ICES Journal of Marine Science, 63: 1118–1135 (2006)
doi:10.1016/j.icesjms.2006.03.014

Interannual changes in distribution of age-0 walleye pollock near the Pribilof Islands, Alaska, with reference to the prediction of pollock year-class strength

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Winter, A. G., and Swartzman, G. L. 2006. Interannual changes in distribution of age-0 walleye pollock near the Pribilof Islands, Alaska, with reference to the prediction of pollock year-class strength. – ICES Journal of Marine Science, 63: 1118–1135.

Walleye pollock (*Theragra chalcogramma*) is a key species and a major commercial fishery target in the eastern Bering Sea (EBS). Recruitment of juveniles to the adult stock is largely determined by first-year survival in favourable nursery areas, and the waters around the Pribilof Islands are an important nursery area. Based on a six-year acoustic survey programme (September 1994–1999) to investigate abundance and distribution variations of age-0 pollock, we developed a set of predictive indices relating the age-0 Pribilof population to the EBS pollock stock at recruitment (age-3). EBS year-class strength at recruitment correlates with age-0 density, the spatial relationship between juveniles and euphausiids, and the degree of centricity of the age-0 distributions around the Pribilof Islands, i.e. neither too far inshore nor offshore. Seabird numbers and density ratios of predatory groundfish also influenced age-0 pollock distribution, but did not provide consistent discrimination among year classes. We hypothesize that age-0 pollock must transition from a copepod diet to a euphausiid diet by September to maximize their survival potential and to establish a strong adult cohort.

Keywords: acoustic surveys, Pribilof Islands, walleye pollock, year-class strength.

Received 29 September 2005; accepted 17 March 2006.

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Introduction

Predicting juvenile recruitment is considered key to managing marine fish stocks that have variable abundance (Russell and Yonge, 1936; Bradford, 1992). In the eastern Bering Sea, Alaska, juvenile stages have been the focus of studies on walleye pollock (*Theragra chalcogramma*) year-class strength (Brodeur *et al.*, 1996; Macklin *et al.*, 2002). Walleye pollock is a key species in the Bering Sea ecosystem (Macklin *et al.*, 2002) and is the mainstay of major commercial fisheries (National Research Council, 1996; Ianelli, 2005). Variability of eastern Bering walleye pollock year classes (cf. Table 1.14 of Ianelli *et al.*, 2003) is compatible with a lognormal distribution. Hennemuth *et al.* (1980) first proposed this statistical distribution for marine fish stocks because of the common characteristic of having mostly years of low-to-average abundance interspersed with occasional very strong ones.

Efforts to develop a year-class strength index for walleye pollock (hereafter referred to as pollock) have focused on the waters surrounding the Pribilof Islands, near the edge of the eastern Bering Sea (EBS) shelf (Swartzman *et al.*, 2002, 2005; Winter *et al.*, 2005). The Pribilof area has been noted as a centre of abundance of age-0 juveniles (Nishimura *et al.*, 1996; Traynor and Smith, 1996) and characterized as a pollock nursery (Brodeur, 1998; Macklin *et al.*, 2002; Swartzman *et al.*, 2002). Swartzman *et al.* (2005) synthesized the results of multiple surveys and estimated that in some years, as much as half the EBS stock of age-0 pollock may come from the Pribilof Islands. Schumacher and Macklin (2004) cited evidence suggesting that the age-0 pollock population around the Pribilof Islands can provide a useful index of year-class strength.

Research cruises by the National Oceanic and Atmospheric Administration (NOAA) surveyed the Pribilof area each year in September from 1994 through 1999, with emphasis on measuring the distribution of age-0 pollock and associated biological and oceanographic data. Through summer and autumn, the Pribilof area is structured by a hydrographic front that separates the tidally mixed nearshore zone from stratified offshore waters (Stabeno *et al.*, 1999). Zooplankton aggregate at this front (Coyle

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and Cooney, 1993) and they attract consumers including seabirds and juvenile and adult pollock (Kinder *et al.*, 1983; Decker and Hunt, 1996; Springer *et al.*, 1996; Brodeur *et al.*, 2000). The limited foraging ranges of age-0 pollock suggest that close proximity to prey is an important determinant of feeding success, especially in times of limited prey abundance (Swartzman *et al.*, 1999a). Predation pressure can force juvenile pollock away from their food (Swartzman *et al.*, 2002), but stratification of the water, where present, may keep juveniles segregated from cannibalistic adults (Francis and Bailey, 1983; Bailey, 1989; Swartzman *et al.*, 2002).

The 1994–1999 NOAA Pribilof cruises collected primarily two-frequency acoustic data which, through validated algorithms, are scalable as biomass indices of fish and zooplankton (Swartzman *et al.*, 2002). We utilized this database to investigate the potential of Pribilof age-0 pollock as an early predictor for year-class strength by analysing the acoustically derived biomass indices in the context of (i) the distribution of age-0 pollock in relation to the distribution of euphausiids, a major prey item (Brodeur *et al.*, 2000; Schabetsberger *et al.*, 2000, 2003; Ciannelli *et al.*, 2004); (ii) the distribution of age-0 pollock in relation to the distribution of groundfish and seabird predators; and (iii) the distribution of age-0 pollock in relation to frontal regions and relative north–south (latitudinal) distance from the Pribilof Islands. Interannual variations in these acoustic density and distribution relationships were then compared with the subsequent abundance of EBS pollock year classes at recruitment (age-3). Specifically, we tested the null hypothesis that age-0 population abundance alone in the Pribilof area predicts year-class strength in the EBS. The alternative hypotheses were that one or more of the three relationships investigated (age-0 pollock distribution vs. euphausiid prey, predators, distance) are important in predicting year-class strength.

Methods

Surveys

The Pribilof surveys were carried out each year between 5 September and 22 September (exact dates varied by year), and run along four transect lines radiating north and south of St Paul and St George Islands (Figure 1). In addition to acoustic sampling, CTD casts were used to derive temperature profiles, bird counts at the sea surface were recorded, and trawl data were collected. Transect lines were perpendicular to the frontal gradient, and each transect consisted of distinct habitat regions on the basis of its hydrographic or bathymetric structure (Swartzman *et al.*, 1999a, 2002). Transect A was divided into a tidally mixed nearshore region, a front region that is partially stratified, and an offshore, fully stratified region. The nearshore boundary of the front region was defined at the first CTD station, showing a well mixed (or weakly stratified) vertical profile. The offshore boundary of the front was defined at the location of the stratified region, where the depth range of the thermocline increased by a factor of two over its average width farther offshore (Stabeno *et al.*, 1999). By these criteria, the front extended 13.5–28.5 km from shore in 1994, 7–33 km from shore in 1995, 6–18 km from shore in 1996, 6–30 km from shore in 1997 (Ciannelli *et al.*, 2004), and 8–26 km from shore in 1998 and 1999 (Swartzman *et al.*, 2002). On transects B, C, and D, the tidally mixed nearshore zones

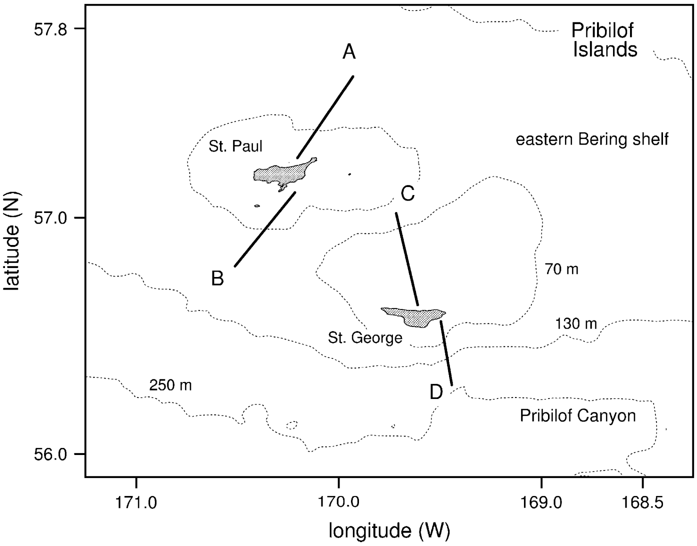

Figure 1. Pribilof Islands study area, showing transects A–D surveyed in 1994–1999. The 70 m isobath delimits shallow and deep habitat regions on transects B and C; the 130 m isobath delimits slope and basin regions on transect D. A depth of 250 m represents the approximate maximum that can be sounded at 120 kHz.

were absent or <1 km wide, and therefore not considered a separate habitat. Instead, transects B and C were each divided into a shallow and a deep region by the 70 m isobath. Transect D was divided into a slope region (<130 m) and a basin region (>130 m; Swartzman *et al.*, 2002).

Generally, each transect was passed over at least once during daylight and once at night per survey year (see Table 1 of Swartzman *et al.*, 2002, for a summary of transect passes). Exceptions were transects C and D in 1994 and B in 1999, which were run by day only. Some transect passes included twilight, and to quantify the proportion of each pass' runtime in daylight we calculated the sum of multiplying 1, 0.5, 0, times the fraction of extent by day, twilight, and night (available from interpolating the sunrise, sunset, and twilight time points of the corresponding date and coordinates on the US Naval Observatory website: aa.usno.navy.mil).

