



PERGAMON

Deep-Sea Research II 49 (2002) 6051–6067

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Interannual and regional variability in distribution and ecology of juvenile pollock and their prey in frontal structures of the Bering Sea

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Abstract

The distribution, size, length-specific weight, growth, and feeding of age-0 walleye pollock (*Theragra chalcogramma*) were examined along with their prey distribution patterns in two contrasting transects over a 4-year period (1994–1997) in relation to biophysical properties of frontal regions around the Pribilof Islands, Bering Sea. There were significant interannual differences in catch of age-0 pollock, but transect and habitat differences (inshore vs. front vs. offshore) were not significant for either catch or size of pollock. There were significant variations in length-specific weight and growth of pollock, but the trends were inconsistent. Copepods dominated the zooplankton biomass in all habitats and years; there were no consistent differences in the densities of the dominant zooplankton taxa among the habitats. There were, however, strong habitat and transect differences in juvenile pollock diet, particularly for the larger and presumably rarer prey taxa (euphausiids, chaetognaths, fish). We did not find any evidence that occupying a particular habitat was beneficial to young pollock, although other factors (e.g. bioenergetic advantage and predation refuge) that we did not examine here could have been more variable and critical to pollock survival. In a physically dynamic system such as the Pribilof Islands, age-0 pollock may need to continuously search for optimal conditions of high prey availability and low predation pressure.

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1. Introduction

Mesoscale hydrodynamic features such as fronts affect the distribution and productivity of planktonic organisms in many coastal systems (see

reviews by Denman and Powell, 1984; Daly and Smith, 1993). Frontal regions are generally productive relative to surrounding waters and concentrate planktonic organisms in a relatively restricted area (Franks, 1992; Perry et al., 1993; Olson et al., 1994; Longhurst, 1998). Early life stages of many marine fishes also concentrate in fronts (Govoni et al., 1989; Kingsford et al., 1991; Munk, 1993; Munk et al., 1995; Sabatés and Olivar, 1996; Lough and Manning, 2001), although the benefit to young fish in occupying

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these areas of enhanced prey concentrations is equivocal (Lochmann et al., 1997; Marchand et al., 1999).

The southeast Bering Sea shelf is a wide (> 600 km), productive continental shelf that is separated in spring and summer into three distinct hydrographic domains (Coachman, 1986; Schumacher and Stabeno, 1998). Each domain has its own unique biophysical characteristics and associated planktonic community (Cooney and Coyle, 1982; Vidal and Smith, 1986; Coyle et al., 1996). This shelf ecosystem is characterized by high primary productivity that responds rapidly to biophysical forcing to produce large amounts of organic matter that supply both planktonic and benthic food webs (Walsh and McRoy, 1986; Springer et al., 1996). Physical forcing plays a strong role in determining food availability for larval fish on the southeast Bering Sea shelf (Napp et al., 2000).

The waters surrounding the Pribilof Islands, at the outer edge of the shelf, offer a unique habitat in that they are the only location on the outer Bering Sea shelf shallow enough to allow tidal mixing throughout the water column. Previous studies have shown a strong interaction of tides and topography around these islands that produces strong shelf-sea tidal fronts completely surrounding St. Paul and St. George, the two main islands in the Pribilof Archipelago (Schumacher et al., 1979; Kinder et al., 1983; Stabeno et al., 1999). By virtue of the shoaling isobaths around these islands, a well-mixed, near island zone is separated from a two-layer regime by a narrow (10–20 km wide) tidal front (Stabeno et al., 1999). The front around the islands is analogous to the 1000-km-long inner front on the interior of the SE Bering Sea shelf (Kachel et al., 2002). In theory, these fronts should be regions of enhanced primary production where deep (below pycnocline) nutrients from the stratified offshore domain are upwelled into sunlit waters and enhance late summer primary production (Kachel et al., 2002; Hunt et al., 2002). This nearly continuous resupply of nutrients after the spring bloom is hypothesized to augment in situ secondary production and hence increase the prey available to higher trophic levels. These fronts exhibit elevated abundances of

phytoplankton, zooplankton, and micronekton (Coyle and Cooney, 1993), even against the background of high productivity of the eastern Bering Sea. This elevated biomass attracts many mobile predators such as seabirds to these frontal regions (Kinder et al., 1983; Coyle et al., 1992; Decker and Hunt, 1996; Hunt et al., 2002).

The research described here is part of a long-term study of distribution, growth, and survival of age-0 walleye pollock (*Theragra chalcogramma*) in nearshore frontal zones of the Pribilof Islands. Within these frontal regions are found high concentrations of age-0 pollock (Brodeur et al., 1997; Swartzman et al., 1999a; Schabetsberger et al., 2000). Concentrations of age-0 pollock also are found in and around the coastal inner front (Coyle and Pinchuk, 2002). The productive fronts around the Pribilof Islands may be late summer and fall nursery areas for fish spawned in spring in the southeastern Bering Sea; drifters deposited in larval pollock patches in this area were advected to and entrained within the local circulation around the Pribilof Islands by late summer (Stabeno et al., 1999). Previous summer and fall surveys on the large-scale shelf distribution of the juvenile pollock (Traynor and Smith, 1996; Brodeur and Wilson, 1999) indicated that high abundances may be found around these islands.

Juvenile walleye pollock are a nodal species in the food web and a major prey for many higher trophic level carnivores in the eastern Bering Sea (Springer, 1992; Livingston, 1993; Mito et al., 1999; Livingston and Jurado-Molina, 2000; Lang et al., 2000). The Pribilof Islands in particular, are a location where intense predation on juvenile pollock occurs due to large numbers of seabird and marine mammal breeding and rearing sites located on these islands (Kinder et al., 1983; Coyle et al., 1992; Springer, 1992; Sinclair et al., 1994). The high abundance of juvenile pollock around the Pribilof Islands suggests that the benefits of occupying this habitat outweigh the disadvantages of increased risk to predation.

This paper presents results from intensive, multidisciplinary late-summer sampling around these tidal fronts during four oceanographically contrasting years. We compare results from two transects that extend into different oceanographic

domains. The hydrological conditions and associated acoustically determined biomass distributions for these two frontal regions over the same period of time have been examined elsewhere (Stabeno et al., 1999; Ciannelli et al., 2002a). In this paper, we examine the corresponding biological conditions across these fronts, including zooplankton and micronekton, and discuss how changes in physics and biology in these habitats affect juvenile pollock growth and feeding.

