Abstract—Nurseries play an important part in the production of marine fishes. Determining the relative importance of different nurseries in maintaining the parental population, however, can be difficult. In the western Gulf of Alaska, the Kodiak Island vicinity may be particularly well suited as a pollock nursery because of a prey-rich nearshore environment. Our objectives were 1) to examine age-0 pollock body condition, growth, and diet for evidence of a nearshore-shelf effect, and 2) to determine if variation in the potential prey field of zooplankton was associated with this effect. This was a pilot study that occurred in three bays and over the adjacent shelf off east Kodiak Island during 5–18 September 1993. Sampling occurred only during night at locations where echo sign indicated the presence of age-0 pollock. Echo sign was targeted to increase the chance of collecting fish given the limited vessel time. Fish condition was indicated by length-specific body weight. Growth rate indices were estimated for three different periods by using fish length-age data and daily otolith increment widths: 1) from hatching date to capture, 2) 1–5 d before capture, and 3) 6–10 d before capture. Fish diet was determined from gut content analysis. Considerable variation among areas was evident in zooplankton composition, and fish condition, growth, and diet. However, relatively high prey densities, as well as fish condition and growth rates indicated that Chiniak Bay was particularly well suited as a pollock nursery. Hatching-date distributions indicated that most of the age-0 walleye pollock from bays were spawned earlier than were those from the shelf. The benefit of being reared in nearshore areas is therefore realized more by individuals that were spawned early than by individuals spawned relatively late.

Geographic variation among age-0 walleye pollock (*Theragra chalcogramma*): evidence of mesoscale variation in nursery quality?*

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The location of suitable fish nurseries has long been of interest to fishery scientists (Kendall and Duker, 1998). Such areas are a link in the chain of resources that sustain the productivity of a population and shape its evolution. Although the presence of juvenile fish in an area may indicate a nursery, relative importance among nursery areas ultimately depends on the number and reproductive fitness of reared individuals that contribute to the parental population. These qualities, however, are usually not measurable. Instead, we focus on measuring the size of juveniles, their body condition, diet, growth, and other characteristics that are accessible and relevant to fish survival. However, because these indices are not free of measurement error, it is advisable to consider more than one index (Suthers, 1998).

In the North Pacific Ocean, walleye pollock (*Theragra chalcogramma*) have adapted to the heterogeneity and productivity of coastal areas; they now support one of the world's most productive fisheries. Walleye pollock are a semidemersal gadid. Spawning typically occurs in mid-water during the spring at locations near, or over, the continental shelf (Kendall and Picquelle, 1989; Bailey et al., 1997). Fertilization is external. The eggs and larvae are pelagic, remaining in the plankton for *ca.* 4 months while they are dispersed over large areas. At 25–40 mm standard length (SL), larvae transform to juveniles (Brown et al., 2001) and become increasingly nektonic. Juveniles are referred to as "age-0" when they are between transition and 12-months old (40~130 mm SL, Brodeur and Wilson, 1996a). They are zooplanktivorous, feeding mostly on copepods and euphausiids, but other taxa sometimes dominate their diet (Brodeur and Wilson, 1996a). Age-0 juveniles commonly occur in various habitats from nearshore to the outer continental shelf (Nakatani and Maeda, 1987; Sobolevskiy et al., 1992; Carlson, 1995; Natsume and Sasaki, 1995; Brodeur and Wilson, 1996a; Wilson, 2000). Occasionally, they are found farther offshore (Tang et al., 1995), but probably in small numbers (Brodeur et al., 1999; Shida et al., 1999).

The early life stages of walleye pollock have been extensively studied in the Gulf of Alaska (GOA) (Kendall et al., 1996). In the Gulf, young pollock are most abundant in the western region (Brodeur and Wilson, 1996a). This region is naturally divided into two areas by the Shelikof Sea Valley, which cuts through the shelf at *ca.*156°N longitude (Fig. 1). To the east, the Kodiak vicinity includes the continental shelf around the Kodiak Island Archipelago. To the west, the lower Alaska Peninsula vicinity extends to Unimak Pass at the Peninsula's southwestern terminus. During the 1980s, age-0 abundance in the
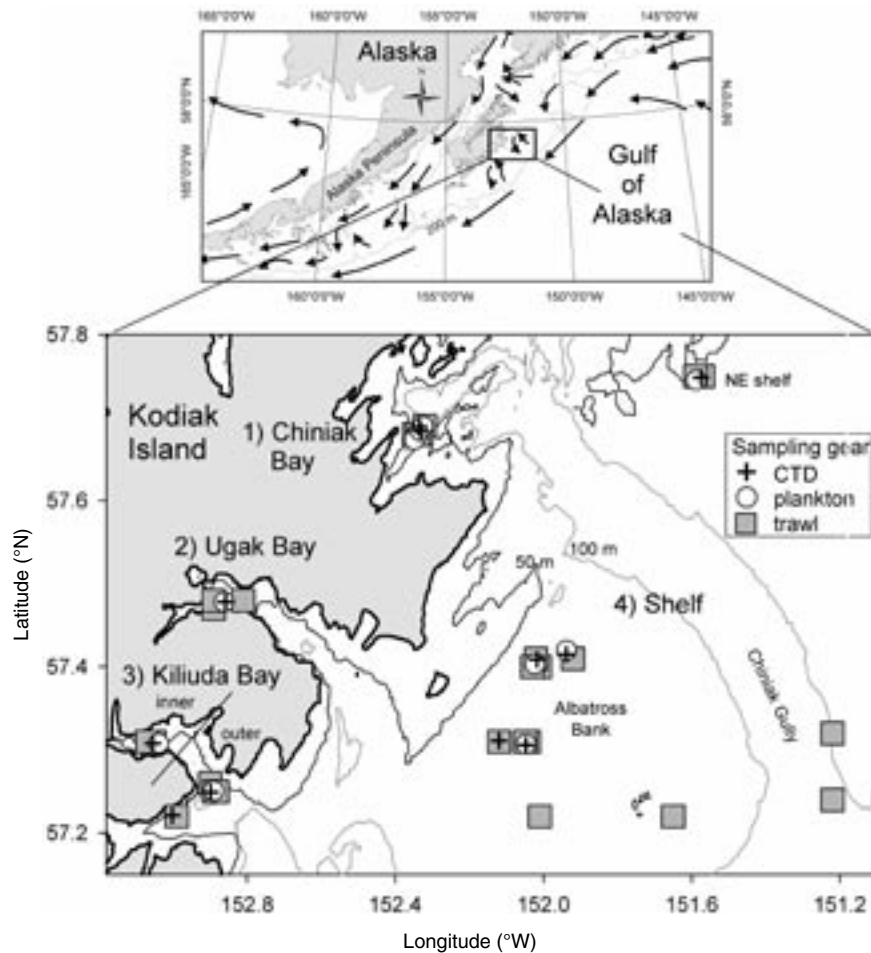
Figure 1

