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Relationship of age-0 pollock abundance and distribution around the Pribilof Islands, to other shelf regions of the eastern Bering Sea

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Abstract

The Pribilof Islands region is recognized to be a major nursery for age-0 walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. However, the Pribilof Islands' importance for the recruitment of pollock in the Bering Sea has not been quantified. In this paper, we define the geographic extent of the Pribilof Islands region based on ocean circulation, location of major fronts, and trophic interactions. The abundance and distribution by oceanographic habitat (nearshore, frontal and offshore), of acoustically determined age-0 pollock are compared between the Pribilof Islands and the Inner Front of the eastern Bering Sea, for the summers of 1997–1999. Net samples collected during surveys in 1995–2002 are used to compare the abundance of age-0 pollock in the Pribilof Islands region to locations eastward along the Bering Sea shelf.

We found densities of age-0 pollock near the Pribilof Islands to be generally higher than on the surrounding shelf, and higher or non-significantly different from the Inner Front. Through synthesis of our data and inferences of pollock growth and mortality, we estimate the Pribilof Islands region to have comprised 12.5% (1997), 53.7% (1998), and 24.7% (1999) of the total stock of age-0 pollock in the eastern Bering Sea. Since the Pribilof Islands region comprises only 14% of the total eastern Bering Sea area, evidence is given that a disproportionately large fraction of the age-0 pollock population inhabits the Pribilof Islands nursery. © 2005 Elsevier B.V. All rights reserved.

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1. Introduction

Bering Sea walleye pollock (*Theragra chalcogramma*) sustains one of the largest commercial

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fisheries in the world, averaging between 0.9 and 2.2 million metric tonnes annually since 1977 (Ianelli et al., 2003). Management of the fishery is based on annual stock assessments utilizing bottom-trawl and acoustic surveys, observer data, and virtual population analysis (VPA) models (Ianelli et al., 2003). Concurrently, increased recognition that year-class strength of a pollock stock is determined primarily through conditions affecting the pre-recruit, juvenile stages (Bailey et al., 1996a; Bailey, 2000; Hunt et al., 2002; Hunt and Stabeno, 2002), has led to the goal of developing indices for pre-recruit pollock abundance (Macklin et al., 2002; Swartzman et al., 2002). The Pribilof Islands region of the eastern Bering Sea has been identified as a major nursery area for age-0 pollock (Brodeur and Wilson, 1999; Brodeur et al., 2002), and particular interest is given to the question of whether age-0 abundance around the Pribilof Islands could be used as an advanced indicator for large adult year-classes of pollock (Swartzman et al., 2002).

Evidence pointing to the Pribilof Islands as a major nursery for Bering Sea pollock can be summarized by the following five factors:

- (1) High primary and secondary production around the Pribilof Islands associated with the Bering Sea green belt (Springer et al., 1996).
- (2) A prevailing current moving northwest along the Bering Sea shelf break toward the Pribilof Islands (drifter studies: Stabeno et al., 2002), which can deliver pollock larvae from major spawning areas near Bogoslof Island and Unimak Pass to the Pribilof region by summer.
- (3) The existence of a clockwise circulation pattern around the Pribilof Islands, which can retain young fish near the Pribilof Islands (Kowalik and Stabeno, 1999; Stabeno et al., 1999).
- (4) The great abundance of piscivorous seabirds (Decker and Hunt, 1996) and marine mammals (Baretta and Hunt, 1994; Robson, 2002) that breed and feed in the Pribilof Islands region, and have diets dominated by pollock (Dragoo et al., 2000).
- (5) The presence of pollock spawning areas near the Pribilof Islands (e.g., Pribilof Canyon) that can deliver pollock larvae to the Pribilof region earlier than those arriving by drift along the shelf break (Napp et al., 2000).

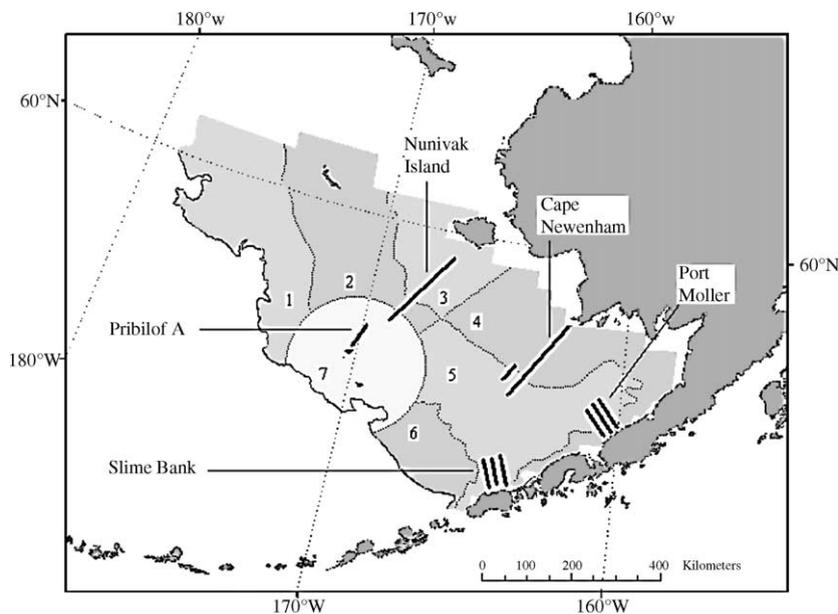


Fig. 1. Acoustic transects of the Pribilof Islands and Inner Front surveys. Eastern Bering Sea shelf regions are shaded; clockwise from north-west: EBS Edge-North (1, light gray); EBS North (2, medium gray); Nunivak (3, light gray); Inner Front (4, medium gray); EBS South (5, light gray); EBS Edge-South (6, medium gray); Pribilof (7, off-white circle). The shelf is bounded by the 200-m isobath.

Traynor and Smith (1996) and Nishimura et al. (1996) found higher than average abundance of juvenile pollock around the Pribilof Islands during summer. However, given the large expanse of the eastern Bering Sea on a shallow continental shelf, and the year-to-year variability of its environment, other nursery areas may be equivalently productive, and it is not a certain premise that the Pribilof Islands region plays a dominant role. This paper examines the importance of the Pribilof Islands region as a pollock nursery, by comparing the acoustically determined abundance and distribution of age-0 pollock between the Pribilof Islands and the Bering Sea Inner Front. The Pribilof Islands and Inner Front are characterized by similar oceanographic structure (Brodeur et al., 2002; Kachel et al., 2002), but considerably different spatial extent (e.g., Fig. 1). Comparing these two areas will address the question of whether the relatively small Pribilof Islands region is potentially suitable as an indicator for the much larger Bering Sea ecosystem. Furthermore, we used net survey data to compare age-0 pollock abundance near the Pribilof Islands with abundance in areas eastward along the Bering Sea shelf.

We synthesized these comparisons to estimate over 3 years (1997–1999), the percentage of the total eastern Bering Sea age-0 pollock population originating from the Pribilof Islands region. Our objectives are to quantify the contribution of the Pribilof Islands as a pollock nursery and to examine similarities and differences in the distribution of age-0 pollock among the frontal regions of the eastern Bering Sea. Besides providing a broad ecosystem comparison, this study represents a first step in the possible application of the Pribilof Islands age-0 pollock abundance as an index of future recruitment.

