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Variations in age-0 pollock distribution among eastern Bering Sea nursery areas: A comparative study through acoustic indices

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Abstract

Cohort abundance of walleye pollock (*Theragra chalcogramma*) is subject to strong interannual variation in the eastern Bering Sea, and this variation is known to be determined largely at the age-0 stage. We estimated the spatial distributions and densities of age-0 walleye pollock in five nursery areas around the eastern Bering shelf in three successive years (1997–1999) from acoustic survey data. Concurrently, we calculated estimates of the spatial distribution of euphausiids, a major prey of age-0 walleye pollock, and estimates of spatial overlap of groundfish predators with the age-0 walleye pollock. The analyses showed that all nursery areas had low densities of age-0 walleye pollock in 1997, which ultimately produced the weakest adult year-class. In the intermediate year of 1998, age-0 densities were low to medium, and in 1999, which produced the strongest of the three adult year-classes, all nursery areas had medium to high age-0 walleye pollock densities. Euphausiid distributions had a consistently positive spatial relationship with age-0 walleye pollock. Groundfish predator density ratios were positively related to age-0 walleye pollock density when age-0 walleye pollock were displaced relatively northward. Our results suggest that abundance of age-0 walleye pollock, and hence of adult cohorts in the eastern Bering Sea, can be predictable from a concise set of indicators: the densities of age-0 walleye pollock at nursery areas in mid- to late-summer, their spatial relationship to euphausiids and groundfish predators, and the latitudinal trend of their distributions. The 3 years 1997–1999 had significant differences of physical conditions in the eastern Bering Sea, and represent an advantageous framework for testing these hypotheses.

Keywords: Walleye pollock; Euphausiid; Nursery areas; Echo survey; Eastern Bering Sea

1. Introduction

Walleye pollock (*Theragra chalcogramma*) is a key species of the Bering Sea food web and the target of important commercial fisheries (Springer, 1992; NRC, 1996). Cohort abundance of walleye pollock populations is subject to strong interannual variation (Ianelli et al., 2004), and a major research objective has been to address the predictability of this variation (Ohtani and Azumaya, 1995; Quinn and Niebauer, 1995; Swartzman et al., 2002). Previous studies have found that cohort abundance of a walleye pollock stock is determined primarily through conditions affecting the pre-recruit, juvenile

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stages (Bailey et al., 1996; Bailey, 2000; Hunt et al., 2002a). Recent investigations have therefore focused on regions of the Bering Sea where juvenile walleye pollock aggregate and grow through their first year (Brodeur and Wilson, 1999; Swartzman et al., 2002, 2005).

The Pribilof Islands, near the Bering Sea shelf edge, have been recognized as a center of abundance of age-0 walleye pollock (Traynor and Smith, 1996; Nishimura et al., 1996), and described as a walleye pollock 'nursery' (Brodeur, 1998; Brodeur et al., 2002a; Macklin et al., 2002; Swartzman et al., 2002). Important concentrations of age-0 walleye pollock likewise have been observed at sampling stations on the inner shelf of the eastern Bering Sea (Coyle and Pinchuk, 2002a). The Pribilof Islands and inner-shelf areas were surveyed in mid- to late-summer of 3 consecutive years (1997–1999) during, respectively, the Southeast Bering Sea Carrying Capacity (SEBSCC) and Inner Front projects, to investigate processes of the southeast Bering pelagic ecosystem (Macklin et al., 2002). Swartzman et al. (2005) concluded that age-0 walleye pollock densities were variable, but generally of the same magnitude among Pribilof Islands and Inner Front areas in 1997–1999. In this paper, we hypothesize that similar densities in different areas are characterized by similar spatial relationships of the age-0 walleye pollock with their prey and predators.

Both the SEBSCC (Pribilof Islands) and Inner Front projects included two-frequency acoustic data collection on repeated transects (Swartzman, 2004). We utilize these acoustic data to delineate and quantify spatial distributions of age-0 walleye pollock in comparing the different areas surveyed. The 3-year series of parallel SEBSCC and Inner Front surveys are not long for the purpose of a comparative study, but the period of 1997–1999 was significant for its strong environmental changes in the eastern Bering Sea. Summer sea-surface temperatures were unusually high in 1997 (Napp and Hunt, 2001), and low in 1999 with heavy sea-ice cover in late spring (Stabeno et al., 2001). Bottom water temperatures were above average in 1998 (Stabeno et al., 2001). A coccolithophore bloom was recorded in the eastern Bering Sea for the first time in 1997 (Sukhanova and Flint, 1998; Stockwell et al., 2001), and recurred each year until 2001 (Hunt, 2004). Conditions associated with coccolithophore blooms may present inferior nutritional quality for zooplankton (Nejstgaard et al., 1995; Hunt et al., 1999). A climatic regime shift (Hare and Mantua, 2000), with accompanying shifts in species composition and abundance in the Northeastern Pacific, appears to have happened around 1998 or 1999 (Ingraham et al., 1998; McFarlane et al., 2000). The Oscillating Control Hypothesis (Hunt et al., 2002a; Hunt and Stabeno, 2002) proposes, in part, that during cold periods, the survival of juvenile walleye pollock will be bottom-up controlled by decreased production of copepods (Huntley and Lopez, 1992), which are a food source for euphausiids (Ohman, 1984) as well as for juvenile walleye pollock (Schabetsberger et al., 2000; Brodeur et al., 2000). During warm periods when zooplankton are plentiful, the Oscillating Control Hypothesis predicts that juvenile walleye pollock will be top-down controlled by adult walleye pollock predation, to the extent that the adult population experienced large year-classes through previously favorable conditions (Hunt et al., 2002a; Hunt and Stabeno, 2002).

Whichever control dominates in a given year, juvenile fish will seek to maintain feeding satiation and minimize energy expenditure while avoiding predators. For the SEBSCC and Inner Front survey transects, we analyzed the acoustically determined densities and spatial distributions of age-0 walleye pollock in relation to: the acoustically determined distributions of euphausiids (a major zooplankton prey of age-0 walleye pollock), the distributions of groundfish predators, the frontal zones, and the relative northward displacement of the age-0 walleye pollock biomass. Frontal zones refer to the hydrographic structuring of the water column that separates tidally mixed nearshore waters from thermally stratified offshore zones (Stabeno et al., 1999). Such hydrographic structuring can create zones of increased environmental heterogeneity (Sournia, 1994) and concentrated nutrient availability (Coyle and Pinchuk, 2002a; Flint et al., 2002). Nearshore, front, and offshore zones in a nursery area may represent distinct habitat conditions for age-0 walleye pollock (Ciannelli et al., 2002; Swartzman et al., 2002). The relative northward displacement of age-0 walleye pollock biomass may serve as a potential indicator for effects of current transport or water temperature (cf. Wespestad et al., 2000; Overland and Stabeno, 2004). The estimated densities of age-0 walleye pollock in eastern Bering Sea survey areas varied by a factor of more than five between the cohorts of 1997–1999 (Swartzman et al., 2005), providing a useful basis for characterizing conditions that may regulate walleye pollock survival.