Location of sampling operations (CTD, plankton, and trawl) conducted during 5–18 September 1993, Kodiak Island, Alaska, to examine geographic variation among age-0 walleye pollock (*Theragra chalcogramma*). The ocean currents, shown as arrows on upper map, are adapted from Reed and Schumacher (1986).

Kodiak vicinity was related to the recruitment of pollock to the GOA fishery (Wilson, 2000). Furthermore, age-0 juveniles in this vicinity were large in comparison to those collected elsewhere (Wilson, 2000). The large size of the "Kodiak" juveniles may reflect faster growth (Bailey et al., 1996) due to a rich diet of euphausiids (Merati and Brodeur, 1996). In contrast, the diet of age-0 pollock along the Lower Peninsula was dominated by larvaceans (Merati and Brodeur, 1996). Interestingly, high densities of age-0 pollock were closer to shore in the Kodiak vicinity than along the Lower Peninsula where the shelf is relatively broad.

The apparent richness of the Kodiak Island vicinity may reflect its relative upstream position in the Alaska Coastal Current (ACC) (Fig. 1). Stabeno et al. (2004) integrated much research on the ACC to provide a comprehensive view of its importance in circulation over the GOA shelf. The ACC is wind driven and structured by seasonal influxes of fresh water. Flow is generally

southwestward over the shelf but there is considerable topographic influence. For example, landmasses at the northern entrance to Shelikof Strait (Kennedy-Stevenson Entrance) allow only about 70% of the ACC water to enter the Strait. The remaining 30% of the water flows south around the northeastern end of the Kodiak Archipelago. This bifurcation of flow occurs in an area of vigorous tidal mixing and localized upwelling, both of which contribute to increased biological productivity. Off the northeastern Archipelago, Stabeno et al. (2004) have shown that the ACC follows bathymetric contours into and out of sea valleys, thus, providing some across-shelf movement of water. Advection of water was found by Coyle et al. (1990) to be important in the enhancement of zooplankton in Auke Bay, which is in the eastern GOA. Less is known about the exchange of water and zooplankton between the bays and fjords of the western GOA and the adjacent shelf. Thus, the ACC probably helps enrich the waters off northeastern

Kodiak Island, but we do not yet understand how this actually affects walleye pollock in nearshore nurseries.

In this article, we present information from a pilot study to better understand the environmental basis for the apparent richness of the Kodiak Island vicinity as a pollock nursery. Our objectives were 1) to examine age-0 pollock size, body condition, growth, and diet for evidence of geographic effect (nearshore versus shelf), and 2) to determine if their potential prey field (i.e., zooplankton) was associated with this effect.

Materials and methods

This study was conducted as an ancillary project during a research cruise off east Kodiak Island, 5–18 September 1993 (Fig. 1). In this area, the shelf is about 50 nmi wide and has an offshore bank (Albatross Bank) crossed by deep gullies (Barnabas and Chiniak gullies) extending from the slope to the coast. Bays form the upper reaches of these troughs and receive seasonal influxes of freshwater (Rogers et al.[1]). Over the shelf, net transport is southwestward (*ca.* 5 cm/s) (Stabeno et al., 1995). A boundary current, the Alaska Stream, exists farther offshore and flows rapidly to the southwest (Reed and Schumacher, 1986).

Sampling was conducted from the NOAA ship *Miller Freeman* (Fig. 1). Sampling occurred only at night to avoid complications of diel fish movement (Brodeur and Wilson, 1996b) and feeding patterns (Merati and Brodeur, 1996). A 38-kHz, Simrad-EK500 echo-sounder system was used to help guide our sampling to locations where age-0 pollock were likely present. The targeting of echo signs resulted in an irregular sample-location pattern and biased estimation of fish abundance; however, it focused our sampling at locations where age-0 pollock were likely present and thereby contributed to successful fish collections. Sampling was accomplished in four areas: Chiniak Bay, Ugak Bay, Kiliuda Bay, and over the adjacent shelf. All data analyses included these four areas as geographic strata; finer divisions (e.g., inner and outer Kiliuda Bay, and NE and Albatross Bank) were not possible given the available data and chosen analytical methods.

Age-0 pollock were obtained from the four areas with a bottom trawl and a midwater trawl (Wilson et al., 1996). The codend of each trawl was lined with a 3-mm mesh net. Towing speed averaged 4.5 k/h. Previous comparisons between these trawls indicated no significant difference with regard to estimation of age-0 pollock size or abundance (Brodeur and Wilson, 1996a; Wilson et al., 1996). Differences in the sampling effort

used to collect each sample were corrected by dividing the age-0 catch by the volume filtered. Volume filtered was estimated by multiplying the distance fished (meters traveled while at depth) by the mouth opening of the trawl (m^2) (Wilson, 2000). Thus, age-0 catches are reported as number of fish per m^3.

Size composition of walleye pollock for each area was estimated by measuring the standard length (SL) of fresh age-0 pollock to the nearest millimeter. For large catches, a random subsample of about 300 individuals was used to represent the entire catch; otherwise, SL on every individual was measured. Length frequencies were expanded to the standardized catch estimates. Age-0 juveniles were clearly distinguishable from older pollock (<130 mm versus >150 mm SL) as indicated by Brodeur and Wilson (1996a). Random subsamples of age-0 pollock were also frozen at sea for subsequent determination of body condition, age, growth, and diet.

In the laboratory, length-specific weights of 776 age-0 pollock were used to examine area differences in body condition (Table 1). The fish were thawed within four months of collection. Excess water was blotted from each individual, and each specimen was measured to the nearest millimeter SL and weighed whole to the nearest 0.01 gram. Afterwards, each carcass was stored in 95% ethanol for eventual gut content analysis. Lengths and somatic weights, obtained from the subset of fish used in the gut analysis, were also analyzed to verify that geographic differences in condition were not dependent on whole versus somatic weight.