2. Data and methods

2.1. Sources

The Pribilof Islands ecosystem has been a major focus for study as part of the Southeast Bering Sea Carrying Capacity Program (SEBSCC) and the Bering Sea Fisheries-Oceanography Coordinated Investigations (FOCI) projects (Macklin, 1999; Macklin et al., 2002), supported by the NOAA coastal ocean program. During late summer of each year from 1994 to 1999, acoustic

surveys, with concomitant physical and biological sampling, were taken along transects representative of different habitats around the Pribilof Islands (Swartzman et al., 2002). Acoustic and biological surveys of the Inner Front were conducted between late July and early September of 1997–1999, through sponsorship of the National Science Foundation (Coyle and Pinchuk, 2002). Net samples for age-0 pollock were taken during late July of 1995–2002 at stations throughout the southeast Bering Sea by the Hokkaido University T/S *Oshoro Maru* (Wilson and Brodeur, 1998; Napp et al., 2002).

2.2. Pribilof Islands versus Inner Front acoustic survey comparisons

The acoustic surveys were conducted along study transects running perpendicular to the bathymetry, thus sampling three sequential oceanographic habitats: nearshore (tidally mixed water column); offshore (fully stratified); and frontal (partially stratified transition zone between near- and offshore), defined according to Stabeno et al. (1999). Boundaries between habitats depend on the degree of vertical mixing, and are described in Ciannelli et al. (2002), Kachel et al. (2002) and Swartzman et al. (2002). The transects are shown in Fig. 1: north of the Pribilof Islands, and at four locations along the Inner Front, Port Moller along the Alaskan peninsula, Slime Bank near Unimak Pass, Cape Newenham and Nunivak Island off the Yukon-Kuskokwin river delta.

Acoustic data on the Pribilof Islands surveys were collected using a hull-mounted SIMRAD EK-500 split-beam echo-sounder system operating at 38 and 120 kHz, and integrated to horizontal-vertical resolutions of $\sim 9\text{ m} \times 0.5\text{ m}$ in 1997 and 1999, and $\sim 9\text{ m} \times 1\text{ m}$ in 1998. Fish samples were collected along the transects with anchovy and Methot trawls, and used to determine fish size and species composition. Zooplanktons were collected using a 1-m multiple opening/closing net and environmental sampling system (MOCNESS) with 500- μm mesh (Schabetsberger et al., 2000). Conductivity–temperature–depth (CTD) profiles were taken at stations along each transect. Current information was collected using an acoustic doppler current profiler (ADCP) and surface temperature, salinity and fluorescence were measured. We restricted our analysis to transect line A, north

of St. Paul Island (Fig. 1), which has been the most comprehensively studied for juvenile pollock in the Pribilof Islands region (e.g., Schabetsberger et al., 2000; Brodeur et al., 2002; Ciannelli et al., 2002), and best represents the hydrographic structure typical of the eastern Bering shelf (Stabeno et al., 1999).

The Inner Front surveys collected acoustic data with an HTI model 244 split-beam system operating at 43 and 120 kHz. The transducers were towed beside the vessel 4 m from the hull and 2 m below the surface. Echo data were integrated to horizontal-vertical resolutions of $\sim 180 \text{ m} \times 2 \text{ m}$ in 1997, and $\sim 45 \text{ m} \times 1 \text{ m}$ in 1998 and 1999. CTD and chlorophyll data were collected at selected locations along the transects. Biological sampling included 1-m MOCNESS tows with a 500- μm mesh fished at night for zooplankton and juvenile fish.

The acoustic data were processed to identify and quantify shoals of fish. To maximize comparability of the biomass estimates between the Pribilof Islands and Inner Front, the same algorithm (Swartzman et al., 1999, 2002) was applied to both sets of surveys. All acoustically determined fish shoals were assumed to be age-0 pollock (Swartzman et al., 2002). This assumption is justified by the evidence of trawl catches accompanying both the Pribilof Islands and Inner Front surveys (Schabetsberger et al., 2000; Coyle and Pinchuk, 2002; Ciannelli et al., 2002; Swartzman et al., 2002), with over 95% of midwater trawl biomass being age-0 pollock.

Briefly, the acoustic algorithm imposes a threshold on all spatial echo-integration units (pixels) of a transect to identify those pixels in the range of backscattering strength expected for age-0 pollock aggregations at the appropriate frequency: -53 to -40 dB at 38 or 43 kHz, depending on the echo-sounder (120 kHz is used for zooplankton). The difference between 38 and 43 kHz is negligible to the backscattering threshold, as evidenced by target strength versus length plots calculated from the Kirchhoff ray-mode model (J. Horne and E. Hazen, University of Washington, personal communication). Pixels exceeding this threshold are morphologically filtered to retain only contiguous areas (shoals) greater than a given minimum size: 3 horizontal \times 2 vertical pixels (Swartzman et al., 2002).

After processing the data, acoustic biomass estimates for each fish shoal were calculated as the sum of the product of area backscattering coefficient (s_a ;

$\text{m}^2 \text{ m}^{-2}$) per pixel times pixel area (m^2), over all pixels in the shoal. Acoustic biomass thus represents an index linear-proportional to the actual biomass of the target organisms (Swartzman et al., 1999). Acoustic biomass totals were compared between survey locations, years, and habitats within each region.

To compare acoustic biomass distributions statistically, the data were averaged into 250 m along-transect (full water column) bins. The 250 m standard was used by Swartzman et al. (1999), who determined that statistical analyses were not sensitive to bin widths in the range of 100–1000 m. Mean, median and quartile values of the 250 m bins are summarized in Fig. 2. We used generalized additive models (GAM; Hastie and Tibshirani, 1990) to examine the variation in acoustic biomass as a function of distance along-transect. In order to standardize between transects having different lengths (Fig. 1) and to highlight the effect of fronts, distances were scaled such that the front habitat of each transect goes from 0 (nearshore boundary) to 1 (offshore boundary) (Fig. 3). We used ANOVA (analysis of variance) to test the biomass variability by survey location (random effect), year (random effect) and habitat (fixed effect), with the acoustic index values of the 250 m bins as replicate sampling units. Inner Front acoustic transects were only run during daytime, and therefore only daytime data were included for comparison. In the Inner Front surveys, 2–3 parallel transect tracks were occupied in some locations (Fig. 1), and the Pribilof Islands transect was run more than once per survey. Such repeated transect-runs were aggregated in the analysis.

Almost all transects covered all the three habitats. Transect-habitats (the horizontal extent of a transect in the nearshore, front, or offshore) comprised 22–87 250-m bins (~ 5.5 –22 km) in the Pribilof Islands and 7–350 bins (~ 1.75 –85 km) in the Inner Front, reflecting the greater extent of the stratified and frontal habitats in the Inner Front. Since the 250 m bins are contiguous sections of continuous survey tracks, we examined their acoustic index values for serial autocorrelation before computing the ANOVAs (ANOVA assumes non-autocorrelation, i.e., independence of the variates). With the transects running along bathymetric gradients, it is plausible that the pollock biomass distributions would follow onshore–offshore trends unrelated to autocorrelation. Therefore, we removed linear trend from each transect by modeling acoustic

