



PERGAMON

Deep-Sea Research II 49 (2002) 6109–6126

DEEP-SEA RESEARCH  
PART II

www.elsevier.com/locate/dsr2

# Physical and biological factors influencing the spatial distribution of age-0 walleye pollock (*Theragra chalcogramma*) around the Pribilof Islands, Bering Sea

Lorenzo Ciannelli<sup>a,\*</sup>, Richard D. Brodeur<sup>b</sup>, Gordon L. Swartzman<sup>c</sup>, Sigrid Salo<sup>d</sup>

<sup>a</sup> School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105, USA

<sup>b</sup> Northwest Fisheries Science Center, Hatfield Marine Science Center, Newport, OR 97365-5296, USA

<sup>c</sup> University of Washington, Applied Physics Laboratory, Seattle, WA 98105-6698, USA

<sup>d</sup> NOAA, Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA

## Abstract

The waters around the Pribilof Islands, in the southeast Bering Sea, are a main nursery area for age-0 pollock. Each summer, the islands are surrounded by a well-mixed inshore region, separated from a stratified offshore region by a frontal zone. To study the spatial distribution of age-0 pollock around this frontal structure in relation to physical and biological factors that are likely to influence it, such as advection, age-0 pollock feeding, and predation, samples were collected during September of four consecutive years, 1994–97, along two transects. Samples collected included water column hydrography and currents, acoustic backscatter, and groundfish predator density.

Our analysis suggested that different mechanisms may be involved in controlling age-0 pollock distribution north and south of the islands. On the shelf area north of the islands, high age-0 pollock density was significantly associated with areas of high potential for growth only in years or portions of the frontal transect in which predator numbers were relatively low, indicating the importance of predation in controlling fish distribution in this area. In contrast, south of the islands, age-0 pollock distribution was associated more with prey availability, which appeared to be determined by vertical spatial overlap between predators and prey. Moreover, south of the islands, the stronger geostrophic currents, typical of the slope region, were more likely to affect the overall standing biomass of juvenile pollock, by constantly advecting fish away from the area.

© 2002 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

The age-0 stage of walleye pollock (*Theragra chalcogramma*) is a nodal element at both the population and community levels of the Bering Sea and Gulf of Alaska (Brodeur and Wilson,

1996, 1999). In the Gulf of Alaska, the generational mortality of a typical pollock cohort is highly correlated with age-0 mortality (Bailey et al., 1996). In the Bering Sea, cycles of high adult pollock abundance follow exceptionally high juvenile stage densities, in particular age-1 densities, indicating that survival of fish younger than age-1 has a critical impact on adult recruitment (Wespestad et al., 2000). At the community level, juvenile pollock are intense consumers of

\*Corresponding author. NOAA/AFSC/RACE, 7600 Sand Point Way, NE, Seattle, WA 98115, USA..

E-mail address: lorenzo.ciannelli@noaa.gov (L. Ciannelli).

zooplankton due to their abundance and feeding rate (Ciannelli et al., 1998; Brodeur et al., 2000). Juvenile pollock are also the main prey items of many fish, marine mammal, and seabird species (Livingston, 1993; Sinclair et al., 1994; Hunt et al., 1996).

The waters around the Pribilof Islands provide habitat for a rich and diverse community in the southeast Bering Sea. In previous surveys the Pribilof Islands have been identified as one of the centers of juvenile pollock abundance (Traynor and Smith, 1996). Predators upon juvenile pollock, such as groundfish, seabirds, and marine mammals, as well as pollock prey, such as euphausiids and copepods, are present at high densities in regions around the islands (Hunt et al., 1996; Brodeur et al., 1997; Lang et al., 2000; Flint et al., 2002). The physical features of the water around the Pribilof Islands may play an important role in creating and concentrating such a rich community. The Islands are the only landmass on the eastern Bering Sea shelf near the Bering Sea slope. During summer, tides and winds create a frontal system around each island (Stabeno et al., 1999). The frontal system is composed by an inner front that divides a well-mixed inshore domain from a typical two-layered thermally stratified offshore domain (Flint et al., 2002). The inner front may be from 1 km to more than 10 km wide, depending mainly on the strength of water stratification, wind forcing and bottom morphology (Stabeno et al., 1999).

Fronts are an important mechanism through which habitat heterogeneity is generated in open seas (Sournia, 1994). Habitat heterogeneity can have a considerable impact on growth, survival and distribution of juvenile and adult pelagic fishes (Brandt, 1993; Munk, 1993; Munk et al., 1999). Fronts are also important because they aggregate particles and replenish nutrients in the water column and thus generate higher than average biological production (LeFèvre, 1986; Franks, 1992; Sournia, 1994).

In spite of the high densities of age-0 pollock around the Pribilof Islands, the major factors affecting their distribution and survival are still unknown. Given the co-occurring high density of prey and predators, it is possible that growth-

related factors, as well as predation, are competing to control the distribution and survival of age-0 pollock (Ciannelli, in press). Also, because of the spatial heterogeneity associated with the frontal structure, it is possible that local events, on the scale of 1–10 km, play an important role in age-0 pollock population ecology (Brandt, 1993; Ciannelli, in press). Our objective was to examine the distribution of age-0 pollock around the islands in relation to physical and biological features that are likely to have an impact on fish distributions and that were available to us. Specific features investigated included ambient fish growth potential estimated from bioenergetics modeling, advection potential inferred from tidal and geostrophic currents, and groundfish predator density and distribution inferred from bottom trawls.

## 2. Methods

### 2.1. Study site

We examined 4 years of sampling, 1994–1997, along transect Lines A and D (Fig. 1). These lines lie within different bathymetric domains. Line A is north of St. Paul Island, in the middle domain of the Bering Sea shelf. Depth along Line A ranges from 30 m at the south end to 65–70 m at the north end. Line D extends south from St. George Island to the Bering Sea slope and intersects Pribilof Canyon, which intrudes northward onto the shelf (Fig. 1). Depth along Line D starts at 40 m near the island and quickly descends offshore to more than 300 m near the Pribilof Canyon. Surveys along these lines took place during the first half of September. Data collected included water column properties, acoustic backscatter, zooplankton and age-0 pollock densities, and in some years and locations, groundfish predator densities.

### 2.2. Hydrography, currents and advection of fish and zooplankton

Water-column properties were measured with conductivity temperature depth (CTD) casts made prior to conducting acoustic and biological sampling (Stabeno et al., 1999). We calculated the

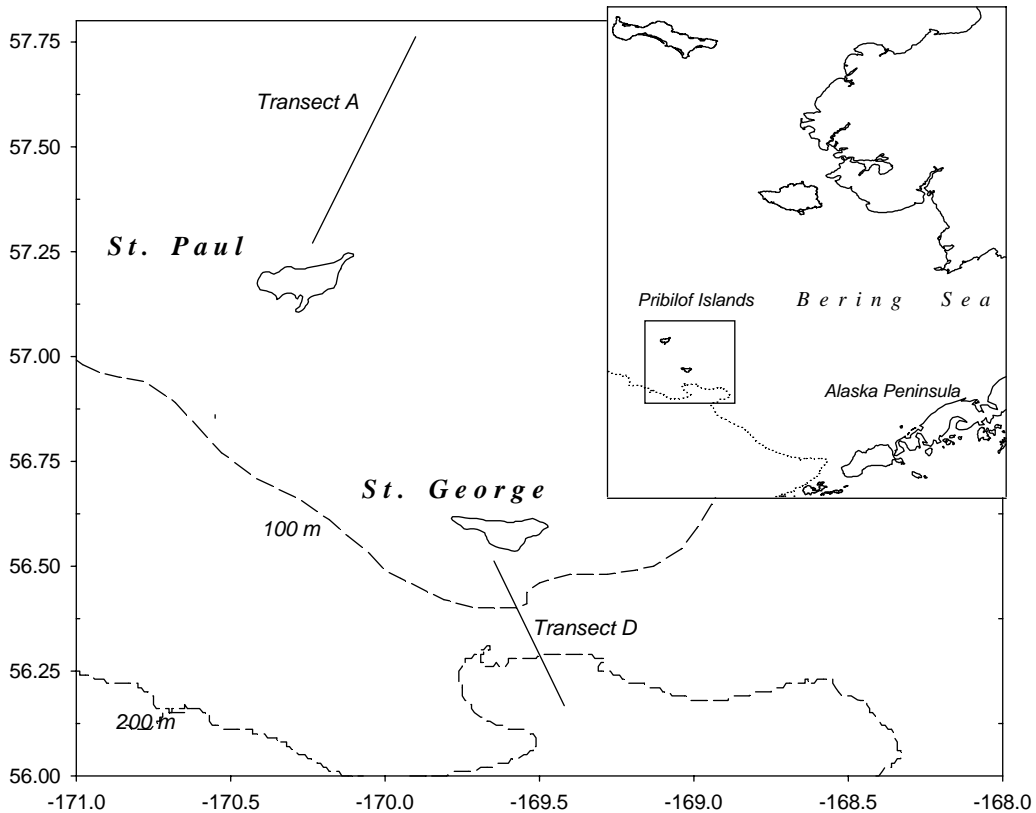


Fig. 1. Study area and sampled transect lines around the Pribilof Islands.

geostrophic currents perpendicular to each transect from the variation in dynamic height obtained from the salinity and temperature data from each cast. Geostrophic currents from 1994 both Lines A and D and from 1996 Line D only were not included in the analysis because CTD casts for these year and transect subsets were questionable due to the presence of salinity spikes. Tides can adversely affect geostrophic calculations, especially if the variation in tidal height is much greater at one end of the transect than the other. To minimize the effect of tides on the geostrophic calculations we used pairs of neighboring casts that were occupied an hour or less apart.