Growth rate was estimated for 128 individuals by using fish length and age data. Age, in days, was estimated as the number of daily increments visible in the microstructure of sagittal otoliths following Brown and Bailey (1992). Length-age relationships were examined for evidence of an area effect on growth rates integrated over the period from hatching to capture. We used these relationships to convert the length composition for each sample to a hatching-date distribution, and by summing across samples we then obtained area-specific hatching-date distributions.

To estimate growth rate realized near the point of capture we measured the width of recent daily otolith increments. Following Bailey (1989), we measured the width of the two outermost, nonoverlapping 5-increment bands on each of 97 sagittal otoliths. These widths were assumed to relate directly to body growth during the first (1–5 days) and second (6–10 days) 5-d periods before capture, and that the increments were deposited while individuals were near the point of capture. Thus, growth rate indices were obtained for three different periods: 1) hatching date to capture date, 2) 1–5 days before capture, and 3) 6–10 days before capture.

Gut content analysis was conducted on 300 individuals according to the method of Merati and Brodeur (1996) to determine feeding intensity and taxonomic composition of age-0 prey. No more than 15 fish per sample were examined. Each fish was measured (SL), blotted dry, and weighed immediately prior to dissection. Stomachs were excised between the esophagus and

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[1] Rogers, D. E., D. J. Rabin, B. J. Rogers, K. J. Garrison, and M. E. Wangerin. 1979. Seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island—including ichthyoplankton, meroplankton (shellfish), zooplankton, and fish. Annual rep. OCSEAP RU553, FRI-UW-7925, 291 p. Fish. Res. Inst., Univ. Washington, Seattle, WA.

Table 1

Number of age-0 walleye pollock (*Theragra chalcogramma*) collected near Kodiak Island, Alaska, September 1993, measured for standard length, and examined in the laboratory to estimate condition, growth, and the weight and taxonomic composition of stomach contents. Sample is the number of trawl hauls.

						Laboratory examinations (no. of fish)				
				Condition		Growth				
		At-sea collections (no. of fish)						Band width		Evaluated for gut content weight and composition
Location	Sample (n)	Caught	Measured for SL	whole[1] wt.	somatic[2] wt.	Age		1–5[3]	6–10[4]	
Chiniak Bay	7	1858	709	223	75	23		17	17	75
Ugak Bay	4	2506	773	218	91	28		12	12	91
Kiliuda Bay	7	562	279	165	66	41		33	33	66
Shelf	14	358	358	170	68	36		35	35	65
All combined	32	5284	2119	776	300	128		97	97	297

[1] Whole wet weights from thawed fish.

[2] Somatic wet weights from fish preserved in 95% ethanol after freezing at sea.

[3] Collective width of daily otolith increments 1–5; numbering begins with the most peripheral increment.

[4] Collective width of daily otolith increments 6–10.

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pylorus. Gut contents were dissected from the specimens and weighed to the nearest 0.001 gram. Somatic weight represented whole wet weight minus the gut content weight. Three fish were omitted from further consideration because of apparent regurgitation. Taxonomic composition of age-0 diets was determined by counting the organisms in the gut after sorting them into broad taxonomic groups.

Zooplankton was collected by using a 1-m Tucker net (333-μm mesh) to sample where age-0 pollock had been collected. The net was fished through acoustic echo layers believed to be age-0 pollock in order to characterize their immediate prey field. Potential prey items were sorted into broad taxonomic groups and enumerated at the Polish Plankton and Identification Center, Szezcin, Poland.

Temperature and salinity profiles (near surface to 10 m off bottom) were obtained by using a Seabird SBE-911+ CTD system. Profile data were collected during deployment at a descent rate of ca. 0.5 m/s.

Statistically significant differences in age-0 condition, growth, and feeding intensity among geographic areas were detected with split-plot analysis of covariance (AN-COVA) and *post hoc* multiple comparison tests (Proc Mixed, SAS software, Littell et al., 1996). The covariates were fish length or age (days since hatching). Following Milliken and Johnson (2002), we first tested for covariate significance (H_0: all slopes=0) and homogeneity of slopes (H_0: equal slopes) to ensure appropriateness of the following reduced, common-slope model:

$$Y = \alpha + \beta x_{ij} + Area_j + Sample_i\{Area_j\} + e_{ijk},$$

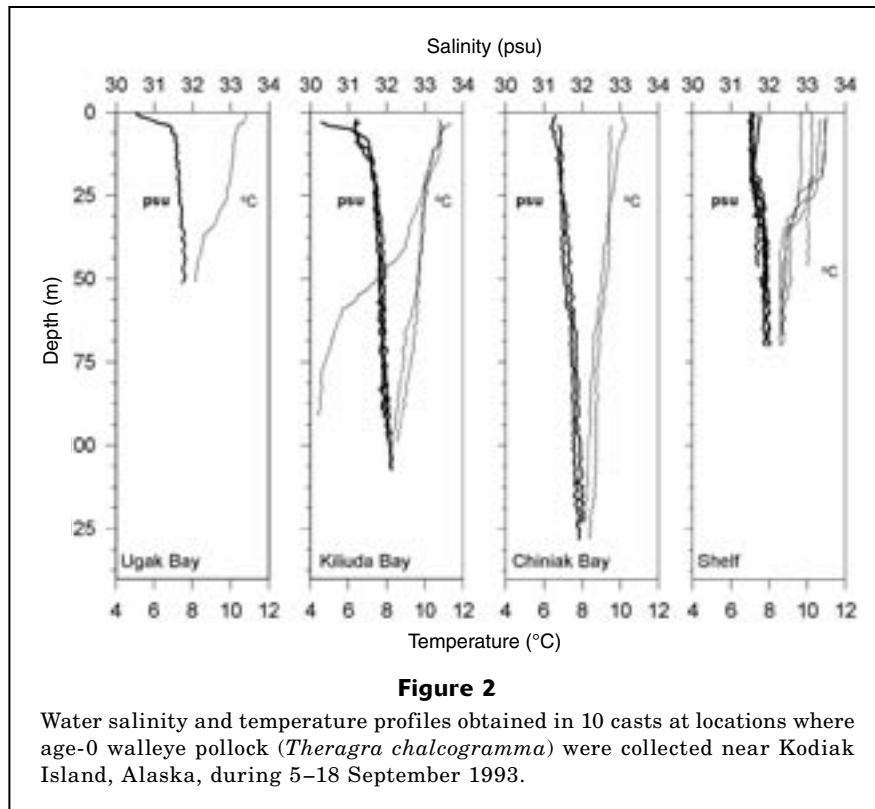where Y = dependent variable;

α = intercept parameter;
β = slope parameter;
x_{ij} = covariate for sample i and area j; and
e_{ijk} = replicate error for sample i, area j, and fish k.

