

Size-dependent, Spatial, and Temporal Variability of Juvenile Walleye Pollock (*Theragra chalcogramma*) Feeding at a Structural Front in the Southeast Bering Sea

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Abstract. The waters surrounding the Pribilof Islands are an important nursery ground for juvenile walleye pollock (*Theragra chalcogramma*), an important forage fish in the pelagic food web of the productive Bering Sea shelf region. The diet of juvenile pollock was studied in two consecutive years along a transect line crossing from a well-mixed coastal domain, through a frontal region to stratified water farther offshore. Variability in stomach fullness was high and evidence for increased feeding intensity in the front was weak. Prey diversity and prey size generally increased with increasing fish size, shifting from predominantly small copepods to larger, more evasive prey items such as euphausiids, crab megalopae and fish. The diet of the fish reflected changes in the relative abundance of copepods and euphausiids in the prey fields between years. Juvenile pollock showed increased feeding rates at dusk, and stomach fullness as well as prey condition were generally lowest just before sunrise; however,

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the proportion of euphausiids increased in the diet of pollock caught at night, suggesting that some food was also ingested during darkness. Juvenile pollock and their euphausiid prey both vertically migrated above the thermocline at night, although each had a different daytime depth.

Problem

The age-0 stage of walleye pollock *Theragra chalcogramma* (Pallas) is a nodal species in the pelagic food web of the Southeast Bering Sea (Springer, 1992; Livingston, 1993). Juvenile pollock are the dominant prey for a variety of demersal fishes (Livingston, 1993; Lang *et al.*, 2000), seabirds (Decker & Hunt, 1996) and marine mammals (Sinclair *et al.*, 1994; Antonelis *et al.*, 1997). In years of high abundance they may also inflict high mortality on zooplankton, causing local prey depletion (L. Ciannelli, pers. comm.). Walleye pollock are also a major component of a large US domestic fishery; annual catches have an ex-vessel value of several hundred million dollars.

Large-scale surveys in the Bering Sea showed high abundance of pollock around the Pribilof Islands, which are located near the edge of the 400 km-wide eastern Bering Sea shelf (Traynor & Smith, 1996; Brodeur *et al.*, 1999). Smaller-scale surveys identified a second region of relatively high abundance in the inshore structural front separating the middle-shelf and coastal domains (Coyle & Pinchuk, 2002). The waters adjacent to the Pribilof Islands exhibit elevated zooplankton densities compared to the shelf and are considered to be an important nursery ground for juvenile pollock (Flint *et al.*, 2002). They are a unique habitat in that they are the only location at the outer Bering Sea shelf that is shallow enough to allow tidal mixing. Each summer, St. Paul and St. George, the two main islands of the Pribilof Archipelago, are completely surrounded by a structural front separating a well-mixed inshore domain from a thermally stratified offshore region. The width of the front varies annually between 5 and 20 km, depending mostly on the strength of water column stratification and summer winds (Stabeno *et al.*, 1999).

Theoretically, oceanographic fronts should be regions of enhanced primary production where deep nutrients from the stratified offshore domain are upwelled into sunlit waters. This resupply of nutrients should increase secondary productivity and hence increase prey availability. Additionally, these fronts should generate enhanced feeding conditions due to mechanical aggregation of particles (Le Fèvre, 1986; Franks, 1992). The empirical evidence, however, is inconsistent and the role of hydrographic fronts as potential nursery areas for juvenile fish is under debate (Mann & Lazier, 1996).

Recruitment models of pollock show that much of the interannual variation in mortality occurs at the juvenile stage (Megrey *et al.*, 1996; Bailey, 2000). Since feeding success ultimately determines individual growth and recruitment, much effort has gone into studying various aspects of feeding ecology in relation to the frontal structure. Although strong habitat differences in pollock diet were detected, there was no consistent trend of increased survival and growth within the front (Brodeur *et al.*, 1997, 2002).

To better understand variations in feeding intensity in relation to the front, the confounding effects of variations in stomach fullness and diet choice throughout the day have to be examined. Previous studies indicated that feeding intensity increases during the afternoon and evening hours during the upward co-migration of predators and prey (Brodeur *et al.*, 2000). At a sampling station north of St. Paul Island at approximately 60 m water depth, juveniles migrated from daytime maxima at 40 m depths to less than 20 m at night. Their upward migration coincided with the concentration of euphausiids, large copepods and chaetognaths in shallow water during darkness (Schabetsberger *et al.*, 2000).

Direct observations with a remotely operated vehicle (ROV) had shown that, during daytime, juveniles were often associated with dense aggregations of scyphomedusae close to the thermocline (~ 35 m depth), whereas at night they left the shelter provided by the jellyfish and formed loose aggregations in near-surface waters (Brodeur, 1998a). The tentacles of the medusae probably offered protection from predation by diving seabirds (*Uria* spp.) (Coyle *et al.*, 1992; Decker & Hunt, 1996) and northern fur seal (*Callorhinus ursinus*) (Livingston, 1993; Sinclair *et al.*, 1994) from above and by demersal fishes such as arrowtooth flounder (*Atherestes stomias*) (Lang *et al.*, 2000) from below. The strategy “to eat and avoid being eaten” seemed to drive the apparent migration and feeding pattern.

Limited sample sizes of different size classes of fish, however, prevented a rigorous analysis of changes in diet choice of different-sized juveniles throughout the diel period (Schabetsberger *et al.*, 2000). Additionally, previous studies did not address potential differences in diel feeding patterns in the front and the stratified offshore region. Therefore two intensive diel sampling studies – one in the front and the other in the stratified region – were once again conducted in 1999. They are presented here together with additional diet data from 1998 to better understand spatial and temporal variation in the diet of different size classes of juvenile pollock in relation to a structural front.

Material and Methods

1. Study area

Samples were taken between 13 and 15 September 1998 aboard the Russian research vessel ‘Professor Kaganovsky’ and between 9 and 13 September 1999 aboard the NOAA Research Vessel ‘Miller Freeman’ along the same 30 km-long transect line north of St. Paul Island in the Bering Sea (Fig. 1). A structural front separates a well-mixed coastal domain (0–40 m) near the island from the two-layered middle shelf water (60–100 m) further offshore (Fig. 2; Stabeno *et al.*, 1999). This frontal region shows elevated chlorophyll concentrations relative to the non-frontal zones (Brodeur *et al.*, 1997).

2. Fish collections and stomach analysis

Juvenile pollock were caught with an anchovy trawl (140 m² mouth opening; ~ 10 m vertical net opening; 3 mm mesh liner; described in Wilson *et al.*, 1996) which was targeted at layers of high acoustic backscatter (38 kHz; Brodeur & Wilson, 1996).

In 1998 two anchovy trawls each were taken in the inshore, front and offshore region between midnight and 04:20 (Fig. 1). In 1999 an extensive diel sampling program was conducted at one station offshore and one station in the front (darkness: 21:45–08:45). A total of 5 and 6 hauls were taken in the front and offshore stations, respectively. A diel sampling program at the inshore station was attempted but abandoned after the first tow when jellyfish (*Chrysaora melanaster*) filled the net; however, some fish

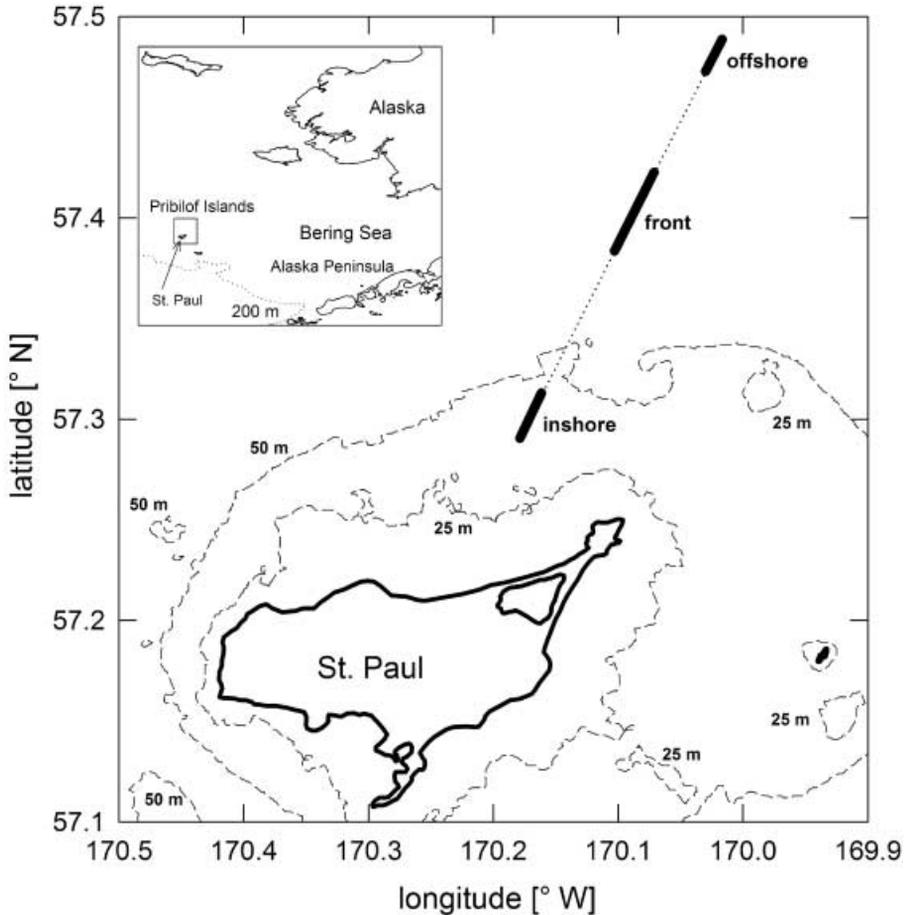


Fig. 1. Locations of the inshore, front and offshore sampling sections (bold lines) on the transect (dotted line) north of St. Paul Island, Bering Sea.

from this trawl were available for stomach content analysis. Bottom depth ranged from ~ 48 m (inshore) to ~ 60 m (front) and ~ 67 m (offshore) in both years. On average, the net was at the target depth for 8–10 min. Juvenile pollock were sorted from the catch and a subsample of approximately 50 fish was preserved in a 5 % buffered formaldehyde-seawater mixture for stomach content analysis.

