



The influence of pelagic habitat selection and interspecific competition on productivity of juvenile walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*) in the Gulf of Alaska

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ABSTRACT

Here we investigate processes affecting productivity of capelin and walleye pollock in the Gulf of Alaska. We examine pelagic habitat selection by comparing the distribution of juvenile fish and their prey with oceanographic properties and we evaluate the potential for interspecific competition by comparing diets and measures of foraging. The primary field study was conducted in Barnabus Trough, Kodiak Island, Alaska, during September 2005. The distribution of fish was assessed acoustically and trawls were used to collect individual fish for stomach content analyses. Physical and biological data were collected with conductivity–temperature–depth probes and zooplankton tows. Age-0 pollock were distributed in cool waters offshore of a mid-trough front, coincident with the distribution of euphausiids, their preferred prey. In contrast, capelin and their prey (copepods) were distributed throughout the trough. We observed that sympatric capelin (occurring with pollock) often had reduced foraging success compared to allopatric capelin (occurring alone). Results of a bioenergetic model also suggest that the exclusion of capelin from foraging on euphausiids can have negative consequences for capelin growth.

Key words: capelin, fisheries acoustics, foraging, growth, Gulf of Alaska, interspecific competition, *Mallotus villosus*, oceanography, pollock, *Theragra chalcogramma*

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INTRODUCTION

Walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*) are key forage fish in the Gulf of Alaska (GOA). Pollock is a dominant species in the Alaska groundfish complex and a target species for one of the world's largest fisheries. It is important prey for other groundfish, such as Pacific cod (*Gadus macrocephalus*), arrowtooth flounder (*Atheresthes stomias*) and Pacific halibut (*Hippoglossus stenolepis*) (Yang, 2003), and for marine mammals (Sinclair and Zeppelin, 2002). Capelin is also an important forage fish, serving as prey for seabirds (Hatch and Sanger, 1992), groundfish (Jewett, 1978) and marine mammals (Sinclair and Zeppelin, 2002). Capelin and juvenile pollock are both zooplanktivorous, foraging primarily on calanoid copepods and euphausiids (Vesin *et al.*, 1981; Naumenko, 1984; Brodeur and Wilson, 1996; Sturdevant, 1999); O'Driscoll *et al.*, 2001; Orlova *et al.*, 2002), but also on larvaceans, amphipods and other zooplankton prey (Gjørseter, 1998; Wilson *et al.*, 2005).

The GOA is a shelf system that is punctuated by a series of submarine troughs that create varying areas of shelf and canyon regions. The region supports a high level of primary production from April to November with seasonal blooms in May and October (Stabeno *et al.*, 2004). GOA shelf waters are characterized by a seasonal phytoplankton bloom of large diatoms and dinoflagellates that supports a copepod-dominated grazing assemblage (Cooney, 2005; Coyle and Pinchuk, 2005). Euphausiids such as *Euphausia pacifica* are commonly found in oceanic waters, reaching peak abundance in winter (Cooney, 1986; Coyle and Pinchuk, 2005). They are locally abundant on the shelf and slope as a result of onshore transport (Kendall *et al.*, 1980; Coyle and Pinchuk, 2005).

Previous research in the central GOA shows that the distribution and feeding ecology of juvenile pollock and capelin is often driven by spatial and temporal variability in oceanographic properties on the shelf. In the Semidi Bank vicinity, which includes portions of the Shumagin and Shelikof sea valleys,

juvenile pollock and capelin were densest in proximity to sea valleys, especially along the upstream edge of Semidi Bank, where oceanographic processes resulted in increased prey density (Wilson *et al.*, 2006b). Because these juvenile pollock and capelin often co-occur and share prey resources, there may be a high potential for interspecific competition and fine-scale resource partitioning (Wilson *et al.*, 2006a).

Research conducted in the central GOA off Kodiak Island has similarly highlighted the potential importance of oceanographic processes and competition for the distribution of forage fishes. Fisheries acoustics and oceanographic surveys in a submarine trough off Kodiak Island (Barnabus Trough) showed that a mid-trough front defined water masses of different temperature, salinity and productivity. Inner-shelf waters were warmer, fresher, well-mixed and had higher chlorophyll biomass than the cooler,

high-salinity and stratified waters offshore of the front. The distribution of these two distinct water masses also apparently determined the distribution of juvenile pollock and capelin (Hollowed *et al.*, 2007). Logerwell *et al.* (2007) hypothesized that inner-shelf waters were preferred foraging habitat for juvenile pollock and capelin. They also suggested the potential for interspecific competition. However, these hypotheses are difficult to evaluate without information on the distribution of prey, fish diet and foraging success.

Here we build on the findings of previous studies (Hollowed *et al.*, 2007; Logerwell *et al.*, 2007) with additional field observations that include data on prey fields and fish diet composition that had not been collected in previous years. We investigate local pelagic habitat selection by comparing the distribution of pollock and capelin with oceanographic properties and with the distribution of their prey. We investigate the

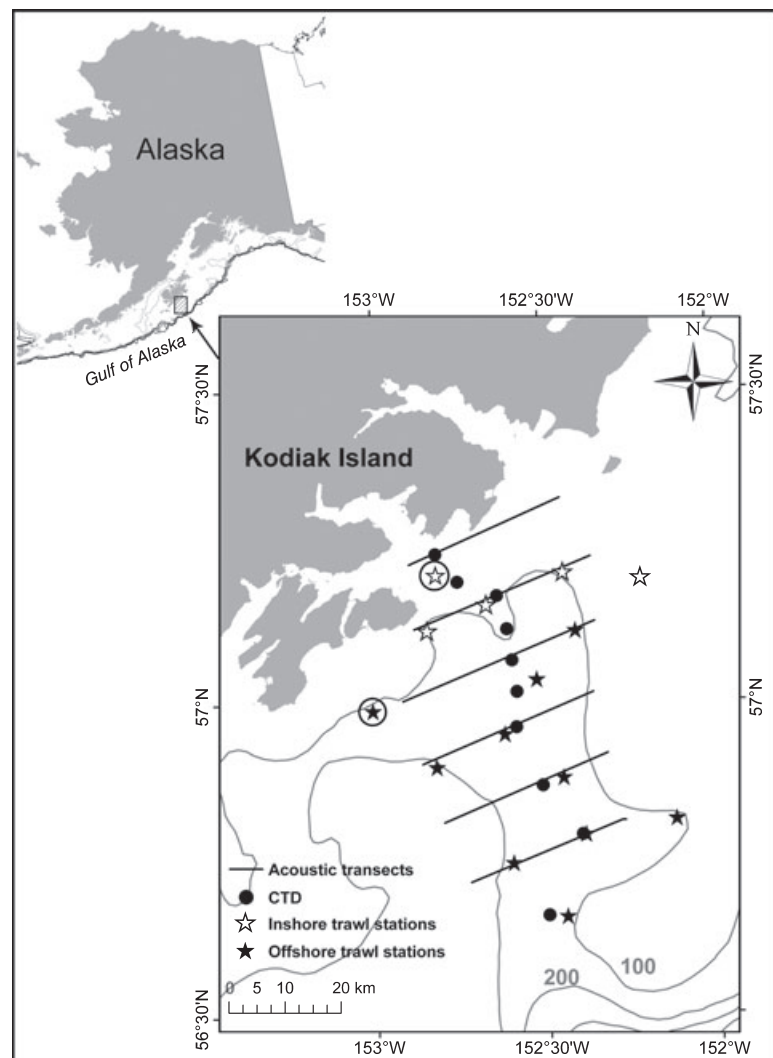


Figure 1. Study area for September 2005 cruise, Barnabus Trough, showing the location of acoustic transects, CTD stations and trawl stations (Stauffer and Tucker trawls). White stars are 'inshore' stations, solid black stars are 'offshore' stations (relevant for Figs 7, 9 and 10). The exceptions are the circled trawl stations. The circled white star represents a station where only a Tucker trawl was deployed. The circled solid black star represents stations where only a Stauffer trawl was deployed. Depth contours are in meters.

potential for interspecific competition by comparing diets and measures of foraging success between juvenile capelin and pollock.

