

Vertical distribution and migration of fish larvae in a Northeast Pacific bay

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ABSTRACT: Fish larvae were collected at 6 depths in Auke Bay, southeastern Alaska, USA, on 4 days in May and June 1987. On 3 dates samples were collected between 08:00 and 13:00 h, on the other date samples were collected every 4 h during 24 h. Vertical distributions of light, temperature, salinity, chlorophyll and copepod nauplii were also measured. Wind speed data were available from a nearby station. Smelt (*Osmeridae*) larvae, the most abundant larval fish taxon, migrated to the surface at midnight, whereas walleye pollock, flathead sole, rock sole, poacher (*Agonidae*) and northern smooth-tongue moved deeper at dusk. During the day, most fish larvae were concentrated from 5 to 15 m, broadly overlapping the highest abundances of copepod nauplii, although poacher and northern smooth-tongue were consistently deeper (15 to 25 m). Diurnally, smelt larvae were shallow (5 to 10 m), and pycnocline depth accounted for more variability in their mean depth than any other biotic or physical variable. Mean depths of the other 5 most abundant taxa were in the same rank order by depth in all 4 sets of daytime samples, and depth of isotherms below the pycnocline accounted for more variation in their mean depths than did any other variable. The diurnal depth distributions we observed apparently result from temperature preferences among marine larval fishes, with descent at dusk as the most common form of diel vertical migration.

INTRODUCTION

In subarctic marine ecosystems many larval fishes hatch in spring, when increasing zooplankton concentrations and higher water temperatures promote rapid growth and enhance survival (Qasim 1956, Cushing 1975). The spring phytoplankton bloom is associated with the formation of a pycnocline; consequently, fish larvae hatched in spring occupy a habitat with vertically structured physical and biotic conditions. Lasker (1978) proposed that persistent vertical stratification was necessary to develop prey concentrations required for survival of larval northern anchovy. His stable ocean hypothesis has been supported by analyses of inter-annual variation in survival of anchovy larvae (Peterman & Bradford 1987), by observations that haddock larvae from stratified waters are in better condition than those from well-mixed areas (Frank & McRuer 1989) and by indications of enhanced feeding by cod larvae in stratified waters (Tilseth & Ellertsen 1984).

Such results imply that larval fishes are able to locate and remain in depths that have high abundances of prey. Vertical coincidence of fish larvae and their prey has been reported for cod (Ellertsen et al. 1981), walleye pollock (Kamba 1977, Nishiyama et al. 1986), mackerel (de Lafontaine & Gascon 1989) and herring (Fortier & Leggett 1983, Munk et al. 1989). Fish larvae, like many other planktonic organisms, perform diel vertical migrations (reviewed by Neilson & Perry 1990), including nocturnal ascent (Kendall & Naplin 1981, Boehlert et al. 1985), nocturnal descent (Boehlert et al. 1985, Yamashita et al. 1985, Munk et al. 1989, Lyczkowski-Shultz & Steen 1991) and nocturnal diffusion (Kendall et al. 1987, Heath et al. 1988, Leis 1991). Larval fishes are visual predators that typically cease feeding at night when light levels fall below the minimum required for successful feeding (Blaxter 1968, Bagarinao & Hunter 1983). To occupy depths with high prey abundance during the day, larvae performing diel vertical migrations must return to the appropriate depth when light levels rise in the morning.

The foraging environment available to larval fishes may influence their growth and survival, and their vertical distributions will, to a large extent, determine the prey concentrations they encounter during diurnal feeding periods. As part of a study on subarctic pelagic production we examined the vertical distribution of larval fishes relative to their prey and other biotic and physical variables. Our objectives were to document depth distributions of fish larvae during the day as the spring production cycle progressed, to identify patterns of vertical migration and to determine which physical and biotic variables may influence the location of fish larvae in a vertically stratified prey environment.

STUDY AREA

These studies were part of the APPRISE (Association of Primary Production and Recruitment in a Subarctic Ecosystem) project, a 5 yr study conducted in Auke Bay (58° 22' N, 134° 40' W), southeast Alaska, USA (Fig. 1). Auke Bay is about 16 km² and varies in depth from 40 to 60 m. Until sometime in April, Auke Bay is cold (<5°C), relatively saline (29 to 32 ppt) and isopycnal (Bruce et al. 1977, Ziemann et al. 1990). In April the water column stratifies, warms and freshens. By June the pycnocline is typically less than 10 m deep and surface water may be above 10°C and have salinity below 20 ppt (Bruce et al. 1977, Ziemann et al. 1990).

In Auke Bay the spring production cycle is initiated in early April by a phytoplankton bloom that peaks in

late April or early May (Williamson 1978, Ziemann et al. 1991). This is followed in May by a large increase in herbivorous copepods (Coyle et al. 1990), especially *Pseudocalanus* spp. (Paul et al. 1990a) and copepod nauplii (Paul et al. 1991). Copepod nauplii display considerable interannual variability in abundance, and are usually concentrated in the upper 15 m (Paul et al. 1991).

In Auke Bay the larvae of many fish species hatched about the time zooplankton abundance was increasing, although several species, notably Pacific sand-lance *Ammodytes hexapterus* and rock sole *Pleuronectes bilineatus*, consistently occurred before the peak in phytoplankton production (Haldorson et al. 1993). Walleye pollock *Theragra chalcogramma*, flathead sole *Hippoglossoides elassodon* and smelt (Osmeridae) larvae were the most abundant taxa that hatched in synchrony with the spring zooplankton increase (Haldorson et al. 1993). Copepod nauplii in the size range 150 to 350 µm were the primary prey of larval walleye pollock and flathead sole in the first month after hatching (Haldorson et al. 1989), so the abundance of nauplii of that size is reported herein.

MATERIALS AND METHODS

Larval fishes. Vertical distributions of fish larvae were determined from depth-specific horizontal tows of an opening-closing 1 m² NIO (Tucker) trawl with 505 µm mesh. The net is designed to have an effective mouth area of 1 m² when towed at 1.5 to 2.0 knots. Daytime distributions were estimated from depth series collected between 08:00 and 13:00 h on 8 May, 15 May and 6 June 1987. Vertical migration was documented from depth series collected every 4 h for 24 h beginning at 08:00 h on 22 May 1987. Times in the following sections identify the start of a 4 h period of sampling. Each depth series consisted of 3 replicate samples at 0, 5, 10, 15, 20 and 30 m. Depth was controlled by measuring wire angle and adjusting cable length. The net was opened for 3 min to collect each replicate, unless rapidly changing wire angle indicated excessive clogging, in which case the net was closed early. Towing speed was about 1.5 knots. A flow meter in the net mouth was used to estimate volume filtered for each replicate. All samples were fixed immediately in 5% seawater-buffered formalin.

