Ichthyoplankton distribution and abundance in relation to nearshore dissolved oxygen levels and other environmental variables within the Northern California Current System

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Ichthyoplankton distribution and abundance in relation to nearshore dissolved oxygen levels and other environmental variables within the Northern California Current System

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ABSTRACT
Nearshore hypoxia along the coast of Oregon and Washington is a seasonal phenomenon that has generated concern among scientists studying this temperate upwelling ecosystem. These waters are affected by coastal upwelling-induced hypoxia mainly during late summer and fall, but the effects of low oxygen levels on fish and invertebrate communities, particularly during the early-life history stages, are poorly known. We investigated the effects of hypoxia and other variables on the species composition, density, vertical and horizontal distribution of fish larvae along the Oregon and Washington coasts during the summers of 2008, 2009 and 2010. Bottom-dissolved oxygen (DO) values ranged from 0.49 to 4.79 mL L⁻¹, but the overall water column DO values were only moderately hypoxic during the 3 yr of sampling compared with recent extreme years. In this study, DO was found to be an environmental parameter affecting the species composition, but other variables such as season, year and depth of capture were also important. Although the overall density of fish larvae increased with increasing bottom-DO values, the effect on individual species density was limited. Slender sole (Lyopsetta exilis) and sand sole (Psettichthys melanostictus) were the only species to have a weak trend of density with DO, but both showed negative relationships and neither relationship was significant. Our results indicate that larval fish spatial distribution was only moderately affected within the range of observed oxygen values, but low DO may be an important factor under intense hypoxic conditions.

Key words: California Current, environmental effects, hypoxia, Ichthyoplankton, larval assemblages

INTRODUCTION
Increasing reports of hypoxic events in coastal and estuarine waters since the late 1990s have garnered the interest of both the scientific and fishing communities. Scientific investigators are trying to understand the driving mechanisms of nearshore hypoxic events and their consequences for local ecosystems (Diaz and Rosenberg, 2008; Vaquer-Sunyer and Duarte, 2008; Rabalais et al., 2010). Low dissolved oxygen (DO) can alter the biogeochemical cycling of elements and the distribution of marine species, thus potentially impacting the economic status of many coastal communities (Helly and Levin, 2004; Rabalais et al., 2010; Zhang et al., 2010). Coastal hypoxia is caused by increased nutrient enrichment and higher respiration in nearshore areas. The mechanisms for nutrient enrichment can vary and are linked to either human activities, as seen in the Gulf of Mexico, Chesapeake Bay and the Adriatic Sea (Diaz, 2001; Breitburg et al., 2003; Rabalais et al., 2010), or the surfacing of nutrient-rich, oxygen-poor, deep water from the oxygen minimum zone (OMZ) by upwelling favorable winds, as seen within eastern boundary current ecosystems (Grantham et al., 2004; Ekau and Verheye, 2005; Barth et al., 2007; Bograd et al., 2008; Rabalais et al., 2010; Zhang et al., 2010). These systems have been shown to support highly productive fisheries, particularly for anchovies and sardines (Pauly and Christensen, 1995; Ekau and Verheye, 2005).

The northern California Current (NCC) along the western United States (Washington, Oregon and northern California coasts) has exhibited inner-shelf hypoxia (≤1.43 mL L⁻¹), severe inner-shelf hypoxia (≤0.5 mL L⁻¹) and even water-column anoxia in recent years (Chan et al., 2008; Connolly et al., 2010; Pierce et al., 2012). These hypoxic regions can cover a
large portion of the shelf along the Oregon and Washington coasts by late summer (Grantham et al., 2004; Connolly et al., 2010; Peterson et al., 2013). Innershelf (<50 m) hypoxia has been documented annually since 2000 along the central Oregon coast (Grantham et al., 2004; Chan et al., 2008; Pierce et al., 2012; Peterson et al., 2013). Hypoxic events along the shelf tend first to occur near the bottom but can extend upward to the water column to within 10–15 m of the surface (Chan et al., 2008). Hypoxia can vary vertically and horizontally throughout the water column, with the most intense hypoxic waters occurring at the bottom boundary layer. Many studies have, therefore, focused on the tolerance of benthic organisms to low DO (Diaz and Rosenberg, 1995; Miller et al., 2002; Vaquer-Sunyer and Duarte, 2008; Zhang et al., 2010), but relatively few studies have investigated the effects of low DO on pelagic fish, particularly during early-life stages and in upwelling-driven systems.

Previous studies have shown that pelagic fish alter their vertical and horizontal distributions to remain above or outside the hypoxic boundary layer when bottom-DO values are more severely hypoxic, reducing the available habitat for these species (Keister et al., 2000; Taylor and Rand, 2003; Klumb et al., 2004; Bell and Eggleston, 2005; Prince and Goodyear, 2006; Parker-Stetter and Horne, 2008; Vanderploeg et al., 2009; Herbert et al., 2010). Vertical migration patterns of pelagic fish have also been interrupted by severe hypoxic events (Taylor et al., 2007; Ludsin et al., 2009; Zhang et al., 2009), creating changes in predator/prey spatial overlap. Fish early-life stages appear to be less tolerant to low DO than their adult conspecifics (Keister et al., 2000; Miller et al., 2002; Zhang et al., 2010). Thus, further investigations into the effects of low DO on pelagic fish early-life stages are needed, to understand the development and survival of larval fishes in areas that experience hypoxia. This research need is particularly relevant for eastern boundary current systems, characterized by both coastal hypoxic events and abundant fish biomass.

