Diel variation in vertical distribution of an offshore ichthyoplankton community off the Oregon coast

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Abstract—We examined the diel vertical distribution, concentration, and community structure of ichthyoplankton from a single station 69 km off the central Oregon coast in the northeast Pacific Ocean. The 74 depth-stratified samples yielded 1571 fish larvae from 20 taxa, representing 11 families, and 128 fish eggs from 11 taxa within nine families. Dominant larval taxa were *Sebastes* spp. (rockfishes), *Stenobrachius leucopsarus* (northern lampfish), *Tarletonbeania crenularis* (blue lanternfish), and *Lyopsetta exilis* (slender sole), and the dominant egg taxa were *Sardinops sagax* (Pacific sardine), *Icichthys lockingtoni* (medusafish), and *Chauliodus macouni* (Pacific viperfish). Larval concentrations generally increased from the surface to 50 m, then decreased with depth. Larval concentrations were higher at night than during the day, and there was evidence of larval diel vertical migration. Depth stratum was the most important factor explaining variability in larval and egg concentrations.

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Early life stages of fishes have long been studied to gain insight into adult spawning locations and biomass (Hunter et al., 1993), trophic interactions between fish larvae and their surrounding zooplankton and piscivore communities (Hunter and Kimbrell, 1980), and the relationship between early life processes and subsequent recruitment success (Bradford, 1992; Houde, 1997). Knowledge of the diel vertical distribution of fish eggs and larvae is critical to understanding the structure and ecological interactions of ichthyoplankton communities, and for the development of appropriate sampling strategies (Gray, 1998). Furthermore, variation in the diel vertical distributions of different larval fish taxa and their associated predator and prey fields may influence the occurrence, degree, and timing of competitive, trophic, and environmental interactions (Neilson and Perry, 1990). In addition, an understanding of the differences in ichthyoplankton depth distribution and concentration is essential for accurate quantitative estimates of whole water-column abundance when the depth to be sampled is limited (Ahlstrom, 1959; Comyns and Lyczkowski-Shultz, 2004). Also, because in many surveys sampling is conducted during both night and day, it is often necessary to separate diel (e.g., visual net avoidance by larvae during daylight conditions) and depth effects when analyzing variable ichthyoplankton distributions (Ahlstrom, 1959; Boehlert et al., 1985).

Larvae of many fish species are known to perform diel vertical migrations (Ahlstrom, 1959; Neilson and Perry, 1990). These migrations can follow several different patterns; the most common is movement into the upper water column during night and into deeper water during the day (Shoji et al., 1999; Tsukamoto et al., 2001). However, the reverse pattern has also been observed (Lyczkowski-Shultz and Steen, 1991; Brodeur and Rugen, 1994). In addition, some fish larvae have been found to disperse during the night and aggregate during the day (Brewer and Kleppel, 1986; Munk et al., 1989).

In the present study the diel variation in vertical distributions and concentrations of fish eggs and larvae was examined by repeatedly sampling fish eggs and larvae from a single offshore station off the central Oregon coast in the northeast Pacific Ocean. We used univariate and multivariate statistical techniques such as ANO-

Table 1

Date, time (Pacific daylight-savings time [PDT]), and number of depth-stratified samples collected during each sampling period. All hauls were conducted at the same station (HH-05), located at 44°00′N, 125°00′W at a station depth of 950 m.

Haul	Date	Time	Day or night	Number of depth-stratified samples
HH-05A	3 Aug 2000	1600	Day	8
HH-05B	5 Aug 2000	2356	Night	8
HH-05C	6 Aug 2000	0330	Night	8
HH-05D	6 Aug 2000	0630	Day	8
HH-05E	6 Aug 2000	1623	Day	9
HH-05F	7 Aug 2000	0343	Night	9
HH-05G	7 Aug 2000	0633	Day	7
HH-05B	11 Aug 2002	0350	Night	9
HH-05C	11 Aug 2002	0722	Day	8

VA, diversity and evenness indices, multidimensional scaling, and cluster analyses to assess the influence of water depth, diel migration, temperature, and salinity on the occurrence and concentration of dominant ichthyoplankton taxa and assemblages. This is the first examination of diel variation in the vertical distributions of ichthyoplankton in the northern California Current since Boehlert et al. (1985), and the only work of its kind for an offshore assemblage. In addition, no similar study has been conducted examining fish egg diel vertical distributions and assemblages in this region. Results from this study are intended to supplement previous spatial and temporal analyses of Oregon coast ichthyoplankton (Richardson and Pearcy, 1977; Auth and Brodeur, 2006)–analyses that were based on samples collected along the Newport Hydrographic (NH) line (44°39′N) over many years.

Materials and methods

Sampling procedures

Ichthyoplankton samples were collected from a single station (HH-05) approximately 69 km off of Heceta Head (44°00′N, 125°00′W) along the central Oregon coast in 950 m of water. Sampling cruises in August 2000 and 2002 resulted in the collection of 74 depth-stratified samples from nine diel hauls: five during the day and four at night (Table 1). Samples collected after the beginning of civil twilight (~0445 Pacific daylight-savings time [PDT]) were considered day samples, whereas those collected after the end of civil twilight (~2006 PDT) were considered night samples. A multiple opening and closing net and environmental sensing system (MOCNESS; Wiebe et al., 1976) with a 1.2-m^2 mouth opening and 333-µm mesh nets was used to collect ichthyoplankton at 7–9 discrete depths. The MOCNESS was fished as a continuous oblique tow from a depth of 350 m to the surface at a retrieval rate of 20–30 m/min and a ship speed of 1.0–1.5 m/s. Ship and retrieval speeds were continually adjusted during each tow so as to maintain the mouth opening at a 45° angle for an effective mouth opening of 1 m^2 at all times. Mean water volume filtered by each net was 210 m^3 (standard error [SE]=18.0), but was always greater in nets from deeper strata and less in nets fished in the upper 50 m. Because strata had unequal depth ranges, towing times were different for each stratum. Throughout the water column during each tow, we recorded volume of water filtered, temperature, salinity, depth of the net, length of wire out, and angle of the net mouth relative to the geoid.

Ichthyoplankton samples were preserved at sea in a 10% buffered-formalin seawater solution. Fish eggs and larvae from each sample were completely sorted, counted, and identified to the lowest taxonomic level possible in the laboratory with a dissecting microscope. The lesser of either all larvae or a random subsample of 50 individuals from each species in each sample was measured to the nearest 0.1 mm standard length (SL) (or notochord length for preflexon larvae) using an ocular micrometer mounted on the sorting microscope.

It should also be noted that *Sebastes* spp. were not identifiable below the generic level based on meristics and pigmentation patterns (see Richardson and Pearcy [1977] and Matarese et al. [1989] for a more complete discussion of this problem); therefore no species-specific inferences are intended for this taxon in this study. Recent work has allowed the identification of rockfishes to species level based on mitochondrial markers (Gray et al., 2006), and this identification should enable future researchers to discern specific patterns in larval rockfish distribution and abundance.

Data analyses

Fish egg and larval concentrations for each depth-stratified sample (D_i) were expressed as the number of individuals per 1000 m^3. Weighted mean water-column densities for each haul (D_{Haul}) were calculated according to the following equation:

$$D_{Haul} = \sum D_i r_i / \sum r_i, \quad (1)$$

where r_i = the depth range (m) of each depth-stratified sample.

Weighted mean depths (*WMD*s) of dominant larval taxa were calculated according to the following equation (Pearre, 1973):

$$WMD = \sum n_i d_i / \sum n_i, \quad (2)$$

where n_i = the number of individuals in each depth-stratified sample; and
d_i = the mean depth (m) of each sample.

