

Early- to late-summer population growth and prey consumption by age-0 pollock (*Theragra chalcogramma*), in two years of contrasting pollock abundance near the Pribilof Islands, Bering Sea

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ABSTRACT

Acoustic survey data were used to estimate the abundance and distribution of age-0 walleye pollock and zooplankton near the Pribilof Islands, Bering Sea, nursery area at two time periods in two consecutive years: the beginning of August, and mid-September, of 1996 and 1997. The 1996 pollock year class ultimately produced a large adult cohort in the eastern Bering Sea, while the 1997 year class produced a below-average adult cohort. Acoustic densities of age-0 pollock were significantly lower in August – and declined more strongly from August to September – in 1997 than in 1996, indicating that the trend to adult cohort strength was already set by August. Diet composition analyses revealed that age-0 pollock ate a much higher proportion of euphausiids in 1997 than in 1996, despite lower acoustic abundance of euphausiids in 1997. We infer that in 1996, age-0 pollock experienced greater feeding success by August, with high concentrations of copepods available for smaller fish to consume, and high concentrations of euphausiids available for larger individuals. In 1997, age-0 pollock had lower body condition in August and may have been limited by the availability of small (<2 mm) copepods. Bioenergetic modeling of prey consumption did not indicate a likelihood that age-0 pollock would

begin to deplete euphausiids until late August in 1996, and not at all between August and mid-September in 1997.

Key words: Bering Sea, copepod, euphausiid, food limitation, Pribilof Islands, *Theragra chalcogramma*, walleye pollock

INTRODUCTION

Walleye pollock (*Theragra chalcogramma*) is a major commercial fish species, and a key component of North Pacific ecosystems (National Research Council, 1996). The abundance of pollock stocks is thus a focus of considerable importance to fisheries managers and researchers. Furthermore, the age-0 juveniles provide an important food resource for seabirds, marine mammals and groundfish (Springer, 1992). Several studies have presented evidence that the ultimate size of a pollock year class is largely determined at its age-0 juvenile stage (reviewed by Brodeur and Wilson, 1999). In particular, Bailey and Spring (1992) found significant correlations between abundance indices of age-0 juveniles and age-2 recruits in the western Gulf of Alaska, including both strong and weak year classes. Brodeur and Wilson (1996) reported that the maximum biomass of a pollock cohort is achieved during the age-0 stage.

In the eastern Bering Sea, abundance of age-0 pollock has been found to center in the vicinity of the Pribilof Islands (Nishimura *et al.*, 1996; Traynor and Smith, 1996), and the Pribilof Islands area is characterized as a nursery for the pollock population (Swartzman *et al.*, 2002). Surveys conducted around the Pribilof Islands between September 5 and September 17 of two consecutive years (1996 and 1997) showed strongly contrasting levels of age-0 pollock abundance: an order of magnitude higher in 1996 than in 1997. In fact, 1996 and 1997 had respectively the highest and lowest abundance during the 6 yr from 1994 to 1999 (Swartzman *et al.*, 2002). That contrast has remained

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evident through recruitment to the adult stock, with 1996 the second-largest eastern Bering Sea cohort from 1990 through 2003, and 1997 the fifth-smallest cohort over the same 13-yr period (Ianelli *et al.*, 2003).

In addition to the September cruises (Macklin, 1999), in both 1996 and 1997 the Pribilof Islands area had been surveyed between August 1 and 3 during the course of the eastern Bering Sea echo-integration trawl (EIT) surveys (Midwater Assessment and Conservation Engineering program – Alaska Fisheries Science Center, NOAA, Seattle, WA, unpublished cruise reports). The combined information of two synchronous sampling intervals, about 40 days apart, in 2 yr of differing juvenile pollock abundance provides an opportunity to examine the development of the pollock population during its crucial first pre-winter growth period. In this paper, we present analyses of the August and September, 1996 and 1997, survey data together with bioenergetic modeling that explores the possibility of food limitation of the age-0 pollock.

METHODS

All four surveys were conducted aboard the NOAA ship *Miller Freeman*. The September surveys of both years occupied identical, straight transect lines (Fig. 1), designed to traverse the hydrographic frontal structures surrounding the Pribilof Islands (Stabeno *et al.*, 1999). In this paper we analyze data from transect A, north of St Paul Island, and transect D,

south of St George. Those two transects have been comprehensively sampled for juvenile pollock (e.g. Brodeur *et al.*, 1997, 2002; Ciannelli *et al.*, 2002) and oceanographic properties (Stabeno *et al.*, 1999), and present a range of different habitats. On transect A, the hydrographic structure creates a tidally mixed nearshore habitat, the partially stratified front, and a stratified offshore habitat. Boundaries between these habitats are defined according to water temperature profiles, as described in Stabeno *et al.* (1999). In 1996, the front extended from 6 to 18 km offshore, and in 1997, from 6 to 30 km offshore. On transect D, the furthest-inshore hydrographic stations were already in water too deep to be mixed by tidal currents and wind (Ciannelli *et al.*, 2002), and therefore habitats could not be zoned precisely according to stratification. Instead, we partitioned transect D using the habitat definitions described in Swartzman *et al.* (2002): a slope habitat extending to the 130 m isobath (about 20 km offshore), and a basin habitat of bottom depth >130 m.

The August EIT cruises followed a track near the Pribilof Islands, but had not been designed to parallel the September studies. Therefore, transects differed from August to September, although they were identical between August 1996 and August 1997, as well as between September of either year. We analyzed the portions of the August track that most closely match transects A and D in September (Fig. 1). To define equivalent habitat regions in August we determined (for line A) the seafloor depths corresponding to the

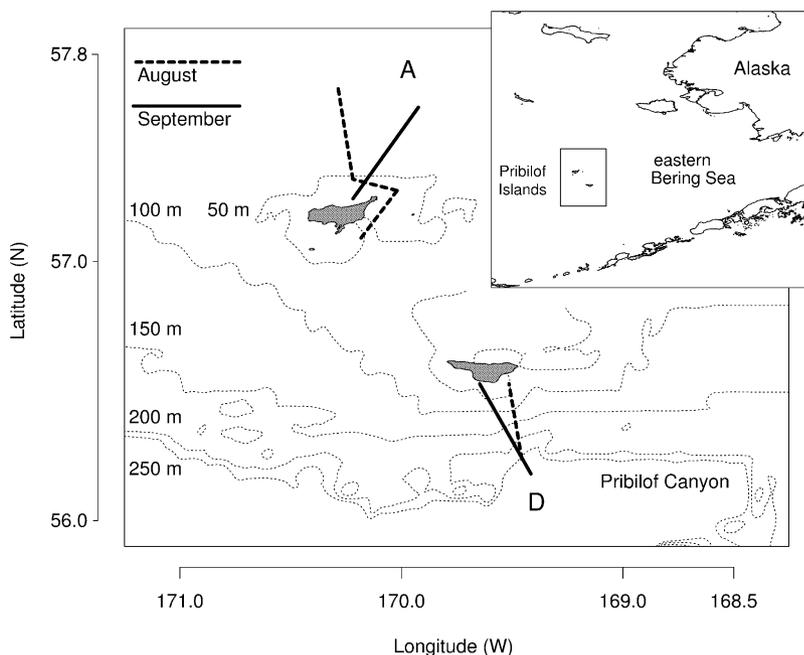


Figure 1. Study area around the Pribilof Islands in the southeast Bering Sea, showing transects A, north of St Paul Island, and D, south of St George, acoustically surveyed during the August (broken line) and September (solid line) cruises.

