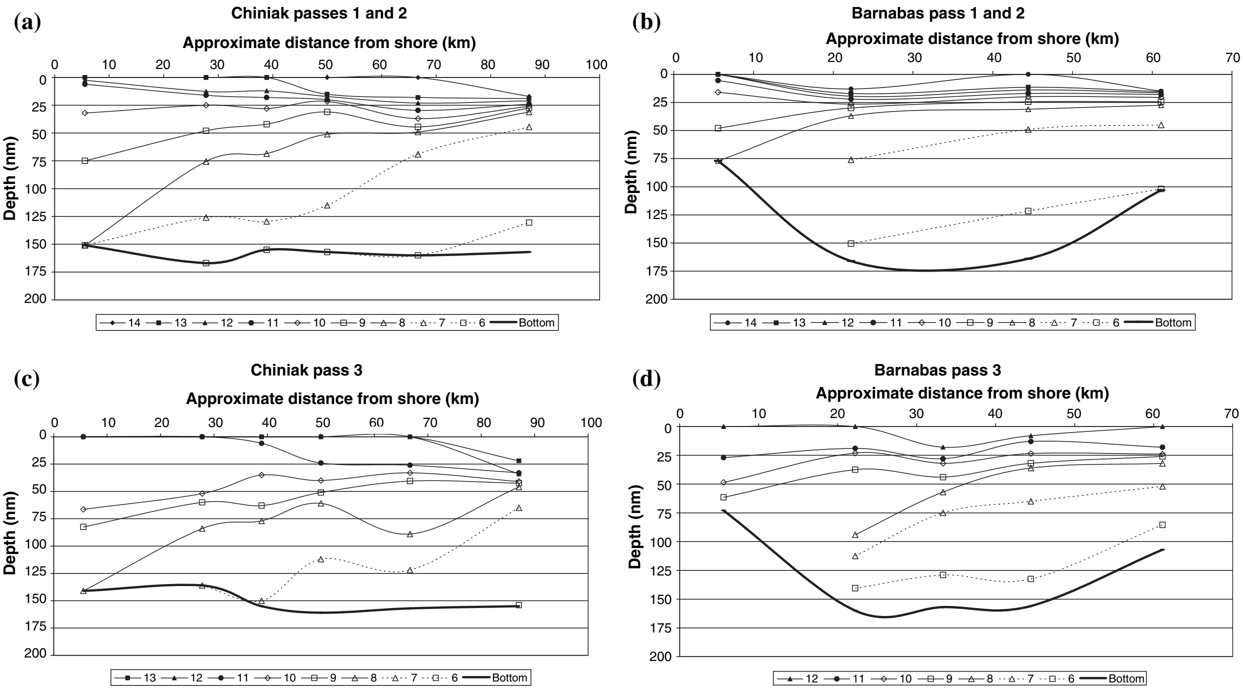


Table 3. Average temperature of upper 15 m at transect lines ≥22.2 km from shore in Chiniak and in Barnabas Troughs.

Trough	Before or after storm	Approximate mixed layer depth (m)	Average temperature of upper 15 m excluding near-shore stations	Number of CTD profiles used to calculate the mean
Barnabas	Before	16	13.94	4
	After	26	11.75	4
Chiniak	Before	18	13.18	6
	After	49	11.48	6

CTD, conductivity temperature depth.

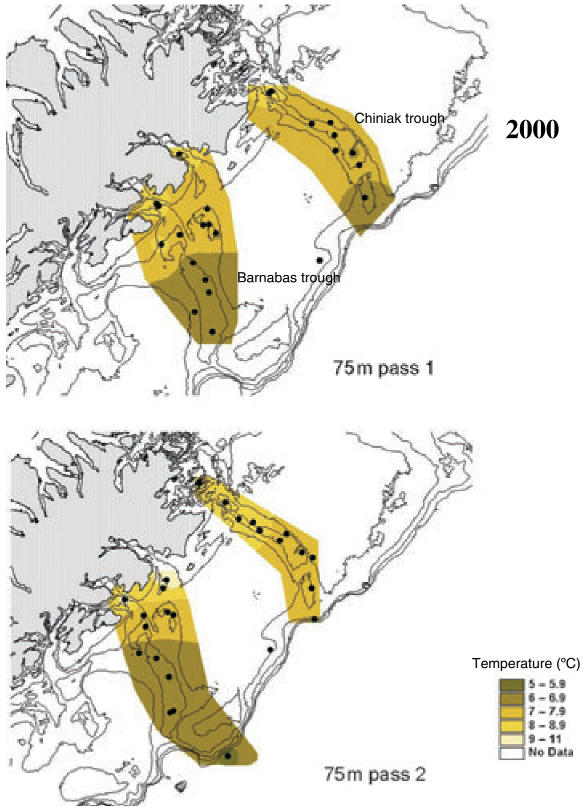
The spatial distributions of adult pollock and capelin, and the association of these sign types with environmental features in 2001, were similar to those observed during 2000. Adult and juvenile pollock were observed throughout Chiniak Trough and in the ‘nearshore area’ of Barnabas Trough (Fig. 13, top). Capelin were concentrated in the region near Cape Chiniak in Chiniak Trough and in the ‘offshore area’ in Barnabas Trough (Fig. 13, bottom).