To facilitate vertical distribution analyses, the water column was divided into seven depth strata: 0–10, 10–20, 20–50, 50–100, 100–150, 150–200, and 200–350 m. The weighted mean density of eggs and larvae in all samples collected in each depth stratum per haul were calculated as the strata densities for each haul. A type-II ANOVA model was used to test the null hypothesis that egg and larval densities did not differ between day and night periods or between depth strata, and that there was no interaction among these factors (Dunn and Clark, 1974; Lough and Potter, 1993). ANOVA and a Tukey's multiple range test were applied to the $\log_e(n+0.1)$-transformed haul and depth-strata densities to test for significant differences between day and night periods and depth strata. Weighted mean (based on density) larval lengths of important species were also calculated for each haul and depth stratum, and were similarly tested for significant differences between day and night periods and depth strata.

Taxa diversity and evenness for day and night and total diversity and evenness for each depth stratum were analyzed for all identifiable egg (n=11) and larval (n=20) taxa. The Shannon-Wiener diversity index (H′) was used to measure egg and larval diversity, where higher H′ values denote greater diversity. Taxa evenness was assessed by using Pielou's evenness index (J′), which ranges from zero to one, with the maximum J′ value indicating that all taxa are represented in the same relative concentrations. Both H′ and J′ were calculated according to the formulas of Shannon and Weaver (1949) and Krebs (1989).

On Field et al.'s (1982) recommendation, we performed a hierarchical cluster analyses in conjunction with nonmetric multidimensional scaling (MDS) ordinations to identify assemblages by potential taxa, depth-strata, and diel egg and larval concentrations. For analyses of taxa assemblages, only those egg (n=4) and larval (n=12) taxa found during more than 5% of the sampling events were included, whereas all identifiable egg (n=10) and larval (n=19) taxa were included in the other assemblage analyses. Concentrations for each egg and larval taxon were averaged for each diel tow (eggs: n=8; larvae: n=9) and each depth stratum from all tows (eggs: n=22; larvae: n=53), which constituted the sampling units in the respective multivariate matrices. Sampling units for which no taxa were found were excluded from the analyses.

Dendrograms of egg and larval taxa, depth strata, and diel presence were created using hierarchical, group-averaged clustering from Bray-Curtis ranked similarities on standardized, fourth root-transformed egg and larval concentrations (Clarke and Warwick, 2001). Dendrograms were cut to produce ecologically interpretable clusters when they were apparent. In order to verify our interpretations of the dendrograms, we performed nonmetric MDS ordinations using similarity matrices from the cluster analyses, with 20 random restarts each to minimize stress levels. A two-dimensional ordination approach was adopted because stress levels were sufficiently low (≤0.08) in all cases and were not appreciably reduced by the addition of a third dimension, and the results were sufficiently interpretable ecologically in two-dimensional space (Clarke and Warwick, 2001).

A nonparametric, multivariate procedure (BIO-ENV) was used to analyze the relationship between select environmental variables and egg and larval community structures. The details of the BIO-ENV algorithm and its suitability for use in analyzing the interactions of biological and environmental data are described by Clarke and Gorley (2001) and Clarke and Warwick (2001). Two separate analyses were performed: one with a similarity matrix of depth-stratified samples by egg taxa (24 samples × 9 taxa), and the other with a similarity matrix of depth-stratified samples by larval taxa (61 samples × 19 taxa). These matrices were analyzed in association with three environmental variables: mean depth (m), mean temperature (°C), and mean salinity of each depth-stratified sample. Both BIO-ENV analyses were performed by using the Spearman rank correlation method on the normalized Euclidean distance similarity matrices of the $\log_e(n+0.1)$-transformed, nonstandardized environmental variables by depth-stratified samples (Clarke and Gorley, 2001). All diversity, evenness, cluster, MDS, and BIO-ENV analyses were performed by using PRIMER statistical software (PRIMER, vers. 5.2.9, PRIMER-E Ltd, Plymouth, UK).

Pairwise correlation analyses were also conducted to assess the relationship between concentrations of several prominent egg (*Sardinops sagax* [Pacific sardine], *Icichthys lockingtoni* [medusafish], and *Chauliodus macouni* [Pacific viperfish]) and larval (*Sebastes* spp. [rockfishes], *Stenobrachius leucopsarus* [northern lampfish], *Tarletonbeania crenularis* [blue lanternfish], and *Lyopsetta exilis* [slender sole]) taxa as well as total eggs and larvae and the environmental variables salinity and temperature. Mean egg and larval densities, salinity, and temperature per depth-stratified sample were used as variable measures. Before inclusion in the analyses, egg and larval concentrations were $\log_e(n+0.1)$-transformed to normalize the data and homogenize residual variances. Statistical significance was determined at α = 0.05. All ANOVA and correlation analyses were performed using the statistical software JMP (JMP, vers. 5.1., SAS Inst., Inc., Cary, NC).

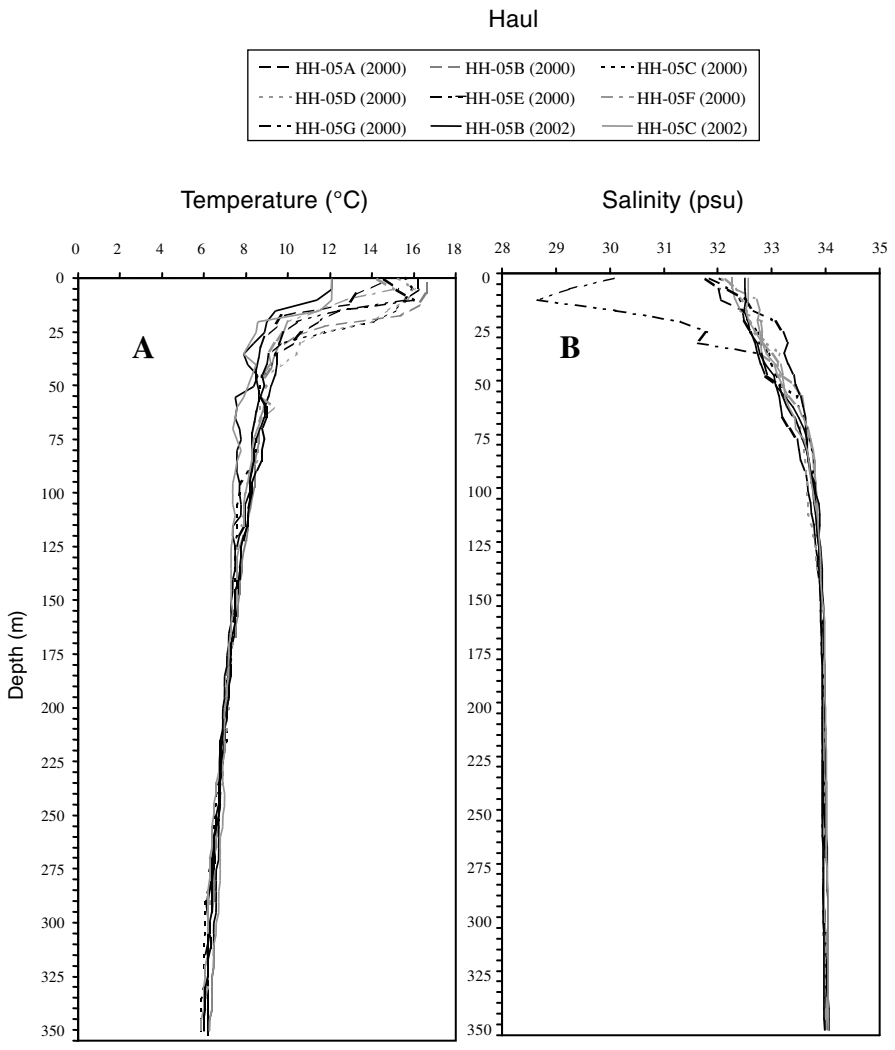

Figure 1

Temperature (**A**) and salinity (**B**) water-column profiles from a single offshore station (HH-05 [44°00′N, 125°00′W]) sampled repeatedly off the central Oregon coast during August in 2000 and 2002.

