

Spatial patterns of pollock and zooplankton distribution in the Pribilof Islands, Alaska nursery area and their relationship to pollock recruitment

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Data from six years, September 1994–1999, of bio-acoustic surveys near the Pribilof Islands, Alaska, (AK), from which age-0 walleye pollock school and zooplankton patch locations have been extracted, were analysed using image-processing methods. Multiple passes along four transects in this major pollock nursery area were examined. The data showed high year-to-year variability in overall abundance of both fish and plankton, but consistent abundance differences between the transects. Juvenile pollock abundance was generally highest in the shallow shelf region to the north of the Pribilof Islands and lowest in the mouth of the Pribilof Canyon to the south. Plankton biomass patterns tended to be the reverse. We identified fronts and regions within the transects based on changes in hydrography (e.g. vertical stratification) and bathymetry. Diel migration patterns of pollock and zooplankton within these regions appear to depend on the degree of stratification, the depth, the size of the pollock and the relative abundance of the pollock and zooplankton. Several hypotheses are also discussed concerning the relationship of pollock recruitment year-class strength to large year classes including differences in the environmental conditions, the pervasiveness of the pollock, the size of juvenile pollock and the density of predators.

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Introduction

There is compelling evidence for many fish stocks that year-class strength is mainly determined by conditions during the first year of life (Helle *et al.*, 2000). What is still unclear is what conditions lead to high and low year-class strength, whether recruitment is determined by the availability and proximity of food resources or predation and possibly cannibalism (Bailey *et al.*, 1998) and how these factors are related to environmental conditions. This study attempts to further our understanding of the relationship between front and bathymetry-defined habitats and the distribution

and diel patterns of age-0 walleye pollock (*Theragra chalcogramma*) and their zooplankton prey through a synthesis of acoustic and supporting environmental and net sampling data collected in September, 1994–1999 near the Pribilof Islands, Alaska. Our emphasis in this paper is on changes in distribution and diel migration patterns between years and habitat regions in the study area of acoustically determined fish schools and zooplankton patches. Through synthesis of acoustic data, net samples, bird observations and environmental data we examine the relationship between fish and zooplankton abundance, their diel migration and various hypothesized factors that may be influencing their

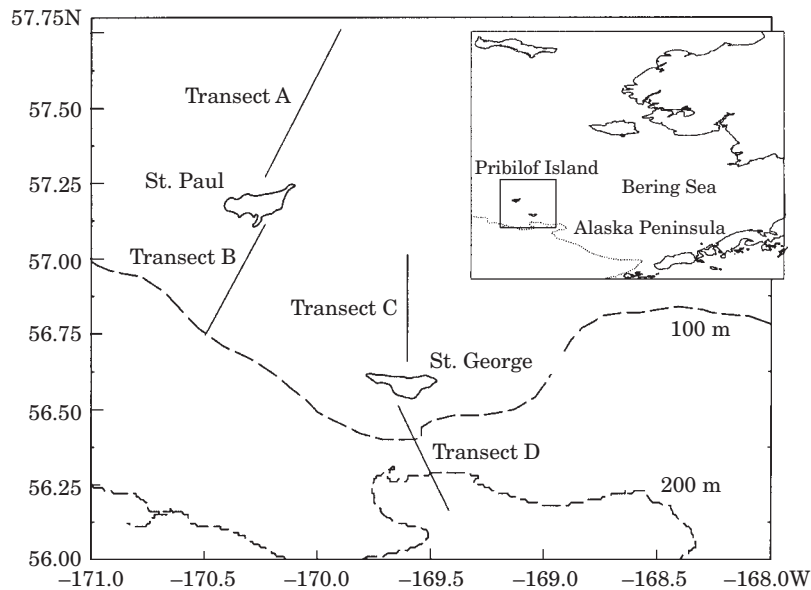


Figure 1. Acoustic survey study area near the Pribilof Islands, showing the four transects A–D studied during surveys each September in the years 1994 to 1999.

patterns including fish size, bathymetry, the strength and depth of the thermocline and the relative abundance of predators and prey.

Age-0 pollock are found in high concentrations in and around hydrodynamic fronts on the Bering Sea shelf. Both the structural fronts around the Pribilof Islands and the 1000-km-long Inner Front on the Southeast Bering Sea shelf support high concentrations of age-0 pollock (Coyle and Pinchuk, 2002). The Pribilof Islands region is a major nursery area for walleye pollock (Traynor and Smith, 1996; Brodeur and Wilson, 1999). It also is a location where intensive predation on juvenile pollock is likely because of the large numbers of seabirds and marine mammals breeding and rearing on the islands (Springer, 1992) and the presence of predatory flatfish and adult pollock. While pollock nursery areas exist in various shelf regions of the Bering Sea (Coyle and Pinchuk, 2002), the conditions for juvenile pollock in the Pribilof Islands region may be indicative of rearing conditions throughout the Bering Sea (Brodeur and Wilson, 1999) and thus serve as a surrogate for Bering Sea pollock production.

The factors influencing diel migration patterns of age-0 pollock are not well understood. Generally, it is thought that diel migration patterns derive as a predator-avoidance mechanism (Sih, 1980). Data and models in lake systems suggest that there is a trade-off in the diel migration of smaller fish between having access to high densities of food and avoiding predation and that the timing of vertical migration at dawn and dusk can depend on the size of the fish (Clark and Levy, 1988). There is evidence from laboratory (Sogard

and Olla, 1996) and field research (Bailey, 1989; Schabetsberger *et al.*, 2000) that larger age-0 pollock diel migrate and smaller age-0 pollock remain above the thermocline. Smaller pollock must be more susceptible to predation than larger pollock though. Some other factor, such as either the strength and depth of the thermocline or the diel migration patterns and abundance distribution of their zooplankton prey, might be expected to influence the onset of diel migration.

Zooplankton patches near the Pribilof Islands, identified from both acoustic data and net samples, have been observed to diel migrate (Swartzman *et al.*, 1999a; Schabetsberger *et al.*, 2000). However, the year-to-year and between-habitat consistency of this diel migration has not been explored. Our intention is to examine the pattern of zooplankton diel migration over the six study-years relative to the diel migration pattern of pollock, the strength and depth of the thermocline, the bathymetry and the ratio of their abundance to that of the pollock.

Methods

Data sources

Acoustic surveys were conducted during September aboard the NOAA ships “Miller Freeman” (1994–1997, 1999) and “Surveyor” (1994–1995) and the Russian research vessel “Professor Kagonovsky” (1998). These surveys collected data using a hull-mounted SIMRAD EK-500 split-beam echo-sounder system with two echo-sounders operating at 38 and 120 kHz (“Miller

Freeman” and “Professor Kagonovsky”), or 120 and 200 kHz (“Surveyor”). Transects A–D (Figure 1) were sampled repeatedly with acoustic soundings using at least two frequencies (38 and 120 kHz; also 200 kHz in 1994 and 1995).

The Pribilof region is unique in the Bering Sea in that it has a wide range of habitats relatively close to shore. These include tidally mixed regions close to shore, thermally stratified (in September) regions of the inner shelf further offshore and a front or “transition, partially stratified region” in between on transect A. Water-column properties were sampled using Conductivity–Temperature–Depth (CTD) casts (Sea-Bird SBE-911+). Stations were spaced about every 5 km along the sampling transects. The temperature profiles were used to identify boundaries between regions on transect A (Figure 1). The boundary between the inshore and front habitats was set by the first mixed (or weakly stratified) vertical temperature profile. The boundary between the front and offshore habitat corresponded to the location where the temperature profile showed a two-fold increase in the distance between the surface and subsurface boundaries of the thermocline (i.e. the depth range defining the thermocline in the clearly stratified region). While the boundaries between these regions depend on atmospheric conditions and tidal forcing (Kachel *et al.*, 2002), and therefore can change from year to year, we found that the boundaries changed very little between 1994 and 1995 (Swartzman *et al.*, 1999b), or for the other years. Consequently we used fixed boundaries between the regions based on those of 1994 and 1995 (Swartzman *et al.*, 1999b). Habitats on other transects were defined by bathymetry thresholds because of both the lack of well-defined front-related boundaries and the increased depth range of these transects compared with Transect A. The boundaries between shallow and deep regions on transects B and C (Figure 1) were defined by the 70 m isobath. Transect D, at the head of the Pribilof Canyon (Brodeur, 2001), is the deepest of the study transects. We divided it into a slope region, up to 130 m in depth, and a deeper, basin region. The nearshore, tidally mixed area on transects B, C and D was either non-existent or extremely narrow (less than 1 km) and thus was not considered in this study as a separate habitat. Having hydrological and bathymetric habitat regions allowed us to treat all fish schools and plankton patches within a habitat as a population whose behaviour can be both statistically as well as graphically explored. The use of habitats also allowed us to relate the observed patterns to the environmental features defining the habitat regions.

Zooplankton was sampled using a 1 m² Multiple Opening/Closing Net (MOCNESS, Wiebe *et al.*, 1976) with a 500 µm mesh size used in the nets in 1994 and 1995 and 333 µm mesh size used in 1996, 1997 and 1999. There was no MOCNESS deployed in 1998. Night-time

tows only were used to reduce the influence of net avoidance. Samples were preserved in 5% buffered formalin/seawater solution and were sorted and identified to the lowest possible taxonomic level at the Polish Plankton Sorting Center in Szczecin, Poland. However, classification for this paper was to the lowest common denominator – zooplankton functional groups, including euphausiids, small copepods (<2 mm), large copepods, amphipods, chaetognaths, pteropods and mixed crustaceans but excluding gelatinous zooplankton.