A split-plot design was necessary to account for the nesting of samples (trawl catches) within area, and individuals within sample. To avoid pseudoreplication, trawl catch was the sampling unit instead of individual fish. Area was a fixed effect; sample was a random effect. For body condition, lengths and weights were $\log_e$-transformed according to the method of Patterson (1992); two points were omitted because of suspiciously low length-specific, whole-body weight. For feeding intensity, gut content weights (GCW) were fourth-root transformed ($GCW^{0.25}$) to linearize the GCW-length relationship and remove heteroscedasticity (Clarke and Warwick, 2001). Significance of *post hoc* pairwise differences was based on a Bonferroni-corrected, 0.05-level of significance. The standardized catch data were not incorporated into these tests; therefore the conclusions pertain to the samples not weighted by catch.

Nonmetric multidimensional scaling (NMS, PC-Ord, McCune and Mefford, 1999) was used to ordinate the diet and plankton samples according to taxonomic composition. Each diet sample represented the average numerical composition of the diet of all fish in the sample. This value was calculated by dividing the sum of all items within each taxonomic category by the number of fish in the sample. The ordinations, one for diet and another for plankton, were based on Bray-Curtis similarity coefficients of fourth root-transformed data. Differences among the four areas were statistically tested by using a two-way nested analysis of similarity

Figure 2

Water salinity and temperature profiles obtained in 10 casts at locations where age-0 walleye pollock (*Theragra chalcogramma*) were collected near Kodiak Island, Alaska, during 5–18 September 1993.

(ANOSIM, PRIMER, Clarke and Warwick, 2001) applied to the Bray-Curtis similarity matrices.

Results

Overall, salinity ranged from 30.3 to 33.0 ppt, and water temperature ranged from 4.4 to 11.3°C (Fig. 2). Shallow surface layers of relatively fresh water were evident from low near-surface salinities in Ugak Bay and in the inner part of Kiliuda Bay. This part of Kiliuda Bay was also well stratified thermally. Unfortunately, it was not possible to include inner Kiliuda Bay as a fifth area in subsequent statistical analyses because of insufficient sampling. Thermal stratification was also evident at shelf sampling locations.

A total of 5284 age-0 pollock were collected in 25 of the 32 successful trawl hauls (Table 1). These fish were absent only at the four most-offshore locations over Albatross Bank and Chiniak Gully (Fig. 3). In addition, no age-0 pollock were caught in shallow (<35-m depth) tows at locations on Albatross Bank; a dense and expansive school of capelin (*Mallotus villosus*) may have displaced them downward. Median age-0 density was 0.0006 fish/m³; the maximum (0.095 fish/m³) was found in Ugak Bay.

Standard lengths of 2119 age-0 pollock ranged from 25 to 121 mm SL (Table 1, Fig. 4). The fish in Chiniak Bay (91 mm SL), Ugak Bay (90 mm SL), and Kiliuda Bay (89 mm SL) all had a median SL that were larger than the median length of fish collected over the shelf (71 mm SL). A surprising number of individuals <50 mm SL were collected in Ugak Bay and inner Kiliuda Bay.

Body condition, based on the reduced, common-slope ANCOVA model, varied among the four areas (Table 2). Because of this effect, area-specific equations were used to describe the length-weight relationship (Table 3, Fig. 5A). After accounting for differences in length, we found that fish from the shelf weighed less than the individuals collected in Chiniak Bay and Ugak Bay. Individuals from Kiliuda Bay were intermediate in weight, differing only from the Ugak Bay fish (Table 4). Similar conclusions from the somatic-weight data of fish used in the diet examinations indicated that gut-content weight was not responsible for the relatively low length-specific weights of fish from Kiliuda Bay and the shelf (Tables 2 and 4).

The fish age-length relationship also varied by area. The relationship was described by using a reduced, common-slope model (Table 2). The common slope was 0.78 mm/d (Table 3, Fig. 5B). Differences in line elevation, or age-specific length, indicated that fish from the shelf grew more slowly during the hatch-to-capture period than did the fish from Chiniak or Kiliuda bays (Table 4). Applying these equations to the length data resulted in hatching-date distributions that ranged from mid March to mid July (Fig.6). The fish collected in Chiniak Bay (17 April), Kiliuda Bay (20 April), and Ugak Bay (25 April) all had earlier median hatching
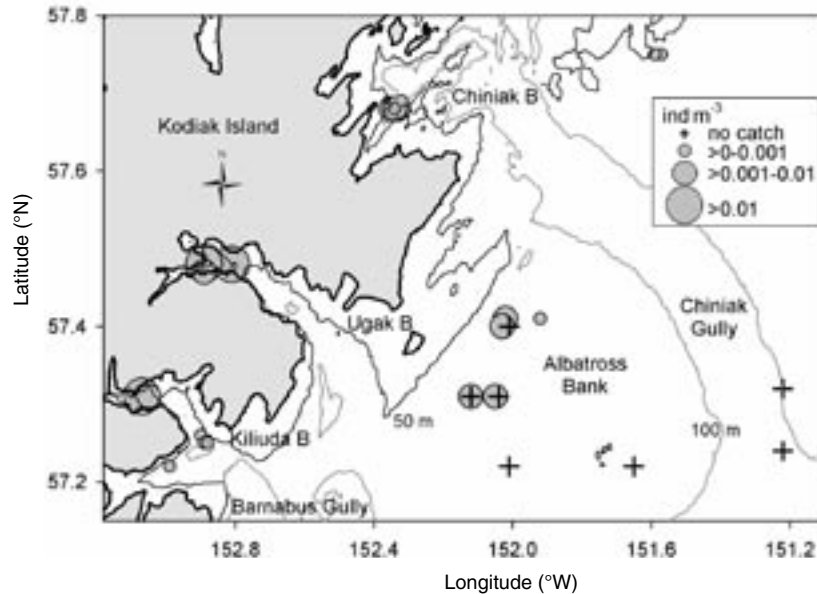
Figure 3

Geographic distribution of standardized catches (no. of individuals/m^3) of age-0 walleye pollock (*Theragra chalcogramma*) collected in trawl hauls conducted near Kodiak Island during 5–18 September 1993.

dates in comparison to fish from the shelf (8 May). Interestingly, the hatching dates of the cohort of small individuals from Ugak Bay and inner Kiliuda Bay ranged from June to July.