In addition to geostrophic flow, we used records of current meters deployed near the Pribilof Islands to predict tidal currents in the area. For the region north of St. Paul Island, we used a

current meter deployed at 25 m of water, in place from September 1995 to August 1996. Tides south of St. George Island were calculated from a current meter deployed at 100 m of water in place from April to September 1999. Current records for both lines were long enough to obtain sufficient tidal coefficients to predict the tides during other years.

Estimated geostrophic current velocities were used to assess fish and zooplankton advection during the course of a day. This analysis was made only for 1995, when we had a favorable combinations of CTD and acoustic passes along both lines. We first estimated the depth of the organisms during each hour of their diel migratory cycle using the acoustic records. Next, we estimated fish and zooplankton net 24-hour geostrophic displacement (hereafter, geostrophic advection) from the

estimates of geostrophic current velocities. Tides were not included in the geostrophic advection analysis because tidal flow was relatively constant with depth, so that fish and zooplankton at their respective depths experienced roughly the same tidal velocity.

### 2.3. Age-0 pollock and zooplankton distribution

Age-0 pollock and zooplankton distributions were detected acoustically using a SIMRAD EK-500 echosounder system at three frequencies (38, 120 and 200 kHz) in 1994 and 1995 and two frequencies (38 and 120 kHz) in 1996 and 1997. Two passes along Line A and one along Line D were conducted in 1994, five passes along Line A and two along Line D were conducted in 1995, four passes along Line A and two along Line D were conducted in both 1996 and 1997. Line A required about 3 h and Line D <2 h to complete each pass. Multiple hydroacoustic passes along the same line were alternated between day and night and were usually completed within 3 days, except for the 1995 pass along Line A, in which two sets of day–night runs were separated by 5 days.

Signal processing analyses were used to distinguish between zooplankton and fish, based mainly on differences in backscatter properties between the two classes of organisms at the different frequencies (Swartzman et al., 1999a,b). Fish acoustic density was calculated by integrating all acoustic backscatter attributable to age-0 pollock along a 42-m vertical bin, divided by the depth at location. In this paper, the term “acoustic density” refers to the density index derived from acoustic data, as described above. Also, age-0 pollock have been shown to dominate the numerical catch of midwater trawls in all areas and years, comprising more than 90% of total fish number caught (Brodeur et al., 1997, 2002). Therefore in the following sections the terms “fish” and “juvenile pollock” are used interchangeably, and refer to age-0 walleye pollock.

### 2.4. Bioenergetic potential for growth

The bioenergetics model used to estimate age-0 pollock spatially explicit growth along the trans-

ects is described in Ciannelli (in press). Here we briefly reiterate the most important aspect of the model. The general bioenergetics model is based on the Winberg (1956) balanced energetics equation, in which, for a non-reproductive fish, all energy ingested ( $I$ ) is allocated between metabolism ( $M$ ), egestion ( $F$ ), excretion ( $U$ ), and growth ( $G$ ):

$$G = I - M - F - U.$$

The above equation is composed by two sub-models, a foraging model to calculate fish consumption ( $I$ ) and a bioenergetics model to allocate consumption between metabolism ( $M$ ), egestion ( $F$ ), and excretion ( $U$ ). We used the Gerristen and Strickler (1976) forage model adapted to juvenile pollock (Ciannelli, in press) to calculate fish consumption. We used the Ciannelli et al. (1998) age-0 pollock bioenergetics model to partition consumption into growth and other metabolic output. The model is made spatially explicit by applying it to many different portions of the environment (Brandt et al., 1992). Such portions of the environment, termed cells, differ from each other by specific physical and biological variables, including temperature, prey density, fish length, and diet composition. In this study, the model is used to predict age-0 pollock growth only within their observed distribution, thus the output should be regarded more as an estimate of fish realized growth rather than an estimate of habitat potential growth.

In each year examined, fish growth potential was calculated over an average zooplankton distribution by transect. For each line, the yearly averaged zooplankton distribution was derived over depth and among multiple passes of the investigated year and transect. By doing so, the average zooplankton transect lost its diel and vertical variability, and preserved the horizontal variability. However, fish growth potential did preserve vertical variability, due to temperature differences throughout the water column. The assumption applied in deriving the average zooplankton distribution transect was that even if zooplankters were vertically distinct from a particular fish school for part of the day, they would eventually overlap with the

school, due to the diel vertical migration of zooplankton (Swartzman et al., 1999b; Schabetsberger et al., 2000).

Age-0 pollock growth potential was not estimated along Line D during 1994 and 1997; in 1994 temperature data were incomplete and in 1997 there were too few fish in the water column to extrapolate an estimate of ambient growth in the areas occupied by fish schools.

Empirical data on fish biomass and estimated potential for growth, both averaged by distance bins, were correlated against each other to study the degree of spatial dependence between fish distribution and their potential for growth. Bin length in the correlation analysis was 2500 m on Line A and 1500 m on Line D. The statistical model used for this analysis was linear:

$$\text{Fish biomass} = k_1 + k_2 \text{ GP} + \text{error},$$

where  $k_1$  and  $k_2$  are the model intercept and slope, respectively.

### 2.5. Groundfish distribution

The main groundfish predators of age-0 pollock were arrowtooth flounder (*Atheresthes stomias*) and adult pollock based upon an analysis conducted during the same sampling season and for the same area considered in this study (Lang et al., 2000). In our study, groundfish predators were collected in a nylon Nor'eastern bottom trawls with 1.5 × 2.1-m steel doors without roller gear. The mean effective path width of the bottom trawl was estimated to be 13.4 m with a mean vertical opening of 9.2 m. Mesh size of the net varied between 13 cm in the forward part to 8.9 cm in the codend (Lang et al., 2000). Catches were reported as a standardized biomass by volume sampled. Along Line A in 1994, there was only one bottom trawl station done at the inshore region, while in 1995 and 1996, each habitat had from 1 to 8 bottom trawls. Along Line D, bottom trawls were performed only in the offshore region in 1995, in the inshore and offshore region in 1994 and in the frontal region in 1996.

## 3. Results

### 3.1. Hydrography, currents and geostrophic advection of fish and zooplankton

Along Line D, the inshore water column was often stratified because the closest-to-shore station was often deeper than the depth (50 m) at which tidal currents and winds were able to mix the water column (Fig. 2). In contrast, Line A always crossed the inner front, which separated a stratified offshore region from a well-mixed inshore region. Among all years included in this study, 1995 stands out as anomalously cold. In 1995, bottom temperatures on both Lines A and D were at least 2°C colder than in other years, and depth of the thermocline was about 10 m shallower than in any other year (Fig. 2). Moreover, in 1995 bottom and top layer temperatures in the offshore stratified region of A differed by about 8°C, while in other years they differed by about 6°C.

Currents at a depth of 25 m north of St. Paul Island were almost exclusively tidal; 54% of the current variance was at semidiurnal frequencies and 37% was at diurnal frequencies. Tides were the largest component of currents throughout Line A (Fig. 3), but their magnitude decreased with distance from the shore (Kowalik and Stabeno, 1999). These authors show that although there was little change in the phase of two major tidal constituents (M2 and K1) along Line A, the maximum velocity associated with each component decreased to roughly 60–62% of its nearshore value by the north end of the transect. Current records on Line D were less strongly tidal than the site north of St. Paul Island, with about 20% of the current variance at diurnal and 15% at semidiurnal tidal frequencies (Fig. 3). The decrease in the relative tidal importance of Line D compared to Line A, is due in part to the proximity of the site to the shelf break and the Bering Slope Current; Kowalik and Stabeno (1999) show that the M2 and K1 tidal velocities more than doubled closer to St. George Island.