Results

Hydrography

The water column at the sampling station was similarly stratified for each of the nine diel hauls, and a thermocline was centered approximately at 20 m (Fig. 1, A and B). Mean water temperature was 14.7°C (standard deviation [SD]=1.6) at the surface, and decreased to 6.2°C (SD=0.2) at 350 m. Salinity increased from a mean of 31.9 psu (SD=0.7) at the surface to 34.0 psu (SD=0.03) at 350 m. The unusually low salinities recorded in the upper 35 m of the water column during the last haul in 2000 (HH-05G) may have resulted from an infusion of low-salinity Columbia River plume water from the north.

Egg concentrations and distributions

A surprisingly small sum of 128 fish eggs representing 11 taxa from nine families was collected throughout the study. Three taxa were dominant according to total mean concentration and frequency of occurrence from all depth-stratified samples: *S. sagax* (3.42/1000 m^3; 0.07), *I. lockingtoni* (2.00/1000 m^3; 0.14), and *C. macouni* (1.07/1000 m^3; 0.12). Together these three taxa accounted for over 71% of the total mean egg concentration. *Trachurus symmetricus* (jack mackerel) eggs were found at a high concentration (241.29/1000 m^3) in a single daytime surface (0–10 m) sample in 2000 but were found in only two other samples and at much lower densities (6.80 and 17.54/1000 m^3). These two samples were collected from two depths

Table 2

Day, night, and total mean densities (number/1000 m^3) of fish eggs collected at all different depth strata from a single offshore station off the central Oregon coast in 2000 and 2002 (1 standard error in parentheses). For between-stratum comparisons of each taxon within each diel category, different superscripts indicate significant differences (ANOVA, $P<0.05$).

	Depth (m)							
Taxa	0–10	10–20	20–50	50–100	100–150	150–200	200–350	Total
Day								
Total eggs	159.90 (79.0)^{a}	31.01 (14.1)^{ab}	18.60 (4.1)^{a}	0.70 (0.7)^{b}	0 (0)^{b}	0 (0)^{b}	1.30 (1.3)^{b}	13.43 (5.8)
Sardinops sagax	84.11 (78.9)	6.26 (6.3)	1.36 (1.4)	0 (0)	0 (0)	0 (0)	0 (0)	5.99 (5.6)
Lipolagus ochotensis	2.10 (2.1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Chauliodus macouni	2.14 (2.1)^{ab}	9.39 (6.3)^{ab}	8.70 (2.5)^{a}	0 (0)^{b}	0 (0)^{b}	0 (0)^{b}	0 (0)^{b}	1.74 (0.8)
Merluccius productus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Trachipterus altivelus	0 (0)	2.09 (2.1)	4.45 (4.4)	0 (0)	0 (0)	0 (0)	0.43 (0.4)	0.75 (0.4)
Trachurus symmetricus	50.36 (47.8)	3.51 (3.5)	1.36 (1.4)	0 (0)	0 (0)	0 (0)	0 (0)	2.10 (1.9)
Icichthys lockingtoni	14.76 (7.9)	6.26 (6.3)	1.37 (1.4)	0.70 (0.7)	0 (0)	0 (0)	0 (0)	1.83 (0.7)
Tetragonurus cuvieri	0 (0)	0 (0)	1.37 (1.4)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Lyopsetta exilis	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Microstomus pacificus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.87 (0.9)	0.28 (0.3)
Undetermined spp.	6.42 (6.4)	3.51 (3.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.44 (0.3)
Night								
Total eggs	42.42 (40.2)	26.66 (11.2)	1.02 (1.0)	0.95 (1.0)	0 (0)	0.67 (0.7)	0.58 (0.6)	3.65 (2.2)
Sardinops sagax	0 (0)	7.28 (7.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.21 (0.2)
Lipolagus ochotensis	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Chauliodus macouni	0 (0)	3.64 (3.6)	1.02 (1.0)	0 (0)	0 (0)	0 (0)	0 (0)	0.24 (0.1)
Merluccius productus	0 (0)	3.88 (3.9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Trachipterus altivelus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Trachurus symmetricus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Icichthys lockingtoni	34.28 (32.0)	11.87 (7.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2.21 (1.9)
Tetragonurus cuvieri	2.71 (2.7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Lyopsetta exilis	0 (0)	0 (0)	0 (0)	0.95 (1.0)	0 (0)	0 (0)	0 (0)	0.13 (0.1)
Microstomus pacificus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.67 (0.7)	0.58 (0.6)	0.31 (0.3)
Undetermined spp.	5.43 (5.4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.28 (0.3)
Total								
Total eggs	107.69 (49.3)^{a}	29.08 (8.7)^{ab}	10.78 (3.8)^{abc}	0.81 (0.5)^{bc}	0 (0)^{c}	0.33 (0.3)^{c}	0.98 (0.7)^{bc}	9.08 (3.6)
Sardinops sagax	46.73 (44.1)	6.71 (4.4)	0.76 (0.8)	0 (0)	0 (0)	0 (0)	0 (0)	3.42 (3.1)
Lipolagus ochotensis	1.17 (1.2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.08 (0.08)
Chauliodus macouni	1.19 (1.2)^{ab}	6.83 (3.8)^{ab}	5.28 (1.9)^{a}	0 (0)^{b}	0 (0)^{b}	0 (0)^{b}	0 (0)^{b}	1.07 (0.5)
Merluccius productus	0 (0)	1.72 (1.7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.06 (0.06)
Trachipterus altivelus	0 (0)	1.16 (1.2)	2.47 (2.5)	0 (0)	0 (0)	0 (0)	0.24 (0.2)	0.42 (0.2)
Trachurus symmetricus	27.98 (26.7)	1.95 (1.9)	0.76 (0.8)	0 (0)	0 (0)	0 (0)	0 (0)	1.17 (1.1)
Icichthys lockingtoni	23.43 (14.1)^{a}	8.75 (4.6)^{ab}	0.76 (0.8)^{b}	0.39 (0.4)^{b}	0 (0)^{b}	0 (0)^{b}	0 (0)^{b}	2.00 (0.8)
Tetragonurus cuvieri	1.21 (1.2)	0 (0)	0.76 (0.8)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Lyopsetta exilis	0 (0)	0 (0)	0 (0)	0.42 (0.4)	0 (0)	0 (0)	0 (0)	0.06 (0.06)
Microstomus pacificus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.33 (0.3)	0.74 (0.5)	0.30 (0.2)
Undetermined spp.	5.98 (4.1)	1.95 (1.9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.37 (0.2)

(10–20 and 20–50 m, respectively) in the same haul (HH-05A).

Fish egg concentrations varied across depth-stratified and diel scales (Table 2). However, depth stratum was the only significant factor explaining variation in *C. macouni*, *I. lockingtoni*, and total egg densities in the type-II ANOVA model ($P<0.05$). Almost 91% of the total egg abundance was found in the upper 100 m of the water column. Egg densities were generally highest near the surface and decreased with depth. There were no *S. sagax*, *C. macouni*, or *I. lockingtoni* eggs found at depths >100 m.