Mean otolith increment width varied with area. It was not necessary to include fish length as a covariate (Table 2). For the 1–5 d precatch period, the large mean increment width associated with fish from Chiniak Bay (0.036-mm band width) was different from the means of

Figure 4

Size composition (mm SL) of age-0 walleye pollock (*Theragra chalcogramma*) by area from samples collected near Kodiak Island, 5–18 September 1993.

each other area (Table 4). The only other difference was between the Kiliuda Bay (0.026 mm) and shelf (0.030 mm) areas. The only difference for the 6–10 d precatch period was again between the Kiliuda Bay (0.029 mm) and shelf (0.036 mm) areas.

No area effect on gut content weight (GCW) was detected (Table 2). There was, however, a significant fish length effect (Fig. 5C), and this was incorporated in the final model (Table 3). After adjusting for length, area-specific mean GCW agreed in rank with area-specific fish weight (Table 4).

Differences in taxonomic composition of age-0 pollock diets resulted in a good separation of samples by area (Fig. 7A, ANOSIM, $R=0.533$, $P=0.001$). Each pair-wise comparison of areas resulted in a significant difference ($P<0.05$) (the one sample of small fish from Kiliuda Bay, and two samples from the shelf of fish with empty stomachs were omitted from the ANOSIM). The diet of fish from Ugak Bay and Kiliuda Bay were mostly crab larvae or copepods, depending on fish size (Table 5A). Over the shelf, fish diets comprised mostly euphausiids (74%). In contrast, fish from Chiniak Bay had a much more varied diet; no single prey category exceeded 40% of the items per stomach. Note the correspondence between the number of prey per fish (Table 5A) and mean gut-content weight (Table 4); both were lowest for fish from the shelf.

Differences in taxonomic composition also resulted in separation of the plankton samples by area (Fig. 7B, ANOSIM, $R=0.886$, $P=0.001$). Pair-wise comparisons indicated a difference between Chiniak Bay and the shelf ($R=0.813$, $P=0.029$). Ugak Bay was not included in the comparisons because only one sample was avail-
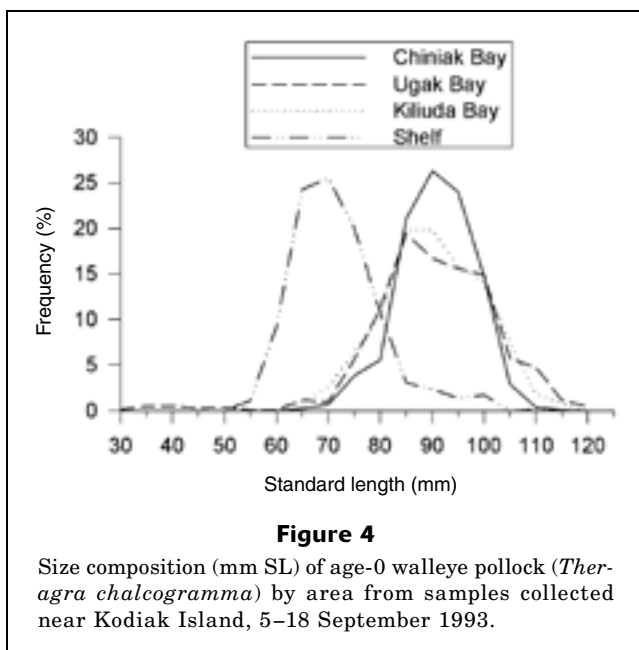
Table 2

Summary results of six ANCOVA tests of an area effect on six dependent variables obtained from laboratory analysis of age-0 pollock: body condition (whole or somatic weight), three indices of growth, and gut content weight. NDF and DDF are numerator and denominator degrees of freedom for the *F* test, respectively.

Dependent variable	H_0: all slopes = 0	Ho: equal slopes	Reduced model				
			Source	NDF	DDF	Type III *F*	*P > F*
Condition							
whole weight	*P*=0.0001	*P*=0.3340	Area	3	14.2	6.81	0.0045
			ln(SL)	1	769	105824	0.0001
somatic weight	*P*=0.0001	*P*=0.3115	Area	3	17.8	10.01	0.0004
			ln(SL)	1	294	31000	0.0001
Growth							
age-specific length	*P*=0.0001	*P*=0.4140	Area	3	4.3	14.43	0.0106
			Age	1	117	475.39	0.0001
1–5 d band width	*P*=0.2645		Area	3	93	8.05	0.0001
6–10 d band width	*P*=0.2267		Area	3	5.76	3.89	0.0768
Gut content weight	*P*=0.0001	*P*=0.7208	Area	3	16.2	0.36	0.7850
			SL	1	285	201.99	0.0001

able. Copepods dominated the catches in Chiniak Bay and over the shelf, whereas larval crabs were most prevalent in the Ugak and Kiliuda samples (Table 5B). In terms of overall abundance, mean prey densities were lowest among samples collected from the shelf and highest for the Chiniak Bay samples.

Discussion

The presence of age-0 pollock in bays and over the inner shelf, but not over the outer shelf, indicates that the principal pollock nursery off east Kodiak Island during autumn is relatively close to shore. Earlier studies of age-0 pollock in the western GOA focused on nearshore areas (Smith et al., 1984; Wilson, 2000) and did not document the absence of age-0 pollock over the outer shelf. Our results point to prey resource as a likely explanation for the observed distribution of and differences among age-0 walleye pollock.