All fish larvae were removed from each replicate and enumerated by species or family. Identification below the family level was not used for Osmeridae, Agonidae,

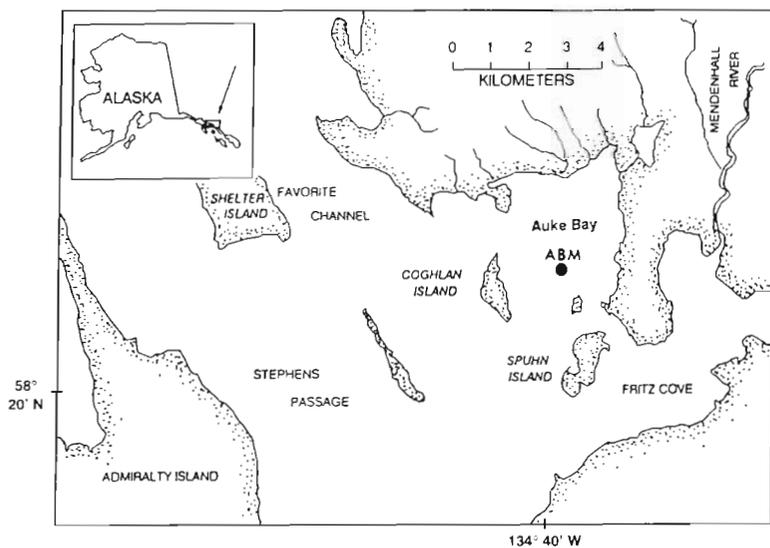


Fig. 1. Study area, Auke Bay, southeast Alaska. Samples were collected at the station designated ABM

Cottidae and Cyclopteridae, as reliable keys or identification guides were not available for those species. The mean volume of water filtered per tow in the diel migration study was 155 m³. Therefore, abundance of larvae per tow was calculated as number per 100 m³ in order to standardize numbers in the same approximate range as the actual numbers in the samples (Barnett et al. 1984).

Physical and biotic measurement. Temperature and salinity profiles were determined from 40 m to the surface on the day preceding the date larval fish were sampled, with the exception of the first date when they were measured on 4 May. Measurements were taken with a CTD (Conductivity, Temperature, Depth) meter with built-in memory (Applied Microsystems, Inc.).

Light levels at depth were estimated based on measurements of extinction coefficients on the day preceding larval fish sampling, and on incident light at the surface on the day fish samples were collected. Extinction coefficients were determined by measuring light at depth every 2 m from the surface to 10 m with a profiling quantum scalar irradiance meter (Biophysical Instruments, Inc., Model QSP-200). Surface incident light was measured with an integrating quantum scalar irradiance meter (Biophysical Instruments, Inc., Model QSP-250) averaged every 15 min with an averaging data logger. Our estimates of incident light levels are the mean of the 15 min averaged values for the period from 06:00 to 12:00 h on the day fish larvae were sampled.

Chlorophyll concentrations were measured on the day preceding larval fish sampling. Water samples were collected at depths of 0, 2, 4, 6, 8, 10, 15, 20, 25, 30 and 35 m with a 5 l Niskin bottle. Chlorophyll concentrations were determined with the fluorometric method for acetone-extracted samples (Strickland & Parsons 1972).

Microzooplankton samples were collected at 0, 5, 10, 15, 20 and 30 m depths with a 30 l Niskin bottle on the day preceding larval fish sampling. Water from the bottle was passed through a 64 µm mesh sieve and the concentrated samples were preserved in buffered formalin. Copepod nauplii were measured and counted in length categories of < 150, 150 to 350 and > 350 µm.

Data analyses. The null hypothesis that larvae were evenly distributed over depth in each horizontal sample series was tested with the Kruskal-Wallis nonparametric test or with ANOVA on log(x+1)-transformed data. ANOVA was used for the most abundant taxa; however, we used the Kruskal-Wallis test for others because the frequent occurrence of zero values violates assumptions of normality in a way that is not corrected by transformation (Barnett et al. 1984). Data are reported as means with standard errors for consistency within tables. If results of ANOVA were

significant ($p < 0.05$), we used Scheffé's *a posteriori* contrast tests, corrected for multiple pairwise tests, to identify the pattern of aggregation, based on groupings of depths with no significant differences among group members. If a given depth could be assigned to either of 2 groups (i.e. did not differ significantly from the depths in either group) it was included in the group with which it had the lowest average *F*-values.

To test the null hypothesis that time of day had no effect on vertical distributions of fish larvae, we used the heterogeneity chi-square test (McCleave et al. 1987). If this test was significant, we examined the standardized residuals for each time period to identify those depths that were responsible for most of the heterogeneity among times.

The mean depth of larvae in each sample series was calculated as the center of density:

$$Z = \sum_{i=1}^n P_i Z_i$$

where Z_i is the depth of the i th sample and P_i is the proportion of larvae at depth i (Fortier & Leggett 1983). We examined the relationship between physical and biotic variables and the distribution of fish larvae on the 4 sample dates with simple linear regression, with mean depth of larvae as the dependent variable. The independent variables were depth of the chlorophyll maximum, mean depth of copepod nauplii (150 to 350 µm), depth of the pycnocline, depth of the 5 and 6°C isotherms, depth of the 1×10^{15} quanta cm⁻² s⁻¹ irradiance level and wind speed.

RESULTS

Physical conditions

In southeast Alaska, 1987 was a year of unusually stormy, cloudy weather (Ziemann et al. 1991); consequently, in early May the pycnocline was poorly developed with a weak temperature and salinity discontinuity near 15 m (Fig. 2). During May the surface layer actually cooled, as the 6°C isotherm rose from 15 m during the first week of May to 5 m in the third week (Fig. 3). However, by early June surface warming had occurred and a relatively strong pycnocline was at 5 to 10 m and temperature isotherms turned sharply deeper.

Day length was increasing during the sampling period. Sunrise and sunset (Pacific daylight time) were at 05:48 h and 22:03 h on 8 May and at 04:58 h and 22:56 h on 5 June. On the days larval fish were sampled there was considerable variability in light at the surface due to weather patterns over southeast Alaska. On 8, 15 & 22 May and 5 June the average

