Marine Biology (2004) 144: 515–526
DOI 10.1007/s00227-003-1215-4

RESEARCH ARTICLE

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Foraging impact on zooplankton by age-0 walleye pollock (*Theragra chalcogramma*) around a front in the southeast Bering Sea

Received: 20 March 2003 / Accepted: 6 September 2003 / Published online: 22 November 2003

Abstract The waters around the Pribilof Islands in the southeast Bering Sea are a center of abundance for age-0 walleye pollock (*Theragra chalcogramma*). Each spring and summer a tidal front is formed around the islands separating a well-mixed inshore habitat from a stratified offshore habitat. The objective of this study was to assess the foraging impact on zooplankton by age-0 pollock in the vicinity of this frontal structure. A bioenergetic model was used to estimate age-0 pollock food consumption from field estimates of water temperature, age-0 pollock density, diet and growth. Sampling of field variables took place over three hydrographic habitats along an inshore–offshore transect located north of the islands. The bioenergetics analysis was applied for a 2-week period during the late summer of four consecutive years, 1994–1997. Model results of age-0 pollock food consumption indicated variable levels of food depletion, changing with prey type, year and habitat. The foraging impact of age-0 pollock on copepods and euphausiids (most common prey) ranged from about 3% to 77% of the biomass available at the start of the simulation. Copepod depletion was typically greater than euphausiid depletion. Consequently, juvenile pollock <60 mm in standard length were more likely to experience food limitation due to the greater proportion of copepods in their diet. We present evidence of severe foraging impact during 1996, when one of the primary prey items of juvenile pollock (i.e. large copepods) was scarcely represented both in their diet and in the water column. In all years, most instances of prey depletion were found at the inshore and front habitats; age-0 pollock densities were too low relative to their prey to severely impact the offshore zooplankton populations. We discuss these results with respect to modeling assumptions and in the context of previously acquired knowledge of fish behavior around frontal regions.

Communicated by T. Ikeda, Hakodate

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Introduction

The feeding success of juvenile fishes during late summer determines their nutritional status and size in the first winter of life. Nutritional status and size of fish residing in highly seasonal environments are thought to affect their survival through the winter (Paul and Paul 1998; Sogard and Olla 2000; Sutton and Ney 2001), thereby strongly influencing recruitment to the adult stage (Sogard 1997; Schindler 1999). Consequently, it is clear that a better understanding of the trophic requirements of juvenile fish during late summer could lead to a better understanding of factors affecting their recruitment to adult stages. The objective of the present study was to examine the late summer foraging impact of planktivorous juvenile walleye pollock (*Theragra chalcogramma*, Pallas) around the Pribilof Islands, in the southeast Bering Sea.

Walleye pollock is currently the world's second largest single-species fishery (FAO 2002; second only to the Peruvian anchoveta). Annual catch of walleye pollock in the United States has averaged around 1.5 million metric tons since 1970, and the vast majority of it comes from the Bering Sea (Ianelli et al. 2000). Recently, the age-0 stage of walleye pollock has received increased scientific interest, not only because of its importance as a prey and predator in the Bering Sea ecosystem (Springer 1992; National Research Council 1996), but also because of its pivotal role in the recruitment dynamics of adult pollock (Brodeur and Wilson 1999; Bailey 2000; Wespestad et al. 2000). Walleye pollock fit the characteristics of the "cod-like" group for which Houde (1987) hypothesized predominant control of the adult recruitment dynamics during the early juvenile stage.

The waters around the Pribilof Islands are a center of abundance for age-0 pollock (Traynor and Smith 1996; Brodeur and Wilson 1999). Locally, age-0 pollock dominate the small pelagic fish biomass (Brodeur et al. 2002a), and are an important component of the food web, being primary consumers of zooplankton (Brodeur et al. 2000) and prey for several species of adult groundfish (Lang et al. 2000), marine mammals (Sinclair et al. 1994), and seabirds (Decker and Hunt 1996). Primary and secondary production around the Pribilof Islands are high compared to other shelf areas of the Bering Sea (Flint et al. 2002), and are probably enhanced by a tidal front that surrounds the islands during spring and summer (Coyle and Cooney 1993; Stabeno et al. 1999a). The frontal system consists of a transition domain, which divides a well-mixed inshore domain from a two-layered thermally stratified offshore region. Each habitat varies in width from 2 km for the inshore region, up to 10 km for the frontal region, depending on the intensity of water stratification and wind forcing (Stabeno et al. 1999a). Besides enhancing primary production (Franks 1992; Olson et al. 1994), oceanic frontal areas are known to generate habitat heterogeneity within a relatively narrow spatial scale (Sournia 1994; Olson 2002). In turn, habitat heterogeneity around fronts can affect both the distribution and the feeding success of juvenile fishes, due to different feeding, growth, and predation risk conditions along the frontal system (Brandt 1993; Munk 1993; Ciannelli 2002).

Despite elevated productivity around the Pribilof Islands (e.g. Flint et al. 2002), it is possible that by late summer age-0 pollock can significantly impact their food resources, generating instances of local food depletion. For example, studies focusing on the spatial distribution of juvenile pollock and their prey along the Pribilof frontal system indicated that during some years there was a negative correlation between predator and prey abundance (Ciannelli 2002; Ciannelli et al. 2002a). However, a quantification of the foraging impact of the age-0 pollock population on their prey around the Pribilof Islands is presently unknown. Age-0 pollock feed primarily on copepods and euphausiids, and secondarily on chaetognaths, larvaceans, crab larvae and pteropods (Brodeur et al. 2000; Schabetsberger et al. 2000). In addition, their diet is variable by size, with euphausiids becoming more important in larger fish (typically, larger than 50 mm standard length, SL; Schabetsberger et al. 2000). The SL range of age-0 pollock collected around the Pribilof Islands in September can be as much as 60 mm (Brodeur et al. 2002a); thus, individuals within the same population, but of different sizes, will feed on different prey and will experience different degrees of food availability at the same site and time.

We examined the foraging impact of age-0 pollock residing around the Pribilof Islands. This is in fact the first study that quantifies the foraging impact of age-0 pollock in an important nursery area of the Bering Sea. The analysis was conducted along each of the frontal habitats and for each size group sampled. Consumption by age-0 pollock was estimated using a bioenergetics model applied to the late-summer conditions of four consecutive years (1994–1997), with contrasting environmental features, prey and predator densities. Both 1994 and 1995 were cold years, and had average densities of early summer age-0 pollock (Brodeur and Wilson 1999). Years 1996 and 1997 were both warm, but early summer age-0 pollock density was above average in 1996 and below average in 1997 (Brodeur and Wilson 1999). In addition, during the summer of 1997 an extensive bloom of coccolithophores occurred throughout most of the eastern Bering Sea shelf, including the area around the Pribilof Islands (Napp and Hunt 2001; Stockwell et al. 2001).