Age-0 pollock size was estimated using targeted mid-water anchovy trawls with a 140 m² mouth opening and oblique Methot midwater tows with a 5 m² mouth opening. The anchovy trawl had a 3 mm mesh in the codend and the Methot frame was mounted with a 3 × 2 mm oval mesh in the body and a 1000 µm mesh in the codend (Brodeur *et al.*, 1997). Only night-time Methot tows were included to minimize gear avoidance though daytime anchovy hauls were used as well as night-time because no diel effect in anchovy trawl catches has been found in early, targeted studies (Brodeur *et al.*, 2002).

Data analysis

The size, shape and acoustic backscatter (proportional to biomass) of fish and zooplankton patches was mapped using image-processing methods that included taking image differences, thresholds, and morphological filters applied to the images (Swartzman *et al.*, 1999a,b).

Acoustic backscatter images, collected at 38 and 120 kHz (and 200 kHz in 1994 and 1995) were available in segments 5 nautical miles long. Because between 95 and 99% of the fish biomass collected during the surveys using anchovy trawl hauls were pollock (Brodeur *et al.*, 1997, 2002) we defined the range of backscatter expected for fish schools, –53 to –40 dB at 38 kHz, based on previous studies on backscatter for pollock (Traynor, 1996). Pixels in the expected backscatter range to be included as part of a fish school must constitute a contiguous area greater than a given minimum size. This step was accomplished by using a morphological opening and closing operation (Haralick and Shapiro, 1992) on the image after thresholding, with a 3 × 2 pixel-structuring element (dimensions 27 m horizontal × 1 m vertical).

Zooplankton threshold-backscatter range was between –62 and –45 dB, based on models of backscatter from euphausiids and copepods (Stanton and Chu, 1992; Stanton *et al.*, 1993). These thresholds suggested a range of backscatter expected for zooplankton at 38 and 120 kHz (120 and 200 kHz for zooplankton in 1994 and 1995). Backscatter from zooplankton depends on their size relative to the acoustic wavelength and their density. Zooplankton patches comprised of larger zooplankton (e.g. euphausiids in the 15–25 mm

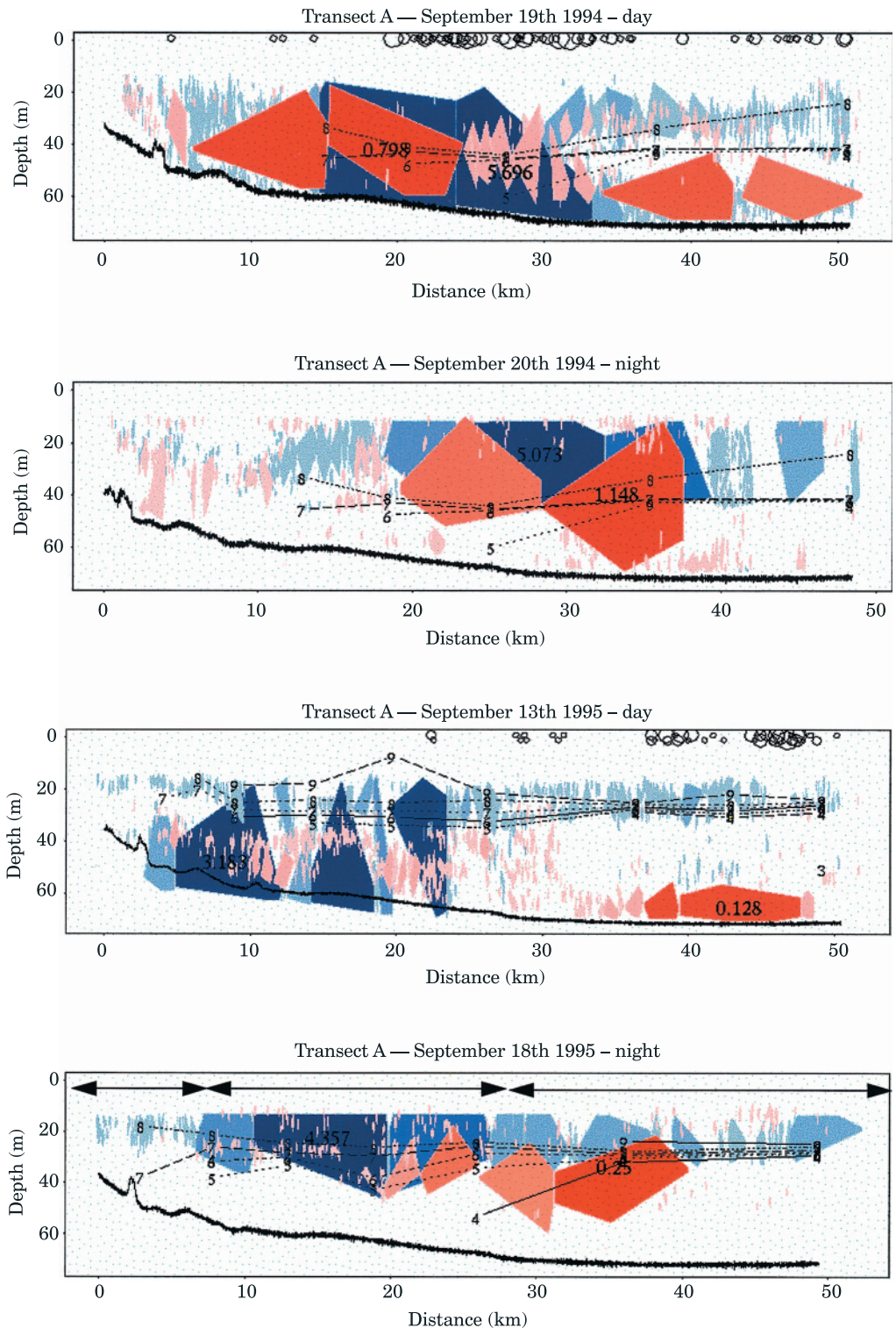


Figure 2. (a).

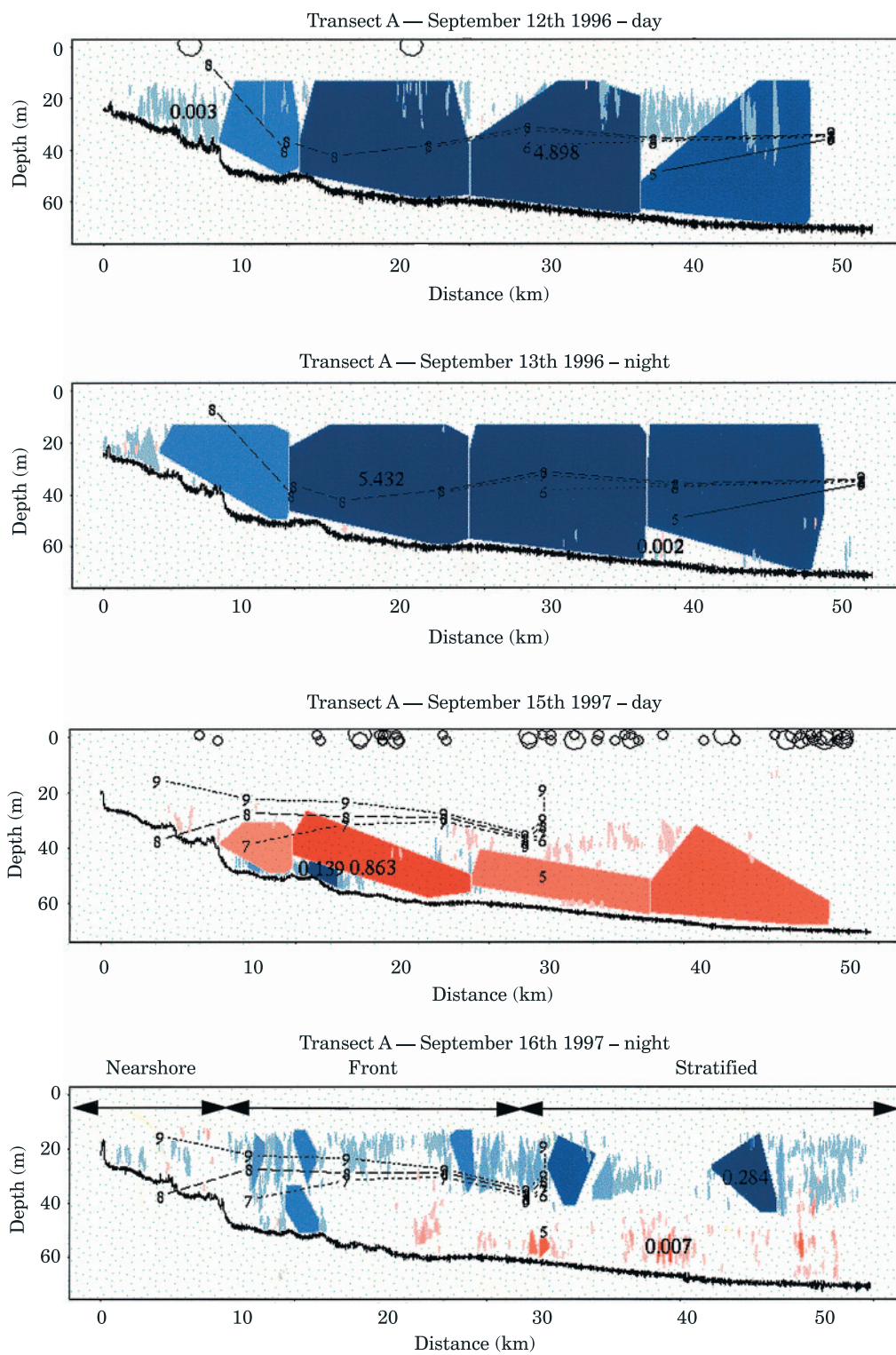


Figure 2. (b).