Seasonal declines in zooplankton density underscore the importance of nearshore areas as pollock nurseries. Rogers et al.[1] and Kendall et al.[2] observed an order-of-magnitude autumnal decline in prey[3] density off Kodiak Island during 1977–79 (Fig. 8). This decline was accompanied by a shoreward shift in the region of highest eu-

Table 3

Least-squares linear relationships used to describe the condition, growth, and feeding intensity of age-0 walleye pollock collected September 1993, Kodiak Island, Alaska. GCW = gut content weight.

Relationship	Location	Equation
Condition		
whole weight	Chiniak Bay	$\ln(g) = 3.228(\ln SL\text{mm}) - 12.646$
	Ugak Bay	$\ln(g) = 3.228(\ln SL\text{mm}) - 12.609$
	Kiliuda Bay	$\ln(g) = 3.228(\ln SL\text{mm}) - 12.659$
	Shelf	$\ln(g) = 3.228(\ln SL\text{mm}) - 12.698$
somatic weight	Chiniak Bay	$\ln(g) = 3.127(\ln SL\text{mm}) - 12.708$
	Ugak Bay	$\ln(g) = 3.127(\ln SL\text{mm}) - 12.702$
	Kiliuda By	$\ln(g) = 3.127(\ln SL\text{mm}) - 12.774$
	Shelf	$\ln(g) = 3.127(\ln SL\text{mm}) - 12.816$
Growth		
length-at-age	Chiniak Bay	$\text{age}(d) = 0.782(SL\text{mm}) - 22.294$
	Ugak Bay	$\text{age}(d) = 0.782(SL\text{mm}) - 26.928$
	Kiliuda Bay	$\text{age}(d) = 0.782(SL\text{mm}) - 21.346$
	Shelf	$\text{age}(d) = 0.782(SL\text{mm}) - 31.011$
Gut content weight		
	All combined	$\text{GCW}(g^{0.25}) = 0.007(SL\text{mm}) - 0.192$

[2] Kendall, A. W., Jr., J. R. Dunn, R. J. Wolotira Jr., J. H. Bowerman Jr., D. B. Dey, A. C. Matarese, and J. E. Munk. 1980. Zooplankton, including ichthyoplankton and decapod larvae, of the Kodiak shelf. NOAA NWAFC proc. rep. 80-8, 393 p. Alaska Fishery Science Center, Seattle, WA.

[3] All invertebrate zooplankters are considered potential age-0 pollock prey except cnidarians, ctenophores, siphonophores, and larval shrimps and crabs. Shrimp and crab were omitted from Figure 8 because density estimates were not available separately for the shelf and slope regions.

phausiid density. Similar to our findings, the estimates of larval crab densities from Rogers et al.'s and Kendall et al.'s studies were always highest in bays. In autumn,

Figure 5

Least-squares regressions of age-0 walleye pollock (*Theragra chalcogramma*) length on weight (**A**), length on age (**B**), and gut content weight on length (**C**) for individuals collected from four areas off east Kodiak Island, 5–18 September 1993.

the larger zooplankters are of principal importance to age-0 pollock because of size-related changes in diet (Table 5A, Merati and Brodeur, 1996).

By all accounts, age-0 pollock collected from Chiniak Bay fared as well or better than individuals in each of the other areas sampled. Wilson (2000) found that the density of age-0 pollock in the Chiniak Bay vicinity predicted Gulf-wide recruitment. However, these fish represent a minuscule part of the Gulf-wide population of age-0 pollock. Even if two cohorts, from spring- and summer-spawnings, were produced, it seems unreasonable to expect that local production would dramatically affect gulf-wide recruitment. Alternatively, the abundance and condition of age-0 pollock in this vicinity might reflect larger-scale processes that relate to gulf-wide recruitment. Identifying large-scale processes based on small-scale sampling, however, is complicated by variation at high spatial and temporal frequencies. For example, the relatively high density of pea crab (*Fabia subquadrata*) megalopae in combination with influxes of freshwater (Epifanio, 1988) indicate that local dynamics are important in sustaining prey populations in Ugak and Kiliuda bays. In contrast, Chiniak Bay might be more affected by influxes of oceanic prey. Such influxes could be facilitated by cross-shelf sea valleys, which extend into all the fjords that we sampled. Indeed, Kendall et al.,[2] Lagerloef (1983), and Stabeno et al. (2004) have all shown that the local sea valleys induce cross-shelf flow in the ACC. Furthermore, Inzce et al. (1997) found that zooplankton density was elevated in the Shelikof Sea Valley above the density found at adjacent shelf areas; a similar phenomenon, however, was not observed off northeastern Kodiak Island (Kendall et al.[2]). Compared to the other bays, Chiniak Bay might be best positioned to receive enriched ACC water that flows south from where it bifurcates at the entrance to Shelikof Strait. Such enriched water may also be an important transport mechanism for immigrating larval and juvenile pollock (Wilson, 2000).