Materials and methods

Field sampling

We restricted this analysis to sampling conducted in 1994–1997 along a single transect, line A, that extended northeast from St. Paul Island toward the Bering Sea shelf (Fig. 1). Sampling along line A took place over a 2-week period in three adjacent hydrographic regions (inshore, at the front, and offshore) during the first half of September. Water column properties were determined from conductivity–temperature–depth (CTD) measurements (Sea-Bird SBE-911+). Stations were spaced about every 5 km along the sampling transect. Hydrographic sections were made in the shortest time possible (usually 3–4 h), to minimize the confounding effects of tidal-generated currents on water-column structure. Hydrographic sections of temperature were used to identify boundaries between habitats (Stabeno et al. 1999a). The boundary between the inshore and the front habitat was set by the first mixed (or weakly stratified) vertical temperature profile. The boundary between the front and offshore habitat was the location where the vertical extent of the thermocline (i.e. distance between upper and lower layer) was twofold that of the clearly stratified offshore region.

Zooplankton was sampled using a 1 m^2 multiple opening/closing net and environmental sampling system (MOCNESS). The multiple nets used on retrieval were 500 μm mesh in 1994 and 1995 and 333 μm in 1996 and 1997. Additionally, during all years except 1996, the MOCNESS was equipped with 153 μm nets to collect small copepods that were not quantitatively retained by the larger mesh. During 1996, small zooplankters were sampled with a 20 cm Clarke–Bumpus net (153 μm mesh) mounted in the Methot frame (see below), also towed obliquely through the water column (Schabetsberger et al. 2000). To reduce bias due to net avoidance by euphausiids only nighttime tows were examined.

Zooplankton samples were preserved in 5% buffered formalin/seawater solution for later analysis. Sorting and identification were done at the Polish Plankton Sorting Center in Szczecin, Poland. Individual zooplankters were identified to the lowest possible taxonomic level, often to species and stage. However, in this study the data were grouped at higher taxonomic levels to match the coarser

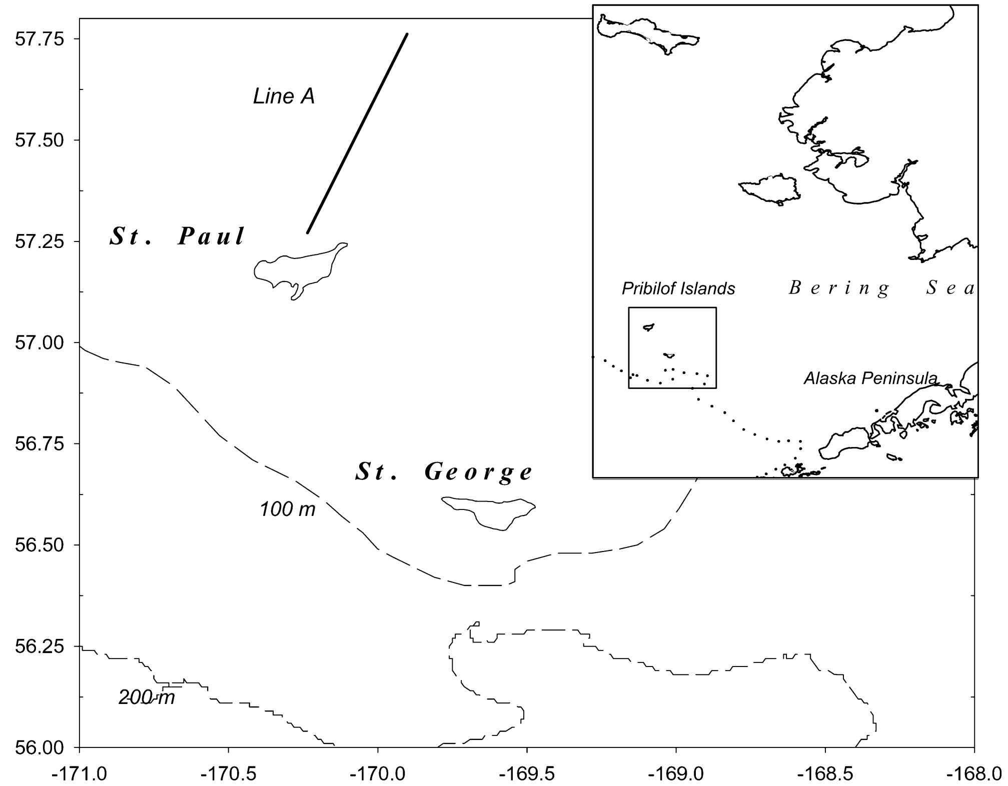

Fig. 1 Map of Pribilof Islands in southeast Bering Sea showing the location of the sampled transect (*line A*) during September of 1994–1997

taxonomic resolution of the stomach content analyses (Brodeur et al. 2002a). For the 1995–1997 zooplankton samples, the following prey categories were formed: euphausiids (adults and furcilia stages), small copepods (<2 mm; *Pseudocalanus* spp., *Acartia* spp., *Oithona* spp., <2 mm copepodites of other species), large copepods (>2 mm; *Calanus marshallae*, *Neocalanus* spp.), chaetognaths, other (amphipods, pteropods, ostracods, crab larvae, euphausiid calyptopsis larvae, cumaceans). In 1994 small and large copepods were combined in a single category in both the diet and the zooplankton studies. In all years, gelatinous zooplankton were not included, although they were present in high densities in the area around the Pribilof Islands (Schabetsberger et al. 2000). To estimate prey biomass, we weighed (to the nearest 0.01 mg wet weight) multiple (i.e. >2) representative samples of at least 20 individuals from each zooplankton category. Prior to weighing, the excess moisture was removed by placing the sample on tissue paper for about 10 s. The sample weight was divided by the total number of individuals in the sample to estimate an individual wet weight for each zooplankton category. Loss of wet weight due to preservation in formalin was assumed to be negligible (Williams and Robins 1982), although there is also evidence of the contrary (Postel et al. 2000).

Age-0 pollock density was estimated using midwater anchovy trawls (140 m^2 mouth opening) targeted for hydroacoustic layers, or a Methot trawl (5 m^2 mouth opening) obliquely towed from 10 m off the bottom to the surface. The relative efficiency of the two sampling gears (Methot or anchovy trawl) for age-0 pollock abundance is unknown. Therefore, we decided to use both gears to estimate age-0 abundance, and to account for increased variability of density estimates in the predictions of population food consumption (see below). The anchovy trawl had a 3 mm mesh net in the codend. The Methot frame had a 3×2 mm oval mesh in the body and a 1000 μm mesh in the codend (Brodeur et al. 1997). To minimize gear avoidance by the fish, only nighttime Methot tows were included in the analysis of age-0 pollock density. However, both day and night anchovy trawls were used because in a previous study no diel effect on pollock catches was found in the anchovy trawl (Brodeur et al. 2002a). Age-0 pollock size distribution was estimated from a sub-sample of about 100 individuals taken from the anchovy trawl.

Foraging impact analysis

Age-0 pollock food consumption was estimated using the Kitchell et al. (1977) bioenergetics model, parameterized for age-0 pollock by Ciannelli et al. (1998). The model predicts food consumption (C) based on measures of fish body growth (ΔG), size, diet, environmental temperature, and from species-specific physiological equations relating food consumption to body growth, metabolic output (R) and unassimilated food (F and U): $C = R + F + U + \Delta G$.