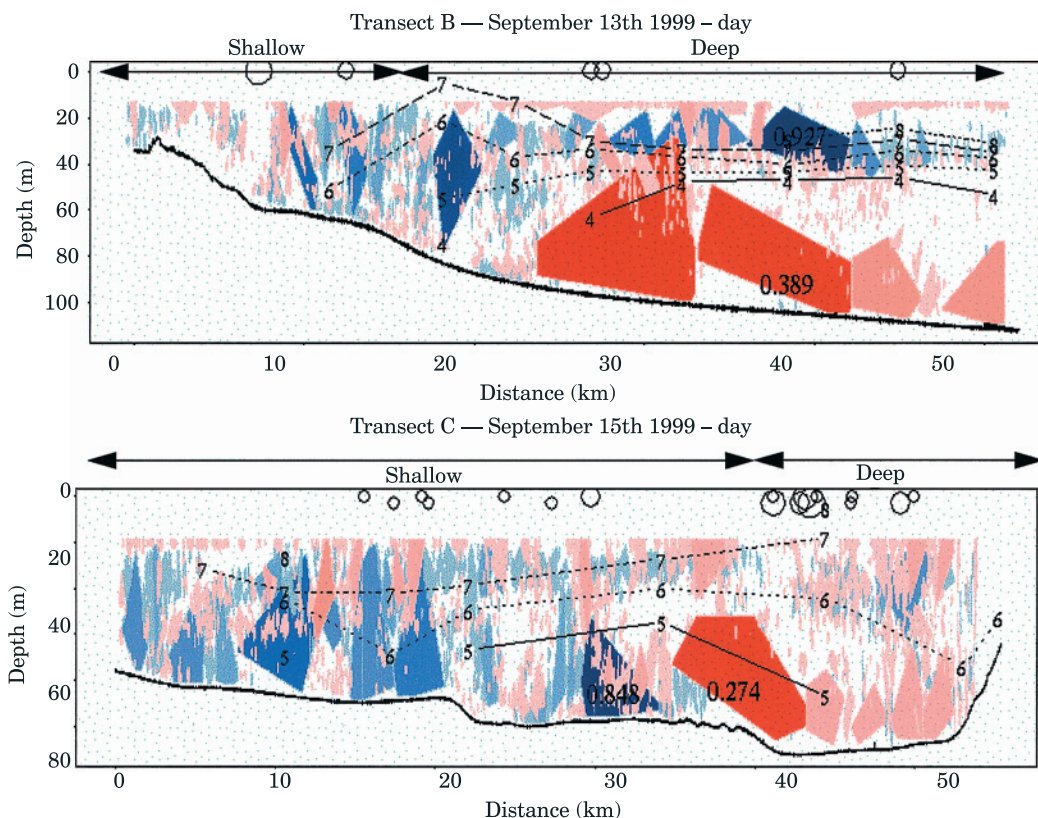


Figure 2. (d).

Figure 2. Transect plots for 1994–1999 of transect A (cf. Figure 1) showing fish schools shaded blue and plankton patches shaded red. Colour hue is used to give relative biomass, with darker hues meaning higher biomass. A heavy line indicates the sea bottom and temperature isotherms are shown where available from CTD data. Locations of murre passes during the daytime passes are shown by ovals at 0 depth, with oval size proportional to the numbers of birds sighted. The largest patch and school (acoustic) biomass are labeled in each image.

length range) have higher backscatter at 120 kHz than at 38 kHz as expected from theoretical backscatter models for zooplankton sizes in the Rayleigh scattering range. Fish schools, on the other hand, do not have higher backscatter at 120 kHz than at 38 kHz. Based on backscatter models we calculated that euphausiids should have at least 5 dB higher backscatter at 120 kHz than at 38 kHz. Therefore, we subtracted the 38 kHz image from the 120 kHz image (after zooplankton backscatter thresholds were applied to both images) and used a 5 dB threshold on the resulting image followed by a 3×3 pixel (27 m horizontal \times 1.5 m vertical) morphological opening and closing operation. Other, smaller zooplankton also scatter sound at 120 kHz when they occur in high enough densities. However, euphausiids, because of their larger size, dominate the backscatter at 120 kHz, while other zooplankton, because of their low target strength at 120 kHz, are not likely to be dense enough to show significant backscatter at 120 kHz. This assertion is supported by MOCNESS samples taken during the cruises, which showed euphausiids to be in the same

biomass range as other zooplankton (Schabetsberger *et al.*, 2000; Ciannelli *et al.*, 2002), including large and small copepods, pteropods, chaetognaths and other crustacea. In some years chaetognath biomass is an order of magnitude larger than euphausiid biomass, but, because of their much smaller size and elongated shape, they have significantly smaller backscatter based on the truncated, fluid-sphere model of Stanton and Chu (1992). We do not, however, identify the acoustically derived zooplankton patches to species or size groups. The MOCNESS data showed the dominant euphausiid to be adult *Euphausia pacifica* between 15 and 25 mm in length.

Previous comparisons of the depth distribution of MOCNESS hauls with the predicted depth distribution of euphausiid and copepod biomass from the patch identification algorithm have indicated that it is effective (Swartzman *et al.*, 1999b). Effectiveness, however, is tempered by the degree of physical separation of fish and plankton. If the fish schools and plankton patches overlap then pixels having both zooplankton

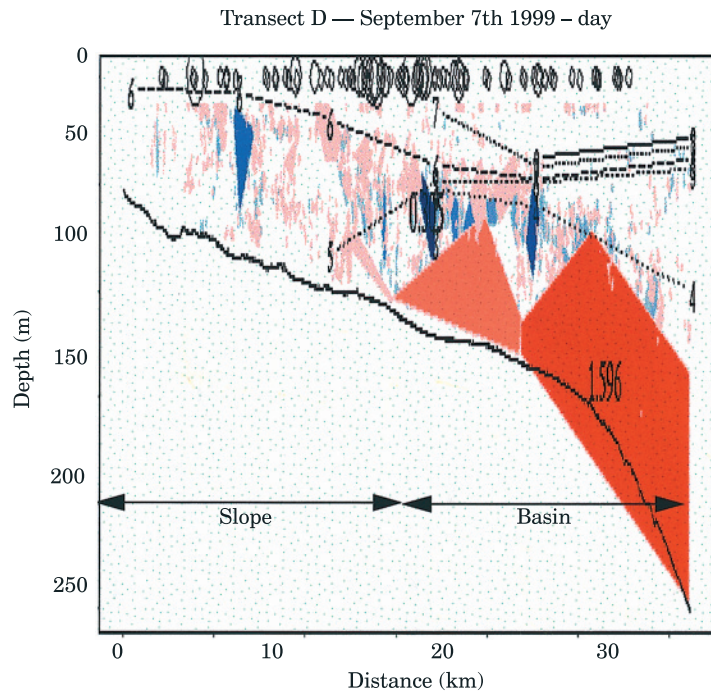


Figure 3. Transect plots for 1999 daytime passes of transects B, C and D (cf. Figure 1) showing fish schools shaded blue and plankton patches shaded red. All transect plots go from the Pribilof Islands outward. A heavy line indicates the sea bottom and temperature isotherms are shown where available from CTD data. Ovals at zero depth show murre sightings along the survey track, with oval size proportional to the numbers of birds sighted. The largest patch and school biomass are labeled at their center in each image.

and pollock may be dominated by fish backscatter, as may have occurred on transect A in 1996 and 1999, when fish schools spanned the entire water column both day and night (Figure 2).

After identification of fish schools and plankton patches on the backscatter images a connected component algorithm was run on each image (Haralick and Shapiro, 1992). This produced a table in which each row was one school or patch and each column contained patch attributes. These include patch location (latitude, longitude and depth of the geometric patch centre, distance from the start of the current transect and from the start of the survey), patch size (length, width, area, perimeter and locations of eight points along the edge of the patch), environmental information (bottom depth below the patch, time in GMT and date) and backscatter information, including the mean and variance in backscatter cross section area s_a ($\text{m}^2 \text{m}^{-2}$) an index of total biomass, and the minimum, maximum and mean target strength in the patch (dB).

Combining data from the school and patch tables with CTD, bathymetry and the locations of the survey transects we plotted the convex hull for each patch and school with octagons, from the 8 patch-edge points, along each pass of the transects together with the

temperature isotherms and the bathymetry (Figures 2 and 3). The temperature plots were obtained by interpolating between the CTD casts while the bathymetry was taken from the acoustic system at a horizontal resolution of 1 pixel (9 m). The locations of piscivorous birds [murre (*Uria* spp.)] observed along the survey tracks (Swartzman and Hunt, 2000) were added to the daytime plots, when available, as ovals at the surface on the plots (i.e. 0 m depth).