September front boundaries: 43 m depth at 6 km along-transect, 60 m depth at 18 km, and 67.5 m depth at 30 km, then used those depths to delimit the habitats (e.g. the August 1996 front is thus defined as the portion of the transect in waters 43–60 m deep). For transect D, the 130 m depth threshold between slope and basin was applied in August as in September.

The surveys collected acoustic data using a hull-mounted EK-500 split-beam echo-sounder system (Simrad Kongsberg Gruppen ASA, Kongsberg, Norway) operating at 38 and 120 kHz. Transects were run day and night during the September cruises, but only in daytime in August. Therefore, only daytime acoustic data were included in this study. Juvenile pollock and zooplankton diel migrate (Bailey, 1989; Schabetsberger *et al.*, 2000), and some may rise above the depth of the echo-sounder at night. Mixing day and night data would potentially bias quantitative estimates. The daytime survey was run three and two times, respectively, over transects A and D during the September cruises, and once over each transect during the August cruises.

Acoustic data were processed according to the algorithms described in Swartzman *et al.* (1999a,b, 2002) to identify and locate shoals of age-0 pollock and patches of zooplankton. Further, we retained backscatter information within each shoal and patch at the spatial scale of the individual echo-integration unit (i.e. 'pixel'; typically ~ 9 m horizontal \times 0.5 m vertical) instead of averaging backscatter strength across the shoal. This resolution enabled us to identify more numerous small aggregations of pollock and zooplankton, especially near-surface and near-bottom, than were previously detected (Swartzman *et al.*, 2002). Fish shoals were delineated by morphologically filtering 38 kHz pixels within the threshold range of -53 to -40 dB, and retaining contiguous areas >3 horizontal by 2 vertical pixels (Swartzman *et al.*, 2002). The identification of these shoals as pollock was supported by trawl samples during the surveys, which yielded age-0 pollock at $>95\%$ of the fish catch (Brodeur *et al.*, 2002). Zooplankton patches were delineated by morphologically filtering pixels within the range of -62 to -45 dB at 120 kHz, and backscattering at least 5 dB higher at 120 kHz than at 38 kHz. Contiguous areas >3 horizontal by 3 vertical pixels were retained (Swartzman *et al.*, 2002). The zooplankton algorithm was based on theoretical target strength modeling ('bent cylinder' model, Stanton *et al.*, 1993) which predicts that larger zooplankton (e.g. euphausiids in the range of 15–25 mm body length) backscatter more strongly at 120 kHz than at 38 kHz. Other, smaller zooplankton (e.g. pteropods or

large copepods) also scatter sound at 120 kHz when occurring in high densities. However, Multiple Opening/Closing Net and Environmental Sampling Systems (MOCNESS, 333 μm mesh; Wiebe *et al.*, 1976) samples taken during the September cruises (Schabetsberger *et al.*, 2000; Ciannelli *et al.*, 2004) obtained biomass densities of copepods and pteropods that, in relation to these organisms' sizes and expected target strengths (copepods: 'truncated sphere' model, Holliday and Pieper, 1995; pteropods: 'spherical elastic shell' model, Stanton *et al.*, 1994), would not significantly augment the backscatter retained by the thresholds (above), compared with euphausiids. We thus identified the acoustic zooplankton patches as dominantly representing euphausiids.

Method (1986) midwater tows were used to capture fish for size distribution and stomach content analyses. Weighted average age-0 pollock lengths were calculated for each transect habitat from measurements of the fish caught in or near that habitat. In the August 1997 survey, tow sample stations were not specifically located on the transects, and an overall average from five tows around the Pribilof Islands was used for all habitats (Table 1). The length averages were converted to estimates of backscattering cross-section (σ_{bs} ; m^2) at 38 kHz based on an extrapolation of the Kirchhoff ray-mode model (John Horne, Univ. Washington, Seattle, WA; Personal communication), and the σ_{bs} estimates were divided into the area backscattering coefficients (s_a ; $\text{m}^2 \text{m}^{-2}$) of each echo-integration unit (pixel) that the acoustic algorithms (Swartzman *et al.*, 1999a,b, 2002; see above) identified as fish. The factor $s_a \sigma_{\text{bs}}^{-1}$ is thus a measure of the number of 'average' pollock m^{-2} of the pixel. An estimate of pollock density (numbers m^{-3}) was then obtained by multiplying $s_a \sigma_{\text{bs}}^{-1}$ by the horizontal resolution of the pixels, summing over all pollock pixels in a given habitat, and dividing by the horizontal distance multiplied by the vertical depth of that habitat. Individual weight estimates for the pollock were calculated from length-to-weight equations in Brodeur *et al.* (2002).

Acoustic densities of euphausiids were likewise computed by inferring an 'average' animal, and dividing the s_a of zooplankton pixels by the σ_{bs} value corresponding to that average. We used Coyle and Pinchuk's (2002) estimate calculated from 200 MOCNESS-caught euphausiids: an averaged euphausiid 18.2 mm long, weighing 40.2 mg, $\sigma_{\text{bs}} = 1.66 \times 10^{-8} \text{m}^2$.

For both pollock and euphausiids, the acoustic density estimates were summarized by 250 m horizontal bins (full water column) along the length of

Table 1. Average weights and densities from respectively trawl samples and echo-integration transects during the surveys. Transect habitats 'near.' and 'off.' abbreviate nearshore and offshore. Euphausiid mean individual weights are fixed at 40.2 mg.

Transect habitat	Year	August			September		
		Age-0 pollock		Euphausiid	Age-0 pollock		Euphausiid
		Mean wt. (g)	Density (no. m ⁻³)	Density (no. m ⁻³)	Mean wt. (g)	Density (no. m ⁻³)	Density (no. m ⁻³)
A – near.	1996	0.17	0.39	7.50	1.02	0.04	3.52
A – front		0.16	0.54	7.08	0.72	0.17	9.42
A – off.		0.20	0.28	5.74	1.04	0.13	11.69
D – slope		0.16	0.18	9.24	0.81	0.05	5.07
D – basin		0.49	7e–3	2.36	0.99	0.02	6.74
A – near.	1997	0.17	0.16	8.93	0.95	8e–5	0.29
A – front		0.17	0.19	6.48	0.95	7e–3	5.35
A – off.		0.17	0.19	9.03	0.95	4e–4	4.26
D – slope		0.17	0.07	4.95	0.61	8e–4	2.15
D – basin		0.17	8e–3	5.68	0.61	9e–5	2.06

each transect-habitat. Two hundred and fifty meters is the standard used by Swartzman *et al.* (1999b), who found that biomass analyses were not sensitive to a range of bin sizes from 100 to 1000 m. Bin densities were taken as replicate sampling units to statistically test differences among habitats, years and survey periods. As the bins represent consecutive sections of continuous survey tracks, we examined their density values for serial autocorrelation prior to further statistical testing. With the transects running along bathymetric gradients, it is plausible that the pollock and zooplankton biomass distributions would follow onshore-offshore trends by water depth or distance from land, unrelated to autocorrelation. Therefore, we modeled each transect's vector of binned density values as a linear regression, and tested for autocorrelation on the residuals of the regression. Residuals were randomly permuted 1000 times, and the sum of absolute differences between consecutive values was calculated for every permutation. Autocorrelation was assumed significant if ≤ 50 of the 1000 permutations (i.e. $\alpha = 0.05$) had sums of absolute differences less or equal than the original vector of residuals. The permutation test was calculated for lags of 1 and 2.