2. Methods

2.1. Survey databases

Acoustic transects analyzed in this paper are mapped on Fig. 1. Pribilof A was surveyed through the SEBSCC project, and Nunivak Island, Cape Newenham, Port Moller and Slime Bank were surveyed through the Inner Front project. Survey transect dates are summarized in Table 1, together with the distance from shore and width of the oceanographic front in each area, by year. Locations of the front were determined according to the criteria of Stabeno et al. (1999): nearshore, the front is delineated at the first water column sampling station that shows a well-mixed (or weakly stratified) vertical profile, and offshore, it is delineated where the depth range of the thermocline increases by a factor of two over its average width. Survey transects were generally designed to track perpendicular to the front, thus sampling each of the nearshore, front, and offshore zones. The Inner Front survey areas were covered by 1–3 parallel transect lines (Fig. 1) per survey, and Pribilof line A was replicated 3–5 times per survey. The surveys operated mostly during daytime, although some transects ran into twilight and night. Conductivity–temperature–depth (CTD) samples and trawls for biological data were taken along the survey tracks.

2.2. Acoustic data processing

Acoustic data on Pribilof line A (SEBSCC surveys) were collected using a hull-mounted SIMRAD EK-500 split-beam echo-sounder system operating at 38 and 120 kHz. The data were echo-integrated to horizontal–vertical resolution units (pixels) of ~9 × 0.5 m in 1997 and 1999, and ~9 × 1 m in 1998. Acoustic data on the Inner Front surveys were collected with an HTI model 244 split-beam towed 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. Inner Front acoustic data were echo-integrated to ~180 × 2 m pixels in 1997, and ~45 × 1 m pixels in 1998 and 1999.

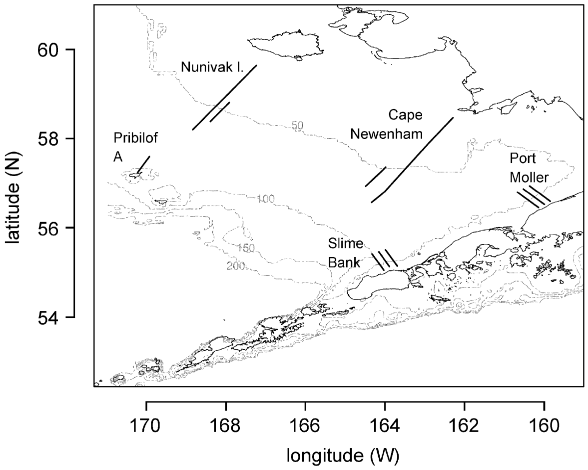

Fig. 1. Survey transects of the SEBSCC Pribilof Islands and Inner Front studies, late summer 1997–1999.

Table 1
Summary of survey dates and extents of the oceanographic front over transects analyzed in this study

Transect area	Transect surveyed dates	Offshore distance (km) of front zone
Pribilof A	15, 16 September 1997	6–30[a]
	12–14 September 1998	8–26[b]
	9, 11, 17 September 1999	8–26[b]
Nunivak Isl.	5 September 1997	135–165[c]
	28 August 1998	125–169[c]
	12 August 1999	145–164[c]
Slime Bank	8, 10, 11 September 1997	8–33[c]
	20, 21 August 1998	11–32[c]
	27–29 July 1999	12–25[c]
C. Newenham	2–4 September 1998	49–161[c]
	6, 8 August 1999	117–142[c]
Port Moller	31 July 1999	7–24[c]

[a] From Ciannelli et al., 2004.
[b] From Swartzman et al., 2002.
[c] From Kachel et al., 2002.

The acoustic processing algorithms described by Swartzman et al. (1999, 2002) were used to identify and spatially locate aggregations of age-0 walleye pollock and zooplankton from the echo-integration. These algorithms defined a range of backscatter expected for fish as −53 to −40 dB at 38 kHz. Pixels within this threshold range were morphologically filtered to retain only aggregations greater than a minimum size of 3 horizontal × 2 vertical pixels, to eliminate isolated backscatter not forming part of a fish shoal (Swartzman et al., 2002). Target strength vs. length comparisons calculated from the Kirchhoff ray-mode model (Clay and Horne, 1994; Horne and Jech, 1999) showed that the difference between echo sounding at 38 and at 43 kHz was negligible to the backscatter in this range. The same threshold parameters (−53 to −40 dB) were therefore applied to the HTI as well as the SIMRAD data.

The backscatter range for zooplankton was defined as −62 to −45 dB at 120 kHz. Zooplankton at sizes in the Rayleigh scattering range are expected to have higher backscatter at 120 kHz, whereas fish schools do not have higher backscatter at 120 than at 38 or 43 kHz (Swartzman et al., 2002). Therefore, the processing algorithm (Swartzman et al., 2002) set an additional threshold for zooplankton pixels to backscatter at least 5 dB higher at 120 kHz than at 38 kHz. This 5 dB frequency-differencing threshold had been designed for the ~9 × 0.5-m echo-integration resolution used in the 1997 and 1999 SEBSCC surveys. For the lower resolutions (larger pixel sizes) used in the 1998 SEBSCC and the Inner Front surveys the threshold was reduced according to the formula of dividing 5 dB by the square root of the resolution ratio (Swartzman, 2004). For example, transects with a pixel size twice the area of 9 × 0.5 m would be processed for zooplankton with a differencing threshold of $5\,\text{dB} \times 2^{-0.5} = 3.54\,\text{dB}$. Since each pixel averages the echo return over its area, a larger pixel size requires a lower backscatter-difference value to represent the same level of discrimination between the two frequencies.

An example of the processed echo-integration distributions, for one transect, is given in Fig. 2. We assumed fish pixels to represent age-0 walleye pollock, as midwater trawls taken during the SEBSCC and Inner Front surveys showed over 90% of fish catch to be age-0 walleye pollock (Coyle and Pinchuk, 2002a; Brodeur et al., 2002a). We assumed zooplankton pixels to be primarily euphausiids, based on geometric models (e.g., Stanton et al., 1993) for which backscatter retained by the processing algorithm would be dominated by zooplankton in the size range of adult euphausiids. Smaller or weaker-scattering zooplankton (e.g., copepods, chaetognaths) are unlikely to occur at densities high enough to be detectible (Swartzman et al., 2002). Jellyfish attained high biomass levels in the eastern Bering Sea during 1997–1999 (Brodeur et al., 2002b), and at high densities may produce scattering levels equivalent to fish with swimbladders (Colombo et al., 2003). However, Winter (2005) compared jellyfish net catches with the distribution of fish and zooplankton pixels on the Inner Front surveys, and did not find evidence of significant confounding.

