Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea

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The diel vertical migration of age-0-walleye pollock (*Theragra chalcogramma* Pallas) and their principal prey organisms were examined at a productive frontal region in the Bering Sea using 38 kHz acoustic measurements and net samples. Small copepods dominated the catch of depth-stratified plankton tows. Two copepod species (*Calanus marshallae* and *Metridia pacifica*), euphausiids and chaetognaths, exhibited strong diel vertical migrations, although the magnitude and timing of the migrations varied among taxa. Age-0 pollock dominated midwater trawl catches (92% by number) that targeted layers of strong acoustic backscatter. Distributions of target strengths (TS) recorded within the layers corresponded well with predicted values based on empirical length/TS relationships for age-0 walleye pollock. Juvenile pollock in these layers migrated from daytime maxima at 40 m depths to less than 20 m at night. The proportion of large copepods, euphausiids, and chaetognaths in the diet of juvenile pollock increased with increasing fish size, but prey composition did not change significantly throughout the diel period.

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Introduction

Walleye pollock (*Theragra chalcogramma*) is one of the dominant species in the Bering Sea ecosystem and has been the mainstay of a large US domestic fishery since the 1970s, with annual landings valued in the hundreds of millions of dollars range. The juvenile stage has received considerable attention due to its importance in the trophic budget of the Bering Sea where they function as an important forage fish for many mammals, seabirds

and fishes (Livingston, 1993; Brodeur *et al.*, 1996; Brodeur and Wilson, 1999).

The Pribilof Islands are located near the edge of the 400 km-wide eastern Bering Sea shelf. Large-scale surveys of the eastern Bering Sea shelf indicated that high levels of abundance of juvenile walleye pollock are found around the Pribilof Islands (Brodeur *et al.*, 1999). The waters surrounding the Pribilof Islands are characterized by elevated phytoplankton, zooplankton, and micronekton biomass that support large numbers of

apex land-based predators such as seabirds and pinnipeds (Coyle et al., 1992; Coyle and Cooney, 1993; Sinclair et al., 1994; Decker and Hunt, 1996). This biomass concentration is sometimes localized in well defined structural fronts delineating well-mixed coastal water close to the islands from highly stratified offshore water (Brodeur et al., 1997; Stabeno et al., 1999).

To understand the factors controlling the distribution and survival of juvenile pollock in this important nursery area, annual late summer sampling has been conducted since 1994. Studies have focused on top-down effects of higher trophic level carnivores (Lang et al., 2000; Decker and Hunt, 1996) and bottom up effects of zooplankton density (Brodeur et al., 2000). Much effort has gone into studying pollock–plankton spatial relationships as a initial step in understanding the role of prey availability in pollock year-class strength (Swartzman et al., 1999). Hydroacoustic data have shown diel vertical migrations by both juvenile pollock and their prey along inshore–offshore transects, but these migrations have not been studied at one location throughout the diel period.

Diel vertical migrations (DVM) of fish and zooplankton are nearly ubiquitous in both freshwater and marine systems and thus are well documented in the literature (see Lampert, 1989 and Neilson and Perry, 1990 for reviews in zooplankton and fish, respectively). In this paper we describe DVM of juvenile pollock and some of their prey within the nursery area north of St Paul Island and we investigate diel differences and ontogenetic shifts in their diet.

Materials and methods

Study area

All data used in this study were collected between 12 and 15 September 1996 aboard the NOAA Research Vessel "Miller Freeman" in a 1.3 km^2 area 9 km north of St Paul Island in the Bering Sea (Fig. 1). Our sampling was within the structural front that separates a well-mixed coastal domain (0–40 m) near the island from the two-layered middle shelf water (60–100 m) further offshore (Stabeno et al., 1999; Fig. 2). This frontal domain shows elevated chlorophyll concentrations relative to the non-frontal zones (Brodeur et al., 1997). Stabeno et al. (1999) found that the width of the frontal zone on this transect in 1996 was on the order of 12 km, about half the width found on the same transect during September 1995 and 1997. The nearshore velocity field around the Pribilof Islands is dominated by the semi-diurnal tidal currents which are very dynamic in our study area (Kowalik, 1999). Results from satellite-tracked drifters suggest that the circulation is counter-clockwise around St Paul Island (Stabeno et al., 1999). To minimize the effect of advective losses and along-shelf exchange of plankton, we conducted our study during a period of minimum tidal amplitude (Fig. 3), although sampling occurred at different phases of the tidal cycle.

Zooplankton

Zooplankton samples were collected in 10 m depth intervals with a 1 m^2 MOCNESS (333 µm mesh nets; Wiebe et al., 1976). The nets were towed between 1.8 and 3.7 km h^{-1}. A total of nine tows was taken in the study area. All large macrozooplankton (e.g. medusae >5 cm bell diameter) were removed from the catch at sea and the remaining sample was preserved in a 5% buffered formaldehyde-seawater mixture. Additionally, smaller zooplankton were collected with a 20 cm Clarke-Bumpus (C-B) net (153 µm) mounted inside a Methot trawl towed obliquely from the bottom to the surface. The volume filtered was estimated from a General Oceanics flow meter placed in the mouth of the net. All plankton samples were sorted and counted at the Polish Plankton Sorting Centre in Sczcezin, Poland. The 153 µm C-B sample was used to estimate the concentration of small copepods that were not quantitatively retained by the MOCNESS 333 µm nets. Different species of chaetognaths were not discriminated. Wet preserved weights were determined for each taxon in the laboratory.

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

$$WMD = \frac{\Sigma n_i d_i}{\Sigma n_i}$$

where n_i is the number of a given taxon in depth stratum i and d_i is the midpoint of the stratum. Mean daytime and nighttime WMDs were compared using a Student's t-test.

