ANALYSIS OF THE SPRING-FALL EPIPELAGIC ICHTHYOPLANKTON COMMUNITY IN THE NORTHERN CALIFORNIA CURRENT IN 2004–2009 AND ITS RELATION TO ENVIRONMENTAL FACTORS

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ABSTRACT

The taxonomic composition, distribution, concentration, and community structure of ichthyoplankton off the Oregon and Washington coasts were examined in 2004–2009 to investigate annual, seasonal, latitudinal, and cross-shelf variability. Larval concentrations and community structure were also analyzed in relation to several local and larger-scale environmental variables. The dominant taxa, comprising 94% of the total larvae collected, were *Engraulis mordax*, *Sebastes* spp., *Stenobrachius leucopsarus*, *Tarletonbeania crenularis*, and *Lyopsetta exilis*. Larval concentrations and diversity generally varied across the temporal and spatial scales. Several seasonal and cross-shelf assemblages were identified, and annual, seasonal, latitudinal, and cross-shelf gradients of taxonomic associations with significant indicator taxa were found. Distance from shore, salinity, and temperature were the local environmental factors that explained the most variability in larval fish concentrations, while Columbia River outflow and sea-surface temperature were the larger-scale factors that explained the most variability in 2–4 month lagged larval fish concentrations and diversity.

INTRODUCTION

The northern California Current (NCC) is a highly dynamic and productive upwelling environment similar to other eastern boundary current regions around the world (Bakun 1993; Fréon et al. 2009). Like these other regions, the NCC supports a wide array of ecologically and commercially important forage and predatory taxa such as anchovy, lanternfish, flatfish, and rockfish (Brodeur et al. 2006; Checkley and Barth 2009). A key component to understanding the processes that influence the spawning, trophic dynamics, recruitment, and survival of these important fish stocks is an understanding of the ichthyoplankton communities, and the environmental factors that influence them, within these upwelling regions (Brodeur et al. 2008; Auth et al. 2011).

Many ichthyoplankton studies have been conducted in the NCC region over the past 40 years, but these have been generally limited with respect to spatial and temporal coverage. Past studies have incorporated only coastal (<50 km from shore) stations (Mundy 1984; Boehlert et al. 1985; Brodeur et al. 1985; Brodeur et al. 2008; Parnel et al. 2008), or were based on sampling efforts limited to one year (Waldron 1972; Richardson 1973), one transect (Richardson and Pearcy 1977; Auth and Brodeur 2006; Auth et al. 2007; Auth 2009 [although a second transect was sampled one time]), or one season (Richardson et al. 1980; Auth 2008). During 1980–1987, Doyle (1992) collected ichthyoplankton in conjunction with temperature and salinity data from multiple cross-shelf transects during multiple seasons along the northern and central California Current, but did not conduct any formal statistical analyses of the observed spatial and temporal patterns. Subsequently, several studies have suggested that local and larger-scale environmental variables can influence larval fish communities in the NCC (Doyle 1995; Brodeur et al. 2008), Gulf of Alaska (Doyle et al. 2009), Humboldt Current off Peru (Suntsov 2000), the North Sea (Beaugrand et al. 2003), and elsewhere (Hsieh et al. 2007).

The present study is the first to incorporate such a large data set of ichthyoplankton samples collected from multiple cross-shelf stations, latitudinal transects, seasons, and years into a comprehensive analysis of the ichthyoplankton community structure in relation to both local and larger-scale environmental factors within the NCC ecosystem. The objectives of this study are to (1) identify and describe the variability within the taxonomic, annual, seasonal, latitudinal, and cross-shelf ichthyoplankton assemblages within the NCC, (2) identify larval taxa indicative of each temporal and spatial assemblage, and (3) identify the local and larger-scale environmental factors that may influence changes in ichthyoplankton concentrations. The results of this study establish basic information on the distribution, composition, and variability of NCC ichthyoplankton assemblages and their dominant taxa with respect to dynamic environmental factors that influence them. This information should be of great use to fisheries researchers and managers in assessing the impact of environmental processes on early-life histories and subsequent recruitment of important forage and commercial stocks.

METHODS

Sampling Procedures

A total of 489 ichthyoplankton samples were collected from 28 monthly cruises between May and October/November 2004–2009. Samples were collected primarily at five stations extending ~20–100 km offshore at ~20 km intervals along each of four transects (i.e., Willapa Bay [WB: 46.67°N], Columbia River [CR: 46.16°N], Newport Hydrographic [NH: 45.65°N], and Heceta Head [HH: 44.00°N]) for a total of ~20 stations per monthly cruise off the southern Washington and central Oregon coasts from May to September. Additional stations extending as far inshore as 9 km and as far offshore as 238 km were sampled occasionally (fig. 1). The 9 km inshore station along the NH transect was only sampled in June and September 2004 and May 2006, the 116 km far-offshore station along the CR transect was only sampled in May 2006, the far-offshore stations along the HH transect were only sampled in August 2004, and the far-offshore stations along the NH transect were only sampled as follows: 120 km station in June, August, September, and November 2004, October 2005, May 2006, and June 2008; 139 km station in August 2004; 157 km station in June and September 2004, May 2006, and June 2008; 208 and 238 km stations in June 2008. No sampling was conducted in May and July 2004, May 2005, or July 2006. However, additional samples were collected in November 2004 and October 2005. Not all stations were sampled during all cruises due to inclement weather or equipment malfunctions. Sampling was done primarily at night (n = 372), although some samples were collected during crepuscular periods (n = 117) due to the lack of sufficient night hours during the summer months. Since no diel pattern of variability in larval concentrations (no. 1000 m^{-3}) was found through ordination analysis or ANOVA ($p > 0.34$), all samples were used in subsequent analyses regardless of time of sampling.

Samples were collected using a bongo net with a 60-cm (70-cm in June, September, and November 2004, October 2005, and May 2006) diameter mouth opening and fitted with 335-μm mesh. The bongo was fished as a continuous oblique tow from ~100 m (or within 5 m of the bottom at stations <100 m) to the surface at a retrieval rate of 33 m min^{-1} and ship speed of 1.0–1.5 m s^{-1}. A depth recorder and flowmeter placed in the net during each tow allowed determination of tow depth and volume of water filtered. The mean water volume filtered was 161.6 m^3 (standard error, SE = 2.6). Temperature (°C), salinity, density (sigma theta, kg m^{-3}), fluorescence (mg m^{-3}, an indicator of chlorophyll), and turbidity (mg m^{-3}) were measured throughout the water column during most cruises using a Seabird SBE 25 CTD (Sea-Bird Electronics Inc., Bellevue, WA, USA). Seabird model SBE 911 was used in November 2004, October 2005, and May 2006. During 2008 and 2009, dissolved oxygen concentration (DO, ml L^{-1}), and DO saturation (%) were also measured. Not all environmental parameters were measured at all stations due to periodic instrumentation malfunctions.

Ichthyoplankton samples collected in 2004–2008 were preserved at sea in a 10% buffered-formalin seawater solution. Samples collected in 2009 were preserved at sea in 95% ethanol for ~72 hours, then filtered and re-preserved in fresh 95% ethanol. Larval fish from each sample were completely sorted, counted, and identified to the lowest taxonomic level possible in the laboratory using a dissecting microscope. Most *Citharichthys* spp., *Cyclothone* spp., osmerids, *Pholis* spp., *Scopelosaurus* spp., *Sebastes* spp., and *Sebastolobus* spp. larvae were not identifiable below the generic or family level based on meristics and pigmentation patterns, so no species-specific inferences are intended for these taxa in this study. However, the majority of individuals classified as *Citharichthys* spp. are either *C. sordidus* or *C. stigmaeus* based on the larger, identifiable individuals collected and dominance of these paralichthyid species in the NCC ichthyoplankton (Matarese et al. 1989). All larvae of rare taxa or a random subsample of 30 individuals of abundant taxa in each sample were measured to the nearest 0.1 mm standard length (SL), or notochord length (NL) for preflexion larvae, using UTHSCSA Image Tool Version 3.0 image processing and analysis software (http://ddsdx.uthscsa.edu/dig/itdesc.html 2010).

Data Analyses

Hierarchical cluster analyses in conjunction with nonmetric multidimensional scaling (MDS) ordinations were used to identify potential larval fish taxonomic, annual, seasonal, latitudinal, and cross-shelf assemblages (Field et al. 1982). For analyses of taxonomic assemblages, only those larval taxa (n = 13) found in >5% of the samples were included, while all identifiable taxa (n = 60) were included in the other assemblage analyses. Samples lacking larval fish were not included in the cluster and MDS analyses.

Taxonomic, annual, seasonal, latitudinal, and cross-shelf dendrograms were created using hierarchical, group-averaged clustering from Bray-Curtis similarities on fourth root-transformed larval fish concentrations (Clarke and Warwick 2001). Larval concentrations for each taxon were averaged for each cruise (n = 28) and station (n = 30), which constituted the sampling units in the respective multivariate matrices. In order to verify dendrograms interpretations, nonmetric MDS ordinations were preformed using similarity matrices from the cluster analyses with 20 random restarts each to minimize stress levels. A two-dimensional ordination

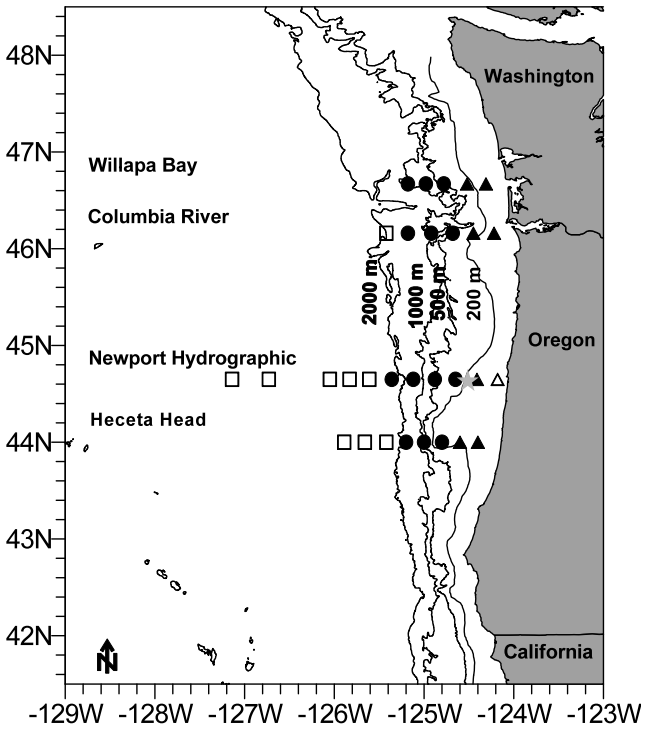

Figure 1. Locations and classifications (coastal [triangles], offshore [circles], and far-offshore [squares]) of stations sampled during this study off the Oregon and Washington coasts in 2004–2009. Contour lines representing the 200-, 500-, 1000-, and 2000-m isobaths are shown. Filled symbols depict normally-sampled stations, and open symbols depict irregularly-sampled stations. The filled star symbol represents the location of the National Oceanic and Atmospheric Administration's (NOAA) Stonewall Banks buoy.

approach was adopted because stress levels were sufficiently low (≤0.16) in all cases and results were sufficiently interpretable ecologically in two-dimensional space (Clarke and Warwick 2001).