Echo-integration

Acoustic data were collected by the survey ship at 38 and 120 kHz using a hull-mounted SIMRAD EK-500 split-beam echosounder. In 1994 only, the 38 and 120 kHz frequencies were recorded separately on two survey ships operating in tandem. The echo data were integrated to units (pixels) of approximately 9 m horizontal × 0.5 m vertical resolution (1.0 m vertical resolution in 1998), and processed according to the image-analysis methods described in Swartzman *et al.* (1999a, 2002). Briefly, pixel echo-integration was classified as fish if it was within the threshold range -53 dB to -40 dB backscattering strength at 38 kHz. Echo-integration was classified as zooplankton if it was within the threshold range -62 dB to -45 dB at 120 kHz; plus ≥ 5 dB higher at 120 kHz than at 38 kHz. Acoustic evidence to distinguish fish from zooplankton by $120 - 38$ kHz differencing is discussed in Miyashita *et al.* (1997) and Kang *et al.* (2002). For the 2× lower pixel resolution in 1998, the $120 - 38$ kHz differencing spread was rescaled to $5\ \text{dB} \times (0.5\ \text{m}/1\ \text{m})^{0.5} = 3.54$ dB, according to the calibration algorithm in Swartzman (2004). Pixels retained by the respective thresholds were morphologically filtered (Haralick and Shapiro, 1992) to delineate contiguous shoals of fish or zooplankton, while scattered or isolated pixels were eliminated. Figure 2a shows an example of a transect with fish backscatter in blue and zooplankton backscatter in red. Shading of the pixels in Figure 2a is proportional to backscatter strength.

The area backscattering coefficient of a pixel, s_a ($\text{m}^2\ \text{m}^{-2}$) (where backscattering strength, $\text{dB} = 10 \log_{10}(s_a)$; MacLennan *et al.*, 2002), is linearly proportional to the sum of individual acoustic targets (i.e. fish or zooplankton) within the perimeter of that pixel (Foote, 1983). By extension, Σs_a of contiguous pixels making up a shoal, normalized for the horizontal and vertical resolutions of the pixels, represents an acoustic index of biomass within that shoal. Acoustic fish shoals in the Pribilof surveys were assumed to be juvenile pollock, because juvenile pollock comprised $>90\%$ of fish catch in trawls taken along transects (Brodeur *et al.*, 2002; Schabetsberger *et al.*, 2003). Acoustic zooplankton shoals were assumed to be euphausiids. Target-strength models (Stanton *et al.*, 1993) together with survey catch data indicate that euphausiids of 15–25 mm body length (*Thysanoessa* spp.; Schabetsberger *et al.*, 2000, 2003) would dominate the acoustic backscatter in the zooplankton threshold range, as described above (Swartzman *et al.*, 2002).

Data analyses of these acoustic indices assumed that the algorithms correctly partition age-0 pollock and euphausiid components from the backscatter integration. These assumptions were included in the variance components of the analyses, and the same algorithms were applied to each year's data.

Acoustic target strength

Individual target-strength values (TS) were collected by the echosounder system in conjunction with echo-integration. TS values can be converted to estimates of fish length through standard equations in the fisheries acoustics literature (Love, 1971; Foote and Traynor, 1988; Traynor, 1996). Strong TS can thus be taken to represent fish of a size likely to be predators of age-0 pollock (as shown in Figure 2b for one acoustic transect). Around the Pribilof Islands, predators are predominantly adult and sub-adult pollock, followed by Pacific cod (*Gadus macrocephalus*) (Lang *et al.*, 2003), which present a similar acoustic profile as inferred from studies of the morphometrically analogous (Schultz and Welander, 1935) congener *Gadus morhua* (Foote, 1987; Rose and Porter, 1996). As pollock and Pacific cod are acoustically indistinguishable at this scale of analysis, we refer to them together as groundfish predators. We used Foote and Traynor's (1988) standard equation of mean acoustic target strength at 38 kHz as a function of pollock fork length (L, in cm):

$$\text{TS} = 20 \log L - 66.0.$$

For the 1994 survey, TS data were not available at 38 kHz and we derived target strengths from the 120 kHz data using Hazen and Horne's (2004) equation:

$$\text{TS} = 20 \log L - 68.5.$$

Groundfish lengths derived from these equations were divided into four categories corresponding to relationships between nominal year class and length cited in Dwyer *et al.* (1987) for pollock ages 1, 2, 3, and 4+ (Table 1). TS values were upper-limited to the equivalent of 100 cm, based on Hart's (1973) length maximum for Pacific cod (slightly bigger than Hart's reported length maximum of pollock: 91 cm). TS values corresponding to age-0 pollock lengths were based on extrapolations of mean backscattering cross-section σ_{bs} ($\text{TS} = 10 \log_{10}(\sigma_{\text{bs}})$) from the Kirchhoff ray-mode model (J. Horne, University of Washington, pers. comm.). Dates of age-0 pollock surveys varied interannually, so a length range for age-0 pollock was set for

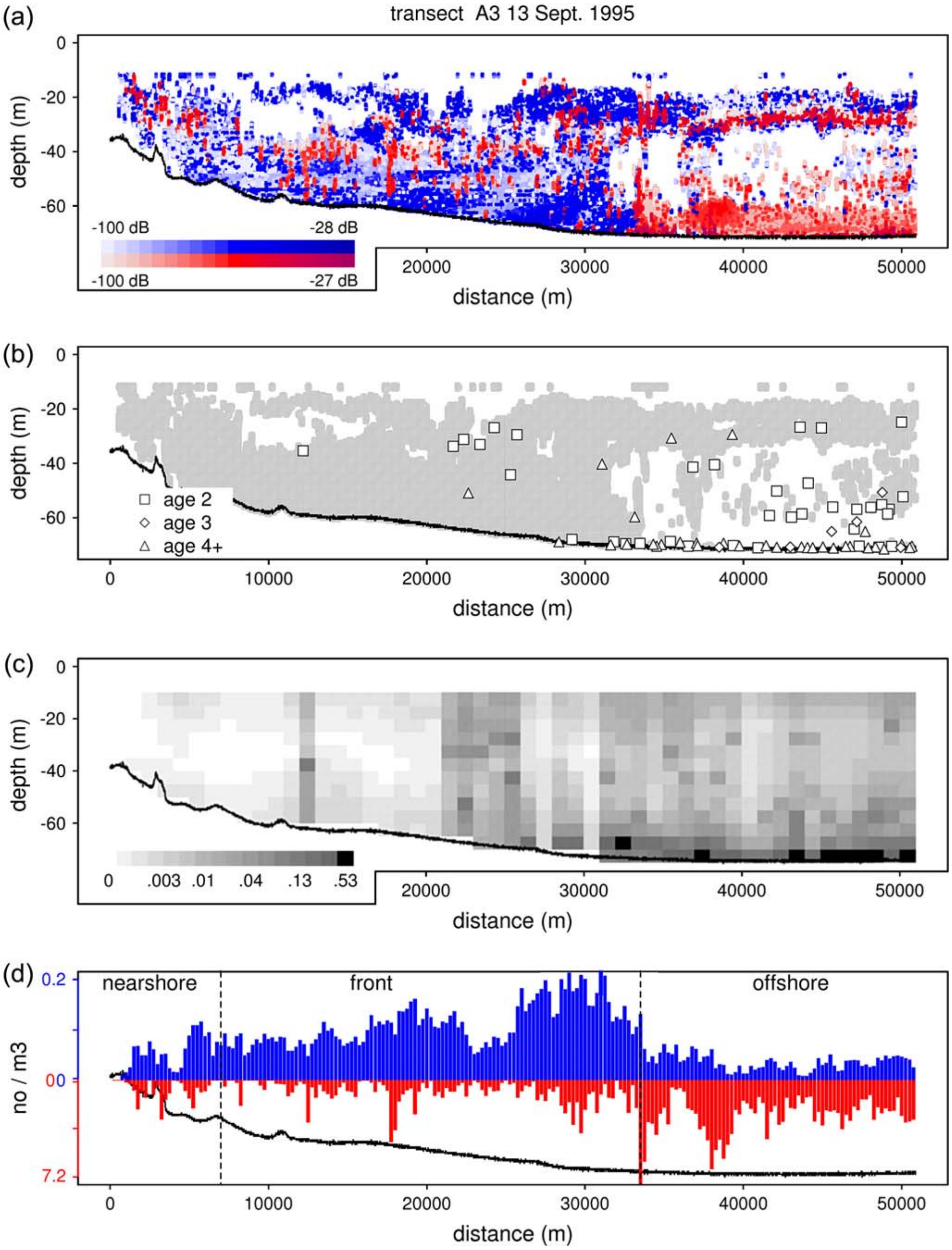

Figure 2. One example survey transect pass (A3 95) representing: (a) age-0 pollock (blue) and euphausiid (red) echo-integration pixels, (b) individual target-strength data corresponding to age-2, age-3, and age-4+ pollock, superimposed on the age-0 pollock echo-integration distribution, (c) the TS ratio distribution of ages 2, 3, and 4+ over age-0 pollock estimated from the TS processing algorithm, by 5 × 1000 m bins, (d) depth-normalized densities of age-0 pollock (blue) and euphausiids (red) from the echo-integration, by 250 m bins, with habitat region boundaries indicated as vertical lines.

each year separately based on Methot trawl samples. As measured target strength of any fish varies with its tilt angle (Blaxter and Batty, 1990; MacLennan *et al.*, 1990), TS thresholds must be considered an approximate index of true size categories. However, observations by Horne (2003, cf. his Figure 5) showed that pollock predominantly maintain a horizontal aspect without bias towards positive or negative inclination or lateral roll. We therefore considered the categorization sufficiently precise for qualitatively discriminating size groups.