Fish collections and stomach analysis

A total of eight Anchovy trawls (100 m^2 mouth opening; ∼10 m vertical net opening; 3 mm mesh liner; described in Wilson et al., 1996) were taken in the study area (Fig. 1). Anchovy trawls alternated with MOCNESS and C-B tows taken throughout the diel period. The equilibrium depth of the anchovy net was set to sample the highest concentrations of juvenile pollock in the water column, based on 38 kHz acoustic backscatter data displayed as an echogram (Brodeur and Wilson, 1996). On average the net was in the water for 21.9 (±1) min (±s.e.) and during that time period, the target depth was sampled for an average 4.6 (±0.4) min. Juvenile pollock were quickly sorted from the catch and a subsample of 200 fish was measured to
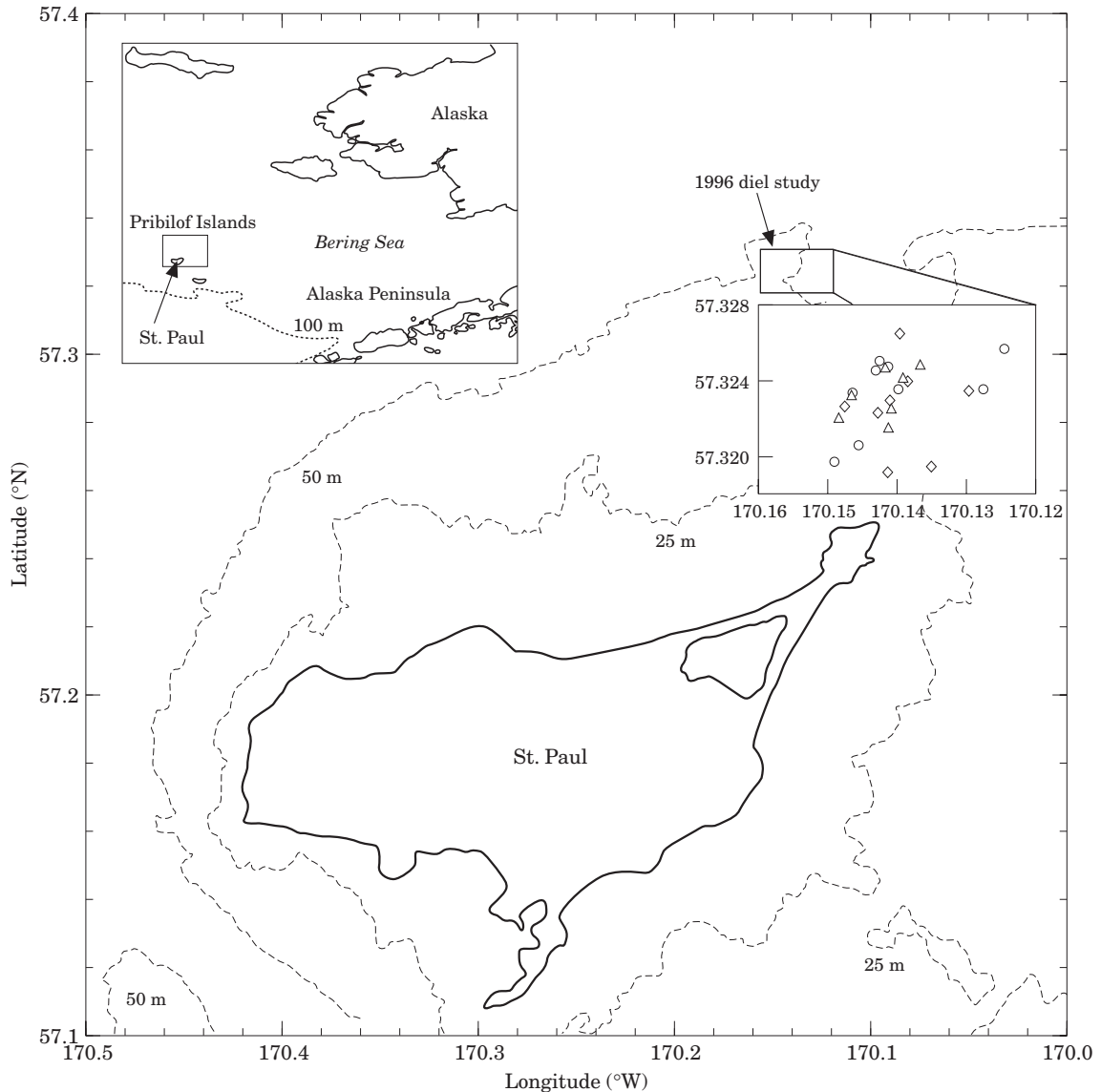
Figure 1. Location of the 1996 diel study north of St Paul Island, Bering Sea (diamond=anchovy trawls, circle=MOCNESS tows, triangle=C-B tows).

the nearest millimeter and then approximately 50 fish were preserved in a 5% buffered formaldehyde-seawater mixture for stomach analysis.

In the laboratory, a random subsample of 20 fish from each trawl was selected for diet analyses. Sample processing is described in detail by Brodeur (1998a) and Brodeur *et al.* (2000). Briefly, fish were again measured, weighed and the stomach was excised. Stomach contents were removed, blotted on absorbent paper to remove excess moisture and weighed to the nearest 0.1 mg. The stomach contents were examined under a binocular microscope and each prey item was assigned to the lowest possible taxonomic category. Most prey items

were digested to the point that species identification was impossible. Each prey taxon was enumerated and individually weighed for every stomach examined.

For the statistical analysis of prey choice, the food items were grouped into five major categories (small Copepoda: *Acartia* spp., *Oithona* spp., *Pseudocalanus* spp.; large Copepoda: *Calanus marshallae*, *Eucalanus bungii*, *Metridia pacifica*; Euphausiacea Calyptopis and Furcilia; Euphausiacea Adult and Juvenile Chaetognatha) and the percentage composition of prey by number and biomass calculated for each stomach. Other prey items such as epibenthic Cumacea, Ostracoda and Polychaeta comprised only a minor part
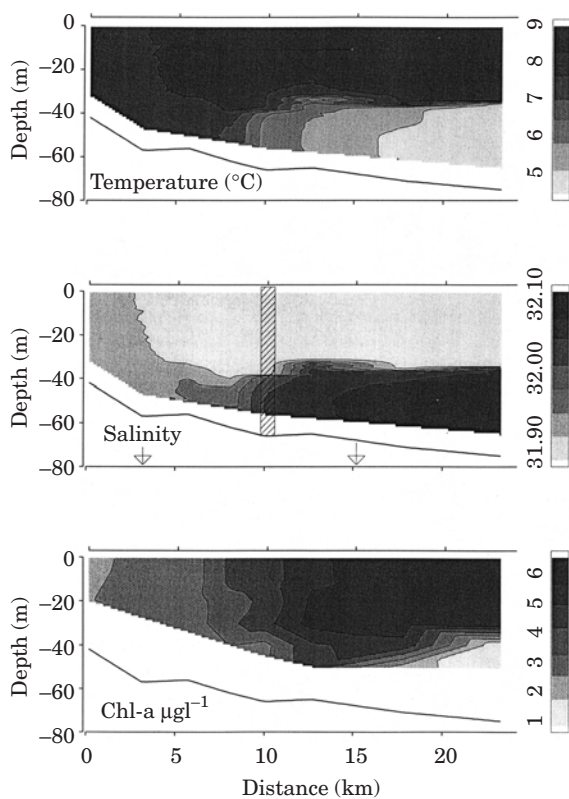
Figure 2. Cross-shelf distribution of temperature, salinity, and chlorophyll along a transect radiating to the northwest off St Paul Island. Frontal region (arrows) and diel sampling area (box) are indicated.