Unlike tidal currents, geostrophic currents along Line D were stronger than along Line A (Figs. 4a and b). Along Line D flow occurred in bands roughly 10 km wide and went mainly to the west at

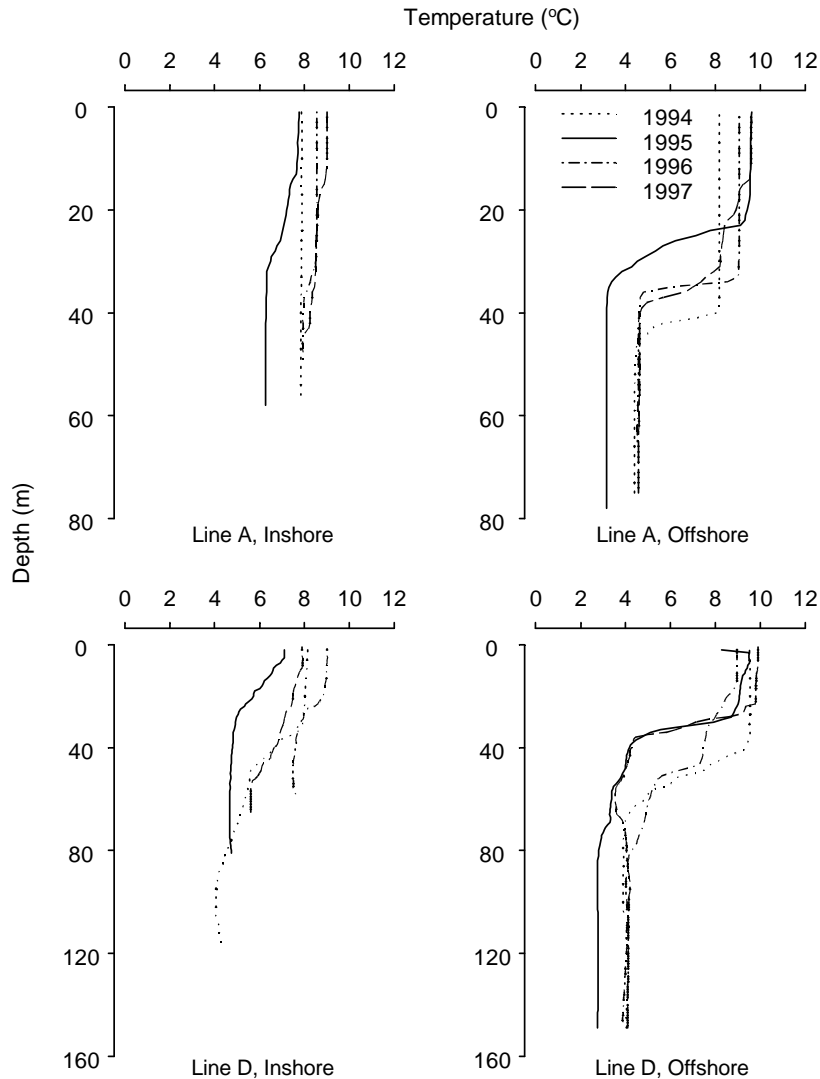


Fig. 2. Temperature profiles in late summer 1994–97 along Line A (top figures) and Line D (bottom figures) at an inshore (left figures) and offshore (right figures) site.

magnitudes greater than  $15 \text{ cm s}^{-1}$ . There were narrow bands of weak eastward flow toward the nearshore area. Geostrophic flow along Line A was about  $5 \text{ cm s}^{-1}$  in both eastward and westward components (Fig. 4a).

Two patterns emerged from the geostrophic advection analysis of fish and zooplankton. First, total 24-hour geostrophic advection of fish and zooplankton along Line D was greater than along Line A; on Line A it ranged between 0.4 and

$5.2 \text{ km d}^{-1}$ , while on Line D it ranged between 0 and  $15.5 \text{ km d}^{-1}$  (Fig. 5). Second, fish geostrophic advection was always greater than zooplankton geostrophic advection, especially along Line D. North of St. Paul Island, the maximum difference between fish and zooplankton advection was about  $1.7 \text{ km d}^{-1}$ , while south of St. George Island, in the core of the westward flow, the maximum difference between the two net advections was  $5.2 \text{ km d}^{-1}$ .

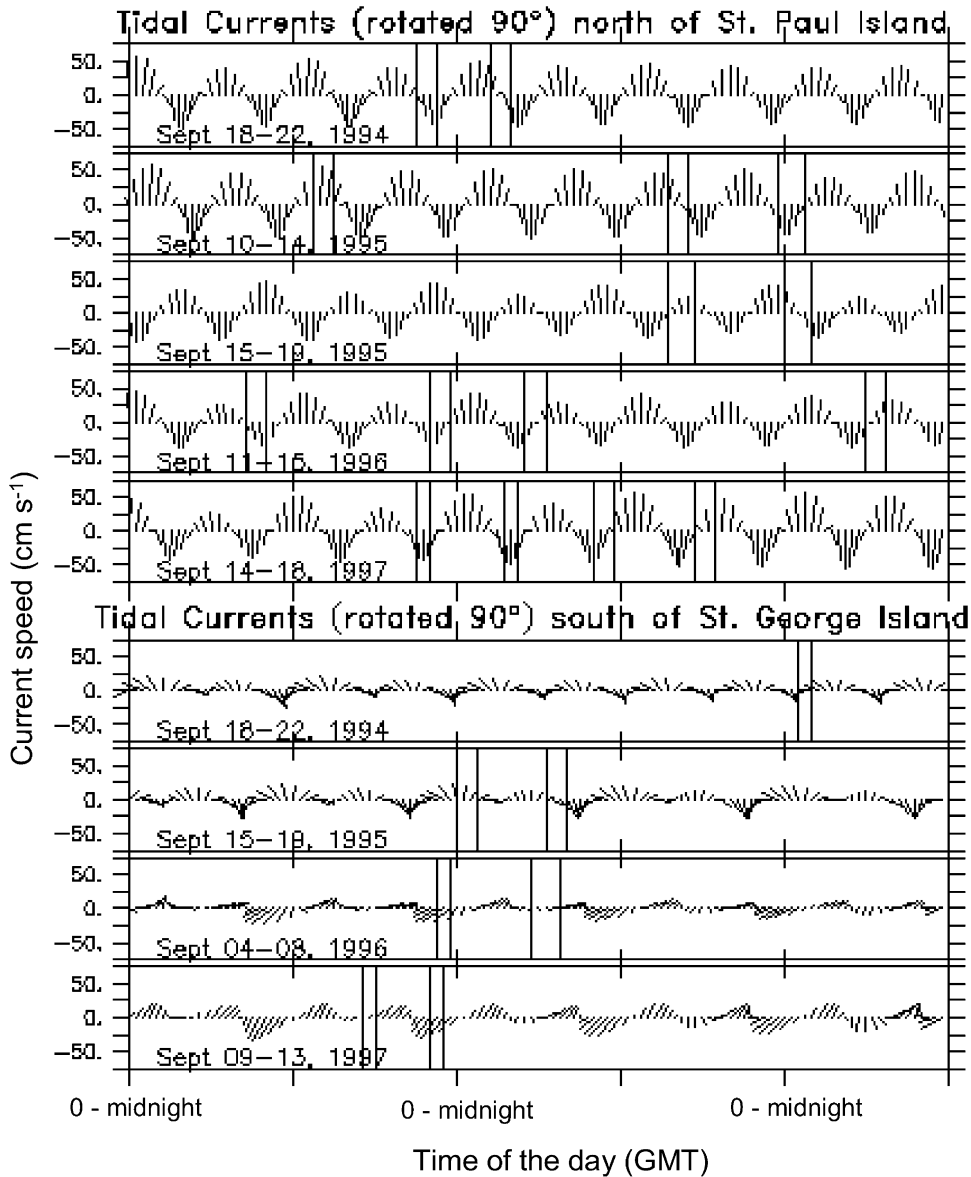


Fig. 3. Estimated tidal currents along Line A (top five panels) and Line D (bottom four panels) during the time of hydroacoustic survey in the study area. Vertical bars on each panel indicate beginning and ending time of hydroacoustic pass. The currents have been rotated  $90^\circ$  to be better displayed. Thus, an upward vector is eastward. Time refers to Greenwich Meridian (GMT) and it is 8 h forward with respect to Alaska daytime.