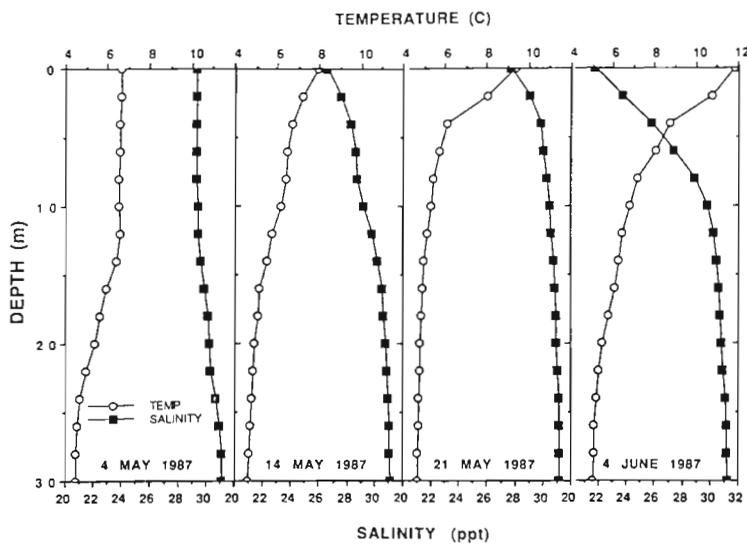


Fig. 2. Temperature and salinity depth-profiles at Stn ABM in Auke Bay, Alaska on 4 dates in 1987

incident light for the period from 06:00 to 12:00 h was 47.9, 101.4, 40.7 and 27.8 ($\times 10^{15}$ quanta $\text{cm}^{-2} \text{s}^{-1}$). Extinction coefficients on 7, 14 & 21 May and 4 June were 0.73, 0.49, 0.44 and 0.39; consequently, highest light levels at all depths occurred on 15 May, while the lowest levels were in the preceding week (Table 1).

To assess effects of the physical environment on depth distributions of larval fishes, we used depth of the pycnocline determined from Fig. 2, depth of the 5 and 6°C isotherms, and the depth of the 1×10^{15} quanta $\text{cm}^{-2} \text{s}^{-1}$ isolume. The 2 isotherms and the isolume values were selected because they occurred in approximately the same depth range as the mean depths of larval

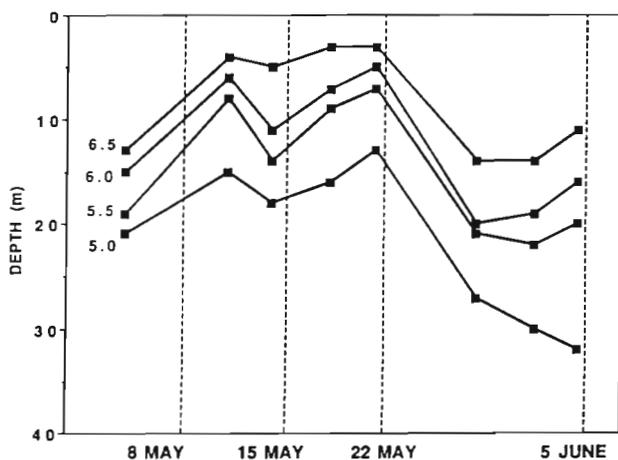


Fig. 3. Depth of isotherms in Auke Bay over the sampling period. Dates when larval fishes were sampled are indicated

fishes. Below the pycnocline water temperatures gradually decreased from over 6°C to just above 4°C (Figs. 2 & 3). The 2 isotherms were chosen to represent the temperature structure of the water column below the pycnocline. We also used the mean wind speed for the date larval fishes were sampled, as recorded in NOAA weather records at the Juneau airport about 4 km east of Auke Bay (Table 2).

Biotic conditions

The spring production cycle was in a state of transition during the month of this study. The initial sampling of vertical distributions occurred at the end of the phytoplankton bloom, while the last 2 sampling dates were during the annual increase in herbivorous copepods (Fig. 4). Chlorophyll was typically at highest concentration in the upper 10 m, with a chlorophyll maximum of over 20 mg m^{-3} on all but the last sampling date (Fig. 5). The mean depth of nauplii (150 to 350 μm lengths) occurred from 5 to 10 m. On the last 2 sampling dates there were relatively few nauplii available, as maximum densities were below 20 ind. l^{-1} (Fig. 5).

We used depth of the chlorophyll maximum and mean depth of copepod nauplii to study effects of biotic variables on depth distributions of larval fishes (Table 2).

Vertical migration: 22 to 23 May

Larval fishes most abundant in the 24 h vertical migration study were osmerids, walleye pollock, agonids, northern smoothtongue, flathead sole and rock sole. Other species were at densities too low for us to assess their patterns of vertical migration.

Table 1. Amounts of light (units = 10^{15} quanta $\text{cm}^{-2} \text{s}^{-1}$) at depths of 0, 5, 10 and 15 m in Auke Bay on 8, 15, 22 May and 5 June 1987, calculated from the average incident light from 06:00 to 12:00 h on those dates (the light at depth 0 in the table), and extinction coefficients (k) measured on the preceding day

Depth (m)	Light			
	8 May	15 May	22 May	5 June
0	47.9	101.4	40.7	27.8
5	1.24	8.75	4.51	3.95
10	0.03	0.76	0.50	0.56
15	0.001	0.065	0.055	0.080

Table 2. Depth (m) distributions of physical and biotic variables measured in Auke Bay, Alaska, on 4 dates from 4 May to 5 June 1987, and used as independent variables in linear regression analyses with mean depth of larval fishes as the dependent variable

Variable	4-7 May	14 May	21 May	5 June
Pycnocline	15	10	5	8
6°C isotherm	15	11	5	16
5°C isotherm	21	18	13	32
Light (1×10^{15} quanta $\text{cm}^{-2} \text{s}^{-1}$)	5	9	8	8
Wind speed (miles h^{-1})	4.8	11.2	6.2	8.1
Phytoplankton (maximum)	3	10	10	5
Nauplii (mean depth)	6.8	10.8	10.0	10.5

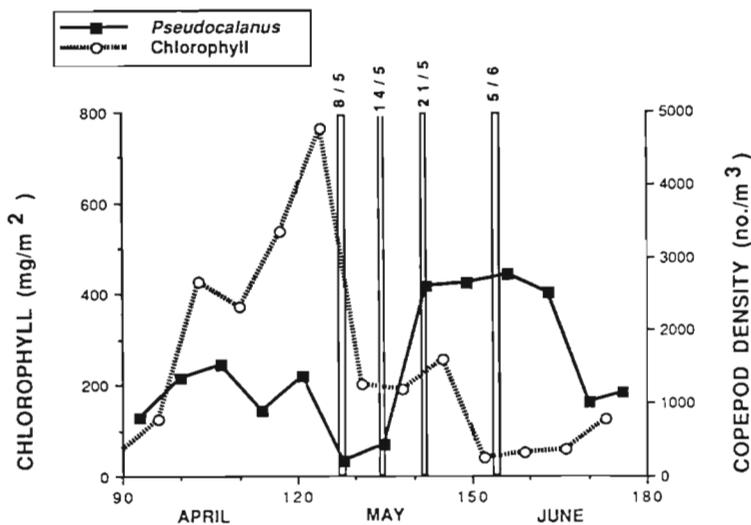


Fig. 4. Densities of chlorophyll and *Pseudocalanus* spp. copepods during spring 1987 (data from Coyle & Paul 1990, Ziemann et al. 1990), with marks on the dates larval fishes were sampled for vertical distribution studies