in the diet and were not included. For each prey category differences in feeding were tested for effects of fish size, time of capture (day or night), haul effect and interaction between time and fish size, by calculating a MANOVA. Since data were non-normally distributed, the response variables, prey weight and prey counts, were included as ranks (Conover, 1982). The final statistical model was:

Diet in ranks=
 constant+time+size+(time × size)+haul (time)+error,

where size is "standard length of fish" in millimeters. Haul (time) is a nested factor to incorporate the effect of haul. One trawl (6:29 h local time) was omitted from the analysis because it had briefly touched the bottom and the high proportion of empty stomachs suggested that most fish had regurgitated their food.

Hydroacoustic data

Acoustic data were collected using a SIMRAD EK-500 echo sounding system. The instrument was calibrated

with a standard target on axis (Foote et al., 1987). A 38 kHz split-beam transducer was mounted in the centreboard of the ship at a depth of 10 m. The pulse width was set at 1 ms, the nominal beam width was 6.7°, and the acoustic threshold was − 75 dB. Output data strings from the EK-500 system's echo-integrator were printed as colour echograms and were saved onto optical disks for later analysis. Data were recorded with a vertical resolution of 0.5 m and a horizontal resolution of ∼ 5 m, but were later binned into 2 m vertical and 185 m (0.1 nm) horizontal increments. The data were then transferred to a personal computer and analyzed. The split-beam transducer provides information on both backscatter intensity and target strength. The area back-scatter coefficient (S_A) normalized to 1 nm^2 is:

$$S_A = \frac{\sigma 1852^2}{\psi z^2}$$

where σ=back-scattering cross-section of the target, z=target depth (m) and ψ=solid angle of the equivalent beam.

The ability of a fish to reflect sound is described by the target strength (TS) which is related to backscattering cross-section:

$$TS\,(dB) = 10 \log \frac{\sigma}{4\pi}$$

The length distributions of fish caught in relatively monospecific hauls of pollock were converted into an expected target strength frequency distribution using an empirically derived relationship for walleye pollock (Traynor, 1996):

$$TS\,(dB) = 20 \log (L) - 66$$

where L is standard length in cm. These length-derived TS frequency distributions from the anchovy hauls were compared to the acoustically measured TS frequency distributions for the entire water column. Although some biases are inherent in this methodology due to fish behaviour (Barange and Hampton, 1994) and density of fish schools (Soule et al., 1995), for our purposes these effects are assumed to be minor.

Differences in vertical distribution of fish between day and night were tested using a Student's t-test on the WMDs of the overall backscattering intensity (S_A) recorded during the anchovy trawls.

Results

Zooplankton

In terms of numbers, small copepods dominated the zooplankton catches with Acartia spp. (Adults), Oithona
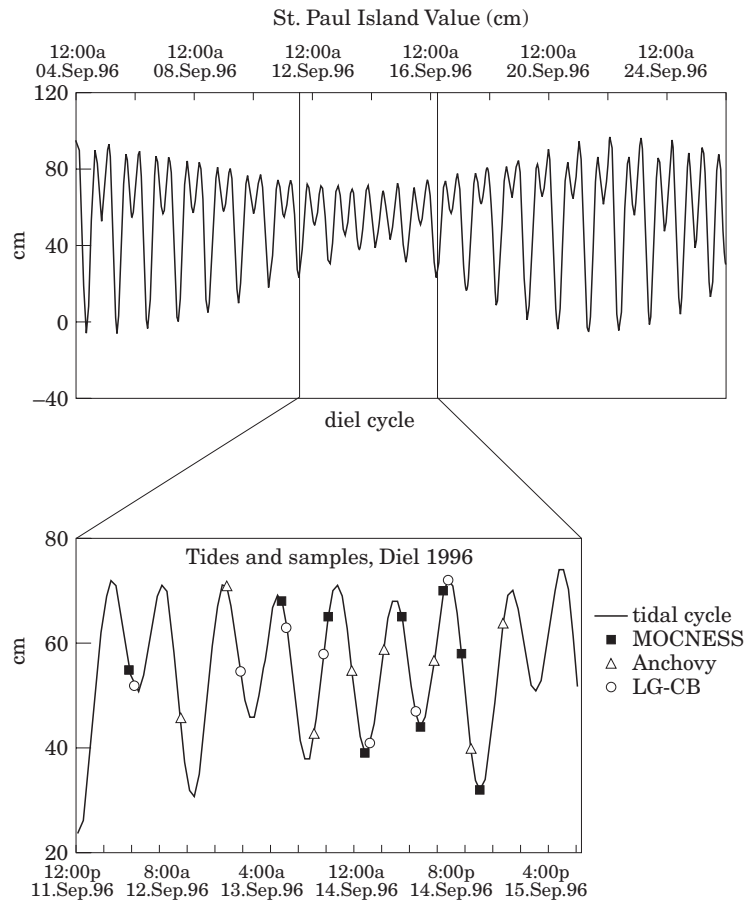
St. Paul Island Value (cm)

Figure 3. Tidal amplitudes off St Paul Island during 4–24 September showing an expanded view of the period of our diel sampling.