2. Materials and methods

2.1. Field sampling

During September 1994 through 1997, we occupied transects extending northwest of St. Paul Island and south of St. George Island (Transects A and D, respectively, Fig. 1). Sampling occurred both day and night using mainly the NOAA research vessel *Miller Freeman*, although supplemental sampling took place aboard the NOAA research vessel *Surveyor* during 1994 and 1995. The vessels, separated by about 0.3–0.5 nm, conducted acoustic transect sampling (Swartzman

et al., 2003) and collected underway temperature, salinity and fluorescence data transecting at a ship speed of 14 km h^{-1} . Hydrographic stations were then occupied nominally 5 km apart along these transects, but were often more closely spaced in the nearshore frontal region. Conductivity-temperature-depth casts (SeaBird SBE-911+) were made from surface to near-bottom to delineate frontal position and structure.

The intent was to sample different habitats both at the fronts and to each side, so net sampling for zooplankton and nekton was done primarily at stations clustered inshore, at, and offshore of the front. Zooplankton was sampled with a 1-m^2 MOCNESS frame containing up to eight nets used to sample specific depth layers or was towed obliquely through the water column. The nets used to collect depth-stratified samples had mesh sizes of $500 \mu\text{m}$ (1994 and 1995) or $333 \mu\text{m}$ (1996 and 1997). The nets that were fished obliquely had mesh sizes of $153 \mu\text{m}$, and sampled from near-bottom to the surface (1994 and 1995), or from the bottom of the mixed layer to the surface (1997). Samples were preserved in a 5% buffered formalin/seawater solution for later analysis.

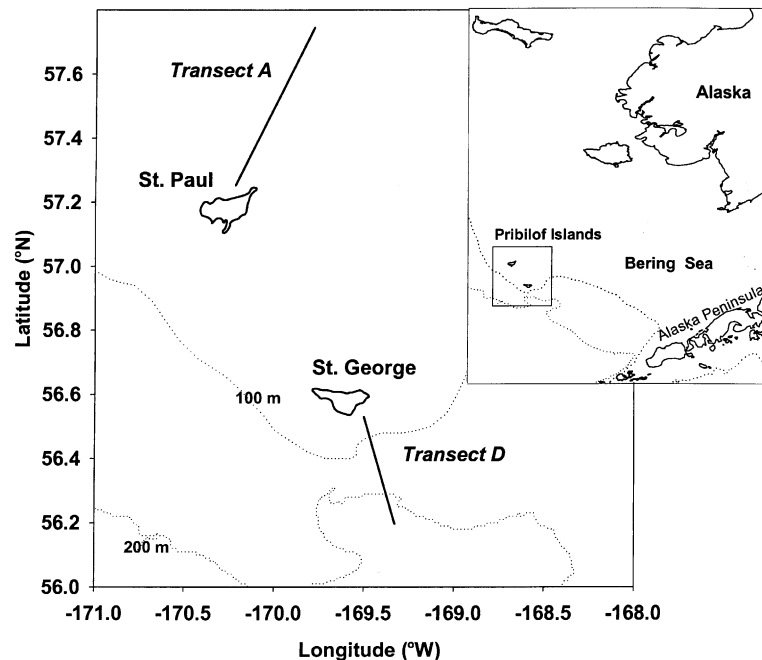


Fig. 1. Location of sampling area around Pribilof Islands, Bering Sea.

Fish sampling was done in midwater using a 140-m² anchovy trawl containing 3-mm mesh in the codend (Wilson et al., 1996). The net was fished to target vertical layers of acoustic scatterers believed to be age-0 pollock. Fifty-six tows were successfully completed. At sea, counts and weights were taken on each taxon collected in the anchovy trawl. Standard lengths of fresh juvenile pollock were measured on a subsample of up to 100 fish from each haul. Where caught, some age-0 pollock were preserved in 10% formalin for subsequent analysis of length-specific weight and diet, and others were frozen for otolith analysis.

2.2. Laboratory processing and data analysis

Habitat was the factor of primary interest in the analysis of age-0 pollock catch and size, but we recognized several other confounding effects (year, transect, and diel period). Inclusion of all effects in one statistical model was not possible due to a high number of empty cells. The diel effect was ignored because a day–night comparison within blocks created by unique combinations of year, transect, and habitat (blocked analysis of variance (ANOVA)) indicated no significant diel variation in fish density ($F = 0.315$, $P = 0.579$) nor mean length ($F = 0.171$, $P = 0.682$). Subsequent statistical analysis of catch and length data was restricted to Transect A due to a possible transect effect and paucity of data from Transect D. The length–frequency data were reduced to an average length per haul to avoid using a nested ANOVA design. The model examined was

$$\text{Catch or Length} = \text{constant} + \text{year} + \text{habitat} \\ + \text{year} \times \text{habitat} + \text{error}.$$

To evaluate possible differences in condition of age-0 pollock, we used an analysis of covariance (ANCOVA) to determine the significance of factor effects on the relationship between fish weight and standard length (Patterson, 1992). Somatic wet weight and length of fish preserved in 10% formalin were measured in the laboratory prior to processing gut contents. Both length and weight were log₁₀-transformed to linearize the relationship. A post hoc multiple comparison test, Fisher's least significant difference (LSD), was used to

detect which pairwise differences among effect levels were significant. A Bonferroni adjustment was used to maintain $\alpha = 0.05$. Transects were analyzed separately due to a transect effect on the year–habitat interaction, which was indicated by a significant three-way interaction in an ANCOVA using only data from 1995–97 ($F = 5.526$, $P \ll 0.001$), and due to a paucity of data along Transect D during 1994. Separation by transect eliminated comparability of line intercepts and adjusted least-squares means among transects, but it allowed more data to be included in the examination of the habitat effect on the length–weight relationship.