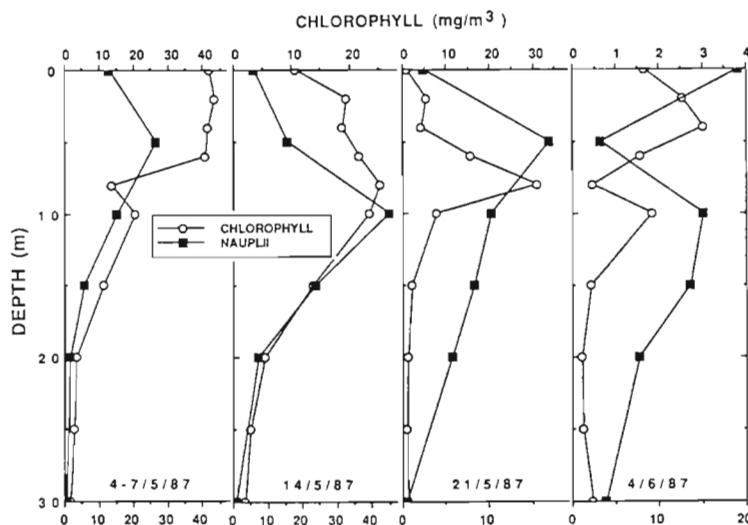


Fig. 5. Vertical distributions of chlorophyll and copepod nauplii (150 to 350 μm lengths) in Auke Bay prior to collection of larval fish samples

Smelt (*Osmeridae*)

Osmerids were the most abundant fish larvae in the vertical migration study. All time periods had significant differences among depths ($p < 0.001$). Larvae were concentrated at 5 m during the day and at the surface at midnight (Fig. 6A), whereas in the other time periods they were apparently more diffuse, as their abundances tended to be homogeneous through mid-depths (Table 3). There was a significant difference among the 6 time periods, due largely to concentration at the surface at midnight (24:00 h).

Walleye pollock *Theragra chalcogramma*

During the brightest daylight hours (08:00 to 16:00 h) walleye pollock larvae were found in highest numbers at 5 to 10 m depths (Fig. 6B). In the evening they descended and remained relatively deep through the night, with highest numbers at 15 to 20 m during the 20:00 and 24:00 h periods. By early morning (04:00 h) they had ascended to typical daytime depths of 5 to 15 m. Differences among depths were significant at all times, with surface and deeper strata forming homogenous groupings in most of the time periods (Table 3). At 20:00 h all depths formed a homogeneous set (based on a *posteriori* Scheffé tests), even though ANOVA found a significant difference among depths. This occurred because of the relatively low power of the *a posteriori* test.

Among time periods there was a highly significant difference in depth distribution, mainly because of higher than expected numbers at 5 or 10 m depths at 08:00, 12:00, 16:00 and 04:00 h, and at 15 to 20 m at 20:00 and 24:00 h.

Flathead sole *Hippoglossoides elassodon*

During the day flathead sole were concentrated at 5 m (Fig. 6C). At twilight they appear to descend somewhat, but still had peak concentrations at 5 to 10 m. This distribution apparently continues through the night, although at midnight there were relatively high numbers at the surface. Differences among depths were nonsignificant only at 20:00 h ($p = 0.07$), and margin-

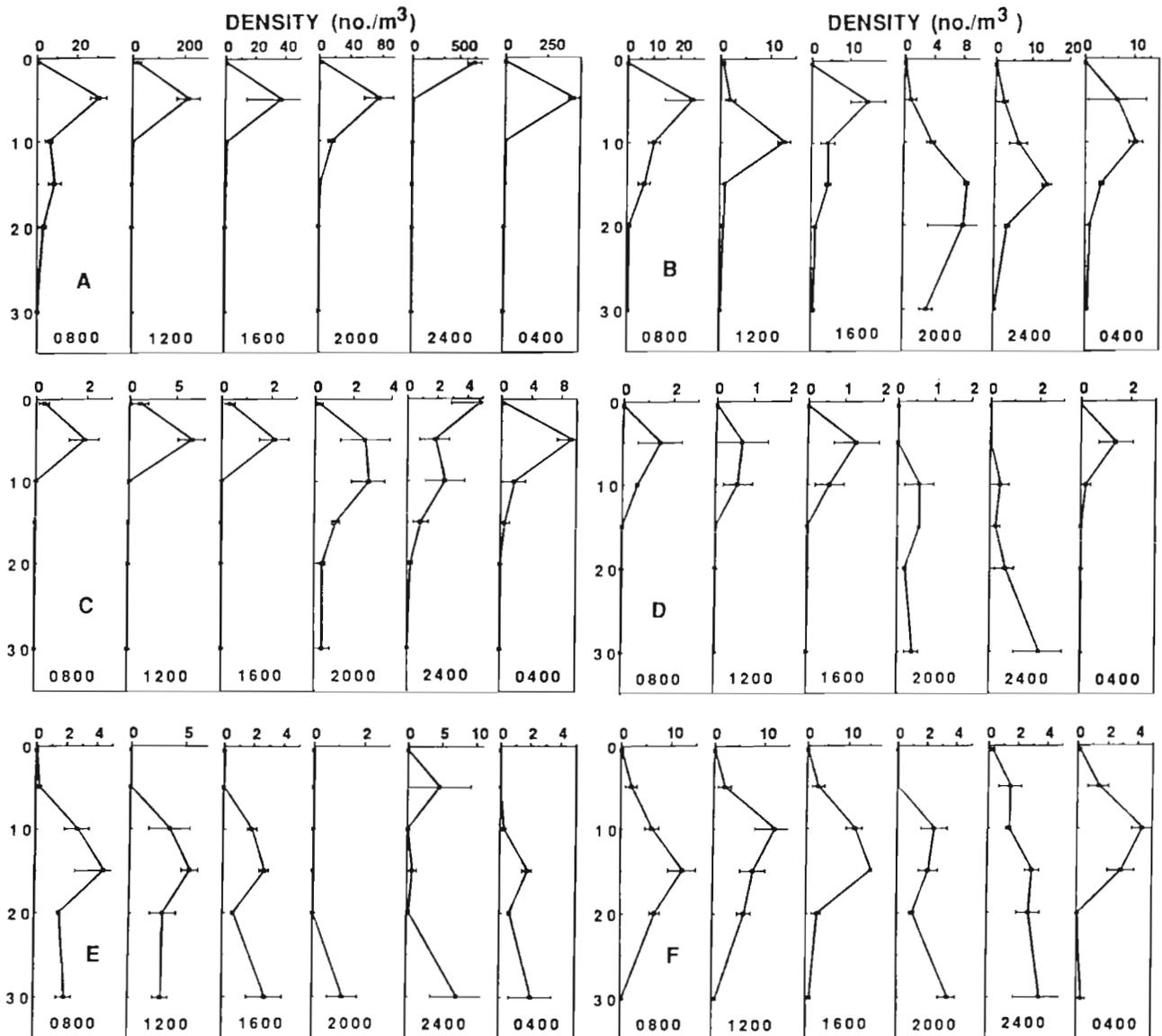


Fig. 6. Vertical abundance profiles of larval fishes in 6 time intervals beginning at 08:00 h on 22 May 1987 and ending at 08:00 h on 23 May 1987. Data points are the mean of 3 replicates, error bars are 1 SE. Species: A, osmerids; B, walleye pollock; C, flathead sole; D, rock sole; E, northern smoothtongue; F, agonids

ally significant at 24:00 h ($p = 0.046$). At 24:00 h all depths were homogeneous in the paired *a posteriori* Scheffé tests (Table 3).