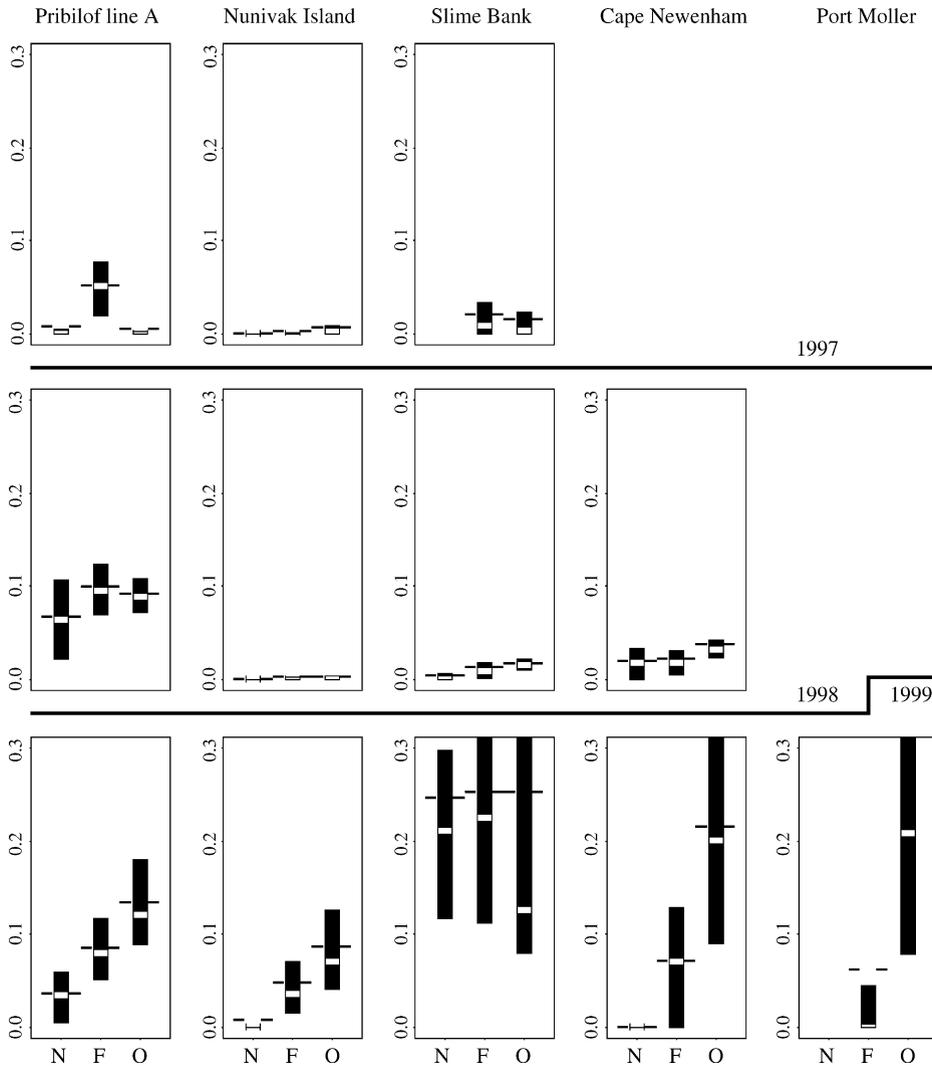


Fig. 2. Acoustically derived densities (no. m^{-3} ; standardized to 1 September) of age-0 pollock in the Pribilof Islands and Inner Front surveys, averaged by 250-m horizontal bins across the nearshore tidally mixed (N), transitional front (F), and offshore stratified (O) habitats. The box plots show the 25–75% quartiles (shaded areas), median (middle bars), and mean values (side bars).

biomass as a function of distance along-transect by linear regression, then tested for autocorrelation on the residuals of the regression. Residuals were randomly permuted 1000 times, and the sum of absolute differences between consecutive values was calculated for every permutation. Autocorrelation was considered significant if fewer than 50 of the 1000 permutations (i.e., $\alpha = 0.05$) had sums of absolute differences less than the sum of absolute differences for the original

vector of residuals. The permutation test was calculated for lags of 1–4 bins (the resolution of distance in the model is the 250 m bin length). Of 78 transect-habitats tested, 59 had significant linear trends, but only 13 showed significant autocorrelation in de-trended residuals at lag 1, and 6 at lag 4 (~1 km). We concluded that serial autocorrelation is not an important factor for these data and proceeded with the ANOVAs directly.

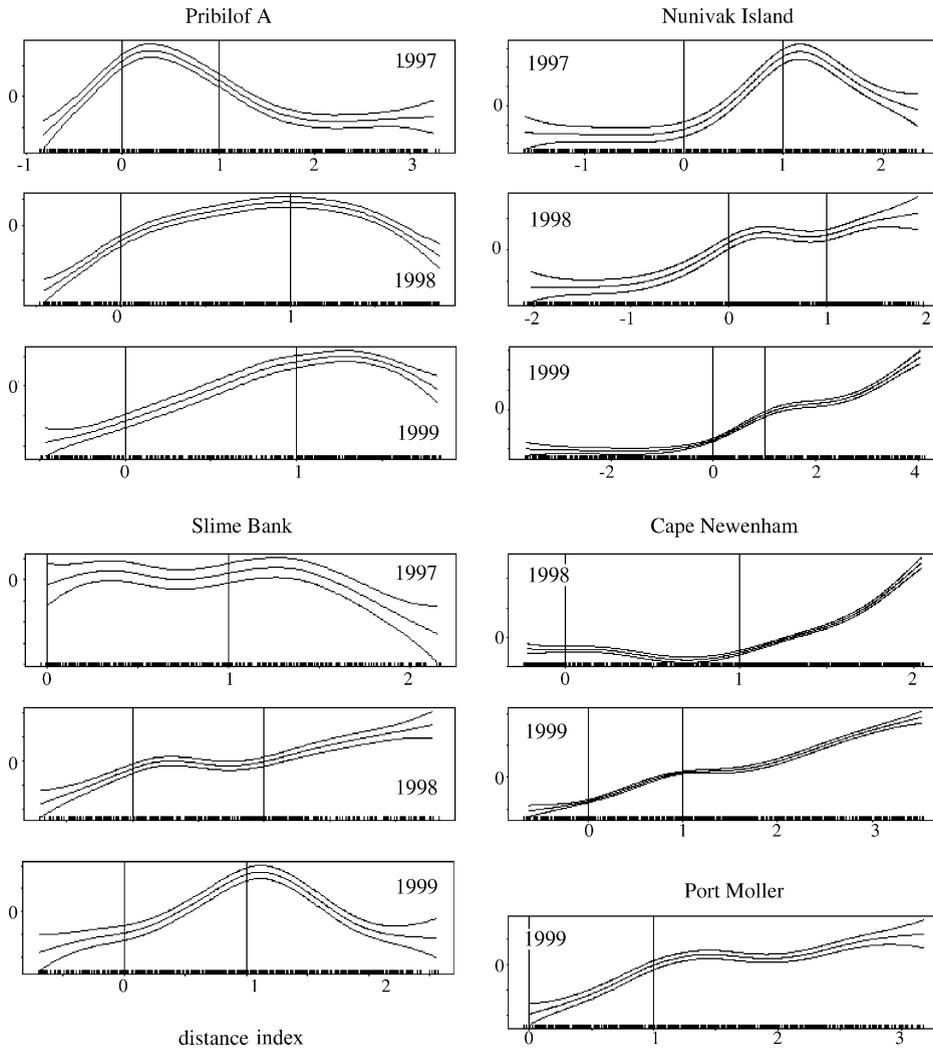


Fig. 3. GAM smooths ± 1 standard error of the effect of relative distance on age-0 pollock acoustic densities by year and survey location. Vertical lines on the plots mark the inner (0) and outer (1) boundaries of the hydrographic fronts.

All locations of the Inner Front were not surveyed in all years. To avoid the problem of empty “cells” (missing years at some Inner Front sites), separate analyses were done for blocks of complete data. Pribilof line A, Nunivak Island, and Slime Bank were surveyed in 1997, 1998 and 1999 for a $3 \times 3 \times 3$ ANOVA. Cape Newenham was added in 1998 and 1999; resulting in a $4 \times 3 \times 2$ design. Port Moller was further added to the survey in 1999, giving a 5×3 ANOVA. Note that this procedure results in the ANOVAs databases overlapping from one test to another (i.e., the tests are not independent).