Mean total water-column concentrations were greater during the day than at night for *S. sagax* (5.99/1000 m^3

[day]; 0.21/1000 m^3 [night]), *C. macouni* (1.74/1000 m^3 [day]; 1.07/1000 m^3 [night]), and total eggs (13.43/1000 m^3 [day]; 3.65/1000 m^3 [night]), although differences were not significant (ANOVA, $P>0.05$). However, *I. lockingtoni* eggs occurred in slightly higher concentrations in the water column at night (2.21/1000 m^3) than during the day (1.83/1000 m^3). Egg concentrations were generally higher during the day than at night at each depth stratum for most taxa (Table 2).

Larval concentrations and distributions

A total of 1571 fish larvae representing 20 taxa from 11 families were collected throughout the study. Three families accounted for 97.4% of the total standardized larval concentration: Scorpaenidae (55.6%), Myctophidae (35.6%), and Pleuronectidae (6.2%). Within these families, four taxa were dominant based on total mean concentration and frequency of occurrence from all depth-stratified samples: *Sebastes* spp. (57.75/1000 m^3; 0.42), *S. leucopsarus* (25.23/1000 m^3; 0.45), *T. crenularis* (8.81/1000 m^3; 0.35), and *L. exilis* (3.78/1000 m^3; 0.15). Several other taxa were documented at relatively high frequencies but at lower mean concentrations: *Glyptocephalus zachirus* (rex sole) (2.10/1000 m^3; 0.18), *Protomyctophum thompsoni* (northern flashlightfish) (1.17/1000 m^3; 0.16), *I. lockingtoni* (1.01/1000 m^3; 0.11), *Diaphus theta* (California headlightfish) (0.91/1000 m^3; 0.11), and *Liparis fucensis* (slipskin snailfish) (0.66/1000 m^3; 0.11).

Larval concentrations varied across depth-stratified and diel scales (Table 3). For *S. leucopsarus* larvae, both factors and their interaction term (depth, diel presence, and depth×diel presence) in the type-II ANOVA model were significant ($P<0.05$). However, depth stratum was the only significant factor explaining variation in *L. exilis*, *Sebastes* spp., *T. crenularis*, and total larval densities in the model. More than 96% of the total larval abundance was distributed in the upper 100 m of the water column. Mean concentrations of *Sebastes* spp., *S. leucopsarus*, *T. crenularis*, and total larvae generally increased from the surface to the 20–50 m depth, then declined steadily as depth increased. No *Sebastes* spp. larvae were collected below 100 m. In addition, *L. exilis* larvae were found only in the 20–100 m depth range, where concentrations were greater than 3× higher in the 20–50 than in the 50–100 m depth stratum.

Mean larval densities were generally greater at night than during the day at all but one depth stratum for *Sebastes* spp., *S. leucopsarus*, *T. crenularis*, and total larvae (Table 3). These differences were significant for *S. leucopsarus* and total larvae at the 0–10 and 10–20 m depth strata (ANOVA, $P<0.05$). However, higher larval densities were found during the day than at night for *Sebastes* spp., *S. leucopsarus*, and total larvae at the 50–100 m depth stratum. In addition, *L. exilis* larvae were found at higher densities during the day than at night at all depths at which they were collected.

Analysis of the dominant larval taxa depth distributions over a 16-h period revealed evidence of diel vertical migration (Fig. 2). Weighted mean depth (WMD) of *L. exilis* and *Sebastes* spp. larvae increased from 2324 to 1550 PDT, whereas larval *S. leucopsarus* WMD decreased slightly between 2324 and 0303 PDT before increasing as the day progressed. In contrast, *T. crenularis* larvae appeared to move up in the water column from 2324 to 0604 PDT but were not found in any sample from the haul conducted at 1550 PDT.

Weighted mean standard lengths (SL) of *L. exilis*, *Sebastes* spp., *S. leucopsarus*, and *T. crenularis* larvae generally increased with depth (Table 4). Mean SL for *S. leucopsarus* larvae collected during night and during both day and night combined was significantly greater at the 20–100 m than at the 10–20 m depth stratum (ANOVA, $P<0.05$). *Lyopsetta exilis*, *Sebastes* spp., and *T. crenularis* larvae collected at night were generally the same size or larger than those collected during the day at each depth stratum, although these differences were not significant (ANOVA, $P>0.05$).

Diversity and evenness

Larval and egg diversity and evenness varied across depth strata. Larval diversity generally increased with depth. Egg diversity increased from the surface to 20 m then declined with increasing depth. Egg and larval evenness generally increased with depth before declining slightly at the 200–350 m depth stratum. Egg diversity and evenness could not be assessed at the 100–150 and 150–200 m depth strata because no eggs were found between 100 and 150 m, and only one egg (*Microstomus pacificus* [Dover sole]) was found at the 150–200 m depth stratum. There was no appreciable difference in egg and larval diversity and evenness between day and night samples.

Assemblages

Several taxa and depth assemblages were identified on the basis of cluster analyses and MDS, although no diel assemblages were apparent (Fig. 3, A–C). Larval taxa separated out into four assemblages (Fig. 3A). In more than 5% of the samples too few egg taxa ($n=4$) were present to permit identification of any assemblages. Cluster analyses and MDS also indicated the presence of two egg and larval depth assemblages: <100 m and >100 m (Fig. 3, B and C).

Environmental relationships

BIO-ENV and correlation analyses revealed significant relationships between several environmental factors and egg and larval mean concentrations. A depth-stratified BIO-ENV analysis, which included mean depth (m), mean temperature (°C), and mean salinity of each depth-stratified sample, showed that depth alone explained 46% of the variability in mean egg concentrations and 44% in larval concentrations. No multiple-factor combination explained more variability in egg or larval concentration data. Pairwise correlation analyses revealed significant

Table 3

Day, night, and total mean densities (number/1000 m^3) of fish larvae collected at different depth strata from a single offshore station off the central Oregon coast in 2000 and 2002 (1 SE in parentheses). For between stratum comparisons of each taxon within each diel category, different alphabetic supercripts indicate significant differences (ANOVA, $P<0.05$). For diel comparisions of each taxon within each depth stratum, different numeric superscripts indicate significant differences (ANOVA, $P<0.05$).