Larval fish distributions during upwelling seasons along the Oregon and Washington coasts have been analyzed in relation to shelf dynamics, depth, temperature and salinity (Auth and Brodeur, 2006; Auth et al., 2007; Auth, 2008, 2011; Brodeur et al., 2008; Parnel et al., 2008), but with the exception of Auth (2011), no studies have investigated the relationship of larval fish to DO in this region. Any changes to larval fish community dynamics can alter the success of local adult fish stocks in an ecosystem (Sherman et al., 1983; Houde, 2008). The nearshore larval fish community along the central Oregon coast is relatively diverse with over 70 taxa represented (Richardson and Pearcy, 1977; Brodeur et al., 2008). The dominant taxa of coastal larval fish collected during spring and summer along the nearshore Oregon and Washington coasts are: Engraulis mordax (Northern anchovy), Sebastus spp. (rockfishes), and members of the families Osmeridae, Pleuronectidae, Hexagrammidae, and Cottidae (Richardson and Pearcy, 1977; Doyle et al., 1993; Auth and Brodeur, 2006; Brodeur et al., 2008).

The aim of this study was to investigate the effects of hypoxia and other environmental variables on the density, composition, horizontal and vertical distribution of fish larvae along the Oregon and Washington coasts during three summers: 2008, 2009 and 2010. We focused this study on the shelf system (<100-m depth) and locations of previous coastal hypoxic events, which are seasonal phenomena with a peak intensity during summer (Barth et al., 2007; Rabalais et al., 2010; Adams et al., 2013). We hypothesized that (i) hypoxia would have a negative effect on the local density of fish larvae, which would ultimately result in changes in horizontal distribution patterns and community structure, and (ii) the proportion of the water column inhabited by fish larvae will decrease during intense hypoxic events (Taylor and Rand, 2003; Prince and Goodyear, 2006; Vanderploeg et al., 2009). Thus, as a corollary of these two hypotheses, we predicted that densities of larval fish would be positively correlated with DO concentrations.

METHODS

Sampling methodology

We sampled during 25 different cruises, some single day and some multiple days, between late May and early September from 2008 to 2010. Cruises occurred on the OSU R/V Elakha, OSU R/V Wecoma and the NOAA R/V Miller Freeman. The sampling sites occurred along the continental shelf between Yachts, Oregon (~44°N) and Neah Bay, Washington (48.5°N) (Fig. 1). The depth of sampling sites ranged from 20 to 400 m, but most of the sampling (95%) occurred at depths ≤100 m with an overall average sampling depth of ~80 m. We collected samples using the Hydro-Bios Multi Plankton Sampler MultiNet Type Midi system (Hydro-Bios, Kiel, Germany, http://www.hydrobios.de) with a mouth area of 0.5 m². This system has five 300-µm mesh nets attached to the main unit that are opened and closed via a motor either preprogrammed based on depth prior to deployment, or signaled by a live-wire connection. The
MultiNet is equipped with an integrated pressure sensor and two electronic flow meters that allow for monitoring of tow speed and net orientation in the water column, as well as determination of volume of water filtered per sample. Mounted on top of the net frame was a CTD-DO unit that contained conductivity, pressure, temperature and DO sensors.

At each site, the first net was opened when the MultiNet was deployed to <10 m from the bottom. The remaining nets were opened every 10–20 m depending on the depth of the sampling site. For deeper sites, nets remained open longer, sampling a greater vertical distance (e.g., at 150-m bottom depth nets were opened every 20 m, whereas at 80-m bottom depth, nets were opened every 10–15 m). The depths at which nets were opened-closed were referenced from the bottom, rather than the surface, as gradients of DO content are sharper closer to the bottom. Throughout this paper, the maximum depth at which each net, during one tow, was opened will be referred to, as the ‘sample depth,’ whereas the depth at that station will be referred to as the ‘bottom depth’. The MultiNet was towed obliquely at a ship speed of 1–2 m s \(^{-1}\) and a wire-retrieval speed of 10 m min \(^{-1}\) with an average net volume filtered of 40 m\(^3\). At the end of each tow, samples were removed from the five cod ends and stored in a 10\% formaldehyde/seawater mixture. In the lab, each sample was measured for biovolume, biomass, and larval fish were counted and identified to the lowest possible taxon. At each sampling location, we also made an additional deployment of a CTD (Sea-Bird Electronics Model 25, Bellevue, WA, USA) equipped with a flow-through DO sensor throughout the water column.