In the laboratory, up to 20 fish from each of 3 different size categories were selected for stomach analysis ('small': 25–39 mm; 'medium': 40–60 mm; 'large': 61–85 mm). Sample processing is described in detail by Brodeur (1998b) and Brodeur *et al.* (2000). In the laboratory, fish were rinsed in water for at least 72 h and were then again measured and weighed. The stomach was excised and the stomach contents were removed and teased apart under a dissecting microscope. Prey items were assigned to different prey categories, enumerated and their relative condition was subjectively rated on a scale from 0 to 4 ranging from totally digested to fresh prey (0 = fully digested, 1 = some items identifiable to major categories, 2 = most items identifiable to major categories, 3 = some items identifiable to species, 4 = all items identifiable to species). Using the condition of prey items, mean stomach condition was calculated.

The dominant copepod prey were grouped into two size classes: small copepods of less than 2 mm total length such as *Acartia* spp., *Oithona* spp. and *Pseudocalanus* spp. and large copepods of more than 2 mm

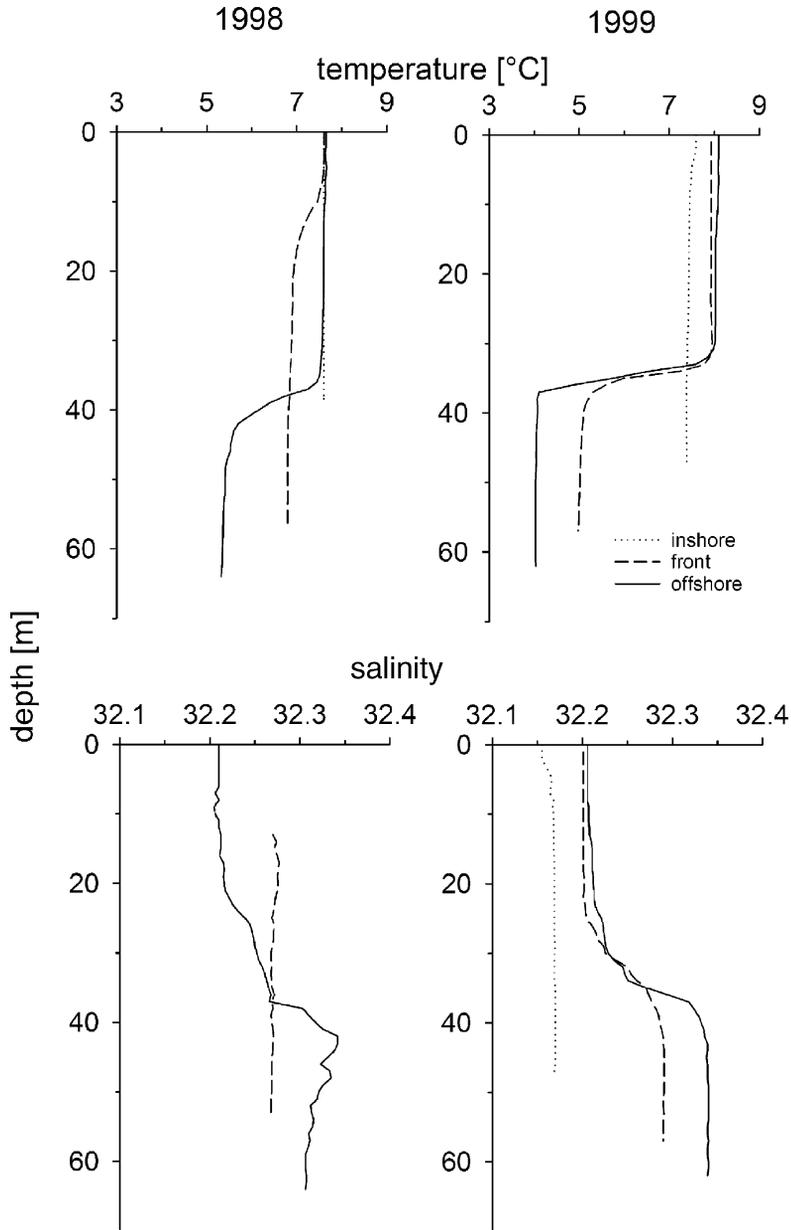


Fig. 2. Temperature and salinity at the inshore, front and offshore stations in 1998 and 1999. In 1998, either no or only limited salinity data were available for the inshore and front region, respectively.

total length such as *Calanus marshallae*, *Eucalanus bungii* and *Metridia pacifica*. Additional prey categories were pteropods, developmental stages of euphausiids (furciliae and juveniles), adult euphausiids, chaetognaths, larvaceans and other prey. The category 'other' was composed of diatoms, mollusc larvae, polychaete larvae, unidentified copepod nauplii, cirripede larvae, decapod larvae, crab

megalopae, cumaceans, amphipods and fish larvae. Totally digested food and mucus were pooled in the category 'unidentified'. Each prey category was blotted on absorbent paper to remove excess moisture before it was weighed to the nearest 0.1 mg.

We used Classification and Regression Trees (CART; Breiman *et al.*, 1984) to distinguish different-sized fish (small, medium and large) based on diet composition (% weight of major categories), time of day (hh:mm), habitat (inshore, front, offshore) and total stomach contents expressed as % body weight. With CART we were seeking a set of decision rules for distinguishing small, medium and large age-0 pollock, based on ranges of values for the covariates. When the dependent variable is categorical (in our case 3 size classes), CART is a tree-based classification method. The CART model uses binary partitioning to split the data recursively into two groups based on the range of those predictor variables that provide maximal distinction between the classes of the dependent variable. The split is chosen as the one which maximally reduces the deviance from that resulting from the previous split. Deviance is a measure of variability within a class, similar to the error sum of squares used in regression. CART uses a one-step look ahead. As it moves down the tree, CART chooses the next split in an optimal way, without attempting to optimize performance of the whole tree. The stopping rule for the splittings is either that the number of individuals on each side of the split is less than some pre-chosen minimum number (in our case 10 individuals) or that the split completely distinguishes the two resulting classes (*i.e.*, the resulting groups consist of individuals all in the same class). The points at the end of a set of recursive splits are called the leaves of the tree. Good classification is achieved if the final splits are, for the most part, fairly unequivocal about what size fish one would expect with that combination of determining covariates.

We tested for differences in the number of euphausiids ingested by each of the three different size classes of juvenile pollock during day and night using $R \times C$ contingency tables (Crow, 1982; Cortés, 1997). Only the last samples during daytime and darkness (18:35 vs. 06:59 in the front and 17:58 vs. 06:51 offshore) were compared to ensure that prey not ingested during the time period in question had been evacuated from the stomach.

3. Zooplankton collection

Samples for zooplankton were taken between fish trawls, CTDs and hydroacoustic transects. In 1998, samples were obtained with a 1 m² mouth opening Tucker trawl equipped with 333 μm mesh nets. Inside each of the two Tucker nets was mounted a 20 cm-diameter Clarke Bumpus net frame with a 150 μm mesh net. Calibrated General Oceanics flow meters were located inside the Clarke Bumpus nets. After descent to near bottom with a drogue net, the next net was used to sample from near bottom to the thermocline and the last net sampled from the thermocline to the surface. The number of zooplankton tows was limited to only one tow in each habitat. Only samples collected with the Clarke Bumpus net were used in this study and average densities were computed using both nets.