There was a highly significant difference in depth distribution among the 6 time periods, due to high numbers at 5 m at 08:00, 12:00, 16:00 and 04:00 h, and occurrence of larvae at the surface at 24:00 h.

Rock sole *Pleuronectes bilineatus*

By mid-May, rock sole were at relatively low density. During daylight they occurred mainly at 5 to

10 m, with highest numbers consistently at 5 m (Fig. 6D). At twilight (20:00 h) they were deeper, and by midnight were concentrated at 30 m. By early morning they were again found mainly at 5 m. Differences among depths were significant only at 04:00 and 08:00 h, however even at those times all of the depths were homogeneous in *a posteriori* testing (Table 3).

There was a significant difference in depth distribution among time periods, principally because of relatively high numbers at 30 m at 24:00 h, and at 5 to 10 m at 08:00, 12:00, 16:00 and 04:00 h.

Table 3. Groupings of homogeneous depths in diel depth studies conducted on 22 to 23 May 1987 in Auke Bay, Alaska, for 6 species of larval fishes, as determined by Scheffé's *a posteriori* *F*-tests on log(*x*+1)-transformed data. All: no significantly different pairs among all of the pairwise comparisons. *No significant difference among depths at that time when tested by ANOVA

	Time (h)					
	08:00	12:00	16:00	20:00	24:00	04:00
Osmerid	0,20,30 5,10,15	5 0,10,15,20,30	5 0,10,15,20,30	0 5 10 15,20,30	5 0,10,15,20,30	0,20,30 5 10,15
Walleye pollock	0,20,30 5,10,15	10 0,5,15,20,30	5 0,10,15,20,30	All	0,5,20,30 10,15	10 0,5,15,20,30
Flathead sole	5 0,10,15,20,30	5 0,10,15,20,30	5 0,10,15,20,30	All *	All *	5 0,10,15,20,30
Rock sole	All *	All	All	All	All	All *
Agonid	0,5,30 10,15,20	0,5,30 10,15,20	0,5,20,30 10,15	0,5 10,15,20,30	All *	0,5,20,30 10,15
Northern smoothtongue	0,5 10,15,20,30	0,5 10,15,20,30	0,5,20 10,15,30	0,5,10,15,20 30	All *	All

Poachers (Agonidae)

Poachers were distributed somewhat deeper than most other species, with peak daytime abundances from 10 to 20 m (Fig. 6F). At twilight they descended, as their highest numbers in the 20:00 and 24:00 h periods were at 30 m. By early morning (04:00 h) they had reoccupied daytime depths of 5 to 15 m. Differences among depths were significant at all times except 24:00 h (*p* = 0.15). Mid-depth strata (5 to 15 m) tended to form homogeneous groupings in *a posteriori* tests (Table 3).

There was a significant difference among depth distributions in the 6 time periods, due mainly to deeper distributions in the darkest periods (20:00, 24:00 h).

Northern smoothtongue *Leuroglossus schmidti*

Larvae of this deep-sea smelt species (Bathylagidae) displayed vertical migration similar to poachers, with daytime densities highest from 10 to 20 m, although even during the day there were relatively high numbers at 30 m (Fig. 6E). At twilight (20:00 h) these larvae apparently descended, as they were found only at 30 m. At 24:00 h there were notable numbers at 5 m, and by 04:00 h they were commonly occurring above 30 m. Differences among depths were significant in all time periods except 24:00 h. During the day depths below 10 m tended to form a homogenous group (Table 3). Difference in depth distribution among the 6

time periods was significant, with most of the variability due to deeper distribution at night.

During daylight hours mean depth of the above taxa ranged from 15 to 20 m for northern smoothtongue to about 5 m for osmerids and flathead sole (Fig. 7). The 6 taxa remained in approximately the same rank order by depth throughout the 24 h period. Osmerids rose to the surface at midnight, whereas the other 5 taxa moved deeper around sunset (20:00 h), followed by ascent back

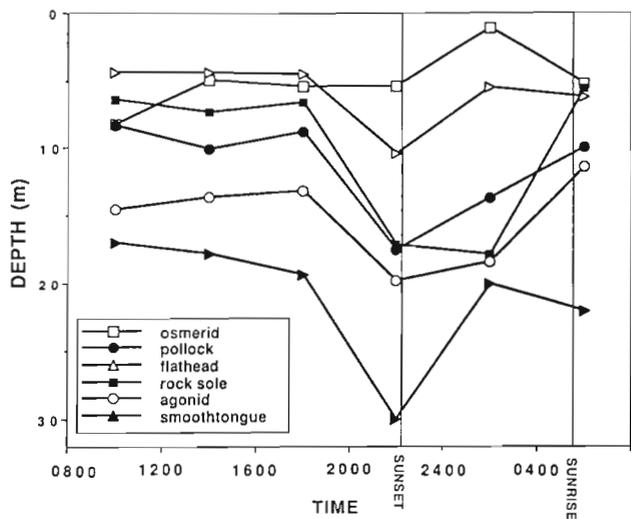


Fig. 7. Mean depths of the 6 most abundant taxa in Auke Bay in 6 sampling periods from 08:00 h on 22 May 1987 through 08:00 h on 23 May 1987. Sunset and sunrise are indicated with vertical lines

Table 4. Mean densities, in numbers per 100 m³, of fish larvae by depth, with standard errors (in parentheses) and results of statistical tests for differences among depths for samples collected on 8 May 1987. Underlined probabilities resulted from ANOVA on log(x+1)-transformed data, others are from Kruskal-Wallis nonparametric tests