### 3.2. Age-0 pollock and zooplankton distribution

Zooplankton acoustic density along both transects was consistently higher toward the offshore region. In contrast, distribution of fish density

along the transects showed high year-to-year variability, especially along Line A (Fig. 6). In 1994 on Line A, peak acoustic densities of age-0 pollock were associated with the central portion of the transect (15–35 km from start), where on

average densities values were two to three times higher than on either side. In 1995 fish acoustic density was 1–2 orders of magnitude higher in the

inshore portion of the transect (less than 20 km from start) than in the offshore part. In both 1996 and 1997 fish acoustic density remained constant

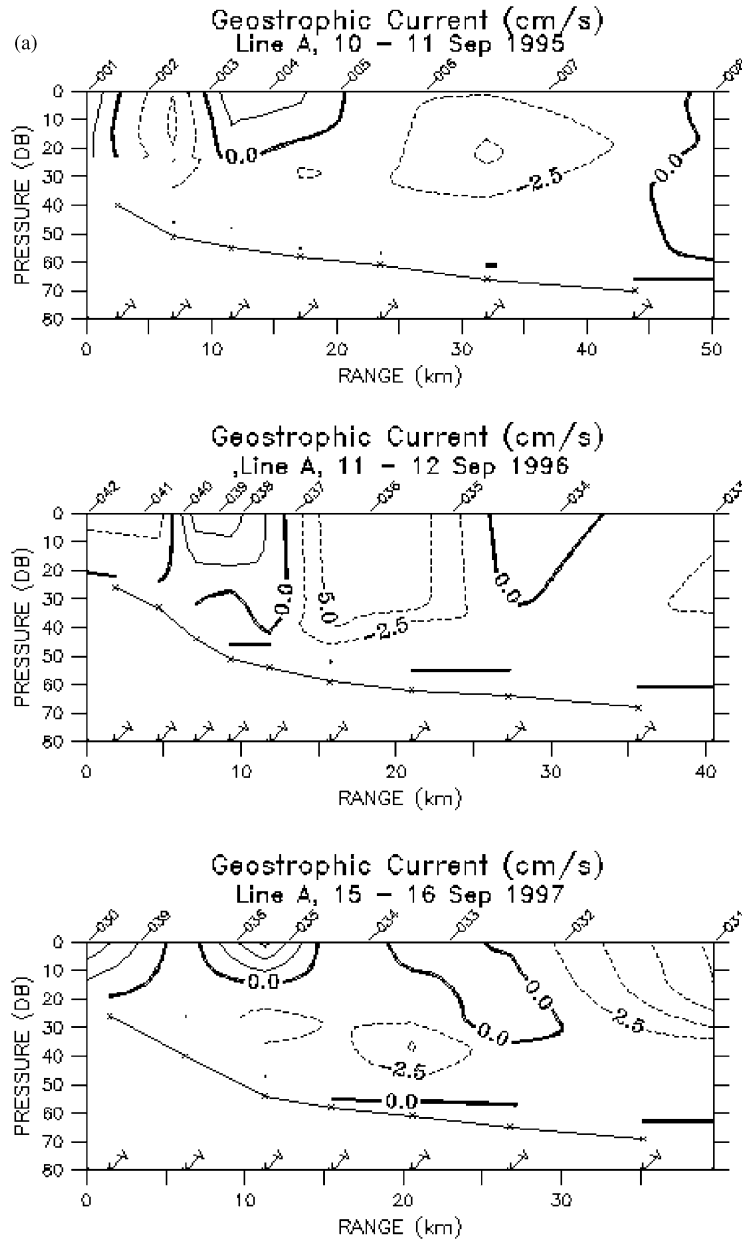


Fig. 4. (a) Estimated geostrophic flow calculated from temperature and salinity at Line A in 1995–97. In these plots, a positive velocity indicates that flow is to the left (west) as one moves out along the transect, (b) estimated geostrophic flow calculated from temperature and salinity at Line D in 1995 and 1997. Here, a positive velocity indicates that flow is to the left (east) as one moves out along the transect.



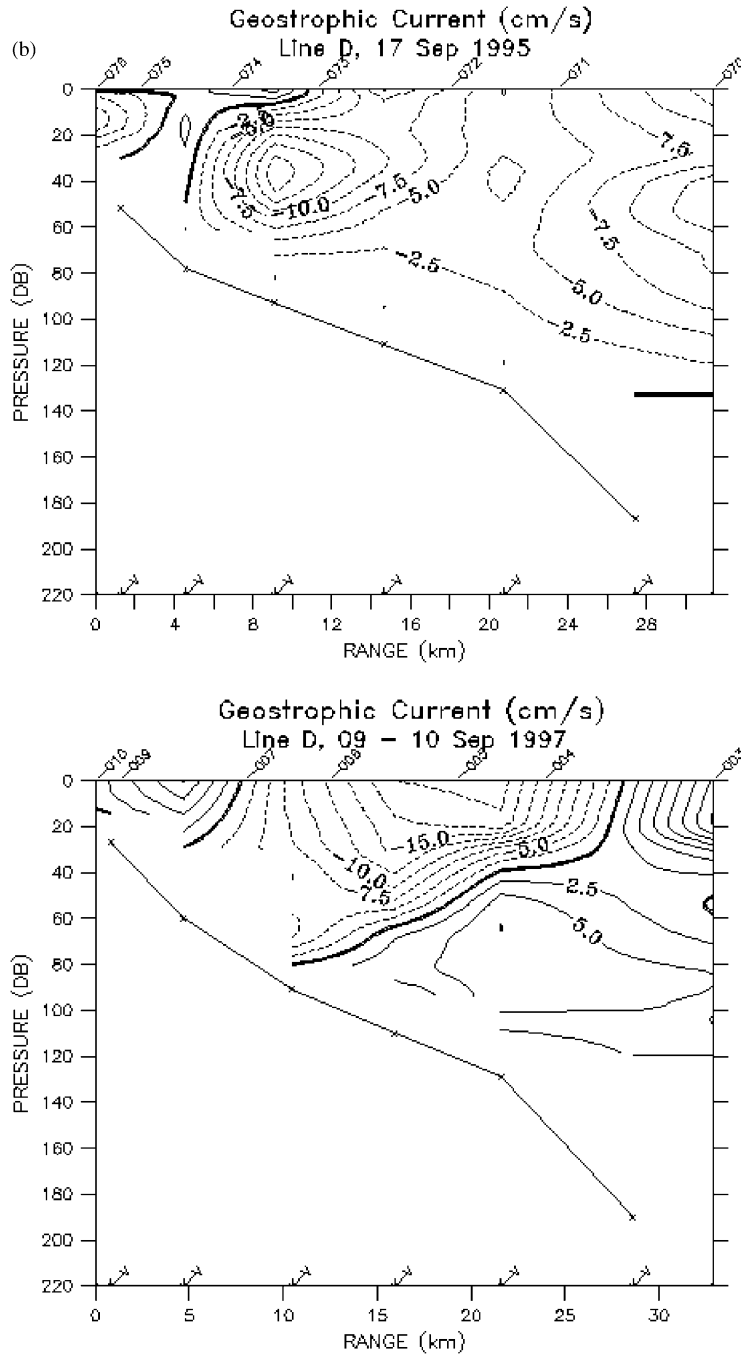


Fig. 4 (continued).

throughout most of the transect length, except for a 5-km portion of the inshore region where it dropped considerably (Fig. 6).

During all years, fish density was from two to three times lower along Line D than along Line A. Furthermore, on Line D, year-to-year variation in