Table 1. Lengths-at-age (from Dwyer *et al.*, 1987) and equivalent target strengths (from Foote and Traynor, 1988) of pollock age categories.

Age category	Nominal length (cm)	Equivalent TS (dB)
0*	1.5–7	−65.05 to −45.65
1	13–22	−43.72 to −39.15
2	22–30	−39.15 to −36.46
3	30–35	−36.46 to −35.12
4+	35–100	−35.12 to −26.00

*Age-0 length ranges and corresponding TS ranges were parameterized separately for each survey. All other age categories are treated as constant averages.

Interannual comparisons of average pollock density

To compare Pribilof Islands densities of age-0 pollock with the eventual size of the adult cohort, we set up a simple ratio table of the NOAA stock assessment estimates for abundance at recruitment (age-3) and the average acoustic age-0 densities by transect, in each year, expressed as a fraction of the 1996 age-3 abundance and age-0 density, respectively (Table 2). Average age-0 pollock densities (m^{-3}) were estimated from the survey echo-integrations by dividing area backscatter s_a ($m^2\,m^{-2}$) of pollock pixels by pixel depth (m) and mean backscattering cross-section σ_{bs} (m^2) of age-0 pollock, i.e. number $m^{-3} = s_a\ \text{depth}^{-1}\ \sigma_{bs}^{-1}$. As Pribilof surveys were not all taken over the same days of the year, age-0 densities for this table were standardized to 22 September (the latest date of any transect) by forward-calculating from the date of each survey an instantaneous mortality rate of 0.055 day^{-1} (the average instantaneous mortality rate from Swartzman *et al.*, 2005). The 1996 eastern Bering pollock year class was by far the most abundant of the study years 1994–1999, as evidenced by pre-recruit surveys (Swartzman *et al.*, 2002) and subsequent stock assessments (Ianelli *et al.*, 2003). Using 1996 as a benchmark, the relative success of the other year classes could be gauged. As body size influences the viability of juvenile fish (Sogard, 1997), we estimated length distributions of the age-0 pollock from anchovy trawls taken during the surveys. Lengths were also standardized to 22 September, using an average growth estimate of 0.5 mm day^{-1} (Swartzman *et al.*, 2005). Significance of length difference among years was tested by nested ANOVA (anchovy trawls nested within years) and Tukey's method for pairwise *a posteriori* comparisons. Ciannelli *et al.* (2002b) found 80 mm body length to represent a threshold beyond which energy content (kJ g^{-1}) of age-0 pollock no longer increases with size. Therefore, we calculated the proportion of age-0 pollock ≥80 mm by the 22 September standardization for each survey.

Table 2. EBS age-3 pollock abundances (from Table 1.14 of Ianelli *et al.*, 2003) and Pribilof age-0 pollock densities (from the acoustic surveys), per year class, expressed as fractions relative to 1996. Fractional values are per column. Pribilof age-0 densities were standardized to the estimated equivalency of a common date (22 September). The subheading "Average" is the mean of transects A, B, C, and D.

Year	Age-3 EBS* stock assessment	Age-0 Pribilof survey A	B	C	D	Average
1994	0.27	1.12	1.36	1.05	0.20	0.93
1995	0.64	0.38	0.20	0.22	0.94	0.44
1996	1.00	1	1	1	1	1
1997	0.45	0.07	0.09	0.03	0.03	0.06
1998	0.48	0.21	0.15	0.11	0.09	0.14
1999	0.67	0.43	0.49	0.41	0.50	0.46

*Numbers in this column refer to the year class that *originated* in each given year.

Spatial distributions of age-0 pollock density

Spatial distributions of age-0 pollock acoustic densities[1] were analysed as a function of (i) the spatial distributions of euphausiid acoustic densities, (ii) the ratio of potential groundfish predators relative to age-0 pollock, and (iii) the distribution of seabirds on the water. Details of these three effects are described below. Analyses were carried out per individual transect pass, using non-parametric regression generalized additive models (GAM; Hastie and Tibshirani, 1990) with spline smoothing (s) at 4 degrees of freedom (1 d.f. would imply a linear fit). For sampling units, each transect pass was subdivided at a spatial scale of 5-m depth × 1000-m distance bins (cf. Figure 2c). In GAM, covariates are assumed to affect the dependent variable through unspecified (not necessarily linear) additive functions or smooths (denoted by s(covariate)), and data can come from any distribution in the exponential family (Swartzman *et al.*, 1992). Here, we assumed the age-0 pollock densities to come from the normal distribution that was verified by Kolmogorov–Smirnov goodness-of-fit tests.

For each transect pass we retained the best fitting GAM model among possible combinations of covariates s(euphausiid density), s(predator/prey ratio), s(seabird effect), and s_i(pairwise interactions). Covariates were ranked by their pseudo-R^2 values (1 minus the ratio of model deviance over null deviance; Swartzman *et al.*, 1992) and added to the model by forward selection. The second-highest pseudo-R^2 covariate was added to the highest pseudo-R^2 covariate if it improved the model as evaluated by an approximate F-test (Hastie and Tibshirani, 1990):

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[1] In this paper, spatial distributions of density always refer to vertical density, i.e. the "curtain" underneath each transect as in Figure 2, rather than a "carpet" covering a surface area. The use of vertical density allows for normalization of different depths of water.

$$\frac{(\text{Deviance}_1 - \text{Deviance}_2)/(\text{d.f.}_{\cdot\text{res.1}} - \text{d.f.}_{\cdot\text{res.2}})}{\text{Deviance}_2/\text{d.f.}_{\cdot\text{res.2}}} \sim F_{(\text{d.f.}_{\cdot\text{res.1}} - \text{d.f.}_{\cdot\text{res.2}}),(\text{d.f.}_{\cdot\text{res.2}})},$$

where subscripts 1 and 2 refer to the 1- and 2-covariate models. If $F_{(\text{d.f.}_{\cdot\text{res.1}} - \text{d.f.}_{\cdot\text{res.2}}),(\text{d.f.}_{\cdot\text{res.2}})} \leq 0.05$, then the next covariate was added and the F-test repeated between the 2- and 3-covariate models. If $F_{(\text{d.f.}_{\cdot\text{res.1}} - \text{d.f.}_{\cdot\text{res.2}}),(\text{d.f.}_{\cdot\text{res.2}})} > 0.05$, the calculation was performed between the highest and third-highest covariate (the third highest might add significance even though the second highest did not, by being more orthogonal to the highest). This was repeated until each covariate was either included or rejected. As bird effects at different depths in the same (1000 m wide) columns were autocorrelated, degrees of freedom of any model including birds were adjusted before the F-test, to allow only one degree of freedom per column per bird effect. GAM plots for an example transect are shown in Figure 3a.

Euphausiid density

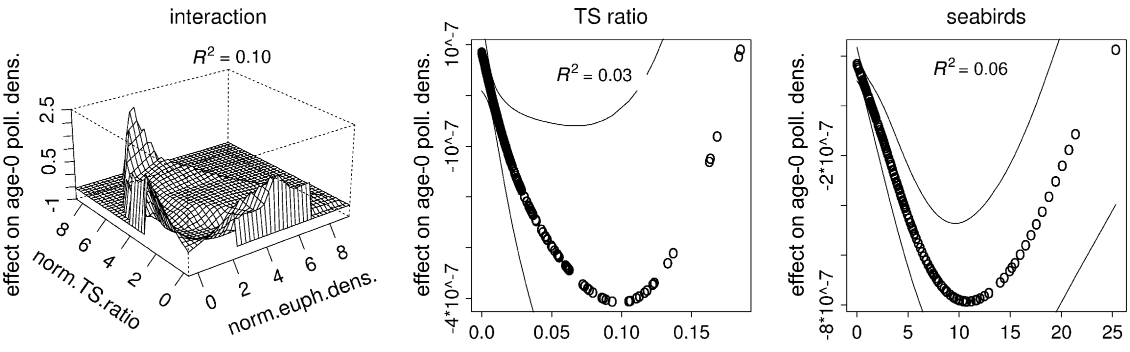
As for age-0 pollock, euphausiid densities were estimated by dividing echo-integration backscatter of pixels identified as euphausiids by pixel depth and backscattering cross-section (σ_{bs}). A mean euphausiid σ_{bs} value of $10^{-7.78}$ m^2 (Coyle and Pinchuk, 2002) was used across all surveys.