spp. (CV-Adult) and *Pseudocalanus* (CI-Adult) together reaching densities of 16 000 individuals m^{-3} (Table 1). Other abundant zooplankton taxa were pteropods, chaetognaths, larvaceans and euphausiids. No diel vertical migration was observed in Cnidaria (t-test on WMD; p=0.32) or *Eucalanus bungii* (p=0.19; stages CIII-Adult, CIV dominating; Fig. 4). All the other large zooplankton organisms exhibited pronounced diel vertical migrations (adult and juvenile euphausiids, Furcilia, *Calanus marshallae*, *Metridia pacifica*: p<0.001; chaetognaths: p<0.016). *C. marshallae* (CII-Adult, CV dominating) and *M. pacifica* (CV-Adult, CV dominating) were concentrated below 30 m during the day. Whereas *C. marshallae* was distributed evenly throughout the water column at night, *M. pacifica* had a density maximum in the top 20 m. *Thysanoessa raschii* was the dominant euphausiid species (Table 1). Other euphausiid species were *T. inermis*, *T. longipes* and *T. spinifera*. Diel vertical migrations were more prominent in furcilia than in later developmental stages (Fig. 4). In chaetognaths (mainly *Sagitta elegans*) the upward migration during darkness was a slower gradual process

and they did not reach notable concentrations in the surface layers before 3:06 h (p=0.016).

Catch data and hydroacoustics

Anchovy trawl catches were relatively monospecific and were, on average, comprised of more than 92% age-0 walleye pollock (Table 2). Conversely, large medusae (mostly *Chrysaora* sp., diameter>20 cm) made up more than 92% of the total biomass (Table 2). Body lengths of age-0 walleye pollock ranged from 30–92 mm with the mode around 46 mm. Expected target strengths estimated from pollock size distribution and observed target strengths both peaked at approximately −53 dB, indicating that many targets throughout the water column were probably age-0 walleye pollock (Fig. 5).

In the frontal region acoustic backscatter at 38 kHz was high throughout the diel period. Highest values were normally measured below 30 m during the day; however, patchily distributed and densely aggregated fish shoals were occasionally seen in shallow depth above 20 m. At

Table 1. Average concentration and biomass of the dominant zooplankton categories at the diel station north of St Paul Island.

	Concentration (no. m^{-3})	Biomass (mg m^{-3})
Cnidaria	2.0 ± 0.3	37.1 ± 5.6
Pteropoda	75.9 ± 21.5	32.8 ± 9.2
Copepoda		
Acartia spp.	178 ± 59	1.34 ± 0.45
Oithona spp.	9508 ± 1931	71.8 ± 14.6
Pseudocalanus spp.	6270 ± 839	154.6 ± 20.7
Calanus marshallae Frost, 1974	2.4 ± 0.7	2.92 ± 0.85
Eucalanus bungii Giesbrecht, 1892	0.3 ± 0.03	0.12 ± 0.01
Metridia pacifica s.l. Boeck, 1864	14.9 ± 5.3	2.87 ± 1.02
Euphausiacea		
Thysanoessa raschii (M. Sars, 1864)	0.11 ± 0.02	4.63 ± 0.84
Thysanoessa inermis (Kroyer, 1846)	0.01 ± 0.004	0.21 ± 0.09
Thysanoessa longipes Brandt, 1851	0.002 ± 0.001	0.05 ± 0.02
Thysanoessa spinifera Holmes, 1900	0.002 ± 0.001	0.02 ± 0.008
Calyptopis and Furcilia	63.0 ± 14.6	31.3 ± 7.3
Unidentified Juveniles	4.9 ± 1.0	118.3 ± 24.1
Amphipoda	0.03 ± 0.01	0.48 ± 0.16
Mysidacea	0.001 ± 0.0003	0.01 ± 0.001
Natantia	0.06 ± 0.02	0.85 ± 0.27
Decapoda larvae	0.012 ± 0.007	0.05 ± 0.04
Chaetognatha	82.4 ± 34.4	54.2 ± 22.6
Larvacea	85.9 ± 20.1	28.6 ± 6.7

night the echosign was more dispersed. Backscattering intensity (S_A) recorded during the anchovy trawls was greatest between 30 and 40 m during the day with an occasional second maximum near the surface, whereas the highest values during the night were above 20 m (t-test on WMD of S_A: p=0.008; Fig. 6). The overall decrease in acoustic backscatter during the night relative to the day suggests that a portion of the population migrated above the transducer depth after dusk.

Diet

Small copepods were the dominant food items for the small size class of fish (49–59 mm) in terms of numbers and biomass (Table 3). Large copepods, adult and juvenile euphausiids, and chaetognaths became more important in the diet of larger fish. However, considering their abundance in the environment, the proportion of chaetognaths and pteropods in the diet of juvenile pollock was low and pelagic cnidaria and larvaceans were completely avoided.

Significant differences in number and weights of the five most common prey categories were found as a function of fish size. No significant differences in fish diet composition were found between the day and night collections (Fig. 7). The interaction term between time of day and fish size was found to be marginally significant only for small copepods (Table 4), meaning that there is a potential difference in diel ingestion rate of small copepods between small and large fish.

Discussion

It is still a matter of debate as to the extent to which endogenous rhythms and/or extrinsic factors such as zeitgebers (e.g. light, temperature) control DVM in larval and juvenile fish. An increasing body of literature suggests that multiple factors affect the behaviour of animals in their environment (e.g. Neilson & Perry, 1990). Given the broad array of physical and biological factors and their continual change over space and time, general models of fish behavior are usually unrealistic.