In 2000 and 2001, vertical distributions of adult pollock and juvenile pollock were not significantly different between passes (Wilson *et al.*, 2003). This finding suggests that neither storm-related surface mixing nor commercial fishing impacted school depth of these scatterers. During the day, adult and juvenile pollock and capelin were all concentrated at depths below the thermocline with mean depths of juvenile pollock ranging between 80 and 100 m and mean depths of adult pollock ranging between 110 and 140 m. During the night, age-1 pollock and capelin occupied shallower depths. Stomach collections from selected nighttime tows revealed that off-bottom excursions were probably related to feeding trips.

DISCUSSION

Results of this study do not support the hypothesis that age-1 or adult walleye pollock and capelin respond similarly to habitat characteristics of the study region. Evidence of habitat overlap between age-0 pollock and capelin was observed in 2000. Age-1 and adult pollock exhibit marked distributional differences from capelin

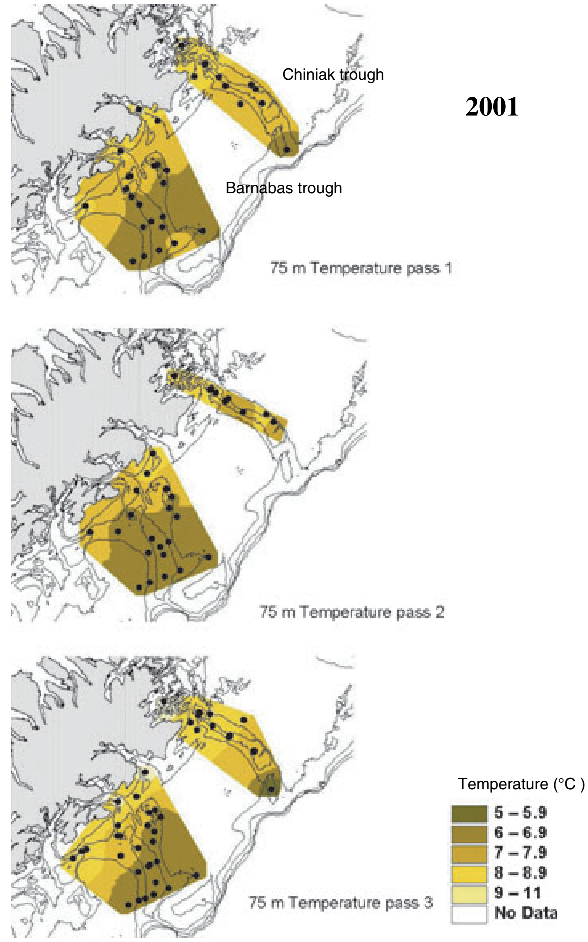
Figure 6. Temperature contours at 75 m for passes 1 and 2 during August 2000. Dots represent trawl or conductivity temperature depth (CTD) locations.



suggesting niche partitioning within each trough. These separations appear to be linked to topographic features and water mass distributions within each trough. Topographic features in the study region appear to influence the flow patterns around troughs to varying degrees on the shelf of Kodiak Island, Alaska. The complex topography and flow patterns through the troughs result in marked thermal features within the troughs. Thermal fronts were observed at the mouth of Chiniak Trough near the shelf-break and midway through Barnabas Trough. These features influenced the spatial distribution of fish within the study region.