In general, study transects were designed to have at least one daytime and one night-time pass (Table 1), and in most years there were multiple day and night passes, especially on transect A; Figure 1. To examine diel migration patterns of fish schools and zooplankton patches, for the day and night fish- and zooplankton-patch data, the abundance density (acoustic biomass, defined as patch area times average patch backscatter cross-section area s_a , per transect km) was computed in each habitat region for each transect pass. The fish-school and plankton-patch abundance per km for each of these regions was computed also by summing the biomass for all fish schools and all zooplankton patches in each region and dividing by the length of the region transected (i.e., biomass/km). These were compared for all study years and regions using boxplots. To examine

Table 1. Data sources available for data synthesis from acoustic surveys conducted near the Pribilof Islands, AK during September 1994–1999. Numbers of day and night passes of each transect in each year are also noted. Processed data are denoted by an “×”. Processed data conform to National Oceanographic Data Center standards.

	1994	1995	1996	1997	1998	1999
Acoustic data – transect A day	1	3	2	3	4	4
Acoustic data – transect A night	1	2	2	2	2	3
Acoustic data – transect B day	1	1	3	2	2	2
Acoustic data – transect B night	1	1	2	4	1	0
Acoustic data – transect C day	1	1	5	2	1	3
Acoustic data – transect C night	0	1	1	1	2	1
Acoustic data – transect D day	1	1	2	2	3	2
Acoustic data – transect D night	0	1	2	1	2	2
Fish schools	×	×	×	×	×	×
Zooplankton patches	×	×	×	×	×	×
Temperature data (CTD)	×	×	×	×	×	×
Bird data	×	×	×	×	×	×
Anchovy net	×	×	×	×	×	×
Method net fish data	×	×	×	×	×	×
Method zooplankton	×	×	×	×	×	×
MOCNESS ¹ zooplankton	×	×	×	×	×	×
Fish predators ²	×	×	×	×		

¹Data reside in two separate databases (1994–1997) and (1998–1999). 1998 data are from Tucker trawls.

²Bottom trawl coverage was sporadic (Ciannelli *et al.*, 2002).

differences in the depth distribution of abundance between day and night transect passes (for diel migration), we divided each transect into habitat regions. The depth distribution for each region was computed as the average school and patch depth weighted by the school or patch biomass, i.e.:

$$\text{depthdistribution}_{\text{patch}} = \frac{(\sum \text{depth}_{\text{patch}} \times \text{biomass}_{\text{patch}})}{\sum (\text{biomass}_{\text{patch}})}$$

These were summarized using boxplots which show the distribution of the average fish school and zooplankton patch depth for each study year and each region for both daytime and night-time transects, along with the depth of the thermocline and the bottom depth. The replicates in the boxplots are the multiple passes of each transect. Walsh t-tests (Venables and Ripley, 1994) were used to compare the day and night depth distribution and abundance of fish schools and plankton patches in each transect habitat region and year without assuming equality of variance of the compared populations. The Walsh t-test did assume independence of the day and night populations; a reasonable assumption since all day and night transects were collected separately in time.

The t-tests and boxplots have different metrics. The boxplots show the day and night median and range for total fish school and zooplankton patch biomass density and average depth (weighted by the biomass in each school or patch) in each habitat. The t-tests compare the mean abundance and depths of all patches and schools

in the daytime “population” with the same parameter for the night-time “population” for each habitat. Unlike the boxplots, the t-tests for depth are not weighted by biomass and those for abundance are not averaged on a per km basis. Replicates in the t-tests are the schools and patches themselves.

To compare the diel migration of age-0 pollock to pollock size we examined the size distribution of pollock from night-time Method hauls for 1994–1999. To encapsulate the age-0-pollock length distribution we recorded and tabulated the pollock length mode for all Method hauls in each region, the second (larger) length mode, if one existed, and the ratio of numbers of sampled pollock with lengths near each of the modes (i.e. the ratio of the heights of the peaks). We also recorded the average bottom depth and the strength of the thermocline in each region. A thermocline was considered strong if it had a 5°C change within 5 m, weak if it had a 3°C change or less in greater than 10 m, and intermediate otherwise.

Results

Graphical comparisons of fish and plankton distribution

The distributions of the fish schools and plankton patches are shown in Figure 2 for selected day and night passes along Transect A (1994–1999). The nearshore, mixed area stands out as having fewer fish and zooplankton in all years (Figure 2). The schools and patches

were much smaller in this region and there was no consistent diel pattern. Plankton in the front and stratified regions in transect A appear to show a distinct diel pattern in 1994, 1995 and 1997 with plankton patches close to the bottom during the day. This pattern is less apparent in 1996 and 1999 on transect A where plankton patches were not abundant, or in 1998, when plankton appeared to stay in mid-water both day and night. There did not appear to be a consistent diel migration pattern over all years for pollock on transect A in the front and stratified regions. In 1995 pollock in the stratified region appeared to stay above the thermocline while in 1998 they appeared to remain below the thermocline and in 1994 showed some diel migration. In 1996 and 1999, years of high pollock abundance, pollock appeared throughout the water column both day and night, although they appeared to be somewhat closer to the surface during the night in 1999.

A similar impression resulted from exploratory data analysis of the acoustic data for transects B–D (Figure 3). Each of these transects was partitioned based on bathymetry, with a 70 m division used for transects B and C and a 130 m division for transect D. Differences between these regions are apparent for 1999 in the large plankton patches near the bottom in the deeper regions. The thermocline was about 40 m for all transects in 1999 (Figures 2 and 3). On transects B and D in 1999 pollock schools appeared to be near the thermocline while on transect C they were below the thermocline during the day.

Fish and zooplankton habitat distribution and diel migration patterns

Results of a Walsh t-test on day versus night abundance (acoustic biomass per km transected) of fish schools and plankton patches (Table 2) suggest that, for most years and regions, there was no significant difference in abundance. A possible exception is 1998 where, for transects A, B and the shallow region of C, there was a consistent difference in pollock school abundance between day and night transects although the difference is significant at the 0.01 level for only the deep region of transect B. Schabetsberger *et al.* (2000) suggested that, because the pollock might be higher in the water column at night, some fish might not be detected since they were above the transducer which is centreboard-mounted at 9 m depth. We did not observe a pattern of lower pollock abundance at night than during the day, except for 1998, although for some regions and years, the pollock were significantly shallower at night (Table 2). The lack of a diel abundance pattern for zooplankton (Table 2) and the general lack of significance in the Walsh t-test for pollock abundance justified combining day and night transects in examining abundance patterns (Figure 4).

Boxplots showing the acoustic abundance of pollock (in schools) and zooplankton (in patches) for 1994–1999 (Figure 4) indicate that the highest pollock abundance (acoustic biomass per km) occurred in the front or stratified regions of transect A. Except for 1995 the basin area of transect D consistently had the lowest pollock abundance. Zooplankton-patch abundance, on the other hand, tended to be higher in the basin and slope of transect D than on other transects. 1996 had the highest overall pollock abundance, with the most even biomass distribution among transects. 1997 was a year of consistently low pollock abundance, with the highest and most even distribution of zooplankton patches among the transect regions. Despite the apparent inverse relationship between pollock and plankton abundance in 1996 and 1997 (i.e. high pollock abundance associated with lower zooplankton abundance and vice versa), this pattern did not appear to be general over all years and regions.

Patterns of fish and zooplankton diel migration are revealed, in part, by the boxplots of the distribution of the average depth for fish schools and zooplankton patches for all passes in each year and in each region (Figures 5 and 6), compared with the bottom and the thermocline. A statistical comparison (Walsh t-test) indicates whether the depth distribution of fish schools and plankton patches in each region and year during the day are significantly different to those at night (Table 2).

We have already noted that for transect A the diel pattern for plankton in 1994, 1995 and 1997 showed plankton patches close to the bottom during the day and higher at night, while pollock appeared to remain above or near the thermocline. This pattern was not apparent in 1996 and 1999 on transect A, when pollock schools were abundant and plankton patches were not, and pollock was distributed throughout the water column (Figures 5 and 6). In 1998 pollock remained below the thermocline both night and day on transect A. 1998 had a very weak thermocline on all transects with only a 2°C temperature gradient (5 to 70°C) between bottom and surface.

A comparison between these diel migration patterns of pollock and the size of pollock from Methot hauls from 1994–1999 (Table 3) showed that many of these hauls had a bi-modal distribution of pollock size with a separation between the length modes of more than 10 mm. If only larger fish diel migrate the ratio of larger to smaller fish in the Methot hauls could indicate what fraction of the pollock were diel migrating.

The results indicate that pollock diel migration through the thermocline (i.e. below the thermocline during the day and above it at night) in a region was generally associated with having a significant number of larger fish (≥ 55 mm) in the Methot samples (Table 3; Figure 5). However there were cases where, even in

Table 2. p-Values for Walsh t-test comparing day and night fish-school and zooplankton-patch abundance and depth.