Stomach contents were examined for a subsample of fish from each habitat and transect to characterize the diets and relative feeding intensity (Brodeur et al., 2000). The effect of habitat on age-0 pollock diet was tested non-parametrically on both prey counts and prey weights. Prey items were grouped into the following categories: copepods, adult euphausiids, chaetognaths, and pteropods. However, in stomachs analysis after 1994, copepods were further differentiated to small (2 mm; *Pseudocalanus* spp., *Acartia* spp., *Oithona* spp.) and large (>2 mm; *Calanus marshallae*, *Neocalanus* spp.) copepodites. The statistical test, on the habitat effect, consisted of five sets of ANOVA done on ranks of prey items by weight and by number where

$$\text{Ranks of prey} = \text{constant} + \text{habitat} + \text{time of day} \\ + \text{size} + \text{all interactions} + \text{error}.$$

Because size of fish and time of day can affect age-0 pollock diet (Brodeur et al., 2000; Schabetsberger et al., 2000), we used ANOVA tests followed by Fisher's LSD pairwise comparisons to detect differences among various levels of interaction between habitat and time of day. Pairwise LSD P -values were altered using the Bonferroni adjustment; i.e., the LSD P -values were multiplied by the number of pairwise comparisons. To balance the model with respect to all of the included variables, only data from 1 year and one transect were included in the analysis (i.e., 1995 Transect A). A similar model also was used to test the effect of transect on age-0 pollock diet by weight and number, again using 1995 data only.

Feeding intensity was measured as percent of body weight of total gut content found in age-0 pollock stomachs ($\%BW = \text{sum of prey weight} / (\text{body weight} - \text{sum of prey weight}) \times 100$). A multi-factor ANOVA was used to detect differences among transect and habitat. The data were not normally distributed and required an arcsine transformation prior to analysis to achieve homogeneity of variances. In an earlier analysis on a smaller data set (Brodeur et al., 2000), it was found that there was no significant difference in feeding intensity by year so we combined all years together in this analysis. However, feeding periodicity does change as a function of fish size (> 51 mm pollock tend to be nocturnal feeders, while < 51 mm pollock tend to be diurnal feeders; Brodeur et al., 2000), so size category (small or large) of juvenile pollock was included in the model. Initial results showed that transect and all interactions involving it were highly significant (all $P < 0.01$), so we subsequently analyzed each transect separately. We performed Bonferroni post hoc pairwise comparisons to further detect differences among single cells included in the model.

Fish age was estimated from otolith microstructure in samples collected at 1–3 stations at each habitat location along Front A from 1994 to 1996. A random sub-sample of 35 frozen fish was removed from each station collection for otolith examination. Standard length (mm) was measured on these specimens and saggital otoliths were removed for processing. The right otolith from each pair was mounted, perpendicular to the saggital plane, on a glass slide with Hard Grade (LR White Resin (London Resin Co.)). Grinding was performed in the frontal plane to reveal the nucleus and, primary growth zone and daily growth increments. Otolith increment deposition is daily for larval and juvenile walleye pollock to at least 100 days, with a well-defined increment formed at hatching (Nishimura and Yamada, 1984; Bailey and Stehr, 1988). Counting of daily growth increments was performed on a Zeiss Compound microscope using transmitted light at $1000\times$ magnification under immersion oil. Three to five counts were carried out on each otolith section and a mean value was calculated and used as an estimate of age in days since hatching. Hatch

dates were computed by subtracting fish ages from sampling dates.

Length at age relationships, as an indication of growth, were investigated among locations and years by performing simple linear regressions using the statistical software SYSTAT 9.0 for Windows (SPSS Inc., Chicago, IL.). A multiple comparison test (Zar, 1984) was performed on each pair of years and locations to compare slopes of regression models, representing growth rates. To control the experiment-wise error rate for these multiple comparisons, a Bonferroni correction was performed. Given that our length and age data approximates normality, we ran an ANOVA testing for differences in location, within each year, for standard length and age of pollock. This was followed by a post hoc, Bonferroni, multiple pairwise comparison to test for significance.

3. Results

3.1. Abundance and size of pollock

Age-0 pollock comprise the bulk of the pelagic community of fishes sampled with this trawl. A total of 38 fish taxa were collected in the 56 anchovy hauls. Age-0 pollock were caught in the majority (90.7%) of these hauls; the next most common species, *Zaprora silenus*, occurred in only 23.7% of the tows. Pollock also dominated the catches in terms of number (99.3% of total catch) and biomass (92.7%).

There were no consistent differences in the catch or size composition of age-0 pollock associated with habitat within each year and transect (Fig. 2). Neither catch ($F = 0.286$, $P = 0.754$) nor mean length ($F = 0.286$, $P = 0.138$) of age-0 walleye pollock varied significantly by habitat along Transect A. The distribution of catch with respect to habitat changed among the years, but the habitat-year interaction was not significant for either catch ($F = 1.818$, $P = 0.138$) or size ($F = 0.933$, $P = 0.490$). The offshore region of Transect A had relatively few fish in 1994 and 1995 compared to the other regions (Fig. 2). In contrast, this region showed the highest concentrations of pollock in 1997, although relatively few fish were