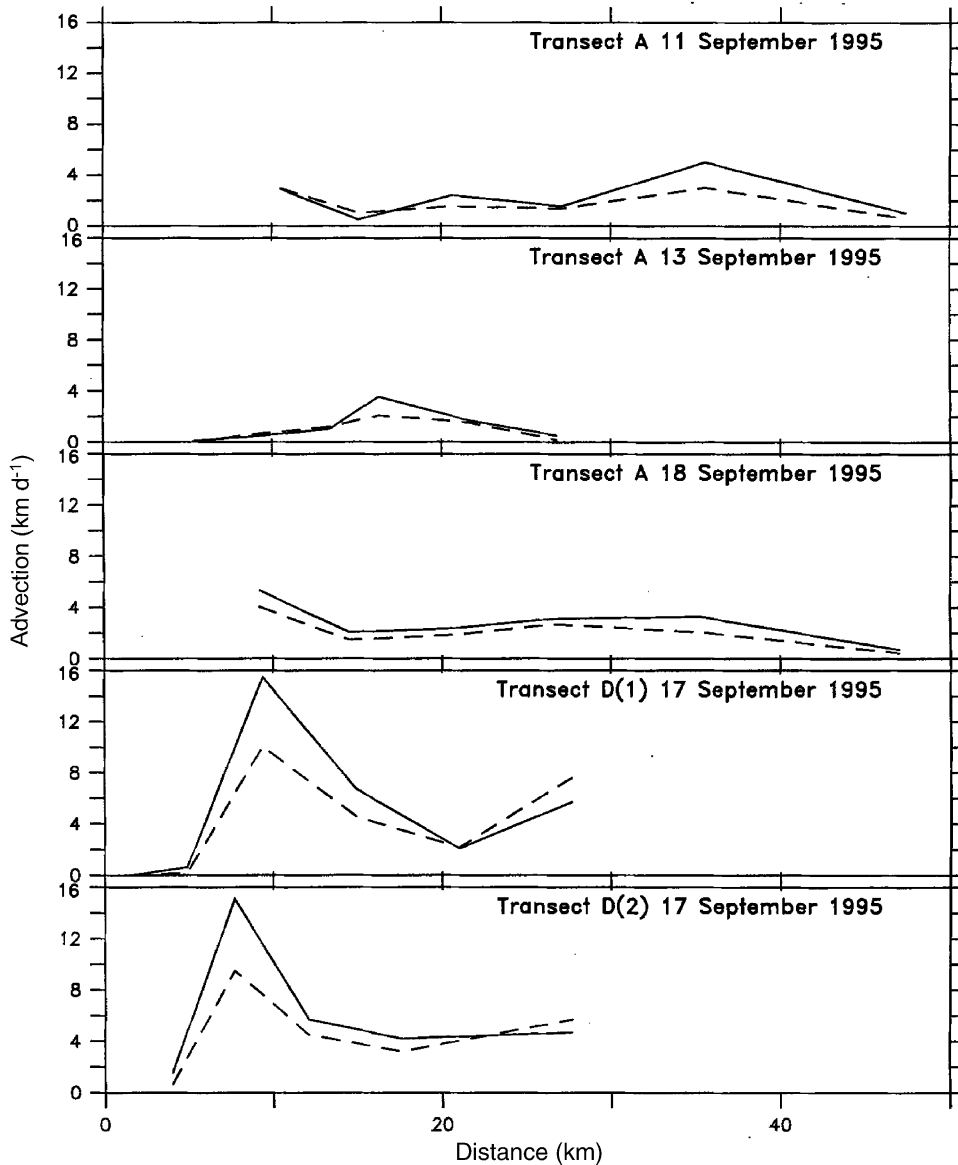


Fig. 5. Net 24-hour geostrophic advection of fish (solid line) and zooplankton (dashed line). Geostrophic advection is calculated from acoustic estimates of diel vertical distribution combined with three realizations of flow calculations along Line A and two along Line D.

fish acoustic density along the transect was not as pronounced as on Line A (Fig. 6). Generally on Line D, fish acoustic density was consistently two to three times higher in the first 10–15 km of the transect than further offshore. One exception occurred in 1995, when there was a peak density

in the offshore region during the night hydro-acoustic pass (Swartzman et al., 1999b). The distribution of fish biomass described in this study for both lines was independently corroborated with midwater net samples reported in Brodeur et al. (2003).

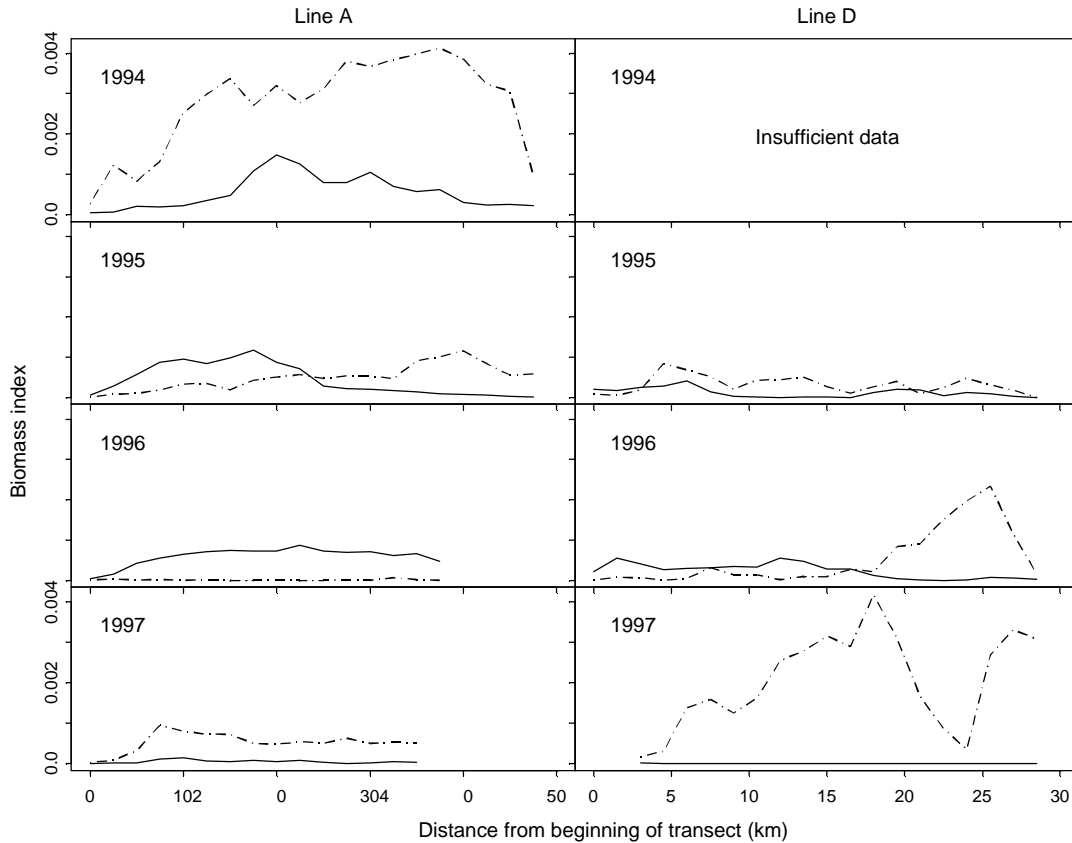


Fig. 6. Hydroacoustic biomass distribution of age-0 pollock (solid line) and zooplankton (dashed-dot line) along Line A (left panel) and Line D (right panel) during 1994–97.

### 3.3. Bioenergetics potential for growth

Age-0 pollock residing in the offshore portions of both lines had growth potential that were two to three times higher than fish residing in any other parts of the surveyed transects (Fig. 7). We estimated the highest fish growth potential on Line A during 1994, and the lowest, again on Line A, during 1996. In 1994 in most locations of Line A, age-0 pollock growth potential was more than twice the average value of all years and transects (gross average, hereafter). Fish growth potential was most strongly affected by habitat type on Line A in 1995, when it was consistently low for all fish schools residing in first 5–10 km of waters and progressively reached a 4-fold increase toward the offshore portion of the transect (Fig. 7).

Along Line D, the lowest estimated fish growth potential also occurred in 1996, but only within the shoreward section of the transect (15–20 km) (Fig. 7). Beyond 20 km from the transect start, corresponding to the Bering Sea shelf edge, fish growth potential showed a 4-fold increase, and reached values equal and occasionally twice as high as the gross average growth potential. In 1995, estimated fish growth potential was about half that of gross average and remained so along the whole transect. Although we do not have estimates of fish growth potential along Line D in 1997, we would expect potential for fish growth to be higher in the offshore region due to the high density of zooplankton found there (Fig. 6).

Results of correlation analysis between binned fish acoustic biomass and growth potential

