Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem

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A B S T R A C T
Climate change-induced ocean deoxygenation is expected to exacerbat hypoxic conditions in mesopelagic waters off the coast of southern California, with potentially deleterious effects for the resident fauna. In order to understand the possible impacts that the oxygen minimum zone expansion will have on these animals, we investigated the response of the depth of the deep scattering layer (i.e., upper and lower boundaries) to natural variations in midwater oxygen concentrations, light levels, and temperature over time and space in the southern California Current Ecosystem. We found that the depth of the lower boundary of the deep scattering layer (DSL) is most strongly correlated with dissolved oxygen concentration, and irradiance and oxygen concentration are the key variables determining the upper boundary. Based on our correlations and published estimates of annual rates of change to irradiance level and hypoxic boundary, we estimated the corresponding annual rate of change of DSL depths. If past trends continue, the upper boundary is expected to shoal at a faster rate than the lower boundary, effectively widening the DSL under climate change scenarios. These results have important implications for the future of pelagic ecosystems, as a change to the distribution of mesopelagic animals could affect pelagic food webs as well as biogeochemical cycles.

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1. Introduction

In some parts of the ocean there exists a permanent subsurface hypoxic layer, called the oxygen minimum zone (OMZ), which arises due to the combination of limited surface ventilation, respiratory oxygen consumption, and ocean circulation (Sverdrup 1938; Wyrk 1962; Karstensen et al., 2008). OMZs are commonly defined by oxygen concentrations of less than 0.5 ml L⁻¹ (Gilly et al., 2013; Helly & Levin 2004; Paulmier & Ruiz-Pino, 2009), however hypoxia tolerances vary greatly by species and environment (Levin 2003; Seibel 2011). The most developed OMZs are in tropical and subtropical oceans and eastern boundary currents, including the California Current off the west coast of the United States.

Increased ocean stratification and changes to global circulation patterns are predicted to accompany global climate change, resulting in decreased dissolved oxygen content, particularly at depths of 200–700 m, and expansion of OMZs (Deutsch et al., 2006, 2011; Shaffer et al., 2009; Keeling et al., 2010). Such expansions have already been observed in tropical and subtropical regions (Stramma et al., 2008, 2010), across the northern North Pacific (Watanabe et al., 2003; Whitney et al., 2007; Crawford and Peña, 2013), and in the southern California Current Ecosystem (CCE) (Bograd et al., 2008; McClatchie et al., 2010) where deoxygenation has been linked to intensification of the California Undercurrent (Bograd et al., 2014). Deleterious effects of ocean deoxygenation have been observed for shallow-dwelling and coastal organisms exposed to extreme hypoxic events such as the summertime “dead zone” appearance in the Gulf of Mexico (Rabalais et al., 2002), entrapment of epipelagic fishes in California harbors (Stauffer et al., 2012), and strong upwelling events along the Oregon coast (Grantham et al., 2004; Chan et al., 2008).

The mesopelagic zone is one of the largest ecosystems on earth, and the resident fauna is both diverse and abundant (Robison, 2009). Many mesopelagic organisms are aggregated into one or more layers in the ocean, referred to as deep scattering layers (DSLs) due to the high acoustic reflectance observed using sonar systems. The animals comprising the DSL are important to global marine food webs, fisheries, conservation, and biogeochemistry (Robinson et al., 2010), yet remain understudied due to inaccessibility and the inadequacy of traditional sampling tools (Robison, 2009; Davison et al., 2013). Anthropogenic disturbances have only recently been recognized to have effects on deep-sea environments (Devine et al., 2006; Robison, 2009; Ramirez-Llodra et al., 2011). With few long-term studies on mesopelagic populations, it is not well understood how these communities respond to perturbations to their environment. The organisms that live in
already hypoxic mesopelagic depths (200–1000 m) of the CCE are living at the limits of their hypoxia tolerance (Childress and Seibel, 1998), and are thus especially vulnerable to declining oxygen levels in their environment. With the predicted and observed global expansion of midwater OMZs, the mesopelagic fauna could undergo changes in abundance and composition that, given the current state of knowledge, may go mostly unnoticed by scientists, marine resource managers and conservation biologists.

Using larval abundance as a proxy for adult abundance, Koslow et al. (2011) inferred that populations of mesopelagic fish in the southern CCE were reduced by over 80% in years with relatively low midwater (200–400 m) oxygen concentrations. The authors hypothesized that the underlying mechanism leading to this decline is that a hypoxic boundary (HB) limits the maximum depth available as suitable habitat for the mesopelagic fauna. In years of low midwater oxygen concentrations, the HB shoals, thereby forcing animals into shallower waters with higher irradiance, where the fishes are more vulnerable to predation by visually-oriented predators. A number of fish species are known to be bound by HBs, including Peruvian anchovy (Engraulis ringens, Bertrand et al., 2010), great white sharks (Carcharodon carcharias, Nasby-Lucas et al., 2009), and istiophorid billfishes (e.g., marlins, sailfish) (Prince and Goodyear, 2006; Stramma et al., 2011).

