Abstract.—The diel vertical distribution patterns of several abundant ichthyoplankton taxa were examined from depth-stratified tows off Kodiak Island in the western Gulf of Alaska during 1986 and 1987. Most larvae were found in the upper 45 m of the water column throughout the diel period but were concentrated in higher densities near the surface (0–15 m) in daylight hours and at greater depths at night. Four of the five dominant taxa examined in detail showed significantly greater weighted mean depths during the night than during the day. This pattern was the opposite to that previously reported for the numerically dominant taxa (*Theragra chalcogramma*) in this area. Since there was no clear relation between the diel vertical distribution of these taxa and the vertical distribution of water temperature and density or copepod nauplii prey, we hypothesize that this reverse migration is either a strategy to minimize spatial overlap with predators that follow a normal diel migration pattern or one to optimize light levels for feeding.

Diel vertical distribution of ichthyoplankton in the northern Gulf of Alaska*

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Planktonic eggs and larvae of marine fishes exist in three dimensions in the open ocean. Unfortunately, traditional ichthyoplankton surveys, which use non-closing sampling gear, provide information only on two dimensions, integrating the vertical indirectly into the horizontal dimensions. It is well known that vertical current shear can be substantial over short distances and that light, temperature, hydrostatic pressure and food show much stronger gradients in the vertical relative to the horizontal dimensions in the water column (Laprise and Dodson, 1993). Thus, a larva can often change not only its geographic position, but also its immediate environment by altering its vertical position in the water column.

Diel vertical migration is well documented for larval, juvenile, and adult life history stages of marine fishes (see review by Neilson and Perry, 1990). The adaptive significance of these migrations is presently in dispute, but it has been attributed to position maintenance, bioenergetic optimization, thermoregulation, and predator avoidance (Kerfoot, 1985; Lampert, 1989). In addition, the degree of migration and amplitude of depths over which a species vertically migrates often changes during ontogenetic development (Brewer and

Kleppel, 1986; de Lafontaine and Gascon, 1989).

Knowledge of vertical distribution patterns of marine fish larvae is crucial not only in understanding ecological processes but also has practical implications in the assessment of abundance. Sampling just the upper depths of a species range can lead to substantial underestimates of abundance, whereas sampling the entire water column for surface-dwelling taxa may waste limited ship time. Despite the importance of the larval phase in recruitment of marine fishes, relatively little is known about larval vertical distribution patterns off the continental shelf in the North Pacific Ocean. With the exception of walleye pollock, *Theragra chalcogramma*, which has been fairly well studied through much of its geographic range (Kamba, 1977; Kendall et al., 1987; Pritchett and Haldorson, 1989; Kendall et al.[1]), the only comprehensive studies on vertical distribution of coastal ichthyoplankton in the northeast Pacific Ocean are from the California Current region (Ahlstrom, 1959; Boehlert et al., 1985; Brewer and Kleppel, 1986; Lenarz et al., 1991). This paper presents information on the vertical distribution of five abundant ichthyoplankton taxa (other than walleye pollock) collected in the

coastal waters of Alaska during spring and examines diel differences in these patterns in relation to environmental and biotic factors.

Materials and methods

Samples examined were collected from two cruises of the NOAA ship *Miller Freeman* in the area southwest of Kodiak Island in the northern Gulf of Alaska (Fig. 1). During May 1986 and 1987, 22 depth-stratified tows were made with a 1-m² Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) (Wiebe et al., 1976) equipped with 153-μm mesh. The net was towed obliquely and nets were opened sequentially at the desired depth strata. The primary purpose of the sampling was to collect information on the vertical distribution of walleye pollock larvae, which are generally found in the upper 50 m (Kendall et al.[1]), and their prey. Therefore, the emphasis during the sampling was on the upper part of the water column. The nets sampled the following nominal depths: 0–15, 15–30, 30–45, 45–60, 60–80, 80–100, and >100 m. Maximum sampling

Figure 1

Location of MOCNESS sampling series in Shelikof Strait used to determine vertical distribution of larvae in 1986 and 1987.

depth varied (range 150–252 m) depending on the depth of the water column at a particular station. There were eight depth strata sampled at most stations but the cutoff depth between the seventh and eighth net was variable. Therefore, we pooled the catches from these two nets into a single depth stratum (>100 m) for analysis. The actual sampling depths are given in Table 1. More complete station and catch information is given in Siefert et al.[2,3]
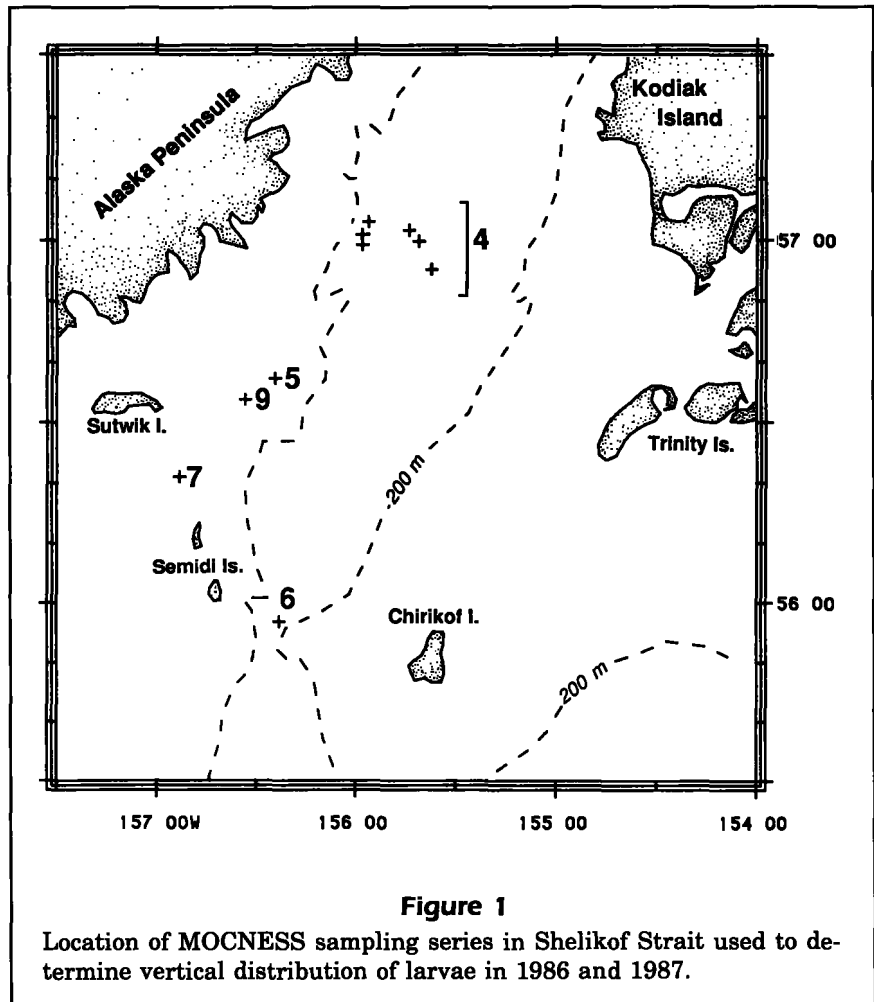
[1] Kendall, A. W., Jr., L. S. Incze, P. B. Ortner, S. R. Cummings, and P. K. Brown. In review. The vertical distribution of eggs and larvae of walleye pollock (*Theragra chalcogramma*) in Shelikof Strait, Gulf of Alaska. Submitted to Fish. Bull.