Taxa	Depth (m)						P
	0	5	10	15	20	30	
Smelt (Osmeridae)	1.8 (0.4)	14.3 (4.0)	1.0 (0.7)	0.6 (0.4)	0 (0)	0 (0)	<u><0.001</u>
Walleye pollock <i>Theragra chalcogramma</i>	0.1 (0.1)	2.4 (0.7)	7.8 (1.2)	8.4 (1.3)	1.1 (1.1)	0.1 (0.1)	<u><0.001</u>
Poacher (Agonidae)	0 (0)	0.4 (0.2)	1.6 (0.9)	5.4 (1.1)	1.1 (0.6)	0.3 (0.3)	<u>0.004</u>
Slender cockscomb <i>Anoplarchus insignis</i>	1.2 (0.7)	1.3 (0.7)	0 (0)	0 (0)	0 (0)	0 (0)	0.006
Northern ronquil <i>Ronquilus jordani</i>	1.3 (0.4)	0 (0)	0 (0)	0.2 (0.2)	0 (0)	0 (0)	0.013
Sandlance <i>Ammodytes hexapterus</i>	0.6 (0.4)	0.4 (0.2)	0.3 (0.3)	0 (0)	0.1 (0.1)	0 (0)	0.362
Northern smoothtongue <i>Leuroglossus schmidti</i>	0.1 (0.1)	0 (0)	2.8 (1.1)	2.4 (1.1)	0.9 (0.1)	1.6 (0.2)	<u>0.003</u>
Rock sole <i>Pleuronectes bilineatus</i>	0 (0)	0.8 (0.6)	1.0 (0.7)	0.1 (0.4)	0.3 (0.1)	0 (0)	0.263
Flathead sole <i>Hippoglossoides elassodon</i>	0 (0)	1.1 (0.6)	0 (0)	0 (0)	0 (0)	0 (0)	0.060
Starry flounder <i>Platichthys stellatus</i>	1.0 (0.3)	0.6 (0.6)	0 (0)	0 (0)	0 (0)	0 (0)	0.344
Sand sole <i>Psettichthys melanostictus</i>	0 (0)	0.4 (0.4)	0 (0)	0 (0)	0 (0)	0 (0)	0.416
Sculpins (Cottidae) > 5 species	0.5 (0.5)	6.2 (0.4)	4.8 (0.6)	3.2 (0.8)	0.8 (0.6)	0 (0)	0.009
Snailfishes (Cyclopteridae)	0 (0)	0 (0)	0 (0)	0.6 (0.4)	0.3 (0.1)	0 (0)	0.084

to daytime depths either during the night or in the early morning. By sunrise the distribution of mean depths was very similar to the distribution at the start of the 24 h sampling in the preceding morning (Fig. 7).

Daytime depth distribution of fish larvae

8 May

On 8 May most fish larvae were located at 5 to 15 m (Table 4). Walleye pollock were the most abundant larvae collected, followed by osmerids and cottids. Osmerids were the only larvae concentrated in depths less than 10 m. Walleye pollock, agonids, and northern smoothtongue were concentrated at 10 to 15 m. Northern smoothtongue was notable in having the deepest distribution, with relatively high numbers at 30 m. Samples from 30 m contained few other species.

15 May

By mid-May osmerids were increasing in number, and were the most abundant taxon. Other species present in relatively high numbers were walleye pollock, flathead sole and agonids, all of which were more abundant than in the preceding week (Table 5). Osmerids and flathead sole were concentrated in relatively shallow water (0 to 10 m depth), walleye pollock somewhat deeper (10 to 15 m) and agonids deeper yet (15 to 20 m).

22 May

We used data from the 08:00 h time period to describe diurnal vertical distributions on 22 May, as this coincided with the times that collections were made on the other 3 dates. Descriptions of depth distributions at

Table 5. Mean densities, in numbers per 100 m³, of fish larvae by depth, with standard errors (in parentheses) and results of statistical tests for samples collected on 15 May 1987. Underlined probabilities resulted from ANOVA on log(x+1)-transformed data, others are from Kruskal-Wallis nonparametric tests

Taxa	Depth (m)						p
	0	5	10	15	20	30	
Smelt (Osmeridae)	53.8 (53.8)	224.3 (22.0)	145.8 (4.5)	3.6 (1.3)	0 (0)	0.2 (0.2)	<u><0.001</u>
Pacific herring <i>Clupea pallasii</i>	0.2 (0.2)	0.4 (0.2)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0.015
Walleye pollock <i>Theragra chalcogramma</i>	2.6 (2.6)	9.9 (1.9)	15.5 (2.1)	11.6 (2.3)	0.8 (0.2)	0 (0)	<u><0.001</u>
Poacher (Agonidae)	0 (0)	0 (0)	1.8 (0.3)	18.7 (7.1)	7.9 (1.1)	0 (0)	<u><0.001</u>
Slender cockscomb <i>Anoplarchus insignis</i>	0.8 (0.8)	2.3 (0.9)	1.3 (0.3)	0 (0)	0 (0)	0 (0)	0.024
Longsnout prickleback <i>Lumpenella longirostris</i>	0 (0)	0 (0)	0.8 (0.5)	1.9 (1.3)	0.8 (0.2)	0 (0)	0.028
Snake prickleback <i>Lumpenus sagitta</i>	0 (0)	0 (0)	0 (0)	0.6 (0.6)	0.8 (0.2)	0 (0)	0.034
Sandlance <i>Ammodytes hexapterus</i>	0.5 (0.5)	3.6 (0.8)	0.5 (0.2)	0 (0)	0 (0)	0 (0)	0.024
Northern smoothtongue <i>Leuroglossus schmidti</i>	0 (0)	0 (0)	0.3 (0.3)	3.0 (0.2)	1.7 (1.0)	0.2 (0.2)	<u><0.001</u>
Rock sole <i>Pleuronectes bilineatus</i>	0.7 (0.7)	1.5 (0.6)	2.1 (0.2)	1.1 (0.2)	0 (0)	0 (0)	<u>0.005</u>
Flathead sole <i>Hippoglossoides elassodon</i>	2.3 (2.3)	11.6 (1.3)	9.3 (2.7)	0.2 (0.2)	0 (0)	0 (0)	<u><0.001</u>
Starry flounder <i>Platichthys stellatus</i>	0.2 (0.2)	0.6 (0)	0.3 (0.3)	0.4 (0.4)	0 (0)	0 (0)	0.186
Sand sole <i>Psettichthys melanostictus</i>	0 (0)	1.7 (0.9)	2.3 (0.4)	0 (0)	0 (0)	0 (0)	0.022
Sculpins (Cottidae)	0.5 (0.5)	4.1 (1.2)	5.7 (1.6)	8.2 (0.6)	1.7 (0.8)	0 (0)	0.014
Snailfishes (Cyclopteridae)	0 (0)	0.2 (0.2)	1.8 (0.2)	1.1 (0.2)	0.4 (0.4)	0 (0)	0.015

this time are included in the preceding section on vertical migration, and summarized in Fig. 6.

5 June

In early June osmerids were at their seasonal peak, with very high relative abundance. Walleye pollock and flathead sole were also at their maximum, as were sand sole *Psettichthys melanostictus* and cottids (Table 6). Osmerid peak numbers were still found at 5 m. Walleye pollock depth distribution was very similar to that in May, with highest abundance from 5 to 15 m. Flathead sole were again concentrated at 5 m, as were sand sole and herring *Clupea harengus*.

Agonids and northern smoothtongue were at 20 to 30 m.

The mean depth of osmerid larvae (the only taxon that ascended at night) was deeper on each successive sampling date (Fig. 8). Among the 6 physical and biotic variables, pycnocline depth had the highest coefficient of determination in the series of linear regressions (Table 7).