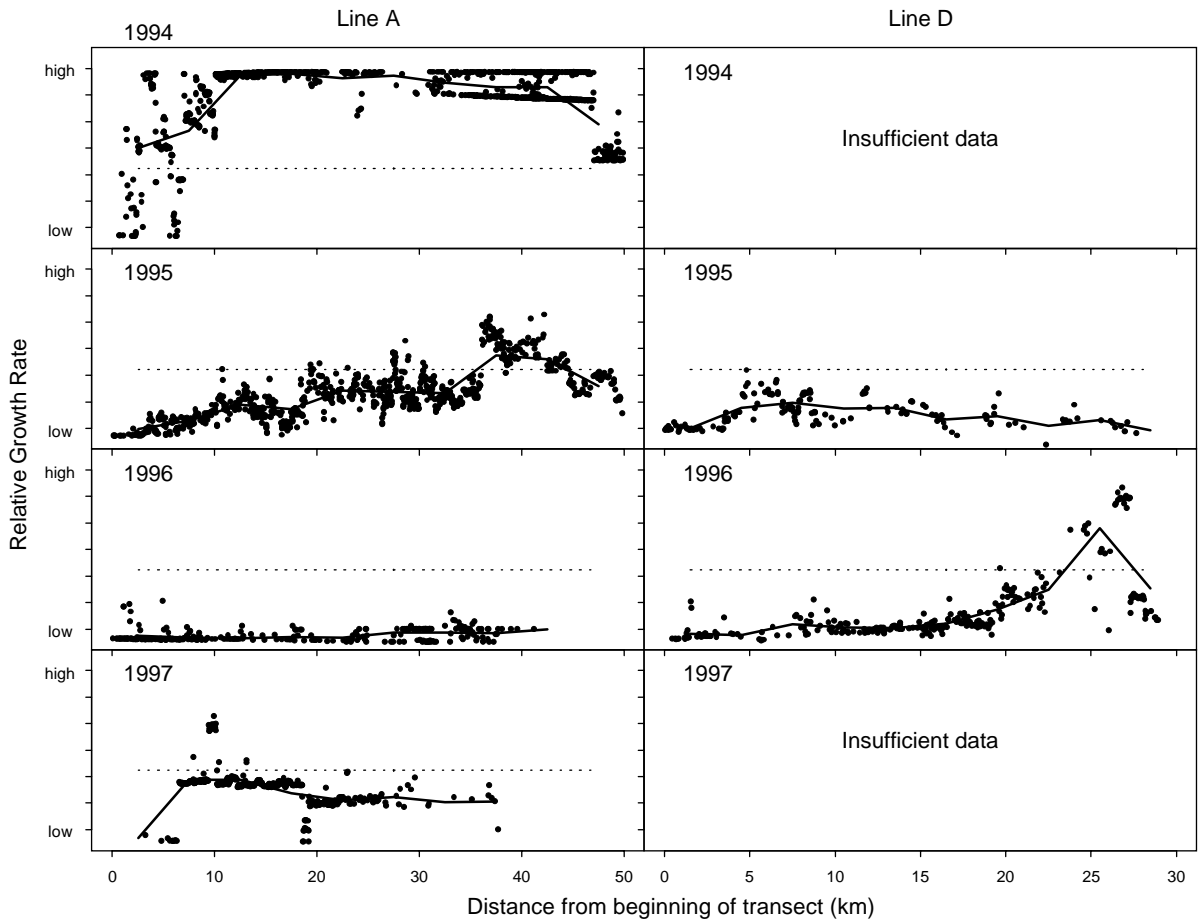


Fig. 7. Estimated age-0 pollock growth averaged under each age-0 pollock school along Line A (left panel) and Line D (right panel). Solid line indicates running average each 2500 m distance bin on Line A, and 1500 m bin on Line D. Dashed line indicates gross average growth potential among all years and transects. Along Line D in 1994 and 1997 there were insufficient data to calculate ambient growth (see text).

Table 1  
Correlation indices (*R*) and probability values (*P*) of regressions between predicted age-0 pollock ambient growth and acoustic biomass along sampling transects A and D in 1994–97

Year	Line A		Line D	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
1994	0.57	0.008	—	—
1995	−0.43	0.057	0.23	0.352
1996	−0.21	0.444	−0.67	0.001
1997	0.63	0.016	—	—

Data points included in the regression analysis are average values obtained from 2500 m vertical bins along Line A and 1500 m vertical bins along Line D.

varied according to year and transects (Table 1). Correlation was not significant in 1996 along Line A and in 1995 along Line D. The correlation was significantly negative on Line D in 1996 and only marginally significantly negative on Line A in 1995, while it was significantly positive on Line A in both 1994 and 1996 (Table 1).

### 3.4. Groundfish distribution

Estimates of groundfish predator biomass changed according to habitat type, year and

Table 2

Combined arrowtooth flounder and adult pollock standardized catch ( $\text{kg ha}^{-3}$ ) from bottom trawls along Line A and D during 1994–97 surveys

Year		Line A			Line D		
		Inshore	Front	Offshore	Inshore	Front	Offshore
1994	CPUE	0.0	NA	NA	0.00	NA	7525.9
	<i>N</i>	1	—	—	1	—	4
	SE	—	—	—	—	—	4328.2
1995	CPUE	4.6	545.8	1931.6	NA	NA	1812.1
	<i>N</i>	2	2	2	—	—	5
	SE	1.2	217.7	154.7	—	—	319.0
1996	CPUE	0.0	97.9	698.8	NA	47.2	NA
	<i>N</i>	1	8	2	—	1	—
	SE	—	76.7	8.4	—	—	—
1997	CPUE	NA	NA	NA	NA	NA	977.7
	<i>N</i>	—	—	—	—	—	1
	SE	—	—	—	—	—	—

Sample size (*N*) and standard error of the catch (SE) are also included.

transect. Unfortunately, our sample size and coverage were neither sufficient nor balanced enough to sustain any statistical test on the groundfish catch data, thus results cannot be statistically validated. Moreover, the spatial resolution at which groundfish data were collected (hydrographic habitat) is lower than the resolution of acoustic zooplankton and fish data (patch and school) and therefore we can only infer regional-scale interactions between age-0 pollock and their predators. Nonetheless, several important trends emerged from the data on groundfish catches. First, within-line groundfish biomass tended to increase toward the offshore region. On Line A in 1995, for example, offshore groundfish biomass was 4 times higher than frontal biomass, which in turn was 10 times higher than inshore biomass (Table 2). There was also an indication of a similar inshore–offshore trend along Line D, but on trawls conducted during different years along different portions of the transect (Table 2). Second, groundfish biomass drastically changed from year-to-year; in 1995 on Line A, groundfish average biomass was up to 5 times higher than that observed in 1996 along the same line, and in 1994 in the offshore region of Line D, groundfish biomass was 4 times higher than in 1995.

## 4. Discussion

### 4.1. Hydrography

Hydrography of the water around the Pribilof Islands was substantially different in only one of the 4 years of this study, i.e. 1995 (Fig. 2). During the winter of 1995, sea ice was present near St. Paul Island for 10 weeks, and retreated only in late April. This caused an extensive cooling of the bottom layer—cooling that persisted through the summer and resulted in a relatively sharp pycnocline. The sharp density gradient observed in 1995 also resulted in a greater differentiation of the inshore mixed region from the offshore-stratified region and in a shallow thermocline. In all other years, the water column overall was warmer and differentiation between bottom and top layers was weaker (Stabeno et al., 1999).

### 4.2. Processes on Line A

Correlation analysis between fish density distribution and fish growth potential seems to explain only part of the interannual variability in age-0 pollock distribution along A. We found two instances of positive correlation—in 1994 and 1997—which suggests that in these 2 years, age-0

pollock distribution was affected by their potential for growth. However, no significant correlation was found in 1996 while an indication of negative correlation was found in 1995. We suggest that the absence of correlation along Line A in 1996 was a consequence of the exceptionally low zooplankton abundance encountered during this year; most of the fish schools were exposed to areas with no food and thus were experiencing equally low potential for growth. In such a scenario where many patches have similar low values of growth potential, it is unlikely that a correlation analysis would be significant.

Particular attention should be devoted to year 1995, when there was an indication of negative correlation between age-0 pollock density and their potential growth along Line A. During 1995, most of the zooplankton was in the offshore region of Line A, while most of the age-0 pollock were in the inshore region (Fig. 6). The question is what prevented age-0 pollock from moving to the offshore region, where there appears to be plentiful food and high potential for growth?

We believe that age-0 pollock in 1995 might have been excluded from the offshore region due to high predation risk or mortality, and forced to remain at higher density in the inshore region in spite of sub-optimal growth conditions. We favor the predation hypothesis based on the following three lines of evidence. First, adult pollock and arrowtooth flounder biomass was extremely high in offshore region of Line A in 1995; offshore biomass in 1995 was 3 times higher than in 1996 (Table 2). Adult pollock are a cold-adapted species and during summer are usually confined to water of less than 5°C, which explains their higher abundance in the outer shelf during 1995. Second, adult pollock and arrowtooth flounder are voracious predators upon age-0 pollock. From a field study (Lang et al., 2000) done during 1995 and 1996 on Line A, age-0 pollock comprised 40–80% of adult pollock diet and 60–80% of arrowtooth flounder diet by weight. Third, in 1995 the divergence between age-0 pollock distribution and their potential for growth occurred only in areas where groundfish predator density was high. For example, on Line A within the inshore region where groundfish predation risk was considerably

lower than elsewhere, age-0 pollock occupied areas of highest possible potential for growth. This is evidenced by a high positive correlation between fish biomass and fish growth potential in the first 18 km of the transect ( $R = 0.9, P = 0.002$ ). Age-0 pollock biomass and fish growth potential started to diverge beyond 18 km (compare Figs. 6 and 7)—the location at which cooler offshore waters infiltrated inshore waters (Stabeno et al., 1999) and groundfish catches started to increase (Table 2).