Among 107 individual transect-habitat runs (continual survey passes over one habitat) tested, only 15 proved to be significantly autocorrelated ($P < 0.05$) at lag 1, of which eight were also significant at lag 2. We thus concluded that serial autocorrelation was not an important factor over these transects, and proceeded to analyze variability among pollock and euphausiid densities directly on the binned data. Analyses of variance (ANOVA) were used to test differences between habitats, years and survey months. The repeated runs over transects A and D during the September

cruises would represent a nested factor within the ANOVA. However, runs had not been repeated during August cruises. To avoid the problem of highly unbalanced design, we first tested differences among all runs (August and September) in each individual transect-habitat by one-way ANOVA. In every case, for both pollock and euphausiids, the outcome was statistically monotonic, i.e. the August acoustic density was never significantly higher than one, and significantly lower than another, of the September run densities. Therefore, we pooled the runs in the September transect-habitats.

We used the Fish Bioenergetics Model 2 (Hewett and Johnson, 1992) to calculate expected prey consumption by age-0 pollock between the August and September surveys, given acoustic densities, diet compositions from stomach analyses, fish size distributions, and water temperatures. Water temperature profiles were recorded with CTD (Conductivity – Temperature – Depth; SeaBird SBE-911+) and XBT (Expendable Bathythermograph) casts. Average diet compositions (weighted by the fish size distributions) and average temperatures (through the water column; weighted by depth distribution of the fish) per transect-habitat were calculated for each survey and linearly-interpolated from August to September (from day 1 to day 36–44, cf. Table 2) in both years. Instantaneous daily mortality rates for pollock in each habitat were derived from the differences in average acoustic density between August and September surveys. Larval pollock drift to the Pribilof Islands from spawning areas around Bogoslov Island and Unimak pass, and possibly the nearby Pribilof Canyon (Napp *et al.*, 2000). The circulating trapped motion around the Pribilof Islands (Kowalik and Stabeno, 1999;

Table 2. Bioenergetics model parameters from the August to September survey periods. Temperatures are at depth of the age-0 pollock distributions. Instantaneous mortality rates potentially include emigration and movement among habitats, as well as actual mortality. Transect habitats 'near.' and 'off.' abbreviate nearshore and offshore. 'C_p' is the proportion of maximum consumption the age-0 pollock would require to fit the observed growth curve.

Transect habitat	Year	August temp. (°C)	September temp. (°C)	Inst. mort. (day ⁻¹)	C _p	Interval days
A – near.	1996	8.1	8.1	0.055	0.32	40
A – front		8.0	7.3	0.029	0.26	40
A – off.		5.9	7.8	0.020	0.31	40
D – slope	1997	7.0	4.9	0.036	0.31	36
D – basin		7.7	5.7	-0.025	0.26	36
A – near.		7.5	7.5	0.173	0.27	44
A – front		7.3	6.5	0.075	0.27	44
A – off.		5.8	5.7	0.140	0.30	44
D – slope		7.2	5.1	0.113	0.22	39
D – basin	7.0	8.3	0.115	0.22	39	

Stabeno *et al.*, 1999) then facilitates their retention. Maturation of the larvae to the juvenile stage also increases their locomotor capability for maintaining position in the nursery area (Haryu, 1980; Olla *et al.*, 1996). We thus assumed that August and September surveys in either year sampled the essentially same age-0 pollock populations, while allowing for some degree of population 'turnover' between survey periods (see Results). Physiological parameters of the bioenergetics model (e.g. respiration, excretion, caloric content of prey items) were set by published values (Ciannelli *et al.*, 1998; Davis *et al.*, 1998). The major prey items, copepods and euphausiids, have breeding seasons that neither start nor end between August and September (Mauchline, 1980; Smith and Vidal, 1986; Smith, 1991) and we assumed that any interseasonal variability in their caloric content per unit weight would be much less than the variability in consumption by age-0 pollock.

The bioenergetics model calculates prey consumption by taking the mortality rate, and the start and end weights of a fish predator over a specified time period, and solving for the proportion of its maximum physiological consumption capacity (C_p) that the fish predator would require to achieve the observed weight and abundance changes (Ciannelli *et al.*, 1998). In a second step, this calculated value of C_p is applied to the fish predator's diet composition, and the model computes the cumulative total of each prey item consumed over the time period. For euphausiids, we then compared this level of prey consumption in each habitat to the available prey biomass (from the acoustic density estimates) and prey productivity (using Smith's (1991) daily P/B ratio of 0.023 for euphausiids).

Age-0 pollock sampled in the surveys were further evaluated for gut fullness and condition. A gut fullness score on a scale of 0–4 (August 1997 survey) or 0–5 (the other three surveys), was visually assessed at the time of each fish's stomach content analysis, with