2.3. Juvenile pollock trawl survey comparisons

Juvenile pollock were collected in net surveys across the southeast Bering Sea shelf during late July 1995–2002, aboard T/S *Oshoro Maru*. The survey grid was fixed (approximately 30 nmi or 54.7 km between the stations), although not all stations were sampled every year (e.g., Fig. 4). The survey used double oblique tows of a rectangular midwater-framed trawl (5-m² mouth opening) with 3 mm \times 2 mm oval mesh in the body of the net and 1 mm mesh in the cod end. A flow meter mounted in the mouth of the

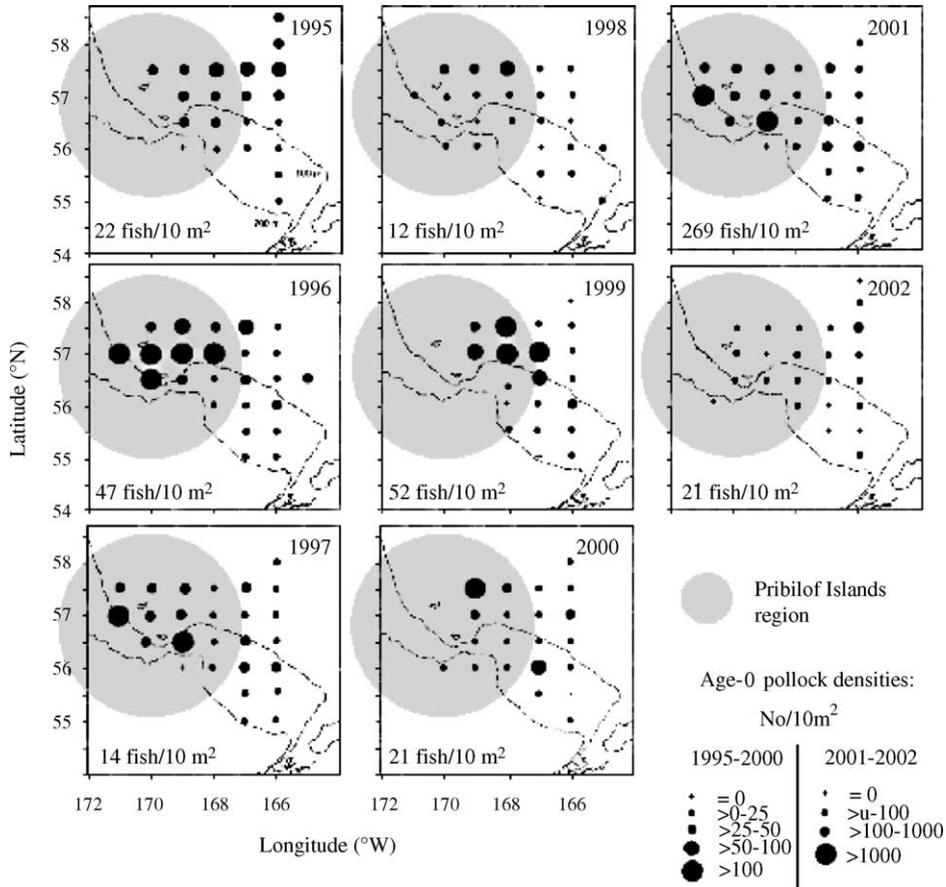


Fig. 4. Distribution of age-0 pollock in July 1995–2002 from trawls taken onboard the T/S *Oshoro Maru*.

net-recorded distance travelled. A count of age-0 pollock was taken immediately after each tow using either a sub-sample or the entire catch. The catch was then preserved and sent for further processing to the Polish Plankton Sorting and Identification Center, Szczecin. The counts were standardized to 10 m² area surveyed (Wilson and Brodeur, 1998).

To compare the abundance of age-0 pollock around the Pribilof Islands with surrounding areas of the Bering Sea required specifying the actual areal extent of the Pribilof Islands region, on ecologically relevant terms. We chose an area of the shelf having water depths less than 200 m (i.e., excluding the Bering Sea basin) and within a 100-nmi radius from the geometric center of the Pribilof Islands. This 100-nmi boundary was based on: (1) the size of the slow clockwise gyre circulating around the Pribilof Islands during summer,

which is thought to retain fish larvae advected from spawning areas (Stabeno et al., 1999); (2) the range of shelf break and shelf partition fronts around the Pribilof Islands (Flint et al., 2002); and (3) the area having the highest ecological efficiency for age-0 pollock. We defined ecological efficiency as the fraction of the energy cycled through the age-0 pollock, which was estimated to come from the region of interest. This was calculated using the ECOPATH compartment model parameterized to the Bering Sea (Ciannelli et al., 2004). The model was run with different area parameters (different radii around the Pribilof Islands). The 100-nmi radius gave the highest ecological efficiency for the ecosystem, compared to greater or lesser geographic areas.

To examine the hypothesis that abundance of juvenile pollock is elevated near the Pribilof Islands, catches within the 100-nmi radius, described above,

Table 1
Area (km²) for each region in the Eastern Bering Sea (excluding the basin area)

Region	Area (km ²)
Nunivak	41329
Inner Front	78703
Pribilof	66000
EBS South	88613
EBS Edge-South	23249
EBS North	88437
EBS Edge-North	79477

were contrasted with catches taken in the rest of the eastern Bering shelf survey area (Fig. 4). A fourth root transformation (Downing, 1979) was applied to the age-0 pollock catch counts to eliminate heteroscedasticity. We then used ANOVAs to test for differences among years, between the two strata (i.e., within or without the Pribilof region), and for interactions between strata and years.

2.4. Proportional contribution of the Pribilof Islands region

We estimated the proportion of total pollock recruitment in the eastern Bering Sea that can be attributed to the Pribilof Islands nursery, for the years 1997–1999. Average density of age-0 pollock in each year was calculated separately for seven regions, subdividing the eastern Bering Sea, one of which is the Pribilof region (Fig. 1; other than the Pribilof region, boundaries were devised by the Alaska Fisheries Science Center Resource Assessment and Conservation Engineering (RACE) division, to represent the natural strata based on bottom depth). The regions' average densities were then multiplied by their areas and summed with the Pribilof Islands' proportion calculated as the following ratio:

age-0 pollock prop._[Pribilof]

$$= \frac{\text{avg. density}_{[\text{Pribilof}]}}{\sum_{\text{region}}^7 \text{avg. density}_{[\text{region}]}} \times \frac{\text{area}_{[\text{Pribilof}]}}{\text{area}_{[\text{region}]}}$$

Topographic areas of the regions are given in Table 1. Average densities of the Pribilof region and the Nunivak region were calculated from the Pribilof Islands and Nunivak Island acoustic transects, respectively. The Inner Front region used the average of the Slime Bank,

Port Moller and Cape Newenham acoustic transects. EBS South, EBS North, EBS Edge-South and EBS Edge-North used the ratio of age-0 pollock abundance within the Pribilof region versus outside the Pribilof region, from the T/S *Oshoro Maru* surveys. Because surveys were conducted at various times of year, ranging from late July–mid-September, the acoustic densities used to compute the Pribilof, Nunivak and Inner Front fractions were standardized to a single reference date: 1 September. Thus, the age-0 pollock density of any given transect was factored by the average daily growth and mortality rates, multiplied by the number of days difference (+ or –) between the date of that transect and 1 September.