Irradiance has consistently been found to be a primary determinant of DSL depths (Kampa and Boden, 1954; Tont, 1975; Frank and Widder, 2002). This effect is attributed to DSL animals taking refuge from visually-oriented predators in darker waters (Lampert, 1993; De Meester et al., 1999). While some studies have considered the role of oxygen content and other variables in constraining DSL depths, many earlier analyses have been conducted either in places that lack an OMZ (e.g., Frank and Widder, 2002), or have only considered a single depth to describe the “DSL depth” (e.g., Tont, 1975; Bianchi et al., 2013). Given that the DSL width can span several hundred meters, it is likely that different environmental factors limit the top and bottom boundaries. The responses of each of these boundaries could be differentially affected by a changing climate.

Several recent studies have suggested a relationship between DSL depths and hypoxia. A global analysis of 38–150 kHz Shipboard Acoustic Doppler Current Profiler (ADCP) data concluded that the depth of the DSL is correlated with the oxygen concentration in the upper mesopelagic (150–500 m) (Bianchi et al., 2013). Their findings indicate that the DSL depth on large scales is limited by climatological oxygen concentrations. Another study within the central CCE attributed a ~300 m change in DSL depth between seasons to potential changes in OMZ depth (Urmy et al., 2012). Neither study collected simultaneous environmental measurements with the acoustic data.

The purpose of the present study is to explore the effects that the predicted decline of oxygen in the southern CCE may have on habitat use by the mesopelagic fish assemblage. Because it is not possible to isolate variation in oxygen concentrations from other natural variability in the environment, we further explore how the DSL responds to light and temperature. The DSL top and bottom boundaries were detected with echosounder-collected acoustic backscatter data, and the relationships between their depths to changes in the different variables were tested using linear regression and general additive models. We tested the following hypotheses:

1. There is a positive relationship between predation risk (using midwater irradiance as a proxy) and DSL depths. We expect this response to be stronger at the DSL upper boundary because predation risk is strongest at the shallower depths.
2. There is a positive relationship between oxygen concentration and DSL depth. We expect this relationship to be strongest at the bottom boundary of the DSL, because this is in closest contact to the most hypoxic waters.
3. There is a positive relationship between temperature and DSL depth, because there is likely an optimal thermal range for basal metabolic and other activities.

To test these hypotheses, we developed an algorithm to detect DSL depths from continuously-collected acoustic backscatter data across the core California Cooperative Oceanic Fisheries Investigations (CalCOFI) stations, accompanied by midwater trawls to characterize the mesopelagic fish fauna on a subset of cruises and stations (Fig. 1). With midwater oxygen levels varying spatially, seasonally, and annually, and concurrent station measurements of environmental variables including temperature, dissolved oxygen, and irradiance, these data allowed us to probe for the mechanisms that lead to the abundance declines observed by Koslow et al. (2011).
Acoustic backscatter data were collected on twelve California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises from 2009 to 2012 and in all 4 seasons with a 5-frequency (18, 38, 70, 120 and 200 kHz) Simrad EK-60 echosounder. Three cruises were omitted from the analysis, because of missing backscatter data. Only the 38 kHz data were used in the determination of DSL depth, as this frequency penetrates to the requisite depths while avoiding some of the resonance effects of air-bladdered fishes at 18 kHz (Kloser et al., 2002; Gode et al., 2009; Davison et al., 2015a). While most small zooplankton do not scatter strongly at 38 kHz (Laverty et al., 2007), the detected DSL layer likely includes some invertebrate taxa, such as squid, decapods, and siphonophores, in addition to fish. In particular, physonect siphonophores have strong backscatter at this frequency due to the inclusion of a gas-fill pneumatophore (Warren, 2001; Benfield et al., 2003; Laverty et al., 2007), and the DSL that we detected at this frequency likely includes both fishes and siphonophores. Siphonophores are not typically well preserved in net catches and were not enumerated for this analysis. However, a detailed comparison of the acoustic and trawl data for these cruises indicates that fish likely dominated the acoustic signal except during the August 2010 cruise in the region around the Channel Islands (Davison et al., 2015b). The cruises for which data were used for this study are presented in Table 1. Transducers were calibrated using a tungsten carbide reference sphere suspended beneath the research vessel at the start or end of each cruise (Foote et al., 1987).

All bioacoustic data were cleaned using EchoView software. The cleaning process involves removal of ship noise, acoustic reflections from the CTD during casts, background noise and false bottom reflections (i.e., acoustic reflections from the seafloor), and filling in areas of removed data with interpolated nearby data. The volume backscatter data were binned into 5 m vertical by 500 m horizontal bins to resolve horizontal and vertical gradients in the backscatter at a scale that can be compared to measurements of water column properties, such as oxygen concentration and temperature, over the CalCOFI sampling region. Backscatter data were converted from nautical area scattering coefficient (NASC, m² nmi⁻²) to area scattering coefficient (σs, in m² m⁻²).