Region	Pollock						Zooplankton					
	Time/year											
	1994	1995	1996	1997	1998	1999	1994	1995	1996	1997	1998	1999
A – near												
Abundance	—	0.16	0.28	—	*	0.18	—	0.16	—	0.13	0.24	0.25
Depth	—	**	**	—	0.32	*	—	0.49	—	**	**	**
A – front												
Abundance	0.18	*	0.4	0.5	*	0.3	0.3	0.23	—	0.49	0.36	0.4
Depth	**	**	0.21	**	**	**	0.18	**	—	*	**	**
A – stratify												
Abundance	0.28	**	0.13	—	*	**	0.49	0.18	0.5	0.29	*	0.4
Depth	**	**	0.22	—	**	0.48	0.19	**	0.1	**	*	**
B – shallow												
Abundance	**	0.45	0.14	0.44	*	—	0.31	0.28	—	0.29	**	—
Depth	0.39	0.4	*	**	**	—	0.06	**	—	**	*	—
B – deep												
Abundance	0.22	0.24	0.44	0.1	**	—	0.28	0.1	**	0.37	0.13	—
Depth	**	**	**	**	**	—	0.19	**	0.08	0.31	**	—
C – shallow												
Abundance	—	0.15	0.12	0.3	*	0.07	—	0.1	0.05	0.34	0.26	0.43
Depth	—	**	**	**	0.3	**	—	**	**	**	0.28	**
C – deep												
Abundance	—	0.50	0.4	0.12	0.5	**	—	0.19	0.14	0.08	0.15	0.28
Depth	—	**	0.24	**	0.14	**	—	**	**	*	*	*
D – slope												
Abundance	—	**	0.28	0.18	0.25	—	—	0.38	0.12	0.38	**	0.4
Depth	—	*	**	**	0.11	—	—	**	0.13	0.12	0.38	0.09
D – basin												
Abundance	—	—	0.12	—	—	—	—	0.41	0.04	0.45	0.39	0.16
Depth	—	—	**	—	—	—	—	0.06	**	**	0.05	**

—, Missing data; **significant at $p < 0.01$; *significant at $p < 0.05$.

regions without larger fish, there was a clear diel-migration pattern and a few cases where, despite the presence of significant numbers of larger fish in the Methot hauls, the fish did not appear to behave in this way.

Discussion

Pollock diel migration

While there was considerable variability in diel-migration patterns from year-to-year and region-to-region (Figure 5), one dominant pattern emerged: larger age-0 pollock (>55 mm) appeared to diel migrate through the thermocline, while smaller fish did not (Table 3). There is evidence from laboratory (Sogard and Olla, 1996) and field research (Bailey, 1989; Schabetsberger *et al.*, 2000) that larger age-0 pollock diel migrate and smaller age-0 pollock remain above the thermocline. In 1999 results from anchovy net trawls suggested that larger pollock did go below the thermo-

cline on transect A during the daytime while smaller pollock stayed above it (Matt Wilson, Alaska Fisheries Science Center, unpublished data). The diel migration pattern of age-0 pollock in all years and regions is also generally supportive of the hypothesis that only larger fish diel migrate (Table 3). For example, weak diel migration was observed in all years and locations where the first mode of pollock size was small (less than 50 mm), the second mode was large (>55 mm) and their ratio was large (>6:1). This suggests that smaller individuals remained above the thermocline while the larger individuals diel migrated. Regions having a large first-length mode (≥ 55 mm) or a large second-length mode with a ratio of less than 7:1 to the first mode tended to show a strong diel migration pattern for pollock (Table 3). Age-0 pollock diets switch at a length above 53 mm from primarily copepods to primarily euphausiids (Ciannelli *et al.*, 2002). We hypothesize that this diet switch is related to the diel migration of pollock, with the larger pollock going below the thermocline eating primarily euphausiids and the smaller pollock remaining above the thermocline eating primarily copepods.

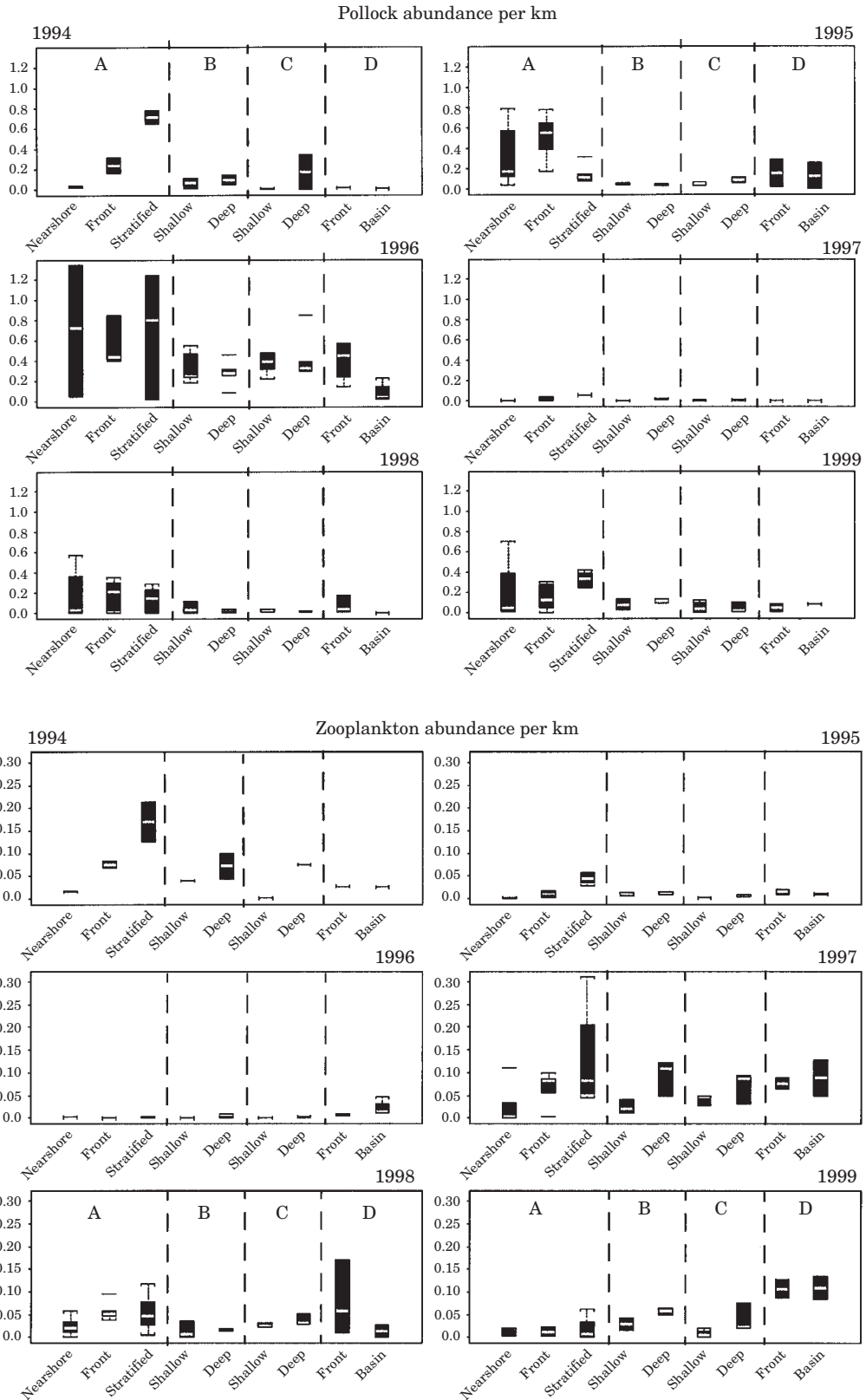


Figure 4. Boxplots showing the pollock (top 6 panels) and zooplankton (bottom 6 panels) abundance for each habitat region of each transect for 1994–1999 acoustic surveys. Replicates for the boxplots are the number of passes of the each transect (Table 1)