One might argue that if age-0 pollock remained in the top layer, as they did in 1995 but only in small numbers, they would avoid groundfish predation. In fact, since the top layer in 1995 was extremely shallow and easily saturated, the predation avoidance hypothesis may explain the observed lack of fish diel vertical migration during this year and location (Table 3). However, such a strategy should meet with only limited success since restriction of occurrence to only the shallow surface waters would result in high predation risk from seabirds, which are abundant in the area and generally forage in the upper water column (Hunt et al., 1996; Swartzman and Hunt, 2000).

It is difficult to determine whether low age-0 pollock densities observed on offshore Line A in 1995 were a consequence of direct habitat avoidance or increased predation mortality. However, it is not uncommon that fish reside in high numbers in areas of sub-optimal growth conditions. Predation is one of the principal factors involved in explaining avoidance of energetically favorable habitats (see Sogard, 1994, for a review). Specifically for walleye pollock, juveniles do not vertically migrate to bottom cold waters in the presence of high adult pollock density (Bailey, 1989), thus reducing their potential to grow faster via behavioral thermoregulation (Sogard and Olla, 1996; Ciannelli et al., 1998).

#### 4.3. Processes on Line D

In all years, we found higher age-0 pollock biomass on Line A than on Line D, in spite of similar and occasionally higher (1996) zooplankton acoustic biomass (Fig. 6) and estimated fish growth potential of Line D (Fig. 7). It is possible that age-0 pollock were constantly advected from

Table 3

Age-0 pollock (fish) and zooplankton (zoop) mean depths during 1994–1999, for each transect and habitat for both day (D) and night (N)

Year	Time of day	Line A						Line D			
		Inshore		Front		Offshore		Shelf		Slope	
		Fish	Zoop	Fish	Zoop	Fish	Zoop	Fish	Zoop	Fish	Zoop
1994	N	21	29	21	29	25	40	NA	NA	NA	NA
	D	24	31	31	41	45	54	NA	NA	NA	NA
1995	N	20	28	24	23	23	26	35	38	24	34
	D	33	34	33	47	23	62	41	87	39	35
1996	N	23	26	33	48	36	59	28	40	37	98
	D	30	43	36	35	35	41	54	73	61	142
1997	N	22	18	30	47	28	55	NA	NA	NA	NA
	D	35	42	45	44	44	42	NA	NA	NA	NA

Mean depths were derived from hydroacoustic data. NA signifies that there were not sufficient data to derive a diel fish or zooplankton mean depth.

Line D as a result of strong unidirectional geostrophic flow across most of this transect (Fig. 5). While at any given time measured standing biomass was low, actual biomass of fish passing through the system could have been substantially higher. Zooplankton may have been able to minimize advection by vertically migrating to depths where flow was slower. In all years considered, as well as in 1998 and 1999, daytime zooplankton patches were considerably deeper than fish schools (Table 3), often reaching depths greater than 120 m where potential geostrophic advection is drastically reduced (Fig. 5).

We did not find a positive correlation between fish acoustic biomass and growth potential along Line D. To increase their potential for growth on this transect, fish should have resided in the offshore region where higher zooplankton density was usually found and where we estimated the highest potential for fish growth (Fig. 7). However, in estimating potential growth, we assumed that zooplankton were equally available to fish throughout the whole depth of the transect. While this assumption was met on Line A where fish and zooplankton often overlapped due to the shallow bathymetry, it was not satisfied on Line D, where the bottom was deeper and where zooplankton

could remain below fish. For example, both fish and zooplankton were actively migrating along the offshore portion of D in 1996, but at their closest proximity, peak zooplankton abundance was still deeper than fish peak abundance by at least 60 m (Table 3). Thus, in 1996, the high zooplankton biomass of the offshore region was probably unavailable to age-0 pollock, making growth potential for the area lower than was estimated. This hypothesis is supported by the low body condition of the offshore fish and by the low percentage of euphausiids represented in their diet (16.75%) compared to fish found inshore (85.33%) or at the front (43.97%) (Brodeur et al., 2002). However, euphausiids were scarcely represented in midwater samples collected in the same year and transect (Brodeur et al., 2003), which could also explain the relatively low percentage of euphausiids found in age-0 pollock diet.

Similar processes might have also occurred along Line D in 1995 in that prey were more readily available to fish residing over the shelf area than to offshore fish, although to a lesser degree than in 1996. During 1995, peak zooplankton and fish abundance were separated by 5–10 m (Table 3), thus increased their vertical spatial overlap with respect to the 1996 scenario.

Euphausiids in 1995 were well represented in the diet of offshore fish (76.4%). The better accessibility of prey items in the offshore region during 1995 also might explain the higher abundance of age-0 pollock found in this region compared to previous years (Fig. 2).

#### 4.4. Summary

In this study, we found a lack of consistent age-0 pollock habitat association across years and among transects, similar to that found by Brodeur et al. (2002). This suggests that different factors intervene in regulating age-0 pollock distribution north and south of the islands and that the relative importance of various factors may vary between years.

We propose that on Line A, groundfish predation has a primary role in setting age-0 pollock distribution, due to the shallow bathymetry that co-locates predators and prey. Groundfish predator distribution may be mainly affected by water column hydrography: in cold years, such as in 1995, the extent of viable groundfish habitat is increased. Increased incursion of groundfish predators into shallower areas reduces the extent of juvenile pollock habitat. In contrast, during warm water years when groundfish predator density is reduced north of the islands, age-0 pollock are able to occupy areas of high growth potential, as they also do within areas for which groundfish predation threat is minimal, such as the inshore and frontal regions in 1995.

Our proposed mechanism for Line A was independently corroborated by a similar study on juvenile pollock distribution around the Pribilof Islands conducted by Evans (1992) during mid-August 1987–88. Evans found that habitat effect on juvenile pollock distribution along a transect line north of St. Paul (analogous to our Line A) was significant only in 1988. Moreover, it was found that the density of age-0 pollock in the middle zone of the transect was 5 times higher in 1988, than in the deeper zone, while in 1987 there was no significant difference in age-0 pollock density between the deep and middle zones. Hydrographic features measured along the same line and years indicated that 1988 was indeed a

colder year, and bottom offshore waters were on average 1.1°C colder than in 1987, corroborating our finding that in colder years juvenile pollock are forced closer to the island.

Along Line D, we propose that prey accessibility has the primary role in determining the distribution of juvenile pollock. Prey accessibility is affected by the extent of vertical spatial overlap between juvenile pollock and their prey. Vertical spatial overlap can be severely reduced in the offshore region of Line D due to the greater depth of the area, and to the fact that zooplankton are capable of much deeper migrations than fish, which are probably limited by predation or other factors such as physiological constraints.

Other potential processes, affecting age-0 pollock distribution, have not been considered in this study. For example, we have not considered the role of jellyfish in age-0 pollock distribution. Jellyfish constitute the bulk of the pelagic biomass around the Pribilof Islands (Schabetsberger et al., 2000; Brodeur et al., 2002) and age-0 pollock are often found in association with them (Brodeur, 1998). Medusae are known to feed on juvenile pollock and consume many of the same prey (Brodeur et al., 2002). Other potential age-0 pollock predators such as seabirds and marine mammals (Sinclair et al., 1994; Hunt et al., 1996; Swartzman and Hunt, 2000) have likewise not been included. Competition from other forage species might also play an important role in age-0 pollock distribution, especially in the slope area of Line D where bathylagid and myctophid fish are abundant (Sinclair and Stabeno, 2002). However in most areas, juvenile pollock comprised up to 95% of the water-column fish densities collected in trawls (Brodeur et al., 1997).

This study generates several new research questions. What is the prevailing mechanism (habitat avoidance versus predation mortality) that causes age-0 pollock low densities in areas at high groundfish predator abundance? How are prey density and production potential related to age-0 pollock foraging demand? Does this relation change in years in which age-0 pollock are hindered from reaching areas of high zooplankton density? And finally, what are the consequences of reduced prey accessibility on the capability of



juvenile pollock to grow and store enough energy to survive the upcoming winter season?

## Acknowledgements

We thank the crew and scientists aboard the R/V *Miller Freeman* and especially M. Wilson for assistance in collecting pollock and physical, acoustic and biological data. We thank Art Kendall for editing earlier drafts of this manuscript. Comments and editing provided by Méta Landys and two anonymous reviewers greatly improved structure and flow of this manuscript. This research was sponsored by the NOAA Coastal Ocean Program through the Bering Sea Fisheries Oceanography Coordinated Investigations (FOCI) and Southeast Bering Sea Carrying Capacity and is Contribution No. FOCI-S397. The Environmental Protection Agency and SEBSCC provided funding for the current meter moorings used to determine tidal currents.