A summary of the model equations is presented in Table 1 and parameter values are listed in Table 2. More information about model structure and parameterization can be found in Ciannelli et al. (1998).

Model computations are in energy units (calories), and outputs are in biomass units (g). The conversion from energy to biomass and vice versa was based on energy-density coefficients obtained from the literature. The energy density of age-0 pollock was set to 1000 cal g^{-1} wet weight (see Ciannelli et al. 2002b), while zooplankton energy content varied according to prey type (Davis et al. 1998). Water temperature used in the bioenergetics model was referred only to the actual area occupied by fish schools throughout a diel cycle (i.e. ambient temperature). The horizontal and vertical distributions of fish schools used to estimate ambient temperatures were derived from analysis of hydroacoustic data (Swartzman et al. 1999). Age-0 pollock body growth was calculated from length–weight and age–length relationships, as reported by Brodeur et al. (2002a). A different weight–length key was available for each simulated combination of year and habitat (Brodeur et al. 2002a), while age–length keys were only available for the years 1994–1996. Therefore, in 1997 an average age–length key from the previous

Table 1 Bioenergetic model equations used to estimate juvenile pollock (*Theragra chalcogramma*) food consumption. Parameter symbols are explained in Table 2 and in Ciannelli et al. (1998) [C consumption; W weight (g); T temperature (°C)]

Process and units	Equation
Consumption ($\mathrm{g\ g^{-1}\ day^{-1}}$)	$C = A_c \times W^{Bc} \times f(T) \times P$
	$f(T) = V^X \times e^{[X \times (1-V)]}$
	$V = (T_{cm} - T)/(T_{cm} - T_{co})$
	$X = \{Z^2 \times [1 + (1 + 40/Y)^{0.5}]^2\}/400$
	$Z = \ln(Q_c) \times (T_{cm} - T_{co})$
	$Y = \ln(Q_c) \times (T_{cm} - T_{co} + 2)$
Metabolism ($\mathrm{g\ O_2\ g^{-1}\ day^{-1}}$)	$R = [A_r \times W^{Br} \times f(T) \times A_m] + [D_s \times (C - F)]$
	$f(T) = V^X \times e^{[X \times (1-V)]}$
	$V = (T_{rm} - T)/(T_{rm} - T_{ro})$
	$X = \{Z^2 \times [1 + (1 + 40/Y)^{0.5}]^2\}/400$
	$Z = \ln(Q_r) \times (T_{rm} - T_{ro})$
	$Y = \ln(Q_r) \times (T_{rm} - T_{ro} + 2)$
Egestion ($\mathrm{g\ g^{-1}\ day^{-1}}$)	$F = F_a \times C$
Excretion ($\mathrm{g\ g^{-1}\ day^{-1}}$)	$U = U_a \times (C - F)$

Table 2 Descriptions and values of the parameters used in the bioenergetics model of age-0 walleye pollock (*Theragra chalcogramma*) consumption

Symbol	Parameter description	Value
P	Proportion of maximum consumption	0–2
A_c	Intercept of the allometric function	0.38
B_c	Slope of the allometric function	−0.68
Q_c	Temperature dependence coefficient	2.6
T_{co}	Optimum temperature for consumption	10°C
T_{cm}	Maximum temperature for consumption	15°C
A_r	Intercept of the allometric function	0.0075
B_r	Slope of the allometric function	−0.251
Q_r	Temperature dependence coefficient	2.6
T_{ro}	Optimum temperature for respiration	13°C
T_{rm}	Maximum temperature for respiration	18°C
D_s	Proportion of assimilated energy lost for specific dynamic action	0.125
A_m	Multiplier for active metabolism	2.0
F_a	Proportion of consumed energy	0.15
U_a	Proportion of assimilated energy	0.11

3 years was applied. Age-0 pollock diet for each hydrographic habitat and year along line A was taken from Brodeur et al. (2000, 2002a), and in the present paper, the diet was partitioned among fish size categories.

The assessment of age-0 pollock foraging impact was made by comparing model predictions of predator food consumption with estimates of prey standing stock, with the result reported as a percentage of prey biomass. In most cases, only euphausiids and copepods, inclusive of both large and small specimens, were incorporated in the foraging impact analysis, since these two taxa constituted the majority of items in the diet of age-0 pollock (Brodeur et al. 2002a). Two different scenarios were simulated. The first scenario, termed local depletion analysis, was applied to each hydrographic habitat along line A, over a time span of 15 days, starting on 10 September. This scenario was assumed to represent the magnitude of age-0 pollock foraging impact, within each habitat during the time of the survey. We used the model output to identify instances in which the cumulative population consumption at the end of the 15-day period was significantly higher (one-tailed, two-sample t-test, see below) than one-third of the prey standing stock available at the start of the run. Assuming no migration and a production to biomass rate (P/B) $< 0.022\ \mathrm{day^{-1}}$, the one-third of standing stock criterion identifies instances in which prey biomass would diminish over time. In fact, to replenish or increase one-third of the standing biomass (B) consumed over a 15-day period, zooplankton production (P/B) should be rapid enough to satisfy the following inequality: $(P/B)15B \geq (1/3)B$, and by rearranging: $P/B \geq 1/(3 \times 15) = 0.022$. This value of P/B is at the lower extremity of the previously estimated copepod and euphausiid P/B in the Bering Sea (Ikeda and Motoda 1978; Vidal and Smith 1986), and is a realistic estimate of large copepod and euphausiid production within the simulated region during late summer (Smith and Vidal 1986), particularly where large univoltine copepods (e.g. *Neocalanus* spp., *Calanus marshallae*) are entering diapause.

The second objective of this study was to examine size-mediated effects on age-0 pollock foraging impact. Thus, a second forage impact analysis, termed size-specific consumption, was done to partition the consumption of age-0 pollock according to size categories. The analysis was applied to each hydrographic region sampled along line A and was inclusive of all prey groups found in the pollock diet. Only 1995, 1996 and 1997 were simulated, since in these years we had more complete and detailed size-specific diet analysis than in 1994. We used information on age-0 pollock size-specific abundance and size-specific diet to partition the total consumption required by a representative population of 100 individuals to generate 1 day of growth. For each of the 3 years considered, age-0 pollock size-specific diet was obtained by combining all samples from different habitats of line A together, because the effect of size on age-0 pollock diet typically outweighed the effect of habitat (Schabetsberger et al. 2000; Brodeur et al. 2002a). However, size-specific consumption can still vary among different habitats due to difference in age-0 pollock size composition and water temperature. In years when diet data were not available for all age-0 pollock size ranges simulated (i.e. 1995 and 1997), the missing diet data were set equal to the diet of the next available size range.