The acoustic surveys also recorded depth- and angle-compensated backscatter strengths of individual target detections. We used the individual target strength values (TS) at 38 kHz to examine spatial relationships between the age-0 walleye pollock and larger, predatory fish. The presence of potential

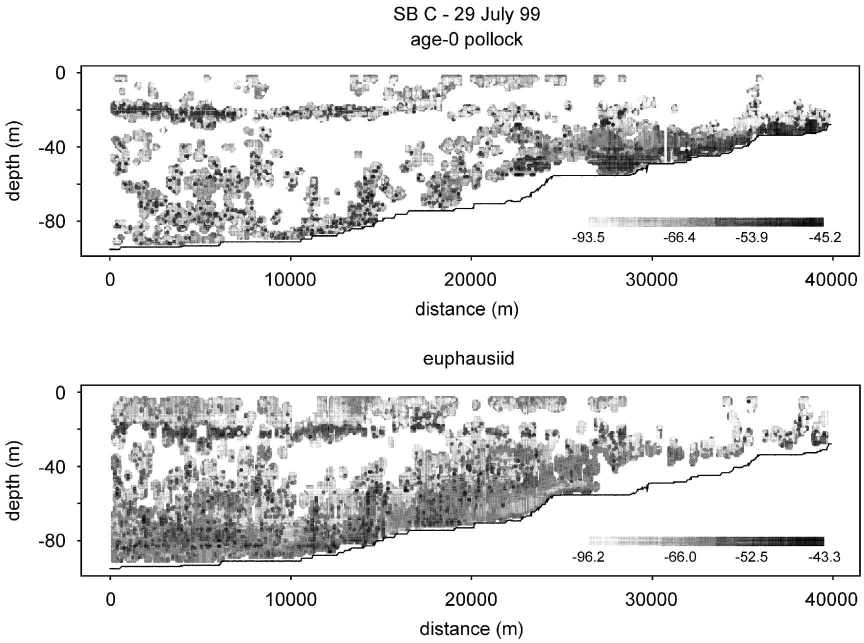

Fig. 2. Transect Slime Bank C in 1999 showing the distributions of echo-integration pixels identified as (top) age-0 pollock backscatter, and (bottom) euphausiid backscatter. Pixel intensities are gray-scaled in dB. The transect is the same as in Fig. 3.

predators is an important factor in the distribution of age-0 walleye pollock (e.g., Lang et al., 2000). However, the SEBSCC and Inner Front surveys took few or no trawls suitable for capturing predator-sized fish (i.e., Aleutian wing or bottom trawls), and publication of such data is otherwise sparse for the eastern Bering Sea. TS are convertible to estimates of fish length through standard equations in the fisheries acoustics literature (Love, 1971; Foote and Traynor, 1988). Strong TS can thus be taken to represent fish of a size likely to be predators of age-0 walleye pollock (as shown in Fig. 3 for one example transect). To classify TS as fish by length, we used Foote and Traynor's (1988) equation for walleye pollock fork length (L; in cm): $\mathrm{TS} = 20\log L - 66.0$. Adult walleye pollock is by far the greatest consumer of age-0 walleye pollock, followed by Pacific cod (*Gadus macrocephalus*) (Lang et al., 2003), which presents 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). Fish lengths derived from this equation were grouped according to nominal walleye pollock year class—length strata obtained from survey net samples, for age 0, or cited in Dwyer et al. (1987) for ages 1, 2, 3, and 4+ (Table 2). These strata represent an approximate index for true length categories, since target strength of a fish varies with its tilt angle (Blaxter and Batty, 1990; MacLennan et al., 1990). Observations by Horne (2003, cf. Fig. 5 therein) showed that walleye pollock do preponderantly maintain a horizontal aspect without bias toward positive or negative inclination, or lateral roll. We therefore considered the categorization sufficiently precise for qualitatively discriminating length groups.

The SIMRAD EK-500 echo-sounder was set to a pulse length of 1 ms and estimated sound speed of $1500\,\mathrm{m\,s^{-1}}$, giving a target resolution of $0.001\,\mathrm{s} \times 1500\,\mathrm{m\,s^{-1}}/2 = 0.75\,\mathrm{m}$. The HTI echo-sounder was

Table 2
Lengths-at-age (from Dwyer et al., 1987) and equivalent target strengths (from Foote and Traynor, 1988) of walleye 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 parametrized separately for each survey. All other age categories are treated as constant averages.

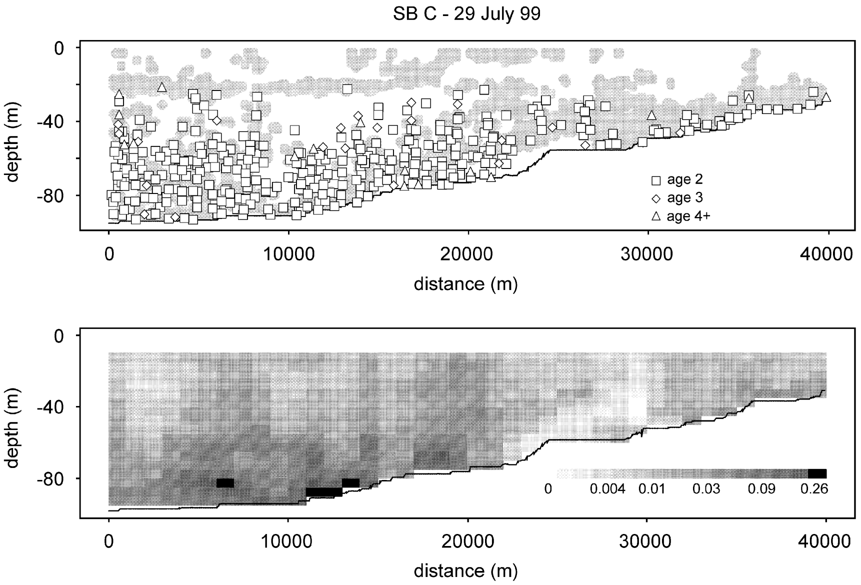

Fig. 3. Transect Slime Bank C in 1999 showing, top: individual target strengths corresponding to age-2 (square), age-3 (diamond) and age-4+ (triangle) pollock overlaid on the age-0 pollock echo-integration, in gray, and bottom: the estimated TS ratio of age-2,3,4+ to age-0 pollock from the target strength processing algorithm. TS ratios are shaded on a logarithmic scale per 5 × 1000 m transect cell. The transect is the same as in Fig. 2.