**Community analyses**

The effects of environmental factors on larval fish composition were examined with a non-metric multidimensional scaling (NMS) analysis, a non-parametric ordination method (Kruskal, 1964). We used Sorensen (Bray–Curtis) distance measure and performed 50 NMS runs using random starting positions. The species matrix contained standardized abundance measures of fish m\(^{-3}\) for taxa that occurred in more than 3.0\% of the samples. The environmental matrix contained five continuous variables (Julian day, maximum depth of each net, lowest salinity of each net, lowest temperature of each net and lowest DO of each net) and the six categorical variables (season, year, time of day, latitude, DO and sample depth). We divided the variable season into two categories: early (samples that occurred before July 15th) and late (samples that occurred on or after July 15th); the variable year into three categories: 2008, 2009 and 2010; the variable time of day into two categories: day (between sunrise and sunset) and night (between sunset and sunrise); the variable latitude into three categories: north (46.00°N – 48.00°N), central (44.65°N – 46.00°N)
and south (44.00°N – 44.65°N); the variable DO was divided into five categories: 1 (0.00–1.49 mL L⁻¹), 2 (1.50–1.99 mL L⁻¹), 3 (2.00–2.99 mL L⁻¹), 4 (3.00–3.99 mL L⁻¹) and 5 (≥4.00 mL L⁻¹); and the variable sample depth into five categories: 1 (0.0–24.9 m), 2 (25.0–49.9 m), 3 (50.0–74.9 m), 4 (75.0–99.9 m) and 5 (≥100.0 m). We established the latitude, DO and sample depth categories based on previous studies (Richardson and Pearcy, 1977; Doyle et al., 1993; Ekau and Verheye, 2005; Auth and Brodeur, 2006; Auth, 2008; Parnel et al., 2008; Vaquer-Sunyer and Duarte, 2008). Specifically, latitude and depth were divided into categories to address differences in species composition (Auth and Brodeur, 2006; Auth, 2008), whereas DO categories targeted lethal, sublethal and non-lethal DO values (Vaquer-Sunyer and Duarte, 2008). No samples were collected at dusk or dawn during this study.

A multi-response permutation procedure (MRPP) was conducted using the Sorensen (Bray–Curtis) distance measure to investigate whether there were significant differences between the groups within each categorical variable. For each categorical variable, an A-statistic and P-value are reported from the MRPP analysis. The A-statistic refers to the chance-corrected, within-group agreement, so that when A = 1 there is homogeneity within groups and when A = 0 there is heterogeneity within groups (McCune and Grace, 2002). The P-value from the MRPP analysis indicates how likely an observed difference between groups is as a result of chance (McCune and Grace, 2002). Where significant differences occurred, an indicator species analysis (ISA) was used to determine if any of the species used in the ordination analysis were significant indicators for those groups (Mielke and Berry, 2001). During the ISA, 4999 permutations were conducted in the Monte Carlo test. Taxa were considered significant indicators at P < 0.05, with a 95% confidence interval. We conducted these statistical analyses using PC-Ord v.6 (McCune and Grace, 2002).

Finally, we measured diversity and evenness of the larval fish community for taxa that occurred in more than 3.0% of the samples across six categorical variables: season, year, sample depth (m), time of day, latitude and DO (mL L⁻¹), as previously defined in the multivariate analyses. Diversity and evenness were measured using the Shannon–Wiener Index (H’) and Pielou’s Index (J’), respectively. Higher H’ values indicate the greatest diversity (Whittaker, 1972). Evenness (J’) values ranged from 0 to 1, with larger values indicating that all taxa are present in the same relative concentrations (Pielou, 1969).

Relationship to the environment

Larval fish abundances, excluding zero catch data, were standardized by volume (m³) then summed over all five nets at each site and correlated with bottom DO to determine if horizontal distribution of fish larvae varied with hypoxia. A Generalized Additive Model (GAM; Wood, 2008) in the statistical package R v. 6.4 (The R Foundation for Statistical Computing, http://www.r-project.org) was used for this comparison. The GAM used a Gaussian family model and identity link function. The response variable, standardized larval fish abundance (Fᵢ), was natural log-transformed to satisfy the assumption of normality. In addition to bottom DO (BDOᵢ), season (M), time of day (D), latitude (L₁), bottom depth (Zₑᵢ), sea surface salinity (SSS; Sₑ) and sea-surface temperature (SST; Tₑ) were also included as covariates in the model. The following variables were included as factors: latitude, season, time of day and bottom depth. Latitude refers to the sample region: north (46.00°N – 48.00°N), central (44.65°N – 46.00°N) or south (44.00°N – 44.65°N). We divided the factor latitude into three regions based on conclusions found in previous studies of larval fish abundance and recruitment and shelf dynamics (Richardson and Pearcy, 1977; Doyle et al., 1993; Auth, 2008; Parnel et al., 2008). We divided the factor season into early (late May – mid July) and late (mid July – September), and the factor time of day into day (sunrise – sunset) and night (sunset – sunrise). The factor bottom depth was divided into four categories (1 = <50 m, 2 = 51–75 m, 3 = 76–100 m and 4 = >100 m). The resulting GAM was the following:

$$\log(Fᵢ + 0.1) \sim s₁(\log(BDOᵢ)) + s₂(Sₑ) + s₃(Tₑ) + Mᵢ + L₁ + Dᵢ + Zₑᵢ$$

where ‘s’ refers to a smoothing function.