In 1999, when a conducting cable was available, zooplankton samples were collected with a 1 m² MOCNESS. Five 333 μm mesh nets were fished from near bottom to the surface (approx. 10 m depth intervals). A total of 9 front tows and 10 offshore tows were completed. As in 1998, zooplankton

Table 1. Year, habitat (number of hauls), average of target depth of the Anchovy trawl, bottom depth, juvenile pollock biomass, weight contribution to total fish catch, juvenile pollock density and numerical contribution to total catch. No densities were available for the inshore station in 1999 (see text).

year	habitat	tow depth [m]	bottom depth [m]	pollock biomass $\text{g} \cdot (10^3 \text{m}^3)^{-1}$	proportion of total catch % biomass	pollock density $\text{indiv} \cdot (10^3 \text{m}^3)^{-1}$	proportion of total catch % number
1998	inshore (2)	33.0	48.0	74.7	61.5	67.3	95.2
	front (2)	20.0	60.0	41.3	99.3	36.6	99.7
	offshore (2)	24.5	67.5	72.1	98.4	47.6	99.7
1999	front (5)	29.2	60.5	53.3	93.5	88.5	97.3
	offshore (6)	28.0	67.0	58.0	95.8	57.9	99.6

collections were made at the same geographic locations as the fish trawls. In each year, large scyphomedusae were removed from the catch, rinsed over a sieve to remove adhering plankton, and the remaining sample was preserved in a 5 % buffered formaldehyde-seawater mixture. The plankton samples were sorted and counted, to the lowest taxonomic level possible, at the Polish Plankton Sorting and Identification Centre in Szczecin, Poland.

To test for diel vertical migration in different zooplankton taxa, we calculated weighted mean depth (WMD) for each taxon and tow in the diel series:

$$\text{WMD} = \frac{\sum n_i d_i}{\sum n_i},$$

where n_i is the number of a given taxon in depth stratum i (individuals·m⁻³) and d_i is the midpoint of the stratum. Mean daytime and nighttime WMDs were compared using a Student's t -test. Samples taken at dawn or dusk were excluded from the analysis.

4. Hydroacoustic data

Acoustic data were collected using a SIMRAD EK-500 echo sounding system (for details about calibration and settings see Schabetsberger *et al.*, 2000). The data were recorded at 38 kHz and integrated into transect images by units (pixels) of ~ 9 m horizontal × 0.5 m vertical resolution. The data were then processed according to the algorithms of Swartzman *et al.* (1999a, 1999b) for the identification of juvenile pollock backscatter. Catches during September were generally monospecific and were on average, comprised of more than 90 % juvenile pollock (Table 1). For this analysis, we retained acoustic data logged within one hour of each anchovy trawl. The backscattering coefficient (S_A) of each pixel identified as pollock was multiplied by its area to give an index of acoustic biomass for that pixel. These indices were then summarized by vertical strata to produce the depth profile of the acoustically defined pollock biomass around each sampling station.

Results

1. Catch data

In both habitats most fish were caught between 20 and 40 m depth, either just above or at the thermocline. Fish densities were similar between years and habitats (Table 1). No significant difference in density was found between front and offshore habitats sampled in 1999 (t -test, $P > 0.05$).

2. Habitat and fish size effects on diet composition and feeding intensity

In 1998, small copepods dominated the stomach contents of all three size classes in the inshore, front and offshore habitats (Fig. 3). Their dominance was most notable in the stomach contents of small fish. They accounted for 91 to 99 % of the identifiable prey items in all three size classes and all habitats except for the large size class at the offshore station, where they still comprised 80.9 % of the total. In 1999, the number of prey groups was much higher, although in the small and medium size classes, small copepods were again dominant by numbers in all

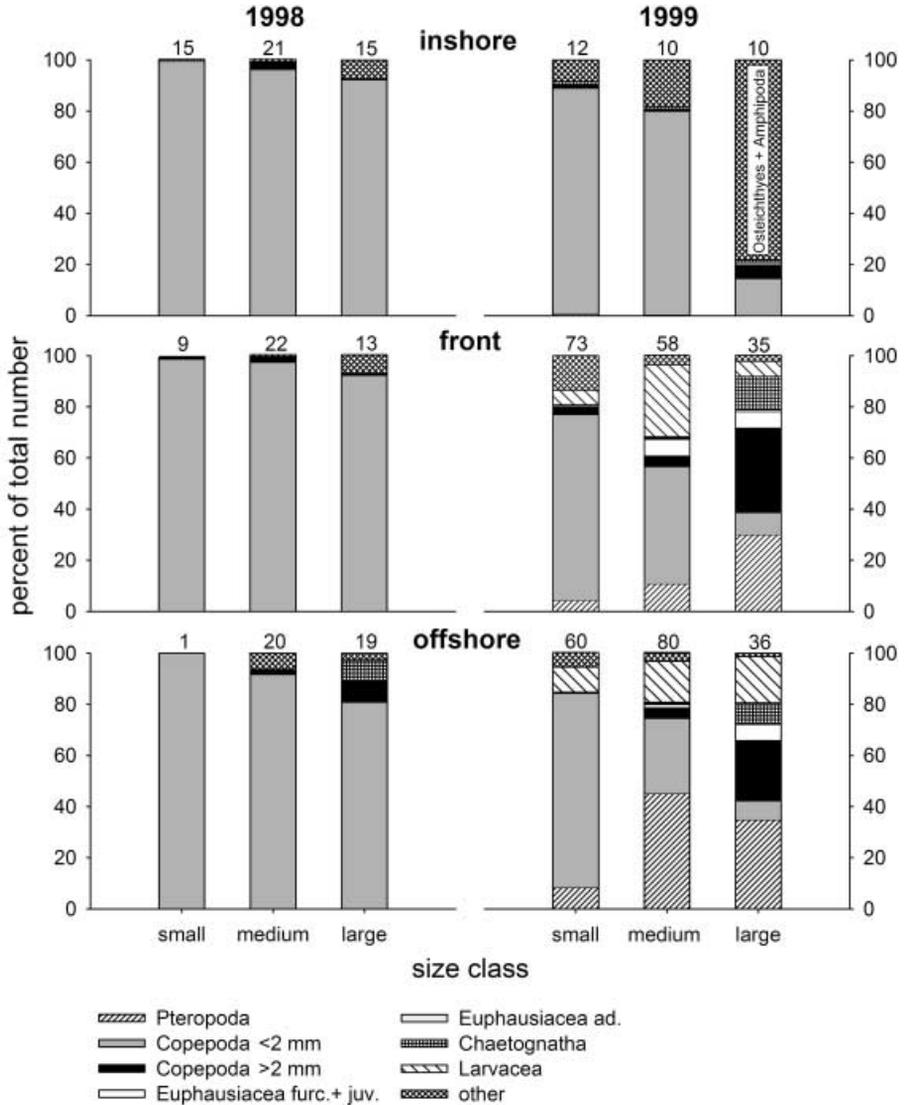


Fig. 3. Percent by number of identifiable prey categories in the diet of 3 size classes of juvenile pollock (small = 25–39 mm, medium = 40–60 mm, large = 61–85 mm) collected in the inshore (top), front (intermediate) and offshore (bottom) habitat during 1998 and 1999. Sample sizes are given on top of each panel. When the category ‘other’ exceeded 40 % of the total, the dominant prey categories are shown in the bars.

habitats, contributing between 48.6 and 88.4 % of all prey items (Fig. 3). Only offshore and only for the medium size class were pteropods more abundant. The overall prey spectrum increased with increasing fish size. Larger fish ingested more amphipods and fish prey in the inshore station, whereas large copepods (*Calanus marshallae*, *Eucalanus bungii*, *Metridia pacifica*) and pteropods became more important at the front and offshore regions.