For the cross-shelf distributional analyses, stations were classified as coastal (<~50 km from shore), offshore (~50–100 km), and far-offshore (>~100 km) (fig. 1) based on the results of the MDS and cluster analyses. The Shannon-Wiener diversity index (*H'*) was used to measure larval diversity, where higher *H'* values denote greater diversity (Shannon and Weaver 1949). Taxa evenness was assessed using Pielou's evenness index (*J'*), although evenness was not included in the analyses because it was highly negatively correlated with diversity ($p < 0.0001$). Analysis of variance (ANOVA) and Tukey's multiple range tests were applied to the $\log_e(n + 0.1)$-transformed larval station concentrations and diversity measures to test for significant differences ($p < 0.05$) between annual, seasonal, latitudinal, and cross-shelf scales. Weighted mean (based on concentration) larval lengths of dominant taxa were also calculated for each sample, and were similarly tested for significant differences between annual, seasonal, latitudinal, and cross-shelf scales.

A non-parametric multi-response permutation procedure (MRPP) was used to test for between-group differences in larval concentrations within several factors by calculating an A-statistic ranging from 0 to 1, with the maximum value indicating complete agreement between groups (McCune and Mefford 1999). Factors and groups within those factors were defined as: (1) year (2004, 2005, 2006, 2007, 2008, and 2009), (2) month (May, June, July, August, September, October/November), and (3) latitude (WB, CR, NH, and HH transects) and (4) cross-shelf (coastal, offshore, and far-offshore). Statistical significance was determined at the $\alpha = 0.001$ level. Indicator species analysis (ISA) was also performed on the fourth root-transformed larval fish concentrations using 5000 random restarts for each Monte Carlo simulation to test taxonomic fidelity within each group (Dufrêne and Legendre 1997). Statistical significance for this test was determined at the $\alpha = 0.05$ level. All MRPP and ISA analyses were performed using PC-Ord Version 5 statistical software (McCune and Mefford 2006).

Because sampling during October (2005) and November (2004) only occurred in one year, the samples were combined into a single seasonal unit (October/November) and only included in between-month cluster, MDS, ANOVA, MRPP, and ISA analyses. Also, because far-offshore stations were only sampled periodically, the data were only included in similar cross-shelf analyses. Unidentified larvae were excluded from all analyses except for ANOVA tests involving total larvae.

A non-parametric multivariate procedure (BIO-ENV) was used to analyze the relationship between select local environmental variables and larval fish community structures. The details of the BIO-ENV algorithm and its suitability for use in analyzing biological/environmental data interactions are described by Clarke and Warwick (2001) and Clarke and Gorley (2006). Sample concentration by taxonomic similarity matrices were analyzed in association with several environmental variables: latitude, station depth (m), station distance from shore (km), and water temperature, salinity, density, fluorescence, and turbidity all measured at 20-m depth. Since DO and DO saturation data were only collected in 2008 and 2009, two separate analyses were performed: one using the sample by taxonomic similarity matrix in association with only latitude, station depth, station distance from shore, temperature, salinity, density, fluorescence, and turbidity (336 samples × 60 taxa), and the other incorporating samples with all environmental data available including DO and DO saturation (151 samples × 60 taxa). Samples containing either no larvae or coincidental environmental data were excluded from analyses. Both BIO-ENV analyses were performed using the Spearman rank correlation method on normalized Euclidean distance similarity matrices of

$\log_e(n + 1)$-transformed, non-standardized environmental variables by fourth root-transformed larval sample concentrations (Clarke and Gorley 2006). All cluster, MDS, and BIO-ENV analyses were performed using PRIMER Version 6.1.7 statistical software (Clarke and Gorley 2006).

Pair-wise correlation analyses were conducted to assess the relationship between concentrations of the most abundant taxa (i.e., *Engraulis mordax*, *Lyopsetta exilis*, *Sebastes* spp., *Stenobrachius leucopsarus*, and *Tarletonbeania crenularis*) and total fish larvae, larval diversity, and both local and larger-scale environmental variables. As noted above, local environmental variables are water temperature, salinity, density, fluorescence, and turbidity for all years, and DO and DO saturation for 2008 and 2009. Larger-scale environmental variables that were easily available and may influence the distribution, concentration, and transport of coastal pelagic fish larvae in the NCC region included: Multivariate El Niño-Southern Oscillation Index (MEI; http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/ 2011), Pacific Decadal Oscillation (PDO; http://jisao.washington.edu/pdo/ 2011), Northern Oscillation Index (NOI; http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix.html 2011), sea-surface temperature (SST, °C; http://www.ndbc.noaa.gov/ 2011) recorded from NOAA's Stonewall Banks buoy located 20 nm west of Newport, Oregon (44.64°N, 124.50°W), and eastward Ekman transport (EET, kg m^{-1}; http://www.pfeg.noaa.gov/products/las.html 2011), north-south Ekman transport (NET, kg m^{-1}; http://www.pfeg.noaa.gov/products/las.html 2011), and Upwelling Index (UPW; http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/PFELindices.html 2011) each for 45°N, 125°W, and Columbia River outflow (COL, 1000 ft s^{-1}; http://www.cbr.washington.edu/dart/river.html 2011) measured at Bonneville Dam located 235 km upriver from the mouth of the Columbia River. SST recorded from NOAA's Stonewall Banks buoy was used as a consistent, general indicator of SST in the study region as a whole (Brodeur et al. 2008; Auth et al. 2011), and thus is referred to as a larger-scale variable. Missing values in the SST data set were due to equipment failure on the buoy. Values for the local environmental variables used in analyses were taken from different depths in the water column at each station corresponding to the mean depth for each taxon as reported by Auth and Brodeur (2006) and Auth et al. (2007): *E. mordax*, 10–m depth; *Sebastes* spp., total larvae, and larval diversity, 20–m depth; *L. exilis* and *S. leucopsarus*, 40–m depth; *T. crenularis*, 50–m depth. Monthly-averaged larval concentrations and diversity were lagged 0–5 months behind the larger-scale environmental variables to account for delayed effects of changes in basin-wide atmospheric-oceanic processes on regional hydrography affecting larval concentrations and diversity. Due to the large amount of zero values in the data set, samples with no larvae were excluded from the local environmental analysis. Similarly, since *E. mordax* and *L. exilis* larvae were highly seasonal and therefore not collected during several cruises in the study ($n = 9$ and 8, respectively), those cruises were excluded from the larger-scale environmental analyses for these species. Prior to inclusion in the analyses, larval concentrations were $\log_e(n + 0.1)$-transformed. Statistical significance was determined at the $\alpha = 0.0l$ level. All ANOVA and correlation analyses were performed using the statistical software JMP Version 7.0 (SAS Institute Inc. 2007).

Non-parametric multiplicative regression (NPMR) analysis was similarly conducted to further assess the relationship between concentrations of dominant taxa and total larvae, larval diversity, and local and larger-scale environmental variables, and to test for interactions between these variables. Details of the NPMR algorithm and its suitability for use in analyzing biological/environmental data interactions are described by McCune (2006). Best-fit models were developed using a local mean estimator with a Guassian weighting function, a predictor ratio minimum of 10, 5% improvement criterion, a minimum average neighborhood size of n (samples) × 0.05, a step size equal to 5% of the range, with 10% maximum allowable missing estimates, a minimal backtracking search method, and leave-one-out cross validation. Prior to inclusion in the analyses, larval concentrations were $\log_e(n + 0.1)$-transformed. Statistical significance for each selected model was evaluated after 1000 random runs. All NPMR analyses were performed using the statistical software HyperNiche Version 2.0 (McCune and Mefford 2009).

RESULTS

Environmental Factors

Larger-scale (i.e., MEI, PDO, NOI, SST, EET, NET, UPW, COL) environmental factors varied annually and seasonally throughout the study (fig. 2). Weak El Niño conditions were prevalent during the 2004 sampling season, while 2005 was marked by highly anomalous late upwelling (mid-July) unrelated to the El Niño-Southern Oscillation (ENSO) (Brodeur et al. 2006; Schwing et al. 2006) followed by a sudden negative shift in the MEI that persisted through mid-2006. La Niña conditions were prevalent during most of the 2007 and 2008 sampling seasons, followed by a switch to El Niño conditions in mid-2009. Monthly-averaged MEI, PDO, and SST values were positively correlated with each other but negatively correlated with NOI values, while SST values were positively correlated with UPW but negatively correlated with EET values ($p < 0.01$).

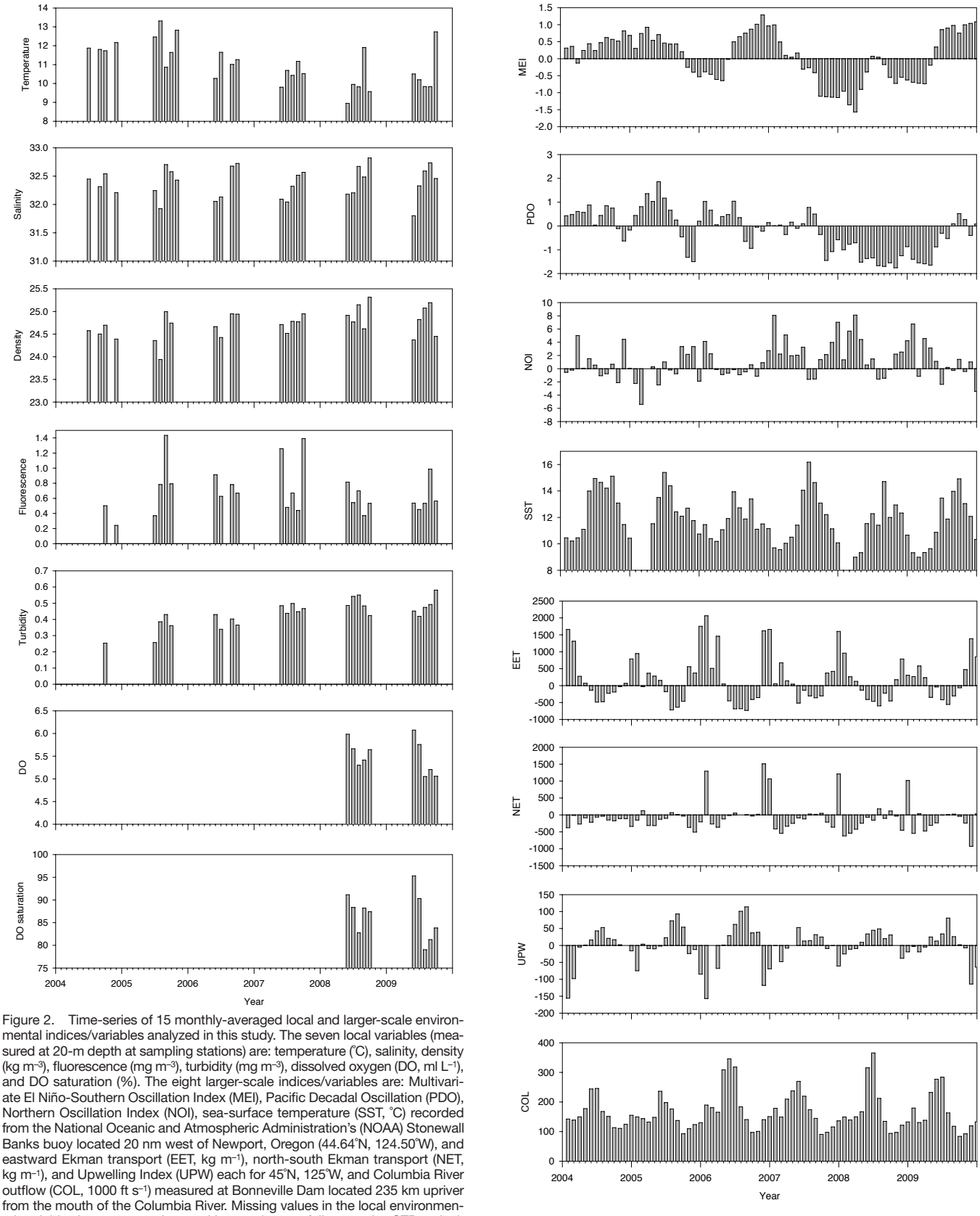

Figure 2. Time-series of 15 monthly-averaged local and larger-scale environmental indices/variables analyzed in this study. The seven local variables (measured at 20-m depth at sampling stations) are: temperature (°C), salinity, density (kg m^{-3}), fluorescence (mg m^{-3}), turbidity (mg m^{-3}), dissolved oxygen (DO, ml L^{-1}), and DO saturation (%). The eight larger-scale indices/variables are: Multivariate El Niño-Southern Oscillation Index (MEI), Pacific Decadal Oscillation (PDO), Northern Oscillation Index (NOI), sea-surface temperature (SST, °C) recorded from the National Oceanic and Atmospheric Administration's (NOAA) Stonewall Banks buoy located 20 nm west of Newport, Oregon (44.64°N, 124.50°W), and eastward Ekman transport (EET, kg m^{-1}), north-south Ekman transport (NET, kg m^{-1}), and Upwelling Index (UPW) each for 45°N, 125°W, and Columbia River outflow (COL, 1000 ft s^{-1}) measured at Bonneville Dam located 235 km upriver from the mouth of the Columbia River. Missing values in the local environmental variable data sets are due to either equipment failure on the CTD or lack of sampling due to inclement weather or other equipment malfunctions, while missing values in the SST data set are due to equipment failure on the buoy.