Individual species responses to changes in DO were measured for the 12 most abundant taxa using linear regression analysis with the statistical package R v. 2.10.1.

Vertical distribution analysis

The effect of hypoxia on the vertical distribution of fish larvae abundance was investigated by first calculating the standardized weighted average depth of fish m⁻³ caught for each tow, and comparing this to different values of bottom DO using an ANCOVA. The analysis was applied to tows with a positive fish catch only (e.g., at least one net within a tow had at least 1 larval fish). The equation used for calculating the standardized weighted average (Zₑᵢ) depth is:

\[ \frac{\sum (F_i d_i)}{\sum F_i} = Z_{d_i} \]
\[ 1 - \frac{Z_{d_i}}{Z_{b_i}} = Z_{d_i} \]

where \( F_i \) equals each standardized fish count for each net (1–5) at each site, \( d_i \) equals the max depth, or sample depth, for each net (1–5) at each site. Bottom depth (\( Z_{b_i} \)) is the bottom depth for that tow. First, we calculated the average depth of fish occurrence for each tow (\( Z_{d_i} \)) by summing the standardized fish abundance (\( F_i \)) multiplied by the sample depth (\( d_i \)) then dividing by the sum of standardized fish abundance (\( F_i \)). We then calculated the weighted average depth of fish larvae (\( Z_n \)) by taking the ratio of (\( Z_{d_i}/Z_{b_i} \)) and subtracting from 1 so that ‘1’ referred to the surface whereas ‘0’ referred to the bottom. The weighted average depth was logit-transformed so that it would not be constrained from 0 to 1 in the statistical analysis. The following ANCOVA model was fitted using the statistical package R (v. 2.10.1):

\[
\logit(Z_{n_i}) \sim \text{BDO}_i + L_i + M_i + D_i
\]

The factors latitude (\( L_i \)), season (\( M_i \)) and time of day (\( D_i \)) are the same as described in the previous GAM analysis. Finally, we conducted a Tukey’s multiple comparison test with a 95% family-wise confidence level for any factor with a significant relationship indicated by the ANCOVA. In addition to the analysis of the vertical distribution of the entire larval community, we also performed an analysis of vertical distribution for each of the top 12 most abundant taxa, using positive fish catches only. In this case, however, we conducted simple linear regressions as opposed to an ANCOVA to compare vertical distributions with DO (mL L\(^{-1}\)).

Because fish larvae can change their vertical distribution in relation to both absolute values of DO and/or the thickness of the bottom hypoxic layer, we also compared the weighted average depth (\( Z_n \)) of ichthyoplankton to the depth of the hypoxic layer (\( H_Li \)). The following factors were again considered in this analysis: latitude (\( L_i \)), season (\( M_i \)) and time of day (\( D_i \)). Again we used an ANCOVA followed by a Tukey’s multiple comparison test with a 95% family-wise confidence level for any factor with a significant relationship indicated by the ANCOVA. We determined the thickness of the hypoxic layer as the distance between the bottom and the depth at which \( DO = 2.0 \text{ mL L}^{-1} \), therefore we only used tows with positive fish catches and bottom DO values of \( 2.0 \text{ mL L}^{-1} \) or less in this analysis. The weighted average (\( Z_n \)) was logit-transformed and standardized to the total depth as in the previous analysis, and we estimated the effects of the hypoxic layer, latitude, season and time of day on the fish weighed at the average depth as follows:

\[
\logit(Z_{n_i}) \sim H_{Li} + L_i + S_i + T_i
\]

**RESULTS**

Overall, 493 samples were collected during the upwelling season between late May and early September in the 3 yr of sampling (Table 1). Fish larvae, representing 23 taxa, were found in 197 of the 493 samples. The bottom DO range, total fish count, and taxonomic standardized abundance (fish m\(^{-3}\)) varied among years with 2010 having the weakest hypoxia event (Table 2). Together, rockfishes (Sebastes spp.) and slender sole (Lyopsetta exilis) made up more than 25% of the total catch for all 3 yr combined. The DO range of fish catch also varied among the taxa (Table 2). Rockfishes, slipskin snailfish (Liparis fucensis), butter sole (Isopsetta isolepis) and slender sole were the only taxa caught when DO was <1.4 mL L\(^{-1}\) (Table 2).

**Community analyses**

The best NMS model resulted in a two-dimensional solution that explained 52.6% of the variance (Fig. 2). Axis 1 explained 34.4% of the variance and was most

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**Table 1.** Summary of sample dates, number of samples collected, percent of samples with fish, total number of fish, total number of taxa and dissolved oxygen ranges for each sample year 2008, 2009 and 2010 and the totals over all three-sample years. Samples refer to each net fished.