Satellite-tracked drifters and moored current meters provided information that suggested that the flow along the shelf-break is steered into the troughs to varying degrees by the topography. The average summer daily flow speed in Chiniak Trough was >13 cm s^{-1} (May–September at 15 m) and the average daily speed in Barnabas trough was approximately 9 cm s^{-1} (May–January at 15 m). This flow is similar to mean flows reported in previous drifter experiments in this area (Musgrave *et al.*, 1992; Stabeno *et al.*,

Figure 7. Temperature contours at 75 m for passes 1, 2 and 3 during August 2001. Dots represent trawl, expendable bathythermograph (XBT) or conductivity temperature depth (CTD) locations.



1995). A notable aspect of flow patterns from moorings was the temporal stability in the strength of flow. In Chiniak Trough, current meter measurements and satellite-tracked drifters show that net flow into the troughs occurs on the upstream, eastern side of the troughs while flow out of the troughs occurs on the downstream, western side. Drifters showed flow into Chiniak Trough at 40 m was variable, with some drifters remaining on the shelf-break, whereas others entered the trough. In Barnabas Trough, temperature profiles suggest that the width of Barnabas Trough allowed slope water to extend further into the trough. All drifter trajectories showed a consistent pattern entering Barnabas Trough on its upstream eastern side. This comparison suggests that the influence of topographic steering on the eastern upstream side of each trough was more consistent in the broader trough.

Figure 8. Satellite images of chlorophyll *a* concentration (mg m^{-3}) taken on August 10, August 13 and August 16, 2000.

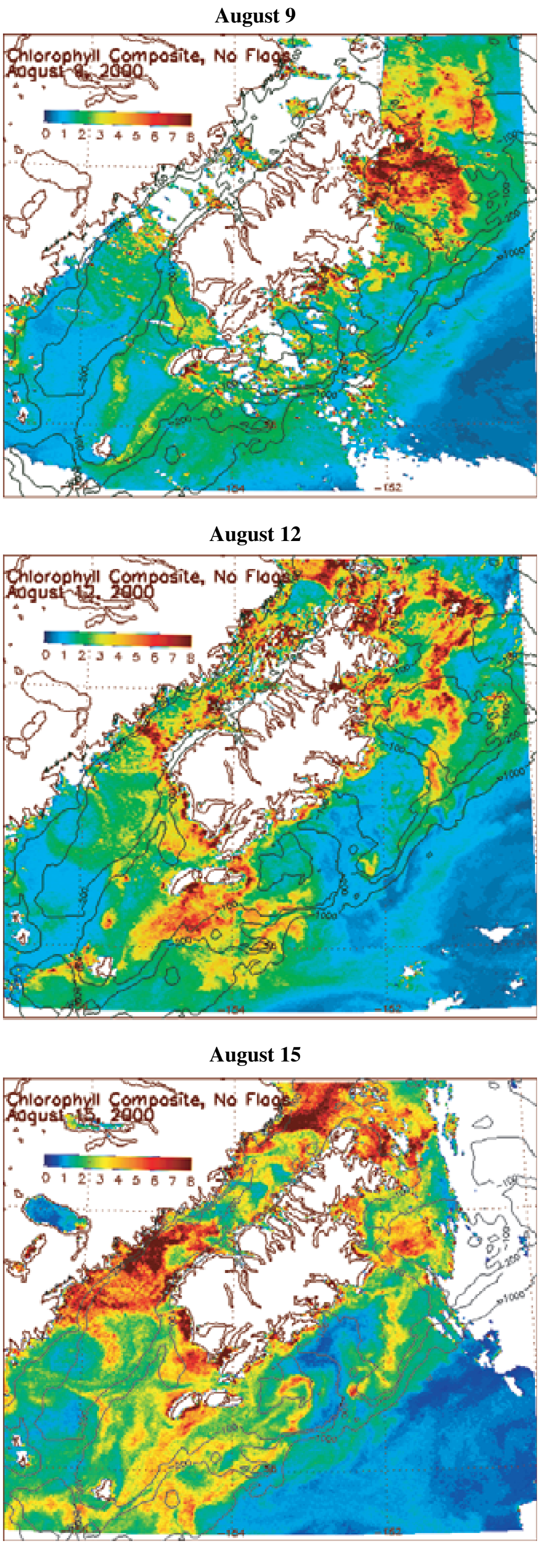


Figure 9. Satellite images of chlorophyll *a* concentration (mg m^{-3}) taken on August 13, August 21 and August 22, 2001.