set to an effective pulse length of 0.18 ms and sound speed of 1470 m s^{-1}, for a target resolution of 0.13 m. Alongship/athwartship beam widths of the EK-500 and HTI were, respectively 6.7°/6.7° and 6.14°/6.17°. An echo-sounder only records TS if returning echoes are sufficiently separated from other backscatter to be resolved as individuals, i.e., separated by at least 0.75 m for the EK-500 and 0.13 m for the HTI sounder. Therefore, counts of strong TS cannot be directly quantified as the number of equivalent-sized (large) fish. However, acoustic resolution of individual fish is independent of fish length (Gauthier and Rose, 2001). An approximation can thus be made that over a given area, the ratio of counts of strong TS to weaker TS relates to the ratio of numbers of large fish (potential predators) to small fish. This approximation may potentially be biased against weaker target detections by backscatter absorption in the water (MacLennan and Simmonds, 1992), by non-random distribution of large and small fish within aggregations, or by the echo-sounder system's algorithm for TS detection (Soule et al., 1995, 1997). Absorption was not considered an important source of bias in this study since transects are less than 100 m deep (Fig. 1). Non-random fish distributions have been found where larger individuals occupy the leading edges of schools (Rose, 1993) or maintain wider spacing within schools (MacLennan and Menz, 1996), either of which would increase the larger fishes' relative probability of single-target detection. Length distributions within walleye pollock schools were not sampled on the SEBSCC and Inner Front surveys (e.g., with a net suitable for capturing all size classes). The possibility of target detection bias therefore cannot be excluded, and TS ratios should not be interpreted as absolute values. However, size-specific positioning of the fish would be consistent across the extent of transects (as would any bias from the echo-sounder's TS detection algorithm), and the distribution of TS ratio values therefore can be utilized as a relative measure of spatial relationship between predators and prey when comparing multiple observations within transects (Winter and Swartzman, 2006). Since larger fish were sparse to begin with (more than 90% of fish biomass had been found to be age-0 walleye pollock; see above), we could also assume that TS ratios were not additionally biased by differential densities of the larger fish (e.g., larger fish being very tightly aggregated in some locations).

To calculate ratios of strong to weak TS, we partitioned transects into subsections (cells) of 5 m vertical × 1000 m horizontal width (Fig. 3). The numbers of TS detected in a transect cell may be confounded by a higher incidence of false multiple-target acceptance at higher fish densities (Sawada et al., 1993; Ona and Barange, 1999; Gauthier and Rose, 2001). Therefore, only transect cells were sampled for TS, which had integrated backscatter below the 10% probability threshold of multiple target detection (calculated as in equation 6.10 of Ona and Barange, 1999). With its lower resolution, the EK-500 potentially has higher acceptance of multiple targets than the HTI sounder (Soule et al., 1997). To examine whether the difference between sounders influenced TS distributions, relative proportions of age-1,2,3,4+ equivalent TS values per survey areas/years were compared (for example: age-1,2,3,4+ = (0.61, 0.20, 0.06, 0.13) for Pribilof A 99, vs. age-1,2,3,4+ = (0.48, 0.18, 0.07, 0.27) for Slime Bank 99). Pairwise Euclidean distances between proportions were found to be no greater on average between EK-500 and HTI-surveyed areas than among HTI-surveyed areas, suggesting that the choice of sounder did not have a significant effect on the TS ratio. In all survey areas, numbers of TS per transect cell were smoothed over unsampled cells to eliminate zero-counts of age-0 equivalents, which would cause infinite ratios (0^{-1}). Smoothing was calculated as the average of neighboring transect cells weighted by the inverse distance of separation (Winter, 2005). This TS ratio algorithm was initially tested on data from the 1997 and 1999 NOAA echo-integration trawl surveys in the eastern Bering Sea, where Aleutian wing and bottom trawls had been taken in conjunction with 38-kHz acoustic transects (Winter, 2005). Normalized CPUEs of walleye pollock were regressed on TS data occurring within ±1000 m horizontal, ±10 m vertical, and ±2 h of each trawl. Application of the TS ratio algorithm improved the fit of linear regression (R^2) from 0.05 to 0.80 for Aleutian wing trawls ($n = 12$) and from 0.15 to 0.43 for bottom trawls ($n = 6$) (Winter, 2005). Correlation between expected mean TS of haul catches (calculated from Foote and Traynor's 1988 equation) and corresponding mean survey TS values was significant at $p < 0.05$ for Aleutian wing trawls, and significant at $p < 0.02$ for bottom trawls (Winter, unpublished data).

2.3. Data analyses

Average densities (no. m^{-3}) of age-0 walleye pollock were estimated from the backscattered energy by dividing age-0 walleye pollock area backscatter (s_a; $m^2 m^{-2}$) by integration depth (m) and mean backscattering cross-section σ_{bs} (m^2). Mean σ_{bs} for age-0 walleye pollock were obtained from the average of lengths measured in each survey (e.g., Brodeur et al., 2002a; Coyle and Pinchuk, 2002a), converted by interpolation of the Kirchhoff ray mode model (J. Horne, pers. commun.). Average euphausiid densities were calculated using the mean TS for euphausiids = −77.8 dB (Coyle and Pinchuk, 2002a).

Walleye pollock biomass comparisons were calculated between the average age-0 acoustic density indices of survey areas, by year, and the NOAA eastern Bering Sea (EBS) stock assessment estimates for 3-year-old recruits of the corresponding year-classes (Table 1.14 in Ianelli et al., 2004). Because the age-0 surveys were conducted in a time range from late July to mid-September (Table 1), we standardized their acoustic densities to a single reference date (September 1) by fore- or back-calculating age-0 walleye pollock mortality and growth (Table 3). We used instantaneous mortality rates of 0.08 day^{-1} for 1997 and 1998, 0.03 day^{-1} for 1999, and a growth rate average of 0.5 mm day^{-1} for all 3 years, as described by Swartzman et al. (2005). Significance for the interannual differences in EBS recruitment abundance (shown as the A and B superscripts in Table 3) was estimated from Ianelli et al. (2004). Significance of the interannual differences in age-0 acoustic densities (per survey area; superscripts C and D in Table 3) was calculated by one-way ANOVA with Tukey's test for multiple comparisons. For statistical units in this calculation the transects were partitioned into 250 m horizontal (full water column) bins, a format that Swartzman et al. (2005) found does not have autocorrelation bias.

Spatial distributions of age-0 walleye pollock densities were analyzed with generalized additive models (GAM; Hastie and Tibshirani, 1990). In GAM, covariates are assumed to affect the dependent variable through unspecified (not necessarily linear) additive functions, and data can come from any distribution in the exponential family (Swartzman et al., 1992). Age-0 walleye pollock densities were modeled using the normal distribution, which was verified by Kolmogorov–Smirnov goodness-of-fit tests. We calculated GAMs at the spatial scale of the 5 × 1000 m transect cells (Fig. 3) using a spline smoother at 4 degrees of freedom and as covariates: (1) the acoustic euphausiid density, and (2) the TS ratio of age-2,3,4+ walleye pollock to age-0 walleye pollock. Age-1 walleye pollock also prey on age-0 walleye pollock to some extent (Dwyer et al., 1987), but have much lower quantitative impact (Lang et al., 2000) and are themselves constrained by efforts to avoid the larger adults. Therefore, age-1 walleye pollock were excluded from the present analysis. Example graphics of these GAMs are shown in Fig. 4. Parameters of the GAM functions calculated per transect are given in Table 4. A covariate was scored 'NS' if inclusion of the covariate failed to improve the explanatory power of the GAM at $p = 0.05$ by an approximate F-test (Hastie and Tibshirani, 1990). TS were not available for Pribilof line A in 1998 and left blank in the table. R^2 values of the GAMs in Table 4 were computed as 1 minus the ratio of model deviance over null deviance (Swartzman et al., 1992).