Mean depths of the next 5 most abundant taxa (walleye pollock, flathead sole, rock sole, agonids and northern smoothtongue, all of which descended at dusk) were in the same rank order in all 4 of the weekly day-time samples (Fig. 8). This pattern is highly significant, as the probability of observing the same rank order 4 consecutive times among 5 randomly assorting variables is extremely small ($p < 0.00001$). The most pro-

Table 6. Mean densities, in numbers per 100 m³, of fish larvae by depth, with standard errors (in parentheses) and results of statistical tests for samples collected on 5 June 1987. Underlined probabilities resulted from ANOVA on log(x+1)-transformed data, others are from Kruskal-Wallis nonparametric tests

Taxa	Depth (m)						P
	0	5	10	15	20	30	
Smelt (Osmeridae)	2.1 (1.4)	519.2 (43.2)	353.2 (45.0)	167.70 (18.4)	207.8 (9.2)	5.8 (3.7)	<u><0.001</u>
Pacific herring <i>Clupea pallasii</i>	1.0 (0.8)	24.9 (8.1)	12.9 (0.8)	3.4 (1.7)	0 (0)	0 (0)	0.020
Walleye pollock <i>Theragra chalcogramma</i>	0 (0)	20.6 (2.7)	27.5 (4.5)	20.8 (1.5)	13.7 (3.5)	0.8 (0.5)	<u><0.001</u>
Poacher (Agonidae)	0 (0)	0.6 (0.3)	0.2 (0.2)	0.6 (0.3)	2.7 (0.1)	2.6 (0.2)	<u><0.001</u>
Northern ronquil <i>Ronquilus jordani</i>	0 (0)	4.1 (1.2)	2.7 (0.5)	0.9 (0.6)	0.4 (0.4)	0 (0)	0.014
Northern smoothtongue <i>Leuroglossus schmidti</i>	0 (0)	0 (0)	0 (0)	0 (0)	1.4 (0.8)	1.7 (0.3)	0.022
Rock sole <i>Pleuronectes bilineatus</i>	0 (0)	1.3 (0.6)	1.7 (0.4)	0.2 (0.2)	0.2 (0.2)	0 (0)	<u>0.193</u>
Flathead sole <i>Hippoglossoides elassodon</i>	0.1 (0.1)	64.2 (3.7)	47.7 (8.9)	10.0 (4.6)	2.1 (0.7)	0 (0)	<u><0.001</u>
Starry flounder <i>Platichthys stellatus</i>	0 (0)	1.9 (1.3)	0.2 (0.2)	0 (0)	0 (0)	0 (0)	0.164
Sand sole <i>Psettichthys melanostictus</i>	0 (0)	9.9 (3.9)	5.3 (2.2)	0.4 (0.5)	0.2 (0.2)	0 (0)	0.014
Sculpins (Cottidae)	0 (0)	21.9 (4.9)	4.6 (0.7)	0.6 (0.6)	0 (0)	0 (0)	0.008
Snailfishes (Cyclopteridae)	0 (0)	0.2 (0.2)	0.4 (0.4)	0.2 (0.2)	0.7 (0)	0 (0)	0.098

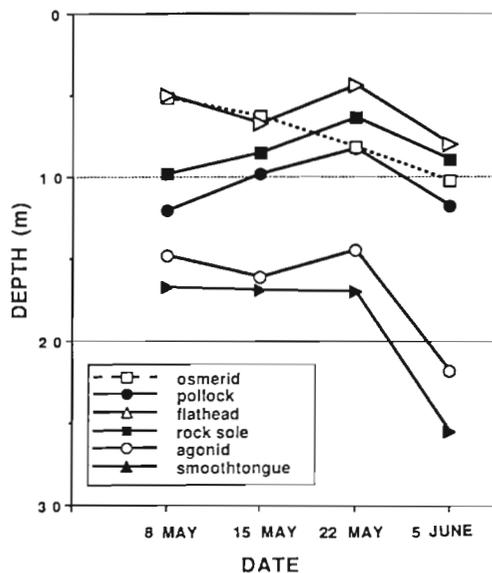


Fig. 8. Mean depths of the 6 most abundant taxa in Auke Bay during the day on 8, 15, 22 May and 5 June 1987

nounced shift in depth among these 5 taxa occurred in the last period (June 5), when their mean depth increased. Among the suite of environmental variables, linear regression with the depth of the 6 or 5 °C isotherm produced the highest coefficient of determination in all 5 taxa (Table 7). The colder of the 2 isotherms accounted for more of the variability in depth of the 2 taxa with the deepest distributions (agonids and northern smoothtongue) than did any other variable.

DISCUSSION

We observed 2 types of vertical migration. Only 1 taxon, osmerids, ascended at night. This pattern has been most frequently reported for larval fishes (Neilson & Perry 1990). Osmerids include species that are freshwater, anadromous and marine. In Auke Bay, osmerids apparently occur predominantly in the mixed layer, rising to the surface at night and returning to relatively shallow depths during the day. Consequently, they occupy the warmest and freshest part of

Table 7. Values of r^2 from simple regression models with mean depth of 6 larval fish taxa on 8, 15, 22 May and 5 June as the dependent variable and the depth of 6 environmental variables in Table 2 as the independent variable. Environmental variables: PYCNO, pycnocline; TEMP, 6 and 5°C isotherms; LIGHT, depth of the isolume; WIND, wind speed; PHYTO, depth of the phytoplankton maximum; COPE, mean depth of copepod nauplii. The highest value for each taxon is underlined

	PYCNO	TEMP		LIGHT	WIND	PHYTO	COPE
		6°C	5°C				
Osmerid	<u>0.53</u>	<0.01	0.28	0.27	0.02	0.01	0.39
Walleye pollock	0.53	<u>0.95</u>	0.62	0.33	0.05	0.86	0.26
Flathead sole	<0.01	<u>0.40</u>	<u>0.68</u>	0.21	0.40	0.02	0.28
Rock sole	0.75	<u>0.89</u>	0.41	0.28	<0.01	0.65	0.25
Agonid	0.04	0.36	<u>0.84</u>	0.11	0.10	0.09	0.20
Northern smoothtongue	0.07	0.30	<u>0.81</u>	0.06	0.02	0.12	0.14

the water column (the mixed layer). Other osmerids have vertical migration patterns that are consistent with these observations. In the St. Lawrence estuary, Canada, rainbow smelt *Osmerus mordax* use tidal vertical migration to move upstream into warmer, fresher water (Laprise & Dodson 1989), while capelin *Mallotus villosus* migrated vertically within the surface layer (Fortier & Leggett 1983).