There is ample evidence from field and laboratory results that walleye pollock juveniles are flexible in their DVM, seemingly weighing the benefits and costs of migratory behavior. They can modify their migrations in response to light, thermal gradients, predators and prey density (Bailey, 1989; Olla and Davis, 1990; Sogard and Olla, 1993, 1996a). Light appears to play an important role in regulating diel activity (Sogard and Olla, 1996a). In laboratory conditions under constant light or darkness juvenile pollock abandon the strong diel activity patterns normally seen in fluctuating light conditions (Fujimori et al., 1999).
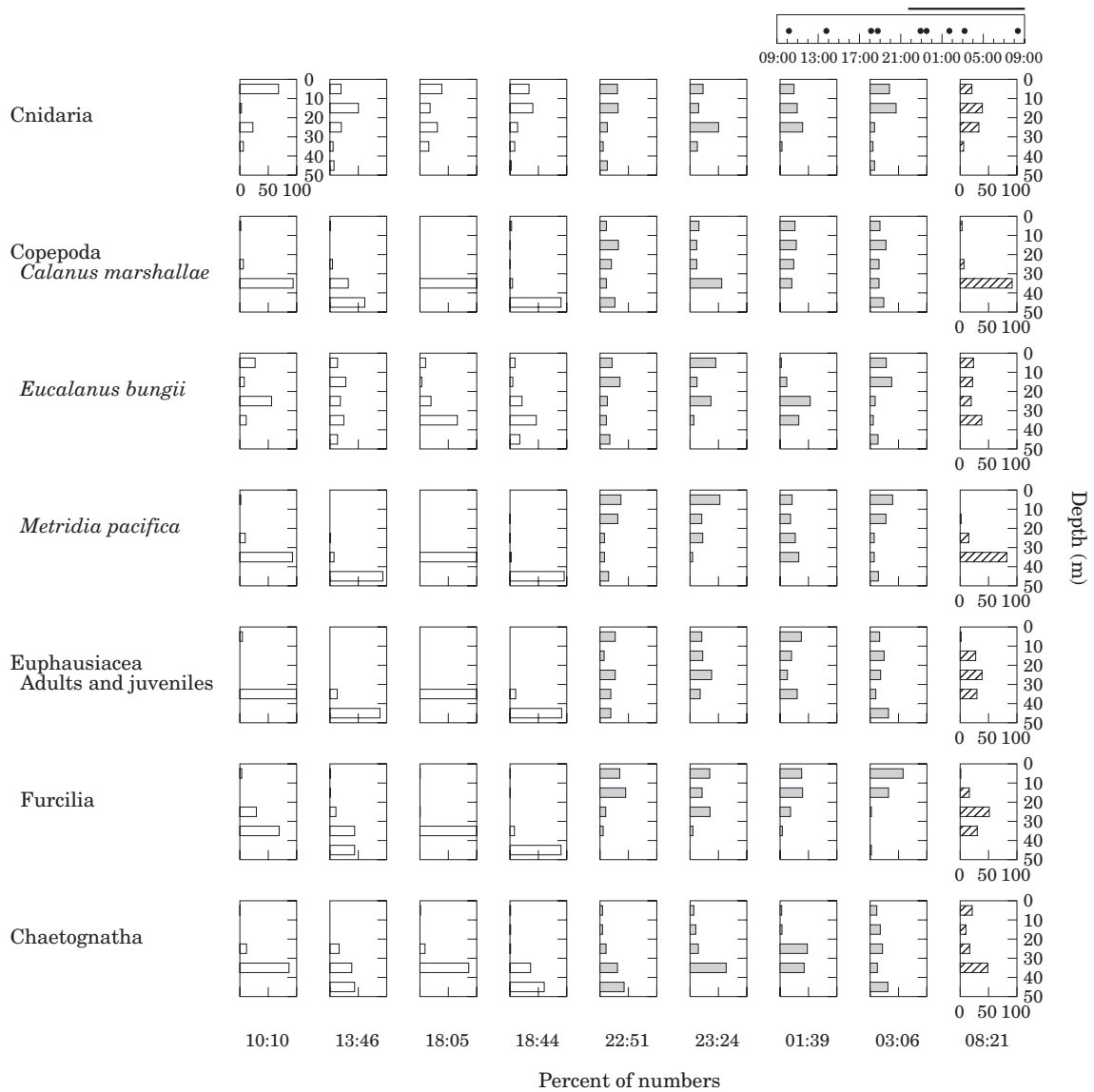
Figure 4. Diel vertical distribution of the dominant zooplankton groups. The panel in the upper right shows how the samples were distributed throughout the diel period. Black and striped bars indicate night and dawn samples, respectively.

In addition to sensory stimuli there must be some selective advantage to maintain migration behaviour in a population (Levy, 1990). Bioenergetic benefits, zooplankton foraging success, predator avoidance or a combination of these factors are the most common explanations for the selective advantage of DVMs (Neilson and Perry, 1990). Migrating juvenile pollock may gain an energetic advantage over non-migrating fish by feeding near the surface during the night and then digesting under colder temperatures in deeper water during the day (Ciannelli *et al.*, 1998). In the laboratory food-deprived juvenile pollock exhibited energy-conserving responses by migrating into 3–4°C colder

water (Sogard and Olla, 1996b), whereas fish maintained at higher rations stayed in the warmer layer. Bailey (1989) found a similar pattern for age-0 walleye pollock in the Bering Sea at high and low food abundance stations. Zooplankton abundance was low in the year of this study (1996) compared to other years (Napp and Brodeur, unpublished data). Moreover, the very weak temperature gradient of less than 0.5°C at the frontal region does not support the hypothesis that juveniles migrated primarily to obtain an energetic advantage.

The strategy "to eat and to avoid being eaten" more likely explains the apparent migration pattern at the front. Elevated abundances of juvenile pollock between

Table 2. Age-0 pollock, other fish and large jellyfish (bell diameter >20 cm) density (N) and biomass (B) by time of day. All times are at the start of the anchovy trawl and are local (Alaska Daylight Time). Numbers in parentheses are percentages of the total catch. The category "other fish" contained a variety of other species including pleuronectids, gadids, cottids, and clupeid fishes.

Time (ADT)	Pollock		Other fish		Jellyfish	
	N $(10^3 \text{ m}^3)^{-1}$	B g$(10^3 \text{ m}^3)^{-1}$	N $(10^3 \text{ m}^3)^{-1}$	B g$(10^3 \text{ m}^3)^{-1}$	N $(10^3 \text{ m}^3)^{-1}$	B g$(10^3 \text{ m}^3)^{-1}$
10:16	44.8 (96.0)	47.5 (2.9)	0.6 (1.3)	4.2 (0.3)	1.2 (2.7)	1611.8 (96.9)
15:00	209.9 (99.7)	157.6 (39.2)	0.2 (0.1)	0.7 (0.2)	0.4 (0.2)	243.5 (60.6)
17:19	82.7 (97.6)	99.6 (4.4)	0.5 (0.6)	6.9 (0.3)	1.4 (1.7)	2143.3 (95.3)
19:44	27.6 (85.8)	46.8 (0.7)	0.6 (1.9)	6.3 (0.1)	3.9 (12.3)	6612.5 (99.2)
22:46	30.8 (93.7)	39.9 (5.4)	1.3 (4.0)	26.9 (3.6)	0.8 (2.3)	671.9 (98.6)
00:50	206.3 (98.7)	210.4 (4.6)	0.7 (0.3)	20.7 (0.5)	2.2 (1.0)	4301.3 (94.9)
06:29	4.4 (72.1)	10.2 (0.3)	0.5 (8.2)	17.6 (0.6)	1.2 (19.7)	3083.0 (99.1)
08:26	20.8 (93.7)	26.4 (0.2)	0.4 (1.8)	8.5 (0.1)	1.0 (4.5)	13661.0 (99.7)
Average	78.4 (92.1)	82.0 (7.3)	0.6 (2.2)	11.5 (0.7)	1.5 (5.6)	4041.0 (92.0)