Statistical uncertainty (standard deviation, SD) in field estimates of copepod and euphausiid standing biomass was derived from habitats that were sampled multiple times (i.e. three or more replicates). These were in 1995 and 1996 and taken at the front. For all other combinations of habitat and year, which had less than three replicate samples, we estimated the SD from an average coefficient of variation (CV = SD/sample mean) derived from the 1995 and 1996 frontal sampling. The SD of the simulated population consumption at the end of a 15-day model run (local depletion analysis) was estimated from a sample of 300 model outputs generated by a random combination of parameters drawn from pre-specified normal distributions. The input parameters with statistical uncertainty were age-0 pollock density, growth and daily mortality rate (M). SDs of pollock density and growth were derived from sampling replicates within the same years and habitats simulated with the model, while the SD of age-0 pollock daily mortality was derived from a life table of early life stages in a pollock population residing in the Gulf of Alaska (Bailey et al. 1996). Mean M was equal to $0.028\ \mathrm{day^{-1}}$ and SD was 0.01.

Instances of prey depletion significantly above the one-third threshold were assessed with a one-sample, one-tailed, t-test applied to each combination of prey, year and habitat examined. We tested for the null hypothesis, H_0: $\bar{a} \leq \mu$, where $\bar{a}$ is age-0 pollock consumption predicted from the bioenergetics analysis and μ is one-third of the prey biomass estimated from field sampling. We used a one-sample rather than a two-sample t-test, because the zooplankton standard deviation was derived from an average CV (see above) and therefore was missing the sample size information necessary to calculate the standard error. The probability level of rejection, α, was 0.05. No adjustments were applied on either α or the predicted P-value to account for multiple, simultaneous testing (e.g. Bonferroni adjustment), because our interest was specific to each combination of habitat, year and prey type examined.

Results

Field sampling

Hydrographic features along line A varied by years. In 1995 bottom offshore temperatures ranged between 3°C and 4°C and were 1.5–2°C colder than in any other year. There was a large thermal gradient between the bottom and top layers of the stratified offshore region, where surface temperature exceeded 9°C (Fig. 2). The depth of the thermocline in 1995 was shallow (20–30 m) compared to other years. In 1994, bottom temperatures were also relatively cold (4°C), but the depth of the thermocline was deeper (about 40 m), and the top layer was colder (9°C) than in 1995. With respect to bottom temperature, 1996 and 1997 were warmer than 1995 and 1994. Bottom temperatures never went below 4.5°C, and the depth of the thermocline was approximately 35 m. The maximum offshore surface temperature was about 9.0°C, consequently there was less of a thermal gradient between top and bottom layers in 1996–1997 compared to 1994–1995 (Fig. 2). There was also interannual variability in the width and location of the frontal habitat. According to Stabeno et al. (1999a), in 1994, the transition zone (front habitat) between inshore-mixed and offshore-stratified regions started at 13.5 km and ended at 28.5 km from the transect's inshore origin. In 1995, it started at 7.0 km and ended at 33.5 km. In 1996, it started at 6.0 km and ended at 18.0 km and in 1997 it started at 6.0 km and ended at 30.0 km.

Total non-gelatinous zooplankton biomass along the sampled transects ranged from 207 to 1481 g per 10 m^2 (Table 3). In all years, chaetognaths, which on average comprised >40% of the total wet weight biomass, dominated the zooplankton community. Copepods, pteropods and euphausiids were also well represented, but their biomass varied with the years and habitats examined. Euphausiid biomass ranged from 20.36 to 163.54 g per 10 m^2, with higher values toward the offshore habitat. Copepod biomass ranged from 22.05 to

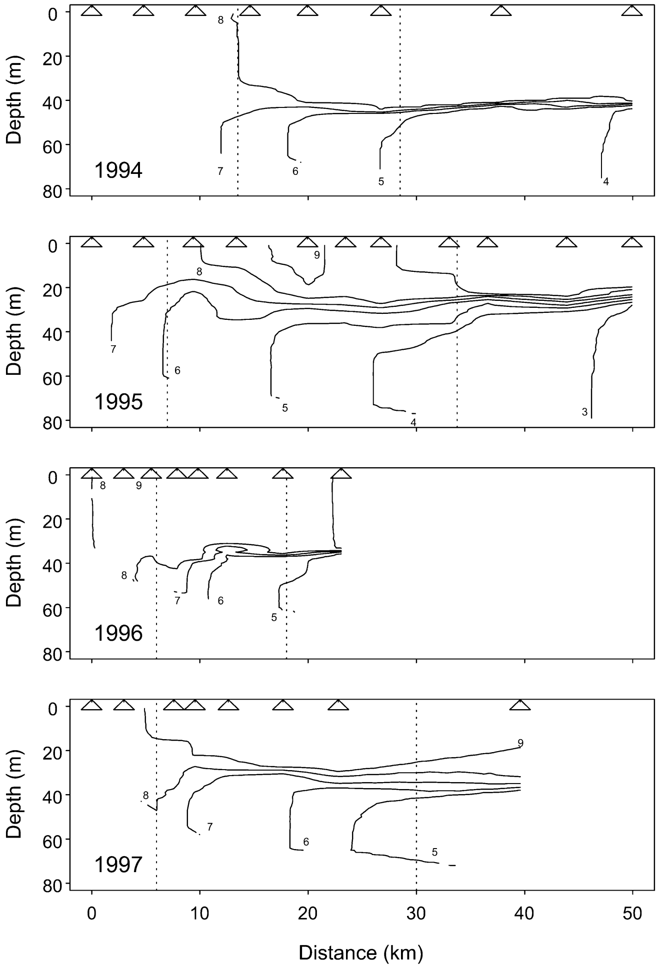

Fig. 2 Temperature (°C) profiles along line A, during September of 1994–1997. *Triangles* indicate locations of CTD samples and *vertical dotted lines* indicate the extent of the frontal habitat

Table 3 Zooplankton biomass (g per 10 m^2) and composition, by habitat and year. Only the main age-0 pollock (*Theragra chalcogramma*) prey items are reported. "Other crustaceans" include ostracods, crab larvae and cumaceans. Sample sizes (*N*) and total biomass (g per 10 m^2) are also given

Year	Taxa	Domain		
		Inshore	Front	Offshore
1994	Amphipods	0.02	0.54	4.22
	Euphausiids	20.36	36.79	42.74
	Chaetognaths	281.70	1207.21	1197.84
	Large copepods	1.80	4.47	83.04
	Pteropods	0.00	0.00	0.00
	Other crustaceans	5.55	20.34	8.35
	Small copepods	20.25	34.80	69.65
	N	1	1	1
	Total weight	329.67	1304.14	1405.82
1995	Amphipods	51.29	102.02	172.11
	Euphausiids	35.29	41.28	36.42
	Chaetognaths	355.94	590.96	141.49
	Large copepods	1.98	41.27	349.13
	Pteropods	80.36	643.78	291.93
	Other crustaceans	20.76	31.02	4.56
	Small copepods	27.90	30.63	33.53
	N	2	4	1
	Total weight	573.52	1480.95	1029.17
1996	Amphipods	–	1.32	7.82
	Euphausiids	–	47.01	163.54
	Chaetognaths	–	17.20	55.08
	Large copepods	–	1.74	8.10
	Pteropods	–	29.37	260.40
	Other crustaceans	–	46.39	33.93
	Small copepods	–	63.84	104.68
	N	–	3	1
	Total weight	–	206.85	633.54
1997	Amphipods	9.31	0.24	3.37
	Euphausiids	46.13	22.88	102.75
	Chaetognaths	78.81	113.56	144.69
	Large copepods	7.48	9.73	17.08
	Pteropods	100.82	225.82	267.42
	Other crustaceans	14.83	10.84	18.07
	Small copepods	26.78	45.43	38.73
	N	2	1	1
	Total weight	284.19	428.51	592.11