We estimated an average growth rate of 0.5 mm day⁻¹, by inspection of the difference in length modes between August and September age-0 pollock samples from 1996 and 1997 (A. Winter et al., unpublished data). Our estimate compares favorably to Walline (1983), who found an average growth of 0.55 mm day⁻¹ (range 0.34–0.69 mm day⁻¹) for age-0 pollock in the Bering Sea.

We estimated mortality from the average differences in acoustically determined densities (age-0 pollock m⁻³) between August and September surveys around the Pribilof Islands in 1996 and 1997. Given the retention characteristics of the Pribilof Islands system, described above, it is assumed that August and September surveys in either year sampled the same populations, although not verifiably the same fish. Numbers of age-0 pollock per m³ on each survey transect were calculated from the ratio of average area backscattering coefficient/average target backscattering cross-section (s_a/σ_{bs}), of age-0 pollock pixels identified according to the threshold and morphology algorithm described above. σ_{bs} (m²) represents the backscatter of a single target. Average lengths of age-0 pollock in each survey were obtained from Methot trawl samples collected during the cruises, and converted to σ_{bs} using an extrapolated Kirchhoff ray-mode model (J. Horne, University of Washington, personal communication). Thus, s_a/σ_{bs} (m² m⁻² m⁻²) gives the estimated number of age-0 pollock per m² of that pixel's horizontal area, and the overall density on a transect is obtained as:

$$\frac{\text{age-0 pollock}}{\text{m}^3 \text{ per transect}} = \frac{\sum ((s_a/\sigma_{bs}) \text{ pixel length})}{\text{depth} \times \text{transect length}}$$

Table 2

Instantaneous mortality rates (z) calculated from the difference between August and September acoustically determined densities of age-0 pollock

Year	Transect	Pollock/m ³ (August)	August–September days (Δ)	Pollock/m ³ (September)	z (day ⁻¹)
1996	A	0.400	40.18	0.122	0.030
	B	0.336	38.14	0.083	0.037
	C	0.223	39.03	0.116	0.017
	D	0.139	35.71	0.038	0.036
1997	A	0.173	44.39	0.005	0.081
	B	0.074	42.16	0.005	0.065
	C	0.142	41.27	0.002	0.106
	D	0.045	39.41	0.0006	0.110

where the summation is over all pixels in the transect identified as age-0 pollock. We used this measure of density as the index of abundance.

Instantaneous mortality rates (day⁻¹) were then calculated as:

$$z = \frac{\ln(\text{age-0 pollock } m_{[\text{August}]}^{-3} / \text{age-0 pollock } m_{[\text{September}]}^{-3})}{\Delta \text{ day}_{[\text{September} - \text{August}]}}$$

This calculation was performed separately for each Pribilof Islands transect A, B, C and D (Table 2). As our primary interest was transect A (see above) we retained the mortality values of 0.03 day⁻¹ (1996) and 0.08 day⁻¹ (1997). The three other transects serve as a measure of variability: 0.02–0.04 day⁻¹ in 1996 and 0.06–0.11 day⁻¹ in 1997. By comparison, Livingston (1993) estimated age-0 mortality in the eastern Bering Sea at 2.84 year⁻¹ (e^{2.84}/365 days = 0.047 day⁻¹). Yoklavich and Bailey (1990) and Hollowed et al. (1996), respectively estimated ≤ 0.02 and 0.014 day⁻¹ for the Gulf of Alaska. The difference between the Bering Sea and the Gulf of Alaska may be a function of cannibalism. While pollock cannibalism is low in the Gulf of Alaska (Brodeur and Wilson, 1996), it can account for upwards of 50% of the age-1+ diet in the Bering Sea (Dwyer et al., 1987). The strong 1996 year-class (e.g., Ianelli et al., 2003), when they were 1-year-old, could have exerted higher than average predation pressure on the 1997 age-0 pollock. Additionally, age-0 growth rates in the Gulf of Alaska are consistently higher than those reported for the Eastern Bering Sea, including the 0.50–0.55 mm day⁻¹, found by our estimation and estimates reported by Walline (1983), 0.60–1.2 mm day⁻¹; Bailey et al. (1996b), 0.91 mm day⁻¹; Brodeur and

Wilson (1996), 0.90 mm day⁻¹; Wilson (2000). The higher growth rates in the Gulf of Alaska may enable juveniles to grow faster and reduce their period of high risk of cannibalism and other predation.

3. Results

3.1. Comparison of Pribilof with Inner Front acoustic transects

Direct comparisons of pollock acoustic abundance between regions, habitats and years were made for 1997, 1998 and 1999 between survey data collected near the Pribilof Islands along-transect A, and across the Inner Front at four locations: at Slime Bank near Unimak Pass and Port Moller along the Aleutian inner front and Nunivak Island and Cape Newenham transects off the Yukon-Kuskokwin river delta (Fig. 1). Net sample data collected by Coyle and Pinchuk (2002) suggest that the abundance of both age-0 pollock and zooplankton in the Inner Front were about the same order of magnitude as in the Pribilof region. This was supported by the current acoustic data comparison. We found that the nearshore habitats in all transects and years generally had the lowest abundance of age-0 pollock, while the stratified offshore habitats generally had the highest abundance (Fig. 2). Also, there was general agreement in year-to-year changes in age-0 pollock abundance between all Inner Front and Pribilof transects, with 1997 having the lowest and 1999 generally having the highest abundance.

The acoustic pollock density comparisons among survey locations are shown in Fig. 2 and GAM plots of the along-transect variation in age-0 pollock density are shown in Fig. 3. Three of the five study locations

Table 3

Three-way factorial ANOVA of acoustic pollock density in Pribilof line A, Nunivak Island and Slime Bank; years 1997, 1998 and 1999

Source	d.f.	SSq	MSq	$F_{[v1, v2]}$	<i>p</i> -value
Location	2	1.42e – 10	7.11e – 11	2.28 _[2,4]	NS
Habitat	2	1.01e – 11	5.07e – 12	2.30 _[2,~2.6(a)]	NS
Year	2	1.03e – 10	5.14e – 11	1.65 _[2,4]	NS
Location:habitat	4	2.31e – 12	5.77e – 13	0.68 _[4,7]	NS
Location:year	4	1.25e – 10	3.12e – 11	312.77 _[4,5058]	<0.001
Habitat:year	4	9.90e – 12	2.47e – 12	2.92 _[4,7]	NS
L:H:Y	7	5.94e – 12	8.48e – 13	8.51 _[7,5058]	<0.001
Error	5058	5.04e – 10	9.97e – 14		

(a) Approximate denominator due to the mixed-model design (Zar, 1984).

were surveyed in all the 3 years. Pribilof line A had its lowest average pollock biomass in 1997, and the acoustic pollock biomass tended to be clustered near the inner boundary of the front. In 1998 and 1999 the pollock biomass density was higher, and more evenly distributed among habitats, with maximum concentration near the outer boundary of the front. By Nunivak Island, average pollock biomass was lowest in 1997 over the nearshore and front habitats, and lowest offshore in 1998. One acoustic transect was recorded in 1997, and showed pollock sign to be maximal near the outer boundary of the front. In 1998, density increased from nearshore outwards, leveled through the front and increased again offshore. In 1999, very little pollock sign was detected nearshore; the acoustic density increased through the front, leveled off around the outer boundary of the front, then increased again offshore. Slime Bank also had its overall lowest pollock densities in 1997 (although the near-shore was not surveyed that year). Pollock density decreased beyond the outer boundary of the front. In 1998, average pollock

densities increased from shore to the front, leveled off across the front then increased again offshore. In 1999, densities increased through the outer boundary of the front, then decreased. Cape Newenham was surveyed in 1998 and 1999. In 1998, pollock density increased from the outer part of the front towards offshore. In 1999, pollock density increased near-monotonically from nearshore to offshore, with a slight plateau at the outer boundary of the front. No pollock sign at all was detected in the nearshore region. Port Moller was surveyed only in 1999, from the front to offshore. Average pollock density increased in the offshore direction until just beyond the outer boundary of the front and then leveled off.