METHODS

The study was conducted in Barnabus Trough off the east coast of Kodiak Island in the GOA (Fig. 1) during 10–13 September 2005. It was nested within a larger grid station survey of the shelf off the east coast of Kodiak Island, conducted by the Ecosystem and Fisheries-Oceanography Coordinated Investigations (Eco-FOCI) Program during 5–14 September (Recruitment Processes Program, Alaska Fisheries Science Center, National Marine Fisheries Service). For comparison we include data on fish distribution and oceanography acquired during a similar survey conducted in the same area in August–September 2004 (Logerwell *et al.*, 2007). New analyses of euphausiid distribution and fish diet composition in samples from 2004 are also included here.

Acoustics

The distribution of fish and large zooplankton (i.e., euphausiids) in Barnabus Trough was assessed using standard acoustic-trawl survey methods during daylight hours aboard the National Oceanic and Atmospheric Administration (NOAA) ship *Miller Freeman* (Traynor, 1997; Wilson *et al.*, 2003; Simmonds and MacLennan, 2005). The acoustic survey consisted of a set of uniformly spaced [6 nautical miles (nmi)] parallel transects (Fig. 1), along which acoustic data were collected with a calibrated Simrad EK 500 echosounder (Kongsberg, Norway) operating at 38 and 120 kHz. These data were logged and later processed using ECHOVIEW software (SonarData Pty. Ltd., Hobart, Tasmania, Australia). A midwater trawl (Stauffer trawl: see below) was deployed opportunistically along transects to identify species composition of the backscatter and collect other biological samples. After the acoustic data were classified to a particular taxonomic group (e.g., walleye pollock or capelin) based on patterns identified in trawl catches and echo signatures, estimates of fish distribution patterns were constructed from the 38-kHz data based on area backscattering values, i.e., nautical area scattering coefficient ($S_A \text{ m}^2 \text{ nm}^{-2}$) defined in MacLennan *et al.* (2002). The distributions of age-0 pollock and capelin were assessed by mapping the area backscatter (S_A) attributed to each species or species mix. The S_A is linearly related to fish/zooplankton density for a given species and size distribution (Simmonds and MacLennan, 2005). The spatial resolution of acoustic data used

to construct fish distribution maps in the vertical was the backscatter for each species integrated over the entire water column between about 14 m depth to within about 0.5 m of the bottom, and in the horizontal was 185.2 m (0.1 nmi).

Euphausiid relative abundances were estimated based on acoustic backscatter measured at 120 kHz. Euphausiid backscatter measurements [mean volume backscatter strength, S_v (dB re 1 m^{-1})] are frequency-dependent between 38 and 120 kHz so euphausiid backscatter at 120 kHz was separated from other backscatter using frequency-differencing methods (Miyashita *et al.*, 1997; McKelvey and Wilson, 2006). Backscatter measurements at 38 and 120 kHz were post-processed using ECHOVIEW software. Measurements at 120 kHz were first processed to remove background noise and then filtered so that only measurements with at least a 10-dB signal-to-noise ratio were used in analysis (De Robertis and Higginbottom, 2007). Volume backscatter measurements were averaged vertically by 5 m, and horizontally across five pings to reduce the random variability due to multiple targets as well as differences in transducer spacing (Korneliussen and Ona, 2002). The bin-averaged backscatter measurements at 38 and 120 kHz were aligned by time and compared. If the averaged backscatter was 10–20 dB higher at 120 kHz than at 38 kHz, then the backscatter at 120 kHz was attributed to euphausiids. Acoustic backscatter ($S_A \text{ m}^2 \text{ nm}^{-2}$) (MacLennan *et al.*, 2002) attributed to euphausiids was integrated from 14 m from the surface to 1 m off bottom along the survey tracklines using a $-80 \text{ dB } S_v$ threshold and mapped at a horizontal resolution of 185.2 m (0.1 nmi).

Fish trawls

A mid-water trawl equipped with a 3-mm mesh codend liner and fished with 1.5×2.1 -m steel-V otter doors (the Stauffer trawl) was deployed opportunistically along the acoustic transects to verify the species constituting the acoustic signal (Fig. 1). The depth and duration of the tows were determined by the distribution of the acoustic signal. The species composition (by number and weight) of all Stauffer trawl catches was assessed by sorting and counting all fish in the catch (or a sub-sample if the catch was large), according to standard Eco-FOCI protocols (Brown *et al.*, 1999; Wilson *et al.*, 2006a). A subsample from each trawl of up to 100 fish of each species was measured to fork length (FL), with the exception of age-0 pollock, which were measured to standard length (SL) because accurate fork length measurements are difficult to obtain from age-0 pollock in the

Table 1. Taxonomic composition of zooplankton collected with the Tucker trawl in Barnabus Trough in September 2005. Copepodite stages 1–6 are indicated as CI–CVI. Taxonomic groups are relevant to Fig. 9.

Taxonomic group	Species	Stage	
Copepoda, small	<i>Acartia</i> spp.	Adult	
	<i>Calanus</i> spp.	CII	
	<i>Eucalanus bungii</i>	CI	
	<i>Metridia pacifica/lucens</i>	CIV	
	<i>Metridia</i> spp.	CIV	
	Metriididae	CI–III	
	<i>Neocalanus cristatus</i>	CII	
	<i>Neocalanus</i> spp.*	CII	
	<i>Oithona</i> spp.	CV + CVI	
	<i>Pseudocalanus</i> spp.	CI–III	
	<i>Pseudocalanus</i> spp.	CIV–V, Adult	
	Copepoda, large	<i>Calanus marshallae</i>	CIII–V, Adult
		<i>Calanus pacificus</i>	CIV–V, Adult
<i>Eucalanus bungii</i>		CII–V, Adult	
<i>Metridia pacifica/lucens</i>		CV, Adult	
<i>Metridia</i> spp.		CV, Adult	
<i>Neocalanus cristatus</i>		CIII–V, Adult	
<i>Neocalanus</i> spp.		CIII–V, Adult	
Chaetognatha			
Cnidaria		Medusa	
Euphausiid furcilia			
Thecosomata			
Euphausiacea, juvenile and adult	<i>Euphausia pacifica</i>		
	Euphausiid (unidentified)		
	<i>Tessarabrachion oculatum</i>		
	<i>Thysanoessa inermis</i>		
	<i>Thysanoessa inspinata</i>		
	<i>Thysanoessa longipes</i>		
	<i>Thysanoessa raschii</i>		
<i>Thysanoessa spinifera</i>			
Natantia		Larva	
		Adult and juvenile	
Larvacea			
Siphonophora			
Amphipoda	Gammaridea		
	Hyperiidia		
Ctenophora			

**Neocalanus flemingeri* and *Neocalanus plumchrus*.

field. All fork lengths were converted to standard lengths using the equations in Buchheister and Wilson (2005). These length data were used to construct length–frequency plots (unweighted by relative catch biomass).

The trawl catch data were not used directly to map the distribution of fish. Following standard acoustic-trawl survey methods (Traynor, 1997; Wilson *et al.*, 2003; Simmonds and MacLennan, 2005) the acoustic data (verified with trawl data) were used for mapping fish. This results in more complete spatial coverage than trawling alone.

Fish somatic weight and food habits

A subsample of up to 50 age-0 pollock and capelin were collected from each Stauffer trawl (if they were caught) for length–weight data and stomach contents analysis by the Eco-FOCI Program. Whole fish were frozen within an hour of landing (at -80°C then transferred to -20°C). Upon return to the laboratory, fish were thawed in seawater and then measured to the nearest 1 mm SL, blotted dry and weighed to the nearest 1 mg. Standard length and whole wet body weight of each fish were used to estimate species-specific length–weight relationships. Differences among length–weight relationships were evaluated with ANCOVA on transformed data (for linearity).

Up to 20 individuals of each species were selected by size from the frozen samples for diet analysis. In this way different sizes in each sample were reasonably well represented. Diet was determined by analyzing fish stomach contents. Stomachs were excised between the esophagus and pylorus and stored individually in a sodium borate-buffered 10% formalin solution. None of the stomachs was flaccid so regurgitation was not believed to be a problem. Stomach contents were dissected from the preserved samples, blotted dry and weighed to the nearest 0.01 mg. The contents were then teased apart and sorted into broad taxonomic categories following Brodeur *et al.* (2000). Taxonomic composition was quantified by prey count, prey weight and frequency of occurrence. Weight was measured to the nearest 0.01 mg.