### Table 1

<table>
<thead>
<tr>
<th>Cruise name</th>
<th>Dates</th>
<th>500 m MOHT trawls</th>
</tr>
</thead>
<tbody>
<tr>
<td>CalCOFI 0911</td>
<td>6–23 Nov, 2009</td>
<td></td>
</tr>
<tr>
<td>CalCOFI 1001</td>
<td>12 Jan–4 Feb, 2010</td>
<td></td>
</tr>
<tr>
<td>CalCOFI 1004</td>
<td>27 Apr–17 May, 2010</td>
<td></td>
</tr>
<tr>
<td>CalCOFI 1008</td>
<td>30 Jul–17 Aug, 2010</td>
<td>✓</td>
</tr>
<tr>
<td>CalCOFI 1011</td>
<td>28 Oct–12 Nov, 2011</td>
<td>✓</td>
</tr>
<tr>
<td>CalCOFI 1101</td>
<td>12 Jan–4 Feb, 2011</td>
<td>✓</td>
</tr>
<tr>
<td>CalCOFI 1108</td>
<td>27 Jul–12 Aug, 2011</td>
<td>✓</td>
</tr>
<tr>
<td>CalCOFI 1202</td>
<td>27 Jan–13 Feb, 2012</td>
<td>✓</td>
</tr>
<tr>
<td>CalCOFI 1210</td>
<td>19 Oct–5 Nov, 2012</td>
<td>✓</td>
</tr>
</tbody>
</table>

2.2. Deep scattering layer depth detection algorithm

A layer detection algorithm was developed (in Matlab v. 2012a) to detect the top and bottom boundaries of the deepest detected DSL at each station using the 38 kHz acoustic backscatter data. The 3 depth bin vertical running mean of the σs was first calculated to smooth the data. The algorithm then searched from the bottom up, starting at the maximum depth for which backscatter data were recorded (750–800 m). A DSL bottom was detected when the following conditions were met: (1) \( \sigma_s \geq a \) threshold value (4×10⁻⁹ m² m⁻² was chosen based on agreement with visual inference), (2) the change in \( \sigma_s \) from the next deepest bin was positive, and (3) the positive gradient persisted for at least 3 depth bins (i.e., 15 m). The top of the layer was similarly defined as the upper-most bin where \( \sigma_s \) was \( \geq \) the cutoff value and the gradient was negative for at least 3 depth bins. In order to compare acoustic backscatter with station-based water column variables, the mean DSL upper and lower boundary depths were calculated for each CalCOFI CTD station from data within 2.75 km on either side of the station (Fig. 1). We only analyzed daytime DSL depth distributions.

Seamounts and continental shelves have an aggregating effect on many organisms. The behavior of the layers near these features was different than in the open ocean region, with high backscatter from the surface to the seafloor in many cases. Therefore the layer detection algorithm for the offshore was not appropriate for waters at nearshore and seamount-associated stations. Data were thus excluded from within 20 km of any region with bottom depths shallower than 600 m. Additional filters were applied to remove detections of anomalous speckle (noise and detections of large individuals that were outside of the core layer) and to ensure that a small gap in the layer did not cause a detected layer to be split into two. In limited cases the algorithm failed to identify the appropriate top or bottom due to anomalous backscatter near the station. In these cases, the DSL top or bottom depth was identified visually.

2.3. Fish assemblages

On five of the cruises in this analysis, there was concurrent daytime oblique trawl sampling to 500 m with a 1.6 mm mesh Matsuda-Oozeki-Hu trawl (MOHT) with a 5-m² mouth opening (Oozeki et al., 2004) and TSK flowmeter (Table 1) at a subset of stations. Although avoidance behavior and escape lead to undersampling with any net system, the MOHT has recently been found to outperform other systems in its capture efficiency (Pakhomov and Yamamura, 2010). No net collections took place at dawn and dusk to avoid sampling during the diel vertical migrations. Efforts were made to allocate the tows evenly across the full CalCOFI grid, and all trawls were conducted using the same approximate ship speed, wire speed, and wire paid out. The collected fish were preserved in 10% sodium tetraborate-buffered formalin and later identified to lowest taxonomic unit possible in the lab. Cluster analysis based on Bray–Curtis dissimilarities of log_{10}(x+1) transformed data has revealed two distinct assemblages based on geographical region: (1) a nearshore/core California Current assemblage (inshore of and including station 80), and (2) an offshore-associated group (beyond station 80 (X. Rojas-Rocha, pers. comm.). Because the number of concurrent fish trawls and acoustic backscatter stations was limited, all CalCOFI stations were assigned a region, with stations ≤ 80 designated the nearshore region and ≥ 90 assigned to the offshore region (Fig. 2). Regressions were fit independently for data collected at each of the two regions.
2.4. Environmental variables

Given previous work done on the subject, irradiance, dissolved oxygen, and temperature were considered as likely explanatory variables for predicting the lower and upper DSL boundary layer depths.

2.4.1. Light level estimates: irradiance index

Due to the inherent difficulties of measuring or estimating light levels at mesopelagic depths, an index of irradiance was calculated based on light attenuation near the surface where most of the light is attenuated, with the assumption that irradiance at depth is proportional to irradiance in the upper water column (Li et al., 2014). The Irradiance Index (II) is: $\text{II} = \text{PAR} \cdot e^{-k_{490} \cdot s}$, where PAR is photosynthetically available radiation at the surface ($E \text{ m}^{-2} \text{ d}^{-1}$) and $k_{490}$ is the diffuse attenuation coefficient at 490 nm light (blue) in the surface mixed layer, which is approximated as 30 m. This index is appropriate as most of the light attenuation per unit depth occurs in the upper 30 m, and satellites are unable to sense below this level. Surface PAR and $k_{490}$ were derived from satellite measurements (SeaWiFS, MODIS-Terra and MODIS-Aqua) by Kahru et al. (2014), using the methods of Frouin et al. (2003) to derive PAR and the standard NASA KD2 algorithm for $k_{490}$ (http://oceancolor.gsfc.nasa.gov/REPROCESSING/R2009/kdv4/). Data were recorded at the pixel closest in time and space to each CalCOFI CTD station as possible.