In addition to the whole-transect analyses, relationships between age-0 pollock and (only) euphausiid densities were analysed by habitat region within transect passes. Echo-integration data were in this case averaged into 250-m horizontal (full water column) bins (Figure 2d), as utilized by Swartzman *et al.* (1999a, b). Density calculations were normalized for bottom depth but restricted to the upper 130 m of the water column (only transect D, basin goes deeper anyway) to avoid biasing the analysis by including depths the juvenile pollock do not habitually enter. GAM results for the habitat regions of one example transect are plotted in Figure 3b, and the directional pseudo-R^2 values (R^2 × the +/− slope of the GAM) for all habitat regions in all surveys are summarized in Figure 4.

Groundfish predators

Direct groundfish predator information from trawls would be optimal for this study. However, the Pribilof surveys took few, if any, trawls suitable for capturing larger,

(a) whole transect



(b) habitats

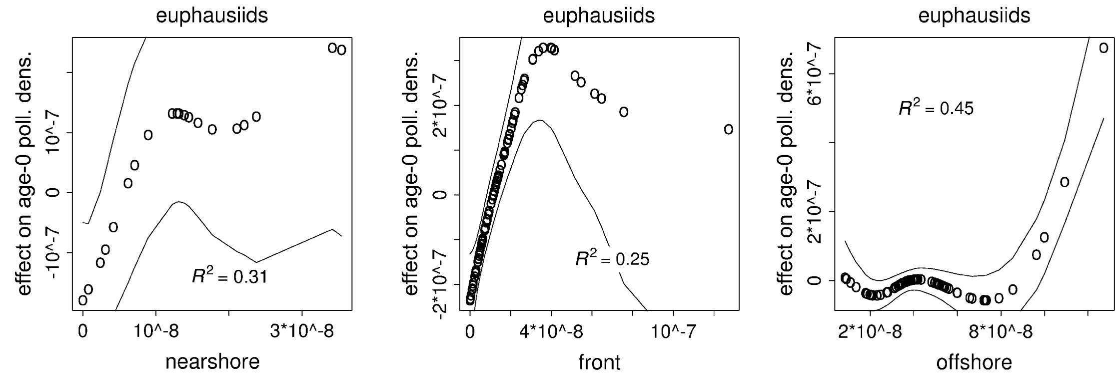


Figure 3. GAM spatial analyses of effects on age-0 pollock density for one example transect pass (A3 95; the same transect pass as in Figure 2) representing: (a) euphausiid density and TS ratio interaction effect, TS ratio main effect, and seabird numbers main effect, by 5 × 1000 m bins across the whole transect, (b) euphausiid density by 250 m × full water column bins, per habitat region. The 2D plots show the covariate data points ± 95% confidence intervals.

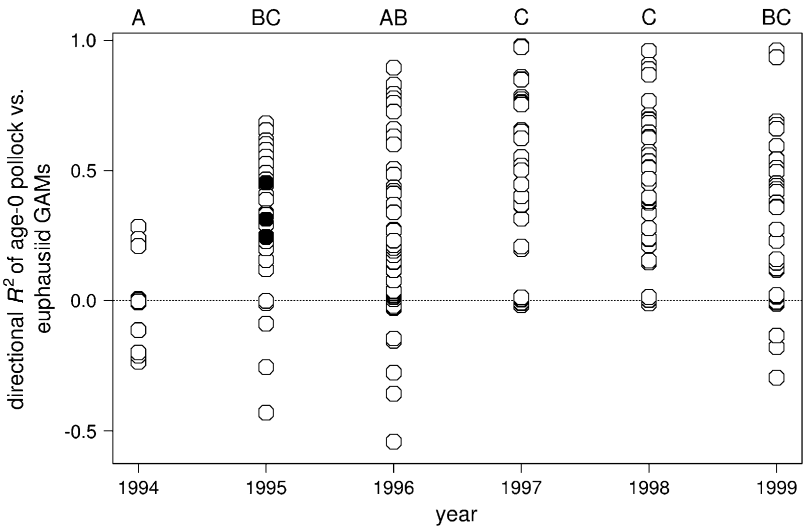


Figure 4. R^2 values × the slope (+/−) of the GAM relationships between acoustic densities of age-0 pollock and euphausiids, per habitat region. As an example, the three 1995 R^2 values from Figure 3b are highlighted in black. Year averages not significantly different from each other by one-way ANOVA are indicated with the same letters above the plot.

predator-sized fish (i.e. trawls taken with an Aleutian wing trawl or a bottom trawl), and publication of such data is otherwise sparse for this area. Lang *et al.* (2000) analysed arrowtooth flounder stomachs in 1995, and adult pollock stomachs in 1996, on Pribilof transect A (Figure 1) only. Ciannelli *et al.* (2002a, cf. their Table 2) summarized bottom trawl catches as combined densities (kg ha^{-1}) of arrowtooth flounder and adult pollock between 1994 and 1997.

To obtain more complete coverage of groundfish predator data, we utilized the distributions of acoustic TS values corresponding to size−age categories that potentially prey on age-0 pollock. The occurrence of TS of a given strength on a transect is not directly quantifiable as an index of the number of large fish present, because the echosounder only identifies TS to the extent that they are demarcated from the overall backscatter. Fish in dense shoals will not be identified individually. But over a given transect interval, the approximation can be made that demarcation of TS is independent of the strength of the TS, e.g. small fish are equally likely as large fish to show up as singles. Gauthier and Rose (2001) noted that at frequencies used in fisheries acoustics (10−200 kHz), fish with swimbladders can be considered point scatterers, and are unlikely to significantly influence reverberation volume as a function of size differences. Under the equally likely assumption, a ratio of large over small TS on a transect interval thus estimates the density ratio of predators to which juvenile fish are exposed (i.e. as an index of predators per prey). Behaviourally, TS detection may favour large fish, which maintain greater separation distance from other fish (MacLennan and Menz, 1996). However, size-specific behaviour would be consistent across the extent of transects. The distribution of TS ratio values can therefore be utilized as a relative measure of spatial relationship between groundfish predators and prey when comparing multiple observations within a single transect.

In this study, spatially explicit predator/prey ratios of age-2+ over age-0 TS were calculated at the resolution of the 5-m depth × 1000-m distance bins (Figure 2c). Age-1 TS were not included in the analysis. Age-1 pollock prey on age-0 pollock to some extent (Dwyer *et al.*, 1987), but have a much lower quantitative impact (Lang *et al.*, 2000). Also, distributions of age-1 pollock are likely to be determined by their own efforts to avoid the larger adults. Before computing this TS predator/prey ratio (hereafter PPR) in each bin, numbers of TS were smoothed to eliminate zero counts of age-0 pollock in a bin, which would cause infinite ratios. Smoothing was calculated as the average TS count of neighbouring bins (and self) weighted by the inverse distance of separation between bins. This PPR method has been validated by correlation with trawl samples in several eastern Bering Sea surveys (Winter, 2005). Target-strength data were available for all four transects in 1995, 1996, 1997, and 1999, and for transect A in 1994.

Seabirds

Seabird counts had been recorded by species along several daylight transects during each survey (Logerwell *et al.*, 1998; Swartzman and Hunt, 2000). To model seabirds' potential influence on age-0 pollock distribution through the water column, we took into account species' different feeding strategies: kittiwakes are surface feeders (Decker *et al.*, 1995), fulmars feed at or near the surface (Hunt *et al.*, 1982), shearwaters dive to at least 40 m (Lovvorn *et al.*, 2001), auklets to 35–40 m (Bedard, 1969), puffins to ~50 m (Burger and Simpson, 1986), and murres to 210 m (Croll *et al.*, 1992). Depth effects of the feeding strategies were calculated as the inverse linear function:

$$\text{depth effect} = 1 - \left(\frac{\text{sample depth}}{\text{species maximum depth}}\right).$$

For example, the presence of a murre would be considered to influence age-0 pollock at 40-m depth 81% as much as it influences age-0 pollock at the surface: $1 - (40/210) = 0.81$. The depth effect was then multiplied by the number of birds (of that species) superjacent, and summed for all birds on a given transect interval.

Latitude distribution

As transects run primarily north–south (Figure 1), a metric of along-transect age-0 pollock distribution was recorded as the latitudinal quantiles of acoustic density. On each transect pass we calculated the latitudes representing the cumulative 10%, 20%, …, etc. of depth-normalized age-0 pollock acoustic biomass. For inter-year comparability, these calculations were restricted to the latitude range common to all passes of each transect. Average latitude quantiles per year and transect are plotted in Figure 5.