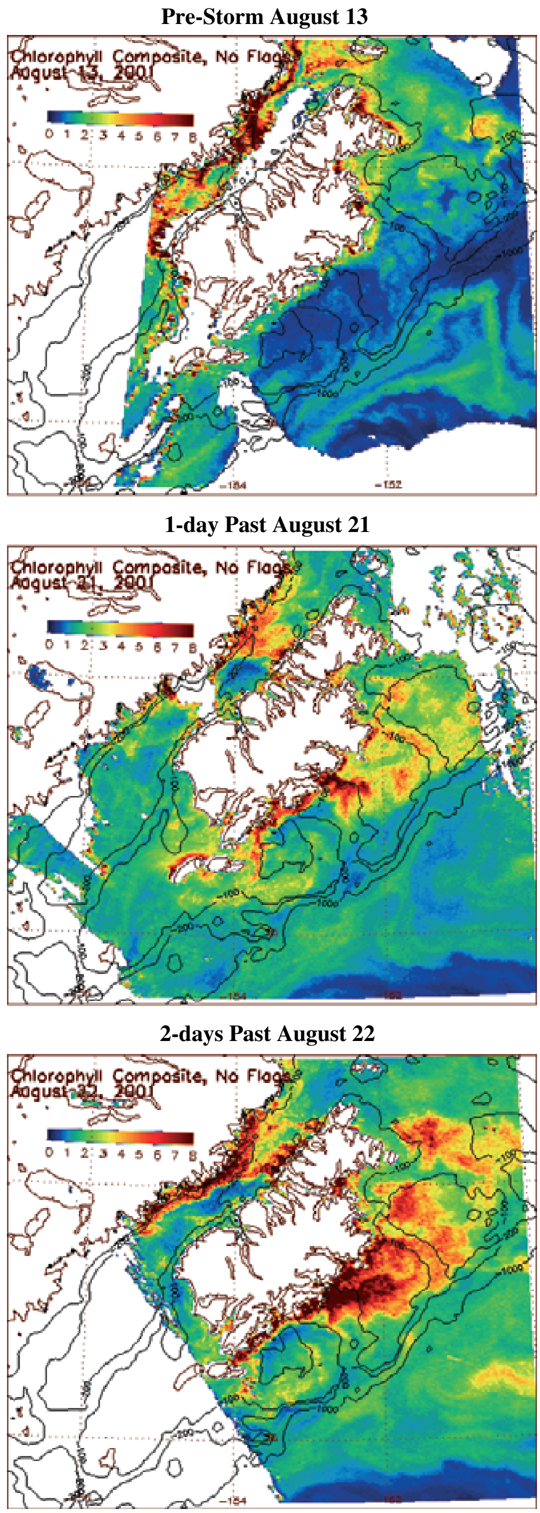


Figure 10. Trajectories of satellite-tracked drifters (depth of drogue approximately 40 m) in August 2001 and flow direction at oceanographic moorings (arrows indicate magnitude of flow, length of the eastern Chiniak arrow is approximately 10 cm s^{-1}).

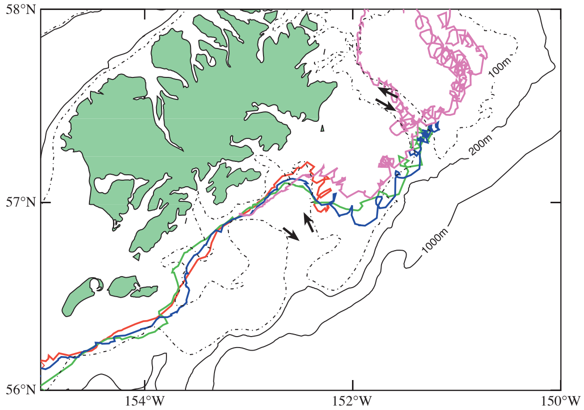
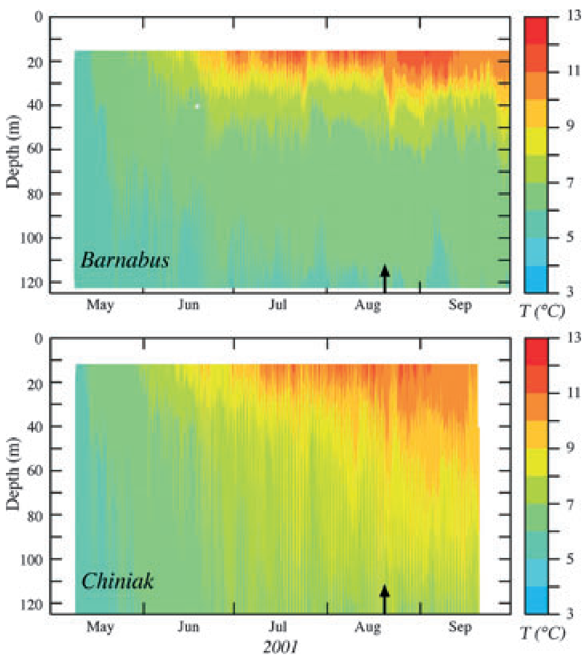