2.4.2. Oxygen

Dissolved oxygen concentrations were measured to ~500 m at each station using a CTD equipped with dual SBE43 oxygen sensors, and corrected with Winkler titration measurements on discrete depth bottle samples at each station. Visual inspection of the DSL indicates a possible hypoxic boundary at ~0.5 ml l$^{-1}$ (Fig. 4 in Koslow et al. (2011)), although the oxygen at the bottom boundary for the present dataset varied from 0.15 to 0.71 ml l$^{-1}$ $O_2$ during the day. Because the bottom of the DSL was often detected deeper than 500 m, the 0.75 ml l$^{-1}$ isopleth was chosen as an appropriate predictor variable due to the availability of data to calculate this metric at all stations. The depth of the 0.75 ml l$^{-1}$ isopleth is strongly correlated with the depth of the 0.5 ml l$^{-1}$ isopleth ($r^2 = 0.803, p < 0.001$) as well as with other deep oxygen isopleths, thus serving as a reasonable proxy for the threshold oxygen concentration. Oxygen concentrations at the upper boundary of the DSL spanned a much greater range than at the bottom boundary, with concentrations ranging from 0.57 to 3.7 ml l$^{-1}$. In order to choose the best oxygen variable to use for the models, we ran regressions for a number of different oxygen isopleths (results not shown). The 2.0 ml l$^{-1}$ isopleth was chosen for the models as it had the strongest correlation with the depth of the upper DSL boundary, and is also near the mean value for oxygen concentration at the top of the DSL (2.16 ml l$^{-1}$).

2.4.3. Temperature

Temperature was measured with dual SBE3plus fast response temperature sensors to ~500 m at each station. Various isotherms were considered, and those with the highest predictive power for each of the top and bottom of the DSL used for the analysis: the 7.5$^\circ$ and 8.5$^\circ$ C isotherm for the bottom and top, respectively.

2.4.4. Statistical analyses

Because there is variability in measurements for both the independent and dependent variables, we fitted the data using Model II regressions (Ricker, 1973). Testing for a difference from zero slope of a Model II regression is uncertain, so we first tested for a significant relationship using Pearson product-moment correlation analysis. Where fits were significant ($p < 0.05$) for both inshore and offshore faunistic regions, we then tested for a significant difference between the slopes of the two lines using the method of Clarke (1980) to determine whether the two characteristic assemblages respond differently to the environmental variables. Both regression equations are presented where the slopes are significantly different between the two regions. If the slopes are not different ($p > 0.05$), we instead fit the entire data set using the Model II regression. Co-variation between variables was...
initially examined with a loess smoother and found to be adequately approximated by a linear fit in most cases.

In order to explore additive effects, a stepwise general additive model (GAM), incorporating all variables, was performed for both the bottom and top of the DSL. The stepwise GAM runs forward and backward at each step. Starting from the null model, the term with the lowest p-value is introduced, and then any terms with a p-value beyond a threshold are removed, before considering the next term.

3. Results

3.1. Lower DSL boundary

Results from the single variable regression analyses for lower boundary depth are illustrated in Fig. 3. The DSL lower boundary depth exhibited a significant positive correlation with the irradiance index for only the nearshore region (p < 0.01). The lower boundary depth was significantly correlated with the depth of 0.75 ml l⁻¹ oxygen concentration for both regions (Nearshore/CC: p < 0.001, Offshore: p < 0.05), with no difference in the slopes. The 7.5 °C isotherm was not significantly correlated with the lower boundary depth (p > 0.10). The results of the stepwise General Additive Model (GAM) were slightly incongruent with the single variable, but not light (Table 2a).

3.2. Upper boundary

Single variable regression analyses for upper boundary depth are illustrated in Fig. 4. The DSL upper boundary depth exhibited significant positive correlation with both the irradiance index (no significant difference between the two regions) and the depth of the 2.0 ml l⁻¹ oxygen isopleths (p < 0.001 for both regions), with different fits for the offshore and nearshore regions. The upper boundary depth exhibited a significant correlation with the 8.5 °C isotherm only for the offshore region (p < 0.01), where it explained only 16% of the variance. Results of the GAM were in agreement with the single variable results, with oxygen (p < 0.001), irradiance index (p < 0.001), and to a lesser extent, temperature (p < 0.05) contributing significantly to predicting the depth of the DSL upper boundary (Table 2b).

4. Discussion

Our algorithm allowed us to define the boundaries of the DSL at a much higher resolution than permissible by depth-stratified trawl sampling, providing insights into the sensitivity of the community to relatively small changes in their environment.