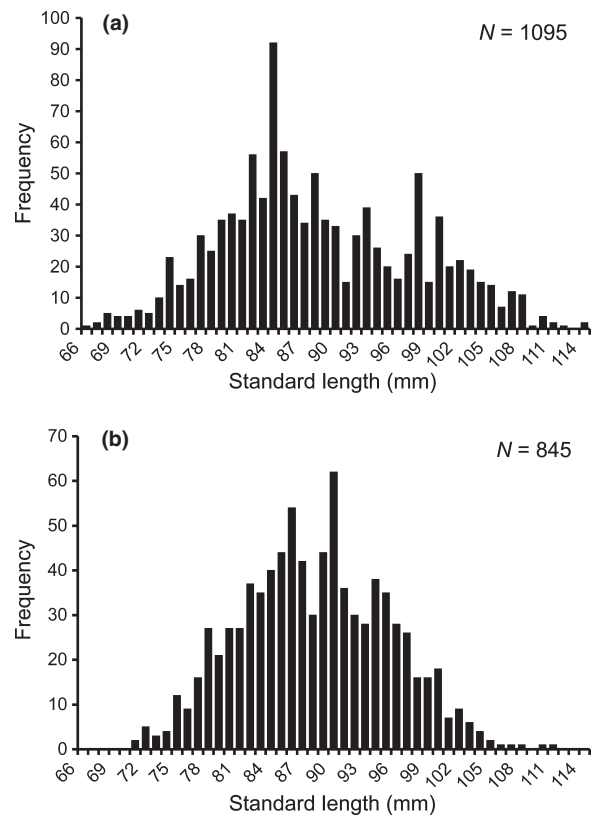
Diet overlap between age-0 pollock and capelin was quantified using Horn's Index of resource overlap (Horn, 1966). This index was chosen because it: (i) performs well in comparison with other overlap indices (Cailliet and Barry, 1979), (ii) has low bias due to variation in sample size and resource categories (Smith and Zaret, 1982), and (iii) was previously used to study age-0 pollock diet in the northeast Pacific (Sturdevant *et al.*, 2001; Wilson *et al.*, 2006a). Horn's Index, R_o , was calculated as

$$R_o = \frac{\sum_{i=1}^m ((p_{1i} + p_{2i}) \ln(p_{1i} + p_{2i})) - \sum_{i=1}^m (p_{1i} \ln(p_{1i})) - \sum_{i=1}^m (p_{2i} \ln(p_{2i}))}{2 \ln(2)}$$

where p_{1i} and p_{2i} are the percentages of the i th group of m prey taxa in the stomach contents of predators 1 and 2, respectively. The value of R_o ranges from 0 (no overlap) to 1 (perfect overlap). Following Sturdevant *et al.* (2001), diets were considered similar for $R_o > 0.6$. Overlap was calculated using prey count. Stomach content data were also used to calculate two measures of feeding success: % empty stomachs (no. fish with empty stomachs/total no. fish sampled) and % body weight (%BW = stomach content weight/somatic wet weight). Calculations of %BW excluded empty stomachs so that the two measures of feeding success were independent. Differences between % empty stomachs and %BW among stations were tested using a two-way blocked ANOVA after applying an arcsine-of-the-square-root transformation. This design accounts for the fact that age-0 pollock and capelin were sampled from the same tows.

The Wisconsin bioenergetics model, version 3.0 (Hanson *et al.*, 1997) was used to explore possible growth consequences of residing in areas with different temperatures and prey. The model computes energy for growth as the total energy consumed minus the energy budgeted for waste, activity and respiration. The model incorporates allometric mass-dependent and temperature-dependent functions for maximum consumption and metabolism. Following Mazur *et al.* (2007), the model for walleye pollock was parameterized for age-0 juveniles and energy for growth was converted to fish body growth (mm d^{-1}) using age-0 walleye pollock energy density (Buchheister *et al.*, 2006). Following Wilson *et al.* (2006a), the model for capelin was parameterized for herring (*Clupea harengus*) (Rudstam *et al.*, 1994), European smelt (*Osmerus eperlanus*) (Karjalainen *et al.*, 1997) and rainbow smelt (*Osmerus mordax*) (Lantry and Stewart, 1993) because capelin-specific parameters were not available. For capelin, energy for growth was converted to body growth using rainbow smelt whole body energy content (Lantry and Stewart, 1993). Model inputs were from 2005 data on integrated water column temperature (from CTD casts, described below, integrated over the water column and averaged across CTD stations), mean fish size (g, whole wet weight), median ration size (% somatic wet body weight) and diet composition by weight. The impact of euphausiids in age-0 walleye pollock diets was explored by comparing the growth potential based on observed taxonomic composition (by weight) to a growth potential based on a hypothetical diet, which was the same as the observed diet except that euphausiids were omitted.

Figure 2. Size distribution of fish (standard length) during the September 2005 survey: (a) capelin and (b) age-0 pollock.

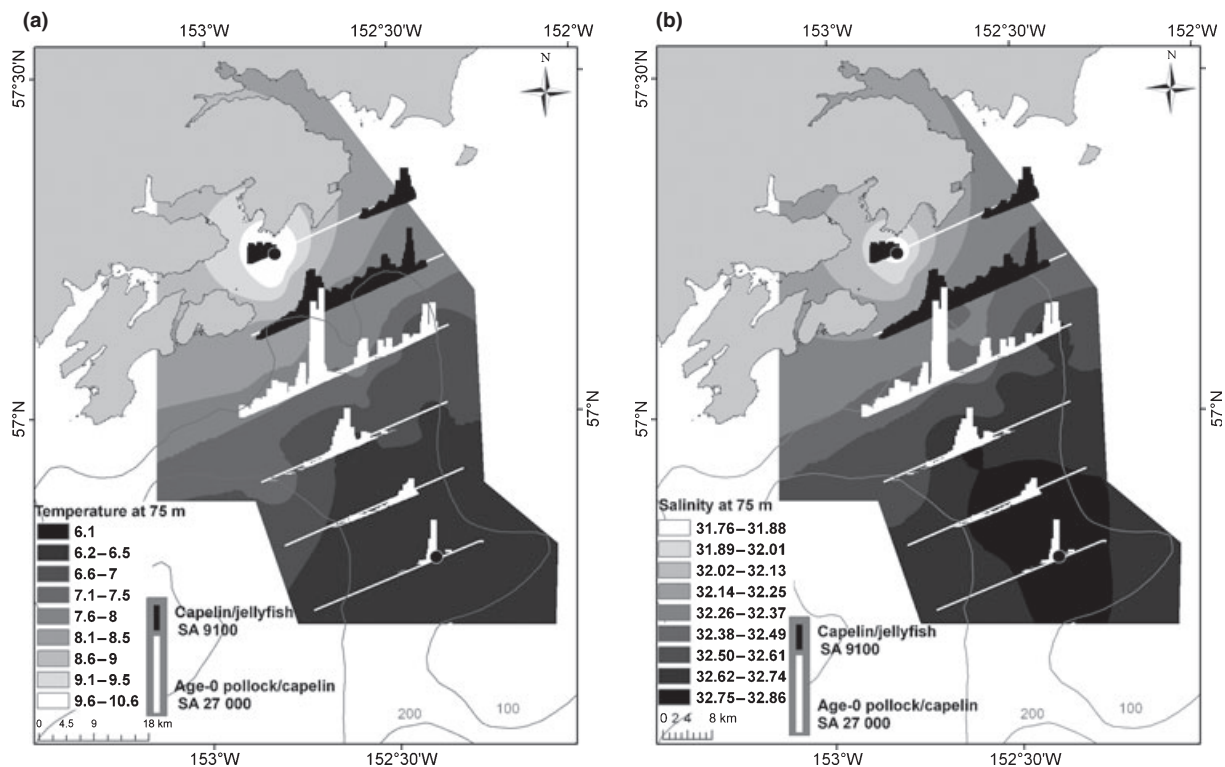


Oceanography

Conductivity–temperature–depth data were collected at selected sites (Fig. 1) using a Sea-Bird SBE 911plus CTD system (Sea-Bird Electronics, Inc., Bellevue, WA, USA) with dual temperature and salinity sensors. Data were recorded during the downcasts. Chlorophyll samples were collected from water samples taken on the CTD upcast at 10-m intervals from the surface to 50 m depth. Water samples for nutrient analyses (nitrate, phosphate and silicate) were collected on the upcast at 10-m intervals from the surface to 50 m depth, and at 150 and 200 m (or 10 m off bottom if total depth was <200 m). Conductivity–temperature–depth data were also collected from a CTD mounted on the zooplankton net (described below). Temperature and salinity data from both the CTDs and zooplankton net tows were used to create horizontal surfaces of temperature and salinity.