[2] Siefert, D. L. W., L. S. Incze, and P. B. Ortner. 1988. Vertical distribution of zooplankton, including ichthyoplankton, in Shelikof Strait, Alaska: data from Fisheries Oceanography Coordinated Investigations (FOCI) cruise in May 1986. NWAFC Processed Rep. 88-28, 232 p.

[3] Siefert, D. L. W., L. S. Incze, and P. B. Ortner. 1990. Vertical distribution of zooplankton, including ichthyoplankton, in Shelikof Strait, Alaska: data from Fisheries Oceanography Coordinated Investigations (FOCI) cruise in May 1987. NWAFC Processed Rep. 90-05, 129 p.

The 22 tows were grouped into five collection series (Table 1) based upon date and location of sampling (see Kendall et al.[1]) and included two complete diel series. The first diel series (Series 4) attempted to sample the same body of water over a four day period during 1986 by following a radar-tracked drifter drogued at 35 m (Incze et al., 1990). The second diel series (Series 9) sampled the same location on three successive days during 1987. Other collections (Series 5, 6, and 7) were taken at various times of the day but in the same general area as these two series (Fig. 1, Table 1).

Retrieved nets were thoroughly washed and contents were preserved in 5% buffered formalin. Samples were sorted to the lowest possible taxon and life history stage at the Polish Sorting Center in Szczecin, Poland. The volume filtered was estimated from a mechanical flowmeter mounted on the MOCNESS frame and abundances were converted to number per 1000 m³. Up to 50 preserved larvae of each taxon from each net were measured to the nearest 0.1 mm standard length. Net depth, temperature, and

Table 1
Station and tow data for collection subset used in the diel series ordered by time of day.

Series	Tow	Year	Date	Bottom depth (m)	Local time	Time period	Net depths (m)						
							1	2	3	4	5	6	7
4	5	1986	10 May	293	0745	Dawn	2–15	15–30	29–45	46–58	59–78	79–99	101–229
4	1	1986	8 May	220	0746	Dawn	1–15	15–31	35–45	45–61	61–80	80–100	101–200
9	4	1987	23 May	201	0747	Dawn	0–15	15–30	30–45	45–60	60–80	80–100	100–150
9	8	1987	24 May	190	0800	Dawn	0–15	15–30	30–45	45–60	60–80	80–100	100–150
6	2	1986	15 May	223	0940	Day	2–14	15–29	30–44	45–60	61–80	80–100	100–175
5	1	1986	13 May	210	1010	Day	2–15	16–30	30–45	45–61	61–80	80–100	101–152
4	6	1986	10 May	296	1341	Day	2–14		30–45			77–99	99–214
5	2	1986	13 May	210	1351	Day	2–14	15–29	30–44	45–59	59–78	80–99	100–176
4	2	1986	8 May	227	1356	Day	2–14	15–30	30–47			79–99	99–200
9	5	1987	23 May	179	1422	Day	0–15	15–30	30–45	45–60	60–80	80–100	100–150
9	9	1987	24 May	190	1543	Day	0–15	15–30	30–45	45–60	60–80	80–100	100–150
7	2	1986	18 May	123	1911	Dusk	2–15	15–30	30–45	45–59	60–79	80–100	
4	3	1986	9 May	235	2006	Dusk	2–13	13–28	29–45	46–59	60–79		100–200
4	7	1986	11 May	293	2011	Dusk	3–14	14–30	31–44	43–59	60–78	78–97	98–252
9	6	1987	24 May	179	2107	Dusk	0–15	15–30	30–45	45–60	60–80	80–100	100–150
9	10	1987	25 May	196	2122	Dusk	0–15	15–30	30–45	45–60	60–80	80–100	100–150
5	3	1986	14 May	210	2200	Night	2–14	14–30	30–45	46–60	60–80	81–101	100–163
7	1	1986	17 May	126	2416	Night	1–15	16–30	31–45	45–59	60–80	80–99	
4	4	1986	9 May	242	0135	Night	2–15	15–30	30–58		59–80	80–100	100–202
9	11	1987	25 May	198	0218	Night	0–15	15–30	30–45	45–60	60–80	80–100	100–150
9	7	1987	24 May	195	0219	Night	0–15	15–30	30–45	45–60	60–80	80–100	100–150
6	1	1986	15 May	229	0353	Night	2–15	15–29	30–44	45–60	60–80	80–100	100–172

salinity were measured continuously in real time during the tow and stored for later analysis.

To examine diel variations in density and size of larvae with depth, collections from the 22 tows were grouped into one of four time periods (hours): dawn (0530–0830), day (0830–1830), dusk (1830–2130), and night (2130–0530). Diel-depth variation in density of eggs and larvae at each depth was examined by using a two-way ANOVA on log-transformed data. The log $(X+1)$ transformation was used to achieve homogeneous variances (Bartlett's Test, all $P>0.05$). In addition, a weighted mean depth of occurrence of eggs or larvae of the dominant species for each time interval was calculated as follows:

$$\overline{D}_t = \frac{\sum_{i=1}^{n_t}\sum_{j=1}^{7} N_{ijt} D_{ijt}}{\sum_{i=1}^{n_t}\sum_{j=1}^{7} N_{ijt}},$$

where n_t = number of tows in time interval t,
N_{ijt} = number of larvae in net j in tow i in time interval t,
D_{ijt} = midpoint depth of net j in tow i in time

interval t with a variance equal to

$$Var(\overline{D}_t) = \frac{n_t}{\left(\sum_{i=1}^{n_t} N_{it}\right)^2 (n_t - 1)} \sum_{i=1}^{n_t} N_{it}^2 (\overline{D}_{it} - \overline{D}_t)^2,$$

where N_{it} = number of larvae in tow i in time interval t.

Differences in the weighted mean depths over the four time periods were tested with ANOVA, and Tukey multiple-comparison tests were conducted when significant differences were observed. Untransformed larval lengths for the three most abundant species were entered as dependent variables in two-way ANOVAs, with time of day and depth as factors.

Results

Species composition

Eggs and larvae of species other than walleye pollock were found in 134 of the 145 samples collected

during the 1986 and 1987 cruises. Flathead sole (*Hippoglossoides elassodon*) eggs were the only pelagic eggs other than walleye pollock collected and were found in 28.4% of the samples. This species had a mean density of 62.99 eggs/1000 m³ (SD=179.66) and comprised 74.9% of the total egg abundance in the 22 tows.