4.1. Bottom boundary

The occurrence of a distinct lower DSL boundary in the southern California Current Ecosystem at depths shallower than in regions that lack an OMZ (Chapman and Marshall, 1966; Williams and Koslow, 1997; Bianchi et al., 2013) suggests that most of the southern California mesopelagic community is bounded by an ecological threshold in the environment. Although a diverse group of metazoans has been found to reside within OMZ cores, this occurs primarily in regions with very shallow OMZs (e.g. the Arabian Sea, eastern tropical Pacific, Humboldt Current, etc.) (Holton, 1969; Childress and Nygaard, 1973; Luo et al., 2000; Cornejo and Koppelmann, 2006; Seibel and Drazen, 2007; Wishner et al., 2008; Karuppasamy et al., 2010; Maas et al., 2014), where die vertical migrations to mesopelagic depths to avoid visually-orienting predators is only possible by migrating into the OMZ and entering a state of metabolic suppression in the day and re-oxygenating in near-surface waters at night (Seibel et al., 2012, 2014; Maas et al., 2012). Our results suggest that the majority of the pelagic fish biomass in the CCE, where the core of the OMZ is

### Table 2

Results from the single variable regression analyses for lower boundary depth as a function of the four predictor variables. Irradiance is a continuous measurement, while the oxygen concentration for both regions (Nearshore/CC: p < 0.001, Offshore: p < 0.05), with no difference in the slopes. The 7.5 °C isotherm was not significantly correlated with the lower boundary depth (p > 0.10). The results of the stepwise General Additive Model (GAM) were slightly incongruent with the single variable, but not light (Table 2a).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>324.93</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Irradiance Index (E m⁻² d⁻¹)</td>
<td>1.177</td>
<td>0.658</td>
<td>1.79</td>
<td>&gt; 0.05</td>
</tr>
<tr>
<td>Depth of 0.75 ml l⁻¹ [O₂] isopleth</td>
<td>0.377</td>
<td>0.059</td>
<td>6.41</td>
<td>&lt; 0.001</td>
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<tr>
<td>Depth of 7.5 °C isotherm</td>
<td>0.151</td>
<td>0.069</td>
<td>2.17</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

(B) Results from the single variable regression analyses for upper boundary depth as a function of three predictor variables. Irradiance is a continuous measurement, while the oxygen concentration for both regions (Nearshore/CC: p < 0.001, Offshore: p < 0.05), with no difference in the slopes. The 8.5 °C isotherm only for the offshore region (p < 0.01), where it explained only 16% of the variance. Results of the GAM were in agreement with the single variable results, with oxygen (p < 0.001), irradiance index (p < 0.001), and to a lesser extent, temperature (p < 0.05) contributing significantly to predicting the depth of the DSL upper boundary (Table 2b).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Estimate</th>
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<td>0.924</td>
<td>4.350</td>
<td>&lt; 0.001</td>
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<tr>
<td>Depth of 2.0 ml l⁻¹ [O₂] isopleth</td>
<td>0.556</td>
<td>0.095</td>
<td>5.940</td>
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</tr>
<tr>
<td>Depth of 8.5 °C isotherm</td>
<td>0.222</td>
<td>0.104</td>
<td>2.135</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

### Fig. 4

Relationships between the depth of the upper boundary of the DSL and each of the four predictor variables. Irradiance is a continuous measurement, while the oxygen and temperature variables are discrete depths. Closed circles represent nearshore and core California Current stations and open circles represent offshore-associated stations. Stars indicate locations where deep (~500 m) MOHT trawls were conducted, with open and closed indicating the two characteristic species assemblages. Black broken lines are fitted to nearshore/CC stations, and the grey broken lines are fitted to the offshore stations. Solid black lines are fitted to the full dataset. (A) Irradiance Index (y = 11.83x + 152.9, r² = 0.39), (B) Depth of [O₂] = 2.0 ml l⁻¹ isopleth (Nearshore/CC: y = 1.058x – 22.1, r² = 0.29, Offshore: y = 1.623x – 183.9, r² = 0.48), and (C) Depth of the 8.5° isotherm (Nearshore/CC: NS, Offshore: y = 2.372x – 277.9, r² = 0.16).
at ~600–800 m depth, is constrained primarily by a minimum oxygen threshold.

4.2. Upper boundary

Irradiance and oxygen concentration (depth of the 2.0 ml l⁻¹ isopleth) were strong predictors of the upper boundary of the DSL for both the single variable regressions and the GAM, and there was a weaker relationship with temperature. A light threshold as predictor of DSL depths is consistent with the view that the animals of the DSL are taking refuge in dark water (Lampert, 1993; De Meester et al., 1999). A relationship between light and the DSL depth has been observed in previous studies (e.g., Tont, 1975), but the relatively strong predictive power of an oxygen threshold as an upper boundary to the DSL was somewhat unexpected. There is no obvious physiological explanation for why the community would need to remain below a given oxygen concentration, although entering a state of metabolic suppression for periods of time may be an adaptive strategy to confer significant energy savings (Seibert et al., 2014). It is likely that the mesopelagic fishes are taking refuge not only in the darkness of mesopelagic waters, but in areas with low oxygen concentrations, such as the CCE, midwater depths are also too hypoxic for their more active predators (as proposed by Bianchi et al., 2013). Supporting this interpretation, the oxygen concentrations at the upper DSL are slightly below levels tolerable to epipelagic visually-oriented predators, such as sharks (1.7 ml l⁻¹, Nasby-Lucas et al., 2009), billfishes (< 3.5 ml l⁻¹, Prince and Goodyear, 2006) and skipjack and yellowfin tunas (< 3.5 ml l⁻¹, Ingham et al., 1977; Cayré, 1991).

For many of the environmental variables, the DSLs of the nearshore and nearshore assemblages responded similarly. However, the relationships between the DSL upper boundary depths and both oxygen and temperature were significantly different between nearshore and offshore regions, with temperature only acting as a significant predictor for the DSL upper depth offshore. Given that the upper boundary likely experiences more frequent environmental variability in the nearshore region than offshore (Bograd et al., 2008; Send and Nam, 2012), the DSL may be better adapted there to this variability. Ongoing collection of acoustic backscatter data in both nearshore and offshore regions over multiple years and seasons would help to resolve the mechanism leading to these observed regional differences.