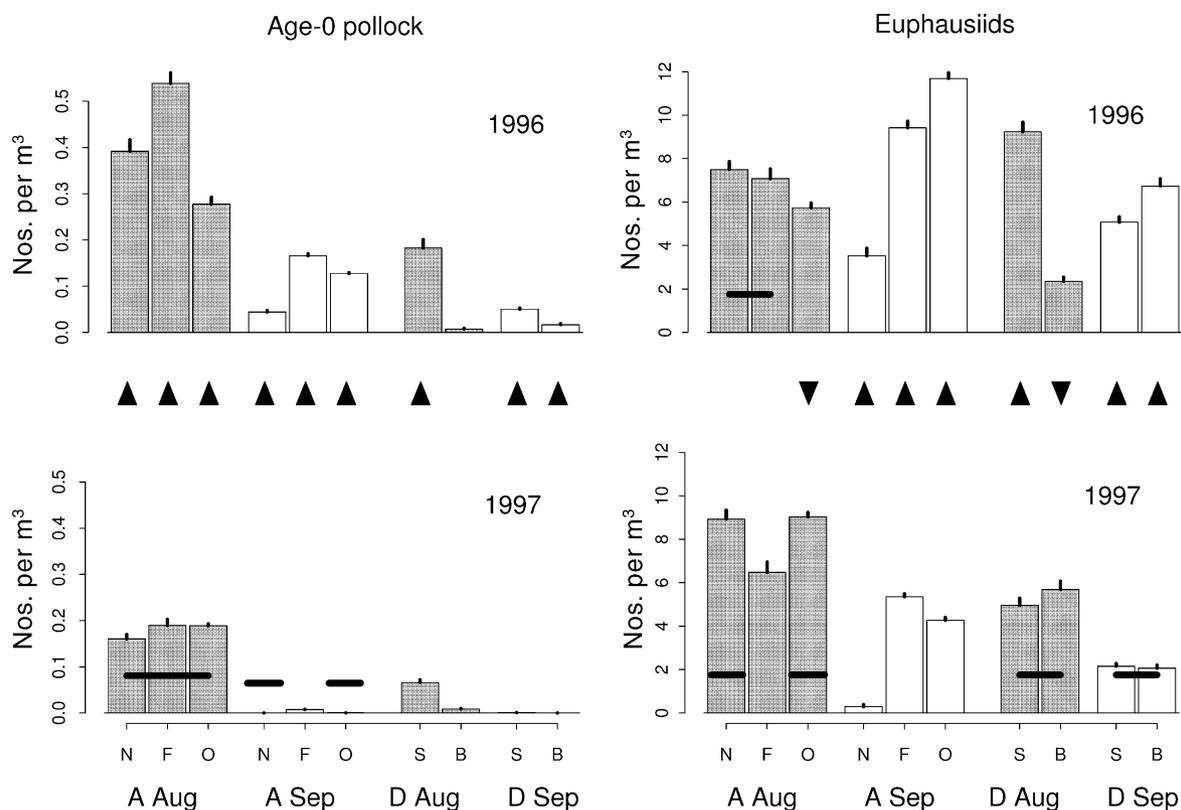
highest score = totally full gut (Merati and Brodeur, 1996). Fulton's condition factor (*K*) was calculated as $K = (W/L^3) \times 10^5$ where *W* is the wet weight (minus stomach contents) in grams, and *L* is the fork length in millimeters (Brodeur *et al.*, 2000). As *K* is a function of length, comparisons should be limited to fish of similar length (Anderson and Neumann, 1996). We compared *K* factors for August 1996 to August 1997, and September 1996 to September 1997, and in either case used sub-samples of the fish whose length distributions were not significantly different ($P > 0.1$, Kolmogorov–Smirnov two-sample goodness-of-fit test) between years.

RESULTS

Average acoustically-derived densities of age-0 pollock and euphausiids, and average individual weights of age-0 pollock, are summarized in Table 1. Density changes between years, months, and habitats were analyzed by one-way ANOVA (with Tukey's test for multiple comparisons, if applicable). All density differences from August to September within habitats and years (for example: August to September on transect A, nearshore, 1996) were statistically significant at $P < 0.05$ (Bonferroni-corrected for the number of separate tests run), except for euphausiid densities in the transect A front in 1997, where $P = 0.053$. ANOVA results of the year-to-year and within-habitat density changes are shown in Fig. 2. Notably, age-0 pollock densities were in almost all cases higher in 1996 than in 1997 (the one exception is that they were not significantly different between years in August on the transect D basin, cf. Fig. 2). Euphausiid densities were always higher in 1996 during September, but on the offshore and basin habitats they were higher in 1997 during August.

Table 2 lists mean water column temperatures and instantaneous mortality rates derived from the differ-

Figure 2. Acoustic density estimates of age-0 pollock and euphausiids by transect-habitat, during the August (gray) and September (white) surveys, with 1 Standard Error bars. Arrows between 1996 and 1997 point to the pairwise significantly higher density estimates. Horizontal segments connect density estimates that are not significantly different within transect groups.



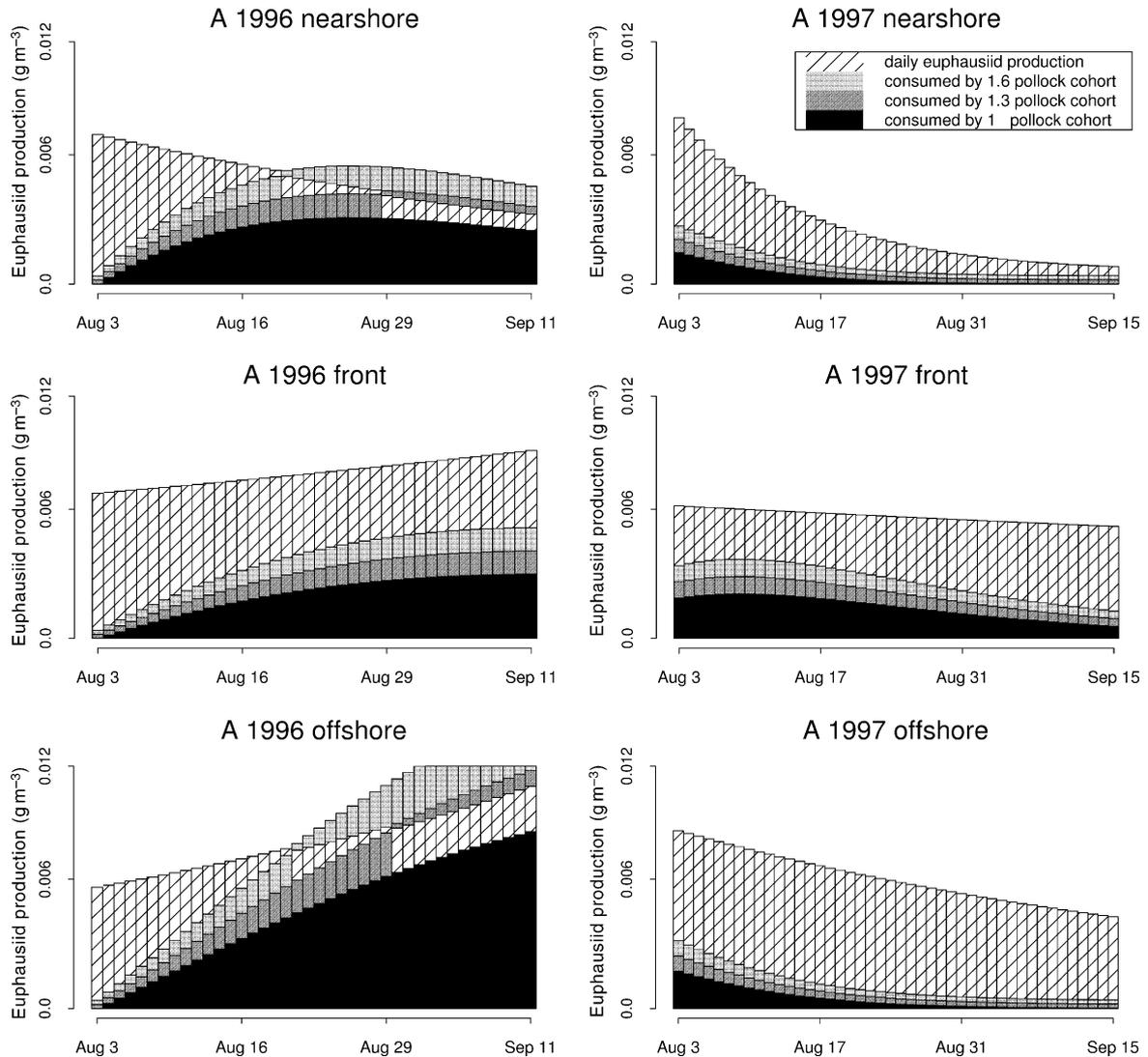
ence between August and September acoustic densities. As well, Table 2 includes the proportionality constant C_p calculated for each set of parameters by the bioenergetics model. For example, the transect A 1996 nearshore value of $C_p = 0.32$ means that in order to achieve the observed average weight gain, given their diet and temperature regime, the fish would have to have been feeding at 32% of their maximum physiological capacity over that time period.