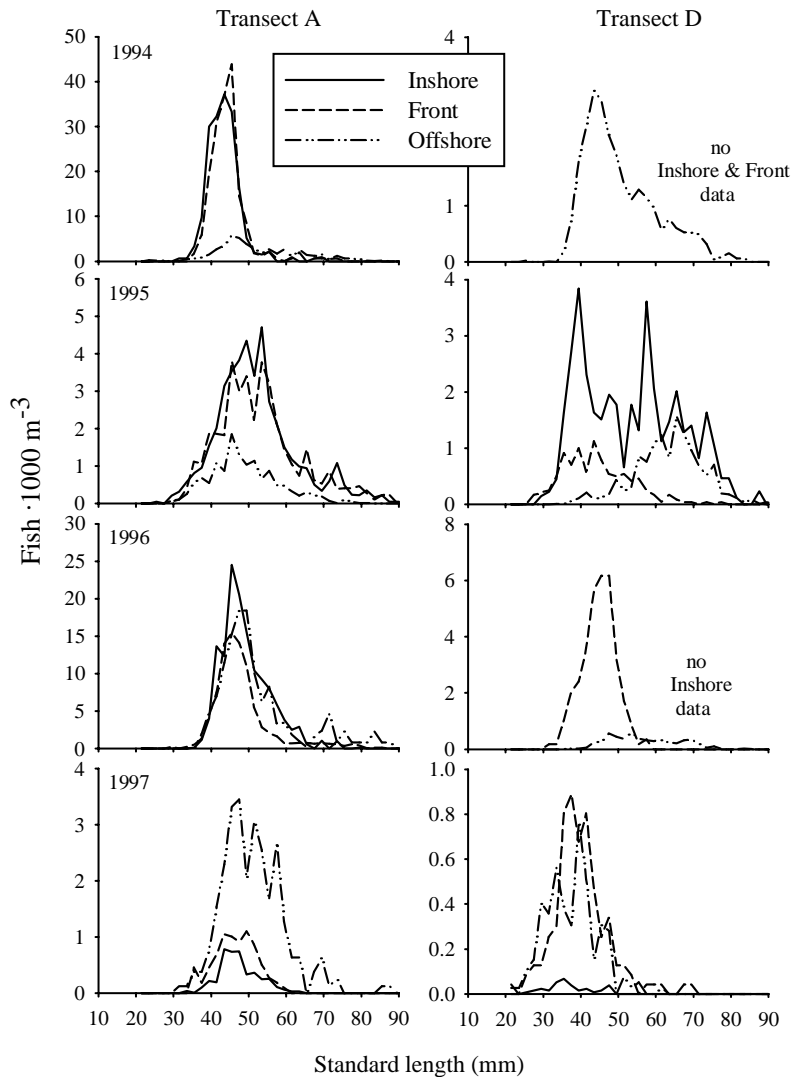


Fig. 2. Size composition, by year, habitat, and transect of age-0 walleye pollock collected in anchovy trawl hauls that targeted midwater echo layers near the Pribilof Islands, Bering Sea, 1994–97.

caught overall that year on either transect. The year effect was significant ($F = 7.732$, $P = 0.001$), with large catches during 1994 and 1996 relative to the other 2 years (Table 1). During 1994, mean fish size along Transect A was relatively small (Table 1; Fig. 2), and the year effect was marginally significant ($F = 3.095$, $P = 0.046$). At Transect D, the data were too sparse to examine statistically for differences in fish size, but in 1995 the size composition was strongly bimodal with fish at the front being small relative to those offshore. The

distribution was also bimodal in 1997 when fish were abundant at the front relative to offshore.

3.2. Length-specific weight

Although habitat was associated with some significant variation in the length-specific weight (intercept of length–weight relationship) of age-0 pollock (Table 2), overall there was no significant relationship between the length-specific weight or length–weight relationships by habitat. The

Table 1

Catch statistics for number of hauls and age-0 walleye pollock density and size collected in anchovy trawl hauls that targeted midwater echo layers near the Pribilof Islands, Bering Sea, by year and transect

Statistic	Transect	Year				All years
		1994	1995	1996	1997	
Number of hauls	A	6	14	12	4	36
	D	8	7	2	3	20
	Total	14	21	14	7	56
Average fish per 1000 m ³	A	132	33	103	11	70
	D	25	20	20	4	20
	Overall Mean	71	29	91	8	52
Average standard length (mm)	A	45.0	52.3	49.2	49.6	48.5
	D	50.6	56.5	46.4	38.9	52.0
	Overall Mean	46.2	53.3	49.1	47.6	48.9

ANCOVA for each transect revealed no differences in slope (length vs. weight), although line elevation did vary with year and habitat (Transect A: $F = 6.52$, $P \ll 0.001$; Transect D: $F = 29.13$, $P \ll 0.001$). Again, between-transect comparisons of intercepts and adjusted means is not valid since the data from each transect were analyzed separately. On Transect A, the 12 relevant pairwise comparisons from the post hoc LSD test indicated a significant habitat effect on the length–weight relation only during 1996 (Table 2). During 1996, the length-specific weight of individual fish collected in three hauls made at the front was lower than that from the other habitats. However, five of the eight trawl hauls at the front were comparable to those from other habitats. We could find no explanation why only those from three hauls had relatively low length-specific weights. On Transect D, the nine relevant pairwise comparisons indicated that habitat-related differences occurred every year. During 1995–96, individuals from the inner habitat had relatively high length-specific weights, but this was reversed in 1997.

3.3. Age, growth, and hatch date

The median hatch-date (where 50% of the population had hatched) occurred progressively earlier from 1994 (median date = 9 June) to 1995 (4 June) to 1996 (1 June), but the only significant difference (Kolmogorov–Smirnov Test, $P = 0.031$)

observed was between 1994 and 1996 (Fig. 3). Regressions of length on age (growth in mm per day) were significant for all year and area combinations, as were pooled yearly and area relationships (Table 3). The results of the ANOVA and post hoc Bonferroni pairwise comparison show that standard length and age of pollock was significantly different ($P < 0.05$) between locations in 7 out of 18 instances of pairing. For the 1994 data, both standard length and age were significantly higher offshore than in either the front or inshore samples. The only significant result for 1995 was that fish were older at the front than offshore. In 1996, fish at the front had a significantly greater standard length and age than inshore fish. The multiple comparison tests performed to compare growth in mm per day among locations, as represented by age–length regression slopes (Fig. 4), indicated that in 1994 and 1995 none of the slopes differed significantly, whereas in 1996, a slower growth rate was apparent at the inshore location.

3.4. Zooplankton distribution and age-0 pollock diet analysis

Small copepods (small adult copepods and the copepodite stages of larger species) dominated the available prey (by numbers) on both transects and in all habitats and years (Table 4). Pteropods, patchily distributed along transects, were often the

Table 2

Least-squares, standard length (SL mm)-somatic wet-weight (g) relationships, by transect, year, and habitat, for age-0 pollock collected near the Pribilof Islands, Bering Sea, during 1994–97

Year	Habitat	# fish	SL (mm)		Intercept a	Wet weight (g), Adj. least squares	
			min.	max.		Mean	SE
<i>Transect A: b = 3.148</i>							
1994	Inshore	31	36	74	−5.361	0.0591	0.00923
	Front	30	39	71	−5.343	0.0774	0.00934
	Offshore	30	40	79	−5.327	0.0926	0.00916
1995	Inshore	60	41	85	−5.384	0.0361	0.00655
	Front	60	41	88	−5.360	0.0597	0.00652
	Offshore	50	40	91	−5.362	0.0582	0.00714
1996	Inshore	30	37	77	−5.366 ¹	0.0541	0.00925
	Front	154	39	81	−5.413 ²	0.0067	0.00404
	Offshore	27	42	83	−5.358 ¹	0.0620	0.00976
1997	Inshore	15	37	64	−5.352	0.0683	0.01295
	Front	15	36	55	−5.351	0.0693	0.01306
	Offshore	15	38	73	−5.343	0.0774	0.01295
<i>Transect D: b = 3.100</i>							
1995	Inshore	29	37	91	−5.282 ¹	−0.0360	0.00679
	Front	15	34	79	−5.275 ¹	−0.0282	0.00945
	Offshore	44	47	84	−5.318 ²	−0.0716	0.00662
1996	Inshore	17	40	68	−5.228 ¹	0.0185	0.00887
	Front	23	35	55	−5.318 ²	−0.0720	0.00787
	Offshore	24	43	83	−5.331 ²	−0.0850	0.00783
1997	Inshore	15	31	48	−5.337 ¹	−0.0902	0.01025
	Front	15	35	65	−5.270 ²	−0.0241	0.00983
	Offshore	15	27	44	−5.272 ²	−0.0253	0.01061