30 and 45 m (10–25 m off the bottom) during the day and above 20 m during the night are consistent with previous results in the more stratified offshore regions around the Pribilof Islands. Direct observations with a remotely operated vehicle (ROV) in 1995 revealed that during daytime juveniles were often associated with dense aggregations of large scyphomedusae close to the thermocline (∼35 m depth; Brodeur, 1998b). At night pollock moved closer to the surface, forming loose aggregations, whereas medusae remained close to the thermocline (Brodeur, 1998b). The shelter provided by the tentacles of the medusae may have decreased the chance of predation by diving seabirds (murres, *Uria* spp.) (Coyle *et al.*, 1992; Decker and Hunt, 1996) and northern fur seal (*Callorhinus ursinus*) (Livingston, 1993; Sinclair *et al.*, 1994) from above and by demersal fishes such as arrowtooth flounder (*Atheresthes stomias*) and adult walleye pollock from below (Lang *et al.,* 2000). Although high concentrations of copepods and euphausiids were found close to the bottom during daytime, feeding in this deep layer would have probably increased the risk of predation by fish, since juvenile pollock at this site constituted more than 70% by weight of the diet of arrowtooth flounder and adult pollock (Lang *et al.*, 2000). Feeding intensity of arrowtooth flounder was highest in the afternoon when juveniles concentrated about 15–20 m above the bottom. Thus, if light and hunger were the only extrinsic factors controlling DVMs, it is difficult to explain why they did not concentrate near the bottom food-rich layers.

Hydroacoustic data suggested that some densely aggregated and patchily distributed fish shoals stayed in shallow water during daytime. There is evidence from laboratory (Sogard and Olla, 1993) and field studies (Bailey, 1989) that smaller juveniles (<60 mm) have a weaker tendency to migrate vertically and that the migration to deeper layers may intensify as the fish gain locomotory and sensory capabilities. The relatively shallow haul (∼24 m) at 1500 h contained no fish larger than 60 mm (Fig. 5) and also less jellyfish than the other hauls (Table 2). However, depth-discrete sampling would be necessary to analyze depth dependent variations in length frequency distributions, if such a stratification by size indeed exists.

Most juveniles and some of their major prey items migrated upwards in the water column around dusk. Walleye pollock undergo a transition from predominantly daytime feeding as larvae (Canino and Bailey, 1995) to nocturnal feeding as juveniles (Merati and Brodeur, 1996; Brodeur *et al.*, 2000). A study in the Gulf of Alaska revealed that juvenile pollock (53–107 mm TL) were migrating upward from near bottom at a 110 m to a depth of 10–40 m at dusk, where individuals dispersed and fed through the night on larvaceans, euphausiids and copepods (Merati and Brodeur, 1996; Brodeur and Wilson, 1996). In the morning they returned to depth around 100 m and decreased their feeding rate. Data collected between 1994 and 1996 near the Pribilof Islands show that the stomach fullness was lowest after sunrise and increased continually throughout the day in juveniles smaller than 50 mm, whereas larger juveniles showed a feeding peak 4–5 h after sunset (Brodeur *et al.*, 2000). For the 1996 diel study, stomach fullness increased during the day and maximum stomach fullness was reached at 2215 h, right after sunset (2150 h), indicating that these fish consumed most food during the afternoon and early evening hours (Brodeur *et al.*, 2000); however we do not know if they cease feeding completely at night. In laboratory experiments small (20–50 mm) juveniles were capable of non-visual particulate feeding during darkness, but feeding was found to be more efficient when adequate light levels permitted visually mediated foraging (Ryer and Olla, 1999).