	Depth (m)							
Taxa	0–10	10–20	20–50	50–100	100–150	150–200	200–350	Total
Day								
Total larvae	^{2}47.47 (22.6)^{abc}	^{2}130.11 (71.3)^{ab}	324.49 (104.4)^{a}	150.55 (59.3)^{a}	6.27 (2.6)^{bcd}	1.93 (1.3)^{d}	2.97 (0.8)^{cd}	75.05 (20.1)
Sardinops sagax	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Pseudobathylagus milleri	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.43 (0.4)	0.19 (0.2)
Chauliodus macouni	0 (0)	0 (0)	0 (0)	0 (0)	1.59 (1.6)	0 (0)	0 (0)	0.11 (0.1)
Tactostoma macropus	2.09 (2.1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Lestidiops ringens	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Myctophidae spp.	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Protomyctophum thompsoni	0 (0)	0 (0)	0 (0)	1.70 (1.1)	3.92 (1.5)	0 (0)	0.62 (0.4)	0.88 (0.3)
Tarletonbeania crenularis	0 (0)^{c}	12.98 (9.6)^{abc}	26.69 (13.8)^{a}	18.63 (13.9)^{ab}	0.76 (0.8)^{abc}	0 (0)^{bc}	0.26 (0.3)^{bc}	8.40 (5.1)
Nannobrachium regale	0 (0)	2.46 (2.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Stenobrachius leucopsarus	^{2}0 (0)^{b}	^{2}3.13 (3.1)^{b}	55.79 (34.4)^{a}	46.50 (16.4)^{a}	0 (0)^{b}	0 (0)^{b}	0.79 (0.5)^{b}	15.42 (5.3)
Diaphus theta	0 (0)	2.46 (2.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Brosmophycis marginata	0 (0)	3.13 (3.1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Sebastes spp.	33.45 (26.0)^{ab}	85.61 (51.0)^{ab}	190.12 (54.4)^{a}	64.04 (38.6)^{a}	0 (0)^{b}	0 (0)^{b}	0 (0)^{b}	38.73 (8.9)
Liparis fucensis	0 (0)	0 (0)	2.69 (1.6)	2.60 (1.7)	0 (0)	0.53 (0.5)	0 (0)	0.81 (0.4)
Icichthys lockingtoni	8.47 (5.2)	10.94 (5.1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.28 (0.6)
Citharichthys sordidus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Glyptocephalus zachirus	0 (0)	9.39 (9.4)	8.43 (5.2)	4.65 (4.7)	0 (0)	0 (0)	0 (0)	2.21 (0.7)
Lyopsetta exilis	0 (0)^{b}	0 (0)^{b}	40.77 (25.7)^{a}	11.72 (5.1)^{a}	0 (0)^{b}	0 (0)^{b}	0 (0)^{b}	5.60 (2.7)
Microstomus pacificus	0 (0)	0 (0)	0 (0)	0.70 (0.7)	0 (0)	1.40 (1.4)	0.87 (0.5)	0.66 (0.3)
Undetermined spp.	3.45 (3.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.19 (0.2)
Night								
Total larvae	^{1}293.20 (131.3)^{a}	^{1}667.70 (153.9)^{a}	630.54 (281.2)^{a}	84.33 (41.4)^{ab}	13.21 (7.8)^{b}	3.66 (1.2)^{b}	2.68 (1.0)^{b}	139.73 (42.4)
Sardinops sagax	4.42 (2.7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.27 (0.2)
Pseudobathylagus milleri	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Chauliodus macouni	0 (0)	0 (0)	0 (0)	3.26 (1.1)	0.94 (0.9)	0 (0)	0 (0)	0.58 (0.3)
Tactostoma macropus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lestidiops ringens	0 (0)	0 (0)	0 (0)	1.45 (1.4)	0 (0)	0 (0)	0 (0)	0.14 (0.1)
Myctophidae spp.	0 (0)	0 (0)	3.05 (3.1)	1.90 (1.9)	0 (0)	0 (0)	0 (0)	0.68 (0.4)
Protomyctophum thompsoni	0 (0)	0 (0)	0 (0)	3.61 (2.5)	8.30 (4.8)	1.29 (1.3)	0 (0)	1.52 (0.7)
Tarletonbeania crenularis	1.34 (1.3)^{ab}	27.65 (19.4)^{ab}	38.98 (27.9)^{a}	19.26 (10.7)^{a}	3.02 (3.0)^{ab}	0.67 (0.7)^{ab}	0 (0)^{b}	9.34 (5.5)
Nannobrachium regale	5.43 (5.4)	12.36 (12.4)	2.03 (1.2)	0 (0)	0 (0)	0 (0)	0 (0)	0.94 (0.4)
Stenobrachius leucopsarus	^{1}5.09 (2.2)^{abc}	^{1}248.31 (170.3)^{a}	175.64 (61.7)^{a}	34.70 (19.4)^{ab}	0 (0)^{c}	1.71 (1.0)^{bc}	1.59 (0.6)^{bc}	37.50 (13.3)

continued

Table 3 (continued)

Taxa	Depth (m) 0–10	10–20	20–50	50–100	100–150	150–200	200–350	Total
Night (continued)								
Diaphus theta	3.05 (1.8)	11.52 (3.9)	9.20 (6.7)	0 (0)	0 (0)	0 (0)	0 (0)	1.88 (1.0)
Brosmophycis marginata	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Sebastes spp.	263.65 (124.1)[a]	356.70 (176.9)[a]	379.92 (209.6)[a]	14.96 (12.0)[ab]	0 (0)[b]	0 (0)[b]	0 (0)[b]	81.52 (25.7)
Liparis fucensis	0 (0)	0 (0)	0 (0)	3.23 (1.9)	0 (0)	0 (0)	0 (0)	0.47 (0.3)
Icichthys lockingtoni	6.45 (4.8)	0 (0)	1.02 (1.0)	0 (0)	0 (0)	0 (0)	0 (0)	0.67 (0.5)
Citharichthys sordidus	1.70 (1.7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.13 (0.1)
Glyptocephalus zachirus	2.07 (2.1)	11.17 (6.9)	7.15 (4.5)	0 (0)	0.94 (0.9)	0 (0)	0.81 (0.8)	1.96 (1.0)
Lyopsetta exilis	0 (0)[b]	0 (0)[b]	9.23 (3.5)[a]	1.95 (2.0)[ab]	0 (0)[b]	0 (0)[b]	0 (0)[b]	1.50 (0.5)
Microstomus pacificus	0 (0)	0 (0)	2.28 (1.3)	0 (0)	0 (0)	0 (0)	0.29 (0.3)	0.34 (0.2)
Undetermined spp.	0 (0)	0 (0)	2.04 (2.0)	0 (0)	0 (0)	0 (0)	0 (0)	0.28 (0.3)
Total mean								
Total larvae	156.68 (69.8)[a]	369.04 (119.5)[a]	460.51 (138.2)[a]	121.11 (37.4)[a]	9.74 (4.0)[b]	2.80 (0.9)[b]	2.84 (0.6)[b]	103.80 (23.3)
Sardinops sagax	1.96 (1.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.12 (0.1)
Pseudobathylagus milleri	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.24 (0.2)	0.11 (0.1)
Chauliodus macouni	0 (0)	0 (0)	0 (0)	1.45 (0.7)	1.26 (0.9)	0 (0)	0 (0)	0.32 (0.1)
Tactostoma macropus	1.16 (1.2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.08 (0.08)
Lestidiops ringens	0 (0)	0 (0)	0 (0)	0.64 (0.6)	0 (0)	0 (0)	0 (0)	0.06 (0.06)
Myctophidae spp.	0 (0)	0 (0)	1.36 (1.4)	0.85 (0.8)	0 (0)	0 (0)	0 (0)	0.30 (0.2)
Protomyctophum thompsoni	0 (0)	0 (0)	0 (0)	2.55 (1.2)	6.11 (2.5)	0.64 (0.6)	0.34 (0.2)	1.17 (0.3)
Tarletonbeania crenularis	0.60 (0.6)[c]	19.50 (9.7)[abc]	32.15 (13.7)[a]	18.91 (8.6)[ab]	1.89 (1.5)[bc]	0.33 (0.3)[c]	0.15 (0.1)[c]	8.81 (3.5)
Nannobrachium regale	2.41 (2.4)	6.86 (5.5)	0.90 (0.6)	0 (0)	0 (0)	0 (0)	0 (0)	0.50 (0.2)
Stenobrachius leucopsarus	2.26 (1.3)[bc]	112.1 (81.8)[ab]	109.06 (37.5)[a]	41.25 (11.9)[a]	0 (0)[c]	0.85 (0.6)[bc]	1.14 (0.4)[bc]	25.23 (7.2)
Diaphus theta	1.35 (0.9)	6.49 (2.6)	4.09 (3.2)	0 (0)	0 (0)	0 (0)	0 (0)	0.91 (0.5)
Brosmophycis marginata	0 (0)	1.74 (1.7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.08 (0.08)
Sebastes spp.	135.76 (66.3)[ab]	206.09 (90.6)[ab]	274.47 (96.2)[a]	42.22 (22.6)[b]	0 (0)[c]	0 (0)[c]	0 (0)[c]	57.75 (13.7)
Liparis fucensis	0 (0)	0 (0)	1.50 (1.0)	2.88 (1.2)	0 (0)	0.27 (0.3)	0 (0)	0.66 (0.2)
Icichthys lockingtoni	7.57 (3.4)	6.08 (3.3)	0.45 (0.5)	0 (0)	0 (0)	0 (0)	0 (0)	1.01 (0.4)
Citharichthys sordidus	0.76 (0.8)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.06 (0.06)
Glyptocephalus zachirus	0.92 (0.9)	10.18 (5.7)	7.86 (3.3)	2.58 (2.6)	0.47 (0.5)	0 (0)	0.36 (0.4)	2.10 (0.5)
Lyopsetta exilis	0 (0)[b]	0 (0)[b]	26.75 (14.7)[a]	7.38 (3.3)[a]	0 (0)[b]	0 (0)[b]	0 (0)[b]	3.78 (1.6)
Microstomus pacificus	0 (0)	0 (0)	1.02 (0.7)	0.39 (0.4)	0 (0)	0.70 (0.7)	0.61 (0.3)	0.52 (0.2)
Undetermined spp.	1.92 (1.9)	0 (0)	0.91 (0.9)	0 (0)	0 (0)	0 (0)	0 (0)	0.23 (0.2)