Our study suggests that vertical distributions of DSL organisms in the CCE are limited by midwater oxygen concentrations. This is in agreement with some previous work in the CCE (Urry et al., 2012), French Polynesia (Bertrand et al., 1999, 2002), and globally (Bianchi et al., 2013), and there is evidence that midwater hypoxia limits distributions of many fish taxa, such as larval fish in the Benguela current (Ekau and Verheye, 2005), Peruvian anchoveta (Bertrand et al., 2010), and billfishes and tuna in the Eastern Tropical Pacific (Stramma et al., 2011). Yet DSLs have been detected acoustically within the OMZ cores of the Arabian Sea (Kinzer et al., 1993; Karuppasamy et al., 2010), and myctophids and other midwater fishes have been collected within OMZs of the Arabian Sea (Karuppasamy et al., 2010), Eastern Tropical Pacific (Maas et al., 2014), and Humboldt Current (Cornejo and Koppelmann, 2006), regions where the OMZ is shallower than in the CCE (on the order of 100 m). Mesopelagic taxa in those areas appear to have adapted to a shallow OMZ by evolving the ability to enter the OMZ during the diel period, undergoing marked metabolic suppression, and migrating at night into near-surface waters to feed and re-oxygenate (Seibert, 2011).

Thin biomass peaks of zooplankton at specific oxygen levels of oxyclines have been revealed by depth-stratified net sampling (Wishner et al., 2008, 2013), and likely result from an advantage of occupying waters at the edge of a species’ hypoxia tolerance. There may be similar zonation of fishes within the CCE DSL that we were unable to detect with our methods. Assemblage-level biomass peaks could potentially be distinguished through more sophisticated algorithms (Cade and Benoit-Bird, 2014), and taxon-specific peaks revealed through depth-stratified trawl sampling. The Eastern Tropical Pacific and Arabian Sea OMZs span a greater depth range, are shallower, and have lower minimum oxygen concentrations than the CCE OMZ, which may lead to different dynamics in habitat utilization of inhabitant organisms. The OMZ in the CCE may be deep enough that mesopelagic fish can simultaneously avoid both predation risk and hypoxia, but in other areas must make a trade-off to avoid predation at the expense of oxygen availability. Paired trawl and acoustic sampling over a range of OMZ depths would shed some light on the discrepancies between our findings and other studies.

Ocean acidification is a compounding stressor on organisms in hypoxic waters because reduced pH decreases the affinity of proteins such as hemoglobin for oxygen (Seibel and Walsh, 2001). As oxygen concentration and pH covary (Alin et al., 2012), this may be especially problematic for organisms already living at the limits of their pH and oxygen tolerances. While we acknowledge that the shift in DSL depths attributed here to oxygen variability may in part be a response to changes in pH, it is not possible to decouple the oxygen and pH variability, so we rely on evidence that mobile fishes are not as susceptible to low pH as to changes in oxygen availability (Melzner et al., 2009; Kroeker et al., 2013) to assume that they are responding primarily to respiratory demands.

4.3. Predicting changes to DSL upper and lower boundary depths due to ocean deoxygenation and increased light attenuation

Oxygen concentrations and irradiance levels are the strongest predictors of the DSL depth in our study region. Dissolved oxygen levels in the ocean have been declining globally (Helm et al., 2011). The North Pacific region is experiencing some of the greatest change in oxygen concentrations, at least some of which is due to decadal-scale climate variability (McClatchie et al., 2010; Deutsch, 2005; Duetsch et al., 2011, 2014). The average decline in oxygen concentration in the southern CCE from the mid-1980s to present was 21% (Bograd et al., 2008, 2014), and global climate models predict a further decline in midwater oxygen concentration of ~20–40% over the coming century or so due to climate change (Sarmiento et al., 1998; Matear and Hirst, 2003; Shaffer et al., 2009). By extrapolating from a linear relationship between the two variables, Koslow et al. (2013) find that midwater fish biomass would approach zero with a further ~30% decline in midwater oxygen concentrations. This implies that midwater fishes will either have to modify their behavior (i.e. descend into the OMZ during the daytime and undergo metabolic suppression) or they will be replaced by a fauna that does. Light attenuation in the CCE has increased over the last half century (Aksnes and Ohman, 2009). Although DSL depths have been found to respond to midwater irradiance levels (e.g., Tont, 1975), no studies have explored the effects of the decreased irradiance on distributions of mesopelagic fauna.