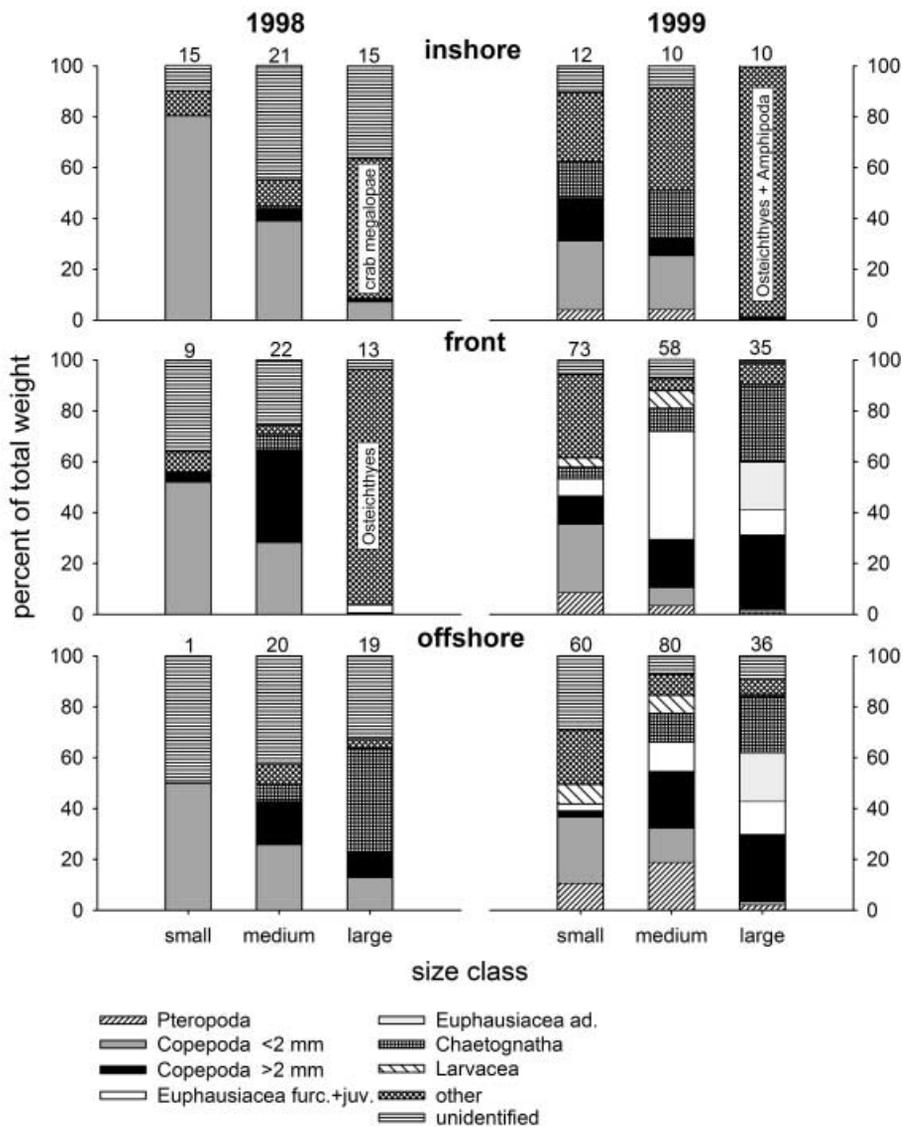


Fig. 4. Percent by weight of identifiable prey categories in the diet of 3 size classes of juvenile pollock (small = 25–39 mm, medium = 40–60 mm, large = 61–85 mm) collected in the inshore (top), front (intermediate) and offshore (bottom) habitat during 1998 and 1999. Sample sizes are given on top of each panel. When the category “other” exceeded 40 % of the total, the dominant prey categories are shown in the bars.

In terms of weight, the contribution of copepods decreased and the importance of larger prey such as crab megalopae (inshore), fish (front) and chaetognaths (offshore) increased with increasing fish size in 1998. In 1999, the diet was generally more diverse than in 1998 (Fig. 4).

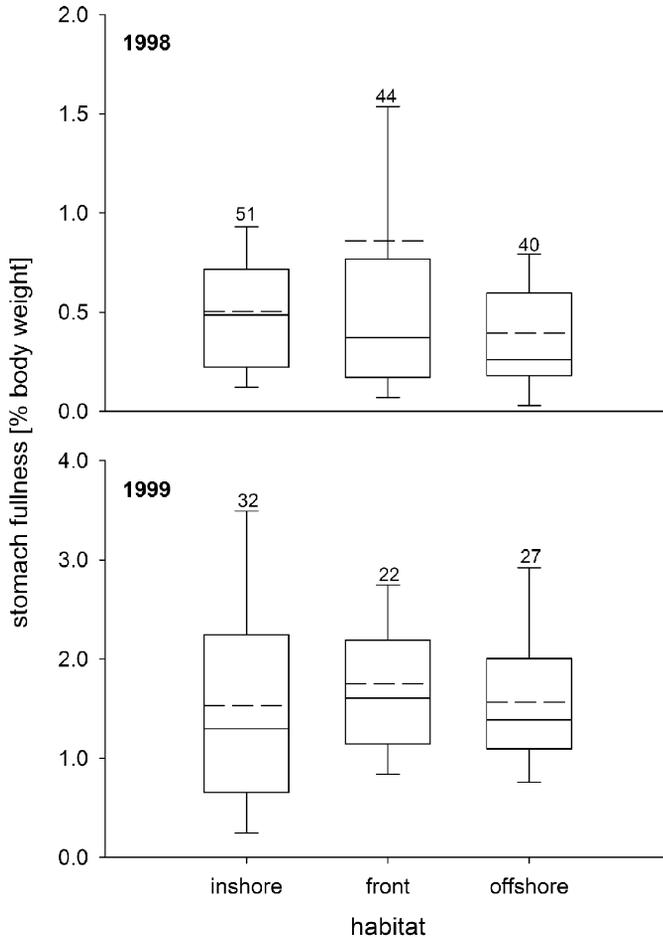


Fig. 5. Box plots of stomach fullness (percent body weight) of all stomachs analyzed for the inshore, front and offshore habitat in the years 1998 and 1999 (solid line: median, dotted line: arithmetic mean, box: 25th and 75th percentile, error bars: 10th and 90th percentile). Sample sizes are given on top of each bar. The inshore sample (18:45) in 1999 was compared to samples taken at similar times at the front (18:35) and offshore (17:58) station.

In both years, mean stomach fullness was highest in the front (Fig. 5); however, variation was high and the fullness in the three habitats was not significantly different in either year when all the fish from different size classes were pooled (Mann-Whitney U-test, $P > 0.05$). The particularly high variance in stomach fullness in the front during 1998 resulted from a few fish that had ingested unidentified fish larvae. In 1999, relative stomach weight was significantly higher than in 1998 for all size classes in all three habitats (U-test, $P < 0.001$). Even when only night-time samples from both years were compared, fish caught in 1999 still had significantly fuller stomachs (U-test, $P < 0.001$).

3. Results of CART analysis

The proportion of small copepods and the total stomach contents expressed as a percentage of body weight were good predictors for fish size class in both years. These covariates, along with the proportion of euphausiid furciliae and juveniles, could be used to characterize diet change with increasing size of juvenile pollock. The effects of capture time and habitat were comparatively minor compared to these top classifier variables.

Table 2. CART results showing probability of falling within a certain size class (small, medium, large juvenile pollock) and the ranges of variables leading to these predictions for the 1998 and 1999 diet data.

small	medium	large	stomach contents (% body weight)	Copepoda < 2 mm (% weight)	Euphausiacea furc. + juv. (% weight)
1998					
0.83	0.17	0	> 0.41	> 55	–
0.80	0.20	0	> 0.79	< 11–55	–
0.16	0.67	0.16	< 0.41	> 55	–
0.03	0.92	0.02	0.26–0.79	11–55	–
0	0.715	0.285	0.14 –0.26	29–55	–
0	0.6	0.4	> 1.34	< 11	–
0	0.58	0.42	< 0.26	11–29	–
0.0	0.172	0.8	< 0.14	29–55	–
0.03	0.172	0.825	< 1.34	< 11	–
0	0	1	< 0.26	29–55	–
1999					
0.88	0.12	0	0.43–0.65	> 42	–
0.81	0.19	0	> 0.65	> 15	–
0.33	0.67	0	–	< 5.7	> 46
0.25	0.75	0	> 0.65	5.7–15	–
0.125	0.875	0	< 0.43	> 42	–
0	1.0	0	> 1.70	2.7–5.7	–
0	0.75	0.25	< 0.65	5.7–42	–
0.09	0.34	0.57	–	< 0.3	< 46
0	0.11	0.89	< 1.70	2.7–5.7	< 46
0	0	1	–	0.3–2.7	< 46

Table 2 shows the ranges of these predictor variables for each leaf of the tree and the probability of having a fish at that leaf being small, medium or large. For example, when more than 55 % by weight of the stomach contents in 1998 were small copepods and the overall stomach contents were less than 0.41 % body weight, the fish had an 83 % probability of belonging to the small size category. Small fish generally had the highest proportion of small copepods in their diet, or alternatively had fuller stomachs. In both years, the medium and large fish that had a large proportion of small copepods in their diet had relatively less food in their stomachs (as % body weight) than small fish having the same diet composition of small copepods. In 1999, large juvenile pollock seemed to feed less on developmental stages of euphausiids than medium-sized fish (Table 2).