<table>
<thead>
<tr>
<th>Sample dates</th>
<th>Samples collected</th>
<th>Samples with fish (%)</th>
<th>Total no. of fish m(^{-3})</th>
<th>Total no. of taxa</th>
<th>Bottom-DO range (mL L(^{-1}))</th>
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<tr>
<td>2008</td>
<td>May 24 to September 1</td>
<td>155</td>
<td>35</td>
<td>0.015</td>
<td>18</td>
</tr>
<tr>
<td>2009</td>
<td>June 12 to August 22</td>
<td>182</td>
<td>19</td>
<td>0.029</td>
<td>10</td>
</tr>
<tr>
<td>2010</td>
<td>June 16–20</td>
<td>156</td>
<td>68</td>
<td>0.041</td>
<td>17</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>493</td>
<td>40</td>
<td>0.027</td>
<td>23</td>
</tr>
</tbody>
</table>

DO, dissolved oxygen.

correlated with dissolved oxygen ($r = -0.192$), whereas the second axis explained 28.2% of the variance and was most correlated with sample depth ($r = -0.208$). For the species relationships, northern anchovy ($r = -0.416$) and padded sculpin ($r = 0.406$) were strongly correlated with axis 1. For the second axis, rockfishes ($r^2 = 0.538$) and northern anchovy ($r^2 = -0.487$) were most strongly correlated (Fig. 2).

There were large overlaps in environmental space when samples were divided by the following grouping factors: season, year, sample depth (m), time of day, latitude and DO (mL L$^{-1}$). An MRPP analysis indicated that all grouping factors had a low $A$-statistic, but only four were significant (all $P < 0.001$) indicating significant differences in species composition within a factor: season, year, sample depth and dissolved oxygen (Table 3). The time of day and latitude of the collection were not found to be significant variables in this analysis.

From the ISA, the factors that were significant had some indicator species for their groups (Table 3). For the category season, only northern anchovy was a significant indicator for late (on/after July 15th) in the season. The category year had significant indicator species for 2008 (northern anchovy), 2009 (slender sole) and 2010 (two sculpin species). The category depth had three significant indicator taxa (northern lanternfish, slender sole and rockfishes) for the deepest strata sampled. Finally, four taxa (northern lanternfish, northern anchovy, flatfishes and padded sculpin) were significant for the highest level of oxygen ($>4.00$ mL L$^{-1}$).

Ichthyoplankton diversity ($H'$) and evenness ($J'$) varied similarly by year, sample depth (m), time of day and latitude (Table 4). For the year, 2010 had the highest diversity value whereas 2009 had the lowest diversity value. Although the diversity and evenness analyses only included species collected in more than 3.0% of the samples, the total species catch for 2009 (Table 1)
Figure 2. Non-metric multidimensional scaling biplot showing individual stations coded by dissolved oxygen level with the centroids of each level indicated by large numerals. The positions of the dominant larvae are overlaid relative to the station data and oxygen levels. The five levels of DO are as follows: 1 (0.00–1.49 mL L⁻¹), 2 (1.50–1.99 mL L⁻¹), 3 (2.00–2.99 mL L⁻¹), 4 (3.00–3.99 mL L⁻¹) and 5 (≥4.00 mL L⁻¹).

had a much lower percent of samples with fish and a lower number of taxa collected than both 2008 and 2010. The diversity index was higher for southern sampling sites than either central or northern sampling sites, and there were no indicator species for the latitude of sampling (Table 3). Diversity was also higher in shallower depths (0–24.99 m and 24.99–49.99 m) than in deeper depths and in samples collected during the day than samples collected at night, but there were no indicator species for time of the day, whereas there were indicator species for sample depth (Table 3).

Relationship to the environment

The best-fitted GAM explained 45.5% of the deviance in observed fish larvae abundance (Table 5). Of the three smooth terms in the GAM model, only Bottom-DO had significant positive effects (BDO, P < 0.05) on larval fish abundance (Fig. 3). Neither SSS nor SST had significant effects on larval fish abundance (Table 5). Two-factor terms in the GAM model had significant differences in mean larval fish abundance explained by the relationship of the coefficients. Samples collected between mid-July and early September (Late season), had significantly lower larval fish abundances (P < 0.001, respectively) than samples collected between late May and the middle of July (Table 5). Sample locations south of Newport, Oregon (southern: 44.00°N – 44.65°N) had significantly higher larval fish abundances than samples collected north of Newport (northern: 46.00°N – 48.00°N) (Table 5).

Of the 12 dominant taxa, no species had significant correlations (P < 0.05) between abundance and DO. However, slender sole and sand sole had negative correlations with DO (P = 0.07 and P = 0.07, respectively), whereas conversely, northern lanternfish (Stenobrachius leucopsarus) showed a positive correlation (P = 0.10), but these relationships were not significant at an alpha level of 0.05.

Vertical distribution analysis

The vertical distribution of fish larvae did not change in relation to bottom-DO (mL L⁻¹, P = 0.130). Latitude had a significant effect on the weighted average depth of fish (Z₁); fish larvae collected between 44.65°N and 46.00°N (central) were deeper in the water column compared with those collected north or south (P = 0.035). None of the 12 dominant taxa, when analyzed individually, showed significant relationships (P < 0.05) in their vertical distributions relative to DO or hypoxia layer thickness.