Analysis of covariance indicated no within-transect variation in slope, thus only the intercepts are tabulated ($\log_{10}(g) = a + b(\log_{10}(\text{mm}))$). Transect D in 1994 was omitted due to insufficient data. Within each transect and year, intercepts with different superscripts are statistically different ($p \leq 0.05$).

second most abundant taxon, but far less abundant than small copepods. Large copepods and euphausiid adults and juveniles were relatively scarce. There was no consistent pattern in total number of available prey by habitat—i.e., numbers of prey potentially available for ingestion were not consistently higher in the front, as originally hypothesized. Total numbers of available prey by habitat were generally much lower on Transect D than on Transect A, the one exception being the inshore habitat in 1996.

Considering all measures of diet used, large and small copepods, pteropods, and adult euphausiids

were most important in the diets of age-0 pollock. Across all years and transects, pollock diet was numerically dominated (>85%) by small and large copepods and pteropods. Average diet by weight was dominated by large copepods and adult euphausiids ($\approx 70\%$ of stomach weight). In terms of frequency of occurrence (FO), adult euphausiids and large and small copepods were also highest, occurring, respectively, in 37% and 51% of all non-empty stomachs (Fig. 5). Minor prey items were chaetognaths and pteropods, composing 5.26% and 4.23% of total age-0 pollock diet by weight, respectively.

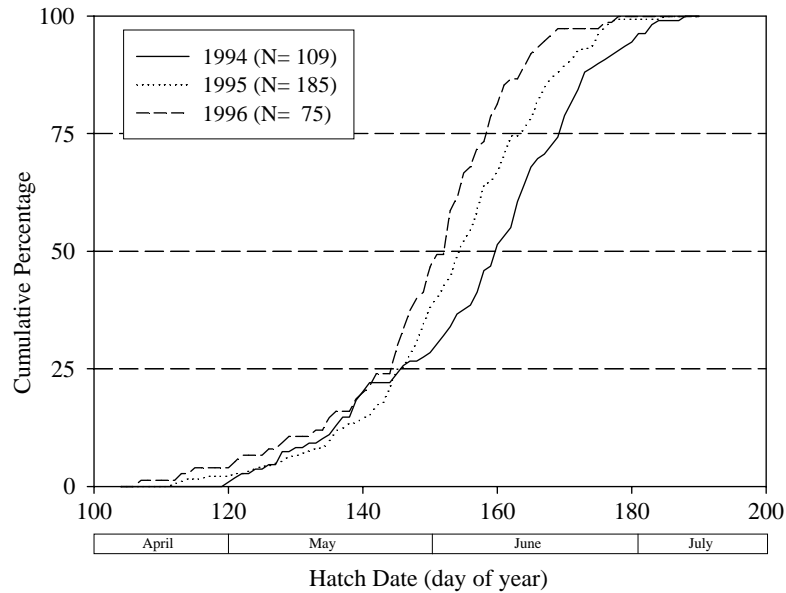


Fig. 3. Cumulative hatch date distributions of age-0 pollock by year for both transects combined.

Table 3

Linear regressions of standard length (SL in mm) on age (days since hatch) for all data subsets on Transect A

Data subset	Regression model	N	R ²
All years combined			
Inshore	SL = -0.946 + 0.491 (AGE)	76	0.587
Front	SL = -23.200 + 0.706 (AGE)	154	0.768
Offshore	SL = -12.365 + 0.631 (AGE)	139	0.624
All locations combined			
1994	SL = -13.558 + 0.605 (AGE)	109	0.758
1995	SL = -19.355 + 0.702 (AGE)	185	0.670
1996	SL = -18.093 + 0.649 (AGE)	75	0.754
1994			
Inshore	SL = -1.720 + 0.485 (AGE)	25	0.844
Front	SL = 5.916 + 0.413 (AGE)	31	0.482
Offshore	SL = -22.747 + 0.687 (AGE)	53	0.746
1995			
Inshore	SL = -8.311 + 0.595 (AGE)	28	0.569
Front	SL = -30.353 + 0.777 (AGE)	94	0.789
Offshore	SL = -20.138 + 0.753 (AGE)	63	0.726
1996			
Inshore	SL = 21.406 + 0.249 (AGE)	23	0.391
Front	SL = -18.136 + 0.655 (AGE)	29	0.807
Offshore	SL = -31.691 + 0.784 (AGE)	23	0.748

All regression slopes were significantly different from 0 ($p < 0.05$).

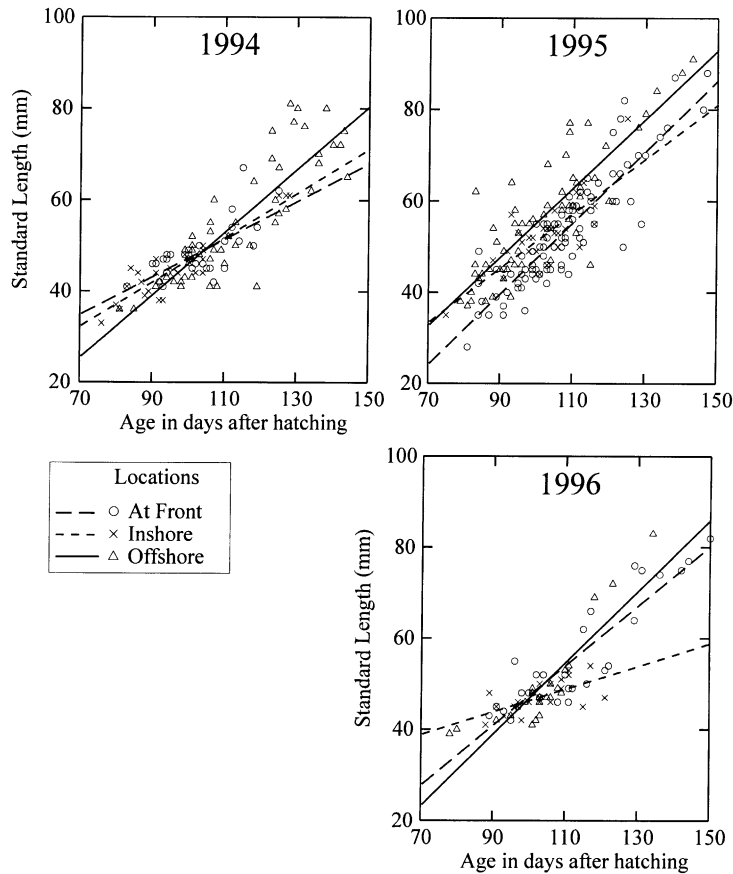


Fig. 4. Regressions of age vs. standard length for age-0 pollock by year and habitat for Transect A.