Results

Interannual comparisons of average pollock density

Inspection of Table 2 shows that the 1994 year class "lost ground" relative to 1996. At the age-0 stage in the Pribilof Islands nursery, 1994 age-0 fish had 93% of the average acoustically derived density of the 1996 benchmark, but by the recruitment age of 3, that proportion had fallen to 27%. Transect D appears to follow different trends from the other transects, being the only transect with lower age-0 pollock densities in 1994 than in 1996. All other year classes gained against 1996 between ages 0 and 3, to varying degrees. Except for 1994, year classes also tended to conserve their rankings from age-0 to age-3, i.e. 1996 > 1999 > 1995 > 1998 > 1997. Age-0 pollock lengths standardized to 22 September were smallest in 1994 and had the lowest proportion ≥80 mm (Table 3). On the actual survey dates, 1994 lengths were intermediate between the other years (Table 3), so the 1994 *in situ* spatial relationships to predators and prey cannot be considered influenced by smaller length of the fish.

Euphausiid density

Spatial relationships between age-0 pollock and euphausiids were predominantly positive, at both the scale of whole transects (5 × 1000 m bins) and of habitat regions

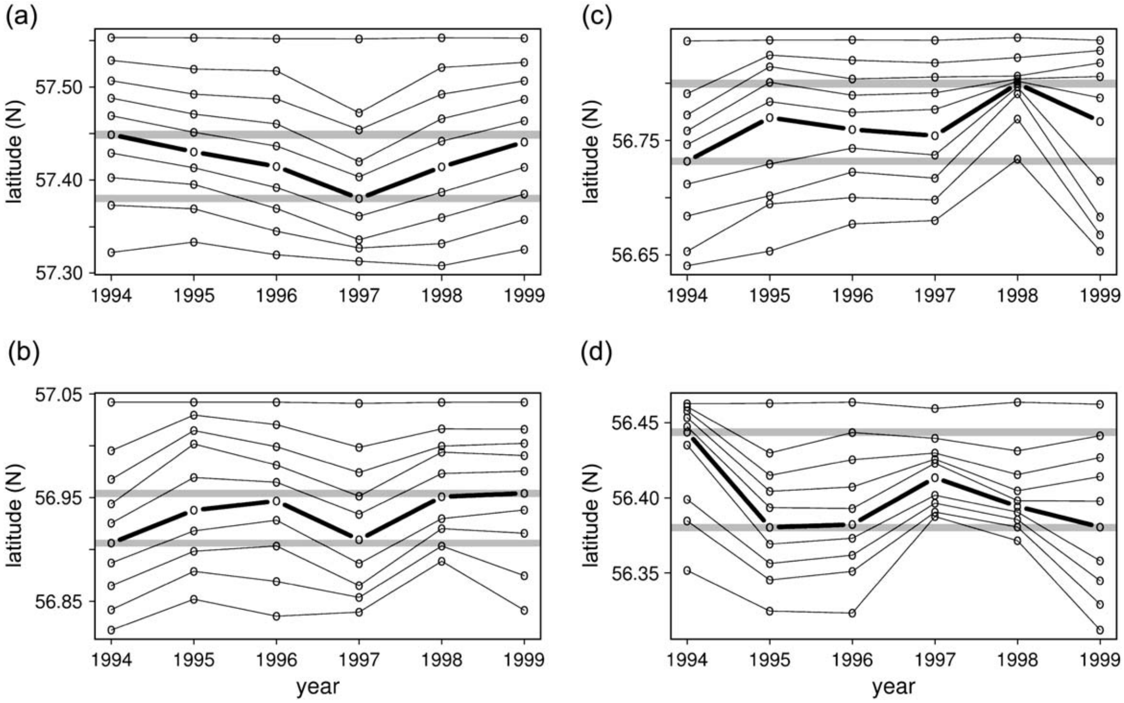


Figure 5. Average 10% latitude quantiles of the age-0 pollock density distributions, per year, along the four transects; 50% quantiles (centroids) are in heavy font and bounded by grey lines at the maximum and minimum latitudes.

Table 3. Mean standard lengths of age-0 pollock from the dates actually sampled, and from extrapolation to 22 September by the factor of 0.5 mm growth day^{-1}. Proportion $\geq$80 mm is the proportion at least 80 mm long. Superscripts A and B indicate length means not significantly different from each other by ANOVA.

September survey		Mean length (mm)		Proportion $\geq$80 mm
Year	Date range	On date	September 22	(September 22)
1994	19–22	48.4	48.9	0.005
1995	11–19	53.4	55.7^A	0.033
1996	05–15	49.0	54.9	0.017
1997	09–17	45.7	50.0^B	0.008
1998	08–14	50.5	55.8^A	0.042
1999	06–17	44.5	49.7^B	0.029

within transects (250 m × full water column bins). Explanatory powers of the relationships (R^2) were higher for the habitat region analyses than for whole-transect analyses (Tables 4–7, Figures 3 and 4). That may indicate in part that full water column bins are more suitable for measuring the relationship than depth × distance strata bins. We conjecture that, as age-0 pollock and euphausiids undertake diel migrations (Swartzman *et al.*, 2002), vertical separation on the shallow eastern Bering shelf may not be an important factor. Analysis of directional R^2 values by habitat regions showed that 1994 had the smallest percentage of spatially positive relationships, followed by 1996, 1995 and 1999, 1997, and 1998 (one-way ANOVA, $p < 0.001$; Figure 4). The outcome suggests that despite 1994 recording the second highest concentration of age-0 pollock in September (Table 2), the fish were relatively unsuccessful at tracking their zooplankton prey.

Groundfish predators

Groundfish PPR main effects were included in whole-transect GAM models on 41 of 63 transect passes (Tables 4–7). Explanatory power contributed by the PPR was almost always less than that of euphausiid density (A3 95, the example transect pass shown in Figures 2 and 3, is exceptional in this regard), and PPR as a sole covariate was never the best model. Statistically significant PPR trends were mostly negative, by a proportion of 2:1 or more on all transects (Tables 4–7). As predators and prey are both mobile, a negative trend is interpreted as age-0 pollock evading high concentrations of larger groundfish (i.e. it would be less plausibly a case of all age-0 pollock having been eaten at such locations, because predators and prey would then redistribute themselves). Occurrence of significantly negative vs. positive or non-significant (n.s.) PPR trends did not show significant differentiation with respect to average values of age-0 pollock, euphausiid, bird, PPR, or daylight parameters (Tables 4–7; logistic regression; Venables and Ripley, 1997). Interactions between PPR and euphausiid density were significant on 33 transect passes. Most of these interactions tended to show a positive effect on age-0 pollock density, with high values of both covariates (Tables 4–7, Figure 3a).

Seabirds

Seabird main effects contributed to the best GAM model on 18 of the 35 transect passes for which bird counts were recorded: 10 positive, 6 negative, and 2 bimodal GAM trends. Seabird interaction effects were mostly not significant (Tables 4–7). Among all transect passes, seabird trends showed no significant relationship with the age-0 pollock, euphausiid, bird, PPR, or daylight parameters (Tables 4–7; logistic regression; Venables and Ripley, 1997).

Latitude distribution

Average latitudinal distributions of age-0 pollock varied among years on the order of 0.04° (~4400 m). On the four transects, 1994 always had either the most northerly or most southerly centroid (50% quantile; Figure 5). For each transect, the absolute difference between each year's centroid and the mean of all years (i.e. the centroid latitude anomaly) was calculated. These anomalies are plotted in Figure 6 against the age-3 EBS abundance fractions taken from Table 2. The highly significant ($p < 0.005$, $r^2 = 0.42$) second-order regression in Figure 6 indicates an inverse relationship between centroid latitude anomaly and recruitment-age year-class strength.

Discussion

Age-0 juvenile abundance from nursery and spawning surveys predicts year-class strength for gadoid populations, including cod (*G. morhua*) along the Norwegian Skagerrak (Tveite, 1984), in the Barents Sea (Helle *et al.*, 2000), and off Iceland (Begg and Marteeinsdottir, 2002), and cod and haddock (*Melanogrammus aeglefinus*) off Nova Scotia (Campana *et al.*, 1989). A predictive correlation from age-0 to age-3 was not detected in Newfoundland coastal cod stocks (Ings *et al.*, 1997), but these authors suggested that recruitment from other nursery areas away from the coast may have concealed a pre-recruit signal. In the eastern Bering Sea, the Pribilof Islands nursery is a primary source of the pollock stock (Swartzman *et al.*, 2005). Initial comparisons between Pribilof age-0 and EBS age-3 indices demonstrated a strong link for some years (Schumacher and Macklin, 2004; Table 2). As in many studies of marine recruitment, an absence of linkage in *all* years motivates investigation.