On transect A, daily individual growth rates interpolated by the bioenergetics model (expressed as a percentage of body weight) went from ~ 8 to $\sim 2\%$ over the period from August to September. According to a simulation by Ciannelli *et al.* (1998), age-0 pollock have daily growth rates of $\sim 9\%$ starting, rather than ending, in September. Bailey *et al.* (1999) reported that age-0 juveniles grow about 1 mm day^{-1} . With the August 1997 fish of this study averaging $\sim 31 \text{ mm}$, assuming weight as proportional to $(\text{length})^3$ and taking the estimate of 1 mm day^{-1} , initial daily growth rates should have been approximately 10% (i.e. $10\% \cong [31 \text{ mm}/(31-1 \text{ mm})]^3 - 1$).

This discrepancy between reported growth and our interpolated growth rates suggests that age-0 pollock of this study were not single, distinct cohorts growing from August to September, but rather the progeny of different spawning events, with fish sampled in September including later arrivals than those sampled in August. We therefore assumed that a continuous and indefinite turnover occurs in the waters surrounding the Pribilof Islands, with movement of some age-0 pollock both in and out of the vicinity, in addition to mortality. There is no unambiguous way to calculate how many times the Pribilof pollock population did 'turn over' between the August and September sampling periods, but following the results above we roughly estimate that it would be about 25% (i.e. calculating that $10\% \text{ daily growth}/8\% \text{ daily growth} = 1.25$; in other words 25% more fish passed through the system than were there at any one time). To cover the full range of plausible outcomes, we modeled consumption totals multiplied by factors of 1, 1.3 and 1.6 (Figs 3 and 4).

Two of the scenarios on transect A (Fig. 3) suggest some potential for age-0 pollock to deplete their

Figure 3. Transect A daily euphausiid production per habitat (calculated as 0.023 of standing biomass; white bars diagonally shaded) interpolated from August to September acoustic surveys, together with the estimated percentage of that production consumed by age-0 pollock. Black bars: Percentage consumption based on the inference of a single cohort of pollock from August to September. Medium gray and light gray: Percentage consumption based on projected turnovers of 1.3 and 1.6 of the pollock population. All plots are to the same scale of euphausiid production (g m^{-3}), and to the same scale as Fig. 4.



euphausiid prey: the nearshore and the offshore habitats in 1996. On transect A nearshore, the average euphausiid density declined by 53% from August to September 1996; and by day 40 (September 11), pollock were estimated to be consuming 81–130% (at 1×–1.6× turnover) of daily euphausiid production. Offshore, pollock were likewise estimated to be consuming 81–130% of daily euphausiid production by day 40. However, the average euphausiid density approximately doubled in the offshore habitat from August to September 1996 (Table 1, Fig. 3). On transect A in 1997, average euphausiid densities

decreased across all habitats from August to September, but estimated pollock consumption nowhere exceeded 61% of daily euphausiid production, even at 1.6× turnover. Daily euphausiid consumption curves reached their highest level between day 34 and day 40 (September 5–11) in 1996, and much earlier in 1997, between day 1 and day 13 (August 3–15; Fig. 3). That difference reflects the higher age-0 pollock mortality rates (Table 2), and the higher proportion of euphausiids in the diet in 1997 (Table 3). The data do not indicate a likelihood for age-0 pollock to deplete euphausiids over transect D in either year. The

Figure 4. Transect D daily euphausiid production per habitat (calculated as 0.023 of standing biomass; white bars diagonally shaded) interpolated from August to September acoustic surveys, together with the estimated percentage of that production consumed by age-0 pollock. Black bars: Percentage consumption based on the inference of a single cohort of pollock from August to September. Medium gray and light gray: Percentage consumption based on projected turnovers of 1.3 and 1.6 of the pollock population. All plots are to the same scale of euphausiid production (g m^{-3}), and to the same scale as Fig. 3.

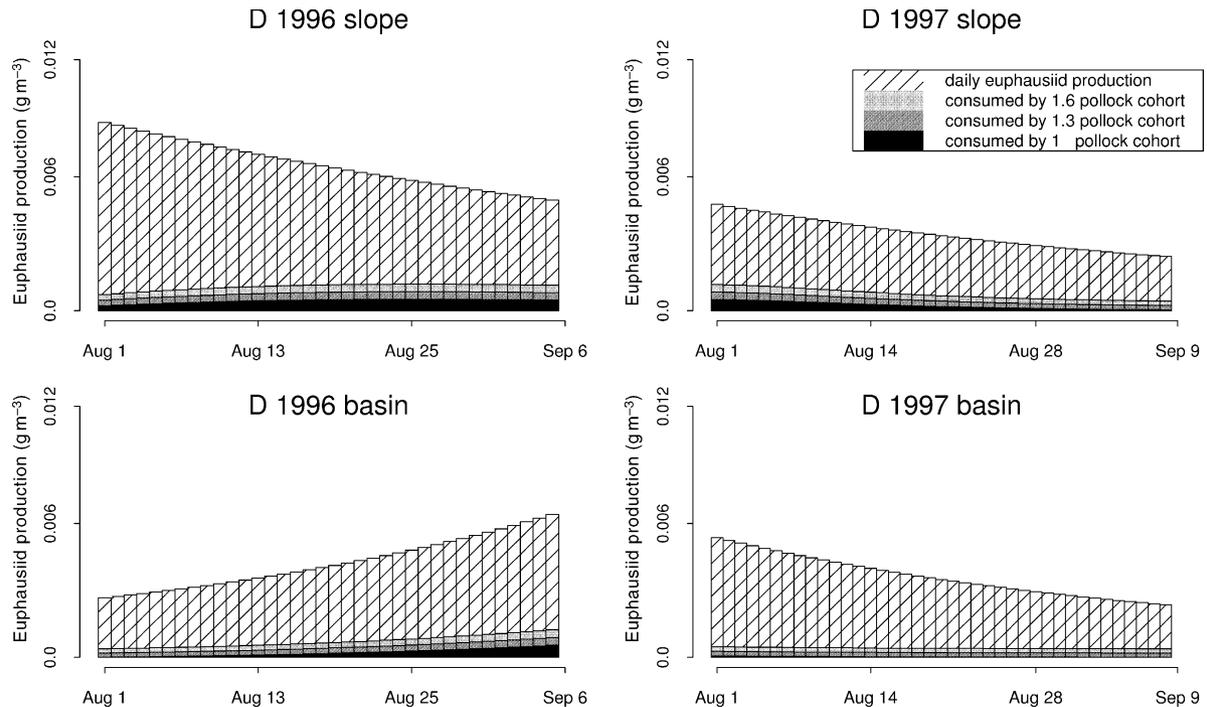


Table 3. Mean age-0 pollock condition factor (K) ± 1 standard error, and average dietary proportion by weight of the four principal prey items, in each survey. Values of K were calculated on sub-samples of fish whose length distributions matched between August 1996 and 1997, and September 1996 and 1997.