TABLE 1

Taxon composition, frequency of occurrence, mean concentration (no. 1000 m^{-3}), percent of total concentration, month (May [M], June [Jn], July [Jy], August [A], September [S], October [O], November [N]), latitudinal transect (north-south: Willapa Bay [WB], Columbia River [CR], Newport Hydrographic [NH], and Heceta Head [HH]), and cross-shelf region (C = coastal, O = offshore, F = far offshore) for all larval fish collected during this study off the Oregon and Washington coasts in 2004-2009. ⋆ = larvae collected during months outside their seasonal spawning period for this region as reported in Matarese et al. (1989).

Taxon	Common name	Frequency occurrence	Mean concentration	Total concentration	Month	Transect	Cross-shelf region
Clupeidae							
Sardinops sagax	Pacific sardine	0.01	0.22	0.11	M, Jy	WB, NH	C, O, F
Engraulidae							
Engraulis mordax	Northern anchovy	0.23	75.94	36.92	M-O⋆	All	C, O, F
Bathylagidae							
Bathylagus pacificus	Pacific blacksmelt	0.01	0.06	0.03	M-Jy⋆	CR, NH, HH	C, O, F
Lipolagus ochotensis	Eared blacksmelt	0.07	0.80	0.39	M-S, N⋆	All	C, O, F
Osmeridae							
Undetermined spp.	Smelts	0.01	0.09	0.04	M-Jn	WB, CR	C
Phosichthyidae							
Cyclothone spp.	Bristlemouths	<0.01	0.01	0.01	O	CR	O
Stomiidae							
Chauliodus macouni	Pacific viperfish	0.04	0.29	0.14	M-O	All	C, O
Tactostoma macropus	Longfin dragonfish	<0.01	0.01	0.01	A	CR	O
Notosudidae							
Scopelosaurus spp.	Paperbones/Waryfish	<0.01	0.01	<0.01	M	NH	F
Paralepididae							
Lestidiops ringens	Slender barracudina	0.01	0.05	0.02	M, A, N	NH, HH	O, F
Myctophidae							
Protomyctophum crockeri	California flashlightfish	0.03	0.24	0.12	M-Jn, A-N	All	C, O, F
Protomyctophum thompsoni	Bigeye lanternfish	0.05	0.41	0.20	M-N	All	O, F
Tarletonbeania crenularis	Blue lanternfish	0.36	6.49	3.16	M-N⋆	All	C, O, F
Nannobrachium regale	Pinpoint lampfish	0.17	2.07	1.01	M-O	All	C, O, F
Nannobrachium ritteri	Broadfin lampfish	<0.01	0.01	0.01	O	CR	O
Stenobrachius leucopsarus	Northern lampfish	0.47	39.55	19.23	M-N⋆	All	C, O, F
Diaphus theta	California headlightfish	0.03	0.70	0.34	M-S	All	O, F
Undetermined spp.		<0.01	0.01	0.01	Jn	WB	O
Merlucciidae							
Merluccius productus	Pacific hake	0.02	0.26	0.13	M-Jn	All	O, F
Gadidae							
Microgadus proximus	Pacific tomcod	<0.01	0.02	0.01	M	WB	C
Ophidiidae							
Spectrunculus grandis	Pudgy cuskeel	<0.01	0.01	<0.01	M	NH	O
Bythitidae							
Cataetyx rubrirostris	Rubynose brotula	<0.01	0.01	0.01	Jn	NH	O
Trachipteridae							
Trachipterus altivelis	King-of-the-salmon	0.01	0.03	0.02	Jn, A-S	CR, NH	O, F
Melamphaidae							
Melamphaes lugubris	Highsnout bigscale	<0.01	0.02	0.01	M, S	WB, NH	O, F
Scorpaenidae							
Sebastes spp.	Rockfishes	0.64	66.48	32.32	M-N	All	C, O, F
Sebastolobus spp.	Thornyheads	0.05	0.77	0.37	M-Jy, O⋆	CR, NH, HH	C, O, F
Hexagrammidae							
Hexagrammos octogrammus	Masked greenling	<0.01	0.03	0.01	M-Jn	WB, HH	O
Cottidae							
Scorpaenichthys marmoratus	Cabezon	<0.01	0.01	0.01	M	WB	O
Chitonotus pugetensis	Roughback sculpin	<0.01	0.01	0.01	Jy⋆	HH	O
Paricelinus hopliticus	Thornback sculpin	0.01	0.11	0.05	M, A-S	NH, HH	C, O
Radulinus asprellus	Slim sculpin	0.01	0.13	0.06	M, Jy	All	C
Ruscarius meanyi	Puget Sound sculpin	0.01	0.03	0.02	M	CR, NH, HH	C
Artedius harringtoni	Scalyhead sculpin	0.03	0.23	0.11	M-Jn, A-S	All	C, O
Cottus asper	Prickly sculpin	<0.01	0.01	0.01	M	CR	C
Undetermined spp.	Sculpins	<0.01	0.01	0.01	A	CR	O
Agonidae							
Xeneretmus latifrons	Blacktip poacher	<0.01	0.03	0.01	M, A⋆	CR, NH	C, O
Bathyagonus pentacanthus	Bigeye poacher	<0.01	0.06	0.03	Jn	NH	F
Psychrolutidae							
Malacocottus zonurus	Darkfin sculpin	<0.01	0.01	0.01	Jn	HH	O

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TABLE 1 (CONT'D.)

Taxon composition, frequency of occurrence, mean concentration (no. 1000 m^{-3}), percent of total concentration, month (May [M], June [Jn], July [Jy], August [A], September [S], October [O], November [N]), latitudinal transect (north-south: Willapa Bay [WB], Columbia River [CR], Newport Hydrographic [NH], and Heceta Head [HH]), and cross-shelf region (C = coastal, O = offshore, F = far offshore) for all larval fish collected during this study off the Oregon and Washington coasts in 2004-2009. ⋆ = larvae collected during months outside their seasonal spawning period for this region as reported in Matarese et al. (1989).

Taxon	Common name	Frequency occurrence	Mean concentration	Total concentration	Month	Transect	Cross-shelf region
Liparidae							
Liparis fucensis	Slipskin snailfish	0.13	1.11	0.54	M-S, N⋆	All	C, O, F
Liparis pulchellus	Showy snailfish	<0.01	0.04	0.02	Jn-Jy	WB, CR	C
Liparis spp.	Snailfishes	<0.01	0.03	0.01	M, Jy	NH, HH	C, O
Carangidae							
Trachurus symmetricus	Jack mackerel	<0.01	0.01	<0.01	A	WB	O
Bathymasteridae							
Ronquilus jordani	Northern ronquil	<0.01	0.04	0.02	M	CR, NH	C
Stichaeidae							
Poroclinus rothrocki	Whitebarred prickleback	<0.01	0.01	<0.01	M	CR	C
Plectobranchus evides	Bluebarred prickleback	0.01	0.08	0.04	M, A	NH, HH	C, O
Pholidae							
Pholis spp.	Gunnels	<0.01	0.02	0.01	M	WB	C
Icosteidae							
Icosteus aenigmaticus	Ragfish	0.01	0.09	0.04	M	WB, CR, NH	C, O, F
Gobiidae							
Rhinogobiops nicholsii	Blackeye goby	<0.01	0.02	0.01	A	NH	O
Centrolophidae							
Icichthys lockingtoni	Medusafish	0.01	0.08	0.04	M-Jn	CR, NH, HH	O, F
Paralichthyidae							
Citharichthys sordidus and *stigmaeus*	Pacific and speckled sanddab	0.15	1.81	0.88	M-N⋆	All	C, O, F
Pleuronectidae							
Atheresthes stomias	Arrowtooth flounder	<0.01	0.02	0.01	M	CR, HH	O
Embassichthys bathybius	Deepsea sole	<0.01	0.01	<0.01	Jn	WB	O
Eopsetta jordani	Petrale sole	<0.01	0.01	<0.01	M	NH	O
Glyptocephalus zachirus	Rex sole	0.09	0.85	0.41	M-S⋆	All	C, O, F
Isopsetta isolepis	Butter sole	0.03	0.24	0.12	M-Jn⋆	WB, CR, HH	C, O
Lyopsetta exilis	Slender sole	0.25	5.20	2.53	M-S⋆	All	C, O, F
Microstomus pacificus	Dover sole	0.06	0.55	0.27	M-S⋆	All	O, F
Parophrys vetulus	English sole	0.01	0.02	0.01	M-Jn⋆	NH, HH	C, O
Platichthys stellatus	Starry flounder	<0.01	0.02	0.01	M⋆	CR	C
Psettichthys melanostictus	Sand sole	0.01	0.07	0.03	M-Jy	All	C, O
Undetermined		0.02	0.14	0.07	M-A	WB, CR, NH	C, O

Taxonomic Composition

A total of 16,524 fish larvae were collected and represented 60 taxa and 30 families (table 1). Five families accounted for 98% of the total standardized larval concentration: Engraulidae (37%), Scorpaenidae (33%), Myctophidae (24%), Pleuronectidae (3%), and Paralichthyidae (1%). Within these families, five taxa were dominant based on total mean concentration (94% of the total standardized larval concentration) and frequency of occurrence from all samples: *E. mordax*, *Sebastes* spp., *S. leucopsarus*, *T. crenularis*, and *L. exilis*. Several other taxa were collected at relatively high frequencies but with lower mean concentrations: *Nannobrachium regale*, *Citharichthys* spp., *Liparis fucensis*, *Glyptocephalus zachirus*, *Lipolagus ochotensis*, *Microstomus pacificus*, *Protomyctophum thompsoni*, *Sebastolobus* spp., *Chauliodus macouni*, *Diaphus theta*, *Artedius harringtoni*, *Isopsetta isolepis*, and *Protomyctophum crockeri* (listed in order of highest to lowest mean concentration).