A question in particular is why 1994 fared so poorly (Table 2). One difference between 1994 and later years was found in the acoustically determined spatial proximity relationships of age-0 pollock and euphausiid density distributions. Spatial proximity between gadoids and their prey

Table 4. Transect A average parameters and results of best-fit GAMs of effect on age-0 pollock density. GAM covariates that were available but did not contribute to best fits are indicated "n.s.". Unavailable covariates are shown as "—". Sub-columns "slope" indicate whether significant data comprised increasing (+), decreasing (−), or partially both (±) trends for that covariate. Superscripts A, B, C, and D, where present, indicate significant pairwise interactions between covariates, and the trends of the interactions are footnoted. Abbreviations: Pollock = age-0 pollock, PPR = predator/prey ratio. Parameter averages and GAMs were calculated per 5 × 1000-m transect bin.

Transect		Average per bin				Best GAM model		
Year/ pass	Daylight	Pollock* (no m^{-3})	Euphausiid (no m^{-3})	PPR (no no^{-1})	Seabird (number)	Euphausiid (slope) R^2	PPR (slope) R^2	Seabird (slope) R^2
94/A1	1	0.15	4.71	0.04	2.60	(−) 0.03	(−) 0.07	(+) 0.13
94/A2	0.10	0.11	4.15	3e−4	—	(+) 0.21	n.s.	—
95/A1	0.99	0.06	2.83	9e−3	1.74	(+) 0.15^{A}	n.s.^{A}	(+) 0.09
95/A2	0	0.05	1.99	0.03	—	(+) 0.18^{A}	(−) 0.12^{A}	—
95/A3	1	0.07	1.85	0.02	3.31	n.s.^{A}	(−) 0.03^{A}	(±) 0.06
95/A4	0	0.05	3.55	0.04	—	(+) 0.43	(−) 0.13	—
95/A5	1	0.04	1.31	0.02	0.17	(+) 0.05	(−) 0.02	n.s.
96/A1	1	0.17	13.36	7e−3	0.23	(+) 0.05	(−) 0.05	(+) 0.02
96/A2	1	0.17	11.11	0.01	0.10	(+) 0.05^{B}	n.s.^{B}	(−) 0.02
96/A3	0	0.16	18.44	1e−3	—	(+) 0.19	n.s.	—
96/A4	0	0.14	18.23	1e−3	—	(+) 0.16	n.s.	—
96/A5	1	0.20	17.25	9e−3	—	(+) 0.14^{A}	n.s.^{A}	—
97/A1	1	7e−3	6.12	0.07	2.47	(+) 0.21^{A}	n.s.	n.s.^{A}
97/A2	1	5e−3	4.86	0.10	—	(+) 0.46^{A}	(−) 0.03^{A}	—
97/A3	0	0.02	12.70	0.01	—	(+) 0.69^{C}	(−) 0.10^{C}	—
97/A4	1	6e−3	7.01	0.05	3.39	(+) 0.50^{AD}	n.s.^{D}	n.s.^{A}
97/A5	0	0.01	10.18	0.01	—	(+) 0.43^{A}	n.s.^{A}	—
98/A1	1	0.03	5.15	—	3.01	(+) 0.23	—	n.s.
98/A2	0	0.05	10.53	—	—	(+) 0.25	—	—
98/A3	1	0.04	7.52	—	—	(+) 0.25	—	—
98/A4	0.91	0.03	6.13	—	0.02	(+) 0.24	—	n.s.
98/A5	0.68	0.04	9.44	—	—	(+) 0.47	—	—
98/A6	1	0.03	4.52	—	—	(+) 0.09	—	—
99/A1	0.31	0.05	8.34	4e−3	—	(+) 0.83	n.s.	—
99/A2	0.16	0.07	9.59	3e−3	—	(+) 0.58^{B}	(+) 0.05^{B}	—
99/A3	1	0.10	5.74	0.02	0.59	(±) 0.09	(+) 0.07	(+) 0.05
99/A4	0	0.10	8.09	0.02	—	(+) 0.28^{A}	(−) 0.10^{A}	—
99/A5	0	0.10	8.16	0.01	—	(+) 0.16^{A}	(−) 0.06^{A}	—
99/A6	0.75	0.07	11.45	8e−3	—	(+) 0.27	n.s.	—

(A) Jointly intermediate covariate values: negative effect.
(B) Jointly low covariate values: negative effect.
(C) Jointly high covariate values: negative effect.
(D) Jointly high covariate values: positive effect.
*Unlike Table 2, these are *not* standardized to 22 September.

has been inferred as an indicator of feeding success for Pacific hake *Merluccius productus* (Mackas *et al.*, 1997; Swartzman, 2001), Cape hake *M. capensis* and *M. paradoxus* (Drapeau *et al.*, 2004), Atlantic cod (Rose and Leggett, 1990), and previously for juvenile (Swartzman *et al.*, 1999a, b) and large (Miyashita *et al.*, 2004) pollock. The acoustic density relationships among age-0 pollock and euphausiids in this study (Table 4) are consistent with consumption data reported by Ciannelli *et al.* (2004; cf. their Figure 3): ~3.5% euphausiid in the age-0 pollock diet in 1994, 15% in 1995, 28% in 1996, and 78% in 1997. Age-0 pollock around the Pribilof Islands in 1994 hatched later and were smaller by September than in the subsequent five years (Brodeur *et al.*, 2002; Table 3), and euphausiid selection is known to increase with size (Merati and Brodeur, 1996; Schabetsberger *et al.*, 2000). Nevertheless, the 48.4 mm mean standard length in 1994 (Table 3) is well within the size range of age-0 pollock that consumed significant proportions of euphausiids in 1996 and 1997 (Winter *et al.*, 2005; cf. their Figure 6).

The corroboration between consumption data (Ciannelli *et al.*, 2004) and spatial relationships observed during the

Table 5. Transect B average parameters and results of best-fit GAMs of effect on age-0 pollock density. See Table 4 for description of entries.

Transect		Average per bin				Best GAM model		
Year/ pass	Daylight	Pollock* (no m^{-3})	Euphausiid (no m^{-3})	PPR (no no^{-1})	Seabird (number)	Euphausiid (slope) R^2	PPR (slope) R^2	Seabird (slope) R^2
94/B1	1	0.17	7.42	—	0.20	(+) 0.22	—	n.s.
94/B2	0	0.04	2.27	—	—	(+) 0.15	—	—
95/B1	1	8e−3	1.90	0.03	0.15	(±) 0.18^{A}	(−) 0.03^{AA}	n.s.^{A}
95/B2	0	8e−3	1.36	0.13	—	(+) 0.50^{A}	(−) 0.25^{A}	—
96/B1	1	0.07	9.81	0.01	0.33	(+) 0.06	(−) 0.02	(+) 0.02
96/B2	0	0.07	8.28	5e−3	—	(+) 0.17^{A}	(−) 0.08^{A}	—
96/B3	1	0.09	9.55	0.02	0.32	(+) 0.17	(−) 0.04	(+) 0.01
96/B4	0	0.08	8.47	7e−3	—	(+) 0.15^{A}	(−) 0.06^{A}	—
96/B5	1	0.09	10.28	0.01	0.05	(+) 0.21^{E}	(−) 0.06	(+) 0.02^{E}
97/B1	1	6e−3	4.50	0.17	—	(±) 0.38^{A}	(±) 0.22^{A}	—
97/B2	0	6e−3	5.54	0.13	—	(+) 0.81^{A}	(−) 0.13^{A}	—
97/B3	1	5e−3	4.51	0.14	3.06	(+) 0.31^{AB}	(+) 0.27^{AB}	(−) 0.11^{BB}
98/B1	1	0.01	3.48	—	0.02	(+) 0.48	—	n.s.
98/B2	1	0.01	2.67	—	—	(+) 0.57	—	—
98/B3	0	2e−3	1.76	—	—	(+) 0.76	—	—
99/B1	1	0.04	5.97	0.09	3.41	(+) 0.38^{A}	(−) 0.08^{A}	n.s.
99/B2	1	0.02	5.37	0.12	0.10	(+) 0.17^{A}	(−) 0.05^{A}	n.s.
99/B3	1	0.03	6.92	0.02	0.02	(+) 0.48^{D}	n.s.	n.s.^{D}

(A) Jointly intermediate covariate values: negative effect.

(B) Jointly low covariate values: negative effect.

(D) Jointly high covariate values: positive effect.

(E) Jointly low covariate values: positive effect.

*Unlike Table 2, these are *not* standardized to 22 September.

acoustic surveys suggests that in 1994, age-0 pollock largely omitted euphausiids from their diet as a function of decreased encounter opportunities. Figures 5 and 6 present a potentially relevant scenario to this effect: age-0 pollock in 1994 occurred on average either farther offshore (transects A and B, St Paul Island) or closer inshore (transects C and D, St George Island) than in any other year. However, neither cause nor effect for this pattern is obvious. Oceanographic studies (Schumacher and Stabeno, 1998; Kowalik and Stabeno, 1999) have revealed a clockwise flow circulation around the Pribilof Islands which, together with the dominant tidal motion, would not have the net result of transporting juvenile fish inshore to St George and simultaneously away from St Paul. Ciannelli *et al.* (2002a) hypothesized that in a cold year such as 1995, groundfish predators foray into shallower water, pushing age-0 pollock closer inshore. According to our analysis, 1995 did have consistently negative PPR GAMs (Tables 4−7), but was unexceptional with respect to the inshore distribution of age-0 pollock. 1994 and 1997 averaged the highest and second highest latitude centroid deviations, respectively (Figure 6), but had the weakest and strongest positive spatial relationships between age-0 pollock and euphausiid distributions. There is therefore a strong statistical correlation between latitudinal deviation and year-class strength (Figure 6), but an absence of connection to any one proximate parameter. Brodeur *et al.* (2002) concluded that juvenile pollock did not benefit more from some habitats than others around the Pribilof Islands, and observed that "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."