Four satellite-tracked drifters were deployed in the Barnabus Trough area. All drifters were drogued at 40 m to reduce direct effects of wind and wind-wave

Figure 3. Distribution of capelin/jellyfish mix (black bars) and age-0 pollock/capelin mix (white bars) during the September 2005 survey. Units are S_A ($m^2 \text{ nm}^{-2}$) and the scale is the same for both scattering types. Fish data are overlaid on: (a) water temperature ($^{\circ}\text{C}$) at 75 m, and (b) salinity at 75 m. Locations of selected inshore and offshore CTD stations are solid circles.



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.

Zooplankton

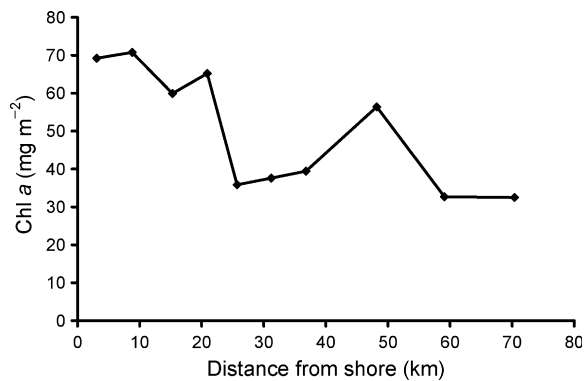
Plankton samples were collected near fish sampling locations to obtain information on the background prey field. Each plankton sample was collected with a 1-m² Tucker trawl (0.333-mm mesh nets) fished obliquely from 200 m (or 10 m off bottom) to the surface. Towing speed was adjusted to maintain a 45° wire angle at a wire retrieval rate of 20 m min⁻¹. A Sea-Bird SBE 19 SeaCat CTD profiler, attached in-line between the wire terminus and trawl, was used for real-time monitoring and recording of net depth, water temperature and salinity. The first net was used to sample that portion of the path below the thermocline (200 or 10 m off bottom to 40 m depth). The second net was used to sample the shallower portion of the path (40 m to the surface). All nets were mechanically tripped to open and close. The catch was preserved in a sodium borate-buffered solution of 5% formalin.

Numerical composition of plankton samples was determined in Szczecin, Poland, by the Polish Plankton Sorting and Identification Center following EcoFOCI protocol (Incze *et al.*, 1997). This protocol mandates a much finer resolution of copepod and euphausiid species and life stages than is practically available from the stomach content data, so individual species and stages were grouped into broad taxonomic categories following Wilson *et al.* (2006b) (Table 1).

RESULTS

In 2005, all midwater acoustic signals were accounted for by two different acoustic scattering types identified from the verification tows: capelin mixed with jellyfish and age-0 pollock/capelin mix. These scattering types were designated as mixes because both members were caught in the same verification tows and there was no apparent spatial or depth separation of the two in the acoustic echograms. Capelin ranged in size from 66 to 114 mm SL (Fig. 2a), indicating that they were juvenile fish, age-0 and -1 (Brown, 2002). Body size of pollock ranged from 71 to 111 mm SL (Fig. 2b), indicating that they were age-0 (Wilson *et al.*, 2003).

Figure 4. Chlorophyll *a* density as a function of distance from shore during the September 2005 survey. Chlorophyll data are from CTD casts only (see Fig. 1).



The acoustic data (verified with trawl data) were used for mapping fish, which provided more complete spatial coverage than trawling alone. The distributions of the two scattering types were non-overlapping.

Capelin/jellyfish were distributed along the two inshore transects, whereas age-0 pollock/capelin (all age-classes of capelin included) were found along the four offshore transects (Fig. 3). The depth distribution of the capelin/jellyfish was centered at approximately 50 m and extended down nearly to the bottom and up to approximately 25 m. The depth distribution of the age-0 pollock/capelin was centered at approximately 125 m, extending down to a few meters off bottom and up to about 75 m.

Water mass properties at depth (temperature and salinity at 75 m) indicate two different water masses separated by a mid-trough front. Inshore water was relatively warmer and fresher than offshore water (Fig. 3a,b). Integrated chlorophyll biomass was higher inshore. (Fig. 4). Water column profiles showed that waters inshore of the mid-trough front were mixed, whereas offshore waters were stratified (Fig. 5a). Inshore waters had higher surface nitrate, phosphate and silicate than offshore waters (Fig. 5b–d).

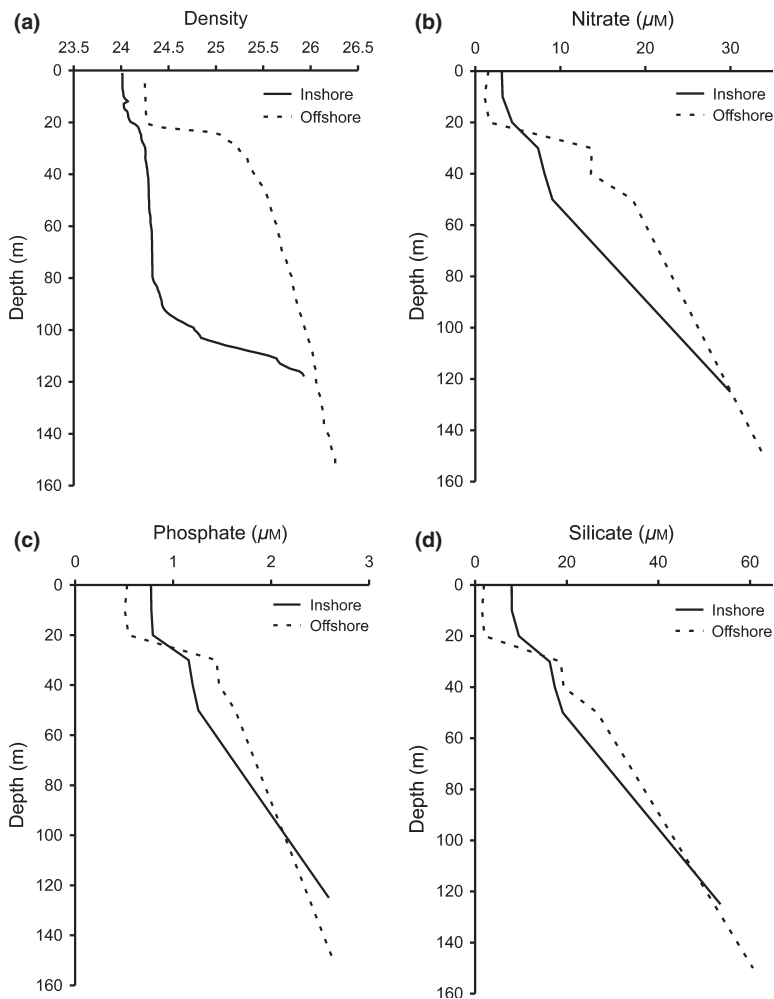
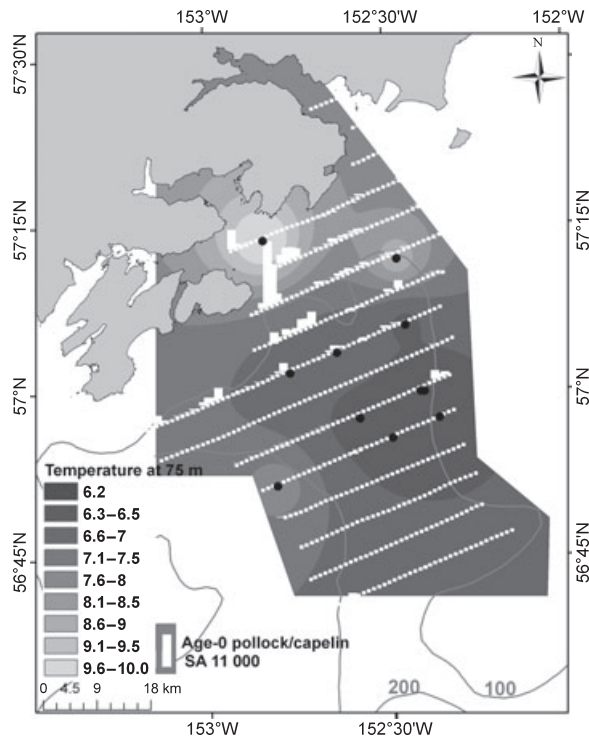


Figure 5. Profiles of water properties with depth (m) at representative CTD stations shown in Fig. 1 during the 2005 survey. Solid line represents the inshore station, dashed line the offshore station. (a) Density (σ_t), (b) nitrate (μM), (c) phosphate (μM), and (d) silicate (μM).