Because of the inconsistency among our various indices (i.e., weight-at-length, length-at-age, otolith increment width), it is difficult to conclude that fish over the shelf and in Ugak and Kiliuda bays were prey limited. Over the shelf, recent growth rates were not low despite relatively small individual size and low prey density. For example, the low prey densities and small fish sizes over the shelf contrasted with recent fish growth that was not low. Age-0 pollock are capable of social foraging behavior to compensate for food scarcity (Ryer and Olla, 1992), but it is unclear that the associated energetic cost (Ryer and Olla, 1997) would depress body weight before slowing otolith growth. In contrast, fish in Kiliuda Bay had relatively slow recent growth and low body weight, but age-specific length was large. The observed differences in age-specific length are somewhat discounted by the fact that such differences may have arisen any time after hatching and are not necessarily indicative of recent differences in growth. Another complication was our inability to reconstruct the spatial history of the sampled fish;
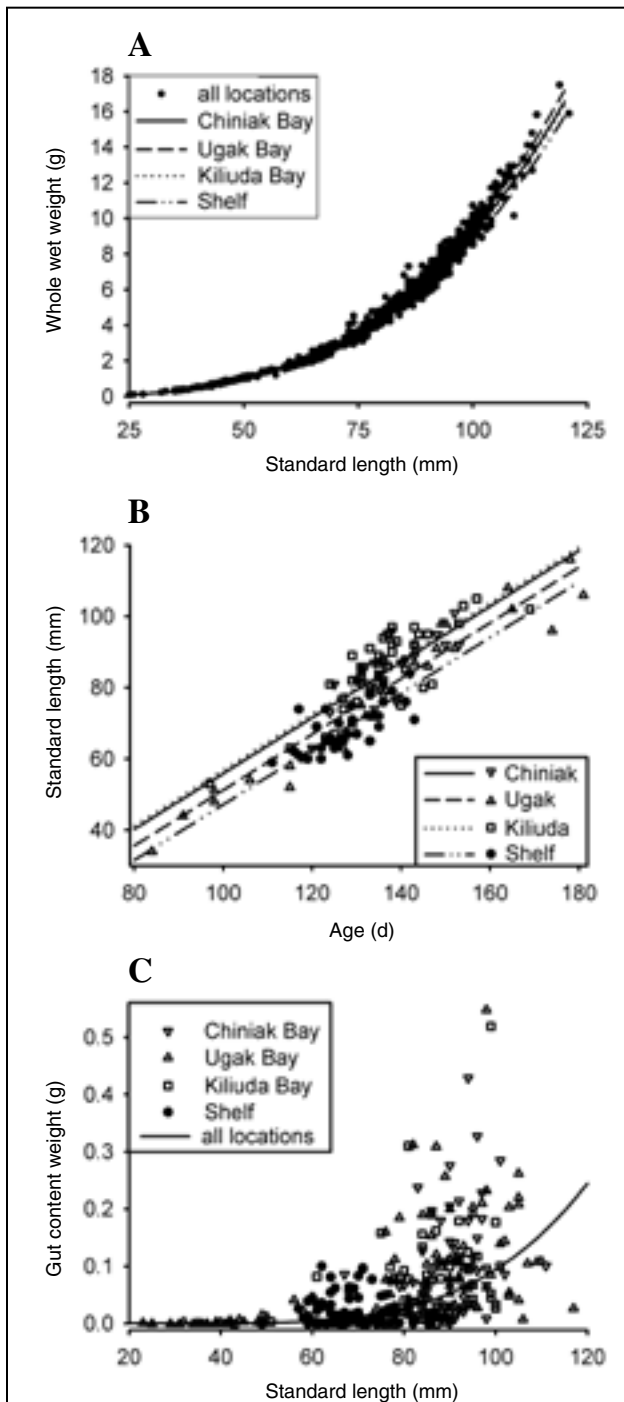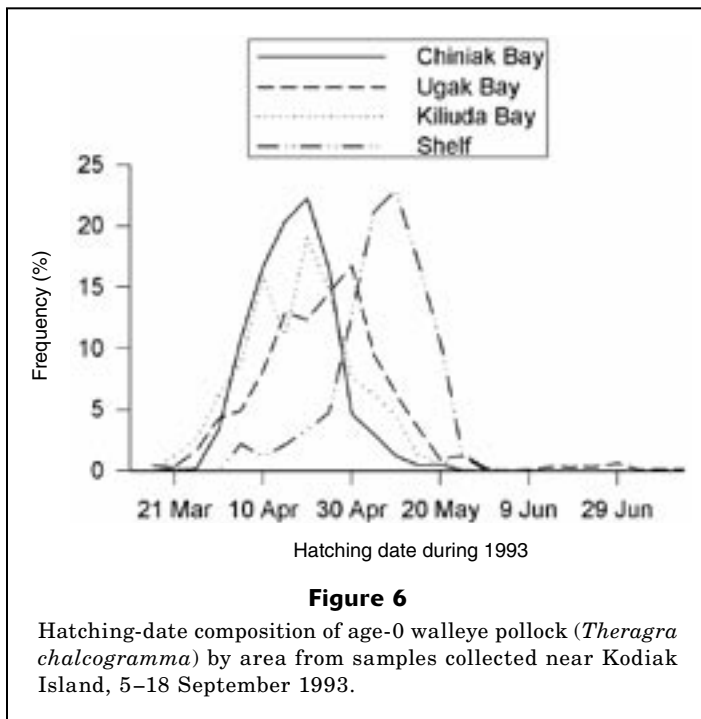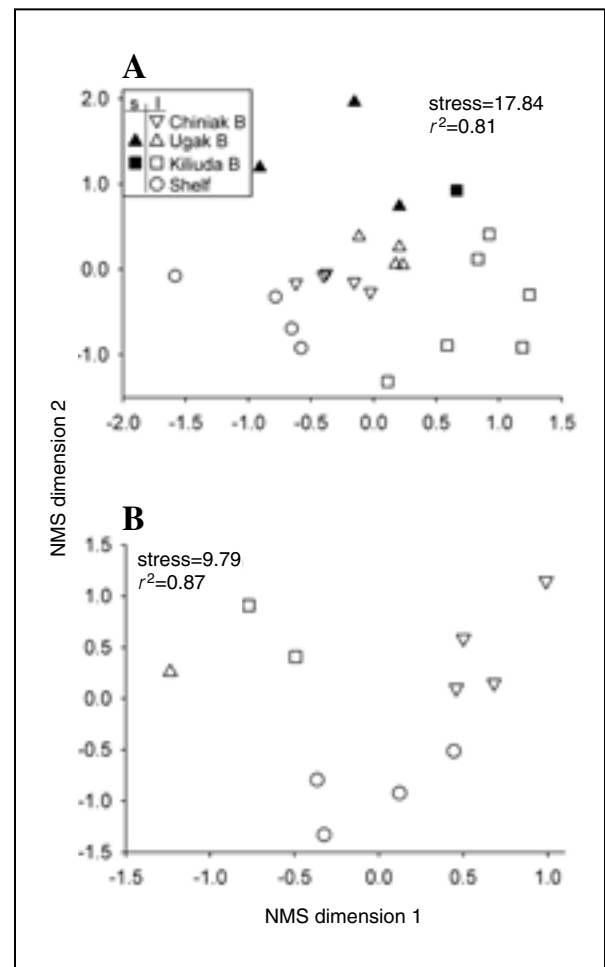
Table 4

Least-squares adjusted means of indices of body condition, growth, and gut content weight (GCW) of age-0 walleye pollock collected September 1993, Kodiak Island, Alaska. Means sharing the same superscript letter are not different (*post hoc* multiple comparison tests, $P>0.05$).