There was such high variability in age-0 pollock stomach contents when the data were partitioned by habitat type, transect and year (Table 5), that it was not possible to detect differences in diet among habitats as has been shown for other species. For example, adult euphausiids ranged from 0% (1994, Line A, inshore and front) to 92.68% (1997 Line A, front) in diet by weight. Fish were consumed (Table 5), but at a low FO (3.3–4.4%).

In 1995, there was a significant difference in the number of small copepods in the stomachs between the two transects ($F = 8.29$, $P < 0.0001$). In addition to small copepods ($F = 3.91$, $P = 0.02$), transect effect was significant in diet by weight for chaetognaths ($F = 12.52$, $P < 0.0001$), large copepods ($F = 36.54$,

$P < 0.0001$) and adult euphausiids ($F = 4.41$, $P = 0.013$). The habitat effect was particularly strong for minor prey items such as chaetognaths, pteropods and small copepods (Table 6). There were no statistically significant differences in ingestion of large copepods by habitat, and the only difference we detected in the ingestion of euphausiids occurred between front and offshore habitat during the night. In addition to habitat effect, the ingestion of small copepods also varied with time of day, both in the inshore and front habitat (Table 6).

3.5. Feeding intensity

For fish collected on Transect A, neither habitat nor size of fish alone was significantly related to

Table 4

Zooplankton catch composition, by habitat, year and transect, indicated as percent of total standardized catch by numbers

	Group	Transect A			Transect D		
		Inshore	Front	Offshore	Inshore	Front	Offshore
1994	Euphausiids juv. and ad.	1.29	1.26	0.54	—	—	0.05
	Large copepods	0.09	0.13	1.41	—	—	8.91
	Small copepods	88.95	83.27	84.94	—	—	82.76
	Chaetognaths	3.21	7.64	4.86	—	—	0.61
	Pteropods	0.00	0.00	0.00	—	—	1.98
	Other crustacea	0.05	1.58	0.27	—	—	0.00
	<i>N</i>	1	1	1	—	—	1
	Total number	172.42	310.77	484.93	—	—	157.62
1995	Euphausiids juv. and ad.	0.77	0.82	0.05	—	—	1.23
	Large copepods	0.04	0.62	6.22	—	—	7.75
	Small copepods	68.42	62.71	82.57	—	—	74.67
	Chaetognaths	2.29	2.64	0.73	—	—	0.28
	Pteropods	3.37	18.79	9.86	—	—	15.78
	Other crustacea	1.63	1.71	0.28	—	—	0.17
	<i>N</i>	2	4	1	—	—	1
	Total number	306.46	440.80	381.13	—	—	151.16
1996	Euphausiids juv. and ad.	—	0.65	1.28	3.88	0.00	0.00
	Large copepods	—	0.12	0.47	0.04	1.60	1.62
	Small copepods	—	94.37	89.19	82.88	97.51	89.10
	Chaetognaths	—	0.56	0.94	0.91	0.00	1.11
	Pteropods	—	0.81	3.75	2.28	0.00	3.34
	Other crustacea	—	2.42	0.94	0.68	0.00	0.02
	<i>N</i>	—	3	1	1	1	1
	Total number	—	468.16	893.07	799.89	155.96	171.60
1997	Euphausiids juv. and ad.	0.21	0.03	0.15	—	0.15	0.40
	Large copepods	0.29	0.21	0.32	—	1.91	2.40
	Small copepods	91.56	90.91	88.68	—	72.04	79.81
	Chaetognaths	0.71	0.54	0.72	—	0.68	1.37
	Pteropods	5.97	6.98	8.72	—	21.88	13.04
	Other crustacea	1.20	0.31	0.82	—	0.59	0.80
	<i>N</i>	2	1	1	—	1	1
	Total number	217.22	416.17	394.78	—	296.69	165.45

Only main age-0 pollock prey items are reported. Other Crustaceans include ostracods, crab larvae and cumaceans. Sample sizes (*N*) and standardized catch (1000 individuals m⁻²) also are included.

stomach fullness. Time of day was a significant ($F = 1.235$; $P = 0.021$) factor, however, with day stomachs containing more food than night stomachs. The interaction between time and habitat was highly significant ($F = 1.934$; $P < 0.001$); based on pairwise post hoc Bonferroni tests, stomach collections from inshore day had significantly more food than inshore night collections while the reverse was true for the offshore samples.

Both daytime and nighttime stomach fullness in the frontal region was intermediate to that in the other habitats. For Transect D, the size of the fish was the only factor that showed significant differences ($F = 2.769$; $P = 0.003$) in stomach fullness, with larger fish having higher feeding intensity than small fish. Habitat again was not related to feeding intensity ($F = 0.628$; $P = 0.139$) on Transect D.

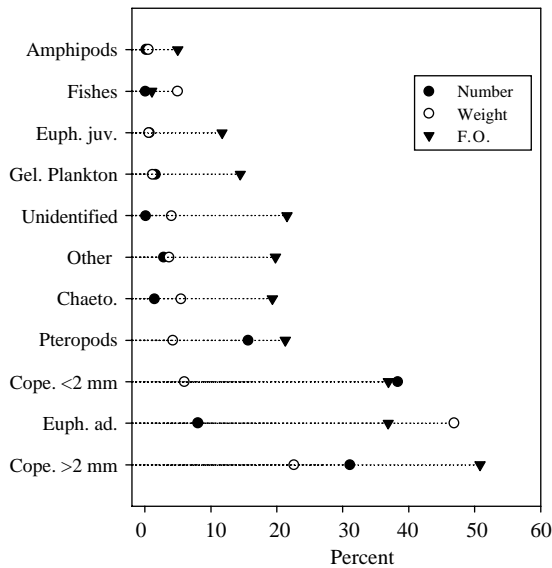


Fig. 5. Percentages of number, weight and FO of principal prey categories of age-0 walleye pollock for all years and transects combined.