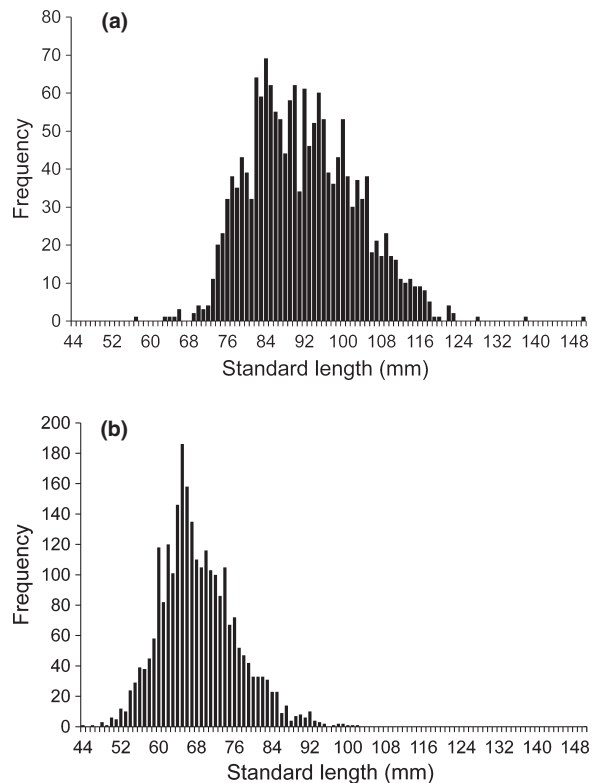
Figure 6. Distribution of age-0 pollock/capelin mix (S_A m^2 nm^{-2}) overlaid on water temperature ($^{\circ}C$) at 75 m during the 2004 survey (Logerwell *et al.*, 2007). Dotted lines indicate acoustic survey transects, black circles indicate stations at which temperature and depth data were collected with CTDs, net-mounted bathythermographs, and expendable bathythermographs. Data are from 2 to 4 September.



In 2004, only the age-0 pollock/capelin acoustic scattering type was observed, and these fish were found along the inshore transects (Fig. 6). Similar to 2005, salinity, temperature and chlorophyll data suggest two different water masses separated by a mid-trough front (Fig. 6; Logerwell *et al.*, 2007), although the front appeared to be weaker in 2004. Capelin length distribution in 2004 (57–150 mm) was similar to 2005. However, age-0 pollock were smaller in 2004 (44–102 mm SL) than in 2005 (Fig. 7).

Tracks of drifters released inshore and offshore of the mid-trough front in 2005 indicate overall flow from the northeast to the southwest (Fig. 8). Drifters released inshore of the front did not cross into offshore waters (Fig. 8a). Drifters released offshore of the front followed the 100-m depth contour towards the inshore head of the trough and then back out, but did not cross into inshore waters (Fig. 8b). The abundance of the dominant zooplankton, including large and small copepods, the most abundant taxa, did not differ from inshore to offshore (Fig. 9). Following copepods in abundance were euphausiid furciliae, larvaceans, cla-

Figure 7. Size distribution of fish (standard length) during the August–September 2004 survey: (a) capelin and (b) age-0 pollock.



docerans and chaetognaths. Euphausiid furciliae were more abundant inshore, but the other groups were equally abundant inshore and offshore. Very few juvenile and adult euphausiids were sampled by the Tucker trawl, possibly because of net avoidance and/or a near-bottom daytime distribution.

The distribution of euphausiids in 2005 shows that, similar to age-0 pollock, euphausiids were found only in the deeper waters of the trough (> 100 m). A consequence of this apparent depth preference was that euphausiids were more widespread along the transects offshore of the mid-trough front (Fig. 10). The euphausiids were distributed at depths in the water column similar to the age-0 pollock, around 125 m and deeper. In 2004, there were greater densities of euphausiids than in 2005, particularly in the inshore end of the trough (Fig. 11).

In 2005, calanoid copepods were prevalent in the diets of capelin inshore and offshore of the mid-trough front (Fig. 12a,b). Larger fish (75–94 mm SL) inshore of the front also consumed larvaceans. Only the largest capelin offshore (105–114 mm SL) consumed euphausiids (furciliae, juveniles and adults combined)

Figure 8. Tracks of drifters released in September 2005 overlaid on temperature (°C) at 75 m. Release locations indicated by a star. (a) Drifters released inshore of mid-trough front. The solid line represents a drifter tracked from 10 September to 16 October, and the dashed line represents a drifter tracked from 11 September to 18 October. (b) Drifters released offshore of mid-trough front. The solid line represents a drifter tracked from 10 September to 16 October, and the dashed line represents a drifter tracked from 9 September to 16 October.

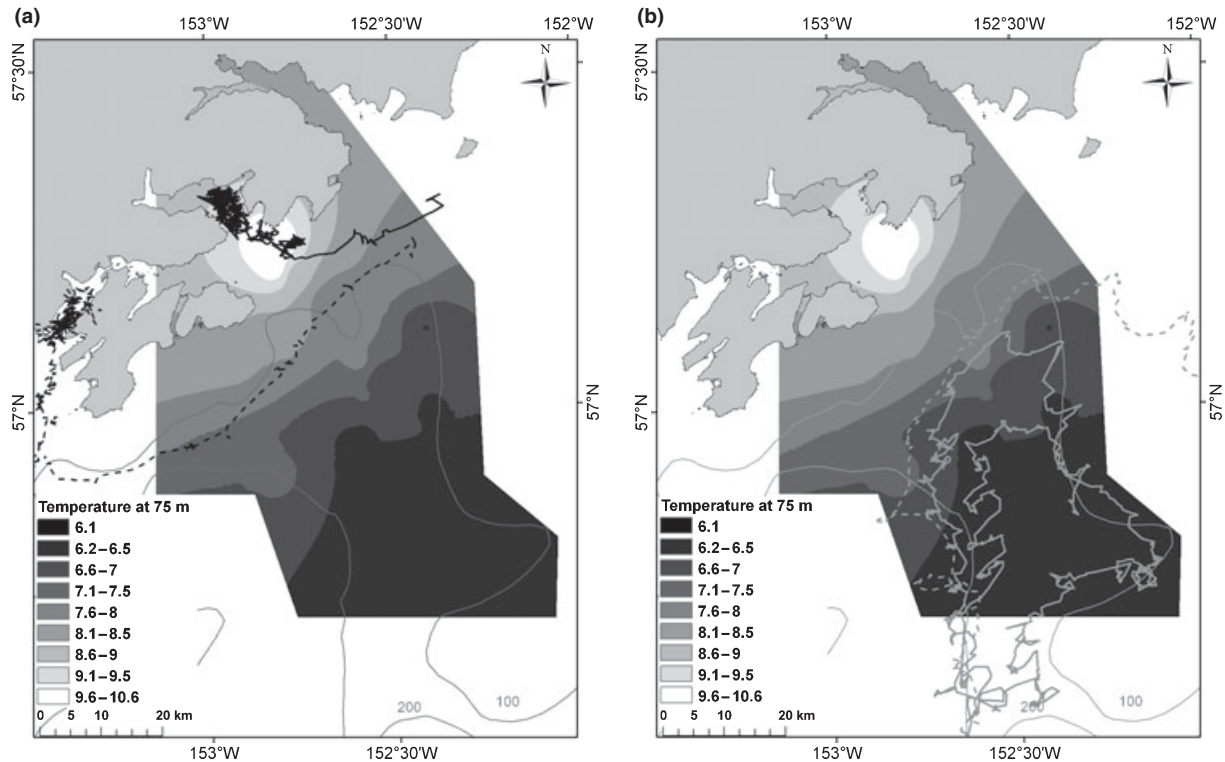
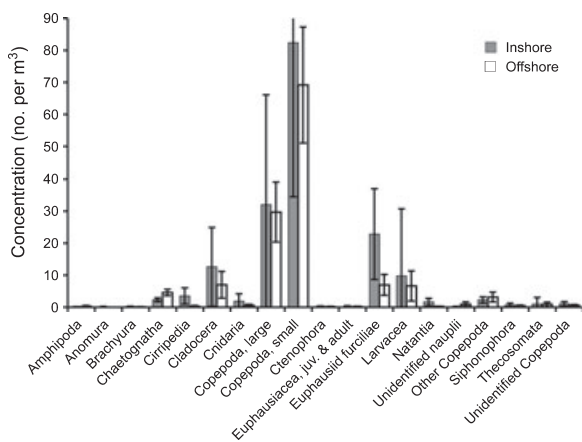


Figure 9. Concentration of zooplankton taxa over the entire water column (10 m off-bottom to the surface), inshore ($N = 5$) and offshore ($N = 11$) of the mid-trough front (mean and 95% confidence intervals). See Fig. 1b for inshore and offshore tow locations.