Figure 11. Temperature contours measured at Barnabas (top, BA2) and at Chiniak (bottom, CH3) based on hourly data. Arrows indicate the approximate date of the storm in August.



Hickey (1997) found similar results in her studies of flow patterns in submarine canyons off the coast of Washington. She showed the width of the trough influenced the amount of topographic steering, with wider troughs showing a higher level of topographic steering.

The exit pattern of flow measured by drifters in Barnabas Trough was not consistent with previous drifter experiments that showed a cyclonic meander around topographic gradients in Barnabas Trough (Lagerloef, 1983). Lagerloef (1983) interpreted flow patterns from current moorings placed in Barnabas Trough as evidence of a cyclonic meander over the trough. We interpret the flow differently. Our review of mooring and drifter data suggests that water flows into Barnabas Trough along the upstream side of the trough, but water exits the trough by a complex combination of alongshore flow though an adjacent trough to the southwest and offshore flow along the downstream side of the trough. This complex circulation pattern may concentrate zooplankton and nutrients in the inner portion of the trough.

Flow patterns appear to influence the spatial distribution of pelagic fish. Spatial distributions of capelin appear to be associated with subsurface intrusions of cool slope water in Barnabas Trough and regions of sharp gradients in topography in Chiniak Trough. This type of distribution has been observed in Atlantic capelin populations. In the Atlantic, aggregations of capelin appear to be associated with strong thermal fronts (Marchand *et al.*, 1999). Atlantic capelin stocks have exhibited marked shifts in distribution resulting from shifts in the distribution of cool water masses as a result of decadal shifts in climate forcing (Carscadden and Nakashima, 1997). The apparent association between capelin in Barnabas Trough and the presence of slope waters over the shelf may explain the rapid disappearance of capelin in near-shore shrimp trawl surveys after a decadal shift in climate forcing in the Pacific that resulted in warmer coastal ocean conditions (Anderson and Piatt, 1999).

The mechanisms underlying the niche separation within the troughs are unknown and will be the subject of future research. Three possible explanations for the observed differences are provided here. Distributions of adult pollock and age-1 pollock tend to be concentrated in warmer regions of the troughs and regions where production may be concentrated by circulation features of the trough. It is possible that pollock exhibit an affinity for warmer waters because they have acclimated to local environmental conditions (Ryer and Olla, 1998). However, it is unlikely that the temperatures in the 'offshore area' exceed the tolerance level for adult pollock and age-1 pollock because pollock are distributed throughout the Aleutian Islands and Bering Sea where ocean temperatures are much cooler.

An alternative explanation for the pollock distribution pattern observed in our study is that pollock