Cluster and Multidimensional Scaling (MDS) Analyses

Several taxonomic, seasonal, and cross-shelf assemblages were identified, although no annual or latitudinal assemblages were apparent (figs. 3a–c, 4a–b). Taxonomic assemblages could not be explained by differences in a single factor (e.g., cross-shelf affiliation), but rather seem to be the result of an association between certain taxa based on the interaction between multiple factors (e.g., annual, seasonal, latitudinal, and cross-shelf). Larvae clustered as four seasonal assemblages along a continuous temporal gradient: spring (May), early summer (June–July), late summer (August–September), and fall (September–October/November). Cluster and MDS analyses indicated the presence of three cross-shelf assemblages: coastal (<~50 km from shore), offshore (~50–100 km), and far-offshore (>~100 km). Although there appears to be a continuous spatial gradient between these assemblages, the offshore

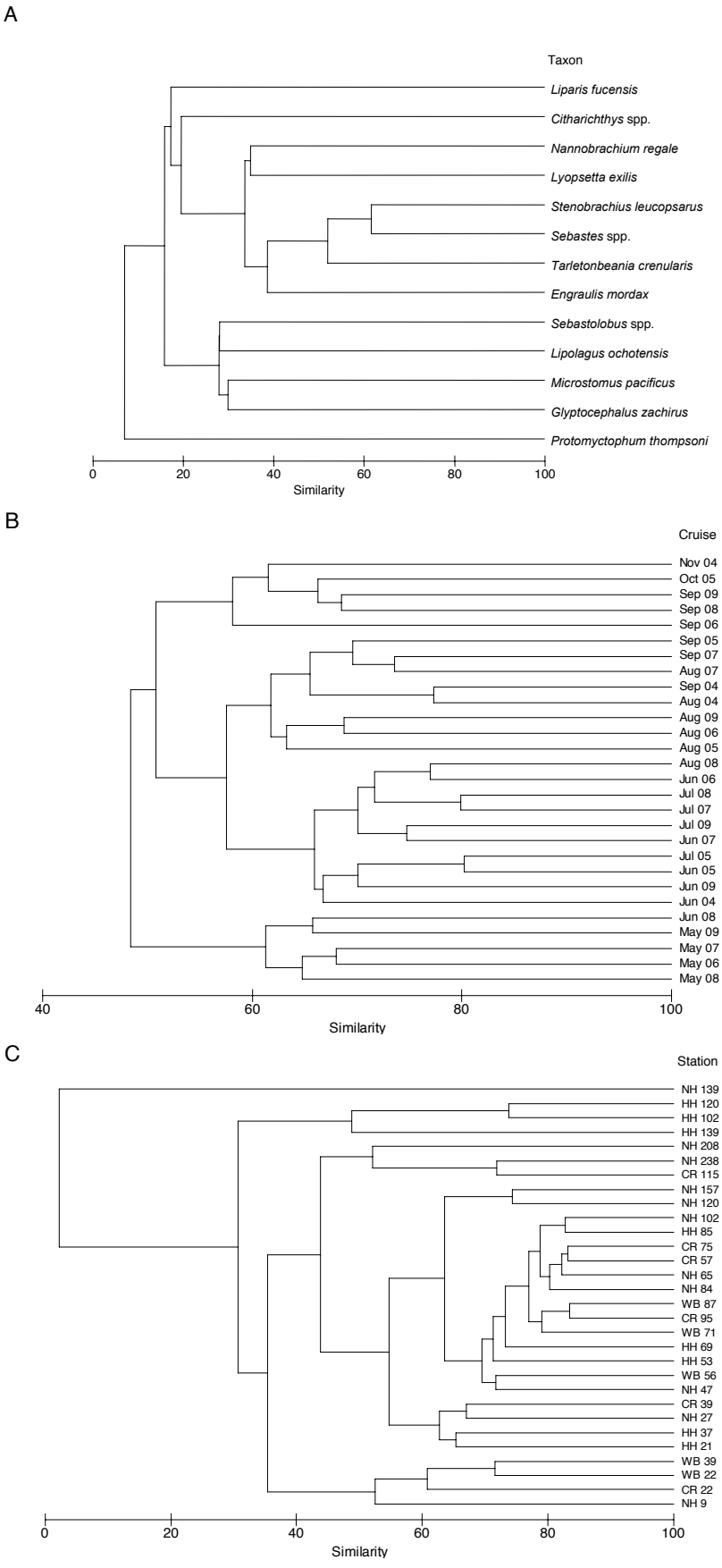

Figure 3. Dendrograms resulting from cluster analysis performed on larval fishes collected during this study off the Oregon and Washington coasts in 2004–2009: (A) taxon, (B) cruise (month and year), and (C) station (transect [north-south: Willapa Bay (WB), Columbia River (CR), Newport Hydrographic (NH), and Heceta Head (HH)] and distance from shore [km]).

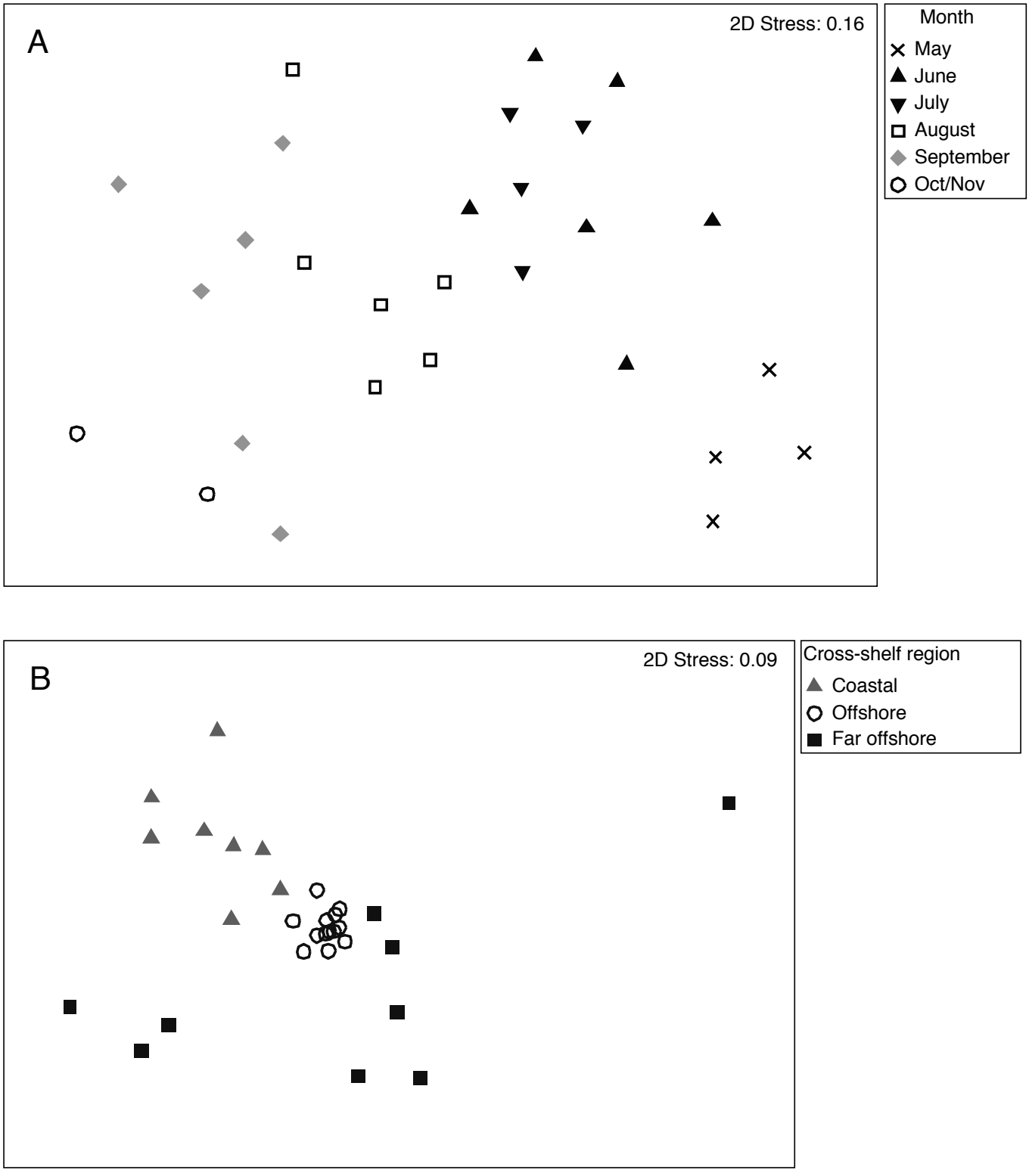

Figure 4. Plots resulting from multidimensional scaling analysis performed on larval fishes collected during this study off the Oregon and Washington coasts in 2004–2009: (A) month and (B) cross-shelf region.

TABLE 2
Annual mean concentrations (no. 1000 m^{-3}) and diversity (H') of fish larvae collected during this study off the Oregon and Washington coasts in 2004–2009 (1 SE in parentheses). For between-year comparisons of each taxon and larval diversity, different superscripts indicate significant differences (ANOVA $p < 0.05$).

	2004	2005	2006	2007	2008	2009
Engraulis mordax	20.6 (9.5)^{ab}	215.3 (78.1)^{a}	4.2 (1.7)^{b}	13.0 (4.9)^{b}	62.3 (56.9)^{b}	141.2 (106.2)^{b}
Lyopsetta exilis	4.0 (1.8)^{ab}	1.3 (0.4)^{b}	3.6 (1.1)^{ab}	10.1 (2.2)^{a}	3.6 (1.2)^{ab}	8.5 (1.7)^{a}
Sebastes spp.	89.2 (28.6)	52.7 (13.6)	22.9 (4.6)	60.5 (18.3)	68.3 (13.7)	129.6 (49.2)
Stenobrachius leucopsarus	4.0 (1.6)^{b}	37.1 (10.7)^{ab}	44.1 (10.9)^{ab}	48.2 (9.6)^{a}	45.3 (9.6)^{a}	36.3 (7.9)^{ab}
Tarletonbeania crenularis	2.6 (1.1)	9.0 (2.2)	5.1 (1.3)	4.9 (0.9)	6.3 (1.4)	7.2 (1.4)
Total larvae	126.5 (40.3)	328.0 (82.4)	92.0 (15.5)	149.5 (26.1)	194.2 (61.0)	337.4 (126.0)
Diversity	0.76 (0.05)	0.68 (0.04)	0.72 (0.03)	0.77 (0.03)	0.69 (0.03)	0.74 (0.03)

TABLE 3
Monthly mean concentrations (no. 1000 m^{-3}) and diversity (H') of fish larvae collected during this study off the Oregon and Washington coasts in 2004–2009 (1 SE in parentheses). For between-month comparisons of each taxon and larval diversity, different superscripts indicate significant differences (ANOVA $p < 0.05$).

	May	June	July	August	September	Oct/Nov
Engraulis mordax	0.2 (0.2)^{b}	206.4 (114.8)^{a}	257.6 (110.9)^{a}	5.6 (1.8)^{b}	0.6 (0.3)^{b}	0 (0)^{b}
Lyopsetta exilis	14.1 (2.0)^{a}	12.5 (2.3)^{a}	2.0 (0.8)^{b}	0.6 (0.2)^{b}	0.1 (0.1)^{b}	0 (0)^{b}
Sebastes spp.	64.6 (17.4)^{ab}	187.2 (53.3)^{a}	85.5 (20.4)^{a}	25.0 (3.6)^{bc}	9.7 (2.3)^{d}	24.7 (18.3)^{cd}
Stenobrachius leucopsarus	72.2 (12.1)^{a}	71.0 (11.0)^{a}	41.6 (10.5)^{ab}	21.2 (5.9)^{b}	1.8 (0.7)^{c}	0.9 (0.5)^{c}
Tarletonbeania crenularis	4.7 (1.1)	9.6 (1.9)	7.5 (1.8)	5.6 (1.0)	4.2 (0.8)	2.5 (0.8)
Total larvae	179.3 (23.6)^{a}	505.4 (134.5)^{a}	400.7 (114.3)^{a}	65.3 (9.4)^{b}	20.1 (2.6)^{c}	30.9 (18.6)^{c}
Diversity	0.74 (0.02)^{b}	0.62 (0.03)^{c}	0.60 (0.04)^{c}	0.82 (0.02)^{ab}	0.87 (0.03)^{a}	0.81 (0.08)^{ab}

TABLE 4
Latitudinal (north-south: Willapa Bay [WB], Columbia River [CR], Newport Hydrographic [NH], and Heceta Head [HH] transects) mean concentrations (no. 1000 m^{-3}), diversity (H'), and weighted (by concentration) mean lengths (mm) of fish larvae collected during this study off the Oregon and Washington coasts in 2004–2009 (1 SE in parentheses). For between-transect comparisons of each taxon and larval diversity, different superscripts indicate significant differences (ANOVA $p < 0.05$).