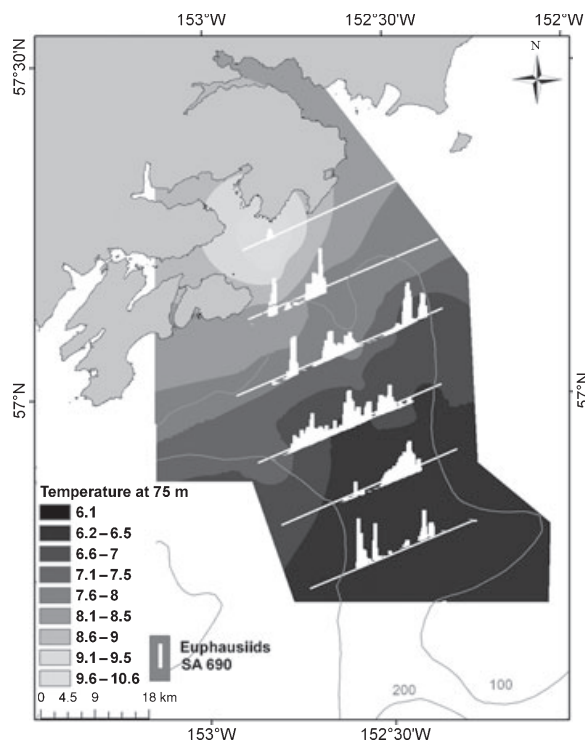


in substantial quantities (>10% of the diet). Horn's Index for capelin inshore versus offshore was 0.79, indicating similar diets. Calanoid copepods and eup-

hausiids made up over 80% of the diet of age-0 pollock in offshore waters (Fig. 12c). Horn's Index for capelin offshore versus pollock offshore was 0.25, indicating dissimilar diets. In 2004, euphausiids and copepods were dominant diet items for both capelin and pollock (Fig. 13). Horn's Index for capelin versus pollock in 2004 was 0.85, indicating similar diet composition. It should be noted that within-site variation in Horn's Index was high (ranging from 0.1 to 0.9) and it is likely that there are differences in feeding and diet within a single geographic area as well as between areas.

Bioenergetic models for capelin were constructed to examine the impact of differences between inshore and offshore habitat on capelin growth. The temperature data were integrated over the water column and averaged across CTD stations inshore or offshore. Model results indicated that despite the relatively warm inshore waters, capelin inshore and offshore of the mid-trough front had similar growth potential, 0.11 g day^{-1} and 0.10 g day^{-1} , respectively (Table 2). Because age-0 pollock were found only offshore, it was not possible to construct bioenergetic models of age-0 pollock in different habitats. Instead, a model of age-0

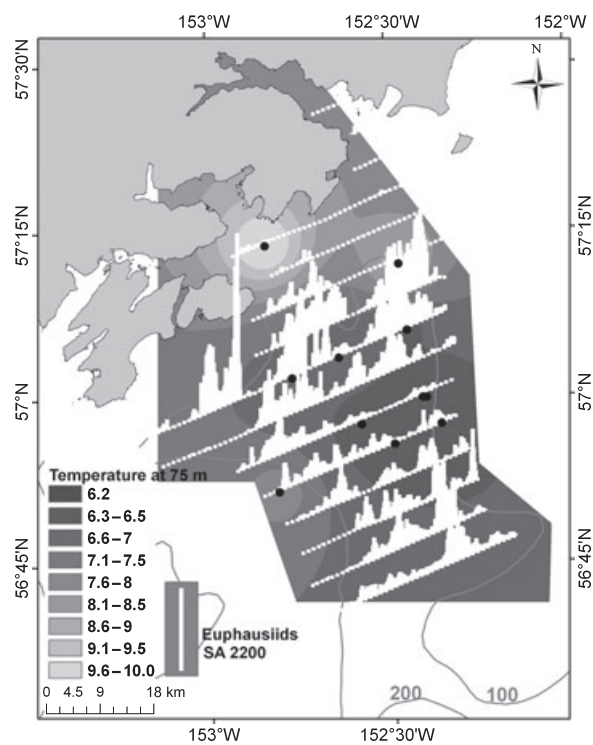
Figure 10. Distribution of euphausiids ($S_A \text{ m}^2 \text{ nm}^{-2}$) in September 2005 overlaid on water temperature ($^{\circ}\text{C}$) at 75 m.



pollock inshore was constructed with observed inshore temperature and a hypothetical diet that was identical to the diet of age-0 pollock offshore except that euphausiids were 'removed' from the diet composition. The model of age-0 pollock offshore was constructed with observed values. The goal of this comparison was to examine the importance of foraging on euphausiids in offshore waters. Age-0 pollock offshore feeding on euphausiids had a higher growth potential than hypothetical pollock inshore not feeding on euphausiids, 0.73 versus 0.60 g day^{-1} .

Length-weight relationships for capelin inshore and offshore in 2005 and inshore in 2004 were all similar according to the ANCOVA test. Feeding measures, % empty stomachs and %BW, for age-0 pollock and capelin collected inshore and offshore of the mid-trough front in 2005 and 2004 are shown in Table 3. In September 2005, the two species were caught together in every tow offshore of the front and thus were sympatric offshore. Capelin were also caught inshore of the front, but without age-0 pollock and thus were allopatric inshore in 2005. In 2004, capelin and age-0 pollock were sympatric inshore. Allopatric capelin in 2005 had 0% empty stomachs, whereas sympatric capelin had 14.4% empty stomachs. There may have been a bias introduced to these data as a

Figure 11. Distribution of euphausiids ($S_A \text{ m}^2 \text{ nm}^{-2}$) in August 2004 overlaid on water temperature ($^{\circ}\text{C}$) at 75 m. Dotted lines indicate acoustic survey transects, black circles indicate stations at which temperature and depth data were collected with CTDs, net-mounted bathythermographs, and expendable bathythermographs. Data are from 2 to 4 September.



result of time of collection. Overall, % empty stomachs of capelin in 2005 was higher during 'morning' (midnight to noon) and a greater proportion of stations were occupied during 'morning' offshore (50%) compared to inshore (25%). According to results of the two-way blocked ANOVA, %BW did not vary among capelin with allopatric and sympatric distributions in 2005. There was no relationship between %BW and time of collection for capelin in 2005. Percent BW was substantially lower for sympatric capelin in 2004 compared to 2005, although the difference was not statistically significant. Sympatric age-0 pollock in both years had lower % empty stomachs than sympatric capelin and higher %BW, although neither difference was statistically significant.