The results of ANOVA comparing acoustic pollock biomass among locations, habitats, and years showed that variability in pollock biomass appeared to be most strongly influenced by the interaction of survey location and year (Tables 3 and 4). Between 1997 and 1998, average biomass increased significantly on Pribilof line A, and showed no significant change for

Table 4

Three-way factorial ANOVA of acoustic pollock density in Pribilof line A, Nunivak Island, Slime Bank and Cape Newenham, years 1998 and 1999

Source	d.f.	SSq	MSq	$F_{[v1, v2]}$	<i>p</i> -value
Location	3	1.79e – 10	5.96e – 11	1.84 _[3,3]	NS
Habitat	2	1.04e – 10	5.20e – 11	3.18 _[2,~3.3(a)]	NS
Year	1	7.28e – 11	7.28e – 11	2.25 _[1,3]	NS
Location:habitat	6	3.60e – 11	5.99e – 12	3.21 _[6,6]	NS
Location:year	3	9.70e – 11	3.23e – 11	283.21 _[3,5793]	<0.001
Habitat:year	2	2.45e – 11	1.23e – 11	6.55 _[2,6]	<0.05
L:H:Y	6	1.12e – 11	1.87e – 12	16.38 _[6,5793]	<0.001
Error	5793	6.61e – 10	1.14e – 13		

(a) Approximate denominator due to the mixed-model design (Zar, 1984).

Table 5
Two-way factorial ANOVA of acoustic pollock density in all Pribilof and Inner Fronts areas, 1999

Source	d.f.	SSq	MSq	$F_{[v1, v2]}$	p
Location	4	3.21e-10	8.02e-11	200.65 _[4,3618]	<0.001
Habitat	2	1.99e-10	9.93e-11	7.21 _[2,7]	<0.05
Location:habitat	7	9.64e-11	1.38e-11	34.47 _[7,3618]	<0.001
Error	3618	1.45e-9	4.00e-13		

Nunivak Island and Slime Bank. Between 1998 and 1999, biomass increased slightly on Pribilof line A, Nunivak Island, and Cape Newenham, and increased strongly on Slime Bank (Fig. 2).

The main effect of survey location was significant in each year examined separately (for 1999, shown in Table 5): Slime Bank had higher biomass than either Pribilof line A or Nunivak Island in 1997; all locations were significantly different in 1998; and all locations except Pribilof line A and Slime Bank were significantly different in 1999 (Tukey's method for pairwise a posteriori comparisons, $\alpha = 0.05$, see also Fig. 2).

The main effect of oceanographic habitat was not significant in the multi-factorial ANOVAs of 1997 and 1998 (Tables 3 and 4). Nevertheless, the GAM analyses indicate significant along-transect variations in biomass distribution (Fig. 3). In every survey location, the peak of biomass was furthest inshore in 1997, and the gradient of biomass density increased through the front (from distance index 0 to 1 on Fig. 3 plots) more strongly in 1999 than in 1998. These data suggest a trend whereby the bulk of the age-0 pollock distribution resided increasingly offshore of the front over the course of the 3 years.

3.2. Net comparisons with other shelf and basin areas

Analysis of the T/S *Oshoro Maru* data from 1995 to 2002 gave significant differences among years ($p = 0.011$) and between the two strata ($p \ll 0.001$), but no significant interaction between year and stratum ($p = 0.101$). The mean abundance of age-0 pollock around the Pribilof Islands was significantly higher than abundance in the 'outside' stratum (Fig. 4). The ratio of abundance within/without the Pribilof region can be used as a rough annual index of juvenile pollock abundance around the Pribilof Islands, relative to the surrounding eastern Bering Sea shelf (Table 6).

Table 6
Ratio of age-0 pollock abundance per 10 m², within the Pribilof Islands region vs. the surrounding shelf area, based on the T/S *Oshoro Maru* survey data

Survey year	Abundance ratio
1995	0.808
1996	5.168
1997	1.035
1998	7.975
1999	3.782
2000	1.487
2001	1.281
2002	2.035
Mean	2.946

Combining these ratios with the survey densities, area measures, and sample date adjustments for growth and mortality, resulted in estimates of 0.125, 0.537 and 0.247 for the fraction of eastern Bering Sea age-0 pollock found within the Pribilof Islands region, in the years 1997, 1998 and 1999, respectively. These estimates are based on assumptions that: (1) growth and mortality rates calculated for the Pribilof Islands apply to the other areas; (2) the densities recorded on survey transects extrapolate to the surrounding areas; and (3) the (often considerable) density variability along-transects is unbiased. Nonetheless, the magnitude of these estimated fractions demonstrates that the Pribilof Islands region is an important nursery for age-0 pollock: in two of three years, this region represents a considerably larger fraction of the total age-0 pollock abundance than expected based on its area.

4. Discussion

The Pribilof Islands region has been identified as a region of unusually high production in the eastern Bering Sea, and is an important part of the 'green belt'

(Springer et al., 1996). This designation is supported by evidence from Sambroto et al. (1986) and Flint et al. (2002), which showed higher primary and secondary production in the Pribilof Islands frontal zones. Flint et al. (2002) argued that current and mixing processes around fronts bring higher nutrient concentrations to the euphotic zone, enhancing production.

Comparison of the acoustic densities of age-0 pollock around the Pribilof Islands, with the Inner Front areas, suggests that their abundance in the Pribilof region is no higher than in other eastern Bering Sea frontal regions (Fig. 2, Tables 3 and 4). However, the T/S *Oshoro Maru* data (Fig. 4) indicate age-0 pollock abundance around the Pribilof Islands to be almost always higher than on adjacent shelf and offshore stations. Other studies, based on data collected by the Alaska Fisheries Science Center Midwater Assessment and Conservation Engineering (MACE) program (unpublished), suggest that abundance of age-0 pollock around the Pribilof Islands changes significantly from year-to-year, relative to nearby shelf and basin areas. This is also supported by the T/S *Oshoro Maru* data (Fig. 4). Traynor and Smith (1996) found that on surveys in 1982, 1984 and 1985, the center of abundance for age-0 pollock occurred in the vicinity of the Pribilof Islands, but other areas had high abundance as well. By contrast, limited sampling in 1999 obtained highest abundances of age-0 gadids (presumed to be primarily pollock) in areas generally outside of the Pribilof Islands (Honkalehto et al., 2002). Although this appears inconsistent with our report of 1999 age-0 pollock abundance around the Pribilof Islands (cf. Fig. 2), the samples were taken at different times of the year. Considering the likely transport of age-0 pollock from spawning areas near Bogoslof Island and Unimak Pass (Stabeno et al., 2002), high densities along the shelf in July 1999 (as found by Honkalehto et al., 2002) may have ended up by September near the Pribilof Islands.