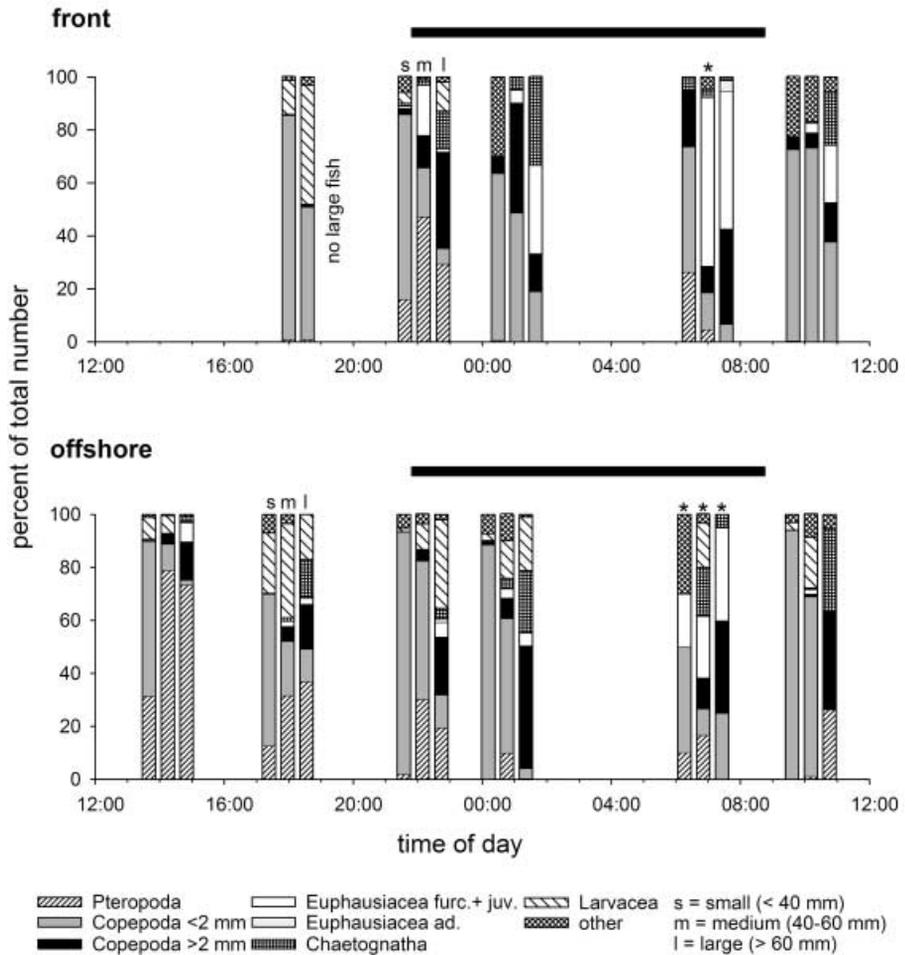


Fig. 6. Percent by number of the major prey categories in the diet of 3 size classes of juvenile pollock collected at different times of the day (Alaska Daytime) during 1999 in the front (top) and offshore habitat (bottom). Bars for the three size classes of fish have been staggered. Black bar on top indicates time of darkness. An asterisk above each bar in the last night-time haul (front: 06:59, offshore: 06:51) indicates a significant difference ($P < 0.01$) in the proportion of euphausiids in the diet when compared to the last day-time haul (front: 18:35, offshore 17:58).

4. Diel and fish size effects on diet composition and feeding intensity

In terms of numbers, copepods, pteropods, euphausiids and larvaceans dominated the diet throughout the diel cycle in 1999, although for the larger fish the proportion of developmental stages of euphausiids increased during the night in both habitats (Fig. 6). In terms of weight, the diet was mostly comprised of chaetognaths and euphausiids (Fig. 7).

All size classes of fish at both locations, except large juveniles offshore, exhibited significant differences in stomach fullness throughout the day (Kruskal-Wallis test;

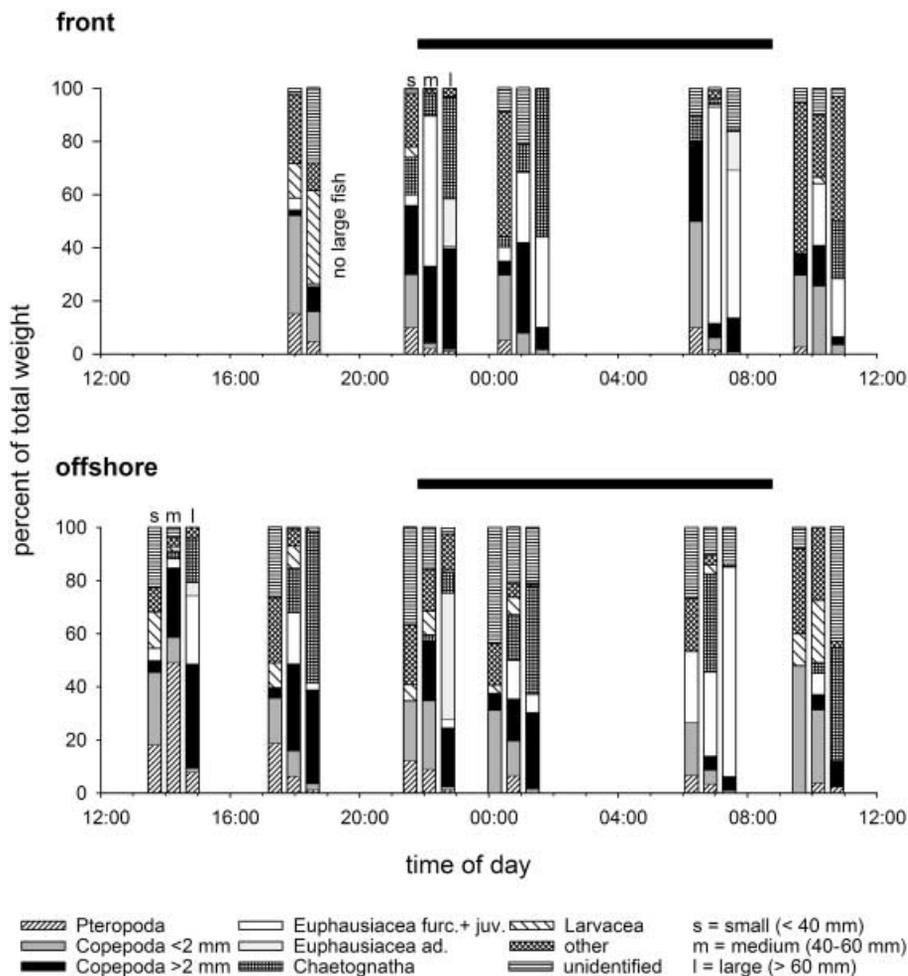


Fig. 7. Percent by weight of the major prey categories in the diet of 3 size classes of juvenile pollock collected at different times of the day (Alaska Daytime) during 1999 in the front (top) and offshore habitat (bottom). Bars for the three size classes of fish have been staggered. Black bar on top indicates time of darkness.

$P < 0.005$). Stomach contents were highest in the evening for all size classes of fish in the front as well as in the offshore habitat (Fig. 8). In the front all size classes showed maximum stomach fullness at 22:11, which was statistically significant only for the medium size class (U-test, $P = 0.041$). At the offshore station stomach fullness remained high during the late afternoon and evening. Only for the small size class was this feeding peak in the late afternoon significantly different from the previous data point (U-test, $P < 0.01$). All size classes in both habitats showed a minimum at around 07:00 in the early morning, which was significant for the small size class in the front (U-test, $P < 0.001$) and the medium size class offshore (U-test, $P < 0.01$). Only the medium size class in the front reached a small peak at dawn and had its minimum stomach fullness at 10:13 (Fig. 8). Some medium-sized juveniles had ingested significantly

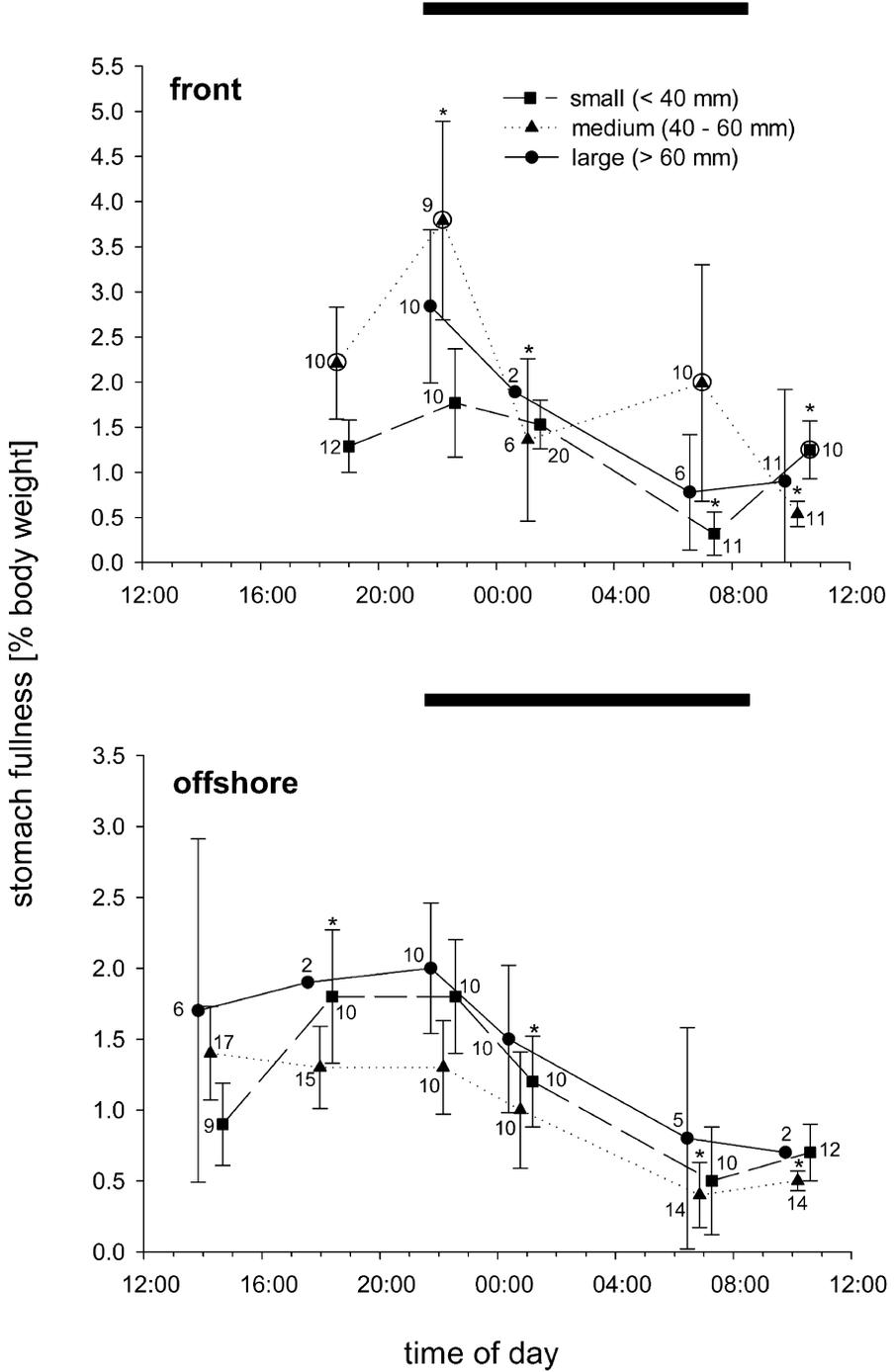


Fig. 8.