A total of 33 larval taxa were identified but only a few taxa occurred in more than 10% of the samples (Table 2). Larvae other than walleye pollock occurred in 92.4% of the collections but made up only 26.3% of the overall total abundance of larvae (total mean density=143.61 larvae/1000 m³; SD=257.03). Larvae of three taxa (*H. elassodon, Ammodytes hexapterus*, and *Bathymaster* spp.[4]) were

[4] Larvae of three *Bathymaster* species known to occur in the study area are presently not identifiable to species. Based on

found at sufficient densities to enable examination of their vertical abundance and length distribution patterns in detail for the four time periods. Two other species (*Gadus macrocephalus* and *Pleuronectes bilineatus*) were found at relatively high densities during day and night but at low densities during the twilight periods; hence, these taxa were examined only for day-night differences.

Vertical distribution

The distribution of *H. elassodon* eggs showed little variation in weighted mean depth by time of day (F=3.10, P>0.05); the highest abundances were

the abundance and distribution patterns of the adults, most of the larvae present in our collections are probably *B. signatus*. (A. Matarese, Alaska Fisheries Science Center, Seattle, WA 98115. Pers. commun. 1992).

Table 2
Summary of all larvae including walleye pollock collected in the 1986–87 vertical distribution study.

Scientific name	Common name	Percent occurrence (n=145)	Mean density (no./1000m³)	Length range (mm)
Osmerus mordax	rainbow smelt	0.69	0.25	21
Leuroglossus schmidti	northern smoothtongue	0.69	0.02	9–15
Stenobrachius leucopsarus	northern lampfish	4.14	3.05	4–7
Protomyctophum thompsoni	bigeye lanternfish	0.69	0.04	10
Myctophidae	unidentified myctophid	0.69	0.06	3
Gadus macrocephalus	Pacific cod	15.86	27.51	3–11
Theragra chalcogramma	walleye pollock	93.79	402.71	3–8
Gadidae	unidentified gadid	2.76	0.36	4
Sebastes spp.	unidentified rockfish	1.38	0.17	4–5
Hexagrammos decagrammus	kelp greenling	1.38	0.05	8–11
Dasycottus setiger	spinyhead sculpin	0.69	0.07	8
Gymnocanthus spp.	unidentified sculpin	0.69	0.07	7–8
Hemilepidotus hemilepidotus	red Irish lord	1.38	0.13	11–13
Icelinus spp.	unidentified sculpin	7.59	0.65	4–5
Malacocottus zonurus	darkfin sculpin	0.69	0.05	6–7
Radulinus asprellus	slim sculpin	1.38	0.10	4–5
Ruscarius meanyi	Puget Sound sculpin	0.69	0.04	4
Agonidae	unidentified poacher	10.34	0.84	5–10
Nectoliparis pelagicus	tadpole sculpin	0.69	0.07	4–8
Cyclopteridae	unidentified snailfish	2.07	0.19	4–5
Bathymaster spp.	unidentified ronquil	13.10	30.67	4–7
Anoplarchus spp.	unidentified prickleback	2.07	0.26	8–10
Lumpenella longirostris	longsnout prickleback	1.38	0.05	10–11
Lumpenus maculatus	daubed shanny	6.21	0.64	12–23
Poroclinus rothrocki	whitebarred prickleback	4.83	0.97	10–15
Cryptacanthodes aleutensis	dwarf wrymouth	1.38	0.19	14
Pholis spp.	unidentified gunnel	0.69	0.04	13–17
Zaprora silenus	prowfish	3.45	0.40	12–14
Ammodytes hexapterus	Pacific sand lance	40.69	12.76	6–19
Hippoglossoides elassodon	flathead sole	17.93	59.81	4–19
Pleuronectes bilineatus	rock sole	13.10	3.71	3–10
Pleuronectes vetulus	English sole	0.69	0.13	8
Psettichthys melanostictus	sand sole	0.69	0.14	4–5
Pleuronectidae	unidentified flounder	0.69	0.10	4

found in the surface layer (0–15 m) during all four time periods (Fig. 2). Although there were significant (P=0.005) differences in density by depth strata, neither the diel density differences alone (P=0.838) nor the interaction between time and depth (P=0.996) was significant.

The majority of larvae, excluding pollock larvae, from all collections combined were collected from the upper three depth strata (Fig. 3). The maximum density overall occurred at the second depth stratum (15–30 m), below which larval density declined with depth. However, this overall vertical distribution pattern was apparently confounded by higher larval densities found during the night when the larvae were mainly caught in the 15–30 m stratum;

during the other three time periods the highest densities were in surface waters (Fig. 4). The weighted mean depth of larvae overall was significantly (P<0.05) greater at night than during the other three time periods (Table 3) and the interaction between time and depth was marginally significant (P=0.05; Table 4), suggesting that there were diel differences in overall larval depth distribution.

Four of the five most abundant larval taxa showed the greatest weighted mean depths (Table 3) and the lowest surface densities (Fig. 4) at night. This general pattern was also evident in the two time periods examined for the fifth species, G. macrocephalus, but the diel differences were not significant (Table 3). Only A. hexapterus and G. macrocephalus showed significant diel differences in larval density, with highest densities occurring at night (Table 4). None of the dominant taxa, however, showed a significant interaction between time and depth strata.

Length distributions

The distribution of larval lengths by time of day and depth showed no consistent pattern among the three most abundant species (Fig. 5). Although time and time-depth interactions were significant (all P<0.03) factors in explaining the variation in mean length of H. elassodon and Bathymaster spp., none of the factors was significant for A. hexapterus. Examining only the strata where more than two lengths were available, we found that the smallest larvae of both Bathymaster spp. and A. hexapterus were caught in the surface stratum at night but in deeper strata during daylight hours (Fig. 5). However, H. elassodon showed an increase in mean length with depth during daylight hours and the reverse pattern at night (Fig. 5). Hippoglossoides elassodon was the only taxon to show a significant difference in length distributions between night and day collections (Kolmogorov-Smirnov Test; Z=3.881; P=0.001). Although the lack of larger larvae in daytime collections might suggest some daytime gear avoidance by this species
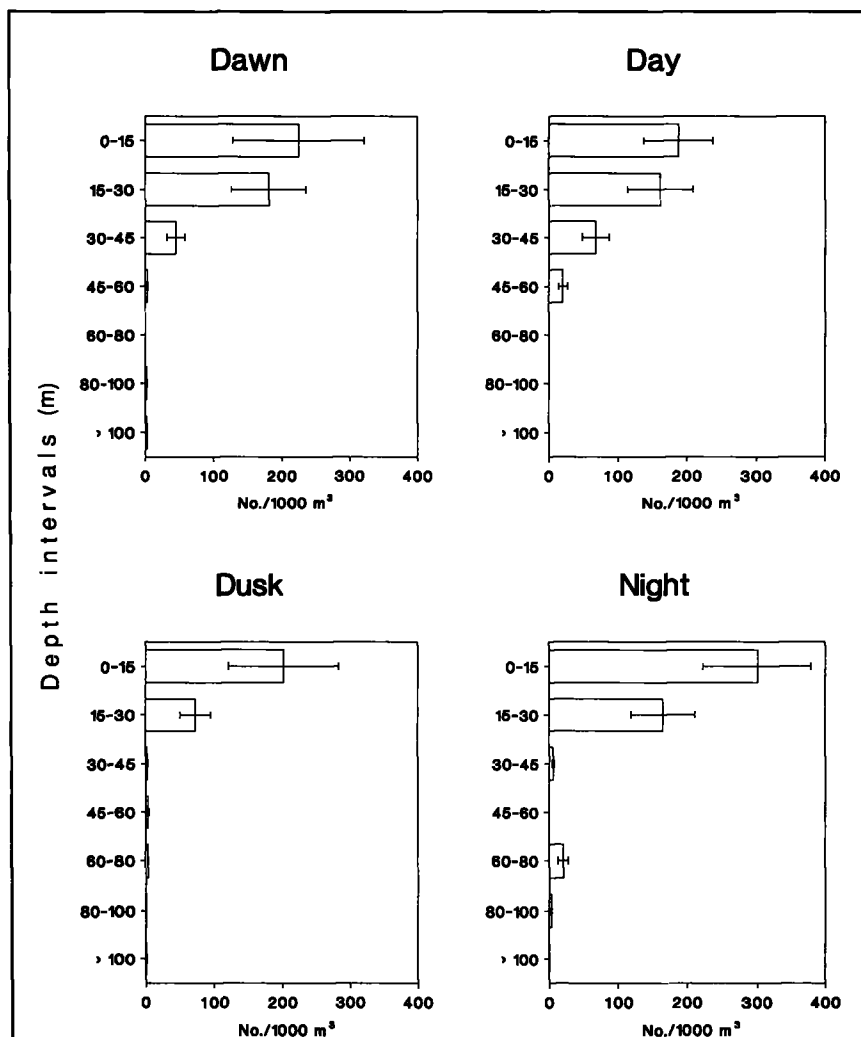