We propose therefore that the advantage of distributions associated with a mid-range centroid may generally be that these are strategically centralized, in the vicinity of the Pribilof Islands nursery, for the juvenile fish to search optimally both shoreward and offshore in the face of varying environmental challenges. In 1994, all 10% density quantiles were monotonically biased either northward (transects A and D) or southward (transects B and C). The other five years were more uneven with some northward- and some southward-biased quantiles on at least half the transects (Figure 5). This pattern is further evidence that in 1994, movement or transport of the age-0 pollock was relatively restricted across the entire latitude extent of transects. Such restriction perhaps supports the Nursery Size Hypothesis described by Abella *et al.* (2005) for European hake (*M. merluccius*), whereby recruitment of cohorts correlates positively with surface area of the nursery grounds.

Table 6. Transect C average parameters and results of best-fit GAMs of effect on age-0 pollock density. See Table 4 for description of entries.

Transect		Average per bin				Best GAM model		
Year/ pass	Daylight	Pollock* (no m^{-3})	Euphausiid (no m^{-3})	PPR (no no^{-1})	Seabird (number)	Euphausiid (slope) R^2	PPR (slope) R^2	Seabird (slope) R^2
94/C1	1	0.07	4.48	—	0.49	(+) 0.14[D]	—	n.s.[D]
95/C1	1	0.02	0.68	0.01	0.34	(+) 0.18	(−) 0.03	n.s.
95/C2	0	0.02	1.96	0.01	—	(+) 0.59[A]	n.s.[A]	—
96/C1	1	0.17	8.31	4e−3	0.60	(+) 0.07	n.s.	(−) 0.05
96/C2	0	0.14	17.45	4e−3	—	(+) 0.17[F]	n.s.[F]	—
96/C3	1	0.13	8.91	0.05	3.75	(+) 0.11	(−) 0.09	(±) 0.06
96/C4	0.12	0.10	13.54	9e−3	—	(+) 0.42	(−) 0.25	—
96/C5	1	0.13	9.15	0.02	0.58	(−) 0.01	(−) 0.02	(−) 0.03
96/C6	1	0.16	10.29	0.04	0.39	(+) 0.24[AG]	(−) 0.06[AA]	(−) 0.05[AG]
97/C1	1	3e−3	3.87	0.11	—	(+) 0.39[D]	(+) 0.20[D]	—
97/C2	1	1e−3	2.68	0.08	4.01	(+) 0.24[DD]	(+) 0.24[DD]	n.s.[DD]
97/C3	0	5e−3	3.09	0.01	—	(+) 0.75	n.s.	—
98/C1	0	9e−3	1.07	—	—	(+) 0.45	—	—
98/C2	0.51	4e−3	2.04	—	—	(+) 0.40	—	—
98/C3	0	0.02	8.37	—	—	(+) 0.63	—	—
99/C1	1	0.04	6.96	0.02	15.16	(+) 0.24[A]	n.s.	(−) 0.02[A]
99/C2	0.69	9e−3	2.16	0.06	—	(+) 0.62	(±) 0.41	—
99/C3	0.68	0.07	9.17	1e−3	—	(+) 0.55[G]	n.s.[G]	—

(A) Jointly intermediate covariate values: negative effect.
(D) Jointly high covariate values: positive effect.
(F) Low TS ratio values: positive effect.
(G) Jointly intermediate covariate values: positive effect.
*Unlike Table 2, these are *not* standardized to 22 September.

Precedent studies have examined large-scale distribution patterns of juvenile pollock in the eastern Bering Sea and postulated that recruitment success varies with the extent of temperature-mediated spatial overlap between juvenile and adult pollock (Francis and Bailey, 1983; Wyllie-Echeverria and Wooster, 1998; Wespestad *et al.*, 2000). Overlap increases in cold years, when reduced current transport keeps juveniles on the outer shelf, resulting in increased cannibalism (Wespestad *et al.*, 2000). Lang *et al.* (2003) reported that from 1993 through 1996, the highest annual level of predation on age-0 pollock (including cannibalism) took place in 1994. However, the data of Lang *et al.* (2003, their Figure 8) do not verify that cannibalism alone would explain the weak year class of 1994 compared with 1995 and 1996 (Table 2). The PPR data available from 1994 indicate significant negative correlation between groundfish predators and age-0 pollock, but not more so than in other years (Table 4). Among all surveys (1994–1999), PPR relationships showed no overall covariance trend with age-0 pollock, euphausiid, or TS density.

Results of this study provide indications that groundfish and seabird predators influenced distributions of age-0 pollock on local scales around the Pribilof Islands, but without incurring significant differentiation among years. Potential seabird influences may have been mitigated by the timing of the surveys: by September, seabirds are less bound to their nesting colonies and can forage farther from the Pribilof Islands than earlier in the season (G. Hunt, University of California, pers. comm.). Winter (2005) found also that frontal zone boundaries and thermoclines showed effects on individual transects, without overall relationship to pollock distribution or year-class strength. It is plausible that all these factors exercised some degree of indirect control on the prevalent spatial correlations between age-0 pollock and euphausiids. Vertical migration of euphausiids is commonly reported to result from predation pressure (Zaret and Suffern, 1976; Iwasa, 1982; DeRobertis *et al.*, 2000). Euphausiid response to thermoclines appears to be species-specific and based on physiological characteristics (Brinton, 1967). Brinton (1967) and Youngbluth (1976), working in the California Current system, found one species each of *Euphausia* and *Thysanoessa* that did not migrate above the thermocline at night, in contrast to all other species of the same genera they encountered in their samples. Brinton (1967) further observed that for those species which did migrate, the thermocline would become the lower limit of the species' night-time range. Swartzman *et al.* (2002) suggested that euphausiids near the Pribilof Islands can locate

Table 7. Transect D average parameters and results of best-fit GAMs of effect on age-0 pollock density. See Table 4 for description of entries.

Transect		Average per bin				Best GAM model		
Year/ pass	Daylight	Pollock* (no m^{-3})	Euphausiid (no m^{-3})	PPR (no no^{-1})	Seabird (number)	Euphausiid (slope) R^2	PPR (slope) R^2	Seabird (slope) R^2
94/D1	1	3e−3	5.83	—	0.51	(+) 0.07	—	n.s.
95/D1	1	0.02	2.14	0.11	6.07	(±) 0.05	(−) 0.04	n.s.
95/D2	0	0.02	1.75	0.01	—	(+) 0.45	n.s.	—
96/D1	1	0.03	6.40	0.25	—	(+) 0.12	(−) 0.06	—
96/D2	0.60	0.03	6.66	0.06	—	(+) 0.21^{C}	(±) 0.04^{C}	—
96/D3	0	0.04	10.68	0.02	—	(+) 0.20	(−) 0.12	—
96/D4	1	0.03	5.75	0.06	—	(+) 0.12	n.s.	—
97/D1	1	1e−3	2.39	0.17	—	(+) 0.28^{A}	n.s.^{A}	—
97/D2	0	1e−3	2.18	0.07	—	(+) 0.24^{D}	(−) 0.05^{D}	—
97/D3	1	2e−4	2.77	0.11	4.38	(±) 0.04^{E}	(+) 0.05^{EE}	(+) 0.04^{E}
98/D1	0	0.01	1.96	—	—	(+) 0.30	—	—
98/D2	1	2e−3	1.01	—	—	(+) 0.08	—	—
98/D3	0.43	1e−3	3.15	—	—	(+) 0.25	—	—
98/D4	0.98	1e−3	1.90	—	—	(+) 0.13	—	—
98/D5	0.09	4e−3	3.14	—	—	(+) 0.51	—	—
99/D1	1	0.03	5.77	0.11	10.99	(+) 0.14^{D}	(±) 0.09	(+) 0.28^{D}
99/D2	1	0.02	6.76	0.26	3.11	(+) 0.08^{D}	(±) 0.02^{A}	(+) 0.04^{AD}
99/D3	0.24	3e−3	3.07	0.24	1.48	(+) 0.34^{F}	(−) 0.03^{F}	n.s.
99/D4	0	0.01	3.71	0.18	—	(+) 0.63^{H}	n.s.^{H}	—

(A) Jointly intermediate covariate values: negative effect.
(C) Jointly high covariate values: negative effect.
(D) Jointly high covariate values: positive effect.
(E) Jointly low covariate values: positive effect.
(F) Low TS ratio values: positive effect.
(H) Low euphausiid values: positive effect.
*Unlike Table 2, these are *not* standardized to 22 September.