## References

- Bailey, K.M., 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theragra chalcogramma* in the eastern Bering Sea, and cannibalism. *Marine Ecology Progress Series* 53, 205–213.
- Bailey, K.M., Brodeur, R.D., Hollowed, A.B., 1996. Cohort survival patterns of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska: a critical factor analysis. *Fisheries Oceanography* 5 (Suppl. 1), 179–188.
- Brandt, S.B., 1993. The effect of thermal fronts on fish growth: a bioenergetic evaluation of food and temperature. *Estuaries* 16, 142–159.
- Brandt, S.B., Mason, D.M., Patrick, V.E., 1992. Spatially explicit models of fish growth rate. *Fisheries* 17, 23–33.
- Brodeur, R.D., 1998. In situ observations of the associations between juvenile fishes and scyphomedusae in the Bering Sea. *Marine Ecology Progress Series* 163, 11–20.
- Brodeur, R.D., Wilson, M.T., 1996. A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fisheries Oceanography* 5 (Suppl. 1), 148–166.
- Brodeur, R.D., Wilson, M.T., 1999. Pre-recruit walleye pollock in the Eastern Bering Sea and Gulf of Alaska Ecosystems. *Proceedings of GLOBEC International Marine Science Symposium on Ecosystem Dynamics*, Tokyo, Japan, pp. 238–251.
- Brodeur, R.D., Wilson, M.T., Napp, J.M., Stabeno, P.J., Salo, S., 1997. Distribution of juvenile pollock relative to frontal structure near the Pribilof Islands, Bering Sea. In: *Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems*, Fairbanks, Alaska. Alaska Sea Grant Pub, AK-SG-97-01, pp. 573–589.
- Brodeur, R.D., Wilson, M.T., Ciannelli, L., 2000. Spatial and temporal variability in feeding and condition of age-0 walleye pollock (*Theragra chalcogramma*) in frontal regions of the Bering Sea. *ICES Journal of Marine Science* 57, 256–264.
- Brodeur, R.D., Sugisaki, H., Hunt, Jr., G.L. 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* 223, 89–103.
- Brodeur, R.D., Wilson, M.T., Ciannelli, L., Doyle, M., Napp, J.M., 2002. Interannual and regional variability in distribution and ecology of juvenile pollock and their prey in frontal structure of the Bering Sea. *Deep Sea Research II*, this issue (PII: S0967-0645(02)00333-8).
- Ciannelli, L. Effects of spatial variability, associated with a frontal structure, on predictions of age-0 pollock (*Theragra chalcogramma*) growth, around the Pribilof Islands, Bering Sea. *Estuarine, Coastal and Shelf Science*, in press.
- Ciannelli, L., Brodeur, R.D., Buckley, T.W., 1998. Development and application of a bioenergetics model for juvenile walleye pollock. *Journal of Fish Biology* 52, 879–898.
- Evans, S.A., 1992. Juvenile walleye pollock, *Theragra chalcogramma* (Pallas), size and abundance in relation to ocean temperatures near the Pribilof Islands, August 1987 and 1988. Master Thesis, University of Fairbanks, Alaska, 95pp.
- Flint, M.V., Sukhanova, I.N., Kopylov, A.I., Poyarkov, S.G., Whitley, T.E., Napp, J.M., 2002. Plankton mesoscale distributions and dynamics related to frontal regions in the Pribilof ecosystem, Bering Sea. *Deep Sea Research II*, this issue (PII: S0967-0645(02)00334-X).
- Franks, P.J.S., 1992. Sink or swim-accumulation of biomass at fronts. *Marine Ecology Progress Series* 82, 1–12.
- Gerristen, J., Strickler, R., 1976. Encounter probability and community structure in zooplankton: a mathematical model. *Journal of Fisheries Research Board Canada* 34, 73–82.
- Hunt, G.L. Jr., Kitaysky, A.S., Decker, M.B., Dragoo, D.E., Springer, A.M., 1996. Changes in the distribution and size of juvenile pollock, *Theragra chalcogramma*, as indicated by seabird diets at the Pribilof Islands and by bottom trawls surveys in the eastern Bering Sea, 1975–1993. In: Brodeur, R.D., Livingston, P.A., Loughlin, T.R., Hollowed, A.B. (Eds.), *Ecology of Juvenile Walleye Pollock*. NOAA Technical Report NMFS 126, pp. 57–59.
- Kowalik, Z., Stabeno, P., 1999. Trapped motion around the pribilof islands in the Bering Sea. *Journal of Geophysical Research* C11, 25667–25684.
- Lang, G.M., Brodeur, R.D., Napp, J.M., Schabetsberger, R., 2000. Variation in groundfish predation on juvenile walleye pollock relative to hydrographic structure near the Pribilof Islands, Alaska. *ICES Journal of Marine Science* 57, 265–271.

- LeFèvre, J., 1986. Aspects of the biology of frontal systems. *Advances in Marine Biology* 23, 169–233.
- Livingston, P.A., 1993. Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasii* in the eastern Bering Sea. *Marine Ecology Progress Series* 102, 205–215.
- Munk, P., 1993. Differential growth of larval sprat *Sprattus sprattus* across a tidal front in the eastern North Sea. *Marine Ecology Progress Series* 99, 17–27.
- Munk, P., Larsson, P.O., Danielssen, D.S., Moksness, E., 1999. Variability in the frontal zone formation and distribution of gadoids fish larvae at the shelf break in the northeastern North Sea. *Marine Ecology Progress Series* 177, 221–233.
- Schabetsberger, R., Brodeur, R.D., Ciannelli, L., Napp, J.M., Swartzman, G.L., 2000. Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near Pribilof Islands, Bering Sea. *ICES Journal of Marine Science* 57, 1283–1295.
- Sinclair, E.H., Stabeno, P.J., 2002. Mesopelagic nekton and associated physics of southeastern Bering Sea. *Deep Sea Research Part II*, this issue (PII: S0967-0645(02)00337-5).
- Sinclair, E.H., Loughlin, T., Percy, W., 1994. Prey selection by northern fur seal (*Callorhinus ursinus*) in the eastern Bering Sea. *Fisheries Bulletin*, US 92, 144–156.
- Sogard, M., 1994. Use of suboptimal foraging habitats by fishes: consequences to growth and survival. In: Stouder, D.J., Fresh, K.L., Feller, R.J. (Eds.) *The Belle W. Baruch Library in Marine Sciences (Eds.), Theory and Application of Fish Feeding Ecology*, Vol. 18, pp. 103–131. Columbia, SC.
- Sogard, S.M., Olla, B.L., 1996. Food deprivation affects vertical distribution and activity of a marine fish in a thermal gradient: potential energy-conserving mechanisms. *Marine Ecology Progress Series* 133, 43–55.
- Sournia, A., 1994. Pelagic biogeography and fronts. *Progress in Oceanography* 34, 109–120.
- Stabeno, P.J., Schumacher, J.D., Salo, S.A., Hunt, G.L., Flint, M., 1999. The physical environment around the Pribilof Islands. In: Loughlin, T.R., Ohtani K. (Eds.), *The Bering Sea: Physical, Chemical and Biological Dynamics*. Alaska Sea Grant Press, AK-SG-99-03, pp. 193–216. Fairbanks, AK.
- Swartzman, G., Hunt, G., 2000. Spatial association between murrelets (*Uria* spp), puffins (*Fratercula* spp) and fish shoals near the Pribilof Islands, Alaska. *Marine Ecology Progress Series* 206, 297–309.
- Swartzman, G., Brodeur, R.D., Napp, J.M., Walsh, D., Hewitt, R., Demer, D., Hunt, G., Logerwell, E., 1999a. Relating predator and prey spatial distributions in the Bering Sea using acoustic backscatter data. *Canadian Journal of Fisheries and Aquatic Science* 56 (Suppl. 1), 188–198.
- Swartzman, G., Brodeur, R.D., Napp, J.M., Hunt, G., Demer, D., Hewitt, R., 1999b. Spatial proximity of age-0 walleye pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska. *ICES Journal of Marine Science* 56, 545–560.
- Traynor, J.T., Smith, D., 1996. Summer distribution and relative abundance of age-0 walleye pollock in the Bering Sea. In: Brodeur, R.D., Livingston, P.A., Loughlin, T.R., Hollowed, A.B. (Eds.), *Ecology of Juvenile Walleye Pollock*. NOAA Technical Report NMFS 126, pp. 57–59.
- Wespestad, V.G., Fritz, L.W., Ingraham, J.I., Mergrey, B.A., 2000. On the relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye pollock (*Theragra chalcogramma*). *ICES Journal of Marine Science* 57, 272–278.
- Winberg, G.G., 1956. Rate of metabolism and food requirements of fishes. Belorussian University, Minsk, 253pp (Translated by Fisheries Research Board of Canada, Translation. No. 164, 1960).