Figure 2

Diel vertical distribution of Hippoglossoides elassodon eggs. Bars are mean abundances per 1000 m³ at each depth interval and error bars are ± one standard deviation about the mean abundance.

(Fig. 6), there were few small larvae caught at night, which cannot be explained by gear avoidance. Since the majority (>95%) of these lengths were from lar-
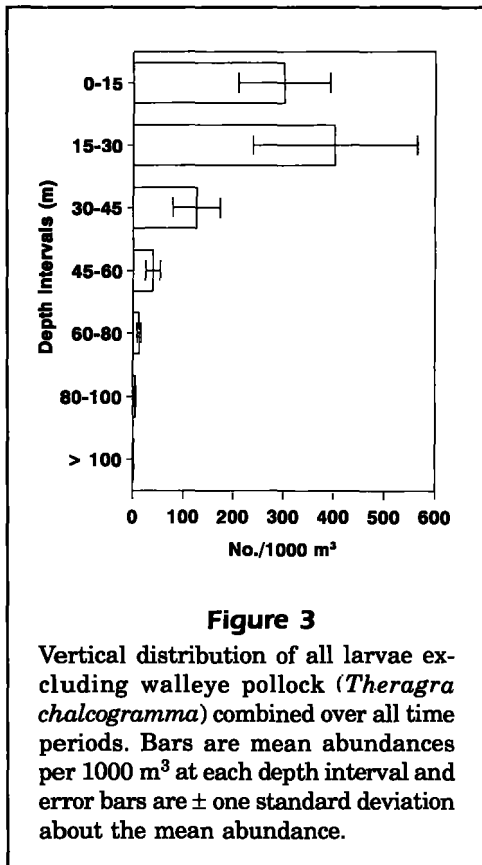

Figure 3

Vertical distribution of all larvae excluding walleye pollock (*Theragra chalcogramma*) combined over all time periods. Bars are mean abundances per 1000 m³ at each depth interval and error bars are ± one standard deviation about the mean abundance.

vae collected from the same location (Series 9), sampling variability cannot be invoked as an explanation for this pattern.

Discussion

Our results indicate that the vast majority (>99%) of pelagic eggs and larvae (excluding walleye pollock) are distributed in the upper 100 m of the water column during the spring months. Therefore, sampling to this depth should be sufficient to characterize the horizontal distribution patterns of these species. Of the common taxa we examined, all but *H. elassodon* have demersal eggs (Matarese et al., 1989). The transit time to surface waters following hatching from demersal eggs is apparently of such short duration that even newly hatched larvae were rarely collected below 100 m. However, this does not appear to be the case for walleye pollock, which spawn at depths greater than 200 m in Shelikof Strait, with mean depths of eggs and yolk-sac larvae generally greater than 100 m (Kendall and Kim, 1989; Kendall et al.[1]).

The diel vertical distribution pattern that we observed for several taxa is not the pattern typically observed for most ichthyoplankton and for zooplankton in general. The more common pattern, termed a 'Type I' migration (Neilson and Perry, 1990), involves a nocturnal ascent into surface waters and is undertaken by larvae of a diversity of fish species.

Table 3

Weighted mean depths (m) and standard deviations of the mean depths (in parentheses) for each taxon and for all larvae excluding walleye pollock by time of day and overall depth for all times combined. Also given are the results of the ANOVAs testing for diel differences in weighted mean depth and the significant ($P< 0.05$) Tukey multiple-comparison tests between time periods.

Dawn	Day	Dusk	Night	Overall	F-value	Tukey test
All Larvae (excluding walleye pollock)						
16.59 (2.72)	17.46 (1.52)	15.45 (2.25)	25.74 (1.52)	21.75 (1.87)	33.17***	Night>Day=Dawn=Dusk
Hippoglossoides elassodon						
14.82 (0.63)	16.94 (2.73)	10.80 (0.42)	20.10 (0.05)	18.06 (1.33)	31.89***	Night>Day=Dawn>Dusk
Ammodytes hexapterus						
31.21(11.45)	27.67 (4.59)	22.67 (2.38)	37.51 (4.45)	32.85 (3.39)	6.05**	Night>Dusk=Day
Bathymaster spp.						
8.21 (0.11)	11.25 (0.08)	11.28 (1.08)	37.95 (2.84)	18.12 (6.05)	441.48***	Night>Dusk=Day>Dawn
Pleuronectes bilineatus						
—	19.75 (1.83)	—	30.73 (1.63)	25.47 (4.64)	128.36***	Night>Day
Gadus macrocephalus						
—	20.36(10.35)	—	24.92 (0.12)	22.12 (6.56)	1.14 n.s.	

*** $P<0.001$.
** $P<0.01$;
n.s. $P>0.05$.

However, the reverse pattern ('Type II' migration), although less frequently documented, has been observed for larvae of several fish species, including many of the taxa we examined. For example, Boehlert et al. (1985) observed larval *G. macrocephalus* at lower depths at night than during the day off the Oregon coast. Walline[5] found that *Bathymaster* spp. in the Bering Sea generally migrated downward at night. Larvae of *A. hexapterus* collected in bays around Kodiak Island were concentrated from 10 to 30 m during the day but were found at lower depths at night (Rogers et al.[6]), and larvae of a congener (*A. personatus*) collected off Japan also exhibited reverse migration (Yamashita et al., 1985). Rogers et al.[6] and Pritchett and Haldor-

son (1989) found that rock sole (*P. bilineatus*), as well as larvae of several other taxa, showed reverse diel migrations during the spring.