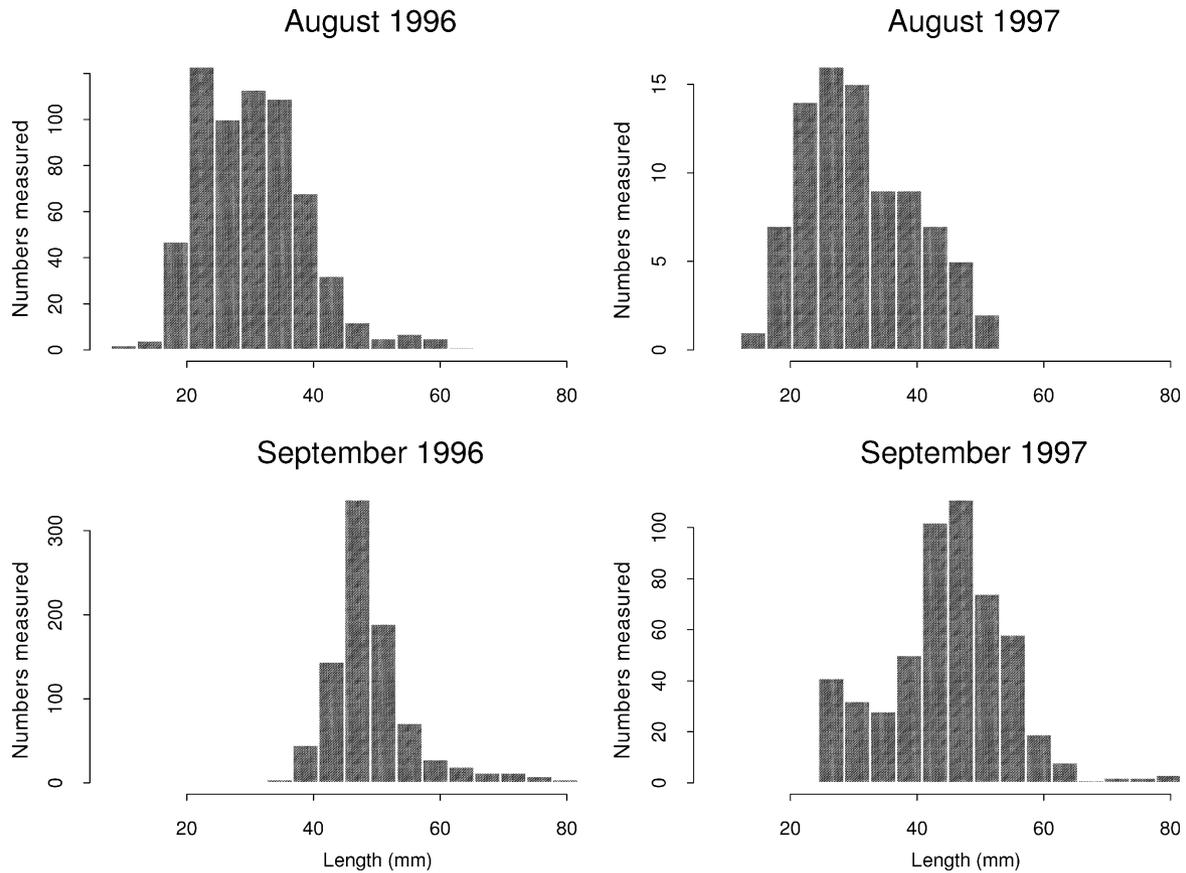
Survey		Condition factor (K)	Prey category			
Month	Year		Chaetognath	Copepod	Euphausiid	Pteropod
August	1996	0.58 ± 0.02	0.02	0.92	0.01	0.00
September		0.71 ± 0.01	0.06	0.51	0.36	0.00
August	1997	0.43 ± 0.01	0.00	0.71	0.21	0.05
September		0.78 ± 0.01	0.04	0.18	0.73	0.04

maximum projected daily consumption on transect D amounted to about 19% of euphausiid production (Fig. 4: slope 1997), and this occurred in the early days of August.

Size distributions of age-0 pollock in August were not significantly different between 1996 and 1997 (Kolmogorov–Smirnov test, $P > 0.4$). Size distributions were significantly different in September ($P < 0.001$): the same mode of length class appeared in both years (45–49 mm), but in 1997 a higher proportion of pollock was smaller than the mode (Fig. 5).

Gut fullness scores are plotted in Fig. 6, by survey, as a function of fish length and euphausiid dietary proportion. While the fullness score is a qualitative assessment by the analyst, consistent patterns are evident of the age-0 pollock. In September 1996, and August and September 1997, fullness was positively correlated with fish length (linear regression, $P < 0.01$), and likewise with the proportion by weight of euphausiids in the diet ($P < 0.001$; shown as open circles on Fig. 6). Mean condition factors (K) of all fish sampled per survey are given in Table 3. Age-0

Figure 5. Length distributions of age-0 pollock measured during the surveys.



pollock in August had significantly higher average condition in 1996 than in 1997 (one-way ANOVA, $F_{[1,156]} = 56.3, P < 0.001$). In September, condition was higher in 1997 than in 1996 ($F_{[1,257]} = 18.6, P < 0.001$).