4. Discussion

This study is the first to examine the distribution of age-0 pollock around the Pribilof Islands at this time of year using gear sufficient to capture a wide size range of juvenile fish. A previous study (Evans, 1992) examined interannual and inshore-offshore differences in catch and size of age-0 pollock along transects extending in all directions from both main islands. However, she used a much smaller 2-m² Tucker trawl a month earlier (in August) and thus caught a much smaller mean size of pollock than we did. Also, her study was not specifically designed to examine the frontal habitat. However, she did find that young pollock abundance was five times higher in a cold year (1988) than during a warm year (1987). Similarly, our age-0 abundance estimates were also highest during relatively cool years (1994 and 1996), as indicated by sea-surface temperature. Low surface temperature corresponded to a relatively deep mixed layer during these years (Stabeno et al., 1999; Ciannelli et al., 2002a).

A number of factors can contribute to the variability in catches of juvenile pollock in trawl sampling. Diel and ontogenetic differences in

vertical distribution and aggregation patterns (Bailey, 1989; Brodeur and Wilson, 1996; Schabetsberger et al., 2000) may affect pollock catchability and confound trawl results. Also, an apparent commensal association of larger age-0 pollock with large cnidarians may provide shelter for juveniles during the day, but also modify their vertical distribution and aggregation patterns in response to the distribution of their hosts (Brodeur, 1998). Some of these problems may be addressed by supplementing trawl data with acoustic backscatter information; this can also reveal finer spatial patterns than are otherwise available (Swartzman et al., 1999b). Based on our anchovy and other trawl sampling (Brodeur et al., 1997; Schabetsberger et al., 2000), the vast majority of small fish scatterers were walleye pollock juveniles.

Age-0 pollock did not appear to preferentially select a particular prey group. The composition of all age-0 diets was similar (small copepods > large copepods > pteropods > euphausiids) to the zooplankton numerical composition in the MOCNESS catches, and presumably in the environment. However, chaetognaths are poorly represented in diet relative to the plankton collections. Prey selection was demonstrated at a single location on Transect A sampled multiple times over a diel period during 1996 (Schabetsberger et al., 2000), when prey size increased with fish size. This fish-prey size relationship probably reflects an increase in prey capture efficiency and an increase in the caloric content per unit prey. Unfortunately, due to sampling limitations, we could not examine this relationship independent of year, transect, and habitat. Diel variation is another possible confounding effect due to vertically migrating prey, particularly the large-sized prey (copepods *Calanus marshallae* and *Metridia pacifica*, euphausiids *Thysanoessa* spp., and chaetognaths), which increased the availability of prey in surface waters at night (Schabetsberger et al., 2000). However, we found no evidence of diel variation in the consumption of prey by age-0 pollock.

One possible reason why our between habitat comparisons were highly variable may lie in the highly contrasting oceanographic conditions

Table 5

Age-0 pollock diet composition, by habitat, year and transect, indicated as percent of total stomach content weight

	Group	Transect A			Transect D		
		Inshore	Front	Offshore	Inshore	Front	Offshore
1994	Euphausiid juv. and ad.	0.00	0.00	34.68	—	—	67.65
	Copepods	47.34	18.24	32.77	—	—	21.70
	Chaetognaths	2.90	8.56	2.01	—	—	0.00
	Fish	0.00	50.68	5.70	—	—	0.00
	Pteropods	2.90	1.13	0.45	—	—	5.44
	Other crustacea	20.77	14.41	17.45	—	—	0.70
	<i>N</i>	31	30	30	—	—	140
	SL	45.42	46.10	55.60	—	—	50.48
1995	Euphausiid juv. and ad.	21.30	56.66	5.36	2.74	10.48	76.40
	Copepods	16.37	25.50	69.39	71.70	54.52	11.79
	Chaetognaths	6.13	10.30	2.96	25.23	0.00	0.21
	Fish	42.96	0.00	8.46	0.00	1.17	0.00
	Pteropods	0.82	3.61	5.36	0.00	25.83	3.09
	Other crustacea	2.94	0.52	1.69	0.00	0.00	2.87
	<i>N</i>	60	60	50	30	15	46
	SL	57.80	56.80	56.90	51.67	48.93	63.07
1996	Euphausiid juv. and ad.	71.81	40.10	76.59	85.33	43.97	16.75
	Copepods	8.76	27.27	12.87	2.31	38.31	79.07
	Chaetognaths	16.29	18.02	0.00	1.18	0.00	3.86
	Fish	0.00	0.16	0.00	0.00	0.00	0.00
	Pteropods	0.00	0.16	0.00	0.02	0.01	0.00
	Other crustacea	0.13	1.38	4.27	0.05	0.09	0.00
	<i>N</i>	30	154	28	17	23	24
	SL	48.30	53.23	60.04	49.88	43.61	58.12
1997	Euphausiid juv. and ad.	67.98	92.68	54.25	75.70	42.09	88.67
	Copepods	0.19	6.10	21.85	11.95	41.94	8.93
	Chaetognaths	0.00	0.00	18.12	0.00	4.44	0.00
	Fish	0.00	0.00	0.00	0.00	0.00	0.00
	Pteropods	31.44	1.22	0.00	8.28	1.91	1.50
	Other crustacea	0.00	0.00	2.41	4.06	5.79	0.90
	<i>N</i>	15	15	15	15	15	15
	SL	51.93	46.40	55.40	38.33	41.67	36.33

Only main prey items of non-empty stomachs are reported. Other Crustacea include ostracods, decapod crab larvae, and cumaceans. Sample sizes (*N*) and standard length (SL) in mm of examined fish also are included.

observed during our study period. In particular, 1997 often showed a markedly different pattern than the other years. For example, there were much higher densities of pollock offshore than inshore of the front, the fish were generally smaller in size (especially maximum size), and the diet contained a higher proportion of euphausiids, particularly offshore on Transect D. The frontal region was anomalously wide (> 30 km compared to only 12 km in 1996) and the mixed layer was

relatively deeper that year (Stabeno et al., 1999). The southeastern Bering Sea shelf was extensively sampled during the summer of 1997 due, in part, to anomalous weather patterns and the unusual occurrence of a massive coccolithophore bloom (Baduini et al., 2001; Napp and Hunt, 2001; Overland et al., 2001; Stabeno et al., 2001; Stockwell et al., 2001). Transport was apparently anomalous, and there were indications that large numbers of oceanic euphausiids were advected