We believe that sampling bias could not have resulted in the observed reverse distributions. Eggs of *H. elassodon*, as expected, showed no differences by time of day in our study and walleye pollock larvae in these same collections exhibited a normal diel migration pattern (Type I), occurring mainly in the 30–45 m range during daytime and above 30 m at night (Kendall et al.[1]; see also Kendall et al., 1987). Net avoidance, although suggested by the higher night catches overall as well as the larger mean size of larvae collected at night, is not a plausible explanation for the observed diel pattern. Light-aided daytime avoidance would be expected to influence the catch of larvae in the surface strata more than those in deeper strata, thus leading to underestimates of near-surface daytime abundances and the magnitude of reverse migration.

The prevalence of the reverse diel migration pattern in our study suggests an adaptive role for this behavior. Temperature gradients are relatively minor (<1°C) over the upper 50–60 m where most of the migration occurs (Fig. 7), and the majority of the larvae appear to be above the seasonal thermocline at all times of the day. Thus, we see no possibility of temperature-mediated energetic advantage related to migration at any time of the day. Similarly, observed density gradients are not pronounced (<0.5 σ_t units) within this surface layer (Fig. 7; Kendall et al.[1]) and there appears to be no physical mechanism that would aggregate either

Table 4

Results of two-way ANOVAs testing for differences in density of larvae by depth and time of day.

Source of variation	df	Sum of squares	Mean square	F-ratio	P-value
All larvae (excluding walleye pollock)					
Time	3	14.60	4.86	9.85	0.00
Depth	6	51.63	8.61	17.40	0.00
Time × depth	18	14.11	0.78	1.58	0.05
Error	4868	2406.73	0.49		
Hippoglossoides elassodon					
Time	3	4.97	1.66	0.48	0.69
Depth	6	93.59	15.60	4.54	0.00
Time × depth	18	15.49	0.86	0.25	0.99
Error	116	398.59	3.44		
Ammodytes hexapterus					
Time	3	55.08	18.36	11.70	0.00
Depth	6	94.13	15.69	9.99	0.00
Time × depth	18	34.27	1.90	1.21	0.26
Error	116	182.03	1.57		
***Bathymaster* spp.**					
Time	3	8.84	2.95	1.24	0.30
Depth	6	44.33	7.39	3.10	0.01
Time × depth	18	21.35	1.19	0.49	0.96
Error	116	276.73	2.39		
Pleuronectes bilineatus					
Time	1	1.68	1.68	1.35	0.25
Depth	6	19.01	3.17	2.55	0.03
Time × depth	6	3.47	0.58	0.47	0.83
Error	69	85.78	1.24		
Gadus macrocephalus					
Time	1	9.12	9.12	4.09	0.05
Depth	6	22.46	3.74	1.68	0.14
Time × depth	6	7.06	1.18	0.53	0.79
Error	69	153.81	2.23		

[5] Walline, P. D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June–July 1979. NWAFC Processed Rep. 81-05, 22 p.

[6] Rogers, D. E., D. J. Rabin, B. J. Rogers, K. J. Garrison, and M. E. Wangerin. 1979. Seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island including ichthyoplankton, meroplankton (shellfish), zooplankton and fish. Univ. Washington, Fish. Res. Inst. Rep. FRI-UW-7925, 291 p.
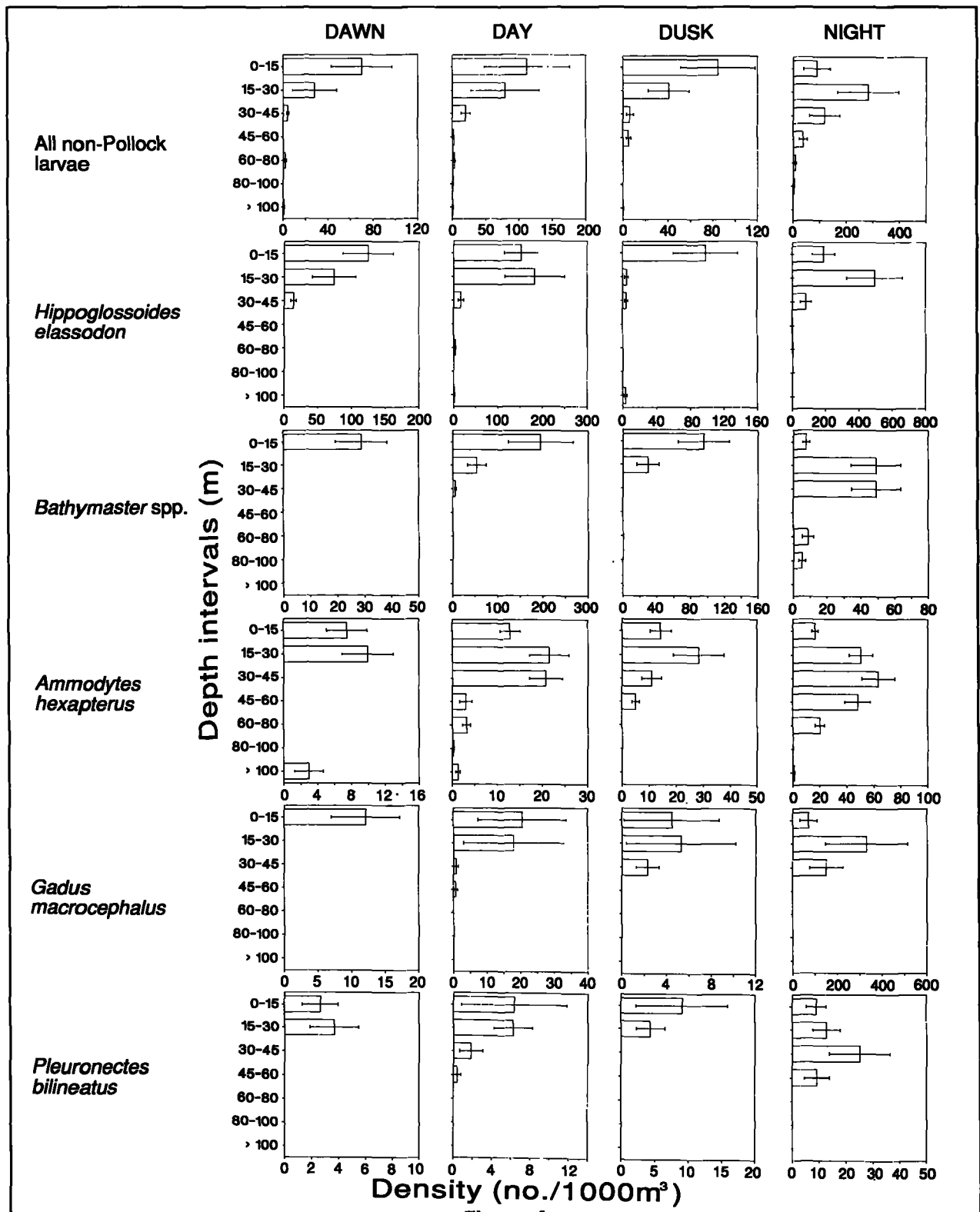
Figure 4