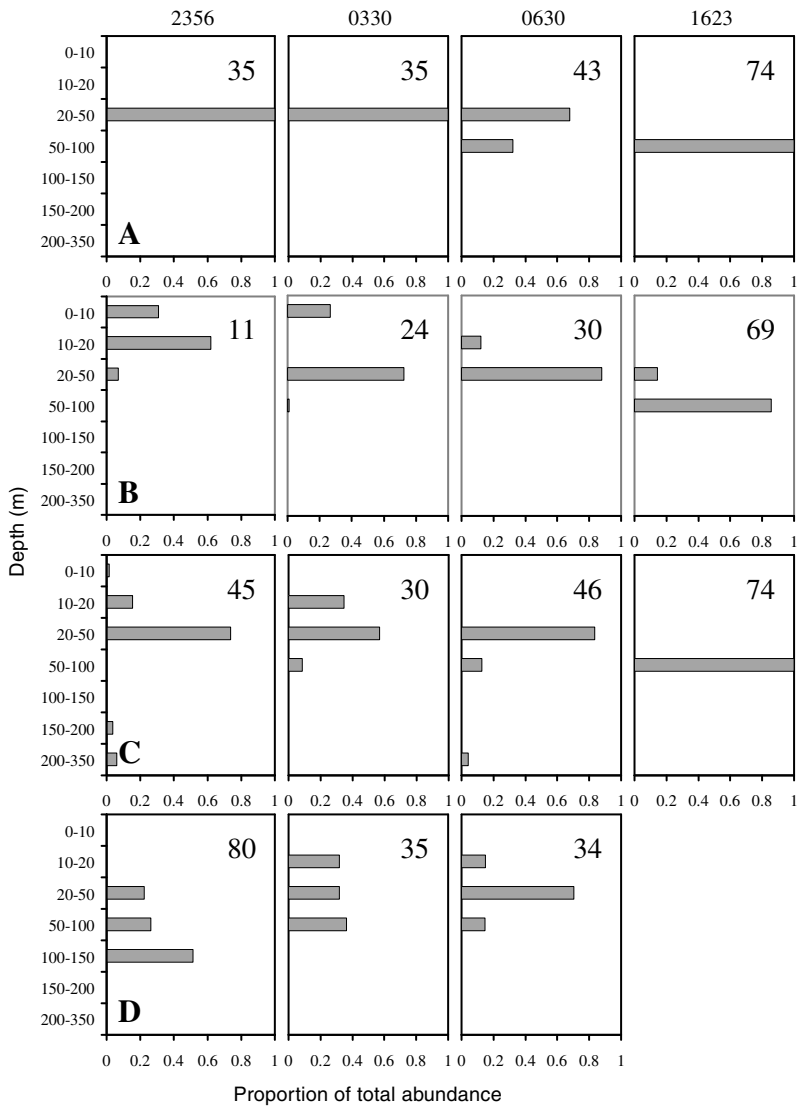

Figure 2

Diel differences in the proportion of total abundances for (**A**) *Lyopsetta exilis*, (**B**) *Sebastes* spp., (C) *Stenobrachius leucopsarus*, and (D) *Tarletonbeania crenularis* larvae collected at different depth strata during a 16-h period at a single offshore station off the central Oregon coast on 5–6 August 2000. No *T. crenularis* larvae were collected in the 1623 PDT haul. The times at which the first MOCNESS net of each haul was opened are given above the panels. Numbers in the upper right corner of each panel represent the weighted mean depth (m) of larvae collected in each haul. During the sampling period, sunset occurred at 2033 and sunrise at 0610 PDT.

correlations between temperature and mean concentrations of *Sebastes* spp. and total larvae, *C. macouni*, *I. lockingtoni*, and total eggs. Significant negative correlations were seen between these same taxa and salinity, and temperature and salinity were negatively correlated with each other ($P<0.05$) (Table 5). Mean concentrations of *L. exilis*, *S. leucopsarus*, and *T. crenularis* larvae, and *S. sagax* eggs were also positively correlated with temperature and negatively correlated with salinity, although the correlations were not significant ($P>0.05$).

Discussion

The species composition, assemblages, and dominant taxa identified in this study were similar to those found