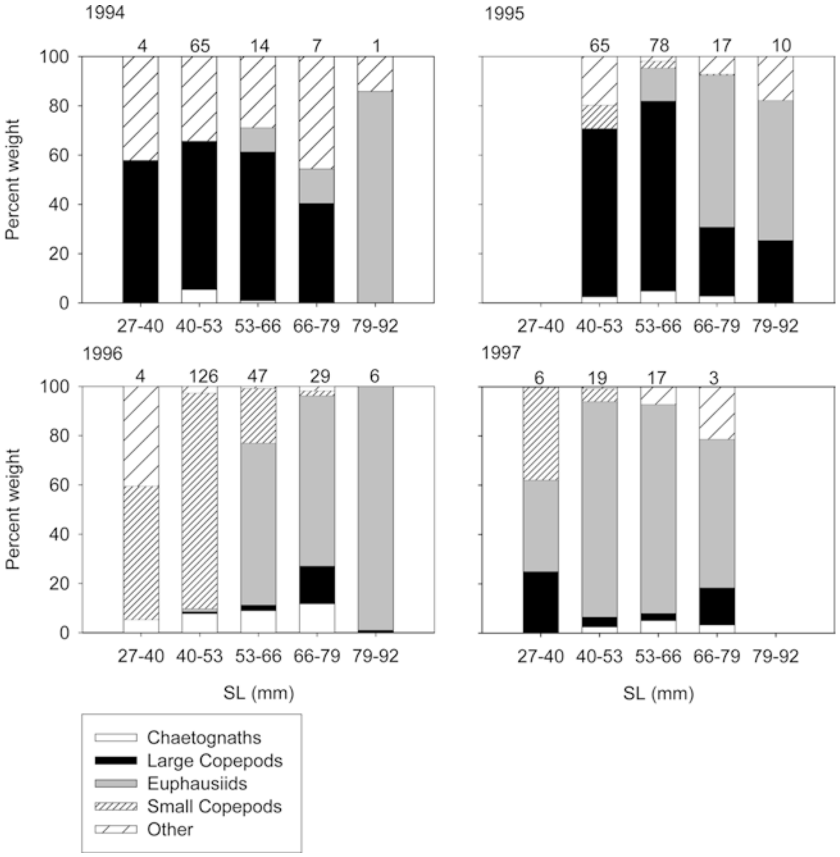

Fig. 3 Age-0 pollock (*Theragra chalcogramma*) diet by size group (standard length, *SL*) during late summer (September) of 1994–1997. Diet is expressed as percentage of total stomach content weight. *Numbers on top of bars* indicate sample size. Prey category "other" includes pteropods, amphipods, crab larvae, ostracods, euphausiid calyptopsis stages, cumaceans and larval fishes. In 1994, small and large copepods are combined in a single copepod category, coded as "large copepods"

382.66 g per 10 m^2, and was dominated by individuals larger than 2 mm in the offshore habitat, while in the inshore and front habitats the biomass was dominated by copepods smaller than 2 mm. Small copepods were particularly dominant and abundant during 1996, when their biomass exceeded 104 g per 10 m^2 at the offshore habitat and comprised $>30\%$ and $>15\%$ of the non-gelatinous zooplankton biomass of the front and offshore habitats, respectively.

Age-0 pollock (*Theragra chalcogramma*) size-specific diet consistently showed a decrease in copepod and an increase in euphausiid consumption with size in all years examined (Fig. 3). However, the size class at which juvenile pollock diet switched to a predominantly ($>50\%$) euphausiid, decreased with year (Fig. 3). Some interesting inter-annual differences in diet were also found with respect to copepod sizes. For example, in 1996 most of the copepods in age-0 pollock diet were small, even at fish size ranges at which pollock typically feed on larger copepods. In contrast, during 1995 the majority of copepods found in pollock diet were large (Fig. 3).

Foraging impact analysis

During the simulation of local food depletion, age-0 pollock specific consumption rate decreased from 26.76% body weight day^{-1} in a 0.38 g pollock, to 13.10% body weight day^{-1} in a 1.57 g pollock (Table 4). Growth efficiency (calculated as the ratio between growth and consumption) varied from 22.14% to 26.32% and averaged 24.16%. At the estimated levels of individual consumption and prey standing stock, the foraging impact of age-0 pollock on their food resources after 15 days varied according to year, prey type and habitat (Fig. 4). There were seven instances (four for copepods and three for euphausiids) in which age-0 pollock cumulative consumption over 15 days was significantly higher than one-third of the available prey biomass. Except for euphausiids in 1996, all instances of consumption above the one-third threshold either occurred at the inshore or front regions (Fig. 4).

In all years and habitats considered in the size-specific consumption analysis, juvenile pollock ranging from 44 to 60 mm in SL contributed to $>70\%$ of the total population consumption. At this size range, the dominant prey in the diet of age-0 pollock varied by year. In 1995 it was large copepods; in 1996, small copepods; and in 1997, euphausiids (Fig. 5).

Discussion

The analyses in this study were based on a bioenergetics model developed for the age-0 stage of walleye pollock (*Theragra chalcogramma*). Predictions from the bioenergetics model were previously independently corrobo-

Table 4 Age-0 pollock (*Theragra chalcogramma*) body weight (*W*), density (*D*) and individual consumption (*C*) at the initial and final period of the food depletion analysis. Final density was calculated assuming an average mortality rate of 0.028 day^{-1}. In all years, the bioenergetics simulation started on 10 September and ended on 25 September. Modeled outputs of age-0 pollock growth efficiency (GE) are also included in the table. *Numbers in parentheses* indicate standard deviation