Pollock larvae in the Bering Sea have been shown to feed almost exclusively on copepod eggs and nauplii of *Metridia*, *Pseudocalanus* and *Calanus* (Hillgruber *et al.*, 1995; Brase 1996). The ontogenetic shift from
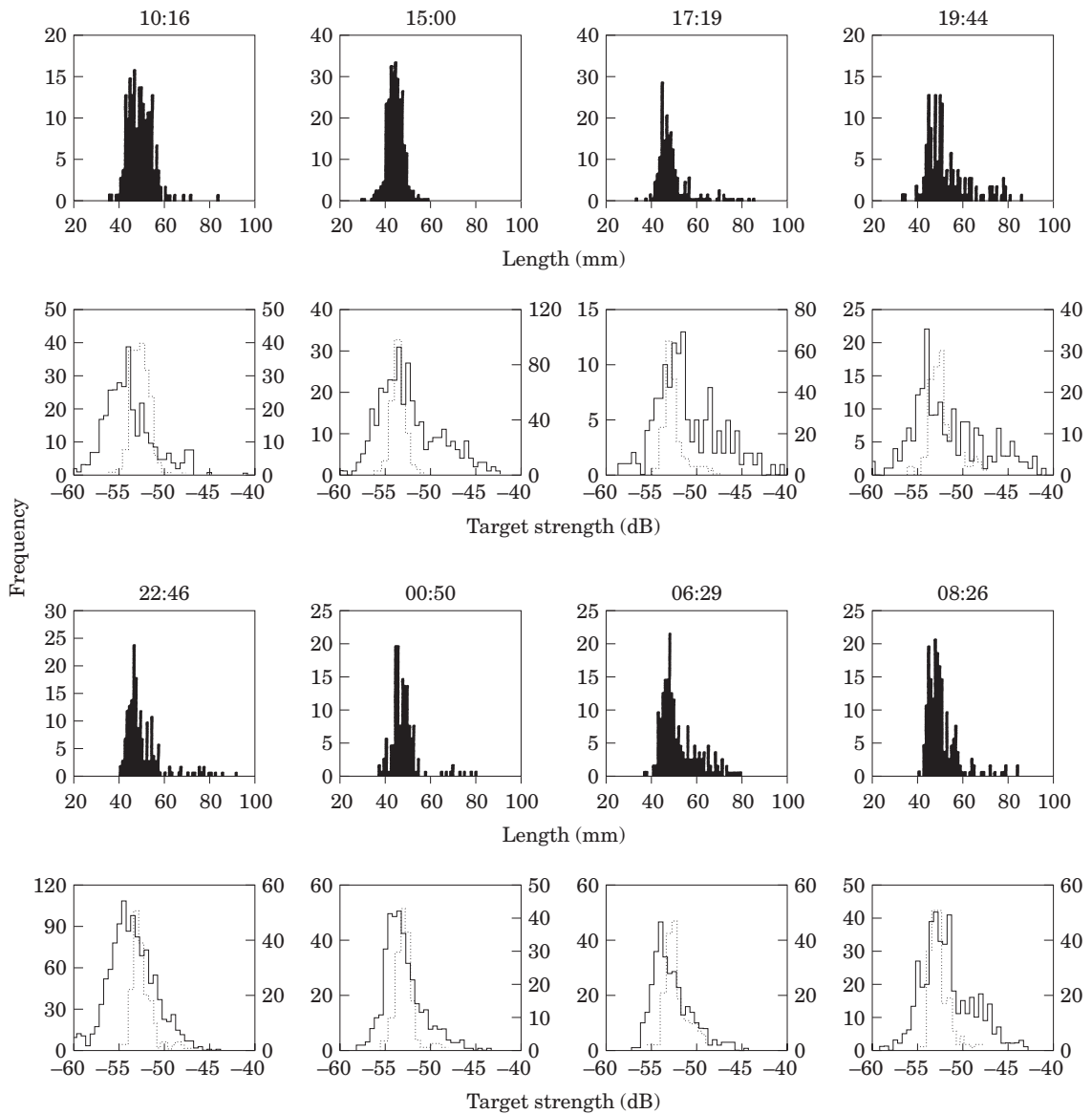
Figure 5. Length frequency distributions for age-0 walleye pollock collected in the anchovy trawls (upper panels, black bars) and corresponding target strengths distributions (below) collected during the trawls (solid stepped line, left axis). Also shown are the expected target strength distributions (dotted stepped line, right axis) based on the observed length distributions and the theoretical length to target strength relationship (see methods). EQ-time for the anchovy trawls is shown on top of each panel.

copepodites to euphausiids in the diet of juvenile pollock had been reported previously from the Bering Sea (Bailey and Dunn, 1979) and the Gulf of Alaska (Merati and Brodeur, 1996). The larger gape size and faster swimming speeds presumably enable the larger size classes of juveniles to capture and ingest the larger, more evasive euphausiids. Larger juvenile pollock (60–110 mm) in the Gulf of Alaska preferred euphausiids and avoided copepods relative to their densities in the plankton (Brodeur, 1998a).

Conversely, the time of capture did not appear to have much effect on prey composition. The slightly larger fish caught at night tended to select more euphausiids and less large copepods, but we were not able to detect significant diel changes in prey choice, although several physiological or sampling factors may have masked our ability to detect them. Among these are the size-related differences in diet, extended gastric evacuation times (Smith *et al.*, 1989), and complex spatial and temporal changes in prey availability. Moreover, different
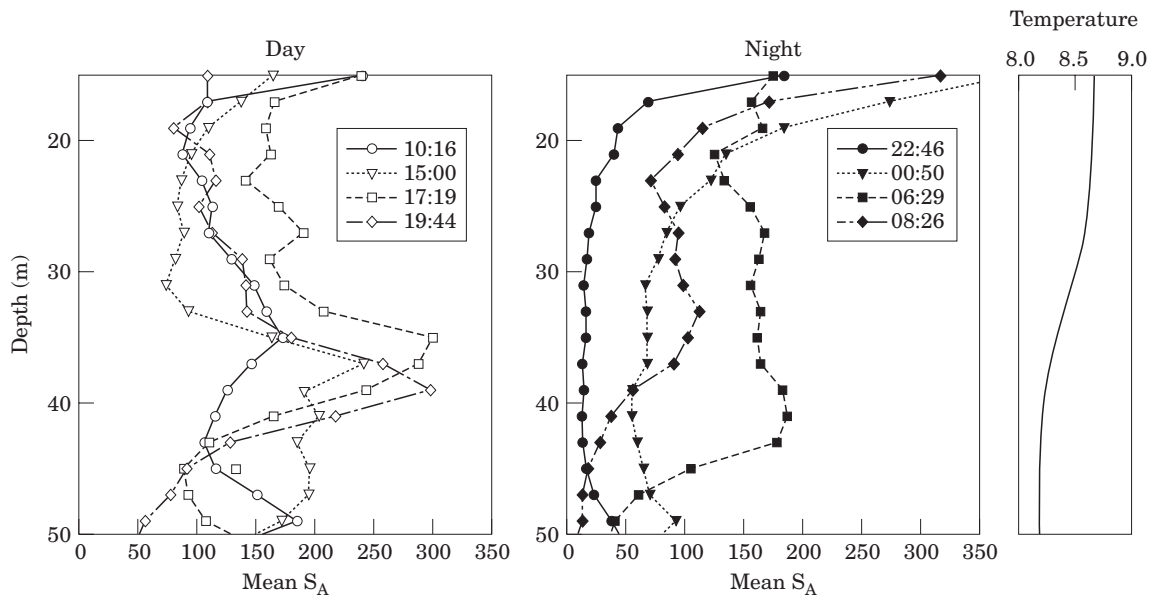
Figure 6. Mean S_A during anchovy trawls as a function of sample time and depth (2 m bins). The temperature profile in the front is in the panel on the right.

Table 3. Percent composition by abundance and biomass of prey found in the stomachs of age-0 walleye pollock (small fish = 39–59 mm, large fish = 60–81 mm). The percentages represent a total of 98 small and 29 large fish.