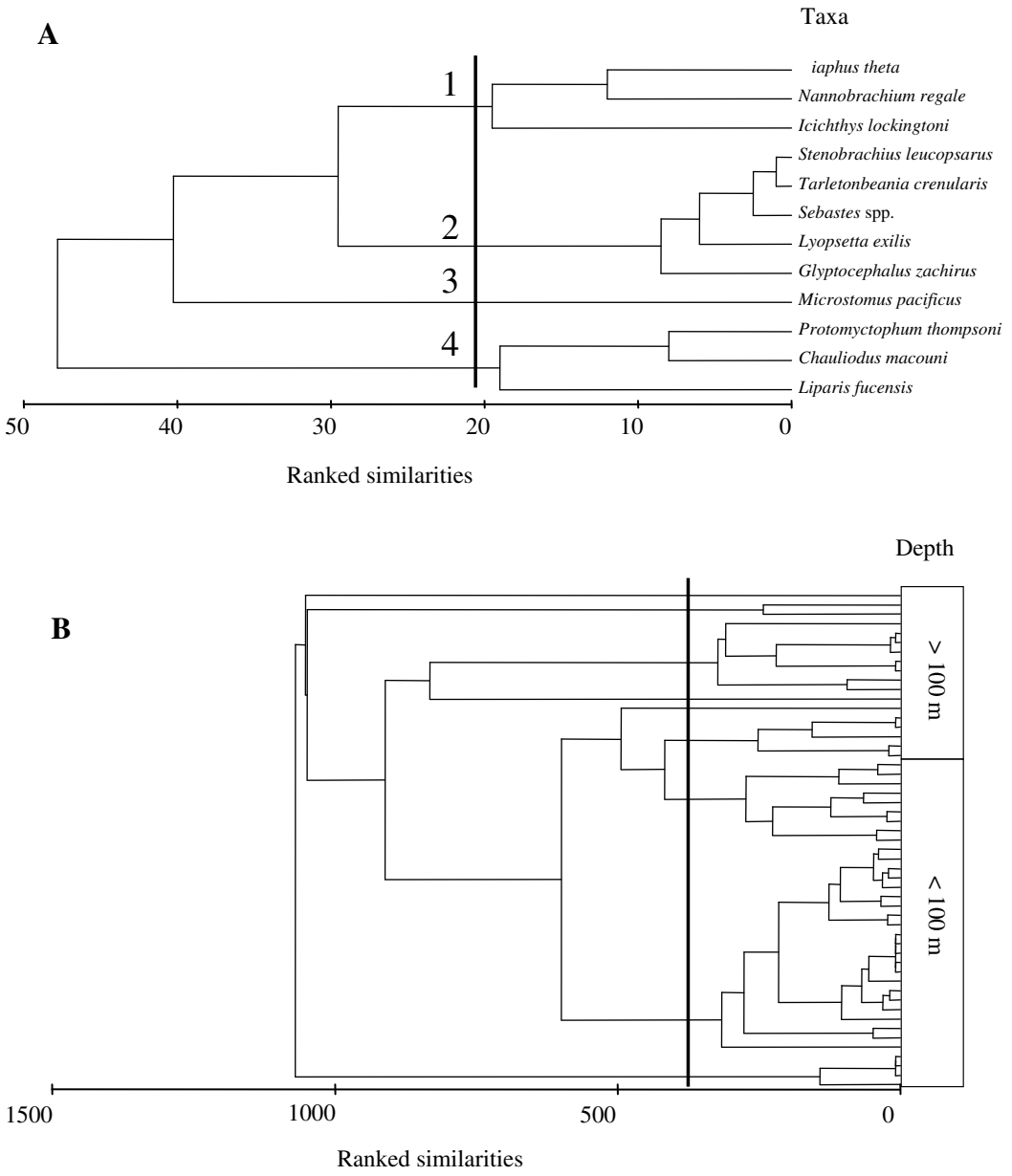

Figure 3

Dendrograms of (**A**) larval taxa, (**B**) larval depth, and (**C**) egg depth. Cluster and multidimensional scaling analyses were performed on fish larvae and eggs collected from a single offshore station off the central Oregon coast in 2000 and 2002. Taxon (A) and depth (B and C) cluster identifications are indicated on each figure. Numbers in figure 3A refer to the four identifiable larval taxa assemblages. Depth strata 1 = 0–10 m, 2 = 10–20 m, 3 = 20–50 m, 4 = 50–100 m, 5 = 100–150 m, 6 = 150–200 m, and 7 = 200–350 m.

in other studies conducted during the summer in offshore waters off the central Oregon coast (Richardson, 1973; Richardson and Pearcy, 1977; Brodeur et al., 1985; Auth and Brodeur, 2006). This similarity may indicate that the composition of dominant larval fishes in this area is resilient to dramatic environmental fluctuations such as those observed during the last 35 years in the northern California Current (Schwing and Moore, 2000; Grantham et al., 2004). It also provides evidence in support of the hypothesis of Auth and Brodeur (2006) that past sampling of ichthyoplankton along the NH line during the summer is indeed representative of summer ichthyoplankton assemblages elsewhere along the Oregon coast.

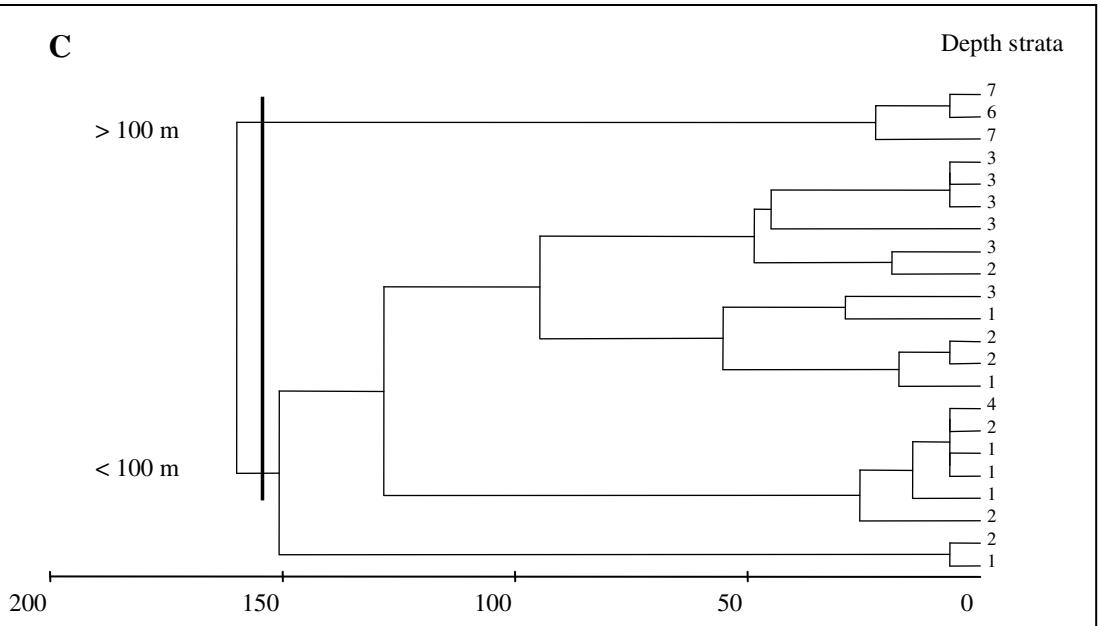

Figure 3 (continued)

Table 4

Day, night, and total mean standard lengths (mm) of fish larvae collected at different depth strata from a single offshore station off the central Oregon coast in 2000 and 2002 (1 SE in parentheses). For between stratum comparisons of each taxon within each diel category, different superscripts indicate significant differences (ANOVA, $P<0.05$).

	Depth (m)							
Taxa	0–10	10–20	20–50	50–100	100–150	150–200	200–350	Total
Day								
Lyopsetta exilis	—	—	8.7 (0.6)	10.3 (0.5)	—	—	—	9.1 (0.4)
Sebastes spp.	4.1 (1.4)	5.1 (0.2)	6.6 (0.7)	7.4 (1.4)	—	—	—	6.2 (0.5)
Stenobrachius leucopsarus	—	13.6	9.3 (0.9)	9.5 (0.6)	—	—	14.7 (0.3)	9.5 (0.5)
Tarletonbeania crenularis	—	9.2 (2.2)	8.9 (1.1)	10.7 (1.4)	14.3	—	16.3	9.6 (0.7)
Night								
Lyopsetta exilis	—	—	9.6 (0.4)	8.6	—	—	—	9.4 (0.4)
Sebastes spp.	6.4 (0.2)	6.2 (0.5)	7.9 (0.5)	10.0 (2.3)	—	—	—	6.9 (0.3)
Stenobrachius leucopsarus	5.6 (0.7)^{ab}	7.6 (0.2)^{b}	9.7 (0.8)^{a}	11.4 (0.3)^{a}	—	14.8 (0.0)^{ab}	15.4 (0.9)^{ab}	8.8 (0.4)
Tarletonbeania crenularis	8.7	7.7 (0.3)	9.4 (0.5)	12.1 (0.9)	13.4	16.0	—	9.6 (0.6)
Total mean								
Lyopsetta exilis	—	—	8.8 (0.4)	10.1 (0.5)	—	—	—	9.1 (0.3)
Sebastes spp.	6.1 (0.5)	6.0 (0.4)	7.4 (0.4)	7.5 (1.1)	—	—	—	6.7 (0.3)
Stenobrachius leucopsarus	5.6 (0.7)^{ab}	7.7 (0.4)^{b}	9.6 (0.5)^{a}	10.2 (0.5)^{a}	—	14.8 (0.0)^{ab}	15.1 (0.6)^{ab}	8.9 (0.3)
Tarletonbeania crenularis	8.7	8.3 (0.9)	9.2 (0.6)	11.3 (0.8)	13.5 (0.4)	16.0	16.3	9.6 (0.4)