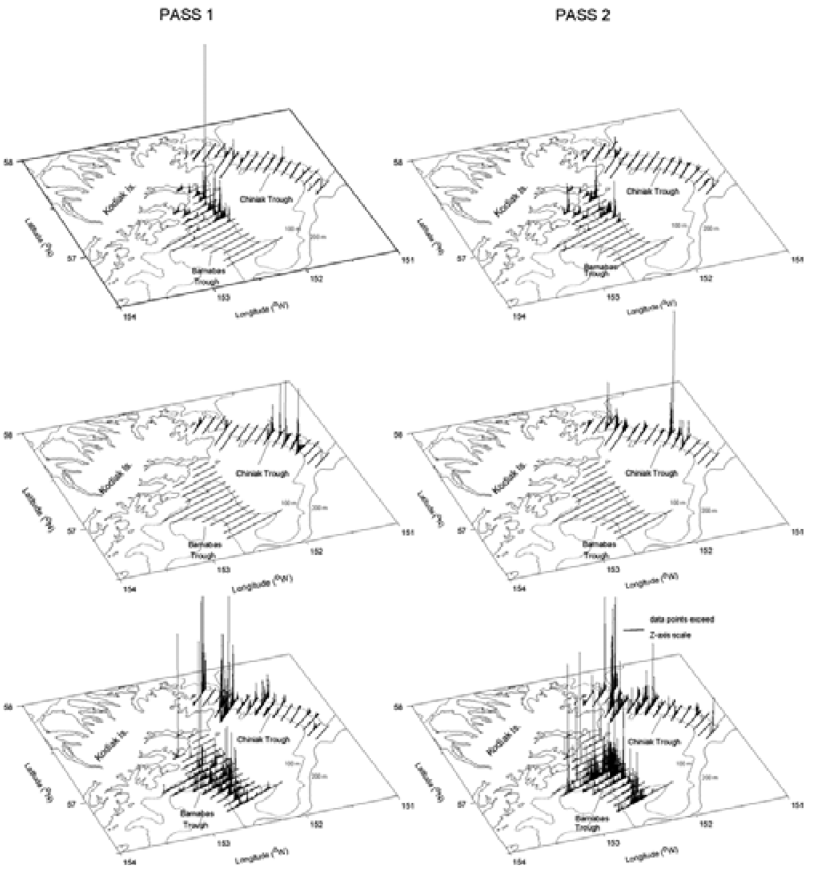


Figure 12. Acoustic backscatter (S_A) attributed to adult pollock (top), age-1 pollock (middle), and capelin–age-0 pollock mix (bottom) during passes 1 and 2 in August 2000. Vertical (*z*-axis) scale is 0–12 000 m^2 nmi^{-2} for adult pollock, and 0–35 000 m^2 nmi^{-2} for age-1 pollock and capelin–age-0 pollock mix.

exhibit a broad temperature tolerance but select habitats where prey availability is likely to be high. The satellite images taken in 2001 demonstrate that primary production is concentrated throughout Chiniak Trough. In Barnabas Trough, primary production was concentrated in the 'nearshore area' landward of the thermal front. Pollock distributions coincided with regions of high primary production. The observation of high production in near-shore regions was consistent with Coyle and Pinchuk (2005) who observed that copepod abundance was consistently higher in the ACC.

A third explanation for the pollock distribution patterns observed in our study is that circulation in Barnabas Trough enhances cross-shelf advection of oceanic zooplankton into the trough. Drifter results indicate that zooplankton would be advected into the trough from the outer shelf. This process has been observed in Barkely Canyon, off Vancouver Island, where zooplankton accumulates in the canyon in response to circulation features along the shelf-break (Allen *et al.*, 2001). Allen *et al.* (2001) found that zooplankton that occupied the deeper portions of the water column was displaced toward the head of the canyon. If zooplankton followed a similar distribution pattern in our study, it could explain why adult and juvenile pollock concentrate in the 'inshore area' of Barnabas Trough.

Our results indicate that adult and age-1 pollock exhibit similar mesoscale horizontal distribution patterns and that these distribution patterns are different from capelin. Spatial partitioning between predators (adult pollock) and prey (capelin) may modulate the strength of interactions between these two species. The importance of scale in interpreting the strength of species interactions has been documented in numerous studies. Rose and Leggett (1990) and Logerwell *et al.* (1998) reasoned that if species exhibited strong interactions, predators would be co-located with their prey at mesoscale spatial scales. Results from 2000 and 2001 surveys show that at the scale of the area of the trough, adult pollock and capelin occupy different portions of the troughs. During the day adult pollock and capelin occupy different parts of the water column. Visual observations showed that adult pollock occupied shallower waters at night; however, overlap between adult pollock and capelin at night was small because the two species occupied different regions of