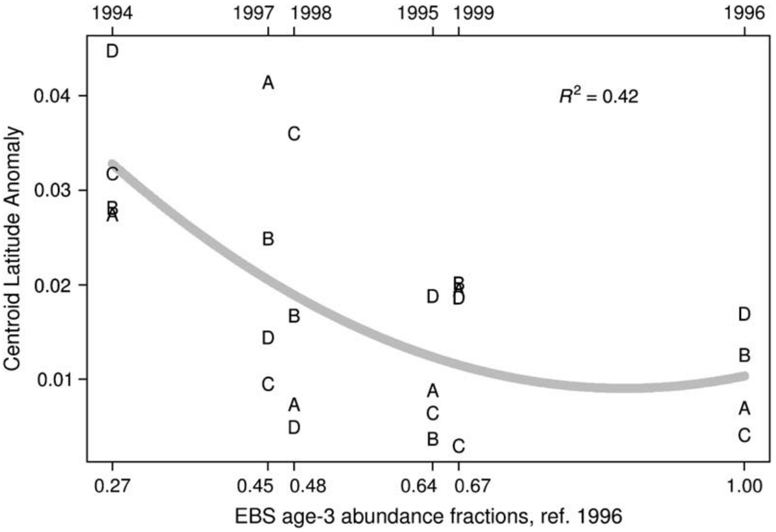


Figure 6. Yearly latitude centroid anomalies by transects A, B, C, and D (cf. Figure 5) vs. EBS age-3 abundance fractions referenced to 1996 (which correspond directly to the second column in Table 2). The R^2 given is of the second-order regression plotted as a grey line.

the thermocline using density cues. Seabirds as well as adult groundfish feed heavily on euphausiids (Bedard, 1969; Lang *et al.*, 2003), and are therefore competitors to as well as predators on age-0 pollock. In fact, age-0 pollock may benefit from a refuge effect of predators selecting euphausiids. As Leggett and DeBlois (1994) remarked for the parallel question of larval fish survival, an "either/or approach" to food vs. predation as the primary determinant of recruitment variability is likely to be inadequate. Given this caveat, the analyses of this study do show spatial correlation between age-0 pollock and euphausiid density distributions to be a potentially useful indicator for year-class strength. The statistically significant GAM relationships often had relatively low R^2 values (Tables 4—7, Figure 4), consistent with findings that a large (in some years majority) proportion of age-0 pollock by September do not feed primarily on euphausiids (Brodeur *et al.*, 2000; Schabetsberger *et al.*, 2003; Ciannelli *et al.*, 2004; Winter *et al.*, 2005). We hypothesize that those age-0 pollock which do feed on euphausiids carry the strength of the cohort.

Euphausiids have the highest caloric density of age-0 pollock's usual zooplankton prey (Davis *et al.*, 1998), and Sogard and Olla (2000) determined that greater energy storage enhances age-0 pollock survival under simulated overwintering conditions. Smith *et al.* (1986) observed that captive juvenile pollock fed every other day, rather than daily, tended to compensate by eating larger meals. If age-0 pollock overwinter by metabolic adaptation and occasional feeding (Ciannelli *et al.*, 2002b), then survival should further be enhanced by access to large prey. Therefore, it is plausible that age-0 pollock cohorts that fail to make the transition to a predominantly euphausiid diet by September will experience greater mortality through their first winter, and recruit as a weak year class. Conversely, a sparse age-0 cohort such as 1997 may still produce a modestly successful year class when the fish achieve high euphausiid consumption. Winter *et al.* (2005) found age-0 pollock near the Pribilof Islands to have significantly higher average condition (W/L^3) in September 1997 than in September 1996, while Brodeur *et al.* (2000) did not find a significant difference in condition factor among the years 1994, 1995, and 1996. As age-0 pollock were smaller in 1994 (Brodeur *et al.*, 2002; Table 3), they would still have been suited to attain satiation from smaller (and less energy-rich) prey such as the copepods on which they were predominantly feeding (Ciannelli *et al.*, 2004). Schabetsberger *et al.* (2003) and Winter *et al.* (2005) concluded from dietary analyses that smaller age-0 pollock had more food in their guts relative to body weight (i.e. gut fullness) than larger individuals when they consumed larger proportions of small prey items. Yamamura *et al.* (2002) found that small pollock off the coast of Hokkaido Island (northern Japan) switched from a predominantly copepod diet in spring to a predominantly euphausiid diet by autumn, and attained maximum body condition in August, followed by gradual decline through winter.

While sufficient body condition of age-0 pollock may be a necessary factor for their overwinter survival potential (Sogard and Olla, 2000), it appears not to be a reliable predictor, as early as mid-September, for comparing interannual differences of year-class strength. Experimental studies on age-0 Atlantic cod found body size but not food ration to significantly influence overwinter survival (Brown *et al.*, 1989; Gotceitas *et al.*, 1999). In this study, the influence of size is unclear. Multiplying the age-0 density fractions from Table 2 by the 80 mm proportions from Table 3, 27.4% as many $\geq$80 mm age-0 pollock were obtained by 22 September in 1994 as in 1996: $0.93/1 \times 0.005/0.017 = 27.4\%$. That estimate is notably close to the age-3 recruitment abundance ratio between the two years (Table 2), and suggests that the relative growth retardation in 1994 might have resulted in fish having too little feeding history on a euphausiid diet before winter, even if they were big enough to take euphausiids by the time the survey was run. However, equivalent growth calculations for the other years were not consistent with subsequent recruitment. For example, 1997 had 2.9% the number of $\geq$80 mm age-0 pollock as 1996 ($0.06/1 \times 0.008/0.017$), yet 45% the cohort strength at recruitment. Possibly, the effect of body size would have become more evident in surveys with older fish.

Summary

Three measures of acoustic survey data were identified that together yield a potentially practical index for pollock year-class strength (Table 8): (i) age-0 density; (ii) spatial correlation with euphausiids; and (iii) centricity of the along-transect distributions.

Inspection of Table 8 suggests that the measures are additive insofar as year-class strength correlates with the sum of their "scores". As the scores at this level are derived from relatively limited survey data, we restrict them to

Table 8. Qualitative summaries of acoustic indices from the Pribilof age-0 pollock surveys in relation to subsequent age-3 eastern Bering Sea year-class strength.

	Pribilof age-0 acoustic indices			
Year	Age-0 pollock density	Correlation with euphausiids	Distribution centricity	EBS age-3 year-class strength
1994	High	Low	Low	Low
1995	Moderate	High	High	Moderate
1996	Very high	Moderate	High	High
1997	Very low	Very high	Moderate	Mediocre
1998	Low	Very high	Moderate	Mediocre
1999	Moderate	High	High	Moderate

qualitative interpretation. This index of measures is predicated on conclusions (Swartzman *et al.*, 2002, 2005, and references therein) that the Pribilof Islands area is highly representative for the eastern Bering Sea. Other areas of the eastern Bering Sea, not sampled or not identified, will contribute to each year class, and further validation of any forecast index should include expanded surveys of additional possible pollock nurseries. Expanded time-series should be pursued as well, because the range of contrast in pollock recruitment among the six years of this study was not exceptionally high for the eastern Bering Sea (cf. Ianelli *et al.*, 2003). It is nonetheless compelling to note that the strong age-0 Pribilof cohort in 1996 led to a strong recruitment-age year class, whereas the almost equally strong age-0 Pribilof cohort in 1994 did not. We propose that this index is suitable for measuring short-term recruitment variation, which may be influenced primarily by episodic events. For example, Bond and Overland (2005) correlated strong pollock recruitment on a short-term scale with the occurrence of strong storms in the early summers of age-0 years (including 1996), and attributed the effect to greater mixing of nutrients into the euphotic zone, leading to enhanced prey concentration available to pollock larvae. On a larger scale of oceanographic processes, the Oscillating Control Hypothesis (Hunt *et al.*, 2002; Hunt and Stabeno, 2002) predicts that cold regimes limit zooplankton production and hence prey for age-0 pollock (bottom-up regulation). In warm regimes, zooplankton is plentiful and predation controls the survival of age-0 pollock (top-down). As predator abundance is itself the result of past recruitment, age-0 pollock are in any year constrained, at the minimum, by some variable combination of the two control mechanisms of food supply and predation. An index that integrates several measures may be the effective approach to forecasting cohort success.

Acknowledgements

We thank M. Brown, A. Cossio, D. Demer, and M. Wilson for providing the acoustic survey data and J. Horne for calculating the Kirchhoff ray-mode model. We also thank A. Bertrand, K. Coyle, D. Gunderson, J. Horne, and two anonymous referees for their critical reading of and suggestions for improvements to the manuscript. The research was sponsored by NOAA's Coastal Ocean Program through Southeast Bering Sea Carrying Capacity, and is contribution of FOCI-S577 to Fisheries-Oceanography Coordinated Investigations. The first author was additionally supported by the Mason Keeler Endowment at the University of Washington.

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