Table 6

P-values of adjusted least-square means based on ranks of prey counts and weights found in age-0 pollock stomachs collected along Transect A during 1995

	Day vs. Night			Daytime among habitats			Nighttime among habitats		
	ID vs. IN	FD vs. FN	OD vs. ON	ID vs. FD	ID vs. OD	FD vs. OD	IN vs. FN	IN vs. ON	FN vs. ON
<i>Weights</i>									
Chaetognaths	ns	<0.0001	ns	ns	ns	ns	0.027	ns	0.009
Large Copepods	ns	ns	ns	ns	ns	ns	ns	ns	ns
Small Copepods	0.099	<0.0001	ns	ns	0.027	0.063	ns	ns	ns
Euphausiid juv. and ad.	ns	ns	ns	ns	ns	ns	0.081	ns	0.036
Pteropods	ns	<0.0001	ns	ns	ns	ns	<0.0001	<0.0001	ns
<i>Numbers</i>									
Chaetognaths	ns	<0.0001	ns	ns	ns	ns	0.036	ns	0.018
Large copepods	ns	ns	ns	ns	ns	ns	ns	ns	ns
Small copepods	0.010	<0.0001	ns	ns	0.018	0.072	ns	ns	ns
Euphausiid juv. and ad.	ns	ns	ns	ns	ns	ns	0.081	ns	0.036
Pteropods	ns	<0.0001	ns	ns	ns	ns	<0.0001	<0.0001	ns

I = Inshore, F = Front, O = Offshore, D = Day, N = Night. "ns" = $P > 0.05$.

onto the shelf in the vicinity of Pribilof Canyon (offshore part of Transect D) that September (Stockwell et al., 2001). Coyle and Pinchuk (2002) also documented unusual transport of juvenile pollock to the northern part of the Eastern Bering Sea shelf, which may explain their low abundance in their usual nursery area around the Pribilof Islands.

The primary data set to which we can compare our growth results is that of Nishimura et al. (1996; unpublished data), which was collected mainly on the Southeast Bering Sea shelf 1989–91 and 1994. They found substantially higher size-at-age for pollock collected in the early 1990s than we found, although their 1994 data were similar to our 1994 fish. Moreover, their hatch date distributions were skewed toward earlier median hatch dates (early to mid-May) than we found. This suggests either that there was a higher mortality of the early spawning fish in our samples or that our fish represented a later spawning cohort, perhaps fish spawned near the Pribilof Islands rather than closer to the Alaska Peninsula (Napp et al., 2000). As indicated from drogue deployments in various areas of the Southeast Bering Sea, offspring of both spawning groups are likely to end up near the Pribilof Islands due to the prevailing circulation on the shelf (Stabeno et al., 1999).

Trawl sampling indicates that high age-0 pollock densities are not restricted to a specific habitat. This contrasts with the distribution of their prey, which tends to be densest offshore of the frontal region (Brodeur et al., 1997). Our data do not provide any insight as to how juvenile fish normally would be transported to, or maintained within, frontal regions. The movement may be active with fish locating higher prey concentrations and maintaining their position with such aggregations. Our sampling was not adequate to detect such aggregations, although spatial and temporal variations in zooplankton abundance make such fine-scale patterns difficult to distinguish with conventional net sampling. Alternatively, the fish may be passively transported and concentrated in these regions by currents. Although such a direct effect may be a plausible explanation for early larval stages, the juveniles that we examined are likely not strongly affected by the weak cross-shelf flows in this area. In contrast, along-shelf flows are quite vigorous, especially tidal circulation inshore on Transect A and geostrophic flow offshore on Transect D in the Bering Slope Current. Ciannelli et al. (2002a) computed geostrophic velocities up to 15.5 km d^{-1} on Transect D and that juvenile pollock in this region would be as susceptible to advection as zooplankton since they

remain in surface waters throughout the diel period.

Regardless of the mechanism that transports larval and juvenile pollock to the region around the Pribilof Islands, the ultimate question is whether individuals at the front have a better survival potential than others located either inshore or offshore of the front. Our empirical results based on a multi-year field study do not support the current theory that frontal regions are beneficial to juvenile fishes. There were no consistent patterns in the condition of juveniles with respect to habitat. Ciannelli et al. (2002b) did find that the energy density (KJ g^{-1}) was significantly higher in juvenile pollock caught in the offshore habitat than inshore, but no differences in energy content were observed between the offshore and frontal habitats. Perhaps a more sensitive indicator of recent growth history such as lipid biomarkers or RNA/DNA (Ferron and Leggett, 1994) could be used to examine the hypothesis that juveniles are in better condition in the fronts. Our stomach fullness data, which may represent a response over a 3–4 h period prior to capture, do not suggest that fish sampled at the front were encountering better feeding conditions than those caught in other habitats. Complications arising from diel and ontogenetic variations in feeding intensity (Brodeur et al., 2000), however, make such comparisons tenuous. We suspect, however, that juveniles actively migrate between the habitats over relatively short time scales, so any advantage to an individual being in the front is not evident when sampling a well-mixed population as a whole (see also Lochmann et al., 1997). Moreover, observed aggregations of mobile predators at these fronts (Kinder et al., 1983; Coyle et al., 1992; Decker and Hunt, 1996) imply higher predation risk, which would obviate any differential feeding and growth benefits accrued to individual fish.

In summary, we did not find any evidence that occupying a particular habitat was beneficial to young pollock, although other factors (e.g. bioenergetic advantage and predation refuge) that we did not examine here could have been more variable and critical to pollock survival (Ciannelli et al., 2002a). In a physically dynamic system such as the Pribilof Islands, age-0 juvenile pollock may

need to continuously search for optimal environmental conditions, high prey availability, and low predation potential in order to survive.

Acknowledgements

We thank the officers, crew and scientists aboard the research vessels for their assistance in making the collections used in this study. Kathy Mier and Susan Picquelle assisted in the statistical analysis. Our manuscript benefited from comments by Art Kendall and an anonymous reviewer. This research was sponsored in part by the NOAA Coastal Ocean Program through the Southeast Bering Sea Carrying Capacity program and is FOCI Contribution No. S396.

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