Pollock school depth

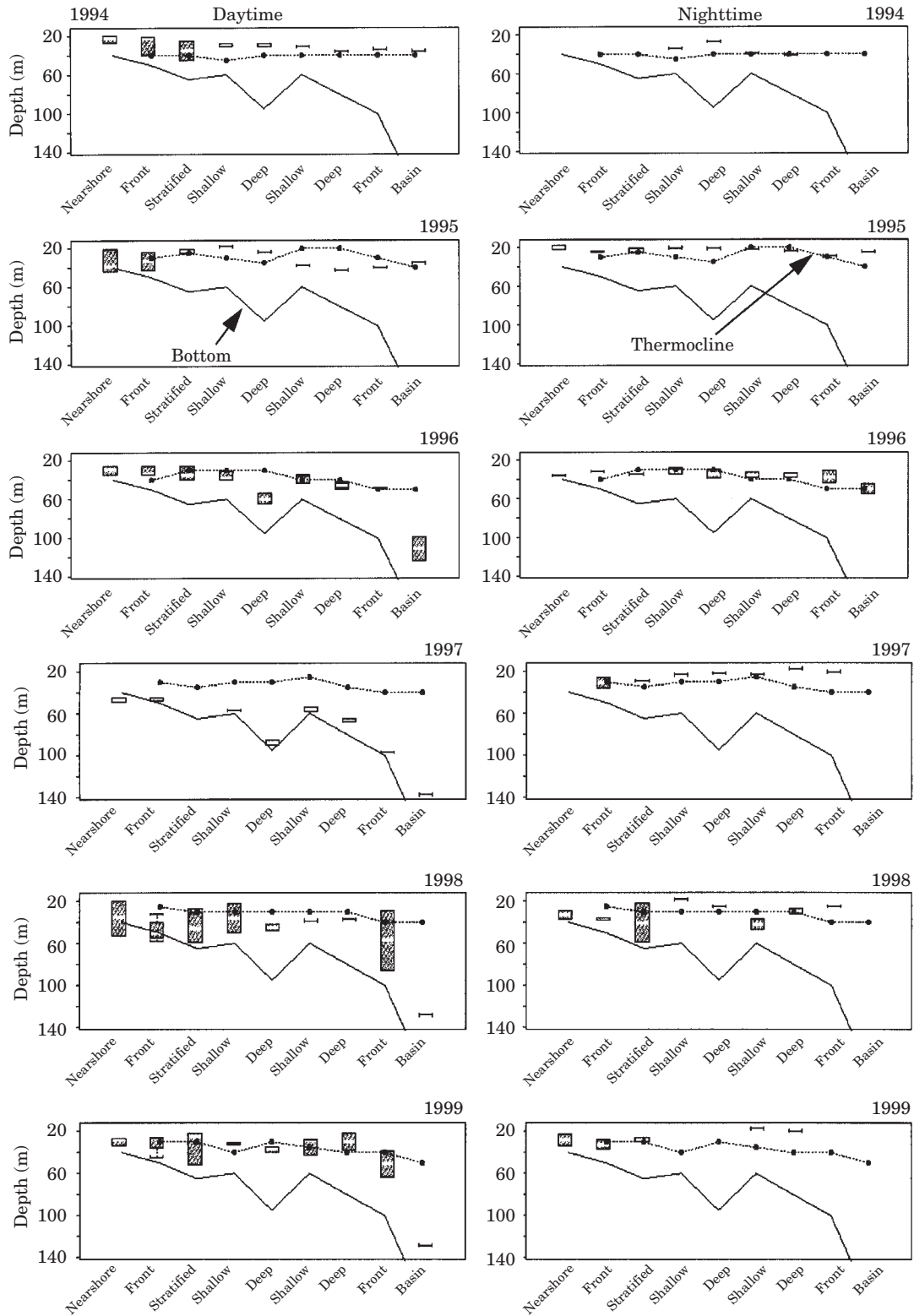


Figure 5. Boxplots showing the pollock-school depth distribution for each habitat region and year (1994–1999) for daytime (left panels) and night-time (right panels). The depth of the thermocline and the bottom depth are shown on the same frames. Replicates for the boxplots are the numbers of day and night passes of each transect.

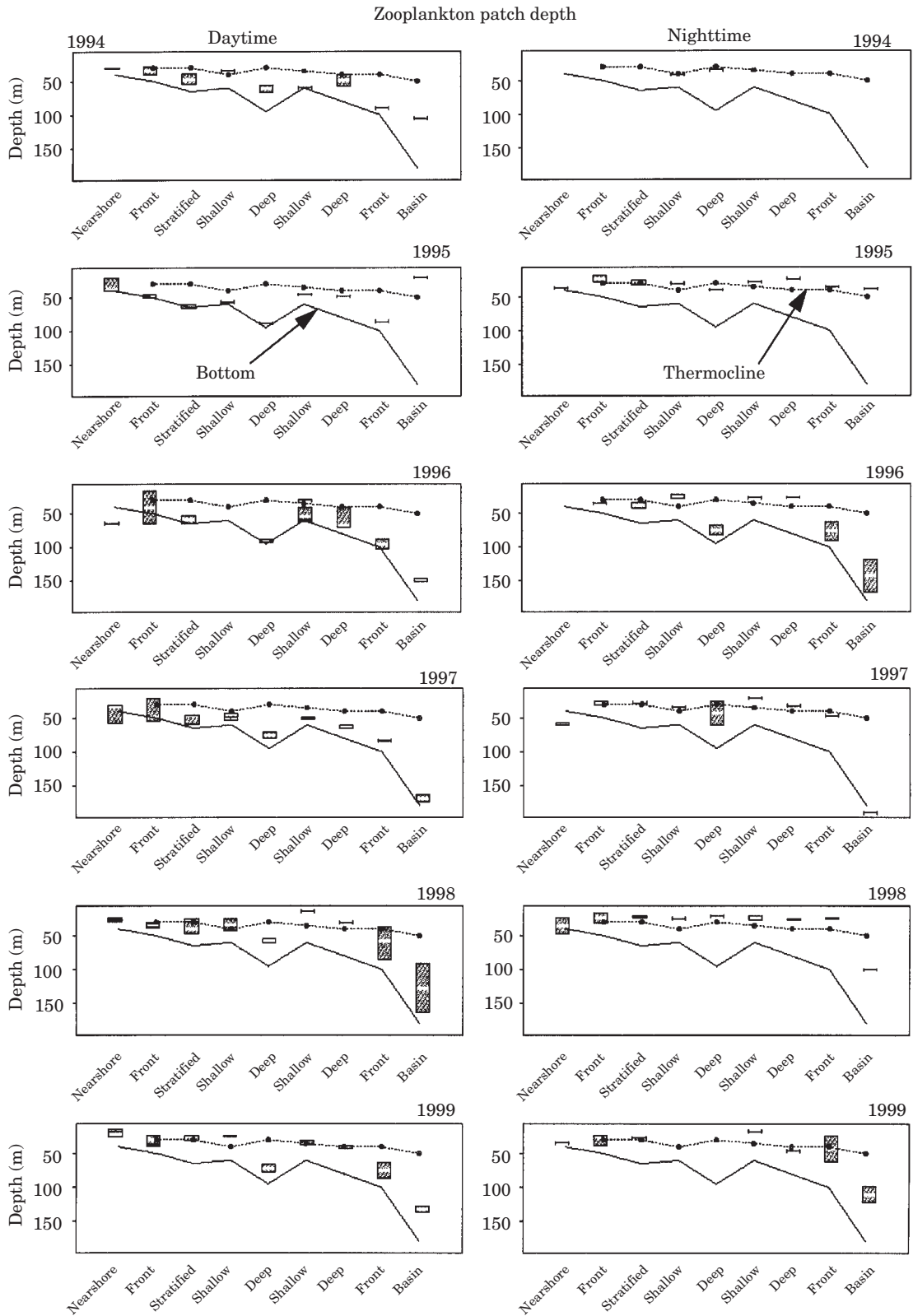


Figure 6. Boxplots showing the zooplankton-patch depth distribution for each habitat region and year (1994–1999) for daytime (left panels) and night-time (right panels). The depth of the thermocline and the bottom depth are shown on the same frames. Replicates for the boxplots are the numbers of day and night passes of each transect.

Table 3. A comparison of pollock diel migration patterns for habitats transected in 1994–1999 with pollock lengths from Methot hauls and thermocline depths and strength. Numbers in parentheses denote results from several Methot samples.

Year	Region	Thermocline	Diel migration	Pollock length mode (mm)	Second length mode (mm)	Abundance ratio
1994	A – stratified	40 m – strong	Weak	42	80	>10:1
1994	B – shallow	40 m – interm.	No	44		
1994	C – deep	40 m – interm.	No	42		
1995	A – nearshore	None	Yes	55		
1995	A – front	25 m – Weak	Yes	(41–55)	(50–70)	3:1
1995	A – stratified	25 m – strong	Weak	(40–55)	73	>10:1
1995	B – shallow	30 m – interm.	No	43		
1995	B – deep	35 m – interm.	Weak	46	66	>10:1
1995	C – shallow	20 m – weak	Yes	32		
1995	C – deep	20 m – weak	Yes	43		
1995	D – slope	30 m – weak	Weak	38	55	2:1
1995	D – basin	40 m – weak	No day fish	62		
1996	A – nearshore	None	No	45		
1996	A – front	40 m – weak	No	45	66	7:1
1996	A – stratified	30 m – strong	Weak	45	67	>10:1
1996	B – shallow	30 m – strong	Weak	(46–52)	66	8:1
1996	B – deep	40 m – strong	Yes	47	70	6:1
1996	C – shallow	40 m – weak	Yes	54		
1996	C – deep	30–40 m – weak	Weak	(43–45)	66	>10:1
1996	D – slope	50 m – strong	Yes	45		
1996	D – basin	50 m – strong	Yes	45	66	4:1
1997	A – nearshore	None	No day fish	40		
1997	A – front	30 m – weak	Yes	(46, 50)	60	8:1
1997	A – stratified	40 m – interm.	Yes – few fish	58	70	6:1
1997	B – shallow	30 m – interm.	Yes	40	60	8:1
1997	B – deep	30 m – strong	Yes	(40, 50)		
1997	C – shallow	25 m – strong	Yes	(42, 46)		
1997	C – deep	30 m – weak	Yes	42	58	3:1
1997	D – slope	35 m – weak	Yes	44		
1997	D – basin	35 m – weak	No day fish	30	42	3:1
1998	A – nearshore	None	No	(37, 47)	(47, 55)	5:1
1998	A – front	25 m – weak	No	(38, 46)	(62, 70)	>10:1
1998	A – stratified	30 m – weak	Weak	(35, 44)	(53, 58)	8:1
1998	B – shallow	30 m – interm.	Yes	48	66	>10:1
1998	B – deep	30 m – weak	Yes	(32, 49)	54	2:1
1998	C – shallow	25 m – weak	No	38	51	1:2
1998	C – deep	25 m – weak	No	42	52	1:1
1998	D – slope	30 m – weak	No	(44–49)		
1998	D – basin	40 m – interm.	No night fish	(38, 44)		
1999	A – nearshore	None	No	(24–42)	58	>10:1
1999	A – front	30 m – interm.	Weak	25	(48, 70)	>10:1
1999	A – stratified	30 m – strong	Weak	(25–48)	(45, 60)	10:1
1999	B – deep	30 m – interm.	No night fish	(34–38)	55	10:1
1999	D – slope	40 m – strong	Weak	(35, 39)	(50, 78)	>10:1
1999	D – basin	30 m – interm.	No night fish	(22, 36)	(48, 54)	10:1

To what extent does the strength of the thermocline influence the diel migration of juvenile walleye pollock? There were considerable environmental differences among transects and years (Table 3; Stabeno *et al.*, 1999; Stabeno *et al.*, 2002). The deepest thermoclines occurred on all transects in 1994 and 1999 (about 40 m for all transects), while 1995 had the shallowest thermocline (25 m on transects A and B, 20 m on transect C and a

weak 40 m thermocline on transect D). There were strong thermoclines in 1996 and 1997 at 30 m on transect A and B, a 25 m strong thermocline in 1997 and a 40 m weak thermocline in 1996 on transect C and 35–50 m thermoclines on transect D (Ciannelli *et al.*, 2002). The weakest temperature gradients occurred in 1998 (less than 2°C) with consistently weak thermoclines at depths from 25 to 40 m. Except for 1998 all stratified

regions had more than a 4°C temperature differential over the thermocline.