Since transects run primarily north–south (Fig. 1), a measure of along-transect age-0 walleye pollock distribution was calculated as the latitude centroid of the distribution weighted by acoustic

Table 3
EBS age-3 walleye pollock recruitment, and average acoustic age-0 pollock density per year-class and survey area

Year	EBS stock assess.	Age-0 acoustic densities (no. m^{-3}; standardized to Sep. 1)				
		Pribilof A	Nunivak I.	Slime Bank	C. Newenham	Port Moller
1997	3732^{A}	0.018	0.003^{C}	0.019^{D}		
1998	4255^{AB}	0.063	0.001^{C}	0.013^{D}	0.030	
1999	5834^{B}	0.088	0.050	0.267	0.184	0.288

EBS: Eastern Bering Sea. From Table 1.14 in Ianelli et al. (2004). Numbers in this column (millions of fish) refer to the year-class that originated in a given year.
Superscripts A, B, C and D indicate values that are not significantly different, by column (year).

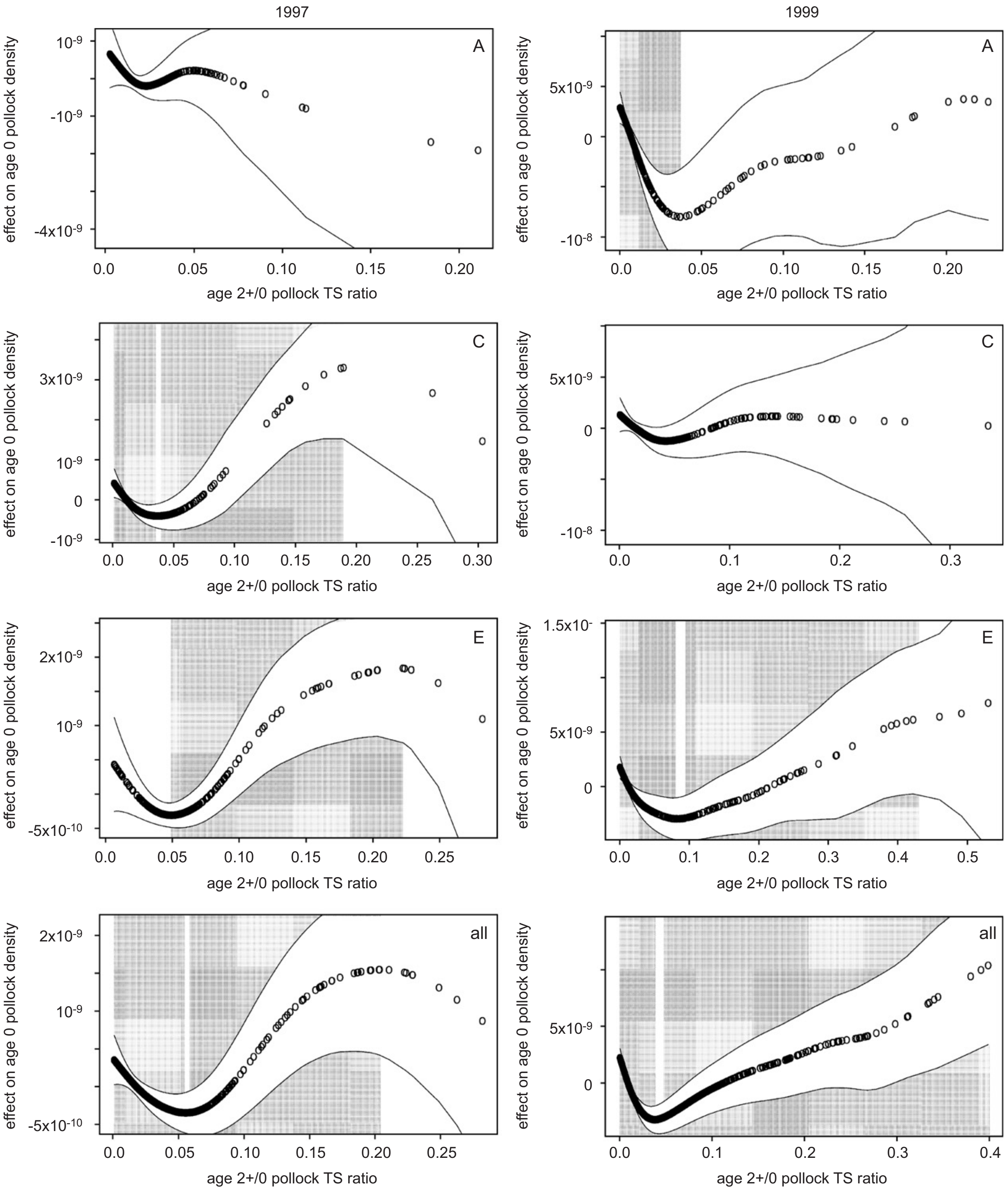

Fig. 4. Smoothed plots ±95% conf. int. of the GAM effect of the TS predator/prey ratio (age-2,3,4+ over age-0) on age-0 pollock density for the Slime Bank transects A, C and E, and the aggregate of the Slime Bank survey area, in 1997 and 1999. Gray undershaded sections of each plot highlight the portion of the distribution giving significantly positive or negative effects (as determined from the rule-of-thumb that a horizontal line would intersect the 95% conf. bounds through that extent of the plot; Swartzman et al., 1992). The data of these plots represent the corresponding entries in Tables 4 and 5.

Table 4
Mean acoustically derived parameters, and summary of GAM results of euphausiid density and predator/prey TS ratio effects on age-0 walleye pollock distributions