more food in the front compared to the offshore habitat, when confounding effects of fish size were minimized by comparing only pollock from the same size class caught in both habitats at similar times of the day (< 45 min difference) (U-test, $P < 0.01$; Fig. 8). Median stomach condition was lowest during the early morning and started to increase after sunrise (Fig. 9).

5. Zooplankton abundance and vertical migration of zooplankton and juvenile fish

In 1998, the zooplankton species composition was numerically dominated by the small copepods *Oithona* spp. and *Pseudocalanus* spp. and larvaceans (Table 3). The limited sampling makes it difficult to arrive at robust conclusions regarding differences in the

Table 3. Average concentration [$n \cdot m^{-3}$] (\pm S.E. in 1999) of the dominant zooplankton categories at the inshore, front and offshore habitat. In 1998, only one sample was taken in each habitat.

	1998			1999	
	inshore	front	offshore	front	offshore
Cnidaria	–	–	–	0.47 ± 0.37	0.88 ± 0.64
Pteropoda	219	28	36	335 ± 83	86 ± 23
Copepoda					
<i>Acartia</i> spp.	196	52	28	125 ± 24	527 ± 408
<i>Oithona</i> spp.	10168	6458	1845	4705 ± 549	6631 ± 1609
<i>Pseudocalanus</i> spp.	5295	10207	5464	64 ± 5.6	113 ± 94
<i>Calanus marshallae</i>	7.9	0.18	0.23	1.5 ± 0.2	3.0 ± 0.4
<i>Eucalanus bungii</i>	6.4	0.26	0.10	0.14 ± 0.04	0.47 ± 0.06
<i>Metridia pacifica</i>	0.8	0.03	–	0.12 ± 0.05	0.06 ± 0.03
Euphausiacea					
<i>Thysanoessa raschii</i>	0.06	–	–	0.02 ± 0.01	0.19 ± 0.1
<i>Thysanoessa inermis</i>	0.04	–	–	0.44 ± 0.17	2.2 ± 0.4
<i>Thysanoessa longipes</i>	–	–	–	0.002 ± 0.002	–
<i>Thysanoessa spinifera</i>	–	–	–	–	0.03 ± 0.03
unidentified furciliae	0.14	0.06	0.005	1.22 ± 0.04	3.20 ± 0.06
unidentified juveniles	–	–	–	0.06 ± 0.03	0.3 ± 0.1
Amphipoda	13.9	–	–	0.007 ± 0.004	0.02 ± 0.02
Mysidacea	0.007	–	–	–	0.01 ± 0.06
Natantia	0.004	0.006	0.065	0.02 ± 0.007	0.02 ± 0.005
Decapoda larvae	0.38	0.057	1.11	0.16 ± 0.03	0.13 ± 0.02
Chaetognatha	144	105	26	75 ± 18	33 ± 9
Larvacea	3583	1184	41	873 ± 166	1306 ± 305

Fig. 8. The relationship between time of day and stomach fullness of three size classes of juvenile walleye pollock collected in 1999 in the front (top) and offshore habitat (bottom). Data are arithmetic means \pm 95 % confidence limits. Data points have been staggered to avoid overlapping error bars. Points with an asterisk above them were significantly different (Mann-Whitney U-test, $P < 0.05$) from those immediately preceding them. Encircled data points indicate that the average stomach fullness during corresponding time intervals (<45 min difference) and a given size class of fish was significantly different between the front and offshore habitat. Sample size is given for each time and size class analyzed. Black bar on top indicates time of darkness.

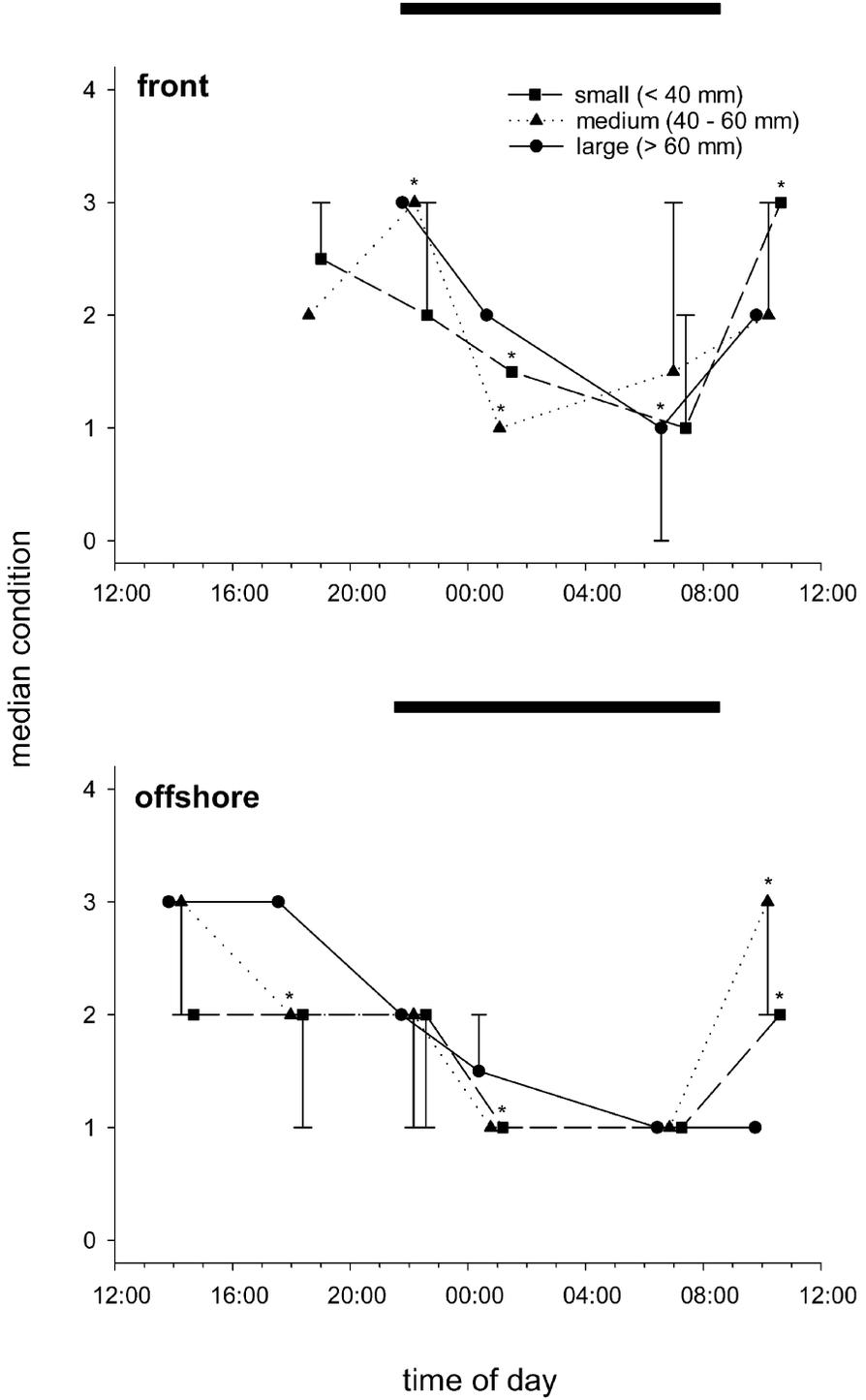


Fig. 9.

plankton community among regions. Many of the taxa were more abundant in the inshore or front region (e.g., Pteropoda, *Oithona* spp., *Acartia* spp., *Calanus marshallae*, *Eucalanus bungii*, *Thysanoessa raschii*, Amphipoda and Larvacea).

In 1999, the zooplankton species composition and abundance was similar at the front and the offshore station. Small copepods of the genus *Oithona* dominated the zooplankton, reaching densities between 4000 and 7000 individuals·m⁻³ (Table 3). The other numerically dominant groups were larvaceans and pteropods. In general, no elevated zooplankton abundances were found in the front.