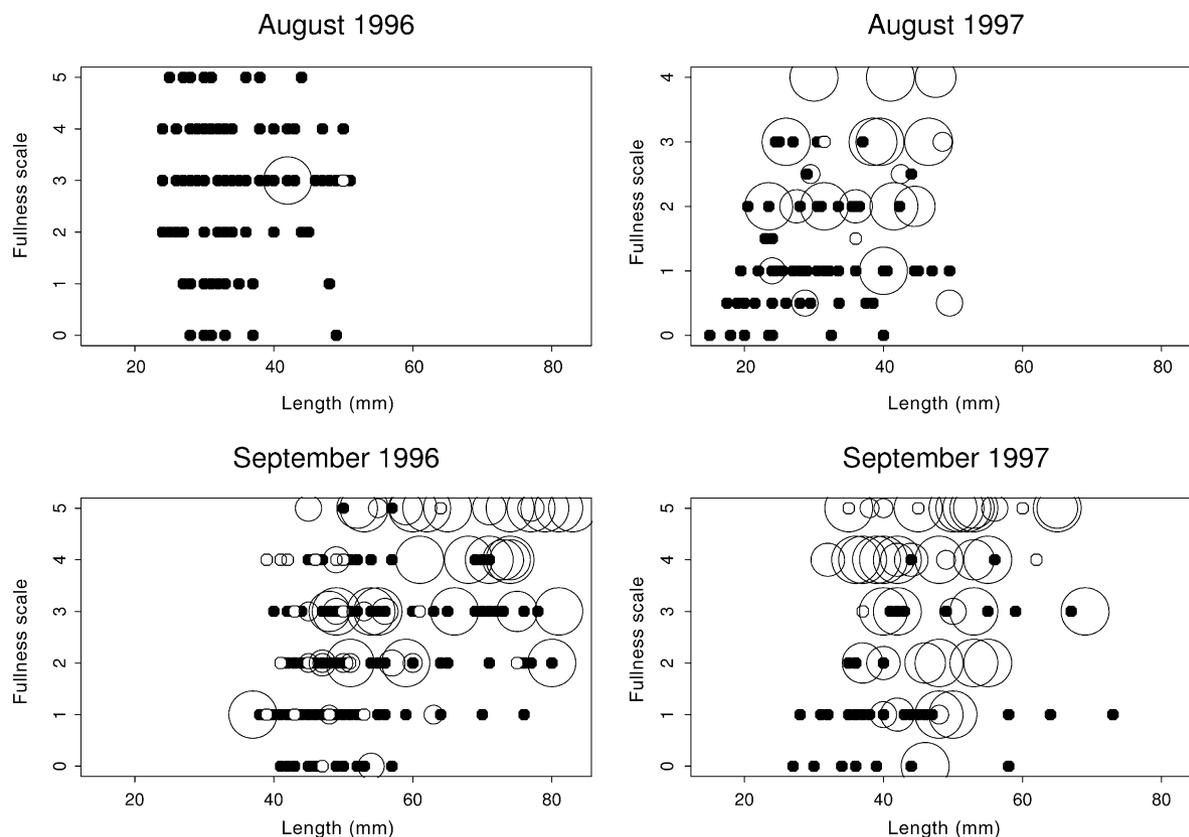
DISCUSSION

The important difference in recruitment resulting from the 1996 and 1997 pollock year classes (Ianelli *et al.*, 2003) was preceded by equally notable differences in the age-0 juvenile stage around the Pribilof Islands nursery area. In 1997, average juvenile pollock densities were significantly lower by early August (Fig. 2 and Table 1), and gross mortality rates to mid-September were significantly higher (Table 2), than in 1996, evincing that the patterns toward adult abundance were initiated by summer and continued to intensify through the fall. The 1996 data show a trend of both pollock and euphausiid biomass occurring progressively farther offshore from August through September. Gross mortality rates in 1996 were [nearshore > front > offshore] on transect A and

[slope > basin] on transect D (in fact, the August–September gross mortality rate came out negative in the basin in 1996; Table 2), while euphausiid density decreased nearshore and on the slope, stayed constant in the front, and increased offshore and in the basin (Figs 3 and 4). In 1997, the highest pollock mortalities were offshore and in the basin, while euphausiid densities decreased everywhere from August to September. This contrast suggests that the strength of the 1996 adult year class may relate to the competency of the juvenile fish at occupying habitat away from the nearshore nursery area, possibly toward offshore feeding grounds more suitable as they grow. However, the distribution shifts could represent changing patterns of current transport in addition to active migration. Ciannelli (2002) found age-0 pollock in September 1995 resided mainly inshore of the front boundary despite better feeding potential offshore. Ultimately, 1995 also became a smaller adult cohort than 1996 (Ianelli *et al.*, 2003).

Our results corroborate previous studies that report the abundances of juvenile pollock in September to be consistently higher on transect A than transect D

Figure 6. Relationship among length of age-0 pollock, gut fullness, and weight proportion of euphausiids in the gut. Black solid circles: <10% (by weight) of gut contents are euphausiid; open circles: $\geq 10\%$ of gut contents are euphausiid. Open circle sizes are scaled to the euphausiid proportion. Fullness scores were visually assessed at the time of dissection of the fish.



(Brodeur *et al.*, 2002; Swartzman *et al.*, 2002), and more variable on transect D (Swartzman *et al.*, 2002). Average pollock densities calculated by the acoustic algorithm agree with densities obtained from anchovy trawl catches (Brodeur *et al.*, 2002) on transect A, and are somewhat lower on transect D. This may be caused by the targeting of anchovy trawls to midwater, above the deep layers of transect D that age-0 pollock typically avoid but which the acoustic estimates include. Transect D extends into Pribilof Canyon (Fig. 1), from which it receives strong current flow and upwelling (Brodeur, 2001; Swartzman *et al.*, 2002). The individual mean weight of pollock in August was more than two times higher in the basin in 1996 than anywhere else in August (Table 1). It is plausible that such larger (and likely older) fish were advected from deeper within the canyon.

Age-0 pollock are cannibalized by age-1 and adult pollock (Dwyer *et al.*, 1987; Bailey, 1989), and preyed upon by birds, mammals and other groundfish (Springer, 1992; Lang *et al.*, 2000). Weststad *et al.*

(2000) hypothesized that eastern Bering Sea pollock recruitment varies interannually with the extent to which ocean transport conveys juveniles into proximity of cannibalistic adults. Predator data are too sparse for rigorous comparison between 1996 and 1997, and from around the Pribilof Islands specifically (e.g. Lang *et al.*, 2000; Ciannelli *et al.*, 2002). Indirect evidence nevertheless suggests that 1996 was not a year of particularly low age-0 predation in the eastern Bering Sea, as would constitute an explanation for its particularly strong cohort. NOAA reports estimate the numbers-at-age of pollock consumed by groundfish (Table 5 in Lang *et al.*, 2003), and the female spawning biomass (Table 1.16 in Ianelli *et al.*, 2003) annually. Using spawning biomass as a surrogate index for numbers hatched (age-0), the ratios of spawning biomass to age-0 numbers consumed give an approximate relative measure of predation pressure. By this measure, the 1996 age-0 pollock experienced more severe predation than five of the six preceding year-classes (1990 through 1995). The report of Lang *et al.*

(2003) only goes to 1996, and thereby also does not permit a direct comparison between 1996 and 1997. However, the outcome that the strong year class of 1996 was not associated with favorably low age-0 predation mortality, in comparison to mostly weaker preceding year classes, suggests that predation mortality is not the primary source of difference between 1996 and 1997 either.

Variations between 1996 and 1997 in dietary composition, and in acoustic densities of pollock and euphausiids, point toward food availability as a factor in the cohort strength difference. Age-0 pollock diet contained proportionally much more euphausiids in August 1997 than in August 1996 (Table 3). That might be expected, as euphausiids were more abundant in August 1997 than in August 1996. However, age-0 pollock diet also contained proportionally more euphausiids in September 1997 than in September 1996, whereby (a) euphausiids were less abundant in September 1997 (Fig. 2), and (b) the pollock were on average smaller in September 1997 (Fig. 5), and thereby less suited to a euphausiid diet. The distributions of fullness scores in this study (i.e. the proportion in each sample that scored 0, 1, 2, ...) were not significantly different between September 1996 and September 1997 (Kolmogorov–Smirnov two-sample test, $P > 0.25$), indicating that fish in September of either year had on average equal feeding success. However, the positive correlation between fullness and euphausiid fraction was significantly steeper in September 1997 than in September 1996 ($t_{[307]} = 4.5$, $P < 0.001$), implying that for an age-0 pollock to achieve satiation in September 1997 was more strongly a function of its capacity to utilize euphausiids for prey (note that by itself, a positive slope between fullness and euphausiid fraction could simply represent longer digestion time of larger prey, e.g. Pearre (1986); but that does not explain why the slope would be significantly steeper in one year than the other).