Transect			Mean acoustic value[a]			GAM	
Year	Area	Line	Pollock (no. m^{-3})	Euphausiid (no. m^{-3})	TS ratio (no. no^{-1})	Euphausiid (slope) R^2	TS ratio (slope) R^2
1997	PrA	A1	0.01	6.12	0.073	(+) 0.21	NS
		A2	0.01	4.86	0.102	(+) 0.45	(–) 0.04
		A3	0.01	7.01	0.054	(+) 0.50	NS
	NI	C	0.00	0.85	0.047	(+) 0.26	(+) 0.01
	SB	A	0.02	0.18	0.022	NS	NS
		C	0.00	3.24	0.023	NS	(±) 0.05
		E	0.00	0.00	0.056	NS	(+) 0.08
1998	PrA	A1	0.03	5.15		(+) 0.23	
		A2	0.04	7.52		NS	
		A3	0.03	4.52		(+) 0.09	
		A4	0.03	6.13		(+) 0.24	
	NI	C	0.00	12.49	0.041	(+) 0.40	(+) 0.03
		E	0.00	9.50	0.019	(+) 0.27	(+) 0.04
	SB	C	0.03	21.10	0.012	(+) 0.33	(+) 0.05
		E	0.02	12.15	0.017	(+) 0.18	NS
	CN	C1	0.01	6.70	0.007	(+) 0.67	(+) 0.06
		C2	0.02	23.80	0.015	(+) 0.28	(+) 0.30
		C3	0.04	25.30	0.030	(+) 0.57	(+) 0.13
1999	PrA	A1	0.05	8.34	0.004	(+) 0.83	NS
		A2	0.10	5.74	0.020	(+) 0.09	(+) 0.07
		A3	0.07	11.45	0.009	(+) 0.27	NS
	NI	C	0.12	5.22	0.001	(+) 0.29	NS
	SB	A	0.42	10.45	0.018	(±) 0.05	(–) 0.06
		C	0.25	11.19	0.030	(±) 0.08	NS
		E	0.23	8.38	0.044	(+) 0.16	(±) 0.16
	CN	C1	0.40	7.03	0.002	(±) 0.07	NS
		C2	0.51	1.75	0.000	NS	(+) 0.07
		E	0.20	4.57	0.001	(+) 0.18	(+) 0.23
	PM	A	0.05	3.73	0.003	(+) 0.75	(+) 0.02
		C	0.38	11.73	0.002	(±) 0.13	NS
		E	0.89	4.37	0.005	NS	(+) 0.08

Transect areas: PrA = Pribilof Islands line A, SB = Slime Bank, NI = Nunivak Island, CN = Cape Newenham, PM = Port Moller. GAM sub-columns 'slope' indicate whether the majority of data were comprised in an increasing (+), decreasing (–), or at least 20% of each (±), GAM trend. Covariates that were available but did not contribute to the best-fitting model are indicated 'NS'. Unavailable covariates are blank.

[a] Note that unlike Table 3, these are not standardized to Sep. 1.

density per distance unit (250-m bin). The latitude centroid thus represents a rough index of the northward trend of habitat occupancy by the age-0 walleye pollock. On each transect line (e.g., Pribilof A, Slime Bank C), the centroid calculation was restricted to the minimal and maximal latitudes common to all survey years, for standardization. Centroid values were averaged per survey area to give qualitative scores of greater- or lesser-northward distribution, by year, of the age-0 walleye pollock. Quantitative scores would be arbitrary since transect extents are only subsections of the total space potentially available to the fish. Cumulative sums per latitude of the age-0 walleye pollock densities were calculated and compared among surveys to verify that relative northward positions of the centroids were not spurious with respect to the total distributions; for example, the centroid being northward while the 20% quantile or the 80% quantile are southward. On Pribilof line A, where the 3–4 transect passes per survey represent actual spatial replicates, the centroids of the replicates were

Table 5
Summary of abundance and distribution factors associated with TS ratio vs. age-0 walleye pollock GAM relationships

TS ratio GAM slope	Survey	Pollock abundance		Latitude centroid
		Age-0[a]	Adult[b]	
–	97 PrA	Low	High	↓
±	99 SB	High	Medium	↓
±	97 SB	Low	Medium	↔
+	97 NI	Low	Low	↓
+	98 SB	Low	High	↑
+	98 NI	Low	Low	↑
+	98 CN	Medium	Medium	↑
+	99 PrA	Medium	Medium	↑
+	99 CN	High	Low	↓
+	99 PM	High	Medium	N/A
NS	99 NI	Medium	Medium	↔
N/A	98 PrA	Medium	Medium	↔

'TS ratio GAM slope' indicates the direction of the relationship of the aggregate of the 1–3 transects per survey. Survey abbreviations are the same as in Table 4. Latitude centroid is the relative northward displacement of the age-0 walleye pollock acoustic biomass. E.g., ↑ for a given survey means the centroid of the age-0 distribution is further north than in other years in the same survey area.

[a] From echo-integration density (cf. Table 3). Low: $<0.02\,\text{no.}\,\text{m}^{-3}$; high: $>0.10\,\text{no.}\,\text{m}^{-3}$.

[b] From NOAA survey CPUE (J. Ianelli, AFSC, NOAA, personal communication). Low: $<25\,\text{kg}\,\text{ha}^{-1}$; high: $>100\,\text{kg}\,\text{ha}^{-1}$.

statistically tested for significant difference among years. For all survey areas, an index of adult walleye pollock abundance was calculated from the 1997 to 1999 NOAA Bering Sea trawl CPUE data (J. Ianelli, NOAA, pers. commun.). These trawls were taken over a regular-spaced grid (e.g., Fig. 1.11 in Ianelli et al., 2004). Using least-squares trend-surface analyses we found no autocorrelation among sampling stations, and calculated the average CPUE per survey area (defined as a quadrangle around the transect coordinates, cf. Fig. 1B in Coyle and Pinchuk, 2002a) by cubic interpolation. Table 5 summarizes the GAM relationships between age-0 walleye pollock density and TS ratio calculated per survey area/year, together with indices of age-0 density and adult abundance, and the age-0 latitude centroid scores. For example, scores of ↓, ↑, and ↔ for Nunivak Island 97, 98, and 99 mean that in the Nunivak Island survey area, acoustically determined distributions of age-0 walleye pollock were the furthest south in 1997 and the furthest north in 1998.

Differences in age-0 walleye pollock density among nearshore, front and offshore zones per transect were analyzed by one-way ANOVA using the 250-m bins as statistical units, and examined in relation to average bottom water temperatures and GAM outcomes of TS ratio vs. age-0 walleye pollock density. Average bottom water temperatures were linear-interpolated from CTD casts. These GAMs were calculated separately per frontal zone within each transect. Results are summarized in Table 6.

3. Results

The EBS age-3 stock assessments and age-0 acoustic survey densities of walleye pollock are given in Table 3. EBS age-3 abundances were significantly below the recent 40-year mean (1964–2004) in 1997 and 1998 (Table 1.14 and Fig. 1.36 in Ianelli et al., 2004) and marginally above the mean in 1999. Compared with the eventual age-3 recruitment, age-0 densities in all surveyed areas were relatively much lower in 1997 than in 1999. For example, around Nunivak Island, average age-0 densities of 1997 vs. 1999 were $0.003/0.050 = 6\%$, while the EBS age-3 ratio was $3732/5834 = 64\%$. Age-0 densities of 1998 vs. 1999 were also relatively much lower than the age-3 EBS ratio ($4255/5834 = 73\%$) around Nunivak Island (2%), Slime Bank (5%) and Cape Newenham (16%), and about equal on Pribilof line A (72%).

The GAM analyses per transect indicated that acoustic distributions of age-0 walleye pollock were more strongly related to euphausiid density than to the density ratio of fish predators. Of the 31 survey transects with euphausiid data, 25 transects had a significant positive GAM relationship between age-0 walleye pollock and euphausiids over at least part of the range of euphausiid densities (Table 4). None had an exclusively negative relationship. Of the 6 (out of 31) non-significant outcomes, 3 were the Slime Bank surveys in 1997; the other 3 occurred in various areas in 1998 and 1999. That 3 of the 6 non-significant outcomes would co-occur in the same survey area in 1 year is itself statistically non-random (permutation test, $p = 0.04$).