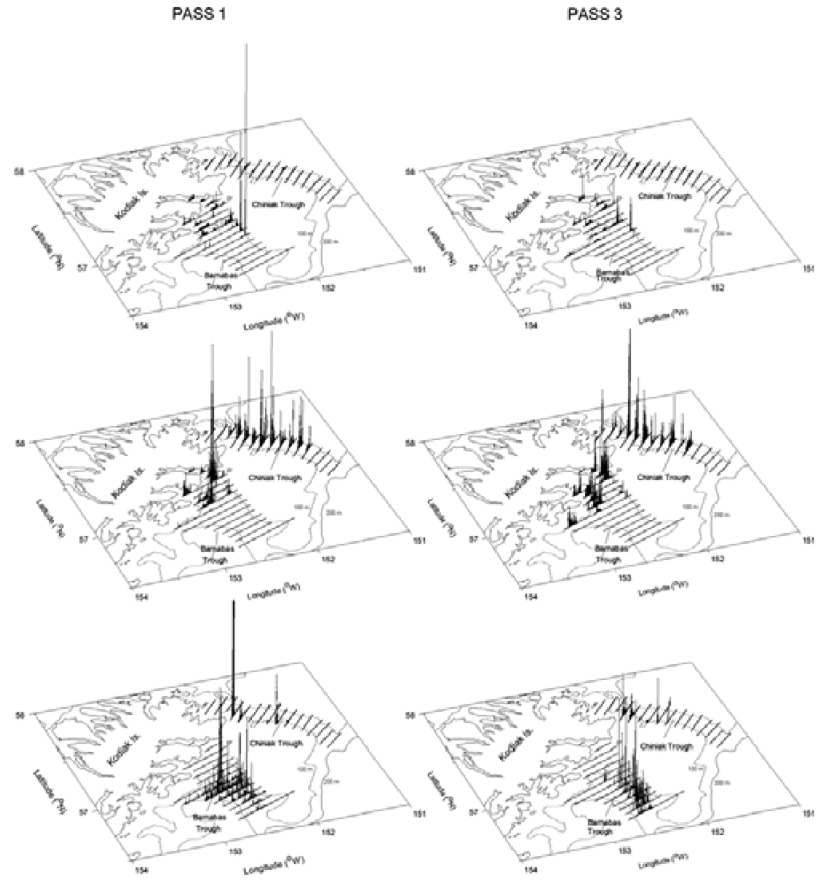


Figure 13. Acoustic backscatter (S_A) attributed to adult pollock (top), age-1 pollock (middle), and capelin (bottom) during a representative pass from the prestorm (pass 1) and post-storm (pass 3) in August 2001. Vertical (*z*-axis) scale is 0–12 000 m^2 nmi^{-2} for adult pollock, and 0–35 000 m^2 nmi^{-2} for age-1 pollock and capelin–age-0 pollock mix.

the trough. These findings do not rule out the possibility that pollock consume capelin when they are co-located. Food habits data collected during the 2000 survey revealed that capelin do occur in pollock diets (P. Livingston, personal communication, Alaska Fisheries Science Center, Seattle, WA). However, our findings suggest it is not likely that predation by adult pollock limits capelin or juvenile pollock populations in the region.

The horizontal distributions of adult pollock and juvenile pollock were similar. Adult pollock and juvenile pollock are separated vertically during the day. During the night, these two size groups overlapped. This finding suggests that competition between juvenile pollock and adults for a shared resource (euphausiids) could be occurring. Age-1 pollock exceed the size range typically consumed by adults, therefore the likelihood of cannibalism is low (Yang and Nelson, 2000).

Our results indicate that age-0 pollock and capelin exhibited similar mesoscale horizontal distribution patterns. This finding suggests that interactions between these two small acoustic scatterers should be investigated further.

The storm event observed in our study deepened mixed layers in both troughs. This event enhanced production in the 'nearshore area' of Barnabas Trough. The storm did not influence the school characteristics or vertical distribution of adult pollock (Wilson *et al.*, 2003). The storm appeared to influence the school characteristics and vertical distribution of juvenile pollock (Wilson *et al.*, 2003). This finding has important implications for future survey planning. Our result suggests that ocean features marked by surface temperature fronts may not be sufficient to describe the location of subsurface features governing fish distributions.

Future studies will evaluate the persistence of niche separation between pollock and capelin. Studies will determine whether capelin and age-1 and adult pollock occupy different regions of the troughs in response to competition and/or in response to predator–prey interactions. Similarly, studies will focus on potential competitive interactions between capelin and age-0 pollock. The common use of euphausiids by these three groups as prey will allow researchers to evaluate the potential interactions between these species. Adult pollock consume a mixed diet of small fish and zooplankton, whereas juvenile pollock and capelin diets are restricted to zooplankton (Yang and Nelson, 2000). The reliance of the three dominant pelagic scatterers on euphausiids should allow for a preliminary analysis of competition among species for zooplankton.

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REFERENCES

Abrams, P.A. (1999) The adaptive dynamics of consumer choice. *Am. Nat.* **153:**83–97.