DISCUSSION

This study provides insight into the effects of DO and other environmental variables on larval fish abundance, community composition and distribution along the Oregon and Washington coasts during the summer upwelling season. The cause of severe hypoxia along the central Oregon coast has been attributed to shelf circulation, shelf productivity and vertical proximity of upwelling source water to the OMZ (Grantham et al., 2004; Chan et al., 2008). Although there were few severe hypoxic values recorded during this study period, during 2002 and 2006, the central Oregon coast became severely hypoxic and even anoxic (2006) for several weeks to months (Chan et al., 2008). Chan et al. (2008) reported that with the onset of anoxia in 2006, severe hypoxia became widespread, at least 3000 km², across the central Oregon shelf between 44.25°N and 45.00°N, from the inner shelf to the shelf break. This hypoxic event also occupied 80% of the water column and persisted from June to October (Chan et al., 2008). Fish larvae that recruit to the central region (44.65°N – 46.00°N), therefore, have a chance of experiencing severe hypoxic and possibly anoxic waters.
Collectively, we found a positive correlation between larval abundance and DO concentration, therefore validating our hypothesis that in very hypoxic waters larval abundance is suppressed. In addition, we found some relationships between levels of DO and the distribution of several larval fish species and on overall community composition. These results are in agreement with previous studies conducted in enclosed basins (Breitburg, 2002; Taylor and Rand, 2003; Vanderploeg et al., 2009) and other upwelling areas (Kreiner et al., 2009). Thus, during most years, variability in the larval fish community composition along the Oregon and Washington coasts is influenced by DO but also other oceanographic variables (e.g., distance from shore, salinity, temperature, upwelling intensity, wind stress, circulation patterns, etc.) (Auth et al., 2007; Barth et al., 2007; Dudas et al., 2009; Auth, 2011). Our data indicated that species composition was most correlated with sample depth and bottom DO, which tend to be correlated with each other. However, depth explained the distribution of only a few of our dominant species in our analysis. Auth et al. (2007) found that depth stratum was a significant factor explaining larval concentrations of L. exilis and Sebastes spp. off the central Oregon coast. We did find that S. leucopsarus, Sebastes spp. and L. exilis were more abundant in deeper samples, which corresponds to the findings in Auth (2011). Auth (2011) also identified peak larval concentrations for L. exilis and S. leucopsarus to be around May/June, and Sebastes spp. and E. mordax around June/July. In our analysis, we found that E. mordax was an indicator species for the late sampling season, on or after 15th July.

Using stationary hydroacoustics and surface-towed split beam echosounders, previous studies have observed fish moving horizontally and vertically to avoid hypoxic regions (Keister et al., 2000; Taylor and Rand, 2003; Klumb et al., 2004; Bell and Eggleston, 2005; Taylor et al., 2007; Parker-Stetter and Horne, 2008; Ludsin et al., 2009; Vanderploeg et al., 2009; Zhang et al., 2009). During this study, the horizontal distribution of fish larvae was affected by bottom-DO, whereas vertical distribution was not. To get an appreciation of how much DO contributes to larval density, it is informative to refer to the results of the GAM analysis shown in Table 5 and to the magnitude of the
Table 4. Taxonomic diversity ($H'$), evenness ($J'$) and sample size ($N$) for ichthyoplankton collected along the central Oregon and Washington coasts by season, year, sample depth (m), day/night, latitude and dissolved oxygen (mL L$^{-1}$).

<table>
<thead>
<tr>
<th>Category</th>
<th>Category division</th>
<th>$H'$</th>
<th>$J'$</th>
<th>$N$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>Early (May–July 14)</td>
<td>0.581</td>
<td>0.783</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td>Late (July 15–September)</td>
<td>0.524</td>
<td>0.646</td>
<td>52</td>
</tr>
<tr>
<td>Year</td>
<td>2008</td>
<td>0.398</td>
<td>0.569</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>0.226</td>
<td>0.296</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>0.593</td>
<td>0.762</td>
<td>54</td>
</tr>
<tr>
<td>Depth</td>
<td>0.00–24.99</td>
<td>0.436</td>
<td>0.635</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>25.00–49.99</td>
<td>0.576</td>
<td>0.749</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>50.00–74.99</td>
<td>0.248</td>
<td>0.332</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>75.00–99.99</td>
<td>0.066</td>
<td>0.044</td>
<td>4</td>
</tr>
<tr>
<td>Day/Night</td>
<td>Day</td>
<td>0.741</td>
<td>0.903</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td>Night</td>
<td>0.280</td>
<td>0.383</td>
<td>25</td>
</tr>
<tr>
<td>Latitude</td>
<td>North</td>
<td>0.244</td>
<td>0.311</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Central</td>
<td>0.423</td>
<td>0.626</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>South</td>
<td>0.604</td>
<td>0.772</td>
<td>57</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>0.00–1.49</td>
<td>0.000</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1.50–1.99</td>
<td>0.240</td>
<td>0.392</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>2.00–2.99</td>
<td>0.511</td>
<td>0.750</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>3.00–3.99</td>
<td>0.331</td>
<td>0.498</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>≥4.00</td>
<td>0.336</td>
<td>0.442</td>
<td>28</td>
</tr>
</tbody>
</table>