In order to explore how the vertical range of the DSL may be altered by continued deoxygenation and changes to light attenuation, we used estimates of annual rates of change in the variables that had the highest predictive power for DSL upper and lower boundary depths, and substituted these values into equations determined by the present study that relate DSL upper and lower boundary depths to the same environmental variables. For these projections we consider only the variables with the strongest and most consistent effects on the bottom boundary (dissolved oxygen) and upper boundary (dissolved oxygen and irradiance).
Bottom

The maximum shoaling rate of the 0.75 ml l\(^{-1}\) oxygen concentration depth in the southern CCE from 1984 to 2013 (calculated as per Bograd et al., 2008) is

\[ \frac{\Delta Z_{O_{275}}}{\Delta t} = 2.74 \text{ m y}^{-1} \]

(This excludes one anomalously high rate of 4.46 m y\(^{-1}\) in the Santa Barbara basin.) The slope relating DSL bottom depth and the 0.75 ml l\(^{-1}\) oxygen isopleths (see Fig. 3b legend) is

\[ \frac{\Delta Z_{DSL_{Bot}}}{\Delta O_{275}} = 0.84 \text{ m m}^{-1} \]

We multiply these terms to arrive at a maximum shoaling of the bottom of the DSL

\[ \frac{\Delta Z_{DSL_{Bot}}}{\Delta t} = \frac{\Delta Z_{O_{275}}}{\Delta t} \cdot \frac{\Delta Z_{DSL_{Bot}}}{\Delta O_{275}} = 2.74 \text{ m y}^{-1} \cdot 0.84 \text{ m m}^{-1} = 2.3 \text{ m y}^{-1} \]

Top

Since oxygen and irradiance are the primary drivers of the upper boundary depth, we explore the effects of each in isolation in order to determine how each may shift the depth of the upper DSL boundary. The maximum shoaling rate of the 2.0 ml l\(^{-1}\) oxygen concentration depth in the southern CCE from 1984 to 2013 (calculated as per Bograd et al., 2008) is

\[ \frac{\Delta Z_{DSL_{Top}}}{\Delta t} = \frac{\Delta Z_{O_{275}}}{\Delta t} \cdot \frac{\Delta Z_{DSL_{Top}}}{\Delta O_{275}} = 3.98 \text{ m y}^{-1} \cdot 1.06 \text{ m m}^{-1} = 4.2 \text{ m y}^{-1} \]

We multiply these terms to arrive at a maximum shoaling of the top of the DSL

\[ \frac{\Delta Z_{DSL_{Top}}}{\Delta t} = \frac{\Delta Z_{O_{275}}}{\Delta t} \cdot \frac{\Delta Z_{DSL_{Top}}}{\Delta O_{275}} = 3.98 \text{ m y}^{-1} \cdot 1.06 \text{ m m}^{-1} = 4.2 \text{ m y}^{-1} \]

Note that we used the regression derived for the nearshore region in this calculation, as the maximum shoaling rates of hypoxic waters is in the nearshore region.

To estimate the potential shift in upper DSL boundary depth due to changes in irradiance, we first rearrange the II equation (Section 2.4.1).

\[ k_{490} = \frac{-1 \ln(II / PAR)}{30} \]

For simplicity, we assume that variation in II is due only to changes in \( k_{490} \), and use a constant PAR value for the calculations \( PAR = 100 \text{ E m}^{-2} \text{ d}^{-1} \)

Given the range of the Irradiance Index values in our dataset, \( 1.118 \times 10^{-6} \text{ E m}^{-1} \text{ d}^{-1} \) at DSL upper depth of 348 m to \( 21.852 \text{ E m}^{-1} \text{ d}^{-1} \) at 187 m, we calculate a concurrent \( k_{490} \) range

\begin{align*}
\min k_{490} &= \frac{-\ln(II / PAR)}{30} = -\frac{-\ln(1.118 \times 10^{-6} \text{ E m}^{-1} \text{ d}^{-1} / 100 \text{ E m}^{-2} \text{ d}^{-1})}{30} \\
&= 0.0507 \text{ m}^{-1} \\
\max k_{490} &= \frac{-\ln(II / PAR)}{30} = -\frac{-\ln(21.852 \text{ E m}^{-1} \text{ d}^{-1} / 100 \text{ E m}^{-2} \text{ d}^{-1})}{30} = 0.610 \text{ m}^{-1}
\end{align*}

We then calculate the change in DSL upper depth per unit of \( k_{490} \)

\[ \frac{\Delta Z_{DSL_{Top}}}{\Delta k_{490}} = \frac{348 \text{ m} - 187 \text{ m}}{0.0507 \text{ m}^{-1} - 0.610 \text{ m}^{-1}} = -288 \text{ m}^{2} \]

From 1949 to 2007, the light attenuation coefficient increased by an estimated \( 9.84 \times 10^{-4} \text{ m}^{-1} \text{ y}^{-1} \) (Aksnes and Ohman, 2009, Table 4), consistent with increases in nutrients and chlorophyll concentrations (Bograd et al., 2014). To obtain the annual shoaling rate of the DSL upper boundary due to changes in light attenuation, we multiply these terms together:

\[ \frac{\Delta Z_{DSL_{Top}}}{\Delta t} = \frac{\Delta Z_{DSL_{Top}}}{\Delta k_{490}} \cdot \Delta k_{490} = -288 \text{ m}^{2} \cdot 9.84 \times 10^{-4} \text{ m}^{-1} \text{ y}^{-1} = 0.274 \text{ m y}^{-1} \]

This value implies that the effect on the upper boundary due to changing irradiance is considerably smaller than the effect due to changing dissolved oxygen, and is therefore unlikely to contribute much to long-term changes in the upper boundary depth.

According to these calculations, the bottom oxygen boundary of the DSL is expected to shoal with continued ocean deoxygenation, consistent with our expectation. Still, the upper boundary will shoal faster than the lower boundary due to changes in the dissolved oxygen concentration, suggesting that there will be expansion of the daytime vertical habitat available to mesopelagic fishes (Fig. 5). However, different types of predators may be differentially limited by either hypoxia or irradiance, and further studies on trophic linkages and predator behavior and habitat use is needed to be certain how the varying effects of shoaling hypoxia and shoaling darkness will ultimately affect the mesopelagic fauna.