Allen, S.E., Viderinho, C., Thompson, R.E., Foreman, M.G.G. and Mackas, D.L. (2001) Physical and biological processes over a submarine canyon during an upwelling event. *Can. J. Aquat. Sci.* **58:**671–684.

Anderson, P. and Piatt, J.F. (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* **189:**117–123.

Carscadden, J. and Nakashima, B.S. (1997) Abundance and changes in distribution, biology and behavior of capelin in response to cooler waters of the 1990s. In: *Forage Fishes in Marine Ecosystems*. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01. University of Alaska Fairbanks, pp. 457–468.

Coyle, K.O. and Pinchuk, A.I. (2005) Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. *Deep Sea Res. Part II* **52:**217–245.

Hickey, B.M. (1997) The response of a steep-sided, narrow canyon to time variable wind forcing. *J. Phys. Oceanogr.* **27:**697–726.

Lagerloef, G. (1983) Topographically controlled flow around a deep trough transecting the shelf off Kodiak Island, Alaska. *J. Phys. Oceanogr.* **13:**139–146.

Logerwell, E.A., Hewitt, R.P. and Demer, D.A. (1998) Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. *Ecography* **21:**212–223.

MacLennan, D.N., Fernandes, P.G. and Dalen, J. (2002) A consistent approach to definitions in symbols in fisheries acoustics. *ICES J. Mar. Sci.* **59:**365–369.

Marchand, C., Simrad, Y. and Gratton, Y. (1999) Concentration of capelin (*Mallotus villosus*) in tidal upwelling fronts at the head of the Laurentian Channel in the St. Lawrence estuary. *Can. J. Fish. Aquat. Sci.* **56:**1832–1848.

Musgrave, D.L., Weingartner, T.J. and Royer, T.C. (1992) Circulation and hydrography in the northwestern Gulf of Alaska. *Deep Sea Res.* **39:**1499–1519.

Reed, R.K. and Schumacher, J.D. (1986) Physical oceanography. In: *The Gulf of Alaska Physical Environment and Biological Resources*. D.W. Hood & S.T. Zimmerman (eds) Washington, DC, USA: Alaska Office, Ocean Assessments Division, National Oceanic and Atmospheric Administration, U.S. Dept. Commer. and U. S. Dept. of the Interior. U. S. Government Printing Office, pp. 57–75.

Rice, J. (2001) Implications of variability on many time scales for scientific advice on sustainable management of living marine resources. *Prog. Oceanogr.* **49:**189–209.

Rose, G.A. and Leggett, W.C. (1990) The importance of scale to predator-prey spatial correlation: an example of Atlantic fishes. *Ecology* **71:**33–43.

Ryer, C.H. and Olla, B.L. (1998) Shifting the balance between foraging and predator avoidance: the importance of food distribution for a schooling pelagic forager. *Environ. Biol. Fishes* **52:**467–475.

Sinclair, E.H. and Zeppelin, T.K. (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *J. Mammal.* **4:**973–990.

Stabeno, P.J. and Reed, R.K. (1991) Recent lagrangian measurements along the Alaskan Stream. *Deep Sea Res.* **38:**289–296.

Stabeno, P.J., Reed, R.K. and Schumacher, J.D. (1995) The Alaska Coastal Current: continuity of transport and forcing. *J. Geophys. Res.* **100:**2477–2485.

Stabeno, P.J., Bond, N.A., Hermann, A.J., Mordy, C.W. and Overland, J.E. (2004) Meteorology and oceanography of the northern Gulf of Alaska. *Cont. Shelf Res.* **24:**859–897.

Traynor, J.J., Williamson, N.J. and Karp, W.A. (1990) A consideration of the accuracy and precision of fish-abundance estimates derived from echo-integration surveys. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* **189:**101–111.

Williamson, N.J. and Traynor, J.J. (1984) In situ target-strength estimation of Pacific whiting (*Merluccius productus*) using a dual-beam transducer. *J. Cons. Int. Explor. Mer.* **41:**285–292.

Wilson, C., Hollowed, A.B., Shima, M., Walline, P. and Stienessen, S. (2003) Interactions between commercial fishing and walleye pollock. *Alaska Fish. Res. Bull.* **10:**61–77.

Yang, M.-S. and Nelson, M.W. (2000) *Food Habits of the Commercially Important Groundfishes in the Gulf of Alaska in 1990, 1993, and 1996*. NOAA Tech. Memo. NMFS-AFSC-112, 174 p.