Because a large temperature gradient across the thermocline has energetic implications for poikilotherms, such as pollock, it might be expected that age-0 pollock migrate below the thermocline during the day to reduce respiration, as well as feed on zooplankton near the bottom. However, diel migration was detected whenever large fish were present, independent of the strength of the thermocline except in the front region of transect A in 1996 and 1998. Both years had weak thermoclines in this region and no apparent diel migration. However, other years with weak thermoclines in this region did show fish diel migration patterns (Table 3). Both 1996 and 1998, as well as 1999, had large fish schools throughout the water column. We surmised that when our school-detection algorithm identified large schools to be pervasive in the water column, as in the 1996 and 1998 front regions, there might be undetected diel migration within the large schools. To check this we examined the diel pattern of pixels within schools in habitats where there were larger fish present (i.e., a second mode of larger age-0 pollock), larger schools, and no clearly detected diel migration pattern based on the average school depths (Table 2). In all cases we found a significant diel migration pattern for pixels within schools. Thus, where schools appeared to span the water column important diel migration information was lost. That there was diel migration of pollock in the front region in 1996 is corroborated by a diel series of net hauls and acoustic measurements taken in that year (Schabetsberger *et al.*, 2000).

In many regions and years there was no diel migration pattern for age-0 pollock when the Methot hauls indicated only smaller fish were present. However in 1997 smaller fish (Methot sampled length modes <50 mm) appeared to diel migrate in the deep region of transect B, the shallow area of transect C and the slope region of transect D. Smaller fish also appeared to diel migrate in 1996 in the slope region of transect D and in 1995 in both regions of transect C. In some cases this diel migration was through a strong thermocline (Table 3). There was no consistent abundance pattern of pollock or zooplankton in these cases to point to food limitation as a general explanation: zooplankton was high and fish were low in 1997, while the reverse was true in 1996, and both were low in 1995 on transect C. Bird abundance observed on the surface was particularly high and pervasive in 1997 on transect C (Swartzman and Hunt 2000). Considering that areas north of the Pribilof Islands (including transect A) had a coccolithophore bloom (Hunt *et al.*, 2002), which may have interfered with piscivorous-bird feeding, birds may have concentrated in areas free of the bloom (like transect C), putting additional predation pressure on the age-0 pollock. Other “exception” regions and years had weaker

thermoclines which might not be as serious an impediment to smaller fish diel migration, particularly since, in 1995 and 1996, prey resources were low in these regions. Another possible explanation for the diel migration of smaller pollock might be the lack of bottom predators in the region. Bottom trawls were made (see Ciannelli *et al.*, 2002 for a summary of these) during the surveys from 1994–1997. These suggest that 1994 and 1995 had higher fish-predator abundance than 1996 and 1997, which might help explain why there was no evidence for age-0 pollock below the thermocline in 1994, and more diel migration in 1996 and 1997 of smaller age-0 pollock through a strong thermocline. It may be the case, also, that individual predation risk is reduced for juvenile pollock (i.e. they swamp their predators) when their abundance is high. Thus the high abundance of pollock in 1996 and 1999 may have reduced fish-predation deterrence to entering the lower water column and thereby increasing the prevalence of diel migration in those years.

The basin area of transect D tended to have low fish densities. For example, there were no fish schools in the daytime surveys in 1995 and 1997 and none at night in 1998 and 1999. It is possible that age-0 pollock on the deeper part of transect D may have migrated between the basin and the slope area, perhaps on a tidal cycle, thus accounting for their absence either during the day or night, but not both, on some surveys. Currents on transect D are stronger than on any other transect (Stabeno *et al.*, 2002) and, particularly in 1995 and 1999, there appeared to be a definite shift on transect D in the abundance of large, patchy schools toward shallower water. This meant that there were large schools in the basin areas at night and in the slope area during the day in 1995 and the reverse in 1999.

In summary, we think that large age-0 pollock (>55 mm) diel migrate through the thermocline unless the thermocline is weak and fish schools are large (i.e. abundance is concentrated), in which case age-0 pollock may remain below the thermocline or saturate the water column. Smaller age-0 pollock generally did not appear to migrate through a strong thermocline. Possible exceptions where smaller fish did diel migrate might involve heavy predation pressure above the thermocline, food limitation, and lower predation pressure from larger fish predators below the thermocline.

Zooplankton diel migration

The transect plots for the distribution of fish schools and plankton patches (Figure 2) show strong evidence of diel migration by zooplankton, especially for the years where pollock were not pervasive in the water column (1994, 1995, and 1997). The transect plots for transect A (Figure 2) show plankton patches close to the bottom during the daytime in these years while they are higher in

the water column during the night. Diel migration of the dominant zooplankton species near the Pribilof Islands was observed in 1996 during intensive MOCNESS sampling over a 48 h period (Schabetsberger *et al.*, 2000). However, during years of extremely high fish abundance (e.g. 1996) or in areas or years having a weak or no thermocline (e.g. 1998 on all transects and transect A nearshore all years) the diel migration pattern of zooplankton is less evident in acoustic data. The most common diel pattern, which occurred in the front and stratified region of transect A in all years except 1998, on transect C in all years except 1994, 1998 and 1999 and in most other regions on at least half the years, was to have diel migration through the thermocline of both fish and zooplankton, with the zooplankton generally being deeper than the fish both during the day and night. In these cases the median-average patch depth of the zooplankton during the night was near the thermocline and was always deeper than the median depth of the night fish schools, which were always clearly above the thermocline (Figures 5 and 6). Zooplankton diel migration appears to be dependent on the thermocline and on the diel migration pattern of the fish.

The zooplankton patches were dominated by euphausiids since these are the dominant zooplankton scatterers at 120 kHz. Euphausiid percentages in the diet of age-0 pollock increase with pollock size with a major switch in diet from primarily copepods to primarily euphausiids occurring at a length around 53 mm (Ciannelli *et al.*, 2002). Under this scenario larger zooplankton, experiencing predation pressure from larger age-0 pollock, would tend to stay near the bottom during the daytime and migrate up into the water column to feed during the night but may be constrained from migrating far above the thermocline by the presence of larger age-0 pollock in the water column above them.

In the deep region of transect B and the slope and basin regions of transect D (except 1998) the zooplankton usually remained below the thermocline both during the day and night. During the daytime these zooplankton were usually close to the bottom (Figure 6). This was particularly evident in 1996, the year of highest pollock abundance. Deeper regions (below 70 m depth) may serve as a refuge for euphausiids from age-0 pollock during periods of intense predation, although fish schools have been observed at depths greater than 100 m. The one year with unusual diel migration patterns for zooplankton is 1998. There was no evidence for a strong thermocline on any of the transects in 1998 (Table 3). As such, the water column may have been mixed down to the bottom in the shallower areas. Zooplankton may have had food available throughout the water column. On transect A in 1998 the fish appeared to stay lower in the water column while zooplankton showed evidence for diel migration and on

transect C fish schools tended to remain deeper than zooplankton patches both day and night: both counter to the general inverse abundance pattern for fish and zooplankton observed in other years. These observations hint at the role of the thermocline for both juvenile fish and larger zooplankton diel migration. Zooplankton may be able to maintain position near the thermocline using density cues to locate it and fish can clearly sense thermocline temperature gradients and respond to them. With the thermocline lacking, as in 1998, food availability patterns for zooplankton changed markedly because larger fractions of the water column may have been productive. Without the reliable, possibly thermocline-punctuated, diel pattern of zooplankton, larger age-0 pollock, present in 1998 (Table 3) may not have diel migrated. The smaller pollock may also have had a larger proportion of the water column available to find their primarily copepod prey, which were also no longer constrained to remain in the upper water column by food availability.

Abundance patterns for fish and zooplankton

In cases where the plankton patches appeared to remain below the thermocline both day and night, food availability in deeper regions might have been the primary incentive for diel migration by pollock. We hypothesize that deeper areas provide protection for plankton from juvenile pollock swimming below the thermocline and therefore the basin areas have higher zooplankton densities. This is supported by the generally higher abundance of plankton in the deeper parts of transects B, C and on transect D than in shallower regions (Figure 4). In part, this may also explain the elevated pollock abundance levels on transect A. Having a shallower bottom may keep the zooplankton from going beyond the effective feeding-depth range of age-0 pollock. However, we could not detect acoustically the entire food resource base for age-0 pollock. Smaller pollock feed largely on zooplankton not detected by acoustics though this depends on their densities: at high enough densities large copepods may reflect enough sound to be detected at 200 and 120 kHz.