	Mean concentration				Mean length			
	WB	CR	NH	HH	WB	CR	NH	HH
Engraulis mordax	203.7 (119.4)	36.8 (11.4)	24.3 (8.7)	85.3 (46.5)	7.4 (0.2)^{b}	10.0 (0.3)^{ab}	7.4 (0.3)^{ab}	10.7 (0.3)^{a}
Lyopsetta exilis	2.0 (0.5)^{c}	2.2 (0.6)^{bc}	7.0 (1.5)^{ab}	10.5 (1.8)^{a}	7.9 (0.6)	9.4 (0.6)	8.3 (0.3)	8.8 (0.3)
Sebastes spp.	37.0 (8.4)^{b}	27.1 (6.0)^{b}	77.1 (18.4)^{ab}	138.5 (42.0)^{a}	5.0 (0.1)^{ab}	5.9 (0.1)^{a}	4.4 (0.1)^{b}	4.5 (0.1)^{b}
Stenobrachius leucopsarus	43.2 (9.3)^{ab}	56.6 (10.4)^{a}	39.2 (7.4)^{a}	22.9 (4.9)^{b}	8.3 (0.1)	7.5 (0.1)	7.4 (0.1)	7.7 (0.1)
Tarletonbeania crenularis	4.1 (0.8)	7.8 (1.4)	7.7 (1.3)	5.2 (1.2)	9.6 (0.6)	9.0 (0.4)	7.1 (0.3)	8.5 (0.4)
Total larvae	300.9 (129.1)	142.7 (21.1)	168.5 (26.7)	272.9 (64.1)				
Diversity	0.71 (0.03)	0.75 (0.02)	0.74 (0.02)	0.68 (0.03)				

assemblage is far more tightly clustered and distinct than the coastal and far-offshore groups.

Concentrations and Distributions

Annual Total mean larval concentration decreased from 328 1000 m^{-3} in 2005 to 92 1000 m^{-3} in 2006, and subsequently increased each year to a high of 337 1000 m^{-3} in 2009 (table 2). Larval *E. mordax* concentration in 2005 was >50 times higher than 2006, and was significantly higher than in subsequent years (2006–2009). In contrast, peak concentrations of *L. exilis* in 2007 and 2009 were significantly higher than in 2005, while *S. leucopsarus* concentrations in 2007 and 2008 were significantly higher than in 2004. *Sebastes* spp. and *T. crenularis* larvae exhibited no significant interannual concentration differences.

Monthly Seasonally, total larval concentrations were highest in May–July, decreased significantly in August, and declined further in September–October/November (table 3). Larval *L. exilis* were found predominantly in May–June, while *S. leucopsarus* concentrations peaked in May and decreased steadily to October/November. Larval *E. mordax* were found almost exclusively in June–July, while *Sebastes* spp. larvae were also found in significantly higher concentrations in June–July than in August–October/November. There were no significant

TABLE 5
Cross-shelf (coastal, offshore, far-offshore) mean concentrations (no. 1000 m^{-3}), diversity (H'), and weighted (by concentration) mean lengths (mm) of fish larvae collected during this study off the Oregon and Washington coasts in 2004–2009 (1 SE in parentheses). For between-zonal comparisons of each taxon and larval diversity, different superscripts indicate significant differences (ANOVA $p < 0.05$).

	Mean concentration			Mean length		
	Coastal	Offshore	Far-offshore	Coastal	Offshore	Far-offshore
Engraulis mordax	24.0 (12.5)^{b}	116.3 (45.5)^{a}	65.3 (39.8)^{ab}	9.9 (0.3)	8.5 (0.2)	6.0 (0.4)
Lyopsetta exilis	4.7 (0.9)	6.2 (0.9)	6.6 (2.3)	9.1 (0.4)	8.4 (0.2)	10.6 (0.8)
Sebastes spp.	15.8 (3.9)^{b}	103.6 (19.1)^{a}	13.2 (4.1)^{ab}	4.0 (0.05)^{b}	4.9 (0.04)^{a}	6.5 (0.5)^{a}
Stenobrachius leucopsarus	1.8 (0.6)^{b}	61.0 (5.9)^{a}	134.6 (44.4)^{a}	7.1 (0.3)	7.7 (0.1)	6.7 (0.1)
Tarletonbeania crenularis	0.3 (0.2)^{c}	9.5 (0.9)^{b}	24.1 (6.3)^{a}	7.7 (1.2)	8.4 (0.2)	6.5 (0.3)
Total larvae	53.1 (13.2)^{b}	311.4 (52.5)^{a}	285.7 (71.2)^{a}			
Diversity	0.82 (0.03)^{a}	0.69 (0.01)^{b}	0.68 (0.06)^{ab}			

TABLE 6
Monthly weighted (by concentration) mean lengths (mm) of fish larvae collected during this study off the Oregon and Washington coasts in 2004–2009 (1 SE in parentheses). For between-month comparisons of each taxon, different superscripts indicate significant differences (ANOVA $p < 0.05$).

	May	June	July	August	September	Oct/Nov
Engraulis mordax	2.2 (0)^{b}	5.0 (0.1)^{b}	12.4 (0.2)^{a}	15.3 (0.7)^{a}	16.3 (3.3)^{a}	—
Lyopsetta exilis	7.7 (0.2)^{b}	8.5 (0.3)^{b}	14.2 (1.0)^{a}	16.2 (1.8)^{a}	14.1 (4.5)^{ab}	—
Sebastes spp.	4.1 (0.1)^{cd}	4.2 (0)^{d}	5.0 (0.1)^{bc}	7.1 (0.2)^{a}	5.0 (0.3)^{b}	4.6 (0.2)^{bcd}
Stenobrachius leucopsarus	7.0 (0.1)^{d}	6.6 (0.1)^{d}	8.7 (0.1)^{c}	10.9 (0.2)^{b}	13.5 (0.6)^{a}	6.2 (2.1)^{d}
Tarletonbeania crenularis	6.9 (0.5)^{b}	6.4 (0.2)^{b}	10.4 (0.5)^{a}	10.5 (0.5)^{a}	8.4 (0.5)^{ab}	6.3 (0.6)^{b}

monthly differences in mean concentration for *T. crenularis* larvae. These seasonal patterns in larval concentrations persisted within each sampled year.

Latitudinal Concentrations of *Sebastes* spp. and *L. exilis* larvae were significantly greater along the southernmost than northern transects, while concentrations of *S. leucopsarus* larvae were significantly higher along the central than southernmost transects (table 4). Concentrations of total larvae and *E. mordax* were highest along the northern- and southernmost transects, while *T. crenularis* larvae showed the opposite pattern. However, despite these regional differences, the distribution patterns of the three groups did not exhibit a significant north to south concentration pattern. These latitudinal patterns were also similar within most sampled months and years.

Cross-shelf Concentrations of the five dominant taxa and total larvae were higher in the offshore and far-offshore regions than in the coastal region (table 5); a pattern that persisted within each sampled month and year. Larval *E. mordax* and *Sebastes* spp. concentrations were significantly higher in the offshore than coastal region, while *S. leucopsarus* and total larval concentrations were significantly higher in both the offshore and far-offshore regions than in the coastal region. Larval *T. crenularis* concentration increased steadily and significantly from onshore to far-offshore direction; a similar sequential increase in *L. exilis* concentration was not significant.

Lengths

Weighted mean length differences of most taxa examined generally exhibited patterns opposite to their concentration differences across monthly, latitudinal, and cross-shelf scales (i.e., largest sizes were in regions with lowest concentrations; table 3–6), and generally within months and years. However, both concentration and length of *Sebastes* spp. larvae were significantly larger offshore than in coastal waters and, on average, the largest larvae occurred far-offshore.

Diversity

Larval diversity varied significantly between months and cross-shelf regions, but not between years or latitudinal transects (table 2–5). Diversity was generally inversely proportional to larval concentration. It was highest in September and lowest in June and July, and decreased with distance from shore. These patterns were generally consistent within months and years.

Multi-response Permutation Procedure (MRPP) and Indicator Species Analysis (ISA)

The results of MRPP analyses revealed significant between-group differences in larval concentrations within each of the annual, monthly, latitudinal, and cross-shelf factors (table 7). A-statistic values indicated that taxonomic association was strongest for the monthly and cross-shelf factors. Significant indicator taxa were also

TABLE 7

Results of the multi-response permutation procedure (MRPP) and indicator species analysis (ISA) for annual (2004–2009), monthly (May–October/November), latitudinal (north-south: Willapa Bay [WB], Columbia River [CR], Newport Hydrographic [NH], and Heceta Head [HH] transects), and cross-shelf (coastal, offshore, far-offshore) differences in composition of fish larvae collected during this study off the Oregon and Washington coasts. Significant indicator taxa ($p < 0.05$) are listed with the factor category with which each taxon is associated in parentheses. Full taxon names are listed in Table 1.

Factor	MRPP A-statistic	*p*-value	Indicator taxa
Year	0.021	<0.001	*Sebastes* spp. (2004); *Citharichthys* spp. and *E. mordax* (2005); *L. ochotensis*, *M. productus*, and *P. crockeri* (2006); *G. zachirus* (2008)
Month	0.076	<0.001	*G. zachirus*, *I. aenigmaticus*, *I. isolepis*, *L. fucensis*, *L. ochotensis*, *L. exilis, M. productus*, *M. pacificus*, *P. evides*, *R. asprellus*, *R. meanyi*, *S. leucopsarus* (May); *N. regale* (June); *E. mordax* and *Sebastes* spp. (July)
Latitude	0.014	<0.001	*L. fucensis,* Osmeridae, *S. sagax* (WB); *P. crockeri* (CR); *L. exilis*, *P. evides*, and *Sebastes* spp. (HH)
Cross-shelf	0.049	<0.001	*A. harringtoni* and *R. asprellus* (coastal); *Sebastes* spp. (offshore); *B. pentacanthus*, *D. theta*, *I. lockingtoni, I. aenigmaticus*, *L. ochotensis, M. productus*, *M. pacificus*, *N. regale*, *S. sagax*, *Scopelosaurus* spp., *Sebastolobus* spp., *S. leucopsarus*, *T. crenularis*, and *T. altivelis* (far-offshore)

TABLE 8

Correlation coefficients for 15 variables collected during this study: station distance from shore (km, Dist. shore), temperature (°C), salinity, density (sigma theta, kg m^{-3}), fluorescence (mg m^{-3}), turbidity (mg m^{-3}), dissolved oxygen concentration (DO, ml L^{-1}), DO saturation (%), $\log_e(n + 0.1)$-transformed concentrations (no. 1000 m^{-3}) of *Engraulis mordax*, *Lyopsetta exilis*, *Sebastes* spp., *Stenobrachius leucopsarus*, *Tarletonbeania crenularis*, and total larvae, and larval diversity (*H'*). Samples containing no larvae were excluded. Values for the environmental variables used in the analysis were taken from different depths in the water column at each station corresponding to either near the surface or the weighted mean depth for each taxon as reported in previous studies: environmental inter-variable comparisons: 1-m depth; *E. mordax*: 10-m depth; *Sebastes* spp., total larvae, and larval diversity: 20-m depth; *L. exilis* and *S. leucopsarus*: 40-m depth; *T. crenularis*: 50-m depth. Sample size (*n*) in parentheses. ⋆ = $p < 0.01$.