DISCUSSION

Our results from the 2005 survey are consistent with the hypothesis that the distribution of age-0 pollock and capelin in Barnabus Trough is driven by oceanographic processes and the distribution of their zoo-

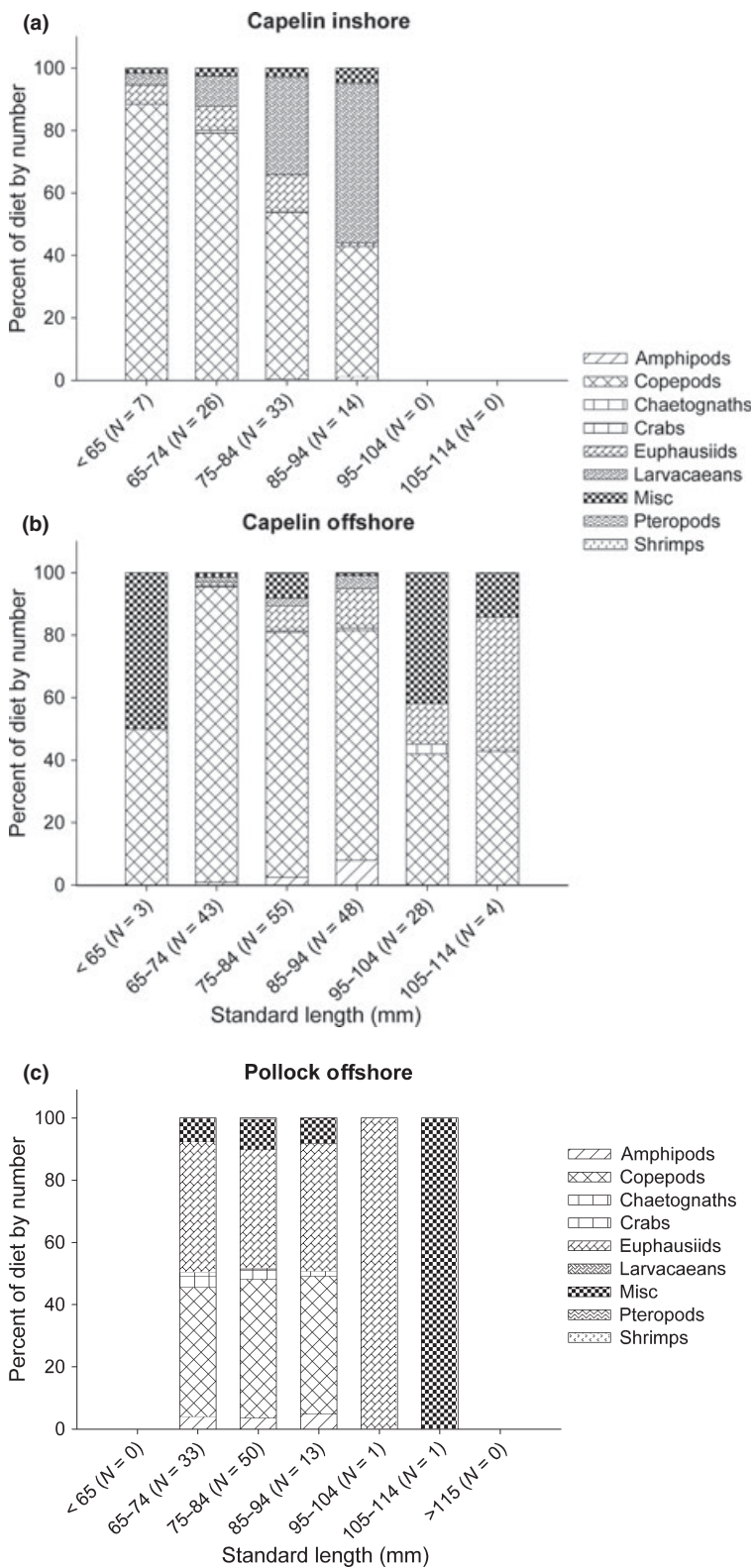


Figure 12. Taxonomic composition (% by number) of fish diet by standard length in 2005: (a) capelin in inshore waters, (b) capelin in offshore waters, and (c) age-0 pollock in offshore waters (see Fig. 1b for tow locations).

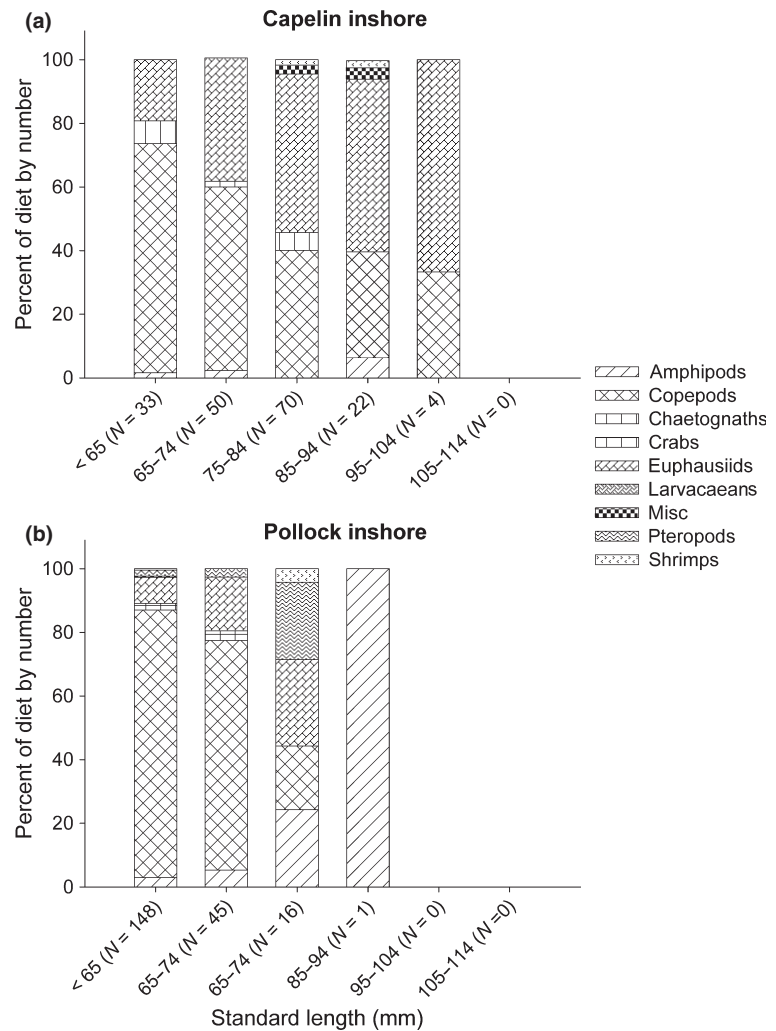


Figure 13. Taxonomic composition (% by number) of fish diet by standard length from the 2004 survey: (a) capelin and (b) age-0 pollock.

plankton prey. We documented two contrasting water masses in the trough, separated by a mid-trough front. Well-mixed inshore waters were relatively warm and fresher. The apparent mixing was likely responsible for the elevated surface nutrients and higher integrated chlorophyll biomass. Offshore waters were relatively cool and had high salinity, consistent with transport of deeper off-shelf waters into the trough (Hollowed *et al.*, 2007). The water column was stratified and surface nutrients and integrated chlorophyll biomass were lower offshore of the front. Drifter tracks indicated transport into the trough on the northeast side and back out of the trough on the southwest side, but with little or no transport across the mid-trough front. Euphausiid adults were distributed primarily in the deeper waters of the trough offshore of the mid-trough front. The water mass properties and drifter tracks indicate that adult euphausiids were likely transported into the trough with the cooler off-shelf waters in

which they are typically found (Kendall *et al.*, 1980; Cooney, 1986) but did not disperse into inshore waters across the mid-trough front. In contrast, copepods were equally abundant inshore and offshore of the front. These smaller zooplankters are typically distributed across the shelf of the Gulf of Alaska (Cooney, 2005).

As indicated by Horn's Index, the diets of age-0 pollock and capelin during this study were different. Pollock diet was dominated by euphausiids and copepods, whereas capelin diet was dominated by copepods, with the exception of the largest capelin, which also consumed euphausiids. In summary, we argue that the distribution of age-0 pollock and capelin in Barnabus Trough represents a response to the oceanographically driven distribution of their prey. Age-0 pollock were found in offshore waters where euphausiids were widespread, and capelin were found throughout the trough with their copepod prey.

Table 2. Inputs and results for bioenergetic models of capelin and age-0 pollock based on 2005 data.

Capelin	Inshore	Offshore
Temperature (°C)	9.25	7.19
Fish size (g, whole wet weight)	5.07	5.07
Ration size (% somatic wet body weight)	0.27	0.27
Diet composition (by weight)	Observed	Observed
Growth potential (g d ⁻¹)	0.11	0.10
Age-0 pollock	Diet w/o euphausiids	Diet w/euphausiids
Temperature (°C)	9.25	7.19
Fish size (g, whole wet weight)	6.43	6.43
Ration size (% somatic wet body weight)	1.09	1.09
Diet composition (by weight)	Hypothetical	Observed
Growth potential (g d ⁻¹)	0.60	0.73

Table 3. Feeding measures for age-0 pollock and juvenile capelin collected inshore and offshore of the front in Barnabus Trough in September 2005 and August 2004 (Logerwell *et al.*, 2007). Species are sympatric when they occur together in- or offshore of the front, and allopatric when they occur without the other species.