Our irradiance index is a relatively coarse proxy for mesopelagic light levels at each station. Neither the effects of differential shading due to plankton patchiness nor midwater bioluminescence have been considered here. The ability to determine the DSL response to light levels would be enhanced by direct in situ light measurements (e.g., Haag et al., 2014). Furthermore, there were some segments of the backscatter data where the algorithm failed to detect an upper DSL boundary due to heightened backscatter throughout the upper water column. If we instead consider the sea surface as the absolute limit for upper boundary of habitat available to mesopelagic fishes, we find that the shoaling of the hypoxic boundary does in fact lead to a decline in total available habitat. With a significant portion of the mesopelagic community...
moving into shallower waters, carbon transport to the deep sea will likely be impacted.

Our predictions for future changes in DSL depth and breadth may be biased by assumptions made in order to estimate these responses. We assumed that recent trends in changes to HB and euphotic zone depths will continue in the same direction and at the same rates. However, McClatchie et al. (2010) showed that the direction of change in HB depth has reversed before, although global climate models generally predict continued deoxygenation into the foreseeable future (Matear and Hirst, 2003; Shaffer et al., 2009). Further, the mechanism leading to the changes in euphotic depth is not well understood (Asknes and Ohman, 2009), so it is unclear whether the observed shoaling trend from 1949 to 2007 will continue. Upwelling rates are expected to continue to increase (Sydeman et al., 2014), which would bring more nutrients and lower oxygen into the surface waters, initially decreasing both oxygen levels and irradiance.

There is no obvious seasonal pattern in the depths of the oxygen variables for the time period of this study, however there was a lot of variation in the depths of both the 0.75 (260–513 m) and 2.0 ml l⁻¹ (115–350 m) isopleths throughout the full dataset, as well as within any given station. For example, at a northern nearshore station, 80.55, the 0.75 ml l⁻¹ oxygen depth ranged from 362 to 448 m and the 2.0 ml l⁻¹ depth from 123 to 184 m. At the southern offshore corner of the CalCOFI grid, station 93.120, the 0.75 ml l⁻¹ isopleth ranged from 424 to 471 m, and the 2.0 ml l⁻¹ level from 288 to 319 m. Given that this within-station variation is greater than that predicted with long-term climatological change, we expect there to be shifts in use of the vertical habitat on seasonal time scales, and even on hourly to daily time scales such as are documented by permanently-mounted echosounders (Urmy et al., 2012). Long-term monitoring with higher temporal sampling (e.g., a bottom-mounted echosounder) would resolve the response time of the DSL fish habitat use to changes in oxygen profiles.

Our results have implications for the availability of suitable habitat for mesopelagic animals as the oxygen levels in the ocean decline. This study was limited to the southern California Current region, however the questions of how habitats of mesopelagic fishes are affected by environmental change over time and space should be further explored throughout the ocean in order to better understand what these changes will mean for mesopelagic communities in other regions. Over the range of the CalCOFI sampling region there is a relatively large range of light levels from oligotrophic gyre water to the very productive nearshore upwelling region (Asknes and Ohman, 2009). In contrast, while there is variation in the range of OMZ depths, the range in the CalCOFI region is only a subset of the range of OMZ depths that exist throughout the global ocean (Stramma et al., 2011). The responses of the DSL should be determined in regions with both shallower and deeper OMZs as well as in areas that lack an OMZ entirely.

This is the first study that we know to investigate the differential responses of the upper and lower boundaries of the DSL to key environmental variables. Tont (1975) found a correlation between light and mean DSL depth, Bianchi et al. (2013) used the location of peak backscatter to identify as DVM depth, and Hazen and Johnston (2010) detected a relationship between integrated water column backscatter and the depth of the oxycline and thermocline. Powell and Ohman (2015) identified a positive relationship between the amplitude of diel vertical migration and euphotic zone depth. The high spatial and temporal sampling provided by the CalCOFI surveys and the overlap of CTD stations with bioacoustic sampling has provided a unique opportunity to explore the responses of the DSL to environmental variability. However, with only three years of bioacoustic data available, we could not resolve responses of the DSL depth over time, and instead had to rely on a space for time exchange, using the natural variation in environmental properties over space as a proxy for future climate change.

Ongoing sampling by the methods outlined here is necessary in order to access how DSL depth and vertical ranges change with natural and human-induced climatic changes. Further refinements to these methods that would assist in better resolving the response of the DSL distribution to environmental variability include obtaining real-time measurements of mesopelagic light levels, collecting CTD data at to at least the bottom depth of the DSL, and conducting depth-stratified sampling to ascertain the differential responses of various taxa of fishes that constitute the DSL.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2015.06.006. These data include Google maps of the most important areas described in this article.

References


Cayré, P., 1991. Behaviour of yellowfin tuna (Thunnus albacares) and skipjack tuna
(Katsuysan wolaimus) around fish aggregating devices (FADs) in the Comoros Islands as determined by ultrasonic tagging. Aquat. Living Resour. 4, 1–12.
Chan, F., Barth, J., Lubchenco, J., Kenichiro, A., Weeks, H., Peterson, W., Menge, B., 2008. Emergence of anoxia in the California current large marine ecosystem. Science 319, 920.