Diel changes in the vertical distribution of all larvae (excluding walleye pollock), and *Hippoglossoides elassodon*, *Bathymaster* spp., *Ammodytes hexapterus*, *Gadus macrocephalus*, and *Pleuronectes bilineatus* larvae. Bars are mean abundances per 1000 m³ at each depth interval and error bars are ± one standard deviation about the mean abundance.
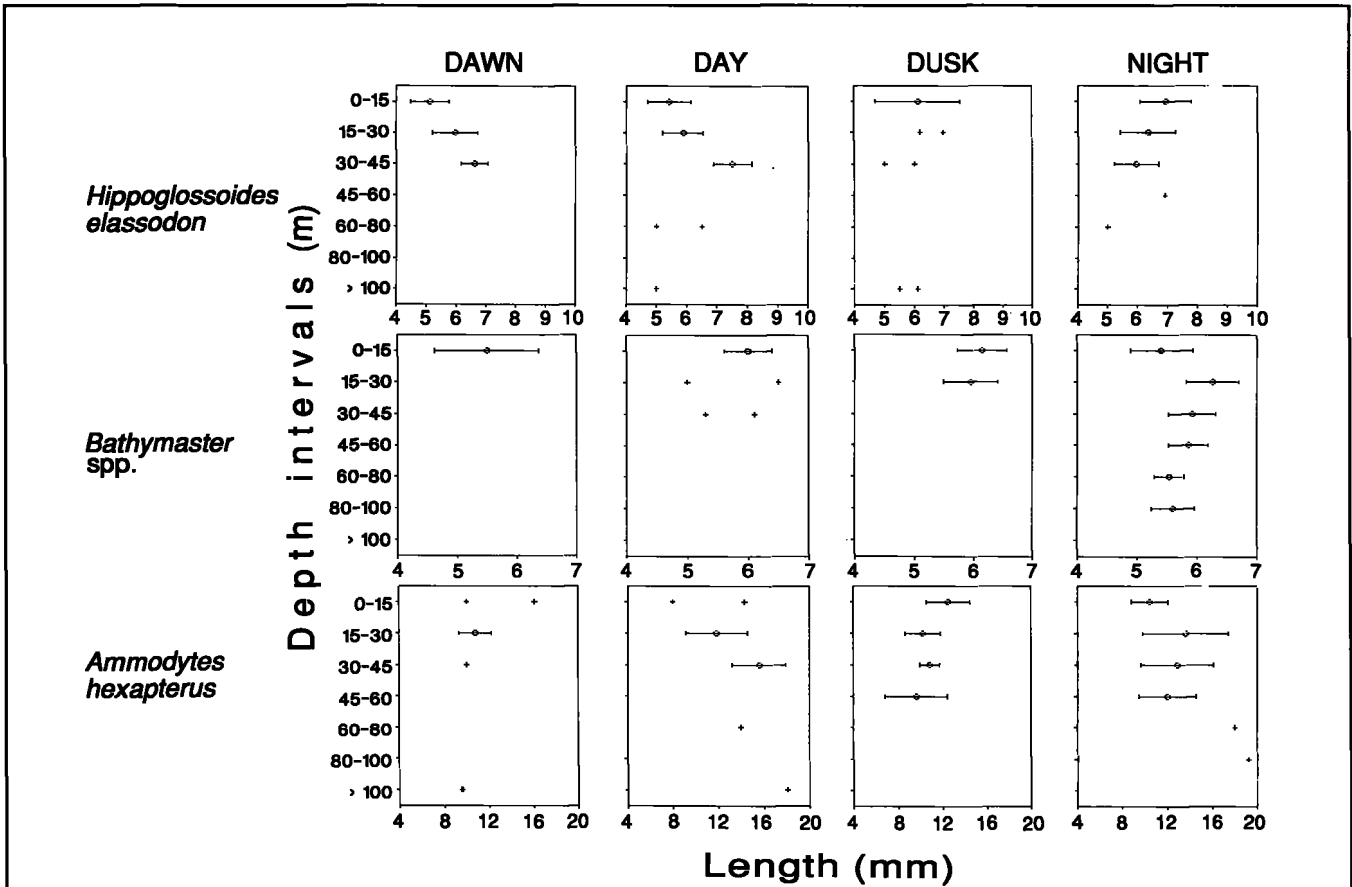
Figure 5

Diel vertical distribution of larval lengths of *Hippoglossoides elassodon*, *Bathymaster* spp., and *Ammodytes hexapterus*. Circles are mean length at each depth interval and error bars are ± one standard deviation about the mean length. The plus signs indicate actual lengths measured when less than three lengths were available from a particular depth stratum.
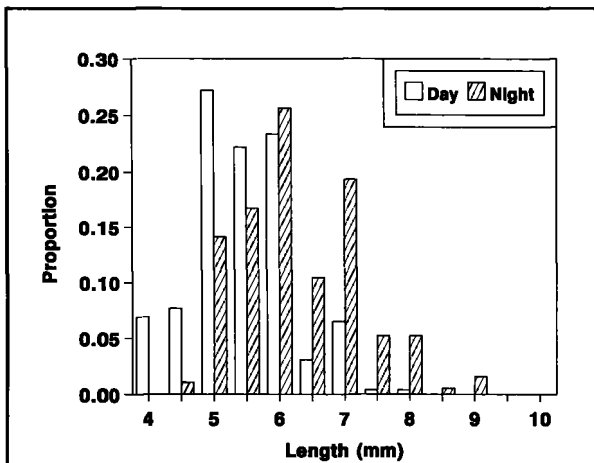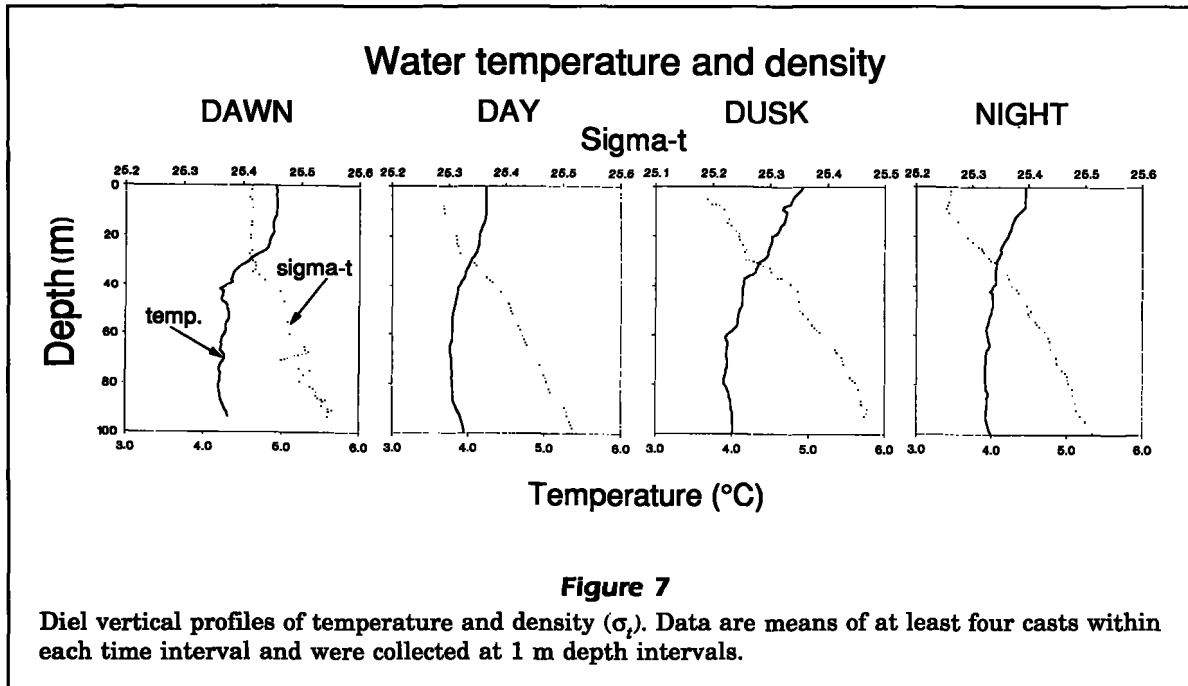

Figure 6

Day versus night proportional length distributions of *Hippoglossoides elassodon* larvae.

larvae or their prey at certain depths or inhibit them from migrating to different depths.