The sampling region was an important factor affecting larval fish horizontal and vertical distributions. The three sample regions varied in both latitude and shelf width. The width of the shelf has been shown to affect physical and biological dynamics (e.g., circulation, productivity, turbulence, etc.) of the waters (Dudas et al., 2009; Kirincich and Barth, 2009), which in turn can impact the recruitment of fish larvae. The Central Region along the northern Oregon coast has a very narrow shelf whereas the Southern Region around Heceta Bank and the Northern Region of the Washington Coast both have a wide shelf with greater primary productivity and water retention (Barth et al., 2005; Hickey and Banas, 2008; Peterson et al., 2013). Peterson et al. (2013) found that the two regions, Heceta Bank (44°N) and the Washington Coast (north of 46°15'N), had lower recorded DO values (<0.5 mL L$^{-1}$) from 1998 to 2012, compared with areas with a shallower shelf. In our study, fish larvae were more abundant in the Southern Region, most probably as a result of its high productivity and water retention features (Kirincich and Barth, 2009). Interestingly, the Newport Hydrographic line (NH; 44°6'N), which is included in this sample region, was identified by Auth (2011) as a transitional region between Heceta Bank and transects to the north, but there were no significant indicator taxa for the NH line. We found no indicator larval taxa for any region we examined.

The thickness of the hypoxic layer is an indicator of quality habitat available for pelagic fish larvae. The expectation is that as the hypoxic layer thickness increases, less suitable habitat is available for pelagic fish larvae. However, in the present study none of the dominant taxa we collected showed significant correlations between their vertical distribution and bottom-DO or hypoxia layer thickness. This is contrary to what other authors have found and may be driven by the relatively mild hypoxic levels that we detected during our sampling. Kreiner et al. (2009) found marked interannual variability in the vertical distribution of sardine Sardinops sagax and anchovy Engraulis encrasicolus larvae in the Benguela upwelling region, which they attributed to changes in bottom layer oxygen concentrations. Lang (2012) observed that postflexion fish larvae vertical movement throughout the water column was reduced under hypoxic conditions compared with the vertical

y-axis in Fig. 3. Specifically, from Table 5, the model intercept is about $-1.8$ on a natural log scale, corresponding to an overall average larval density about 0.06 individuals 100 m$^{-3}$. The predicted effect of DO from Fig. 3, on a log scale, spans from approximately $-0.3$ to $0.5$, which corresponds to an increase of 0.64 individuals 100 m$^{-3}$ above the overall mean. In Table 5 we also note that, with the exception of season and region, no other variable has an effect on overall larval abundance. On a log scale the effect of season is comparable in magnitude to that of DO (fewer larvae later in the year), whereas that of region is about two-thirds that of DO (more larvae to the south).
movement during normoxic conditions. A reduction in available habitat can cause an increase in local fish densities in shallow waters and may increase the risk of predation (Taylor and Rand, 2003; Herbert et al., 2010; McClatchie et al., 2010; Koslow et al., 2011; Campbell and Rice, 2014). Zhang et al. (2009) found that when habitat quality was reduced for pelagic fish during years of severe hypoxia the fish tended to aggregate horizontally along and above the edges of the hypoxic region. Prince and Goodyear (2006) also found that the distributions of tropical pelagic fish [Atlantic blue and white marlins (Makaira nigricans and Tetrapturus albidus), Atlantic sailfish (Istiophorus platypterus), and other species] were reduced to a narrow surface layer as a result of a thick hypoxic layer.

Climate models are predicting the decline of oceanic DO with consequent expansion of the oxygen minimum zone (OMZ) in tropical and subtropical oceans under global warming conditions (Whitney et al., 2007; Stramma et al., 2010). Whitney et al. (2007) identified an 18.6-yr cycle for DO in the North Pacific Ocean and indicated the most recent low period occurred between 2002 and 2006. These results coincide with the lowest DO values recently recorded along the Central Oregon Coast (Grantham et al., 2004; Chan et al., 2008; Pierce et al., 2012). However, while Whitney et al. (2007) recognized that the 18.6-yr cycle was as a result of subarctic water influences, the Central Oregon and Washington Coast upwelling is sourced by both subarctic and equatorial waters (Thomson and Krassovski, 2010). The interannual trend in DO for the upwelled source water along the continental shelf of the Northern California Current has been a gradual decline from 1998 to 2007, with a subsequent increase from 2008 to 2010 before stabilizing in 2011 and 2012 (Peterson et al., 2013). The timing of our study coincided with the subsequent increase in DO in the upwelled source water, so our results need to be considered in the perspective of only a moderately hypoxic period.