	Number (%)		Biomass (%)	
Taxon	Small	Large	Small	Large
Cnidaria	0.94	—	0.82	—
Pteropoda	0.07	—	0.33	—
Polychaeta	2.05	—	1.31	—
Ostracoda	0.35	—	1.80	—
Cumacea	0.12	2.94	0.66	0.54
Amphipoda	0.14	—	0.65	—
Small Copepoda	91.97	30.39	31.64	0.54
Large Copepoda	1.41	26.47	9.84	8.42
Euphausiacea Calyptopis and Furcilia	1.26	—	5.08	—
Euphausiacea Adult and Juvenile	0.33	12.75	22.46	74.47
Chaetognatha	1.34	27.45	25.08	16.03
Osteichthyes	0.02	—	0.33	—

zooplankton species, life stages, and even sexes can have disparate patterns of vertical migration and therefore, we may have missed a diet shift within the broad prey categories we examined. Alternatively, fish of a certain body size may have followed certain search images for prey (Lazzaro, 1987), and did not change their prey choice during the upward co-migration with zooplankton. Juvenile pollock are well adapted to feeding at low-light levels and were found to be size-selective zooplanktivores even under complete darkness, presumably using lateral line input for prey selection (Ryer and Olla, 1999).

In summary, we found that age-0 pollock and most of their major prey were undergoing DVM, residing in deep layers during the day and migrating toward the surface at night. We also found that fish size is an important factor in determining diet choice. Diel variability can also be a factor, especially for larger fish, but to comprehensively test this hypothesis, a wider range of fish sizes collected at different times of the day is needed. This study provided an unique opportunity to describe behavioural and trophic features of juvenile pollock at one site near the Pribilof Islands. Given the high degrees of spatial and
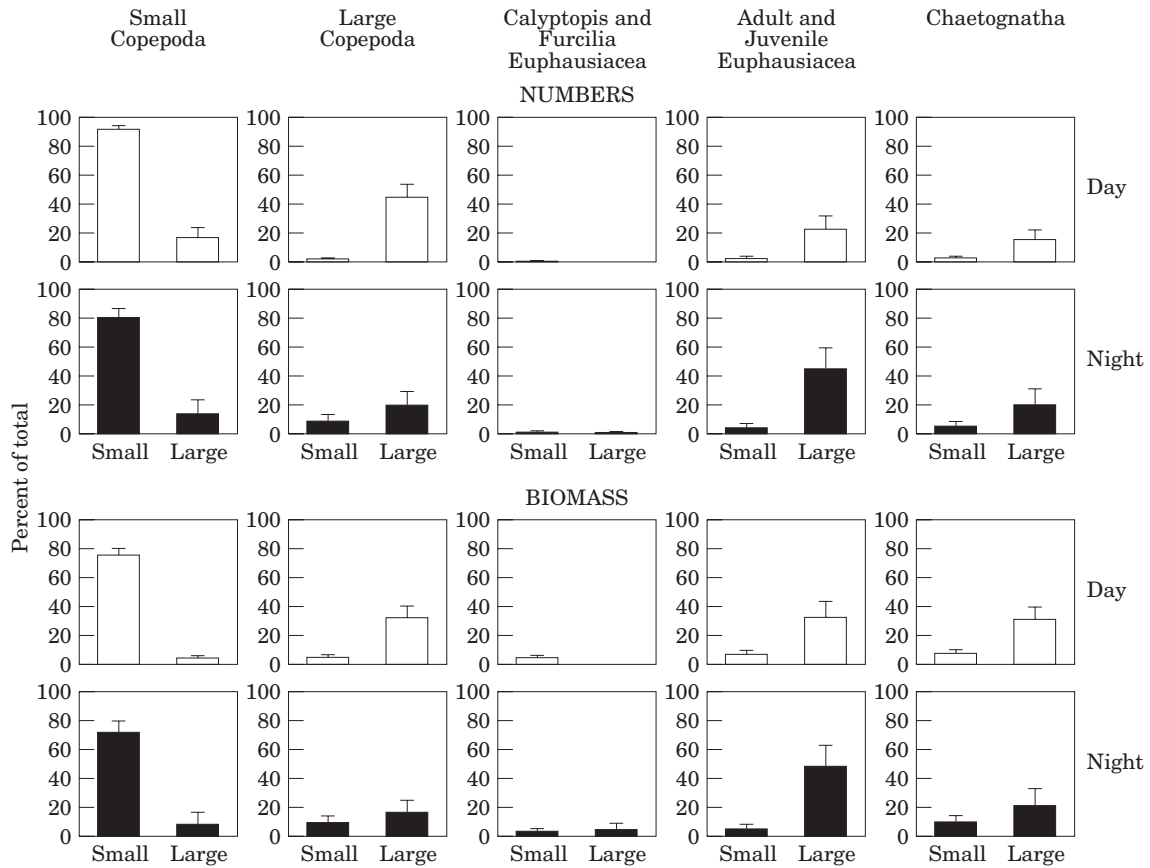
Figure 7. Effects of fish size (SL) and time of capture (day, night) on the diet (prey numbers (top) and biomass (bottom)) for the five main prey categories (small Copepoda, large Copepoda, calyptopis and furcilia, adult and juvenile Euphausiacea, Chaetognatha) of age-0 walleye pollock.

Table 4. Results of MANOVA on ranks of prey counts (Counts) and weights (g).

	Prey item	Time			Size			Time × Size		
		df	F	p	df	F	p	df	F	p
Counts	Large Copepoda	5	0.038	0.853	131	4.172	0.0430*	131	0.073	0.787
	Small Copepoda	5	1.331	0.301	131	54.810	<0.0001*	131	4.278	0.041*
	Chaetognatha	5	0.007	0.937	131	0.551	0.459	131	0.139	0.710
	Adult Euphausiacea	5	1.445	0.283	131	21.224	<0.0001*	131	0.135	0.714
	Calyptopis and Furcilia	5	2.182	0.200	131	2.358	0.127	131	2.795	0.097
Weights	Large Copepoda	5	0.055	0.824	131	3.421	0.067	131	0.118	0.732
	Small copepods	5	0.784	0.416	131	52.111	<0.0001*	131	3.579	0.061
	Chaetognaths	5	0.002	0.967	131	0.400	0.528	131	0.099	0.753
	Adult Euphausiacea	5	0.811	0.409	131	23.957	<0.0001*	131	0.085	0.771
	Calyptopis and Furcilia	5	1.998	0.217	131	2.367	0.126	131	2.759	0.099

Size=Standard Length (mm).
Time=day vs. night collections. *=$p<0.05$.

temporal heterogeneity of the study region, we cannot speculate on the factors that determine such migrations until further information is gathered from contrasting areas.

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