Continuous sampling of age-0 pollock in the greater shelf over the July to September period would help to provide a better indication of interannual spatial variability as well as within-season temporal variability. The timing of sampling is important, since there appears to be evidence for different spatial distributions among adult pollock year-classes (Buckley et al., 2001, in Swartzman, 2004). That may change the dominance among various spawning habitats in different years, in turn affecting the timing of arrival of different cohorts

of age-0 juveniles to the Pribilof region. A comparison between the distributions of age-0 pollock sampled in early July 1999 (Honkalehto et al., 2002), and sampled again in late July 1999 (T/S *Oshoro Maru*; Fig. 4), shows more pollock close to the Pribilof Islands by late July and suggests significant within-season change of the distribution over that summer. The pattern may have been different, however, in 1984 and 1985, when age-0 pollock abundance was highest near the Pribilof Islands in early July (Traynor and Smith, 1996) and in 1987, as shown by data from the Russian/U.S. survey (see Brodeur et al. (1999) for sampling details) aboard the R/V *Darwin* (Fig. 5), when abundance was high near the Pribilof Islands, but higher still near Unimak Pass. Changes in spatial patterns of age-0 pollock in early summer could result from changes in the spawning distribution of different cohorts, as well as from interannual differences in larval advection and cannibalism (Wespestad et al., 2000).

It appears that from late July onward, densities of age-0 pollock are generally elevated around the Pribilof Islands and other frontal areas of the eastern Bering Sea compared to shelf and basin areas. However, the Pribilof Islands' densities are not significantly higher than in other frontal areas. The elevated concentrations of seabirds and marine mammals attracted to the Pribilof area (Dragoo et al., 2000) may be due to the relative isolation of the Pribilof Archipelago, and to the close proximity of its tidal fronts to shore, rather than to increased prey abundance. Further, we found that while age-0 pollock densities are higher in the frontal habitat than nearshore, they are generally highest of all in the stratified waters offshore (Figs. 2 and 3). By contrast, Brodeur et al. (1997) observed higher concentrations of age-0 pollock inshore of the Pribilof Islands front in 1994 and 1995, although a bioenergetics model for 1995 suggested growth and feeding potential to be highest offshore (Ciannelli, 2002). The greater depths of the stratified offshore zone may provide protection from predation for zooplankton and age-0 pollock, both of which undergo diel migration (Schabetsberger et al., 2000; Swartzman et al., 2002). Predation by seabirds and mammals may also be reduced in the stratified zone through its greater distance from shore, and the wider area through which the age-0 pollock can disperse. Finally, stratified waters adjacent to frontal zones may have enhanced production due to transport coming

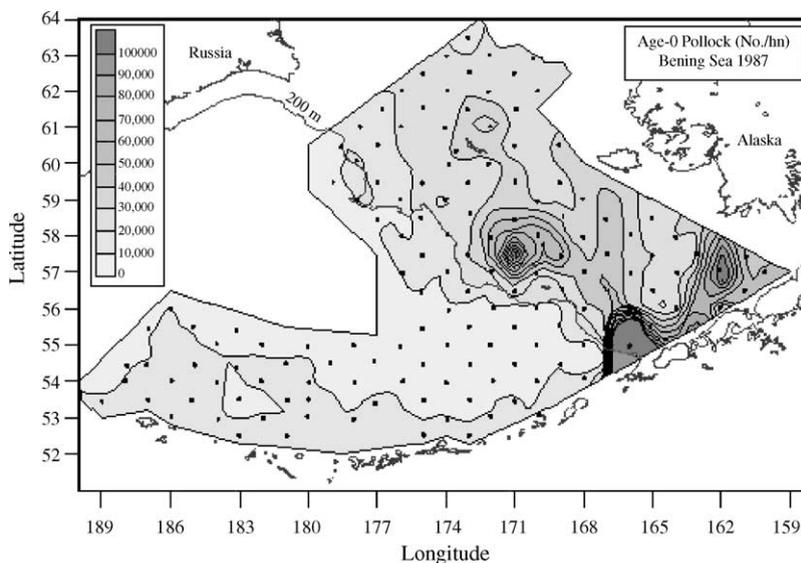


Fig. 5. Age-0 pollock abundance (expressed as catch per hour) during summer of 1987, from fine-mesh midwater trawls taken onboard the R/V *Darwin*.

from the front. The stratified habitat at the distal end of Pribilof transect A (away from the islands) did not show any reduction in age-0 pollock abundance (Swartzman et al., 2002), while the T/S *Oshoro Maru* data showed reduced age-0 pollock abundance in shelf regions more remote from the Pribilof Islands. We hypothesize that the importance of the Pribilof Islands as a nursery area is represented not so much by elevated densities of age-0 pollock, compared to other frontal regions, but by the large area of prime feeding habitat they encompass. Though centered around two small islands, the Pribilof region is only about 16% smaller than the Inner Front region, an extensive area along the Aleutian Islands and the south edge of mainland Alaska to Cape Newenham (Fig. 1, Table 1).

The dominance of particular pollock year-classes, together with their differences in spatial distributions and spawning locations, may explain why in some years early July surveys showed high abundance of age-0 pollock around the Pribilof Islands (e.g., 1984, 1985 and 1987), while in other years (e.g., 1999; Honkalehto et al., 2002) abundance around the Pribilof Islands was lower than in adjacent areas. From 1996 to 2002, the abundance of age-0 pollock sampled in late July by the T/S *Oshoro Maru*, was consistently higher near the Pribilof Islands than in surrounding areas. Perhaps as the age-0 pollock grow and become more able to maintain

position by active swimming, they tend to congregate near the Pribilof Islands. Earlier in the year, happenstance of hatch locality and advection may determine how abundantly age-0 pollock occur near the Pribilof Islands.

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References

- Bailey, K.M., 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Mar. Ecol. Prog. Ser.* 198, 215–224.