Eighteen of 27 survey transects had a significant GAM relationship between age-0 walleye pollock and the TS predator/prey (age-2,3,4+/age-0) ratio. The expected type I error rate at $\alpha = 0.05$ would be 1–2 significant relationships out of 27. Twelve of the 18 significant TS ratio covariates had exclusively

Table 6
Comparisons per nearshore (N), front (F), and offshore (O) zones of age-0 walleye pollock density, bottom water temperatures, and TS ratio GAM trends

Transect			Mean density diffs. per zone	Bottom temp. (°C)			TS ratio GAM		
Year	Area	Line		N	F	O	N	F	O
1997	PrA	A1	$F>\underline{O>N}$	7.8	6.1	5.0	NS	+	+
		A2	$F>\underline{O>N}$	7.6	6.4	5.0	NS	NS	+
		A3	$F>\underline{O>N}$	7.9	6.2	5.0	NS	+	NS
	NI	C	O>F>N	7.8	6.4	3.2	NS	NS	+
	SB	A	F>O		8.5	7.0		NS	NS
		C	F>O		8.7	6.2		NS	+
		E	F		8.5			+	
1998	PrA	A1	$\underline{F>O}>N$	7.0	7.0	5.7			
		A2	$\underline{F>N}>O$	7.0	7.0	5.6			
		A3	$\underline{F>O}>N$	7.0	7.0	5.5			
		A4	$O>\underline{F>N}$	7.0	7.0	5.4			
	NI	C	$\underline{F>O}>N$	7.3	7.1	3.4	NS	+	+
		E	F>O		6.0	3.6		+	NS
	SB	C	O>F>N	10.1	9.0	6.5	NS	+	+
		E	$F>\underline{N>O}$	9.1	7.3	5.7	NS	NS	NS
	CN	C1	N>F	8.9	8.5		+	+	
		C2	O>F		7.4	5.8		±	NS
		C3	O			4.3			+
1999	PrA	A1	O>F>N	7.0	6.2	4.1	NS	NS	NS
		A2	O>F>N	7.0	6.1	4.1	NS	+	+
		A3	O>F>N	7.0	6.2	4.1	NS	NS	−
	NI	C	O>F>N	5.8	4.2	2.7	NS	NS	+
	SB	A	$\underline{F>O}$		6.9	5.1		NS	−
		C	F>O		6.9	4.9		+	±
		E	N>F	6.8	5.0		−	NS	
	CN	C1	O>F>N	6.1	5.1	1.8	NS	NS	−
		C2	O			2.6			±
		E	O						±
	PM	A	O>F		7.2	4.3		NS	NS
		C	O>F		8.1	4.8		±	+
		E	O>F		8.6	5.1		NS	+

Jointly underlined letters N, F and O are not significantly different from each other in mean age-0 walleye pollock density (one-way ANOVA). NS, +, − represent the slope of the GAM between TS ratio and age-0 pollock density, as in Table 4.

positive relationships, two negative, and four included positive and negative trends (Table 4). A positive relationship implies that predator fish concentrate on the age-0 walleye pollock as age-0 walleye pollock densities increase, while a negative relationship indicates that age-0 walleye pollock are distant from high concentrations of predators, implying that they are evading the predators. GAM trends tended to be similar among parallel transects within the same area (e.g., Fig. 4). GAM effects of the TS predator/prey ratio were significantly positive where the latitude centroid was northward (↑), or where the abundance index of adult pollock was low (Table 5). Pribilof A survey transects, which could be tested as true spatial replicates, were significantly different in their latitudinal trends among all 3 years by one-way ANOVA and Tukey's test (df = [2,7], $F = 57.5$, $p < 0.0001$). Across all surveys, significance of the TS predator/prey ratio appeared unrelated to the overall density of age-0 walleye pollock (Table 5).

TS ratio vs. age-0 walleye pollock GAMs calculated per transect frontal zone showed that, proportionally, the greatest number of significant interactions between TS ratios and age-0 walleye pollock occurred offshore, and the fewest significant interactions occurred nearshore (Table 6). Bottom-water temperatures were progressively colder further offshore on every transect. This confounded the effect of temperature with the effects of hydrographic structure or depth. Nearshore, front and offshore zones examined separately had no correlations between bottom temperature and the presence or absence of significant TS ratio vs. age-0 walleye pollock GAMs (*t*-test, $p > 0.15$ in all cases).

4. Discussion

The most consistent trend observed among all surveys was the positive relationships between acoustic euphausiid densities and age-0 walleye pollock densities. Maintaining proximity to their potential prey appeared to be a major determinant of spatial location for the age-0 walleye pollock in the eastern Bering Sea during the years 1997–1999. Age-0 walleye pollock do not prey on euphausiids exclusively, or even predominantly, depending on the zooplankton taxa available (Brodeur et al., 2000; Schabetsberger et al., 2000, 2003). However, by late August–September age-0 walleye pollock were within the size range that has been found capable of consuming euphausiids ($\geqslant 25$ mm length; Winter et al., 2005). Proximity to euphausiids may additionally benefit juvenile walleye pollock by reducing cannibalism through prey switching (Willette et al., 1999), as adult walleye pollock also feed on euphausiids (Lang et al., 2003). Swartzman et al. (1999) analyzed earlier surveys near the Pribilof Islands and likewise observed positive correlation of age-0 walleye pollock with zooplankton—up to a zooplankton density threshold. The notable exception of this study occurred on Slime Bank in 1997, with no significant GAM relationship between age-0 walleye pollock and euphausiids on all three transects. Acoustic densities of both age-0 walleye pollock and euphausiids were low, but not very different in that year from Nunivak Island or Pribilof line A, for which the GAM relationships were strongly positive (Table 4). Slime Bank was surveyed later in 1997 than in 1998 and 1999 (Table 1), which should imply that age-0 walleye pollock were older in 1997 and more, not less, likely to target euphausiids (e.g., Winter et al., 2005). Possibly, high densities of scyphomedusae (for which ‘Slime’ Bank is eponymous; Malakoff, 2001) influenced feeding behavior of age-0 walleye pollock. Possibly also, the first occurrence of the coccolithophore bloom in 1997 may have contributed to this absence of significant GAM relationship between age-0 walleye pollock and euphausiids. Slime Bank was outside the area of the coccolithophore bloom (Hunt, 2004), and in 1997 had significantly higher numbers of live shearwaters (and fewer dead ones) than the Nunivak or Pribilof areas located within the bloom (Baduini et al., 2001). It may be speculated that shearwaters concentrated on Slime Bank where they could still detect euphausiid prey from the air (Lovvorn et al., 2001), thereby disrupting foraging of the age-0 walleye pollock. Baduini et al. (2001) reported mean densities of 189 shearwaters km^{-2} on Slime Bank in 1997, but as many as 300 aggregating on a single dense euphausiid patch, which is the kind of food resource that age-0 walleye pollock would also target. Shearwaters preyed on euphausiids almost exclusively in 1997, but included large proportions of fish in their diets in 1998 and 1999 (Hunt et al., 2002b). Fish and euphausiids were generally deeper in the water in 1997 than in 1998 or 1999 (Swartzman, 2004).