Year	Habitat	*W* (g)		*D* (no. per 10 m^2)			*C* (% day^{-1})		GE (%) Average
		Initial	Final	Initial	*N*	Final	Initial	Final	
1994	Inshore	0.38 (0.18)	0.78 (0.19)	50.28 (14.55)	2	33.03	26.76	16.93	22.79
	Front	0.47 (0.19)	0.91 (0.19)	56.25 (19.47)	2	36.96	24.65	16.02	22.92
	Offshore	0.91 (0.20)	1.57 (0.27)	20.33 (15.15)	2	13.36	18.61	13.10	23.76
1995	Inshore	0.94 (0.24)	1.78 (0.41)	17.25 (18.98)	6	11.34	20.39	13.52	26.17
	Front	0.96 (0.26)	1.81 (0.40)	16.71 (13.58)	8	10.98	21.25	14.11	25.04
	Offshore	0.80 (0.23)	1.57 (0.31)	4.93 (4.25)	5	3.24	24.24	15.67	23.74
1996	Inshore	0.85 (0.29)	1.56 (0.37)	22.56 (14.55)	2	14.82	22.79	15.39	22.14
	Front	0.69 (0.61)	1.31 (0.73)	26.45 (15.31)	9	17.38	23.97	15.83	22.52
	Offshore	1.02 (0.29)	1.88 (0.48)	34.48 (27.02)	4	22.66	20.58	13.89	24.57
1997	Inshore	0.69 (0.28)	1.33 (0.10)	4.59 (5.33)	3	3.01	22.20	14.46	25.31
	Front	0.66 (0.28)	1.24 (0.09)	12.01 (10.45)	2	7.89	19.96	13.30	26.32
	Offshore	0.92 (0.28)	1.68 (0.13)	15.97 (7.40)	2	10.50	20.11	13.67	24.63

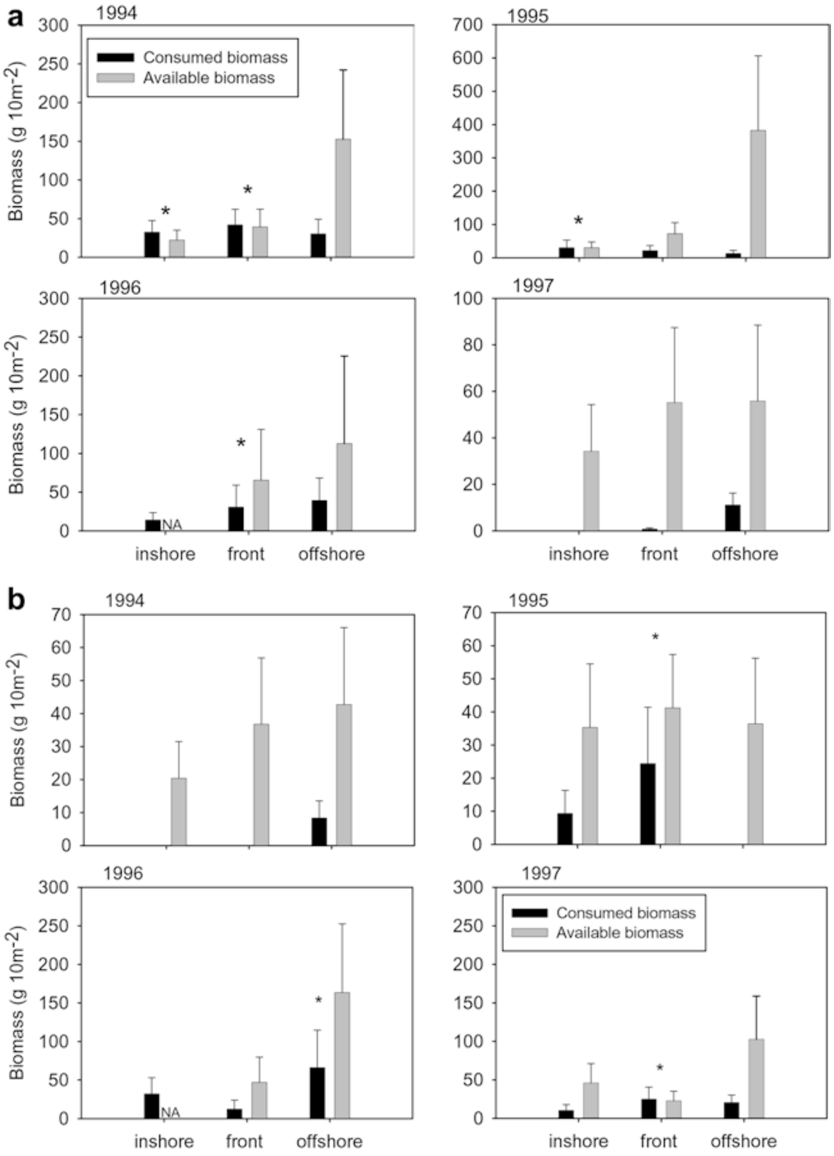

Fig. 4 **a** Age-0 pollock (*Theragra chalcogramma*) population consumption of copepods at the end of a 15-day bioenergetic simulation, compared with field estimates of copepods standing biomass at the beginning of the simulation. *Error bars*: 1 SD. *Asterisks* indicate instances in which age-0 pollock consumption was significantly higher (one-tailed, one-sample *t*-test, rejection at 0.05 probability level) than one-third of the available copepod biomass. **b** As in panel a but for euphausiid consumption