	Dist. shore	Temperature	Salinity	Density	Fluorescence	Turbidity	DO	DO saturation
Temperature	0.24⋆ (478)		-0.12 (464)	-0.35⋆ (445)	-0.40⋆ (401)	-0.12 (386)	-0.46 (169)	–0.09 (169)
Salinity	0.18⋆ (464)			0.97⋆ (445)	-0.009 (401)	-0.34⋆ (386)	-0.16⋆ (169)	-0.06 (169)
Density	0.11 (445)				0.08 (396)	–0.29⋆ (386)	–0.06 (169)	–0.04 (169)
Fluorescence	–0.36⋆ (401)					0.33⋆ (386)	0.59⋆ (169)	0.46⋆ (169)
Turbidity	–0.32⋆ (386)						0.38⋆ (169)	0.30⋆ (169)
DO	–0.21⋆ (169)							0.91⋆ (169)
DO Saturation	–0.14 (169)							
Engraulis mordax		0.10 (107)	–0.25⋆ (107)	–0.23 (107)	–0.29⋆ (100)	–0.25 (100)	–0.26 (37)	–0.34 (37)
Lyopsetta exilis		–0.16 (112)	–0.10 (101)	–0.03 (101)	–0.14 (98)	0.24 (98)	0.002 (48)	–0.003 (48)
Sebastes spp.		0.001 (295)	–0.29⋆ (283)	–0.16⋆ (272)	–0.17⋆ (254)	–0.03 (252)	0.25⋆ (114)	0.24⋆ (114)
Stenobrachius leucopsarus		0.28⋆ (214)	–0.38⋆ (202)	–0.38⋆ (199)	0.21⋆ (194)	0.03 (194)	0.53⋆ (91)	0.54⋆ (91)
Tarletonbeania crenularis		0.04 (168)	–0.19 (158)	–0.17 (152)	0.19 (145)	0.04 (144)	0.35⋆ (66)	0.36⋆ (66)
Total larvae		0.17⋆ (389)	–0.45⋆ (374)	–0.36⋆ (360)	–0.12 (338)	–0.13 (336)	0.45⋆ (151)	0.47⋆ (151)
Diversity		0.02 (315)	0.22⋆ (300)	0.10 (290)	–0.02 (276)	0.03 (275)	–0.26⋆ (127)	–0.22 (127)

identified for most years, months, transects, and cross-shelf regions (table 1). Results from the ISA support those from MRPP analyses, since far more significant indicator taxa were found for the monthly and cross-shelf factors than for annual and latitudinal factors.

Environmental Relationships

BIO-ENV A BIO-ENV analysis, which included local environmental variables (i.e., latitude, station depth, station distance from shore, temperature, salinity, density, fluorescence, and turbidity), revealed that the combination of distance from shore and water temperature at 20-m depth explained the most variability (36%) in larval fish concentrations in 2004–2009. The second BIO-ENV analysis, done with the addition of DO and DO saturation in 2008 and 2009, showed that the combination of distance from shore and DO saturation at 20-m depth explained the most concentration variability (42%) during those years.

Correlations Larval concentrations were generally positively correlated with temperature and dissolved oxygen and negatively correlated with salinity, density, and fluorescence, while diversity generally followed the opposite pattern (table 8). However, concentrations of *S. leucopsarus* larvae were significantly positively correlated with fluorescence, while those of *E. mordax* larvae were negatively (although not significantly) correlated with DO and DO saturation. Among the local environmental variables, distance from shore was significantly positively correlated with near-surface temperature and

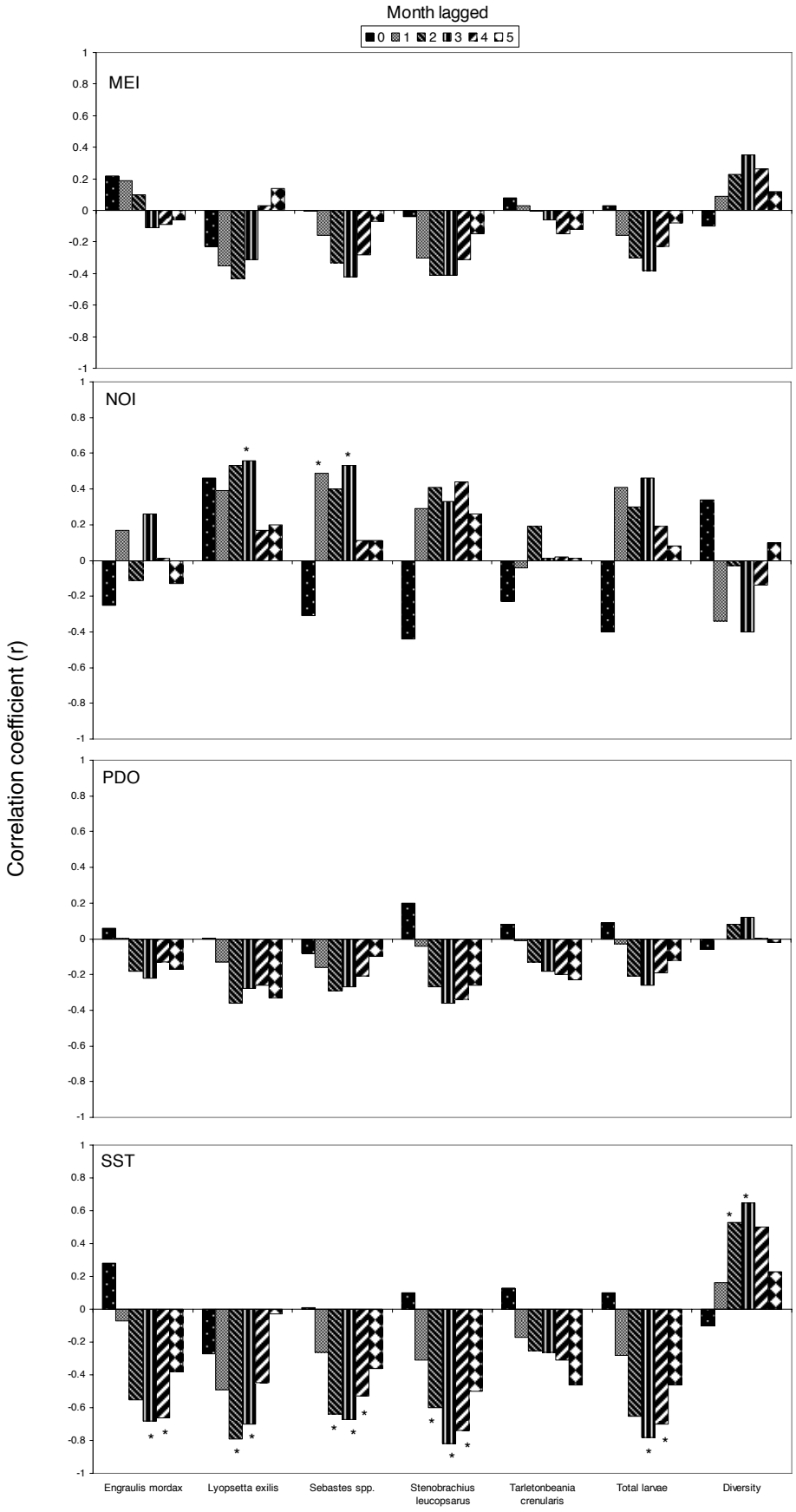

Figure 5. Correlation coefficients for the 0-, 1-, 2-, 3-, 4-, and 5-month lagged $\log_e(n + 0.1)$-transformed concentrations (no. 1000 m^{-3}) of five dominant larval fish taxa and total larvae, and larval diversity, in relation to eight monthly-averaged environmental indices/variables analyzed in this study: Multivariate El Niño-Southern Oscillation Index (MEI), Pacific Decadal Oscillation (PDO), Northern Oscillation Index (NOI), sea-surface temperature (SST, °C) recorded from the National Oceanic and Atmospheric Administration's (NOAA) Stonewall Banks buoy located 20 nm west of Newport, Oregon (44.64°N, 124.50°W), and eastward Ekman transport (EET, kg m^{-1}), north-south Ekman transport (NET, kg m^{-1}), and Upwelling Index (UPW) each for 45°N, 125°W, and Columbia River outflow (COL, 1000 ft s^{-1}) measured at Bonneville Dam located 235 km upriver from the mouth of the Columbia River. * = $p < 0.01$.

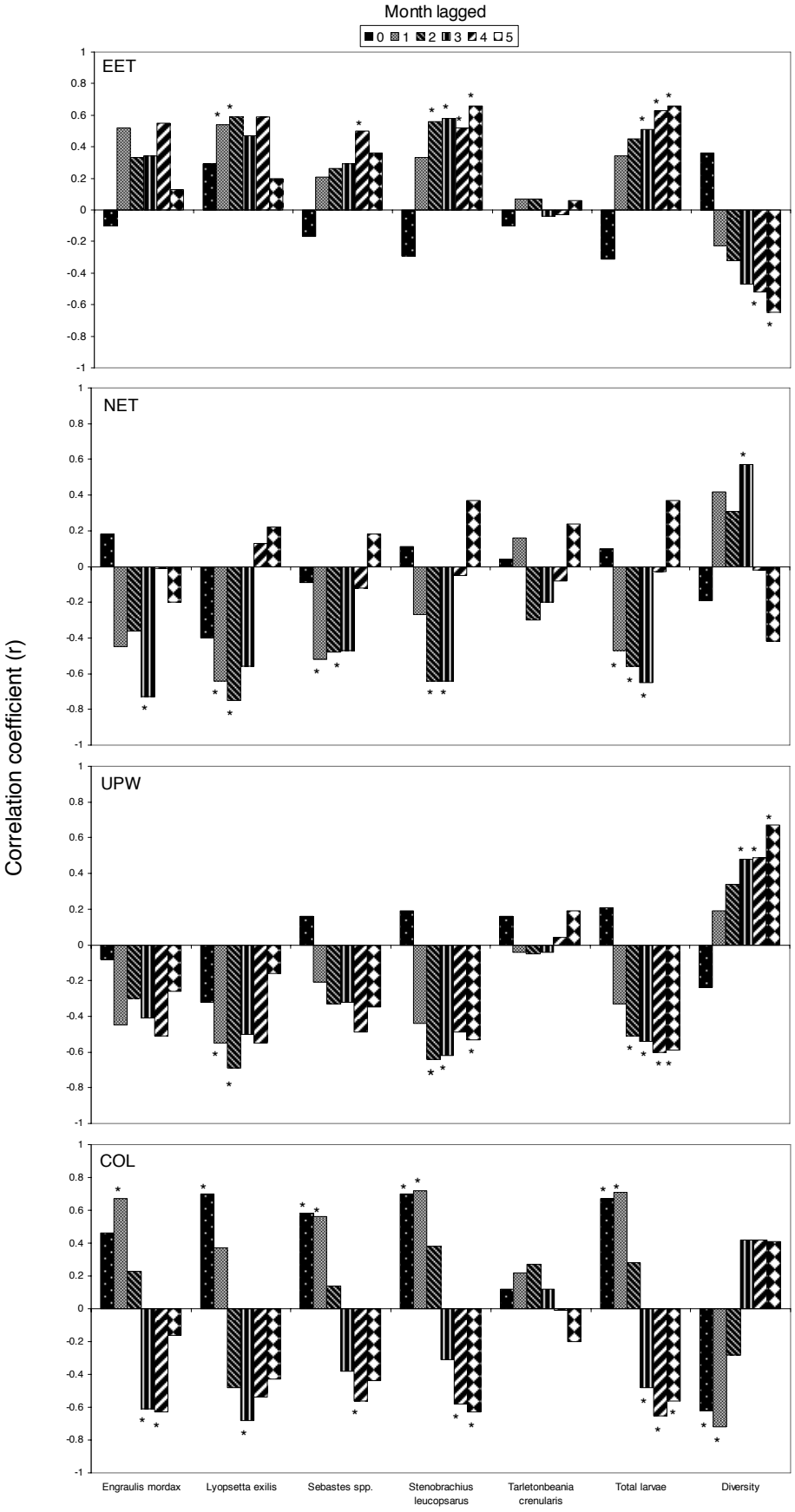

Figure 5. Correlation coefficients for the 0-, 1-, 2-, 3-, 4-, and 5-month lagged $\log_e(n + 0.1)$-transformed concentrations (no. 1000 m^{-3}) of five dominant larval fish taxa and total larvae, and larval diversity, in relation to eight monthly-averaged environmental indices/variables analyzed in this study: Multivariate El Niño-Southern Oscillation Index (MEI), Pacific Decadal Oscillation (PDO), Northern Oscillation Index (NOI), sea-surface temperature (SST, °C) recorded from the National Oceanic and Atmospheric Administration's (NOAA) Stonewall Banks buoy located 20 nm west of Newport, Oregon (44.64°N, 124.50°W), and eastward Ekman transport (EET, kg m^{-1}), north-south Ekman transport (NET, kg m^{-1}), and Upwelling Index (UPW) each for 45°N, 125°W, and Columbia River outflow (COL, 1000 ft s^{-1}) measured at Bonneville Dam located 235 km upriver from the mouth of the Columbia River. * = $p < 0.01$.