Similarly to the trends seen in the Northern California Current, the Southern California Bight has also experienced a decrease in DO (Bograd et al., 2008; Keeling et al., 2010; McClatchie et al., 2010). Nam et al. (2011) identified that recent El Niño/La Niña events have contributed to two to three times lower DO of subsurface ocean waters off Southern California through the enhanced uplifting of isopycnals related to La Niña events. These events occurring in the southern portion of the California Current could affect the source waters in the Northern California Current if they are transported along the poleward undercurrent (Pierce et al., 2012). A moderately strong El Niño occurred during the winter and spring of 2010 which

Table 5. Generalized additive model results for larval the fish abundance [(no. m⁻³), natural log transformed] including sample size (n), generalized cross-validation scores (GCV), deviance explained (Deviance), adjusted \( R^2 \) value \( [R^2 \text{ (adj.)}] \), Scale estimate (Estimate), standard error (SE), \( t \)-value and \( P \)-value for the categorical variables; estimated degrees of freedom (ed.f.), \( F \)-statistic (F), \( P \)-value for the continuous variables; natural log transformed bottom dissolved oxygen (DO), sea surface salinity (SSS) and sea surface temperature (SST). The ‘Intercept’ value is the average response in early season, night time, Northern region and shallowest depth category. All other factor term estimates are expressed as a difference from the model intercept.

<table>
<thead>
<tr>
<th>Variable</th>
<th>( N )</th>
<th>GCV</th>
<th>Deviance</th>
<th>( R^2 ) (adj.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larval fish abundance</td>
<td>106</td>
<td>0.257</td>
<td>45.50%</td>
<td>0.385</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variable (factor terms)</th>
<th>Estimate</th>
<th>SE</th>
<th>( t )-value</th>
<th>( P )-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.822</td>
<td>0.245</td>
<td>-7.429</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Late (season)</td>
<td>-0.645</td>
<td>0.132</td>
<td>-4.897</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Day</td>
<td>0.051</td>
<td>0.185</td>
<td>0.276</td>
<td>0.783</td>
</tr>
<tr>
<td>Central (lat.)</td>
<td>0.196</td>
<td>0.136</td>
<td>1.47</td>
<td>0.145</td>
</tr>
<tr>
<td>Southern (lat.)</td>
<td>0.474</td>
<td>0.164</td>
<td>2.89</td>
<td>0.005</td>
</tr>
<tr>
<td>Depth 2 (51–75 m)</td>
<td>0.279</td>
<td>0.169</td>
<td>1.653</td>
<td>0.102</td>
</tr>
<tr>
<td>Depth 3 (76–100 m)</td>
<td>0.135</td>
<td>0.171</td>
<td>0.791</td>
<td>0.431</td>
</tr>
<tr>
<td>Depth 4 (&gt;100 m)</td>
<td>0.191</td>
<td>0.189</td>
<td>1.016</td>
<td>0.312</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variable (smooth terms)</th>
<th>ed.f.</th>
<th>( F )</th>
<th>( P )-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log (bottom-DO)</td>
<td>2.117</td>
<td>3.029</td>
<td>0.038</td>
</tr>
<tr>
<td>SSS</td>
<td>1.330</td>
<td>0.611</td>
<td>0.489</td>
</tr>
<tr>
<td>SST</td>
<td>1.495</td>
<td>0.375</td>
<td>0.658</td>
</tr>
</tbody>
</table>
resulted in many anomalous larval fish distributions and densities (Auth et al., 2015), but the ocean had transitioned to a strong La Niña by the time of our June sampling that year so it is uncertain how this may have affected DO levels or fish larvae. Koslow et al. (2014) found that the abundance of mesopelagic fish larvae was related to variation in the OMZ off Southern California. Therefore, the decrease in DO of the OMZ in the tropics and subtropics, and the decrease in DO from equatorial events (e.g., El Niño/La Niña) could cause more severe (e.g., longer lasting events and larger area of coverage) hypoxic conditions and have long-lasting effects on fish larvae recruitment along the Oregon and Washington Coasts during the summer upwelling season, particularly for winter or early spring spawners [e.g., rockfishes (Sebastes spp.), rex sole (Glyptcephalus zachirus), slender sole (Lyopsetta exilis), etc.] (Matarese et al., 1989).

The Central Oregon Coast has been a main area of concern among scientists in the last decade owing to the prevalence of severe hypoxic events. There is some evidence presented in this study of larval fish community and density being affected when bottom-DO is low. It is, therefore, critical to continue monitoring the success of larval fish recruitment during the hypoxic season. If the number of larval fish recruits is reduced as a result of predation or prey limitation from habitat suppression in two or more sequential years, there could be a subsequent reduction in adult populations. Even moderate hypoxia during the larval phase has been shown to have long-term effects on fish growth, possibly leading to reduced survival (Vanderplancke et al., 2015). Long-term monitoring will provide a better understanding of the numerous impacts hypoxia is having on this region’s important marine fish species and local ecosystems (Keller et al., 2010, 2015; McClatchie et al., 2010). A number of factors related to climate change, such as temperature, ocean acidification, sea-level rise, precipitation and wind patterns, may act synergistically to increase the occurrence and magnitude of hypoxic zones in coastal waters (Altieri and Gedan, 2015), which may have long-lasting impacts on this productive coastal ecosystem.

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REFERENCES


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