The fact that walleye pollock larvae, which are the dominant fish larvae in this area representing 70–80% of the larvae present in Shelikof Strait in the spring (Rugen[7]; this study), show a normal migration pattern (Kendall et al., 1987) suggests one potential explanation for reverse migration patterns of other larvae. If other larvae feed on the same microzooplankton prey as larval walleye pollock and these prey resources were limiting, then the presence of these other larvae in surface waters at different times of the day than those of walleye pollock would reduce competition with the numerically dominant taxon. Copepod nauplii, an important

Water temperature and density

Figure 7

Diel vertical profiles of temperature and density (σ_t). Data are means of at least four casts within each time interval and were collected at 1 m depth intervals.

component of the diet of many larval fishes including walleye pollock (Kendall et al., 1987), were the most abundant microzooplankton category found in Shelikof Strait, mostly in the upper 30 m during May 1986 and 1987 (Incze and Ainaire[8]). During diel Series 4, copepod nauplii had overall mean depths between 20 and 34 m but showed no obvious diel pattern in depth distribution (Kendall et al.[1]). Although feeding at a different time of day from walleye pollock might reduce interference competition (i.e. behavioral interactions) with the dominant species, it is highly unlikely, based on typical larval fish and copepod naupliar densities, that prey resources could ever be depleted by larval fish (Cushing, 1983; MacKenzie et al., 1990). Moreover, if food were limiting, then it would be advantageous for all larvae to stay in the layer of maximum food concentration throughout the diel period to maximize total intake. Thus, we do not see a trophic benefit accruing from a reverse migration pattern for these larvae.

If feeding by these larvae is periodic and dependent on some minimum light level, then the vertical distribution pattern can be partially explained by larval feeding response. Assuming light levels were limiting feeding at depths below 30 m, then it would be necessary for larvae to ascend to a shallower depth during the daytime when light is at a maximum. Following the cessation of feeding at dusk, larvae would be expected to become inactive

and passively sink to deeper levels at night. Such a mechanism has been postulated for Japanese sand lance (*A. personatus*) by Yamashita et al. (1985) who demonstrated a nocturnal cessation of feeding in this species. Although we lack data on the diel feeding chronology of any of the taxa examined here, it is possible that feeding occurs mainly in the crepuscular periods, with a temporary cessation of ingestion occuring during midday as observed in the field for larval walleye pollock (Canino and Bailey[9]). The shallowest mean depth occurs at either dawn or dusk for the three common species that were examined over the four time periods with slightly greater depths occurring during midday. If larvae were not feeding during the middle of the day, it would be advantageous to cease swimming altogether and sink through the water column to avoid being sensed by mechanoreceptive or visual predators. Following a particular isolume would produce a similar daytime pattern but could not account for the deeper distribution at night that we observed. Larval walleye pollock in the laboratory have been shown to avoid high light levels (Olla and Davis, 1990) but they also require relatively low light levels to initiate feeding (Paul, 1983). Unfortunately, we have no data available on the light levels necessary for feeding in the taxa we examined with which we can evaluate this hypothesis.

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[8] Incze, L. S., and T. Ainaire. In review. Zooplankton of Shelikof Strait, Alaska. I. Micro-zooplankton prey of larval pollock, *Theragra chalcogramma*. Submitted to Fish. Bull.

[9] Canino, M. F., and K. M. Bailey. In review. Gastric evacuation of walleye pollock, *Theragra chalcogramma* (Pallas), larvae in response to feeding. Submitted to Journal of Fish Biology.

A potential disadvantage to a diurnal ascent is increased susceptibility to visually feeding planktivorous fishes. However, acoustic and trawl survey data suggest that epipelagic fish predators are rare during the spring in this area and the majority of the nekton biomass is found in midwater or near the bottom (Brodeur et al., 1991), well below the depth of most larvae. On the other hand, euphausiids, which are possibly the major invertebrate predator on walleye pollock yolk-sac larvae, undergo a nocturnal ascent to surface water and descend to greater depths during the day in Shelikof Strait (Bailey et al., 1993). If euphausiids were also predators on non-pollock larvae and feed only in the surface layer above the nightime depths of these larvae, then a distinct advantage would be conferred upon individuals adopting a reverse diel migration pattern, as has been postulated for copepods (Ohman et al., 1983; Ohman, 1990). Based on field and experimental results, it has become increasingly apparent that predators can alter the diel vertical distribution patterns of invertebrate prey (Ohman et al., 1983; Gliwicz, 1986; Bollens and Frost, 1989; Levy, 1990; Neill, 1990; Frost and Bollens, 1992), but evidence for this effect on larval fish as prey is presently lacking.

Although a variation in depth by time of day was apparent for all species and consistent among species, it was not substantial enough to be statistically significant in all cases (e.g. G . $macrocephalus$). This may be due in part to the lack of resolution of our sampling intervals. The smallest average migration that we could detect is ~15 m; thus, diel vertical migrations less than that were not likely to be detected. Although a daily ambit of 30 m is not exceptional for larger larvae, it may be excessive for newly hatched individuals. For a study specifically examining the diel vertical distribution of the species considered here, we recommend sampling with a multiple net system every 5 m over the upper 40 m of the water column. Some bias may have also resulted from combining tows from different years, weeks, or geographic areas into our four time periods, which was necessitated by the relatively low occurrence rate and densities of these taxa. However, the remarkably strong and consistent diel differences among the different taxa, despite this introduced sampling variability, lend credence to our findings.

If there was differential migration by size classes of larvae, this condition might also obscure some of our results. The vertical distribution of larval lengths of the dominant species did not show any consistent patterns by time of day. The mean length by depth varied significantly for H. $elassodon$; smaller larvae were found at greater depths during the daytime and at the surface at night. This cannot be explained by visual gear avoidance alone since the nighttime pattern would then be expected to be random rather than exhibit the increasing mean length with depth that we observed. A possible explanation for this pattern might be that larger larvae may migrate a greater distance than smaller larvae, a pattern frequently observed in other fish larvae (Neilson and Perry, 1990). It is also possible that the migration of different size classes is asynchronous (Pearre, 1979). However, the available size ranges of the dominant species in our data was not extensive enough to examine diel migration patterns of different size classes. Moreover, caution should be exercised in examining larval length data in multiple net systems. Since larvae shrink upon death (Theilacker, 1980; Hay, 1981) and the likelihood of death may be related to time in net, we may assume that larvae caught in the first (deepest) net may have undergone more shrinkage than those in the last (surface) net.