In August, age-0 pollock had lower average values of Fulton's condition factor in 1997 than in 1996. By September, the 1997 fish surpassed the 1996 fish in Fulton's condition factor (Table 3). These results suggest that in early August, age-0 pollock were comparatively food limited in 1997 and adequately satiated in 1996. Subsequently, starvation-induced mortality in 1997 may have lowered the densities of age-0 pollock below the threshold of food limitation by September, improving average condition of the survivors. Laboratory studies have shown that starved age-0 pollock can respond rapidly to increased food availability (Sogard and Olla, 2000). In particular, food limitation in August 1997 may have selected in

favor of fish capable of consuming euphausiids. By contrast, the initially better-fed fish in 1996 experienced lower mortality from August to September (cf. Table 2), and their higher densities began to deplete prey resources, leading to relatively poorer condition by September. The average length of age-0 pollock was nevertheless significantly greater in September 1996 than September 1997 (Fig. 5), suggesting that an onset of food depletion did not occur until after the 1996 fish had capitalized their early-August growth advantage. Alternatively, a higher proportion of larger fish may have arrived by advection later during 1996. Figure 3 shows that in 1996 potential euphausiid depletion (greater daily consumption than production) existed on transect A – nearshore and offshore for turnover projections of 1.3× and 1.6× the pollock cohort. Ciannelli *et al.* (2004) concluded that by September 1996, large copepods (>2 mm prosome length) were heavily impacted through juvenile pollock grazing. By computing forecast simulations, Ciannelli *et al.* (2004) also found a significant probability that pollock on transect A – offshore would consume more than a third of standing euphausiid biomass over 15 days.

The available data do not provide a direct inference of which – if any one – prey type would have been limiting to age-0 pollock in August 1997. However, the stomach analyses (cf. Table 3, Fig. 5) indicate that it was probably not euphausiids, but possibly copepods and in particular the smaller (<2 mm) species. It has been established that age-0 pollock depend initially on smaller copepods, then switch to larger euphausiid prey as they grow (Merati and Brodeur, 1996; Brodeur, 1998). Schabetsberger *et al.* (2003) analyzed age-0 pollock diets in 1998 and 1999 and found, as this study did (Fig. 6), that smaller individuals had relatively more food in their guts than large individuals when they consumed a high proportion of small prey items. Zooplankton samples were not taken during the August Pribilof Islands survey of either year. In September, zooplankton samples on transect A had lower densities of small copepods in 1997 than in 1996 (Ciannelli *et al.*, 2004). Tows collected east of the Pribilof Islands in April and May showed lower concentrations of small (*Acartia*, *Pseudocalanus*) and large (*Metridia*, *Calanus*, *Neocalanus*) copepods in 1997 than in 1996 (Figs 4–7 in Napp *et al.*, 2002). The mechanisms of the Oscillating Control Hypothesis (Hunt *et al.*, 2002) predict that 1997 should have been a year of lower copepod production in the eastern Bering Sea: in comparison to 1996, ice retreat occurred late, causing an early, ice-associated bloom in water too cold for the copepod population to increase rapidly

and graze down the phytoplankton growth. 1996 and 1997 do not fundamentally represent a 'switch' in oscillating control, as both years appertain to the same climatic regime (e.g. Hare and Mantua, 2000). The mechanisms of temperature-mediated bottom-up control may still have effected significant variation in copepod production at the interannual time scale.

A potentially significant further circumstance is presented by the coccolithophore bloom of 1997. Anomalous atmospheric conditions during spring and summer in 1997 (Overland *et al.*, 2001) preceded a bloom of *Emiliana huxleyi* that persisted from early July through late October in the south-east Bering Sea (Napp and Hunt, 2001; Stockwell *et al.*, 2001), extending as far west as the shelf edge (Sukhanova and Flint, 1998) and reducing visibility in the water to 1–2 m (Baduini *et al.*, 2001). Juvenile pollock are visual foragers, and under those conditions may have been impeded from detecting their prey, in particular the lightly pigmented small copepods (Brodeur, 1998). The coccolithophore bloom may have likewise affected the ability of euphausiids to find their small copepod prey, thus reducing euphausiid growth and density by September 1997.

The visibility factor might also underlie a discrepancy between our acoustically-derived euphausiid densities and euphausiid densities from Methot trawls reported by Stockwell *et al.* (2001). The acoustic data indicate that euphausiid densities were ~1.7–3.3 times higher in September 1996 than September 1997 (Table 1, this paper), while Methot trawls caught densities ~5–20+ times higher in 1997 than either 1995 or 1996 (Table 4 of Stockwell *et al.*, 2001). We speculate that the reduced water clarity of 1997 made euphausiids disproportionately easy to capture with a net. This idea is supported by inspection of the aggregation of euphausiids in either year. On transect A, in 1997 over 90% of nighttime euphausiid acoustic biomass was comprised of a single, huge, low-density patch, as calculated by the patch identification algorithm (Swartzman *et al.*, 2002; and see above). In 1996, 90% of euphausiid biomass consisted of >160 separate patches. The pattern suggests that in 1997, euphausiids dispersed more widely and uniformly in the absence of visually perceived threats.

In relating the abundance and bioenergetics of age-0 juveniles to eventual adult year class strength, caution must be expressed that subsequent stages (e.g. age-1) may also be influential (Bailey *et al.*, 1996), and that the Pribilof Islands are not the only potential nursery area for pollock in the eastern Bering Sea. However, a synthesis of Bering Sea survey data found year-to-year fluctuations in age-0

pollock density to be comparable between the Pribilof Islands and other frontal regions (G. Swartzman, unpublished data), and the Pribilof region has been cited as a 'laboratory' of the Bering Sea for its wide range of habitats in a small area (Swartzman *et al.*, 2002). A grid of trawl-sample stations surveyed in late July 1995–97 also showed higher age-0 pollock densities in 1996 than in 1997, and in both years higher densities near the Pribilof Islands than on the shelf further offshore (that sampling series was not taken close to the Pribilof Islands in 1995; Wilson and Brodeur, 1998; Brodeur and Wilson, 1999). Thus, we propose that the superior year class strength of the 1996 pollock cohort (Ianelli *et al.*, 2003) was established by summer, and was a function of the feeding success of the age-0 fish.

Feeding success in late summer can influence cohort strength by setting the rate at which juvenile fish outgrow predation risks (Sogard, 1997; Ciannelli, 2002), and by establishing their nutritional status at the onset of the first winter (Ciannelli *et al.*, 2004), during which prey availability is probably low in the Bering Sea (Sogard and Olla, 2000). Our analysis of the contrasts between August–September 1996 and 1997 indicates that age-0 pollock survival may be determined well before fall (i.e. in summer), and carry through to the adult year class abundance – a mechanism that to date has received little attention.

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