Descent at dusk was the most common form of vertical migration among larval fishes in Auke Bay. Species that descended at dusk included walleye pollock, flathead sole, rock sole, agonids and northern smoothtongue. Deeper depth distributions at night have been reported for larval fishes (Neilson & Perry 1990) including sandlance (Yamashita et al. 1985), Pacific cod (Boehlert et al. 1985), Atlantic herring (Munk et al. 1989), red drum (Lyczkowski-Shultz & Steen 1991) and gulf menhaden (Sogard et al. 1987); however, it is more common for larval fishes to be nearer the surface at night (Neilson & Perry 1990). Studies in Shelikof Strait of the North Pacific Ocean have found most species of larval fishes to be deeper at night, including rock sole, flathead sole, Pacific sandlance and searchers (Bathymasteridae) (Richard Brodeur, Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA, pers. comm.). In Auke Bay, rock sole was the only species that remained at depth throughout the night. By the 24:00 h sampling period the other taxa that descended at dusk had either returned to, or were intermediate to, typical daytime depths.

Larval fishes may become less aggregated nocturnally (Brewer & Kleppel 1986, Kendall et al. 1987, Heath et al. 1988, Leis 1991). Among the 6 most abundant species in Auke Bay there are indications that nocturnal distributions were more diffuse. Four of the 6 cases where there were no significant differences in abundance among depths occurred at 20:00 and 24:00 h, and 7 of the 12 cases where *a posteriori*

tests found no pairwise differences were also at 20:00 and 24:00 h (Table 3). This trend could have resulted from reduced aggregation or from higher interreplicate variance at night. To determine the cause we compared the coefficient of variation between diurnal (04:00, 08:00, 12:00, 16:00 h) and nocturnal (20:00, 24:00 h) samples, as an increase in the coefficient would be associated with higher interreplicate variance. We found no increase in the coefficient of variation in nocturnal samples, with the exception of northern smoothtongue at 24:00 h, where the average coefficient was unusually high and was almost certainly responsible for the lack of significant difference among depths for that species at 24:00 h. Therefore we conclude that there was a tendency for larvae to become less aggregated nocturnally. This was most pronounced in flathead sole.

The relatively shallow depth distributions of walleye pollock were similar to depths they occupy in Uchiura Bay, Japan (Kamba 1977) and in the Bering Sea (Dagg et al. 1984, Nishiyama et al. 1986). However, in Shelikof Strait, Alaska, they were usually deeper (Kendall et al. 1987). Rock sole and flathead sole had relatively shallow depth distributions in Auke Bay, a pattern observed off Oregon, USA, for rock sole (Boehlert et al. 1985) and in Shelikof Strait for both species (R. Brodeur pers. comm.). Agonids and northern smoothtongue were consistently deeper than most other taxa. Northern smoothtongue are bathylagids, a family with larvae that are found relatively deep off Peru (Sameoto 1982) and Oregon (Boehlert et al. 1985).

Diurnally, larval fishes have often been found concentrated at depths where prey is relatively abundant (e.g. Kamba 1977, Fortier & Leggett 1983, Munk et al. 1989). In Auke Bay, most fish larvae were found at depths with relatively high concentrations of copepod nauplii. Osmerids, walleye pollock, flathead sole and rock sole were consistently aggregated at depths with

high prey abundance, whereas agonids and northern smoothtongue consistently occurred deeper than most copepod nauplii.

Fish larvae may accumulate where prey are concentrated by modifying their behaviour when they find good foraging conditions (Munk & Kiørboe 1985, Batty 1987), or by associating with physical conditions, such as a thermocline, where prey aggregate (Peterson & Ausubel 1984, Frank et al. 1989, Munk et al. 1989). Physical factors that may affect depth of larval fishes include light (Heath et al. 1988, Munk et al. 1989, Olla & Davis 1990), temperature (Ahlstrom 1959, Kendall & Naplin 1981, Olla & Davis 1990) and turbulence (Heath et al. 1988, Olla & Davis 1990).

The persistent rank order of mean daytime depth among the 5 taxa that descended at dusk suggests their depth distributions were determined by the same environmental conditions. Of the variables we measured, temperature was implicated by high coefficients of determination (r^2) in the series of regressions, with depth of the colder of the 2 isotherms accounting for more variation in the deepest-distributed taxa. Fishes, like most poikilotherms, display a preference for ranges of temperatures that are often associated with physiological and growth optima (Brett 1970, Crawshaw 1977, Reynolds & Casterlin 1977). Larval fishes will adjust their depth to avoid unfavorable temperatures (Olla & Davis 1990), and they concentrate at thermoclines (Ahlstrom 1959, Kendall & Naplin 1981, Boehlert et al. 1985, Perry & Neilson 1988). Below the pycnocline temperatures gradually decreased from around 7 to just above 4°C (Figs. 2 & 3). Fishes have the ability to discern small changes of temperature, so it is not unreasonable to suggest that their depth distributions in Auke Bay were a function of temperature preferences.

Although our results suggest that larval fishes select their daytime depths based on temperature preferences, there were indications that light may also have had some effect. Some of the species displayed an increase in depth around midday (e.g. walleye pollock, rock sole); this could result from negative phototaxis at high light levels, as observed in walleye pollock larvae under laboratory conditions (Olla & Davis 1990). Atlantic herring larvae have displayed complex vertical distributional patterns that apparently are a response to multiple and interacting variables including light, turbulence and distribution of prey (Heath et al. 1988, Munk et al. 1989). It is likely that the larvae we observed in Auke Bay also respond to a variety of extrinsic variables, and it would be naive to suggest that they display an absolute response to temperature. For example, in less-protected waters than Auke Bay, turbulence and wind mixing may have important effects on vertical distribution. Also, in areas such as

the Bering Sea, larvae (i.e. walleye pollock) that we observed below the pycnocline are common in the mixed layer. In such systems vertical distribution and migration may differ markedly from patterns we observed in a shallow protected embayment where most larvae were below the mixed layer.

The widespread occurrence of diel vertical migration among fishes and other taxa suggests that there are adaptive advantages associated with this behavior. Possibilities include enhancement of feeding (although for fishes this is most often associated with nocturnal or crepuscular feeding; see review by Neilson & Perry 1990) avoidance of predators (Hunter & Sanchez 1976, Yamashita et al. 1985), metabolic advantages (Wurtsbaugh & Neverman 1988), transport (Fortier & Leggett 1983, Boehlert & Mundy 1988) and retention (Sinclair 1988, Stephenson & Power 1989). Our data do not provide any clear distinction among these possibilities. However, in Auke Bay the diel vertical migrations performed by larval fishes appear to affect 2 important processes. (1) Feeding: larval fishes generally are found at depths with high abundance of copepod nauplii during diurnal feeding periods. (2) Avoidance of predators: fish larvae that descend at dusk appear to minimize their spatial overlap with a suite of micro-nektonic predators that migrate from deep to shallow water at dusk. These predators include euphausiids (Paul et al. 1990b) and small fishes such as juvenile herring, capelin and salmonids (Coyle & Paul 1992).

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