In conclusion, this study shows that all the common larvae exhibit a reverse vertical migration pattern, opposite to that of the overall dominant species, walleye pollock. In Auke Bay, an inland embayment in Southeast Alaska (58°22' N) on the eastern side of the Gulf of Alaska, Haldorson et al. (1993) found a Type I migration for the numerically dominant osmerid larvae in their sampling and a Type II migration for the five next most abundant taxa (T. $chalcogramma$, H. $elassodon$, P. $bilineatus$, $Leuroglossus$ $schmidti$, and Agonidae). These authors attribute this diel-depth distribution pattern to temperature preferences by each species, although their vertical temperature gradients were more pronounced than what we observed in our study. Since most abiotic variables (other than light intensity) and food resources varied little over the depths through which much of the migration occurred in Shelikof Strait, we hypothesize that the reverse migration pattern that we documented was either a predator-avoidance mechanism or else an optimization of light levels for feeding. The prevalence of reverse migration in this and other studies suggests that it may be more common than previously suspected, especially in higher latitude ecosystems, and the factors contributing to this phenomenon merit further investigation.

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Literature cited

Ahlstrom, E. H.
  1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Wild. Serv., Fish. Bull. 60:107–146.
Bailey, K. M., R. D. Brodeur, N. Merati, and M. M. Yoklavich.
  1993. Predation on walleye pollock (*Theragra chalcogramma*) eggs and yolk-sac larvae by pelagic crustacean invertebrates in the western Gulf of Alaska. Fish. Oceanog. 2:30–39.
Boehlert, G. W., D. M. Gadomski, and B. C. Mundy.
  1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull. 83:611–621.
Bollens, S. M., and B. W. Frost.
  1989. Predator-induced diel vertical migration in a planktonic copepod. J. Plankton Res. 11:1047–1065.
Brewer, G. D., and G. S. Kleppel.
  1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217–226.
Brodeur, R. D., K. M. Bailey, and S. Kim.
  1991. Cannibalism on eggs by walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 71:207–218.
Cushing, D. H.
  1983. Are fish larvae too dilute to affect the density of their food organisms? J. Plankton Res. 847–854.
de Lafontaine, Y., and D. Gascon.
  1989. Ontogenetic variation in the vertical distribution of eggs and larvae of Atlantic mackerel (*Scomber scombrus*). Rapp. P.-v. Réun. Cons. int. Explor. Mer 191:137–145.
Frost, B. W., and S. M. Bollens.
  1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. Can. J. Fish. Aquat. Sci. 49:1137–1141.
Gliwicz, M. Z.
  1986. Predation and the evolution of vertical migration in zooplankton. Nature 320:746–748.

Haldorson, L., M. Prichett, A. J. Paul, and D. Ziemann.
  1993. Vertical distribution and migration of fish larvae in a Northeast Pacific bay. Mar. Ecol. Prog. Ser. 101:67–80.
Hay, D. E.
  1981. Effects of capture and fixation on gut contents and body size of Pacific herring larvae. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:395–400.
Incze, L. S., P. B. Ortner, and J. D. Schumacher.
  1990. Microzooplankton, vertical mixing and advection in a larval fish patch. J. Plankton Res. 12:365–379.
Kamba, M.
  1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay, Hokkaido. Res. Inst. N. Pac. Fish., Hokkaido Univ., Spec. Vol., p. 175–197.
Kendall, A. W., Jr., and S. Kim.
  1989. Buoyancy of walleye pollock (*Theragra chalcogramma*) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska. *In* R. J. Beamish and G. A. McFarlane (eds.), Effects of ocean variability on recruitment and evaluation of parameters used in stock assessment models, p. 169–180. Can. Spec. Pub. Fish. Aquat. Sci. 108.
Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
  1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska. Fish. Bull. 85:499–521.
Kerfoot, W. C.
  1985. Adaptive value of vertical migration: comments on the predation hypothesis and some alternatives. Contrib. Mar. Sci. 27:91–113.
Lampert, W. H.
  1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. 3:21–27.
Laprise, R., and J. J. Dodson.
  1993. Nature of environmental variability experienced by benthic and pelagic animals in the St. Lawrence Estuary, Canada. Mar. Ecol. Prog. Ser. 94:129–139.
Lenarz, W. H., R. J. Larson, and S. Ralston.
  1991. Depth distributions of late larvae and pelagic juveniles of some fishes of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 32:41–46.
Levy, D. A.
  1990. Reciprocal diel vertical migration behavior in planktivores and zooplankton in British Columbia lakes. Can. J. Fish. Aquat. Sci. 47:1755–1764.
MacKenzie, B. R., W. C. Leggett, and R. H. Peters.
  1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the field? Mar. Ecol. Prog. Ser. 67:209–225.

Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.

 1989.   Laboratory guide to early life history stages of Northeast Pacific fishes.   U.S. Dep. Commer., NOAA Tech. Rep. NMFS 80, 652 p.

Neill, W. E.

 1990.   Induced vertical migration in copepods as a defence against invertebrate predation.   Nature 345:524–526.

Neilson, J. D., and R. I. Perry.

 1990.   Diel vertical migrations of marine fishes: an obligate or facultative process?   Adv. Mar. Biol. 26:115–168.

Ohman, M. D.

 1990.   The demographic benefits of diel vertical migration by zooplankton.   Ecol. Monogr. 60:257–281.

Ohman, M. D., B. W. Frost, and E. B. Cohen.

 1983.   Reverse diel vertical migration: an escape from invertebrate predators.   Science 220:1404–1407.

Olla, B. L., and M. W. Davis.

 1990.   Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions.   Mar. Ecol. Prog. Ser. 63:105–112.

Paul, A. J.

 1983.   Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae

Theragra chalcogramma.   Mar. Ecol. Prog. Ser. 13:175–179.

Pearre, S.

 1979.   Problems in the detection and interpretation of vertical migration.   J. Plankton Res. 1:29–44.

Pritchett, M., and L. Haldorson.

 1989.   Depth distribution and vertical migration of larval walleye pollock (*Theragra chalcogramma*).   *In* Proceedings of the international symposium on the biology and management of walleye pollock, November 14–16, 1988, Anchorage, Alaska, p. 173–183.   Alaska Sea Grant Rep. 89-1, Univ. Alaska, Fairbanks.

Theilacker, G. H.

 1980.   Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation.   Fish. Bull. 78:685–692.

Wiebe, P. D., K. H. Burt, S. H. Boyd, and A. W. Morton.

 1976.   A multiple opening/closing net and environmental sensing system for zooplankton.   J. Mar. Res. 34:313–326.

Yamashita, Y., D. Kitagawa, and T. Aoyama.

 1985.   Diel vertical migration and feeding rhythm of the larvae of the Japanese sand-eel *Ammodytes personatus*.   Bull. Japan. Soc. Sci. Fish. 51:1–5.