TABLE 9

Best-fit non-parametric multiplicative regression (NPMR) model statistics for the analysis of the $\log_e(n + 0.1)$-transformed dominant larval fish taxa and total larval concentrations (no. 1000 m^{-3}) and larval diversity (H') in relation to five in situ environmental variables: temperature (Temp, °C), salinity (Sal), density (Den, sigma theta, kg m^{-3}), fluorescence (Fluor, mg m^{-3}), and turbidity (Turb, mg m^{-3}). Samples containing no larvae were excluded. Values for the environmental variables used in the analysis were taken from different depths in the water column at each station corresponding to the weighted mean depth for each taxon as reported in previous studies: *Engraulis mordax*: 10-m depth; *Sebastes* spp., total larvae, and larval diversity: 20-m depth; *Lyopsetta exilis* and *Stenobrachius leucopsarus*: 40-m depth; *Tarletonbeania crenularis*: 50-m depth.

Taxon/Group	Best-fit model variables	Cross-validated R^2	*p*-value	*n*
Engraulis mordax	Sal, Temp, Fluor	0.18	0.003	100
Lyopsetta exilis	Temp, Turb	0.17	0.003	98
Sebastes spp.	Sal, Fluor	0.10	<0.001	252
Stenobrachius leucopsarus	Den, Turb	0.23	<0.001	194
Tarletonbeania crenularis	Sal	0.09	0.002	144
Total larvae	Sal	0.22	<0.001	336
Diversity	Sal, Temp	0.07	0.004	275

TABLE 10

Best-fit non-parametric multiplicative regression (NPMR) model statistics for the analysis of the monthly-averaged $\log_e(n + 0.1)$-transformed dominant larval fish taxa and total larval concentrations (no. 1000 m^{-3}) and larval diversity (H') in relation to eight larger-scale environmental variables: Multivariate El Niño-Southern Oscillation Index (MEI), Pacific Decadal Oscillation (PDO), Northern Oscillation Index (NOI), sea-surface temperature (SST, °C) recorded from the National Oceanic and Atmospheric Administration's (NOAA) Stonewall Banks buoy located 20 nm west of Newport, Oregon (44.64°N, 124.50°W), and eastward Ekman transport (EET, kg m^{-1}), north-south Ekman transport (NET, kg m^{-1}), and Upwelling Index (UPW) each for 45°N, 125°W, and Columbia River outflow (COL, 1000 ft s^{-1}) measured at Bonneville Dam located 235 km upriver from the mouth of the Columbia River. Months in which no larvae were collected were excluded.

Taxon/Group	Time lag (months)	Best-fit model variables	Cross-validated R^2	*p*-value	*n*
Engraulis mordax	3	COL, SST	0.59	0.13	19
Lyopsetta exilis	2	COL, SST	0.65	0.09	20
Sebastes spp.	4	COL, EET	0.50	0.04	28
Stenobrachius leucopsarus	4	SST, NET	0.64	0.01	28
Tarletonbeania crenularis	4	NOI, UPW	0.20	0.39	28
Total larvae	4	COL, SST	0.67	0.005	28
Diversity	3	COL, NET	0.65	0.002	28

salinity, and negatively correlated with near-surface fluorescence, turbidity, and DO. Descriptive statistics (mean, SE, median, upper and lower 95% confidence intervals [CIs], range [minimum-maximum values], and sample size [*n*]) for the seven local environmental variables for each of the five dominant larval fish taxa and total larvae (weighted based on concentration) collected during this study are presented in the Appendix.

Lagged monthly-averaged larval concentrations were generally positively correlated with the larger-scale environmental variables NOI and EET and negatively correlated with MEI, PDO, SST, NET, and UPW, while diversity generally followed the opposite pattern (fig. 5). The distributions of the 0–5 month lagged correlation coefficients for most of the larger-scale environmental variables were fairly normal in shape, with a mode at ~3 months for most of the dominant taxa, total larvae, and larval diversity. However, 0–2 month lagged larval concentrations were generally positively correlated with COL, while those lagged 3–5 months followed the opposite pattern. Larval *T. crenularis* showed no correlation pattern or significance when compared to any of the larger-scale environmental variables across all time lags, and no significant correlations were found between any of the 0–5 month lagged larval concentrations or diversity and MEI or PDO.

Non-parametric multiplicative regressions (NPMR) NPMR analyses revealed significant best-fit models for the multiplicative effects of both local and larger-scale environmental variables on larval concentrations and diversity. Salinity was the single most important local variable associated with concentrations of total larvae and most of the dominant taxa as well as diversity, often interacting multiplicatively with temperature and/or fluorescence (table 9). COL and SST were the most important larger-scale variables associated with 2–4 month lagged larval concentrations and diversity (table 10). However, NET was also one of two best-fit model variables explaining 3 and 4 month lagged *S. leucopsarus* concentrations and larval diversity, respectively, while EET was one of two best-fit model variable explaining 4 month lagged *Sebastes* spp. concentrations.

DISCUSSION

Taxonomic Composition

The overall composition of the NCC spring–fall epipelagic larval fish community and dominant taxa in 2004–2009 was similar to that reported in previous studies conducted here over the last 40 years (Waldron 1972; Richardson 1973; Richardson and Pearcy 1977; Doyle 1992; Auth and Brodeur 2006; Auth 2009). However, several anomalies were observed during this study period. Larval *Merluccius productus* and *Sardinops sagax* were collected in concentrations as high as 62 and 82 1000 m^{-3}, respectively, only during June/July 2005 and May 2006. These were periods corresponding to unusual late upwelling (2005) and relatively high positive PDO index values (2005 and 2006). *M. productus* generally spawn in southern California waters. Until recently, their larvae have been rarely sampled in the study area, and those encounters have exclusively been during El Niño events or periods corresponding to positive MEI values (Phillips et al. 2007). *S. sagax* have been spawning in the NCC region since the mid-1990s after an absence of nearly 40 years (Emmett et al. 2005). In addition, larvae of several (n = 16; table 1) taxa were collected during months outside of their spawning seasons as previously reported for this region (Matarese et al. 1989).

Concentrations, Distributions, and Assemblages

Annual The dramatic ichthyoplankton concentration decrease between 2005 and 2006 may have been a delayed response resulting from the adverse effects on spawning stocks of the anomalously late upwelling that occurred in the NCC during the summer of 2005 (Brodeur et al. 2006; Barth et al. 2007). The impact appears to have been especially evident in taxa that spawn farther up in the water column (e.g., *E. mordax*), that were more affected by the increased temperatures, north- and shoreward transport, and decreased productivity in the upper water column resulting from the El Niño-like conditions than more deepwater species (e.g., *L. exilis, S. leucopsarus, T. crenularis*). In fact, the three species that were identified through ISA as indicative of 2006 (i.e., larvae of *L. ochotensis*, *M. productus*, and *P. crockeri*; table 7) were all deepwater and/or more southern spawning species. The gradual increase in concentrations of *E. mordax*, *Sebastes* spp., and total larvae between 2006 and 2009 could be the result of the increasingly beneficial conditions supporting reproductive effort following the deleterious conditions resulting from the anomalous 2005 summer.

Seasonal The seasons of peak larval concentrations for dominant taxa (May/June: *L. exilis* and *S. leucopsarus*; June/July: *E. mordax* and *Sebastes* spp.), and lack of a peak season for *T. crenularis*, have previously been reported (Richardson 1973; Brodeur et al. 1985; Doyle et al. 1993; Auth and Brodeur 2006). The seasonal cycle of larval diversity observed across all six years (i.e., highest levels during the spring–summer and summer–fall transitional periods) is similar to that reported by Auth and Brodeur (2006). The significant concentration reduction of all dominant taxa and total larvae in August–November compared to May–July, along with the lack of any significant indicator taxa for the later period, suggests that the late summer–fall season is not as important as the spring–early summer season in characterizing the ichthyoplankton community in the NCC. In fact, Brodeur et al. (2008) and Auth et al. (2011) both found significantly higher concentrations of larvae in the nearshore region (9–18 km along the NH line) during the winter/spring (January–May) than summer/fall (June–December) periods, most likely resulting from the same increase in food availability during the spring that is characteristic of the NCC ecosystem.

Latitudinal Although three of the dominant larval taxa (i.e., *L. exilis*, *Sebastes* spp., and *S. leucopsarus*) had significantly elevated concentrations along specific transects during some cruises, these differences were not consistently significant between months or years. The southernmost (i.e., HH) transect was generally characterized by highest concentrations of larval *L. exilis* and *Sebastes* spp., an observation supported by the results of the ISA (table 7). Three of the five stations along this transect extend across Heceta Bank ~55 km from shore, an area that includes depths as shallow as 60 m rising from surrounding depths of 100–1000 m, which forms a major nursery area for juvenile *L. exilis* and *Sebastes* spp. (Pearcy et al. 1989; Stein et al. 1992). In contrast, the NH line just north of the HH transect appears to be more of a transitional region between Heceta Bank and transects to the north, as is evident by the lack of significant latitudinal differences between the CR, NH, and HH transects for all larval concentrations (except *S. leucopsarus*) and diversity. This is further supported by the lack of any significant indicator taxa for the NH line.