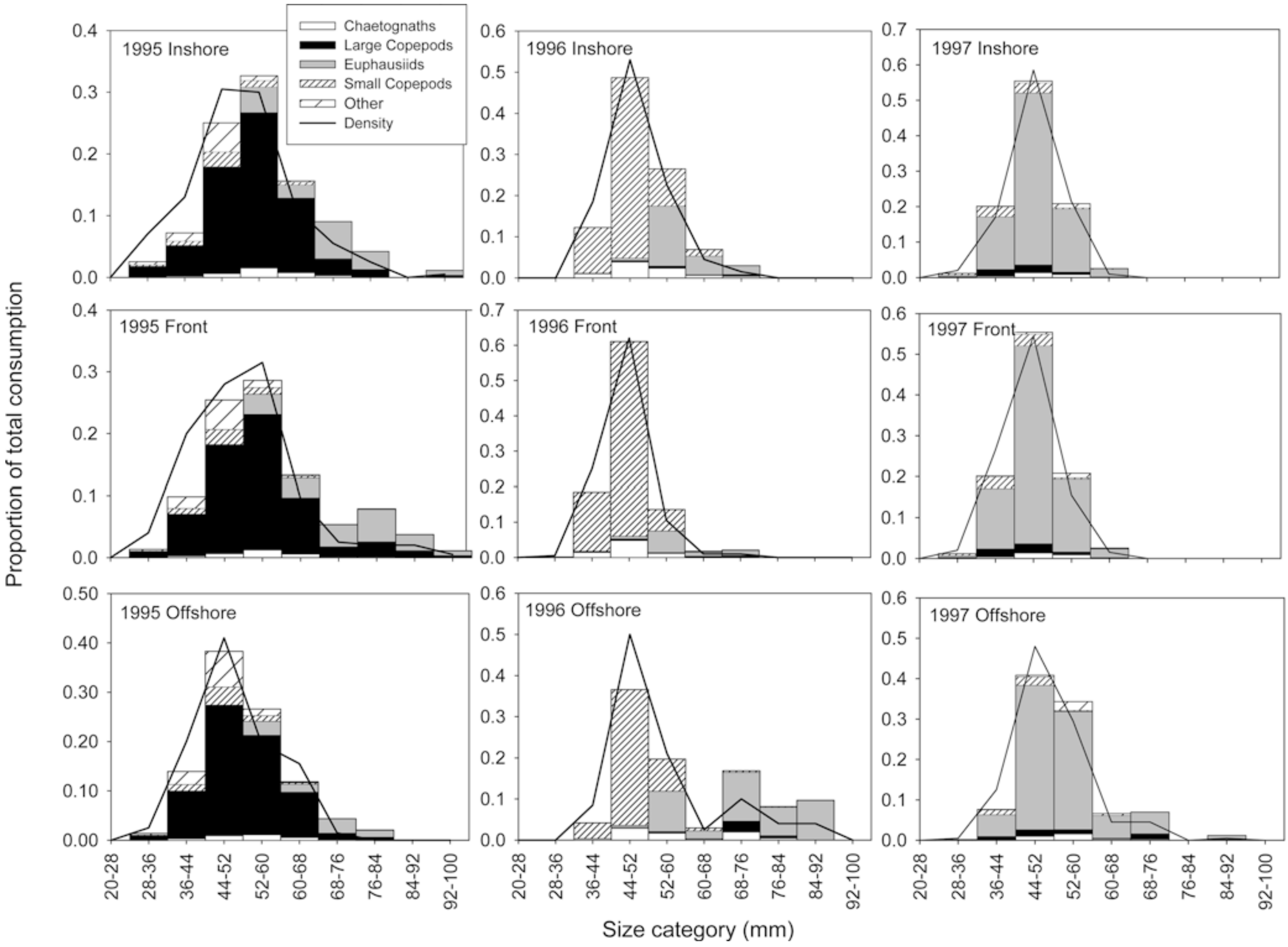

Fig. 5 Size-specific population consumption of age-0 pollock (*Theragra chalcogramma*) partitioned by year (1995, 1996 and 1997), hydrographic habitat (inshore, front and offshore) and prey type. Values for each size group indicate a proportion of the total population consumption. *Solid lines* show size-specific abundance

rated with field estimates of age-0 pollock food consumption in the Gulf of Alaska (Ciannelli et al. 1998). In the Bering Sea age-0 pollock food consumption had only been determined in two previous instances. Nishiyama (1981) estimated for a 1.5 g age-0 pollock a daily specific consumption of 8.9% body weight using a simplified bioenergetics analysis. Our modeled estimates of daily specific consumption for a similar size age-0 pollock ranged from 13.10% to 15.67% body weight, depending on the year and hydrographic habitat considered. However, our results and those of Nishiyama (1981) were obtained from similar methods and therefore are not entirely independent. In a previous analysis, Brodeur et al. (2000) estimated the age-0 pollock daily consumption rate applying a gut evacuation model on diel trajectories of stomach content from fish collected during 1994–1996 in the same area modeled in this study. Estimates of consumption for a 1 g pollock using this method ranged from 1.4% to 2.5% body weight day^{-1}. For a similar-sized fish, our bioenergetics model yields a much higher daily specific consumption, ranging from 16.02% to 21.25% body weight day^{-1}. Near the Pribilof Islands, growth rates for a 1 g age-0 pollock are estimated to be on the order of 4.0–4.5% body weight day^{-1} as measured from age–length and length–weight data (M. Doyle, personal communication, NOAA AFSC, 7600 Sand Point Way NE, Seattle, WA 98115). Thus, the field estimates of age-0 pollock food consumption would not be sufficient to sustain the observed pollock growth rate. As indicated in the original paper (Brodeur et al. 2000) field consumption estimates can be too low due to a combination of factors, including regurgitation of stomach contents in trawl-caught fish and weight loss of preserved stomach samples.

The age-0 pollock population residing around the Pribilof Islands had the potential to deplete their food resources; however, the magnitude of depletion, varied greatly as a function of habitat, prey type and year (a proxy for environmental variables, including temperature and population abundance). The model predicts that copepod depletion was much more likely than euphausiid depletion, given the size distribution of age-0 pollock and our estimates of euphausiid standing stock. This is a conservative statement considering that our estimates of euphausiid biomass may be low due to sampler avoidance (e.g. Hovekamp 1989; Sameoto et al. 1993). Copepod depletion should mainly affect small age-0 pollock (< 60 mm SL) due to their greater diet affinity for copepods. A fundamental question is why age-0 pollock did not switch earlier to euphausiids during years of limited copepod abundance, such as in 1994 or in 1995. We propose that the observed inter-annual variability of age-0 pollock size-specific diet was the result of competitive interactions among individuals of different sizes. Typically, large juveniles (> 50 mm SL) are better adapted to feeding on euphausiids, due to their larger gape size and faster swimming speed (Brodeur 1998), while both large and small juveniles should be equally efficient in capturing copepods. Adult and juvenile euphausiids collected around the Pribilof Islands range 10–20 mm in length. Large copepods (principally CV *Calanus marshallae*) are 3–4 mm and small copepods (principally various stages of *Pseudocalanus* spp.) are < 2.3 mm in length. By virtue of their limited efficiency in capturing euphausiids, small juveniles can exhaust copepod resources before they become large enough to compete with larger juveniles for the euphausiid resources. As a result, small juveniles can suffer from copepod food limitation in the face of high but inaccessible euphausiid abundance.

Particular attention should be devoted to the 1996 year-class for evidence of prey depletion and its consequences. In September 1996, juvenile pollock were feeding mainly on copepods smaller than 2 mm, even at sizes in which they typically feed on larger prey. During early summer of 1996 densities of age-0 pollock were considerably higher than in other years (Brodeur and Wilson 1999). Interestingly, in 1996 large copepods were well represented in the age-0 pollock diet during early summer on line A (Fig. 6). Therefore, we believe that the larger copepods were depleted earlier in the season, and that by late summer only small species of copepods (e.g. *Pseudocalanus*, *Acartia*) remained, which reproduce continuously throughout the summer (Dagg et al. 1984). Ecological theory predicts a reduction in the average size of zooplankton prey when a strong top-down control is in effect (Brooks and Dodson 1965; Möllmann and Köster 1999; Scheffer et al. 2000). This is in line with the low biomass of large copepods found in our zooplankton field samples in 1996 (Table 3). Evidence of food limitation in late summer of 1996 is also supported by other indices of age-0 pollock forage success, such as caloric content (Ciannelli et al. 2002b) and size-specific weight (Brodeur et al. 2002a), which were also found to be low compared to other years.

Except for euphausiids in 1996, we found that the most severe instances of food depletion occurred either at the inshore or at the front habitats, suggesting that the foraging impact of juvenile pollock around the Pribilof Islands is mediated by the local hydrography. In the southeast Bering Sea, the degree of vertical and horizontal thermal stratification during summer depends largely on the extent and residence time of sea ice during the previous winter and on the strength of wind mixing during spring and summer (Stabeno et al. 1999b). A cold winter followed by calm summer results in sharp and intense summer hydrographic stratification, which may create a barrier to free fish distribution and thereby exacerbate situations of potential food depletion. This particular scenario was observed in 1994 and 1995, the 2 years of our series with the greatest vertical and horizontal water mass differentiation. In both years, based on our model simulations, most of the age-0 pollock consumption was taking place at the inshore and front habitats, with the resulting depletion of zooplankton prey. In a previous study on age-0 pollock distribution, Ciannelli et al. (2002a) concluded that during cold summers the predation risk greatly increased in the offshore region, due to the higher density of groundfish that follow cold water masses during summer, such as adult pollock and arrowtooth flounder (*Atheresthes stomias*; Lang et al. 2000). As a consequence, age-0 pollock resided in high numbers in areas at sub-optimal growth potential, but also where predation risk was greatly reduced.