- Bailey, K.M., Brodeur, R.B., Hollowed, A.B., 1996a. Cohort survival patterns of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska: a critical factor analysis. *Fish Oceanogr.* 5 (Suppl. 1), 179–188.
- Bailey, K.M., Brown, A.L., Yoklavich, M.M., Mier, K.L., 1996b. Interannual variability in growth of larval and juvenile walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1983–91. *Fish Oceanogr.* 5 (Suppl. 1), 137–147.
- Baretta, L., Hunt Jr., G.L., 1994. Changes in the numbers of cetaceans near the Pribilof Islands, Bering Sea, between 1975–78 and 1987–89. *Arctic* 47, 321–326.
- 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. *Fish Oceanogr.* 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. In: Proceedings of the GLOBEC International Marine Science Symposium on Ecosystem Dynamics, pp. 238–251.
- 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 structures of the Bering Sea. *Deep Sea Res. II* 49, 6051–6068.
- 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. Alaska Sea Grant Pub. AK-SG-97-01, pp. 573–589.
- Brodeur, R.D., Wilson, M.T., Walters, G.E., Melnikov, I.V., 1999. Forage fishes in the Bering Sea: distribution, species associations, and biomass trends. In: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea. Alaska Sea Grant, pp. 509–536.
- Buckley, T.W., Greig, A., Ianelli, J., Livingston, P., Walters, G., 2001. Spatial distribution and ontogenetic movement of walleye pollock in the eastern Bering Sea presented at the North Pacific Marine Science Organization (PICES) Victoria, BC Canada, 5–13 October, 2001. Alaska Fisheries Science Center, 7600 Sandpoint Way NE, Seattle, WA 98115.
- Ciannelli, L., 2002. Effects of spatial variability, associated with a frontal structure, on predictions of age-0 walleye pollock (*Theragra chalcogramma*) growth around the Pribilof Islands, Bering Sea. *Estuar. Coast. Shelf Sci.* 55, 151–165.
- Ciannelli, L., Brodeur, R.D., Swartzman, G.L., Salo, S., 2002. Physical and biological factors influencing the spatial distribution of age-0 walleye pollock around the Pribilof Islands, Bering Sea. *Deep-Sea Res. II* 49, 6109–6126.
- Ciannelli, L., Robson, B.W., Francis, R.C., Aydin, K., Brodeur, R.D., 2004. Boundaries of open marine ecosystems: an application to the Pribilof Archipelago, southeast Bering Sea. *Ecol. Appl.* 14, 942–953.
- Coyle, K.O., Pinchuk, A.I., 2002. The abundance and distribution of euphausiids and zero-age pollock on the inner shelf of the southeast Bering Sea near the Inner Front in 1997–1999. *Deep-Sea Res. II* 49, 6009–6030.
- Decker, M.B., Hunt Jr., G.L., 1996. Foraging by murre (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Mar. Ecol. Prog. Ser.* 139, 1–10.
- Downing, J.A., 1979. Aggregation, transformation, and the design of benthos sampling programs. *J. Fish Res. Board Can.* 36, 1454–1463.
- Dragoo, D.E., Byrd, G.V., Irons, D.B., 2000. Breeding status and population trends of seabirds in Alaska in 1999. U.S. Fish and Wildlife Service Report AMNWR 2000/02.
- Dwyer, D.A., Bailey, K.M., Livingston, P.A., 1972–1984. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the Eastern Bering Sea, with special reference to cannibalism. *Can. J. Fish Aquat. Sci.* 44.
- 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 of the Bering Sea. *Deep-Sea Res. II* 49, 6069–6093.
- Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman & Hall/CRC, Boca Raton, 335.
- Hollowed, A.B., Bailey, K.M., Brodeur, R.D., 1996. Natural mortality estimates of juvenile walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska. NOAA Tech. Rep. NMFS 126, 218–219.
- Honkalehto, T., Patton, W., De Blois, S., Williamson, N., 2002. Echo-integration-trawl survey results for walleye pollock (*Theragra chalcogramma*) on the Bering Sea shelf and slope during summer 2000. U.S. Department of Commerce NOAA Tech. Memo. NMFS-AFSC-126, p. 66.
- Hunt Jr., G.L., Stabeno, P.J., 2002. Climate change and the control of energy flow in the southeastern Bering Sea. *Prog. Oceanogr.* 55, 5–22.
- Hunt Jr., G.L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A., 2002. The eastern Bering Sea: evidence for change and a new hypothesis linking ecosystem control and climate. *Deep-Sea Res. II* 49, 5821–5853.
- Ianelli, J.N., Barbeaux, S., Walters, G., Williamson, N., 2003. Eastern Bering Sea Walleye Pollock Stock Assessment. Stock Assessment and Fishery Evaluation Report. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, 88.
- Kachel, N.B., Hunt, G.L., Salo, S.A., Schumacher, J.D., Stabeno, P.J., Whitley, T.J., 2002. Characteristics and variability of the inner front of the southeastern Bering Sea. *Deep-Sea Res. II* 49, 5889–5909.
- Kowalik, Z., Stabeno, P., 1999. Trapped motion around the Pribilof Islands in the Bering Sea. *J. Geophys. Res.* 104, 25667–25684.
- 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. *Mar. Ecol. Prog. Ser.* 102, 205–215.
- Macklin, S.A., 1999. Bering Sea FOCI. In: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea. Alaska Sea Grant Press, pp. 733–751.
- Macklin, S.A., Hunt Jr., G.L., Overland, J.E., 2002. Collaborative research on the pelagic ecosystem of the southeastern Bering Sea shelf. *Deep-Sea Res. II* 49, 5813–5819.
- Napp, J.M., Kendall Jr., A.W., Schumacher, J.D., 2000. A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. *Fish Oceanogr.* 9, 147–162.

- Napp, J.M., Baier, C.T., Brodeur, R.D., Coyle, K.O., Shiga, N., Mier, K., 2002. Interannual and decadal variability in zooplankton communities of the southeast Bering Sea. *Deep Sea Res. II* 49, 5991–6008.
- Nishimura, A., Mito, K.-I., Yanagimoto, T., 1996. Hatch date and growth estimation of juvenile walleye pollock, *Theragra chalcogramma*, collected in the Bering Sea in 1989 and 1990. NOAA Tech. Rep. NMFS 126, 81–88.
- Robson, B.W. (Ed.), 2002. Fur seal investigations, 2000–2001, NOAA Tech. Memo. NMFS-AFSC-134, p. 80.
- Sambroto, R.N., Niebauer, H.J., Goering, J.J., Iverson, R.L., 1986. Relationships among vertical mixing, nitrate uptake and phytoplankton growth during the spring bloom in the Southeast Bering Sea middle shelf. *Cont. Shelf Res.* 5, 161–198.
- 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 the Pribilof Islands, Bering Sea. *ICES J. Mar. Sci.* 57, 1283–1295.
- Springer, A.M., McRoy, C.P., Flint, M., 1996. The Bering Sea Green Belt. *Fish Oceanogr.* 5, 205–223.
- Stabeno, P.J., Schumacher, J.D., Salo, S.A., Hunt, G.L., Flint, M., 1999. Physical environment around the Pribilof Islands. In: Loughlin, T.R., Ohtani, K. (Eds.), *Dynamics of the Bering Sea*. Alaska Sea Grant Press, pp. 193–215.
- Stabeno, P.J., Reed, R.K., Napp, J.M., 2002. Transport through Unimak Pass. Alaska. *Deep Sea Res. II* 49, 5919–5930.
- Swartzman, G. 2004. Pribilof Islands: A microcosm for the Southeast Bering Sea. Part 4. In: Macklin, Hunt (Ed.), *The Southeast Bering Sea ecosystem: implications for marine resource management* (final report: SEBSCC). NOAA COP Decision Analysis Series no. 24, Silver Spring, MD, pp. 192.
- Swartzman, G., Brodeur, R., Napp, J., Hunt, J., Demer, D., Hewitt, R., 1999. Spatial proximity of age-0 walleye pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska. *ICES J. Mar. Sci.* 56, 545–560.
- Swartzman, G., Napp, J., Brodeur, R., Winter, A., Ciannelli, L., 2002. Spatial patterns of pollock and zooplankton distribution in the Pribilof Islands. Alaska nursery area and their relationship to pollock recruitment. *ICES J. Mar. Sci.* 59, 1167–1186.
- Traynor, J., Smith, D., 1996. Summer distribution and abundance of age-0 walleye pollock, *Theragra chalcogramma*, in the Bering Sea. NOAA Tech. Rep. NMFS 126, 57–59.
- Walline, P.D., 1983. Growth of larval and juvenile walleye pollock related to year-class strength. Ph.D. dissertation, University of Washington, Seattle, p. 144.
- Wespestad, V.G., Fritz, L.W., Ingraham, W.J., Megrey, B.A., 2000. On relationships between cannibalism, climate variability, physical transport and recruitment success of Bering Sea walleye pollock (*Theragra chalcogramma*). *ICES J. Mar. Sci.* 57, 272–278.
- Wilson, M.T., 2000. Effects of year and region on the abundance and size of age-0 walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska, 1985–1988. *Fish Bull.* 98, 823–834.
- Wilson, M.T., Brodeur, R.D., 1998. Summer collections of age-0 pollock in the eastern Bering Sea aboard the *Oshoro Maru*. *Mem. Fac. Fish Hokkaido Univ.* 45, 62–63.
- Yoklavich, M.M., Bailey, K.M., 1990. Hatching period, growth and survival of young walleye pollock *Theragra chalcogramma* as determined from otolith analysis. *Mar. Ecol. Prog. Ser.* 64, 13–23.
- Zar, J.H., 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ, p. 718.