Comparisons among years were restricted due to the low number of samples collected in 1998. The concentration of small copepods in 1998, particularly *Pseudocalanus* spp., appeared to be equal to or greater than the concentration in 1999 for the front and offshore regions. Conversely, the concentrations of euphausiid adults, juveniles and furciliae were lower in 1998 than in 1999 for these two regions. Except for *Thysanoessa inermis*, no adult or juvenile euphausiids were found in the frontal and offshore regions in 1998.

In 1999, when the MOCNESS was available, we tested for changes in vertical position as evidence of diel vertical migration. Furcilia stages of euphausiids exhibited significant diel vertical migrations at both locations (t-test, $P < 0.001$; Fig. 10). Only at the offshore station did we detect a significant upward migration during darkness of *Metridia pacifica* ($P = 0.02$) and of adult and juvenile euphausiids ($P = 0.003$) (Fig. 10b). Whereas *Calanus marshallae* and *Eucalanus bungii* were distributed throughout the water column, all other prey items were concentrated above the thermocline. Some juvenile pollock also migrated above the thermocline during the night (Fig. 11); however, differences in weighted mean depth between day and night were only significant at the offshore station (t-test, $P = 0.017$).

Discussion

With increasing body size, juvenile pollock diet shifted from mostly small copepods to large copepods, euphausiids, crab megalopae and fish because larger gape sizes and faster swimming speeds enable larger fish to capture larger and more evasive prey items (Bailey & Dunn, 1979; Merati & Brodeur, 1996; Brodeur, 1998b; Schabetsberger *et al.*, 2000). The classification and regression trees reflected this ontogenetic shift in diet and confirmed previous conclusions that the time of capture and habitat have comparatively less impact on diet composition than size

Fig. 9. The relationship between time of day and condition factor of stomach contents of three size classes of walleye pollock from the front and offshore habitat. The 95 % confidence limits were calculated assuming a binomial distribution and hence may not extend in both directions (Zar, 1999). Points with an asterisk above them were significantly different (Mann-Whitney U-test, $P < 0.05$) from those immediately preceding them. Black bar on top indicates time of darkness.

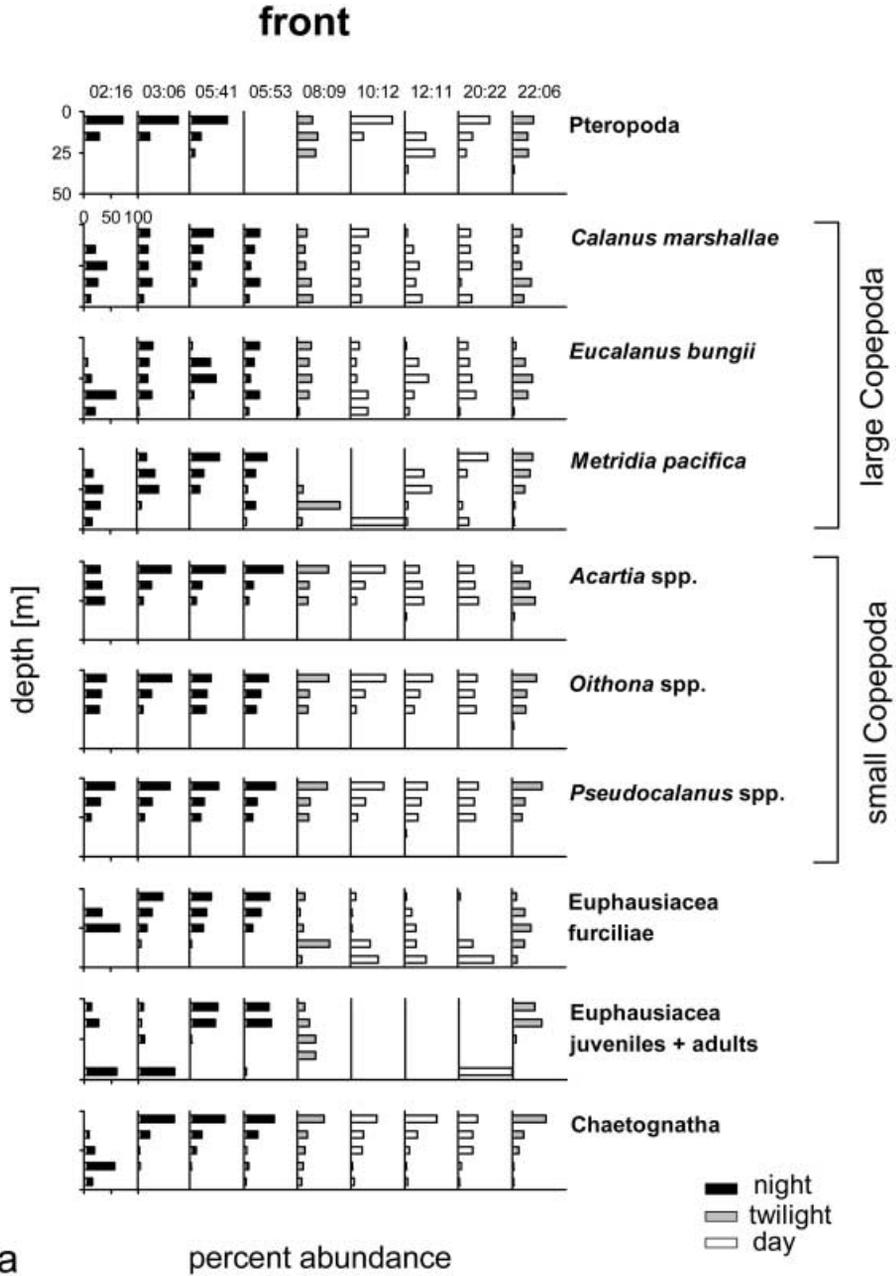


Fig. 10. Diel vertical distribution of the dominant prey taxa at the front (a) and offshore (b) region. Some data for pteropods were missing (crossed-out panels).

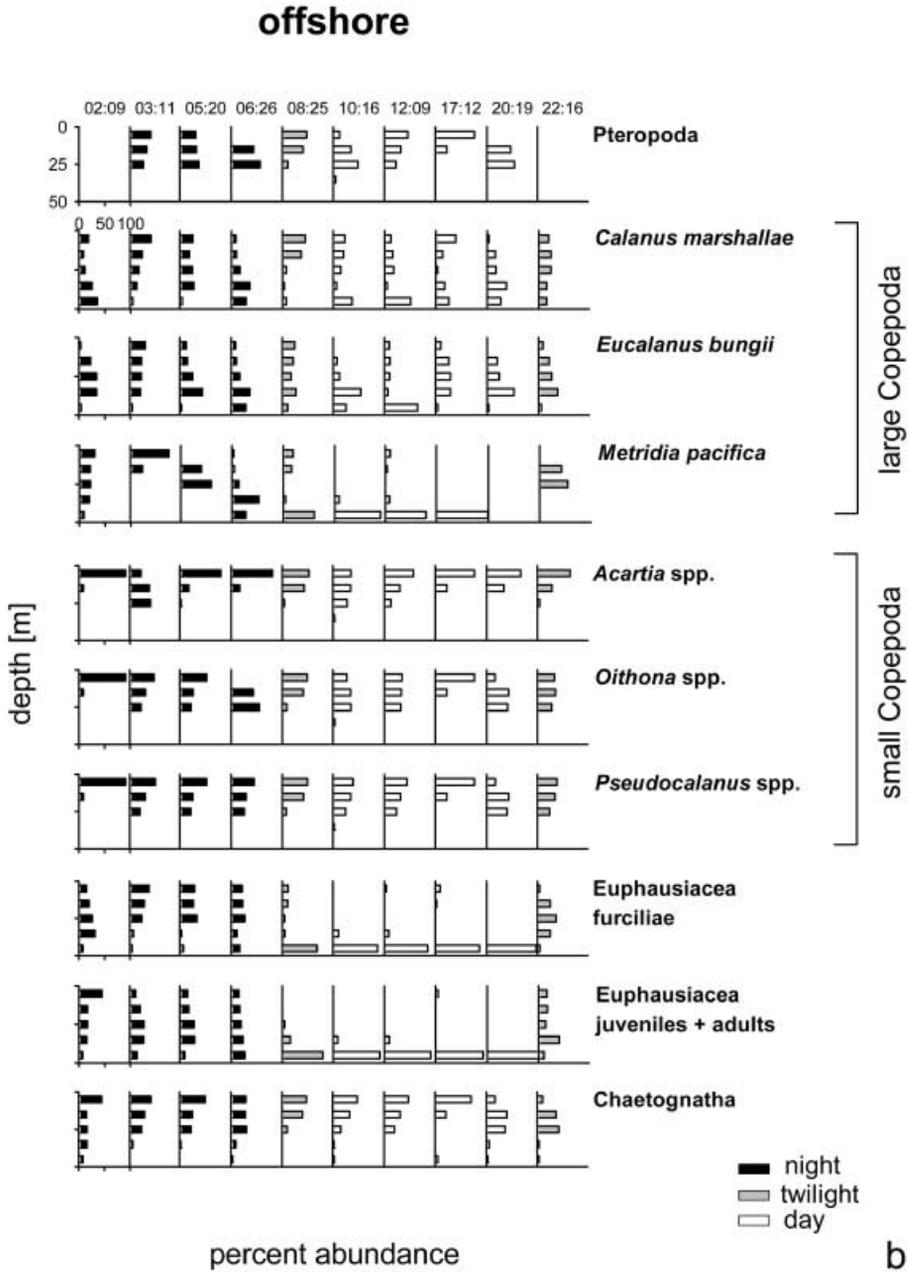


Fig. 10. Continued.