However, in our study we collected no *Engraulis mordax* (northern anchovy) eggs or larvae, which usually comprise a significant portion of the offshore ichthyoplankton in August (Richardson and Pearcy, 1977). *Engraulis mordax* larvae have been associated with warmer, less saline, offshore surface waters from the Columbia River (Richardson, 1973; Auth and Brodeur, 2006). This warmer surface water did not appear to have occurred as far south as our sampling station, except perhaps during the last haul in 2000 (HH-05G) (Fig. 2).

Table 5

Correlation coefficients for the depth-stratified sample means (n=74) of eleven variables sampled during the day and night from a single station (HH-05) off the Oregon coast in August 2000 and 2002: water temperature (°C), salinity (kg/m^3), and $\log_e$-transformed densities (number/1000 m^3) of *Lyopsetta exilis*, *Sebastes* spp., *Stenobrachius leucpsarus, Tarletonbeania crenularis,* and total fish larvae, and *Chauliodus macouni, Icichthys lockingtoni, Sardinops sagax,* and total fish eggs. *=P<0.05, *=P<0.001, ***=P<0.0001.

	Temperature	Salinity
Salinity	−0.82***	
Lyopsetta exilis	0.03	−0.09
Sebastes spp.	0.48***	−0.51***
Stenobrachius leucopsarus	0.16	−0.18
Tarletonbeania crenularis	0.15	−0.14
Total larvae	0.57***	−0.53***
Chauliodus macouni	0.24*	−0.40**
Icichthys lockingtoni	0.63***	−0.47***
Sardinops sagax	0.20	−0.23
Total eggs	0.55***	−0.51***

In addition, we found evidence that *S. sagax* spawn in this region, as documented since the 1990s (Emmett et al., 2005; Auth and Brodeur, 2006). Similarly, we collected *T. symmetricus* eggs, which are normally found off southern California but which have been reported off southern Oregon by Kendall and Clark[1], off Washington by Ahlstrom (1956), and most recently in the Columbia River plume by Parnel et al.[2]

Our finding that the vast majority (96%) of fish larvae were present in the upper 100 m of the water column has been supported by several other studies (Brodeur and Rugen, 1994; Suntsov, 2002; Sabatés, 2004; Auth and Brodeur, 2006). This finding has significant implications for strategies to sample ichthyoplankton off Oregon and potentially throughout the California Current. *Sebastes* spp. primarily occurred in the 10–50 m depth range, as previously reported (Ahlstrom, 1961; Boehlert et al., 1985; Sakuma et al., 1999; Auth and Brodeur, 2006), whereas *L. exilis* larvae were found between 20 and 100 m as observed by Auth and Brodeur (2006) and during daytime collections made by Boehlert et al. (1985). Also, myctophid larvae within the subfamily Myctophinae (*T. crenularis*) were found at greater depths than those within the subfamily Lampanyctinae (*S. leucopsarus*) as reported by Sassa et al. (2002), although the vast majority was still found above 100 m.

One implication from these findings is that sampling in the upper 100 m of the water column should be sufficient to characterize pelagic summer ichthyoplankton abundances and distributions of the majority of fish taxa along the northeastern Pacific coast (Brodeur and Rugen, 1994; Auth and Brodeur, 2006). A further implication is that sampling strategies without discrete vertical strata, which expend additional effort collecting ichthyoplankton below 100 m, may underestimate larval fish abundances by using samples from largely uninhabited portions of the water column.

Differences in the abundance and size of fish larvae collected in diel samples have often led researchers to suspect bias due to net avoidance, resulting in underestimation of larvae (especially larger larvae) collected during the day (Richardson and Pearcy, 1977; Boehlert et al., 1985). These differences can vary depending on such factors as gear type, size, and tow speed. The present study supports this contention, particularly for the upper 20 m of the water column, where light penetration is of greatest concern. Sakuma et al. (1999) found that total adjusted catches of *Sebastes* spp. larvae off the central California coast were significantly greater at night than during the day. Richardson and Pearcy (1977) observed that large *Sebastes* spp. larvae (9–11 mm) were collected exclusively during the night, while smaller larvae (3–4 mm) were collected during both day and night at the 0–50 m depth off the central Oregon coast. However, they did not find evidence of daytime net avoidance for *S. leucopsarus* (5–11 mm) or *Isopsetta isolepis* (butter sole) (14–23 mm) larvae collected during the same study. In addition, Laroche and Richardson (1979) found no evidence of increased net avoidance by larger *Parophrys vetulus* (English sole) larvae collected during the day versus night off the Oregon coast. However, considering results from the present and similar studies on differences in diel ichthyoplankton abundance (Ahlstrom, 1959), we believe that ichthyoplankton sampling should be conducted primarily at night if at all possible to eliminate any potential bias due to net avoidance. Net avoidance should at least be factored into any model estimating abundances and depth distributions of larvae collected during both day and night.

As noted earlier, diel vertical migration (DVM) has been well documented for larvae of many marine fish species. A variety of theories have been put forth to explain DVM in larval fish, including predator avoidance (Hunter and Sanchez, 1976; Yamashita et al., 1985), the pursuit of zooplankton prey (Fortier and Leggett, 1983; Munk et al., 1989), facilitated larval transport in varying tidal currents (Norcross and Shaw, 1984; Hare and Govoni, 2005), optimization of the energetic advantage gained by larvae at certain depths in thermally stratified water (Wurtsbaugh and Neverman, 1988; Neilson and Perry, 1990), and the pursuit of optimum light conditions for larval survival (Heath et al., 1988). Although this study was not designed to

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[2] Parnel, M. M., R. L. Emmett, and R. D. Brodeur. 2006. Interannual and seasonal variation in ichthyoplankton collected off the Columbia River. Unpubl. manuscr., 20 p. Oregon State Univ., Hatfield Marine Science Center, 2030 SE Marine Sci. Dr., Newport, OR 97365.

determine the underlying causes of the DVM of larval fish, it does provide some evidence for type-I DVM (up at night, down during the day) for *S. leucopsarus* and *Sebastes* spp. larvae (and to a lesser extent for *L. exilis* larvae), and type-II DVM (down at night, up during the day) for *T. crenularis* larvae (Fig. 3). Evidence for either type of DVM for larval *Sebastes* spp. has not been found in previous studies (Sakuma et al., 1999; Bjorkstedt et al., 2002). This new type-I DVM could help explain the retention of *Sebastes* spp. larvae close to settlement areas along and inshore from the shelf as observed by Auth and Brodeur (2006)—a retention that is due to the ability of larvae to regulate their position in the water column and to take advantage of selective Ekman transport (Sakuma and Larson, 1995).

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