Year	Inshore/offshore	Species	Allopatric/sympatric	n	% Empty stomachs	Prey % body weight mean (SD)
2005	Inshore	Capelin	Allopatric	80	0	2.0 (0.6)
	Offshore	Capelin	Sympatric	181	14.4	2.1 (1.5)
	Offshore	Pollock	Sympatric	98	7.1	2.9 (1.6)
2004	Inshore	Capelin	Sympatric	179	35.8	0.5 (1.2)
	Inshore	Pollock	Sympatric	210	3.8	1.6 (1.4)

The observed geographic disparity in distribution and diet is more likely due to differences between age-0 pollock and capelin in cross-shelf movements and/or prey preferences than to diel migration or vertical distribution. The acoustic data showed that during the day, when the transects were surveyed and fish were collected for diet determination, euphausiids and age-0 pollock/capelin were found at similar depths. At night, the distributions of age-0 pollock (Brodeur and Wilson, 1996) and capelin (Mowbray, 2002) are expected to expand towards the surface in concert with many zooplankters, including euphausiids (Shaw and Robinson, 1998). This similarity in diel vertical migration between predator groups increases spatial association with regard to distribution of abundance and diet composition.

Bioenergetics modeling of fish growth potential was coherent with the distribution patterns we observed. The growth potential of capelin was virtually the same in inshore and offshore waters, so there would be no advantage to capelin to forage in warmer inshore waters. The bioenergetics model showed that age-0 pollock foraging on euphausiids offshore had higher

growth potential than a hypothetical pollock foraging inshore on a diet devoid of euphausiids. Length-weight relationships, an indicator of fish condition, showed that capelin of a given length were the same weight inshore and offshore of the mid-trough front.

Examination of acoustically derived euphausiid 'biomass' suggests that the distribution of euphausiids may also explain the distribution of fish in 2004. In 2004, there were greater densities of euphausiids observed than in 2005, particularly towards the inshore end of the trough, perhaps due to a relatively weak mid-trough front, across which there may have been greater cross-shelf dispersal. Although the distribution of age-0 pollock and capelin did not track precisely the distribution of euphausiids in 2004, this apparent shoreward shift in the densest aggregations of euphausiids might have played a role in the inshore distribution of fish that year. Further investigation of other factors that could influence the distribution of juvenile pollock and capelin is needed, such as the distribution of predators and the effects of ontogenetic migrations.

We cannot rule out the possibility that age-0 pollock distribution was driven by processes other than

prey distribution and that their diet simply reflects consumption of the dominant prey in the environment. However, studies in other areas of the GOA show that euphausiids are an important prey of age-0 pollock and that euphausiids are often preyed upon preferentially (Sturdevant *et al.*, 2001; Wilson *et al.*, 2006b). These studies support our hypothesis that age-0 pollock distribution is driven by the distribution of euphausiids. It should be noted that prey densities observed in this study are lower than previously reported estimates of zooplankton in the Gulf of Alaska (Coyle and Pinchuk, 2005; Wilson, 2009). At the time of this study, zooplankton densities are beginning to decline seasonally, which could explain some of the variation. However, it is also credible that localized depletion of prey might have occurred in a comparatively small geographic area like Barnabus Canyon. Foraging impacts have been observed in both the Bering Sea and Gulf of Alaska among young-of-the-year walleye pollock and yearling capelin (Cianelli *et al.*, 2004, Wilson *et al.*, 2006b), though the regular influx of water from the slope probably serves to periodically replenish prey resources.

The observed pelagic habitat selection by capelin and age-0 pollock implies that there is the potential for meso-scale to decadal-scale variability in physical and biological oceanographic processes to impact the availability of fish habitat, foraging opportunities, and ultimately growth and survival. Logerwell *et al.* (2007) suggested that variability in GOA area winds and transport at the scale of weeks can influence the distribution of water masses and the pollock and capelin that occupy them. The mechanisms coupling large-scale climate variability to smaller-scale variability in the Alaska Coastal Current are not known but are likely related to the timing of the increase in freshwater runoff and spin-up of the winds which accelerate the ACC (Stabeno *et al.*, 2004). At the decadal scale, the climate regime shift of late 1970s saw a dramatic decline in capelin abundance and an increase in pollock abundance in the GOA (Anderson and Piatt, 1999). This apparent community reorganization was hypothesized to be a result of changes in the timing of seasonal zooplankton production augmented by predation by adult groundfish on capelin. Our results contribute to a growing body of knowledge on pelagic habitat selection dynamics of these important forage fish in the GOA (Hollowed *et al.*, 2007; Logerwell *et al.*, 2007).

Inshore waters, despite being richer in nutrients and phytoplankton biomass, did not appear to be preferred foraging habitat for either age-0 pollock or capelin. This is not consistent with the hypothesis by

Logerwell *et al.* (2007) that inshore waters are preferred, which was based in part on a similar survey conducted in 2004. Instead, our results from 2005 suggest that age-0 pollock preferred offshore waters as habitat to forage on euphausiids and that capelin had no preference relative to water mass, foraging instead on copepods throughout the trough. What is puzzling about this result is that euphausiids are expected to be a higher value prey than copepods because they are generally larger and more energy dense (Mazur *et al.*, 2007), particularly in the fall (Falk-Petersen *et al.*, 2000). Furthermore, capelin have been shown in other areas of the GOA (Shelikof Strait) to forage on euphausiids to the same extent as age-0 pollock (Wilson *et al.*, 2006a). Why were capelin distributed throughout the trough foraging on copepods and not exclusively offshore feeding on euphausiids? We propose that competition with age-0 pollock could have prevented capelin from specializing on euphausiids in offshore waters. Age-0 pollock were similar in length to capelin but greater in weight (Table 2), perhaps giving them a competitive advantage when the two species co-occurred.

We hypothesize that in response to this competition, capelin expanded their distribution throughout the trough to feed on copepods. Although there is no direct evidence, there is indirect evidence consistent with interspecific competition. If competition occurs between two species, then the expectation is that measures of prey consumption would be reduced when species co-occur, a sympatric distribution, compared to when species occupy separate habitats, an allopatric distribution (Sturdevant *et al.*, 2001). Consistent with this expectation, sympatric capelin offshore of the mid-trough front in 2005 had a higher proportion of empty stomachs than allopatric capelin inshore. However, we cannot rule out the possibility that a preference for evening crepuscular feeding (Wilson *et al.*, 2006a) contributed to this pattern, because a greater proportion of offshore stations were sampled during the day. In 2004, sympatric capelin foraged extensively on euphausiids and had an even higher proportion of empty stomachs than in 2005. The other feeding measure, %BW, was also substantially reduced for sympatric capelin in 2004, but there was no difference between allopatric and sympatric capelin in 2005. Indirect evidence in both years suggests that age-0 pollock were the dominant competitor, if competition was occurring. Sympatric age-0 pollock offshore in 2005 and inshore in 2004 had a lower proportion of empty stomachs than sympatric capelin and a trend toward higher %BW as well. Although age-0 pollock are also known to exhibit nocturnal

feeding (Merati and Brodeur, 1996; Wilson *et al.*, 2006a), we observed no patterns in age-0 pollock feeding measures as a function of time of day. No allopatric age-0 pollock were observed in either year, so it is difficult to test fully the hypothesis of interspecific competition. Our results, although not conclusive, are consistent with previous research on competition between age-0 pollock and capelin in the GOA. Wilson *et al.* (2006b) found that age-0 pollock and capelin both foraged preferentially on euphausiids in the Semidi Bank area of the GOA and that there was the potential for the two species to deplete their prey locally. They suggested that capelin may increase foraging mobility while age-0 pollock switch to alternate prey as a competitive response to limited euphausiid availability.

Competition can negatively impact feeding opportunities, which can in turn impact fish nutritional status and size. Because nutritional status and size affect overwinter survival (Paul and Paul, 1998; Sogard and Olla, 2000; Sutton and Ney, 2001) and thus recruitment, a better understanding of forage requirements and the role of competition should lead to a better understanding of pollock and capelin productivity. Improved understanding of local ecological interactions, such as competition and pelagic habitat selection, contributes to improved quantitative ecosystem models that predict the impacts of climate change and anthropogenic stressors on marine ecosystems (Wiebe *et al.*, 1996; Kracker, 1999; Bakun, 2001; Walters and Kitchell, 2001). Further examination of the potential for resource limitation and detailed study of the interactions between individuals of the two species are needed.

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