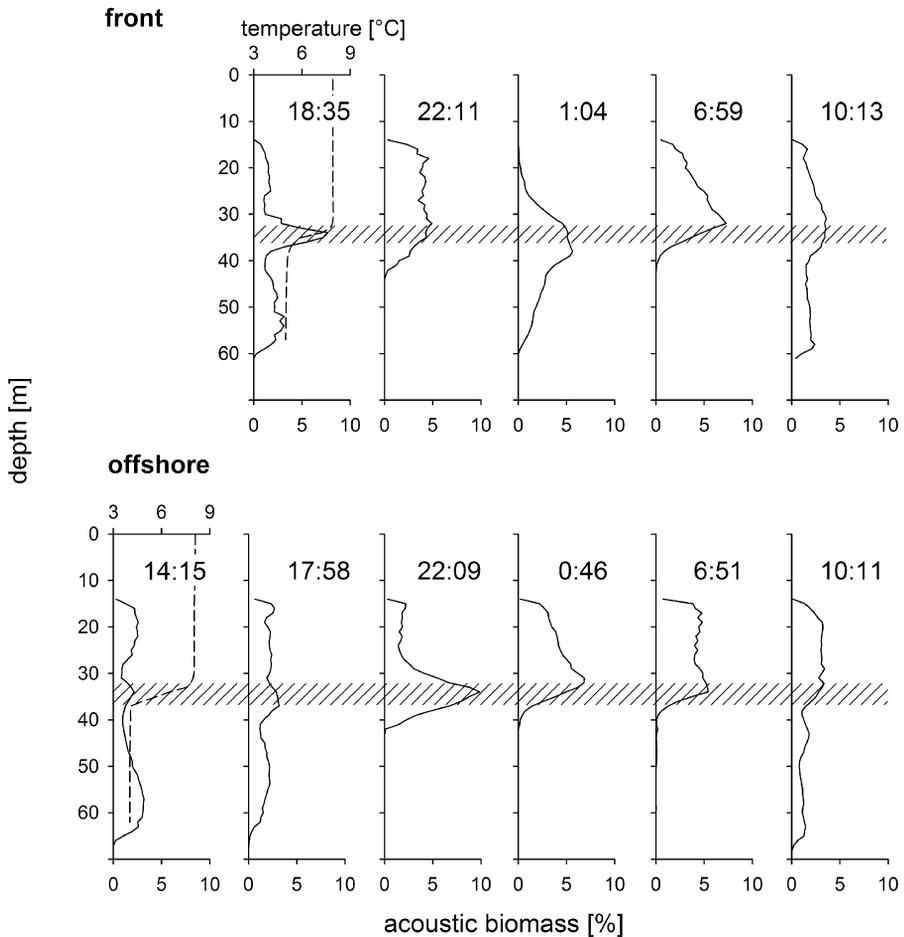


Fig. 11. Proportional distributions of acoustically-detected biomass of juvenile pollock, per meter depth, at front and offshore sampling stations in 1999. The start-time of the corresponding fish-trawl is indicated above each depth profile. The depth profiles include acoustic data from within 1 hour before to 1 hour after the start-times. Temperature profiles are presented in the first panel. Shaded area indicates extension of thermocline.

(Schabetsberger *et al.*, 2000). The CART analysis also revealed that larger individuals had less food in their stomachs relative to their body weight when they included a higher proportion of small prey items into their diet. This may reflect their inability to fill the stomach to the same extent as small juveniles do with easily accessible small copepods. Larger juvenile pollock may therefore not be able to meet their energetic demands by feeding on small copepods over extended periods. Nonetheless, difficulties associated with measuring small amounts of wet weight as well as faster digestion rates for small prey items in larger fish could partly account for these differences.

In 1998, the diet was largely dominated by small copepods, whereas in 1999 various larger prey items were an important component of the diet. This may be explained by prey availability, although 1998 sample numbers were too low to allow a statistical comparison. Small copepods (particularly *Pseudocalanus* spp.) appeared to be more abundant in 1998 than 1999, whereas adult, juvenile, and furcilia stages of euphausiids were probably more abundant in 1999. The availability of larger prey in 1999 may have allowed juvenile pollock to feed more selectively. This presumed abundance of larger prey is also supported by the tendency for stomach fullness to be higher during 1999.

There was weak evidence that at least medium-sized juvenile pollock had fuller stomachs in the front than in the offshore habitat; however, if the juvenile pollock had cued in on densely aggregated prey in the frontal region, a clear difference in stomach fullness between the front and offshore habitat would be expected in all fish size classes. Stomach fullness represents the ingestion rates during the last 3–4 h prior to capture and should reflect feeding intensity in the habitat under consideration (Brodeur *et al.*, 2002). It is unlikely that temperature-dependent differences in gastric evacuation rates were responsible for differences in stomach fullness because the temperature profiles at both locations were very similar.

Conflicting observations have been made on the relative abundance of zooplankton and fish at tidal fronts, and the extent to which these fronts are favorable feeding habitats for juvenile fish is still a matter of debate (Mann & Lazier, 1996). Our results for 1999 and 1998 do not support the idea that the frontal region is a better feeding habitat for juvenile pollock. This is in agreement with results from previous years in which no evidence was found that condition factor and stomach fullness were higher in the front (Brodeur *et al.*, 2002). However, they may still benefit from the hydrographic heterogeneity around the Pribilof Islands, as some areas may offer bioenergetic advantages and reduced predation risk. Additionally, the inter-annual variability in prey availability is generally high in this area (L. Ciannelli, pers. comm.). There is evidence from spatially explicit models that in some years juvenile pollock may deplete their food resources within the inshore and frontal region. Clearly, more multidisciplinary studies measuring physical and biological data on a range of scales are necessary to clarify the role of hydrographic fronts as potential nursery grounds for juvenile fish.

Stomach fullness in 1996 increased continuously during the day, peaking around 22:15, showing that these fish consumed most food during the late afternoon and evening hours (Brodeur *et al.*, 2000; Schabetsberger *et al.*, 2000). Sample sizes of larger juveniles, however, were limited during our 1996 diel sampling (Schabetsberger *et al.*, 2000). The data were therefore pooled with diet data collected at various locations in the two preceding years. The results of this analysis suggested that juvenile pollock switched from predominantly daytime feeding to a more nocturnal feeding at a size threshold of about 50 mm (Brodeur *et al.*, 2000). The present study collected and analyzed enough fish of three different size classes to test for size-specific peaks in feeding, but detected no shift towards a more nocturnal feeding pattern in larger juveniles within the front and in the offshore habitat; a similar diel feeding pattern emerged as described for the 1996 sampling.

Experiments show that juvenile pollock are able to feed during the night, but they are more efficient when adequate light levels permit visually mediated foraging (Ryer & Olla, 1999). Larger juveniles may only be able to ingest larger quantities of food during the night when cloud cover is minimal and/or some moonlight is available; this was probably not the case in September 1999 when cloud cover was present and only approximately one tenth of the moon was illuminated; when sufficient light levels are available, however, ingestion rates may be high during the night due to increased availability of vertically migrating euphausiids and copepods in the surface layers. Stomachs collected during well-lit nights in earlier studies may have reflected a shift of feeding peak to nighttime (Brodeur *et al.*, 2000).

In our 1996 study, we found weak evidence that the proportion of euphausiids in the pollock diet increased during the night (Schabetsberger *et al.*, 2000). The present study confirms an increase in furciliae, juveniles and adult euphausiids in the diet of juvenile pollock during the night. Some of these euphausiids were in good condition, indicating that they had been ingested during darkness, although overall condition of stomach contents decreased during the night due to ongoing digestion of other prey. Juvenile pollock were probably able to capture some of these euphausiids during their upward co-migration with their zooplankton prey, which was more pronounced in the stratified offshore region. During the day euphausiids concentrated in near-bottom water layers where juvenile pollock would be exposed to high predation risk by demersal fishes (Lang *et al.*, 2000).

Conclusions

With increasing body size, juvenile pollock diet shifted from mostly small copepods to larger copepods, euphausiids, decapods and fish. Zooplankton concentrations and stomach fullness of pollock in the frontal region were not significantly higher than in the other two habitats. Thus, our data do not support the hypothesis that frontal regions are superior feeding habitats for juvenile pollock. All available size classes of pollock exhibited a diurnal feeding pattern with highest feeding rates at dusk. During darkness, juvenile pollock concentrated above the thermocline and ingested a larger proportion of vertically migrating euphausiids.

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