Transect D has the greatest depth range (to ~250 m). It had the highest plankton density in many of the years and most consistently had large plankton patches, particularly during the daytime (Figure 3). We hypothesize that the location of transect D at the end of the Pribilof Canyon generates higher currents and upwelling conducive to the development of large zooplankton patches (Brodeur, 2001). Fish abundance on transect D was highly variable and, except in 1995, was the lowest among the transects (Figure 4). Transect D also tended to have the most within-season variability (i.e. between transect passes) in fish and plankton abundance (Figure 4). This may be due to the generally higher currents in

this region than along the other transects. High current shear may make it difficult for age-0 pollock to maintain position near their prey (Ciannelli *et al.*, 2002). More investigation of current conditions during the surveys and the role of the Bering Slope Current and advection in this region may give a clearer understanding of the influence of currents on pollock and zooplankton distribution.

Some insight into the abundance pattern of pollock and zooplankton is afforded by the abundance rankings by year for each habitat region. Pollock abundance was largest in 1996 in all regions except the front region of A and the basin region of D: pollock abundance was at a maximum in 1995 in these regions. Conversely, zooplankton abundance was at a minimum in all regions in 1996. This pattern suggests that 1996 might be a year when the pollock severely depleted their zooplankton prey. Low zooplankton abundance in 1996 on transect A was reported from MOCNESS sampling by Schabetsberger *et al.*, (2000). Zooplankton maxima over all years occurred in 1997 in all regions except in the stratified region of transect A, the shallow region of transect B and in transect D, while pollock biomass was at a minimum in all transect regions in 1997 (Figure 4). Excluding 1994 the pattern of regions having higher pollock and lower zooplankton abundance or lower pollock and higher zooplankton abundance obtained for all years (Figure 4), except on transect D, where pollock and zooplankton abundance appeared to be uncoupled. In 1994, including transect D, higher levels of pollock were associated with higher levels of zooplankton, while some regions had lower levels of both pollock and zooplankton. The other exception to the inverse fish–zooplankton abundance relationship was on transect B in 1999, when higher fish and zooplankton densities both co-occurred. The relatively high currents (Stabeno *et al.*, 1999), high transport from Pribilof Canyon (Brodeur 2001) and increased bottom depth on transect D help to explain why pollock and zooplankton abundance might be uncoupled. The stronger currents and possible onshore–offshore migration of zooplankton patches and the increased bottom depth on transect D may make access to zooplankton prey and effective feeding by age-0 pollock more difficult. Other regions where we might expect less coupling between pollock and zooplankton are the deeper areas of transect B and C. However, only in 1994 and 1999 were there higher densities of both pollock and zooplankton on transect B and only in 1994 on transect C. Thus, the deeper regions of transect B and C, while they might provide some refuge for zooplankton from pollock grazing (as suggested by the zooplankton patches being deeper than pollock schools both day and night; Figures 5 and 6), still had an inverse relationship between pollock and zooplankton abundance in most years (Figure 4). The inverse pollock–zooplankton abundance relationship

found in regions and years of high pollock abundance, suggests there may have been a significant depletion of zooplankton by September. This is supported by the energetics modelling work of Ciannelli *et al.*, 2002, that predicts potential prey extinction by pollock over relatively short time periods (e.g. 15 days).

Toward an index of pollock year-class-strength

This relatively long (6 years) data series has made it possible to improve our understanding of the determinants of year-class-strength in walleye pollock, one of the world's largest single-species fisheries. It would be presumptuous to suggest that the state of age-0 pollock near the Pribilof Islands is synonymous with future recruitment to the entire Bering Sea pollock stock. However, considering the importance of the Pribilof Island region as a nursery area for pollock and the wide range of habitats available in a small region (i.e. several fronts, nearshore region, shelf, shelf break, and canyon areas) the Pribilof Islands may serve as a laboratory for what is occurring in other parts of the Bering Sea (Hunt *et al.*, 2002). Thus, measurements taken around the Pribilof Islands may be like taking the temperature of the pollock nursery system with an eye to the health of the system. The fairly extensive data available on this system makes it a prime candidate to shed light on the connection between conditions during the first year of life and eventual recruitment.

Four aspects that may contribute to age-0 pollock recruitment are:

- (1) The environmental conditions during the first year of life, including such factors as prevailing currents (larval transport), water conditions near the Pribilof Islands (i.e. shelf or slope water), and the degree of stratification;
- (2) The pervasiveness and abundance of juvenile pollock in the autumn, both in their distribution around the Pribilof Islands and in other rearing areas;
- (3) The size and depth distributions of pollock near the Pribilof Islands in the autumn;
- (4) The density and distribution of predators (e.g. fish, birds and marine mammals) and competitors, including scyphomedusae, fish, birds, and marine mammals.

Hydrographic conditions of potential importance to pollock year-class-strength may include the strength and depth of the pycnocline, the intensity and location of the inner front near the islands, the distribution of oceanic water masses on the shelf around the islands and average water temperature. Oceanic conditions and fronts around the Pribilof Islands in 1994–1997 are discussed by Stabeno *et al.* (1999). A major unresolved question for pollock year-class-strength is how strongly larval

transport from major pollock spawning areas to the Pribilof Islands and retention of age-0 pollock around the islands is influenced by large scale circulation patterns and whether such patterns can be predicted from hydrological models (Wespestad *et al.*, 2000).

The highest pollock abundance on transect A and elevated pollock abundance throughout the study region occurred in 1996 (Figures 2 and 4) when there was also a pollock year class much larger than in any of the other study years (Wespestad *et al.*, 2000; J. Ianeli, Alaska Fisheries Science Center, personal communication). We hypothesize that large year classes of pollock must have either elevated juvenile pollock abundance in all transects (A, B, C and D; Figure 1) within the Pribilof study area, a core pollock nursery area, or widespread autumn juvenile pollock abundance in a variety of potential nursery areas (e.g., Nunivak Island, Russian coastal waters) or both (Bailey *et al.*, 1998; Coyle and Pinchuk, 2002). The rationale for this hypothesis is that pervasive pollock abundance increases the probability of a large year class by broadening the habitat range for the age-0 pollock cohort, giving them more chance of encountering favourable habitats having high food abundance and low predator abundance. Under this hypothesis, 1997, which had low but pervasive biomass (Figure 4) should not be a large year class. In 1994, 1995, 1998 and 1999 pollock abundance was relatively high on transect A but was not high on the other study transects (Figure 4) and, under our hypothesis, they should not have produced large year classes unless abundance was also high in other nursery areas.

Successful year-class-strength may also depend on the size of the pollock being sufficient to enhance survival through the coming winter (Sogard and Olla, 1996). Larger size in juvenile pollock might also increase their chances of successful feeding when they diel migrate below the thermocline in the daytime (Bailey, 1989). Having both large and very small (<30 mm) juvenile pollock existing in the same area (e.g. in 1999; Table 3) may result in intra-cohort cannibalism (Brodeur *et al.*, 2000). This might contribute to successful future growth of the largest individuals even when zooplankton food resources are depleted.

We do not yet know how important predation is in affecting pollock year-class-strength. Predation by groundfish may affect pollock diel migration by forcing them to remain above the thermocline (Lang *et al.*, 2000). Large age-0 abundance may also result in pollock diel migration because the pollock saturate the predators. Thus, predators may be important in years of intermediate age-0 pollock abundance by reducing pollock diel migration and by causing the pollock reduced growth rates through separation from their major food sources. Detailed examination of the acoustic target strength data for individual targets may shed some light on whether the higher abundance of groundfish, includ-

ing adult pollock, was associated with the lower abundance of juvenile pollock. Large and small fish can be distinguished in the echograms by looking at acoustic target strengths of fish: larger fish have considerably higher target strength than juvenile pollock. Bird predation during the autumn is not likely to be important to the population as a whole, given the relatively low density of piscivorous birds, although some transects had higher bird abundance in some years (Swartzman and Hunt, 2000). However, earlier in the summer bird predation may be considerable. The apparent association of juvenile pollock with scyphomedusae (Brodeur, 1998) may play an important role in reducing bird predation during the summer. On the other hand, competition for zooplankton resources from the high abundance of scyphomedusae in the study area (Brodeur *et al.*, 2002) may result in reduced food availability for juvenile pollock.

A successful index of pollock year-class-strength will likely depend on a variety of factors and will require integrated research. Many of the proposed factors interact. For example, the pervasiveness and abundance of age-0 pollock near the Pribilof Islands may depend on current conditions that transport larvae from spawning areas, such as the vicinity of the Bogoslof Islands (Napp *et al.*, 2000), to the Pribilof Islands or elsewhere (Stabeno *et al.*, 1999). Similarly, the ice cover of the previous winter, the rapidity of the ice melt and the frequency of summer storms may determine the summer growth conditions for the smaller zooplankton necessary as food for the age-0 pollock arriving at the nursery area (Stabeno *et al.*, 2002). Feeding conditions, initial abundance and the density of bird and fish predators in the area may all influence the abundance and condition of pollock as they enter their first winter. Regression models involving indexes developed to reflect these factors could lead to the evaluation of some of them.

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