Cross-shelf The cross-shelf distribution of fish larvae, with consistently higher concentrations of all dominant taxa and total larvae in the offshore and far-offshore regions than nearshore, was similar to recent reports of ichthyoplankton distributions in the NCC (Auth and Brodeur 2006; Auth 2008; Auth 2009). However, larval diversity exhibited the opposite pattern, being significantly higher in the coastal than offshore region. Auth and Brodeur (2006) reported little cross-shelf variation in larval diversity along the NH line in 2000 and 2002, with the exception of a spike of low diversity at a single station 46 km from shore. Larval diversity may be inversely related to zooplankton community structure. Gómez-Gutiérrez et al. (2005) observed that diversity in the euphausiid community was higher in more off-

shore than inshore stations off the central Oregon coast in 1970–1972, as did Keister and Peterson (2003) for the zooplankton community in the same area in 1998–2000. Brodeur et al. (2008) found that ichthyoplankton diversity was related to zooplankton biomass and the Pacific Decadal Oscillation (PDO) index in a study conducted from 1997–2005 off the central Oregon coast. However, samples for that study were collected exclusively at very nearshore (9 and 18 km from shore) stations along the NH line, and were comprised of a different ichthyoplankton community than the one sampled in the current study. Larval diversity in this study largely reflects the number of species that are spawned in a given location and have pelagic larvae. Nearshore regions have more diverse physical structure and therefore provide many more niches for coastal species. Except for pelagic larval stages of benthic organisms, zooplankton are holoplankton, experiencing their entire life as plankton. Therefore, it is not surprising that zooplankton are more diverse offshore, while ichthyoplankton are more diverse nearshore. It should be noted that larval diversity may be underrepresented due to the difficulty in identifying some larvae to species based on meristics and pigmentation patterns (e.g., Osmeridae, *Sebastes* spp., *Sebastolobus* spp., *Citharichthys* spp.) (Matarese et al. 1989).

Length Distributions

The inverse relationship between weighted mean lengths and larval concentrations may be the result of larval dispersal and growth. Larvae resulting from the late spring/early summer spawning peak (e.g., *E. mordax*, *L. exilis*, *Sebastes* spp., *S. leucopsarus*) should, in conjunction with reduced spawning activity, demonstrate increased mean length as the season progresses. As a consequence, weighted mean length of species with a temporally limited spawning season such as *E. mordax* will progressively increase up to transformation when the early-life stages are no longer planktonic. In contrast, for taxa with more protracted spawning seasons (e.g., *L. exilis*, *Sebastes* spp., *S. leucopsarus*, *T. crenularis*), weighted mean larval lengths will initially increase during the months immediately after the spawning peak then decrease gradually as the older individuals are replaced by fewer, newly spawned larvae. In this respect, a late spring/early summer spawning peak for *T. crenularis* would explain the significant increase in weighted mean length of larvae from a low in June to a high in July/August back to a low in Oct/Nov despite the lack of significant monthly concentration differences (table 6).

The inverse relationship between cross-shelf larval concentrations and weighted mean lengths could result from cross-shelf dispersal during larval growth and development for species with inshore spawning areas. For larval *Sebastes* spp. however, both concentration and weighted mean length were significantly higher in the offshore than coastal region. The occurrence of ~45 different species of the *Sebastes* genus within the NCC (Love et al. 2002), many with different life-history parameters, may contribute to the pattern of variability in cross-shelf concentration and weighted mean length as described by Auth (2009).

Environmental Factors

Local Salinity, temperature, DO saturation, and, to a lesser degree, fluorescence, were the in situ environmental variables with strongest linkage to the distributions and concentrations of the dominant taxa and total larvae in this study. The generally positive relationships between larvae and temperature and DO saturation, and generally negative relationships with salinity and fluorescence, have previously been documented for the NCC (Auth and Brodeur 2006; Auth et al. 2007; Auth 2008; Auth 2009). However, concentrations of *S. leucopsarus* and *T. crenularis* larvae, the only two myctophids represented in the dominant taxa, were also the only taxa positively correlated with fluorescence at 40- and 50-m depth (their respective weighted mean depths), while larval *L. exilis*, a pleuronectid, was negatively (although not significantly) correlated with fluorescence at 40 m. Fluorescence at these depths was on average only 13% and 6%, respectively, of the maximum fluorescence levels recorded at a given station. Although speculative at best, this could be an early environmental cue to the ontogenetic development of the myctophids' bioluminescent photophores in low light, low fluorescence environments within the water column.

The effect of DO concentration and saturation on the distribution, growth, and survival of larval fish is well documented (Breitburg et al. 1999). Most larval taxa are positively related to DO as found in the present study. However, larval *E. mordax* were found to be negatively, although not significantly, related to DO concentration and saturation. This is not surprising since *E. mordax* larvae primarily inhabit the upper 10 m of the water column where DO limitation is not an issue. The significant negative correlation that was found between larval diversity and DO concentration could reflect the increased diversity that was found nearshore, where DO levels may be reduced through organic decomposition or other coastal processes.

Larger-scale The control that water temperature has over the early-life processes of marine fishes is well documented (Houde 2008), as is the influence that the timing and intensity of Columbia River outflow (COL) has on the ichthyoplankton community in the NCC (Parnel et al. 2008). In the present study, COL measured at Bonneville Dam located 235 km upriver from the mouth of the Columbia River and SST measured

from a buoy located 20 nm off the central Oregon coast were the most important larger-scale environmental factors affecting the spring–fall epipelagic ichthyoplankton community in the NCC. The dominance of these factors was fairly consistent for all dominant taxa, total larvae, and larval diversity as shown through both correlation and NPMR analyses (fig. 5, table 10). However, *T. crenularis* larvae were not significantly related to COL, SST, or any other single, or combination of several, larger-scale variables. This is not surprising since this species is distributed farther down in the water column than the other dominant taxa, and is thus less likely to be affected by environmental changes to the surface layer. A particularly interesting finding from this study was that 0–2 month lagged larval concentrations (except for *T. crenularis*) were significantly positively correlated with COL, while those lagged 3–5 months were significantly negatively correlated with COL. This could reflect the positive influence that increased COL—and the increased SST and decreased salinity that accompany higher river outflows—may have on larval survival and the negative influence that COL may have on conditions necessary to maintain healthy gonadal growth in the spawning stock biomass during the months preceding spawning. This is supported by the finding that larvae were generally negatively correlated with in situ salinity and positively correlated with in situ temperature, while negatively correlated when lagged 2–4 behind SST.

Implications for Sampling, Management, and Future Research

The similarity between the taxonomic composition and distribution of the dominant taxa found in this inclusive study to those found in previous studies with varying degrees of temporal and spatial definition suggests that the ichthyoplankton community in the NCC can be adequately described by the current sampling regime. In fact, this study demonstrates that sampling could be reduced to four seasonal collections (i.e., May, June–July, August–September, September–November) and fewer stations within each of three cross-shelf regions (i.e., coastal [<~50 km from shore], offshore [~50–100 km], far-offshore [>~100 km]), and still adequately describe the spring–fall ichthyoplankton community in this area. In addition, the finding that the ichthyoplankton varied similarly in composition, distribution, length, community structure, and relation to environmental variables within years and seasons reflects the robust nature of the larval community within the NCC region. This study has demonstrated that this larval community is influenced by, and can be indicative of, variable local and larger-scale environmental conditions. In particular, fisheries managers may be able to use easily-available indices such as Columbia River outflow and SST measured from a buoy located 20 nm off the central Oregon coast to help predict the spawning success of several dominant taxa 2–4 months in advance. Also, fisheries researchers and managers may be able to incorporate the annual, seasonal, latitudinal, and cross-shelf larval distributions and concentrations, along with the in situ environmental statistics, into fisheries models. Finally, this study will provide a base of information in an attempt to relate the environment and ichthyoplankton to the recruitment of important forage and commercial stocks in the NCC ecosystem in a forthcoming publication.

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APPENDIX

Descriptive statistics (mean, standard error [SE], median, upper and lower 95% confidence intervals [CIs], range [minimum-maximum values], and sample size [*n*]) for seven environmental variables for each of the five dominant larval fish taxa and total larvae (weighted based on concentration) collected during this study: temperature (°C), salinity, density (sigma theta, kg m^{-3}), fluorescence (mg m^{-3}), turbidity (mg m^{-3}), dissolved oxygen concentration (DO, ml L^{-1}), and DO saturation (%). Samples containing no larvae were excluded. Values for the environmental variables used in the analysis were taken from different depths in the water column at each station corresponding to the weighted mean depth for each taxon as reported in previous studies: *E. mordax*: 10-m depth; *Sebastes* spp. and total larvae: 20-m depth; *L. exilis* and *S. leucopsarus*: 40-m depth; *T. crenularis*: 50-m depth.

	Temperature	Salinity	Density	Fluorescence	Turbidity	DO	DO saturation
Engraulis mordax							
Mean	15.0	31.4	23.2	0.24	0.40	5.6	94.9
SE	0.1	0.07	0.07	0.02	0.009	0.03	0.4
Median	14.8	31.6	23.4	0.15	0.38	5.5	95.6
Upper 95% CI	15.2	31.5	23.3	0.28	0.41	5.6	95.8
Lower 95% CI	14.8	31.2	23.0	0.20	0.38	5.5	94.1
Range	8.3-18.5	28.9-33.3	20.9-25.9	0.004-2.73	0.20-1.48	5.2-6.6	90.2-109.6
n	107	107	107	100	100	37	37
Lyopsetta exilis							
Mean	8.8	32.7	25.3	0.25	0.37	5.0	74.6
SE	0.09	0.04	0.04	0.03	0.006	0.2	2.7
Median	8.7	32.5	25.2	0.16	0.36	5.5	82.2
Upper 95% CI	8.9	32.7	25.4	0.30	0.38	5.3	80.0
Lower 95% CI	8.6	32.6	25.3	0.20	0.36	4.6	69.2
Range	7.3-11.8	32.2-33.9	24.7-26.5	0-1.73	0.18-0.54	2.1-6.3	31.1-98.1
n	112	101	101	98	98	48	48
Sebastes spp.							
Mean	11.0	32.1	24.5	0.47	0.42	6.0	94.3
SE	0.1	0.02	0.03	0.03	0.006	0.05	0.9
Median	10.9	32.3	24.6	0.46	0.42	5.9	94.2
Upper 95% CI	11.2	32.1	24.6	0.52	0.43	6.1	96.0
Lower 95% CI	10.8	32.0	24.2	0.42	0.41	5.9	92.6
Range	7.4-18.0	30.6-33.7	22.3-26.3	0.01-6.25	0.19-1.21	1.6-6.9	24.2-109.7
n	295	283	272	254	252	114	114
Stenobrachius leucopsarus							
Mean	9.6	32.5	25.1	0.39	0.35	5.9	90.1
SE	0.07	0.008	0.01	0.02	0.005	0.04	0.7
Median	9.3	32.5	25.1	0.21	0.36	5.9	88.7
Upper 95% CI	9.7	32.5	25.1	0.44	0.36	6.0	91.5
Lower 95% CI	9.5	32.5	25.0	0.34	0.34	5.8	88.8
Range	7.3-11.8	32.2-33.6	24.6-26.1	0-1.91	0.19-0.61	3.5-6.6	52.1-101.7
n	214	202	199	194	194	91	91
Tarletonbeania crenularis							
Mean	9.1	32.6	25.2	0.27	0.33	5.6	84.7
SE	0.07	0.02	0.02	0.03	0.006	0.08	1.2
Median	9.0	32.6	25.2	0.12	0.33	5.7	85.2
Upper 95% CI	9.3	32.6	25.3	0.33	0.35	5.8	87.2
Lower 95% CI	9.0	32.6	25.2	0.21	0.32	5.5	82.2
Range	7.3-12.9	32.3-33.8	24.4-26.4	0-2.19	0.18-0.59	1.6-6.4	23.5-96.6
n	168	158	152	145	144	66	66
Total larvae							
Mean	11.7	32.1	24.3	0.52	0.42	6.0	96.6
SE	0.1	0.03	0.03	0.03	0.005	0.04	0.6
Median	10.8	32.3	24.7	0.46	0.42	5.8	93.5
Upper 95% CI	11.9	32.1	24.4	0.59	0.43	6.1	97.5
Lower 95% CI	11.5	32.0	24.3	0.45	0.40	6.0	95.2
Range	7.4-18.0	30.6-33.7	22.3-26.3	0-6.91	0.19-1.21	1.6-7.2	24.2-111.4
n	389	374	360	338	336	151	151