Unlike the relatively consistent positive association between age-0 walleye pollock and euphausiids, the spatial relationship between age-0 walleye pollock and their fish predators (the TS ratio) varied among survey years and nursery areas. Positive TS ratio GAM trends occurred primarily where centroids of age-0 walleye pollock distributions were northward (Table 5). Northward means offshore on Pribilof A and Slime Bank, but onshore on Nunivak Island and Cape Newenham transects (cf. Fig. 1). Since positive TS ratio GAMs were obtained in each of Pribilof A, Slime Bank, Nunivak and Cape Newenham areas (Table 5), the northward effect is not confounded with the onshore/offshore gradient. This suggests a parallel to the hypothesis of Wespestad et al. (2000), which proposed that strong transport in warm years moves juvenile walleye pollock northward onto the shelf and away from cannibalistic adults. The geographic scales of this study are more restricted, and relative latitude distributions among transects may be related to local movements rather than the large-scale transport mechanisms proposed by Wespestad et al. (2000). However, if more northward age-0 walleye pollock distributions effectively are further out of range for cannibalism, then the TS ratio GAM trends in this study suggest that whatever adult walleye pollock did follow age-0 distributions northward were forced to target them more explicitly than adults that targeted age-0 walleye pollock distributed farther south. This suggestion is made with the caveat of the potential biases in the assumptions of the TS ratio (described in Section 2). As a relative index, the TS ratio is also not as comprehensive as would be an estimate of actual numbers of the age-2+ fish. (Age-2+ numbers could be derived by multiplying the numerator of the TS ratio with the age-0 numbers estimated from echo-integration, but age-2+ and age-0 numbers would then be autocorrelated). The TS ratio has the advantage of being practical to calculate in conjunction with routine acoustic surveying, but further investigation of Bering Sea nursery areas would benefit from midwater and bottom-trawl sampling closely coordinated with acoustic transects.

This summary of GAM relationships suggests a top-down scenario regulating the age-0 walleye pollock population over the 3 years of this study. The predominant outcome among all surveys in this study, of positive GAM relations between acoustic zooplankton and age-0 walleye pollock distributions, indicates that zooplankton availability was not a limiting factor for the age-0 walleye pollock. Potential for such limitation was shown in 1994, when spatial correlation between zooplankton and age-0 walleye pollock around the Pribilof Islands was poor (Winter and Swartzman, 2006), and 1994 produced a weak year-class (Ianelli et al., 2004). The Oscillating Control Hypothesis (e.g., Fig. 18 in Hunt et al., 2002a) anticipates a combination of both top-down and bottom-up regulation with the putative beginning of a cooler climate regime in 1998 or 1999 (Ingraham et al., 1998; McFarlane et al., 2000). Significant differences in copepod densities were found during spring of 1997, 1998 and 1999 (Napp et al., 2002; Coyle and Pinchuk, 2002b; Baier and Napp, 2003). Copepods are major prey for euphausiid and juvenile walleye pollock populations (Ohman, 1984; Schabetsberger et al., 2000). However, Coyle and Pinchuk (2002a, b) found no significant differences in euphausiid biomass or overall late summer zooplankton abundance from 1997 to 1999, despite the 3 years' temperature differences (Hunt and Stabeno, 2002).

ANOVA tests of age-0 walleye pollock density difference by frontal zone were generally consistent in reflecting the latitudinal trends. For example, the Pribilof A transects—of which the deep-end is north (Fig. 1)—were northward biased in 1999 (Table 5) together with average densities Offshore > Front > Nearshore (Table 6). However, nearshore densities in all surveys were almost always lower than front densities regardless of latitudinal trend (Table 6), suggesting that large-scale ocean current transport is constrained by the effects of water column properties closer on-shelf. If the nearshore environment is a less supportive habitat, then width and location of the front, and the considerable variability thereof (Table 1), will influence distribution of the age-0 walleye pollock population. The relatively infrequent occurrence of significant GAM relationships between TS ratios and age-0 walleye pollock in the nearshore zones (Table 6) is likely due, in part, to the nearshore zones being generally smaller (fewer data points). But it is also consistent with prior observations that adult walleye pollock prey more heavily on age-0 walleye pollock further offshore (Lang et al., 2000; Ciannelli et al., 2002).

Late-summer density and distribution measures may provide a useful first index of walleye pollock year-class strength (Schumacher and Macklin, 2004). In this study, all survey areas with applicable data correctly 'predicted' that 1999 would be a stronger year-class than either 1997 or 1998 (cf. Table 3). However, the three Inner Front areas (Slime Bank near the shelf break; Nunivak Island and Cape Newenham on the inner shelf) had much lower relative densities of 1998 vs. 1999 at age-0, than subsequently the EBS age-3 recruitment abundances, whereas the Pribilof area had relatively higher (though still absolutely lower) density of 1998 vs. 1999 at age-0 than at age-3 recruitment (Table 3). Concomitantly, the three Inner Front areas had northward age-0 distributions in 1998 vs. intermediate or southward in 1999, while the Pribilof area had an intermediate latitudinal distribution in 1998 vs. northward in 1999 (Table 5). These latitudinal contrasts suggest that favorable distribution within the habitat range can make up for low density at age-0. That 1999 still produced the largest cohort perhaps relates to the low temperature conditions of that year (Overland and Stabeno, 2004). Adult walleye pollock have been found to avoid cold water (Francis and Bailey, 1983) and were notably absent from the shelf region in the 1999 NOAA trawl survey (cf. Fig. 1.15, Ianelli et al., 2004). This may have created a predator refuge for the age-0 walleye pollock on the inner shelf. The two inner shelf areas in 1999 (Nunivak Island and Cape Newenham) showed the lowest adult walleye pollock CPUEs of all areas (J. Ianelli, NOAA, pers. commun.). At the same time (in 1999), adult walleye pollock CPUE was medium in the Pribilof Islands and Slime Bank, with respectively positive and predominantly negative GAM interactions of age-0 walleye pollock and TS ratios in those areas (Table 5). Evidently, different nursery areas are separately influenced by varying combinations of predator and prey constraints. This study gives evidence that development of age-0 walleye pollock populations relates to such predator and prey constraints over short time and spatial scales. Comparably, Bond and Overland (2005) hypothesized that year-to-year walleye pollock recruitment variability is driven by the impact of short-term weather events on the food chain, within the scale of climatic regimes. Effectively predicting such year-to-year recruitment variability will require further focus on the study of nursery areas.

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