	Condition		Growth			
Location	whole wt. (ln g)	somatic wt. (ln g)	age-specific SL (mm)	1–5 d band width (mm)	6–10 d band width (mm)	GCW ($g^{0.25}$)
Chiniak Bay	1.47[ab]	0.82[a]	82.3[a]	0.036[a]	0.033[ab]	0.40
Ugak Bay	1.50[b]	0.83[a]	77.6[ab]	0.027[bc]	0.032[ab]	0.43
Kiliuda Bay	1.45[ac]	0.76[b]	83.2[a]	0.026[b]	0.029[a]	0.39
Shelf	1.42[c]	0.72[b]	73.6[b]	0.030[c]	0.036[b]	0.36

Figure 6

Hatching-date composition of age-0 walleye pollock (*Theragra chalcogramma*) by area from samples collected near Kodiak Island, 5–18 September 1993.

Figure 7

Nonmetric multidimensional scaling (NMS) of samples based on age-0 walleye pollock (*Theragra chalcogramma*) diet composition (**A**), or zooplankton composition (**B**). Symbols indicate four different sampling areas. For diet, the small (<66 mm SL) fish in bays are represented by filled symbols.

in other words, we did not know where they had been prior to capture.

As evidenced by geographic variation in hatching-date distributions, cohort-specific differences persisted well into the juvenile stage and had important implications for inter-cohort differences in survival. The median hatching dates of fish in bays were similar to those estimated for north Kodiak Island by Brown and Bailey (1992). In contrast, fish over the shelf had substantially later hatching dates. There is little evidence of pollock spawning within our study area; therefore it seems likely that the differences in hatching dates reflect successive immigration of sequential cohorts. However, the presence of the youngest cohort, fish hatched during
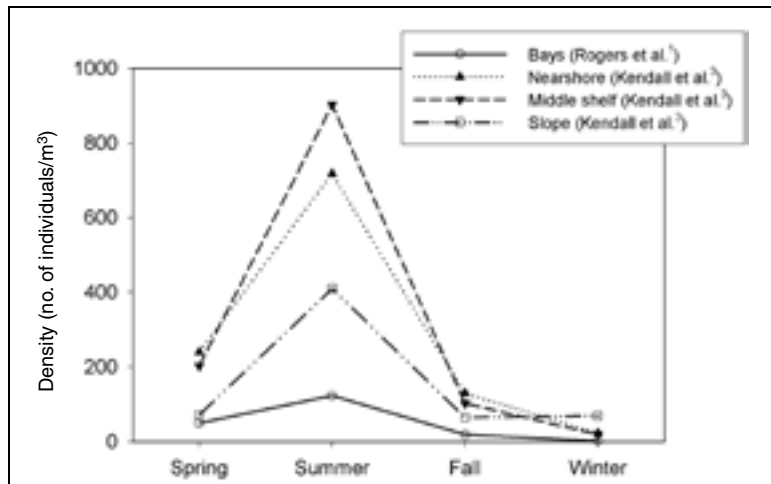
Figure 8

Seasonal variability in densities (no. of individuals/m³) of inverte-brate zooplankton near Kodiak Island based on samples collected with 60-cm bongo nets with 0.333-mm mesh (modified from Rogers et al.[1], Kendall et al.[2]).

June and July, only in the innermost parts of Kiliuda Bay and Ugak Bay, may indicate an alternative mechanism such as local spawning and geographic differences in retention. Regardless, the relationship between fish size and hatching date indicates that large individuals were spawned early; thus, early spawned individuals might experience higher overwinter survival, which often increases with fish size (Sogard, 1997).

We chose to track echo sign in our study to reduce the sampling effort expended in areas devoid of age-0 pollock. This method maximized our chance of collecting the samples needed to study differences among age-0 pollock given the limited vessel time. Unfortunately, this method also introduced a bias, thereby reducing the utility of density estimates to indicate habitat suitability (Brown et al., 2000; Stoner et al., 2001) and to extrapolate from samples to at-sea populations. Our focus, however, was on other measures that might eventually provide a

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Table 5

Numerical composition of age-0 pollock diet by location and predator SL (**A**), and composition of the plankton in 1-m² Tucker samples (**B**) concurrently collected during 5–18 September 1993, Kodiak Island, Alaska. "t" signifies trace (<0.05).

A

Area	Sample (*n*)	no. of fish	amphipod	chaetognath	copepod	crab larvae	cumacean	euphausiid	mysid	shrimp larvae	No. of prey/ fish
Chiniak Bay	5	75	2.8	t	4.1	0.1	0.0	3.7	0.4	t	11.0
Ugak Bay											
≤66 mm	3	31	0.1	0.6	11.2	0.6	0.0	0.1	t	0.0	12.6
>66 mm	4	60	0.1	t	5.9	15.9	t	3.3	0.2	t	25.6
Kiliuda Bay											
≤66 mm	1	5	0.0	0.2	2.2	1.0	0.0	0.2	0.0	0.0	3.6
>66 mm	6	61	t	t	t	6.4	t	2.7	t	t	9.2
Shelf	6	65	0.3	0.0	0.1	0.1	t	2.8	0.4	0.1	3.8

Prey (number of individuals/fish)[1]

[1] $0 < t < 0.05$.

B

Zooplankton (number of individuals/m³)[1]

Area	Sample (*n*)	amphi-pod	chaeto-gnath	copepod	crab larvae	euphau-siid	fish larva	larvacean	mysid	shrimp larvae	total no./ m³
Chiniak Bay	4	t	9	332	1	23	t	4	2	4	375
Ugak Bay	1	t	13	12	48	2	t	3	1	t	80
Kiliuda Bay	2	t	13	40	82	28	t	17	4	3	188
Shelf	4	t	1	51	1	4	t	15	t	2	74

[1] $0 < t < 0.05$. In zooplankton samples, cumaceans were not enumerated.

useful supplement to abundance distribution data (Beutel et al., 1999).

This study enabled us to conclude that Chiniak Bay is particularly well suited for rearing pollock probably because of influxes of zooplankton. It remains to be seen if Chiniak Bay contributes relatively high numbers of recruits, or if other counteracting factors such as predation exist. Nevertheless, we have demonstrated that differences among juvenile pollock exist at mesogeographic scales and that these differences are useful for inferring how specific areas might relate to the population dynamics of walleye pollock.

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