Several model assumptions were adopted to estimate age-0 foraging impact. We assumed an absence of transport into and out of the modeled regions. While we recognize that new zooplankton biomass might have been transported into the modeled region during the time of the simulation, it is equally likely that a similar biomass exited the region or that more juvenile pollock could have accessed the area. Additionally, geostrophic currents across line A are slower than elsewhere around the Pribilof Islands (Ciannelli et al. 2002a), a feature that simplifies the foraging impact analysis due to the reduced fish and zooplankton advection. Also, we

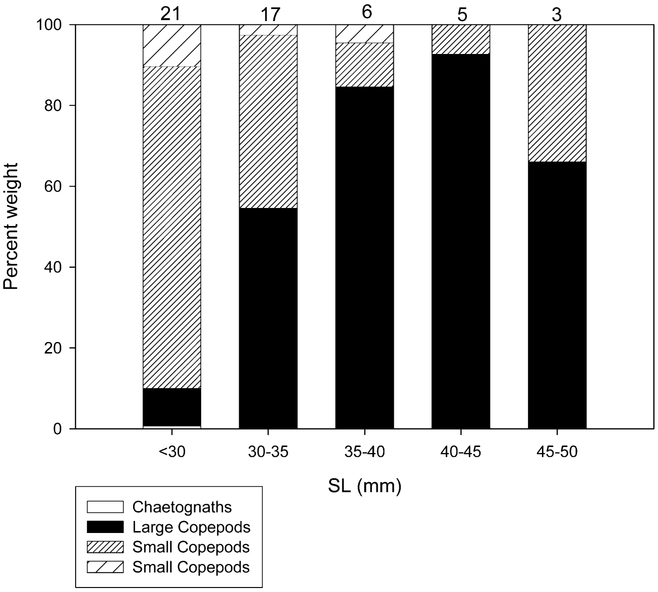

Fig. 6 Age-0 pollock (*Theragra chalcogramma*) diet by size group (standard length, *SL*) during early summer (end of July) of 1996. Legends and shadings as in Fig. 3. The methods applied to analyze pollock stomach content during early summer were the same as those used in the fall (see "Materials and methods")

assumed that juvenile pollock do not change hydrographic habitats during the simulation period (i.e. 15 days). Although there is no definitive way to prove this assumption, we believe that during a period of 15 days, there should be limited movement of juvenile pollock. Typically, water column hydrography, predation and fish size primarily influence the distribution of juvenile pollock around the Pribilof Islands (Ciannelli et al. 2002a). These factors are likely to change over the course of the summer, but during a 15-day period their magnitude of change will have limited effect on juvenile distribution.

With regard to zooplankton production, we proposed a reference threshold (one-third depletion) based on a P/B ratio typical of age-0 pollock prey species from the eastern Bering Sea, including our simulated region (Ikeda and Motoda 1978; Vidal and Smith 1986). We then adopted the low end of the field-estimated P/B, assuming that in late summer many large zooplankton species had already gone through their production peak (Smith and Vidal 1986) and were now either in diapause or had their growth limited by low food levels. On the other hand, production of smaller zooplankton species (e.g. *Pseudocalanus*) may be more responsive to water temperature than food (e.g. Hirst and Lampitt 1998) and still be high during summer, particularly in warm years. From the data available to us it is not possible to test whether the assumptions made with respect to zooplankton production were actually met. Thus, we cannot positively conclude whether the predicted rate of age-0 pollock consumption could eventually result in food limitation. However, it is important to consider that around the Pribilof Islands, age-0 pollock compete for zooplankton prey with substantial numbers of other invertebrate species (e.g. scyphomedusae, Brodeur et al. 2002b) so that our estimates of food depletion are conservative.

Our zooplankton sampling tools (i.e. mesh size) changed in the middle of the study as it became apparent that a wide size range of prey items was eaten by age-0 pollock. In 1996 we reduced the largest mesh size used in the MOCNESS from 500 to 333 μm. Prior to that change, large zooplankton taxa were counted from the 500 μm mesh nets and small- to intermediate-sized taxa were enumerated from the 153 μm mesh nets. After the change, large- and intermediate-sized taxa were counted from the 333 μm mesh net, and small taxa were counted from the 153 μm mesh net (in 1996, Clarke–Bumpus; in 1997, MOCNESS). Thus, we always used the mesh size that was appropriate for retention of each individual prey taxon. The change in mesh size probably did not affect our ability to catch large zooplankton. Although 1-m^2 rectangular nets have been shown to seriously undersample euphausiids relative to acoustics and optics (Sameoto et al. 1993), Stockwell et al. (2001) found no differences in estimates of euphausiid density between our MOCNESS and a Methot net (5 m^2 mouth area, net speed 5.5–7.5 km h^{-1}). Similarly, we assumed that estimates of small zooplankton taxa were not adversely affected by use of the Clarke–Bumpus in 1996 (i.e. no significant avoidance), although we have no proof that this was so. The increase in biomass of small zooplankton in 1996 is contrary to expectation if it was the result of switching net frames. If avoidance of the net by small zooplankton were a problem one would expect the small mouth net frame to collect less, not more biomass than the 1 m^2 MOCNESS. In all years, phytoplankton net clogging was not an issue.

In summary, our study quantifies age-0 pollock foraging impact on zooplankton in a juvenile nursery area of the Bering Sea during late summer. We present evidence of prey depletion during 1996, when one of the primary prey items of juvenile pollock (i.e. large copepods) was scarcely represented in both their diet and in the water column. Further, in the majority of the cases examined we predicted greater risk of depletion in the inshore and in the front regions, suggesting that hydrographic fronts, if acting as barriers around the Pribilof area, could affect the foraging impact of age-0 pollock during late summer. These findings generate new research questions. While age-0 pollock can incur greater risk of food depletion in inshore and front regions when occupied at high abundance, those same habitats may also provide shelter from groundfish predators that mainly reside offshore of the front. Hence, the combination of elevated primary production and the presence of spatial variability associated with the Pribilof frontal system can be the unique feature that, at least from the perspective of juvenile pollock, supercedes the recognized importance of fronts as areas of enhanced feeding.

Acknowledgements We are grateful to the crew of the NOAA ship "Miller Freeman" for help provided in fish collection, and in particular to M. Wilson for assisting in the field. Comments from D. Beauchamp, T. Hurst, G. Swartzman and two anonymous reviewers improved earlier drafts of this manuscript. This research was sponsored by NOAA's Coastal Ocean through Southeast Bering Sea Carrying Capacity and is contribution S442 to Fisheries–Oceanography Coordinated Investigations.

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